

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

Author(s):	Adriano Mazziotta, Annika Kangas, Irene De Pellegrin Llorente, Olli-Pekka Tikkanen & Kyle Eyvindson
Title:	Application of the Global Uncertainty and Sensitivity Analysis to assess the importance of deadwood characteristics for forest biodiversity
Year:	2024
Version:	Published version
Copyright:	The Author(s) 2024
Rights:	CC BY 4.0
Rights url:	http://creativecommons.org/licenses/by/4.0/

Please cite the original version:

Mazziotta, A., Kangas, A., De Pellegrin Llorente, I. et al. Application of the Global Uncertainty and Sensitivity Analysis to assess the importance of deadwood characteristics for forest biodiversity. Stoch Environ Res Risk Assess (2024). https://doi.org/10.1007/s00477-023-02655-2

All material supplied via *Jukuri* is protected by copyright and other intellectual property rights. Duplication or sale, in electronic or print form, of any part of the repository collections is prohibited. Making electronic or print copies of the material is permitted only for your own personal use or for educational purposes. For other purposes, this article may be used in accordance with the publisher's terms. There may be differences between this version and the publisher's version. You are advised to cite the publisher's version.

ORIGINAL PAPER



Application of the Global Uncertainty and Sensitivity Analysis to assess the importance of deadwood characteristics for forest biodiversity

Adriano Mazziotta¹¹ · Annika Kangas² · Irene De Pellegrin Llorente^{3,4} · Olli-Pekka Tikkanen⁵ · Kyle Eyvindson^{1,6}

Accepted: 29 December 2023 © The Author(s) 2024

Abstract

Data acquisition for sustainable forest management has focused on obtaining high quality information to estimate biomass. Improving the quality of non-timber sustainability indicators, like deadwood volume, has been a minor interest. To explore how inventory approaches could be improved, we applied a Global Uncertainty and Sensitivity Analysis (GUSA) to evaluate which factors propagate more errors in deadwood modelling and how better data collection can minimize them. The impact of uncertainty on deadwood characteristics (diameter, collapse ratio, decay class, tree species, and position) was explored under stakeholders' preferences, management actions, and climate change scenarios. GUSA showed that removing the prediction error in deadwood volume was less uncertain for the scenarios where small deadwood volume. We found that assessment of high deadwood volume was less uncertain for the scenarios where small deadwood items were left decaying on the forest floor (BAU) and for high-end climate change scenario (RCP8.5) which resulted in lower deadwood accumulation in forest stands and therefore also in lower likelihood of erroneous estimates. Reduced uncertainty in tree species and diameter class will elevate the certainty of deadwood volume to a similar level achieved in living biomass estimation. Our uncertainty and sensitivity analysis was successful in ranking factors propagating errors in estimate of deadwood and identified a strategy to minimize uncertainty in predicting deadwood characteristics. The estimation of uncertainty in deadwood levels under the scenarios developed in our study can help decision makers to evaluate risk of decreasing deadwood value for biodiversity conservation and climate change mitigation.

Keywords Biodiversity \cdot Boreal \cdot Deadwood \cdot Finland \cdot Global Uncertainty and Sensitivity Analysis \cdot Laser-scanning \cdot Prediction errors

Adriano Mazziotta adriano.mazziotta@luke.fi

- ¹ Natural Resources Institute Finland (Luke), Helsinki, Finland
- ² Natural Resources Institute Finland (Luke), Joensuu, Finland
- ³ Department of Forest Resource Management, Swedish University of Agricultural Sciences (SLU), Umeå, Sweden
- ⁴ Department of Forest Resources, University of Minnesota, St Paul, MN, USA
- ⁵ School of Forest Sciences, University of Eastern Finland, Joensuu, Finland
- ⁶ Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences (NMBU), Ås, Norway

1 Introduction

In Fennoscandia, current forest management prioritizes sustainable provisioning of timber, bioenergy, and bioproducts. This is reflected in data acquisition for forest management: research has focused on improving the precision and reducing the uncertainty in structural forest indicators, like tree density, tree height, tree growth, and forest living biomass resulting from prediction errors from airborne laser scanning (Maltamo et al. 2021). In this context, we identify uncertainty as the knowledge about the environmental indicator, referring to both its accuracy and variability. The uncertainty in the future projections of these forest indicators is related both to the uncertainty in model structure and parameterization and to the uncertainty in the input data inferred via laser scanning. Model uncertainty is related with the propagation of the error in the allometric equations chosen to estimate tree biomass. Uncertainty in the input data is small, as inventory errors involved in biomass prediction derive from small inventory errors in tree basal area and tree height (for both, % Standard Error (SE) < =20% in laser scanning according to Næsset 2004).

Instead, forest management has focused on providing a sustainable supply of timber and has given less priority to sustainably providing other values (Eyvindson et al. 2018), such as deadwood. Deadwood supplies carbon cycling, carbon storage, enhanced soil fertility, the maintenance of soil moisture, habitat creation and biodiversity conservation (Lassauce et al. 2011; Campbell et al. 2019). This is reflected in the few resources dedicated to monitoring the non-timber indicators of Sustainable Forest Management (SFM), such as the deadwood volume accumulated in the forest stand via tree death and decomposition (Woodall et al. 2009; Chirici et al. 2012). Consequently, the estimates of total deadwood volume from laser scanning are affected by large inventory errors (Root Mean-Square Error ranging between 128 and 203% in commercial forest stands, Maltamo et al. 2014). These uncertainties are far larger than those related with biomass estimation.

Quantifying the accumulation of deadwood in the forest depends on three key main drivers: the rate of tree mortality at the stand, the decomposition rate, and the frequency of deadwood removal through human intervention (Stokland et al. 2012). The uncertainties in deadwood volume estimates are impacted by assumptions of the chosen models for tree mortality and decomposition (Harmon et al. 2020). Decomposition occurs in stages, providing specific resources for the life-cycle of different species living in deadwood, and is impacted by the collapse class, decay class, and tree species of the deadwood (Kouki and Tikkanen 2007; Tikkanen et al. 2006, 2007). Deadwood of different tree species decays at different rates, with the fastest decay occurring for deciduous trees (birch and aspen), an intermediate rate for spruce, and the slowest decay for pine (Shorohova and Kapitsa 2014). This different decay rate is the reason for the capacity of different tree species to support a different number of species thriving in deadwood included in the Finnish Red List of threatened species (Tikkanen et al. 2007; https:// punainenkirja.laji.fi/en).

In the Finnish forests, coniferous deadwood hosts a higher number of red-listed species compared with deciduous deadwood, with Norway spruce deadwood hosting more species than Scots pine (Tikkanen et al. 2006). Decay classes are not equally important for hosting red-listed deadwood-dependent species. While deciduous trees host similar number of species in recent deadwood and in advanced decay stages, coniferous trees host far more species in advanced decay than in recent deadwood. Among the coniferous trees, Scots pine hosts the same number of species in the early and advanced decay stages, while Norway spruce hosts far more species in deadwood in advanced decay (Tikkanen et al. 2006). Finally, a substantial proportion of deadwood species are specialized to live in large-diameter trunks (> 30 cm) (Tikkanen et al. 2006). In the heavily managed Fennoscandian boreal forests these types of deadwood fractions (the deadwood of deciduous trees in general and deadwood of coniferous trees in advanced decay classes) are often found in very small quantities, making it rare or impossible to find species depending on these resources (Gibb et al. 2005).

Quantifying uncertainty in deadwood volume is a research gap that must be addressed, given the current pressure of the society to promote multiple values from forests (see, e.g., Mönkkönen et al. 2014; Triviño et al. 2017; Pohjanmies et al. 2017, 2021). Assessing the uncertainties is of utmost importance, as assessments of environmental indicators like deadwood volume are often conducted reporting only the indicator status against target values without ascertaining any confidence interval as measure of uncertainty (Carstensen and Lindegarth 2016). The assessment of uncertainty bounds for environmental indicators helps to verify the effectiveness of management actions targeting conservation values (c.f., McCarthy et al. 2012). Failing to implement them properly can have serious ecological consequences. For example, in Northern Europe 20-25% of the forest-dwelling species are dependent on deadwood habitats (Siitonen 2001) and the availability of a deadwood volume of at least 20 m³ ha⁻¹ is certainly the most important requirement for the presence of threatened wood-inhabiting fungi in the Finnish forests (Junninen and Komonen 2011). Therefore, management actions releasing deadwood below this threshold may lead several species to extinction (Le Saout et al. 2013).

To address this concern, we use an uncertainty and sensitivity analysis approach to evaluate which factors propagate more errors in the estimates of deadwood volume and how these errors can be minimized. According to Campbell et al. (2019), who studied the sources of uncertainty in current field-based deadwood estimates in the northeastern United States, the uncertainty in the estimate of total deadwood volume on the forest floor is mostly determined by the uncertainties in five factors, related to the deadwood characteristics. These factors are (1) the diameter of the deadwood items, which directly relates to their volume, (2) the deadwood item's collapse, a reliable estimate of the proportion of the deadwood volume remaining during the decay process, (3) the decay class of each deadwood item, reflecting the stage of deadwood decomposition, (4) the tree species to which each deadwood item belongs to, reflecting wood density and tree characteristics and, (5) the position of the deadwood item, whether it is standing as a snag or lying as a log on the forest floor, which affects its diameter and the decay rate. Most countries that conduct deadwood inventories

measure deadwood according to the volume categorized by these five characteristics, whose assessment in sample transects or plots is error-prone (Rondeux and Sanchez 2010).

Through the quantification of the relative importance of the uncertainty, it is possible to improve the inferences of a SFM indicator like deadwood volume. This assessment identifies the elements of deadwood monitoring to prioritize so that the total uncertainty is minimized, and the inference errors are reduced. The Global Uncertainty and Sensitivity Analysis (GUSA) (Saltelli et al. 2004, 2008) can be used to estimate how the uncertainties related to deadwood characteristics contribute to the overall uncertainty of the total deadwood (a similar approach was applied by Campbell et al. 2019). GUSA assesses confidence levels around the estimate of an environmental indicator and evaluates which of the errors related to the indicators' factors has a higher impact on the overall uncertainty of the indicator. By indicating where the monitoring design can be improved, GUSA allows decision makers to better allocate monitoring resources to reduce errors in the estimate of the indicators (Campbell et al. 2019).

The aim of this study is to evaluate the potential impact of the uncertainties in the five deadwood characteristics on the overall uncertainty in the total deadwood volume predicted via laser scanning for a production forest landscape in Finland.

In addition to the uncertainty related to the deadwood characteristics, we hypothesize that the uncertainty regarding the total estimated deadwood volume depends upon three factors:

- (a) The forest values preferred by the forest owner, i.e., nature conservation vs. timber production, (Koskela and Karppinen 2020; Juutinen et al. 2021). Biodiversity-friendly forest owners may decide to leave all the wood to decay naturally on the forest floor after clearcut, while forest owners primarily interested in timber production may also collect a considerable proportion of trees felled by natural mortality (i.e., collection of ~75% naturally felled trees to be sold or used for bioenergy production), removing this resource from the forest.
- (b) The management actions applied on the forest, which alter the forest structure and consequently the initial levels of deadwood in the forest (McCarthy and Bailey 1994; Riffell et al. 2011). In Fennoscandia, stands managed for timber production are mostly governed with rotation forestry (Business As Usual, BAU), that uses regeneration harvest methods such as thinning from below and clearcutting producing even-aged stands (e.g., in Finland: Äijälä et al. 2014). Stands managed with Continuous Cover Forestry (CCF) are treated with selection harvest of single large trees (thinning from

above) and natural regeneration instead of planting or seeding (Pukkala et al. 2013). Finally, in stands left growing unmanaged as Set-Asides (SA), timber is not extracted but totally left to grow fully stocked, allowing natural mortality to be high due to self-thinning.

(c) The impact of climate change on the forest, which affects how much deadwood is accumulated (Heinonen et al. 2017; Blattert et al. 2020). Climate change has a direct impact on biomass accumulation in trees and soil (Creutzburg et al. 2017) and conversely on how much deadwood is accumulated in the forest (Blattert et al. 2020) and how fast it decays (Russell et al. 2014; Mazziotta et al. 2016). The uncertainty associated with alternative three IPCC radiative forcing scenarios (i.e., Representative Concentration Pathways (RCP) 2.6, 4.5 and 8.5, van Vuuren et al. 2011) is likely to induce a large variability on the deadwood volume, on the capacity of different tree species to thrive in the stands, and on the time window of persistence of certain deadwood decay classes (Blattert et al. 2020).

To account for these three factors, we explored separately the impact of uncertainty in the five deadwood characteristics on the overall uncertainty in total deadwood volume under alternative stakeholders' choice of deadwood extraction, choice of management actions, and climate change scenarios.

2 Materials and methods

2.1 Study area

The study area is in the Central Finland region and is primarily located in the southern boreal vegetation zone (Fig. 1). It covers 2240 ha and consists of 1475 forest stands of diverse age, productivity, and tree species composition. Among these stands, we have randomly selected 158 stands for simulation (i.e., 10.7% of the total). The area is a typical Finnish production forest landscape, consisting of a mosaic of stands with the current stand age ranging between 0 and 133 years and an average of 48 years (Table 1). The most common tree species are Scots pine (Pinus sylvestris, the dominant species in 50.1% of the stands), Norway spruce (Picea abies, 34.9%), silver birch (Betula pendula, 2.2%), downy birch (B. pubescens, 1.1%) and other deciduous trees (8.1%). While we have no specific information on the past management of the area, the relatively young age-class distribution of the stands suggests that the area has been managed extensively for production forestry, following an even-aged management that was the legally required management system until 2014 (Aijälä et al. 2014). Forests in the study area are privately

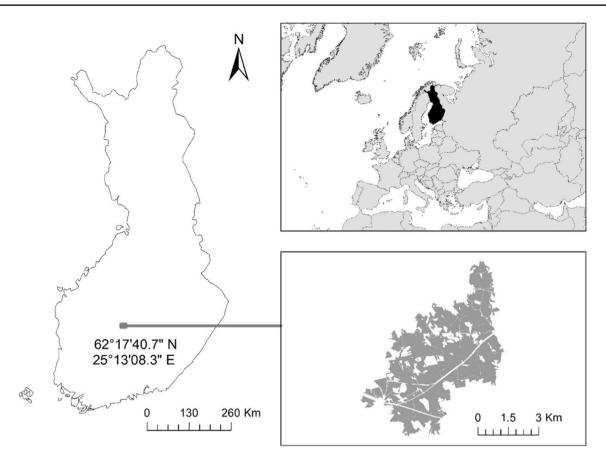


Fig. 1 Locations of the study area in in Central Finland and Finland in northern Europe

	Stand area(ha)	Stand age (years)	Basal area (m ² / ha)	Stem count (n/ha)	Mean diameter (cm)	Mean height (m)	Volume (m ³ / ha)	Sawlog volume (m ³ /ha)	Pulpwood volume (m ³ / ha)
Minimum value	0.03	1	0.0	5	0.0	0.07	0.0	0.0	0.0
25th percentile	0.53	23	1.2	103	9.3	8.42	8.4	0.0	2.8
Median	1.00	47	3.7	315	18.5	16.96	28.5	6.2	15.1
Mean	1.47	48	6.6	837	17.2	14.87	58.2	30.0	26.2
75th percentile	1.77	69	10.2	775	24.3	21.13	84.6	30.9	41.2
Maximum value	15.69	133	39.4	10,733	39.1	28.64	497.8	439.9	177.6

Table 1 Summary statistics for key stand level variables used in the simulations (N=158 stands)

owned and managed using a diverse set of silvicultural treatments (Kuuluvainen et al. 1996).

2.2 Inventory data

The stand-level inventory data derived from airborne laserscanning for our study area was extracted from openly available data managed by the Finnish Forest Centre (FFC 2021) and used as input data in the forest growth simulator. The data used in this study are owned and archived by the Finnish Forest Centre (www.metsakeskus.fi). The data are available from the authors upon reasonable request and with permission of the Finnish Forest Centre.

Key stand level variables used in our simulations are reported in Table 1. Initial deadwood characteristics for Central Finland were obtained from measurements from experimental plots from the Finnish National Forest Inventory (NFI) for the years 1980–2015 (Korhonen et al. 2020). We utilized NFI data of deadwood to simulate them wallto-wall, mimicking laser scanning data suitable for forest planning. Using NFI data for deadwood initialization was necessary, as Forestry Centre currently does not produce deadwood data. Deadwood initialization parameters are summarized by tree species, diameter, decay class, position and years after death (Table 2).

2.3 Simulations of forest growth and decomposition

The simulation of the future states of the forest was conducted using SIMO, an open-source forest simulation and optimization software (Rasinmäki et al. 2009). Using forest growth models, SIMO produces projections of future stand development based on the stand's initial characteristics and the forestry operations to be applied to the stand. The forest simulator creates a wide range of management actions using a decision tree following the Tapio guidelines (Äijälä et al. 2014). The implementation of alternative management actions in the simulator is described in more detail by Eyvindson et al. (2018).

The formation of deadwood and its decomposition from initial deadwood values is predicted with the empirical statistical model developed for Scots pine, Norway spruce, and silver birch by Mäkinen et al. (2006). The models estimate the remaining fraction of deadwood volume based on the years' after death with a Gompertz function. The mortality

Table 2 Summary statistics of the deadwood parameters used to initialize the simulations for NFI stands' estimates for Central Finland (N = 1475)

	Category	Stem number	Volume (m ³)	Volume ad (m ³)	Density (kg/m ³)	Density ad (kg/ m ³)	Biomass (kg)	Biomass ad (kg)
Species	Pine	2.21	0.033	0.013	92	51	17.8	5.6
	Spruce	0.48	0.038	0.010	75	40	22.8	4.4
	Birch	0.29	0.007	0.002	53	24	5.6	1.2
Diameter	2.5	1.98	0.000	0.000	39	20	0.1	0.0
	7.5	4.21	0.001	0.000	71	36	0.7	0.2
	12.5	1.81	0.011	0.002	102	51	7.1	0.7
	17.5	0.70	0.029	0.004	101	53	17.4	1.9
	22.5	0.19	0.052	0.010	105	55	32.3	5.2
	27.5	0.04	0.030	0.010	106	55	17.8	4.7
	32.5	0.01	0.035	0.014	85	44	20.1	5.7
	37.5	0.01	0.037	0.017	31	17	21.9	7.3
	42.5	0.00	0.038	0.019	21	12	21.1	7.9
Decay class	1	4.36	0.087	0.084	417	392	50.3	44.9
	3	7.38	0.081	0.058	393	245	43.9	18.8
	4	8.18	0.068	0.035	422	153	38.1	8.1
	5	10.86	0.070	0.023	409	87	40.0	3.9
Position	Log	1.81	0.047	0.012	125	61	27.7	0.7 1.9 5.2 4.7 5.7 7.3 7.9 44.9 18.8 8.1
	Snag	0.18	0.005	0.005	22	16	3.1	2.4
Years after death	5	1.60	0.034	0.034	175	170	20.4	19.8
	15	1.79	0.027	0.024	162	108	15.9	10.5
	25	1.59	0.034	0.014	141	57	21.9	4.4
	35	2.12	0.017	0.008	83	31	9.4	1.9
	45	2.66	0.017	0.005	81	16	9.2	0.8
	55	0.19	0.125	0.000	80	1	73.5	0.0
	65	0.00	0.006	0.000	12	0	3.7	0.0
	75	0.00	0.000	0.000	0	0	0.0	0.0
	85	0.00	0.000	0.000	0	0	0.0	0.0
	95	0.00	0.000	0.000	0	0	0.0	0.0
Mean \pm SD			0.026 ± 0.005	0.009 ± 0.002	73 ± 15	38 ± 8	15.4 ± 3.2	3.7 ± 0.8

Means and uncertainties (i.e., standard deviations, SD) are estimated on the basis of deadwood inventory errors for each parameter. Density ad, volume ad, and biomass ad are the density, volume, and biomass estimated immediately after tree death (i.e., ad). The density, volumes and biomass after tree death represent means of the values taken only at year 0 after death, while other variables represent means across all the years after death

of single trees in SIMO is determined by a probability model taking into account tree competition and aging, and the tree to die is selected randomly in each simulation (Hynynen et al. 2002).

The 158 stands with the initial deadwood characteristics were simulated for 100 years into the future to account for climate change effects (see the paragraph "uncertainty scenarios" for details). The simulator produced predictions of stand development at 5-year time steps. To evaluate the highest impact of climate change on forest dynamics we compared the last year of each scenario (Kellomäki et al. 2008).

2.4 Management actions

The initial deadwood values used in the simulation were based on the regional level deadwood characteristics of the Finnish NFI (Table 2). These values were used in a spin-up process to construct initial deadwood volumes based on a variation of management regimes (Table 3). We assume that historical management alternatives, as well as natural mortality, are represented in the prevailing deadwood volumes at regional level. Specifically, all the 158 stands were simulated for each combination of management regime (either BAU, CCF, or SA) and deadwood removal levels from the forest floor (either 0%, 40% or 75%) for 30 years into the future at 5-year time steps. The average volume of deadwood was estimated by the end of the simulation horizon. A conceptual model explaining the flow of the deadwood initialization is represented in Fig. 2 (see also Mazziotta et al. 2023).

2.5 Estimate of total volume from deadwood characteristics

We estimated the total volume of deadwood per hectare (V_i) in $m^3 ha^{-1}$) in each forest stand *j* of the total simulated stands (J = 158) at the end of the planning horizon. This is calculated as the sum of the combinations of the volumes for 9 discrete diameter classes as standard output from the simulator (set D, expressed in cm, with mean values from 2 to 42 cm with 5 cm intervals), 5 discrete collapse ratio classes (set C, calculated as ratio between volume after death and volume at each time step, split according to the following intervals: 0.01-0.2, 0.21-0.4, 0.41-0.6, 0.61-0.8, 0.81-1), 3 tree species (set S, i.e., Norway Spruce, Scots pine, and deciduous trees), 4 deadwood decay classes based on time since tree death (set L, i.e., recently dead tree = 1, medium decayed tree = 3, very decayed tree = 4, almost decomposed tree = 5, Stokland et al. 2012; decay class 2 (= weakly decayed tree) is not reported because it lasts only for three years, that is for less time than the minimum 5 year time step of our forest simulator), and 2 positions on the forest floor (set *P*, i.e., snag, upright, or log, lying on the forest floor):

$$V_j = \sum_{d \in D} \sum_{c \in C} \sum_{s \in S} \sum_{l \in L} \sum_{p \in P} V_{j,d,c,s,l,p} \forall j \in J$$
(1)

The five deadwood characteristics affecting total volume are simulated with the SIMO simulator (Rasinmäki et al. 2009) on the basis of the Finnish NFI-derived distributions. Therefore, uncertainty affecting the predictors of total

DW Characteristic	Stakeholders	Management			Climate				
	Scenario	Mean	95%CI	Scenario	Mean	95%CI	Scenario	Mean	95%CI
Decay	DWREM0	14.9	0.076	BAU	6.2	0.054	RCP26	9.4	0.101
Decay	DWREM75	4.0	0.020	CCF	8.4	0.082	RCP45	9.2	0.099
Decay				SA	13.4	0.122	RCP85	9.8	0.105
Position	DWREM0	16.2	0.189	BAU	6.3	0.108	RCP26	10.2	0.218
Position	DWREM75	4.2	0.046	CCF	8.7	0.161	RCP45	9.8	0.204
Position				SA	15.1	0.274	RCP85	10.5	0.230
Collapse	DWREM0	14.9	0.063	BAU	6.2	0.044	RCP26	9.4	0.084
Collapse	DWREM75	4.1	0.017	CCF	8.5	0.068	RCP45	9.3	0.082
Collapse				SA	13.5	0.101	RCP85	9.8	0.087
Species	DWREM0	23.5	0.210	BAU	9.5	0.125	RCP26	20.6	0.238
Species	DWREM75	6.1	0.053	CCF	12.6	0.188	RCP45	15.2	0.249
Species				SA	21.7	0.302	RCP85	14.6	0.234
Diameter	DWREM0	14.1	0.037	BAU	8.3	0.027	RCP26	14.6	0.241
Diameter	DWREM75	4.7	0.012	CCF	8.2	0.044	RCP45	9.2	0.045
Diameter				SA	11.6	0.058	RCP85	9.9	0.047
All	DWREM0	19.5	0.022	BAU	11.8	0.016	RCP26	12.8	0.029
All	DWREM75	6.3	0.007	CCF	10.9	0.025	RCP45	12.8	0.028
All				SA	15.6	0.036	RCP85	13.1	0.028

Table 3 Predicted means and 95% confidence intervals (CI) of deadwood volume for each deadwood characteristics summarized for all the scenarios (All) and for each stakeholders preference (DWREM0% and DWREM75%), management action (BAU, CCF, and SA), and climate change scenario (RCP 2.6, RCP 4.5, RCP 8.5) (N = 158)

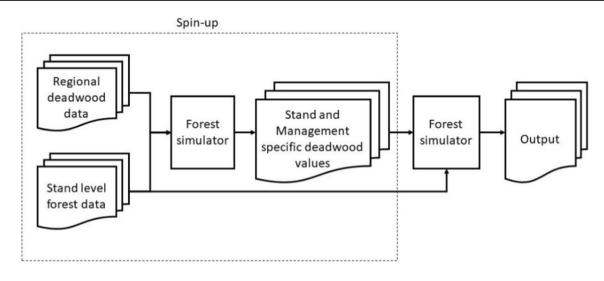


Fig. 2 Flowchart describing the procedure of deadwood initialization

deadwood volume derives both from inventory errors and from assumptions in the models embedded in SIMO. Our metric of uncertainty was the 95% confidence interval (95% CI), calculated as the difference between the 2.5th and the 97.5th percentiles of the distribution of deadwood values.

To evaluate the independent impact of each source of uncertainty on the total deadwood uncertainty, the uncertainty in the total volume was calculated as the sum of the fractions of deadwood volumes for each deadwood characteristic. For example, to evaluate the impact of the volumes of each tree species (V_s) on the uncertainty in the total volume (V_i) , this was calculated for each stand in set *J* as:

$$V_j = \sum_{s \in S} V_{j,s} \forall j \in J$$
⁽²⁾

To evaluate the impact of excluding one source of uncertainty in a certain deadwood fraction from the overall uncertainty in deadwood volume, the uncertainty in the total volume was calculated, via a leave-one-out procedure, as the sum of the volumes of deadwood items with all characteristics but one. For example, to evaluate the impact of the exclusion from the variability in the total volume of the variability derived only from measuring the volumes by diameter class (V_d), total volume was calculated as:

$$V_j = \sum_{c \in C} \sum_{s \in S} \sum_{l \in L} \sum_{p \in P} V_{j,c,s,l,p} \forall j \in J.$$
(3)

2.6 Uncertainty scenarios

Volumes for the deadwood characteristics of the 158 stands were simulated separately under 18 uncertainty scenarios, with a potential impact on the assessment of deadwood volume in the forest. The uncertainty scenarios were a combination of three initial deadwood levels delivered by three management actions (BAU,CCF, and SA), two management decisions from the forest owner (75% or 0% deadwood removal, abbreviated as DWREM), and three climate change scenarios (RCP2.6, RCP4.5, and RCP8.5), as specified below:

(1) INITIAL DEADWOOD VOLUME: The initial quantity of deadwood depends on the history of the management applied in the forest. To simulate the potential deadwood volume assuming different management actions we applied two alternative growth models: both BAU and SA apply the models developed by Hynynen et al. (2002), but BAU assumes even-aged forestry and SA assumes ingrowth, while CCF, assuming uneven-aged forestry, applies the models developed by Pukkala et al. (2013) and Lappi and Pukkala (2020). These two growth models affect differently the stand development, and consequently have a different impact on the quantity of deadwood. In BAU, slash from harvesting is left in the stand, so thinning and clear-felling will increase deadwood volume of small diameter. In CCF and SA deadwood accumulates throughout the forest succession, but as CCF focuses on removing the largest logs when harvesting, this reduces the fraction of large diameter deadwood that enters the litter for decomposition. Finally, in BAU competition is reduced through thinning, inducing faster tree growth of the remaining trees respect to SA and CCF, where ingrowth reduces the diameter growth. In this way, BAU is also likely to reduce the retention time of each decay class of deadwood respect to CCF and SA. The choice of growth model has only a slight impact on deadwood production (Pesonen 2011) and is expected to contribute to the overall uncertainty in total deadwood volume to the same extent.

- (2) VALUES OF THE FOREST OWNER: The forest owners may have different management goals oriented either towards economic or ecological values (Koskela and Karppinen 2021), which can directly affect the volume of deadwood available for forest biodiversity (Deuffic and Lyser 2012). Therefore, we simulated two regimes of deadwood removal: 0% for biodiversityfriendly forest management, and 75%, for intensive forestry.
- (3) CLIMATE CHANGE: The three RCPs (i.e., 2.6, 4.5 and 8.5) chosen to simulate deadwood dynamics represent low, intermediate, and high warming respectively and differ from each other by emission levels. In Finland, the annual mean temperature is projected to increase by 1.9, 3.3 and 5.6 °C by the 2080s under the RCP2.6, RCP4.5 and RCP8.5 scenarios, respectively, compared to the period 1981-2010 (Venäläinen et al. 2020). The mean annual precipitation is expected to increase by 6%, 11% and 18% under these RCPs by the 2080s. The impact of climate variables on forest growth dynamics in SIMO was included based on climate-sensitive statistical growth and yield models (Matala et al. 2005, 2006). The three RCPs were simulated for the General Circulation Model CanESM2 (von Salzen et al. 2013).

2.7 Global Uncertainty and Sensitivity Analysis (GUSA)

We evaluated the relative impact of the uncertainty in the deadwood characteristics on the total deadwood volume with a GUSA. GUSA assesses (1) the propagation of uncertainty from input variables on model outputs and (2) the relative importance of uncertainties in model input variables and their interactions on the uncertainty in model output variables (Saltelli et al. 2004). A variance-based sensitivity analysis is the study of how uncertainty in the output of a model (numerical or otherwise) can be apportioned to different sources of uncertainty in the model input factors (Saltelli et al. 2010). GUSA evaluates the entire parameter space, ranking simultaneously the relative impacts of all the uncertainty sources at once.

We performed the GUSA according to the variancebased Sobol method (Sobol 1993, 2001) and implemented it with the sensobol R package (Puy et al. 2022). The Sobol method provides a quantitative measure of the output variance with respect to the variance associated with the input parameters. These sensitivity indices are described in terms of direct (first order), and interaction (second and higher order) effects of the input parameters (Saltelli et al. 2004). The first-order sensitivity indices (*S*) are calculated as the ratio of the variance associated with the input variable to the total variance of the model output. The total-effect sensitivity (*T*) is calculated as the ratio of the total variance (first order plus all interactions) associated with the input variable to the total variance of the model output (details in Lagerwall et al. 2014).

To calculate the Sobol indices we first selected an integer N to represent the sample size of the forest stands. The sample size was generated using a Monte-Carlo approach looking at the entire distribution of the factor's values (Saltelli et al. 2010). Next, we generated a matrix of size (N, 2 K), the Sobol matrix, where K is the number of input parameters and N is the number of draws to be taken from the parameters' probability distribution function. This matrix is split into two matrices A and B of size (N, K). We then defined matrices Di, Ci which are respectively the same as matrix A and B, except with the *i*th column obtained from matrix B and matrix A. Finally, we computed the model output for all the input values in A, B, Ci, Di. The details of the method are summarized in Lagerwall et al (2014).

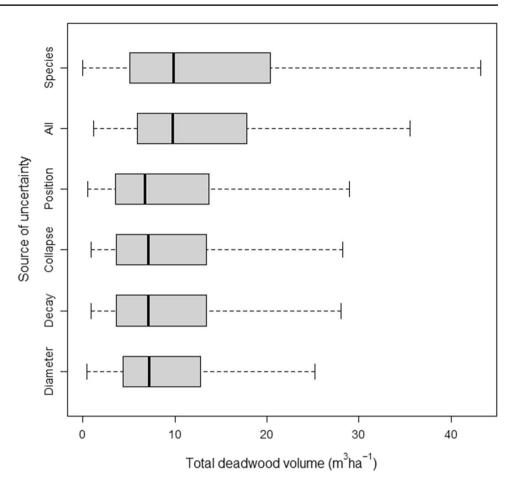
3 Results

3.1 Contribution of sources of uncertainties

The contribution of single sources of uncertainty, i.e., errors in each deadwood characteristics, on the overall uncertainty in deadwood volume was ranked via the GUSA. When all sources of uncertainties were combined, the uncertainty (i.e., 95% CI) was $31.0 \text{ m}^3 \text{ ha}^{-1}$ (Fig. 3). Tree species (95% CI=43.1 m³ ha⁻¹) and deadwood position (95% CI=30.6 m³ ha⁻¹) were the deadwood characteristics projected with the greatest source of uncertainty (being respectively 139% and 98.7% of the joint uncertainties among all the 18 scenarios). All other deadwood characteristics, i.e., collapse ratio (95% CI=23.0 m³ ha⁻¹), decay class (95% CI=22.8 m³ ha⁻¹) and diameter class (95% CI=21.5 m³ ha⁻¹) were all less but similarly important for the total deadwood uncertainty (being 74.2%, 73.5%, and 69.4% of all the joint sources of uncertainties) (Fig. 3).

The relative contribution of each source of uncertainty was also evaluated for each combination of stakeholders' preferences, forest management strategies, and climate scenarios (Fig. 4). The means and 95% CI of deadwood volume inferred by all the sources of uncertainty were four times higher in the scenarios with no deadwood removal from the forest floor (Fig. 4a) than in the 75% deadwood removal scenario (Fig. 4b) (Table 3). Additionally, the relative contributions of each source of uncertainty were similar between Fig. 4a and b. The mean deadwood volume was generally comparable between BAU and CCF and the highest volume

Fig. 3 Contribution of each source of uncertainty, i.e., the five deadwood characteristics, to the total deadwood volume, and of all sources of uncertainty combined among all the 18 scenarios. The boxplots represent the predicted deadwood volumes based on the Global Uncertainty and Sensitivity Analysis. The box represents the interquartile range and the whiskers the reasonable extremes of the data, that is the minimum and maximum values that do not exceed 1.5 times the interquartile range from the middle of the data



was under SA. On the other hand, the 95% CI in the deadwood volume was generally the highest under SA, intermediate under CCF, and the lowest under BAU (Fig. 4a, b, Table 3). The mean of the predicted deadwood volume either decreased (for tree species and diameter class) or remained stable (for decay class, tree position and collapse ratio) under radiative forcing scenarios of increasing greenhouse gas (GHG) concentration, from RCP2.6 to RCP4.5 to RCP8.5, while 95% CI was generally similar under the three climate change scenarios (Table 3, Fig. 4a, b).

3.2 Impacts of sources of uncertainties

To quantify the impact each deadwood characteristic had on the total uncertainty, we conducted a leave-one-out cross validation (Fig. 5). We found that the error in diameter class and tree species affected the most the total uncertainty in deadwood volume, with error-free estimate of these deadwood characteristics increasing of 30.5% and decreasing of 15.9% the total uncertainty, respectively. On the other hand, the exclusion of the uncertainty in deadwood volume induced by errors in volumes by collapse ratio, decay class and position affected only marginally the total deadwood uncertainty, as the total uncertainty increased only by 1.7%, 1.5%, and 0.3%, respectively (Fig. 5).

3.3 Contributions and impacts of uncertainties by scenarios

The relative impact of assessing the uncertainty in total deadwood by excluding each deadwood characteristics was also evaluated for each combination of uncertainty scenarios of stakeholders' preferences, management actions, and climate change (Table 4, Fig. 6a, b). Beside the absolute magnitude of the uncertainties, the relative contributions of the exclusion of each source of uncertainty were similar between Fig. 6a and b. For the stakeholders' preference scenarios, excluding the uncertainty in the decay stage, collapse ratio and species decreased the 95% CI in the total uncertainty under both the scenarios of no deadwood removal (-9.1%, -9.1%, and -13.6%) and 75% deadwood removal (- 14.3%, - 14.3%, and - 28.6%), while the uncertainty increased excluding the error in diameter class more under no deadwood removal (+72.7%) than under 75% removal (+42.9%) (Table 4, Fig. 6a, b). Finally, excluding the error in the position the uncertainty decreased (-4.5%) under no deadwood removal and remained stable at 75% removal.

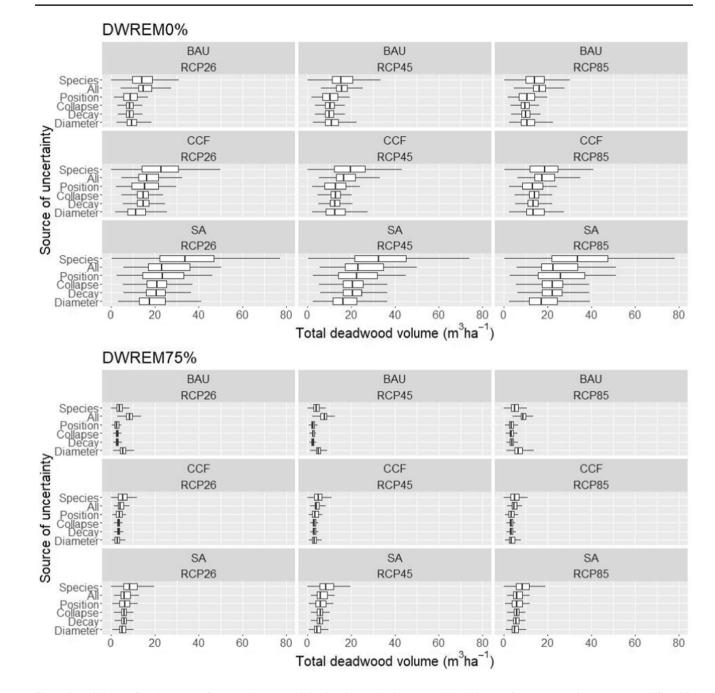
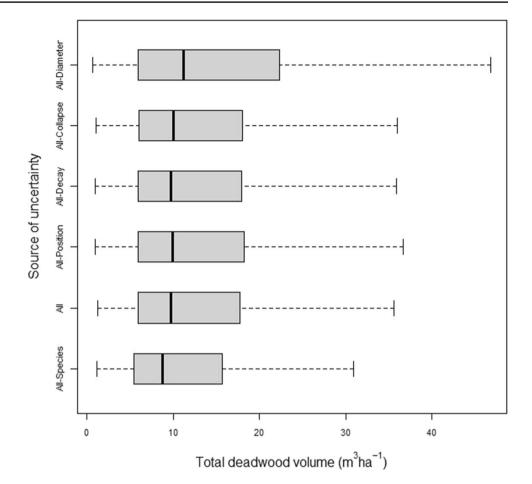


Fig. 4 Contribution of each source of uncertainty to total deadwood volume, and all sources of uncertainty combined for 9 combinations of uncertainty scenarios of climate change (RCP 2.6, RCP 4.5, RCP 8.5) and management actions (BAU, CCF and SA), separated

by the two stakeholders' preference scenarios **a** DWREM0% and **b** DWREM75%. The boxplots represent the predicted deadwood volumes based on the Global Uncertainty and Sensitivity Analysis. Definitions of the box, interquartile range and whiskers as in Fig. 3

When assessing the scenarios associated with the management actions, the error-free estimation of the deadwood volume by decay class, collapse and tree species always caused a decrease in the 95% CI in the total uncertainty (for decay removal: BAU = -6.3%, CCF = -12.0%, SA = -8.3%; for collapse ratio removal: BAU = -6.3%, CCF = -4.0%, SA = -8.3%; for species removal: BAU = -18.8%, CCF = -8.0%, SA = -13.9%) (Table 4, Fig. 6a, b). Interestingly, the exclusion of diameter class uncertainty caused an increase in the total uncertainty, the highest under CCF (+ 64.0%), intermediate under SA (+ 61.1%), and the lowest under BAU (+ 56.3%) (Table 4, Fig. 6a, b). Finally, excluding the uncertainty in the position the uncertainty remained stable under SA and CCF and increased for BAU (+ 6.3%).

Fig. 5 Impact of the exclusion of each deadwood characteristics from the uncertainty in all deadwood characteristics. The boxplots represent the predicted deadwood volumes based on the Global Uncertainty and Sensitivity Analysis accounting for the uncertainties in all the deadwood characteristics but one. Definitions of the box, interquartile range and whiskers as in Fig. 3.



When assessing the impact of the climate change scenarios, excluding sources of uncertainty caused a similar decrease in uncertainty for all GHG concentrations for decay class (RCP2.6 = -10.3%, RCP4.5 = -7.1%, RCP8.5 = -10.7%), collapse ratio (RCP2.6 = -6.9%, RCP4.5 = -7.1%, RCP8.5 = -7.1%) and tree species (RCP2.6 = -13.8%, RCP4.5 = -7.1%) and tree species (RCP2.6 = -13.8%, RCP4.5 = -14.3%, RCP8.5 = -10.7%) (Table 4, Fig. 6a, b). However, in the case of the exclusion of the uncertainty in tree position, the uncertainty decreased only with RCP2.6 (-3.4%) but was stable with RCP4.5 and RCP8.5. On the contrary, the removal of the uncertainty in tree diameter caused an increase in the total uncertainty, the highest under RCP8.5 (+75.0%), intermediate under RCP2.6 (+69.0%), and the lowest under RCP4.5 (+64.3%) (Table 4, Fig. 6a, b).

3.4 Relationships between uncertainties in total deadwood

We plotted the relationship between the predicted overall uncertainty in deadwood volume (in *y*-axes) and the uncertainty in each of the five deadwood characteristics (in *x*-axes) (Fig. 7). The deadwood fractions that gave more "shape" to the curves describing the relationships were the ones whose uncertainty affected more, i.e., were more correlated with, the overall uncertainty in deadwood volume. The shape of the curves did not vary substantially across the 18 scenarios, therefore we reported here the results of the relationships only for a sample uncertainty scenario (i.e., DWREM0 BAU RCP2.6) (Fig. 7), while the relationships for all the scenarios were reported in the Supplemental online material (Appendix Scatterplots).

We found that the overall uncertainty in the total deadwood volume was primarily determined by the uncertainty in the volumes of deadwood fractions with large diameter classes, especially of the last three classes, with trees larger than 30 cm (see Fig. 7a), recently dead (decay class 1), (Fig. 7b) characterized by limited loss in volume due to decomposition (collapse ratio ≥ 0.61) (Fig. 7c), from either spruce or pine trees (cf., Fig. 7d) and lying as logs on the forest floor (Fig. 7e).

3.5 Sensitivity indices

Sobol indices were calculated by partitioning the uncertainty in the total deadwood volume with respect to the uncertainty in the five deadwood characteristics (Fig. 8). The ranking of the Sobol indices did not vary substantially across the Table 4Impact of theexclusion of each deadwoodcharacteristics from theuncertainty in all deadwoodcharacteristics

DW characteristic	Stakeholders			Management			Climate		
	Scenario	Mean	95%CI	Scenario	Mean	95%CI	Scenario	Mean	95%CI
All-decay	DWREM0	19.6	0.020	BAU	11.9	0.015	RCP26	12.8	0.026
All-decay	DWREM75	6.3	0.006	CCF	11.0	0.022	RCP45	12.8	0.026
All-decay				SA	15.7	0.033	RCP85	13.2	0.025
All-position	DWREM0	19.7	0.021	BAU	12.1	0.017	RCP26	12.8	0.028
All-position	DWREM75	6.4	0.007	CCF	11.1	0.025	RCP45	12.9	0.028
All-position				SA	15.7	0.036	RCP85	13.4	0.028
All-collapse	DWREM0	19.8	0.020	BAU	11.9	0.015	RCP26	13.1	0.027
All-collapse	DWREM75	6.5	0.006	CCF	11.3	0.024	RCP45	12.9	0.026
All-collapse				SA	16.0	0.033	RCP85	13.4	0.026
All-species	DWREM0	17.3	0.019	BAU	10.1	0.013	RCP26	11.0	0.025
All-species	DWREM75	5.5	0.005	CCF	9.9	0.023	RCP45	11.4	0.024
All-species				SA	14.0	0.031	RCP85	11.9	0.025
All-diameter	DWREM0	24.8	0.038	BAU	10.2	0.025	RCP26	15.9	0.049
All-diameter	DWREM75	6.7	0.010	CCF	14.4	0.041	RCP45	15.3	0.046
All-diameter				SA	22.1	0.058	RCP85	16.0	0.049
All	DWREM0	19.5	0.022	BAU	11.8	0.016	RCP26	12.8	0.029
All	DWREM75	6.3	0.007	CCF	10.9	0.025	RCP45	12.8	0.028
All				SA	15.6	0.036	RCP85	13.1	0.028

Predicted means and 95% confidence intervals (CI) of deadwood volume summarized for the exclusion of each deadwood characteristic from the total (All) uncertainty and for each stakeholder's preference (DWREM0% and DWREM75%), management action (BAU, CCF, and SA), and climate change scenario (RCP 2.6, RCP 4.5, RCP 8.5) (N=158)

18 uncertainty scenarios of stakeholders' preferences, management actions and climate change; therefore, we reported here the plots for first order (S) and total order (T) Sobol indices for a single uncertainty scenario randomly selected (i.e., DWREM0 CCF RCP2.6), while the plots for all the scenarios are reported in the Supplemental online material (Appendix Sobol Indices).

For the diameter classes, we found that the uncertainty in total deadwood was increasingly explained (higher % of the Sobol index) by deadwood fractions of increasing diameter (Fig. 8a), with deadwood of 2 cm explaining on average among scenarios only -0.015% (Sobol index range: min. = -0.034%, max. = 0.0042%) of the total deadwood uncertainty and deadwood of 42 cm explaining on average 17% of the uncertainty (range: 4.7%, 30.4%). However, among the diameter classes of deadwood only the items of 42 cm diameter, whose average S value was the only one above the red dotted line of the *S* dummy parameter, could be considered influential for the uncertainty of total deadwood (Fig. 8a).

For the decay classes, deadwood in decay class 1, i.e., recently dead tree with the longest retention time was responsible on average for 44.9% of the uncertainty in total deadwood (range: 23%, 74.7%), while the decay classes 3 (medium decayed tree), 4 (very decayed tree) and 5 (almost decomposed tree) were respectively responsible only for

10.2% (range: 5.6%, 13.8%), 8.7% (range: 4.7%, 14%) and 10.3% (range: 4.6%, 30.7%) of the uncertainty (Fig. 8b). However, only the average S value in deadwood fractions in decay class 1 was above the horizontal red dashed line, therefore their uncertainty could be considered influential for the uncertainty of total deadwood (Fig. 8b).

For collapse ratio, we found that the uncertainty in total deadwood was increasingly explained by deadwood fractions with lower loss in volume (Fig. 8c). Deadwood which had lost almost all its volume respect to the initial value (i.e., in collapse class 0.01–0.2) explained on average only 2.1% of the total deadwood uncertainty (range: 0.03%, 12.9%) while deadwood which still retained all its volume (in collapse class 0.81–1) was responsible on average for 33.7% of the uncertainty (range: 10%, 68.1%). Only the average S value of the deadwood belonging to this latter collapse class could be considered influential for the uncertainty of total deadwood (Fig. 8c).

For tree species, spruce deadwood fractions were responsible on average for 33% of the uncertainty in total deadwood (range: 15.5%, 45.4%) and pine fractions for 30% of the uncertainty (range: 13.8%, 48%) (Fig. 8d). Deciduous fractions were less influential, representing on average only the remaining 2.7% of the uncertainty (range: 0.7%, 5.9%), likely because the bulk of deadwood was from coniferous trees. Only the two coniferous deadwood fractions showed

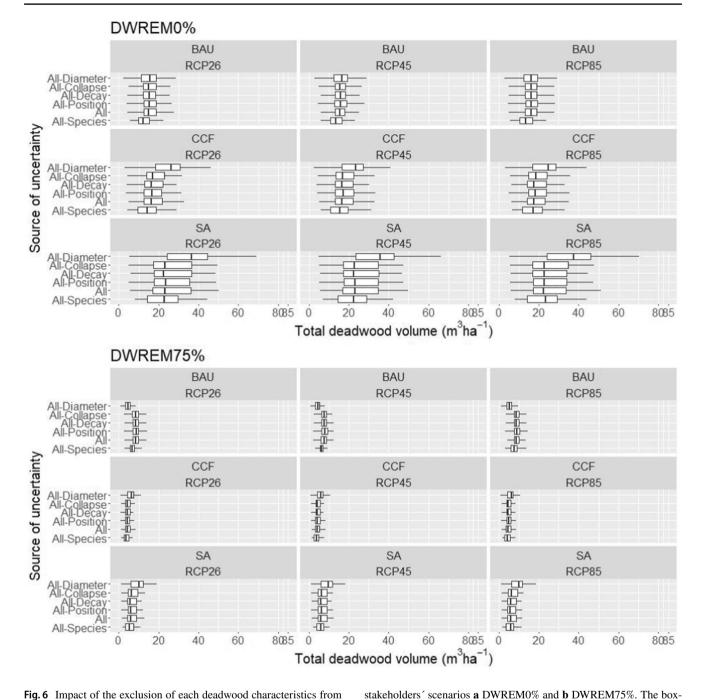


Fig. 6 Impact of the exclusion of each deadwood characteristics from the uncertainty in all deadwood characteristics for 9 combinations of uncertainty scenarios of climate change (RCP 2.6, RCP 4.5, RCP 8.5) and management actions (BAU, CCF and SA), separated by the two

plots represent the predicted deadwood volumes based on the Global Uncertainty and Sensitivity Analysis. Definitions of the box, interquartile range and whiskers as in Fig. 3

an average S value above the horizontal red dashed line, therefore their uncertainty was influential for the uncertainty of total deadwood (Fig. 8d).

Finally, log deadwood fractions were responsible on average for 67% of the uncertainty in total deadwood (range: 46.2%, 92.6%), while snag fractions were much less influential, representing on average only 6.2% (range: 3.6%, 14%) of the uncertainty (Fig. 8e). Only the uncertainties in log deadwood fractions were influential for the uncertainty of total deadwood (Fig. 8e).

The overlap between the confidence intervals of the first order (S) and total order (T) Sobol indices in all the dead-wood fractions revealed an absence of relevant interactions among uncertainties affecting the overall deadwood uncertainty (Fig. 8).

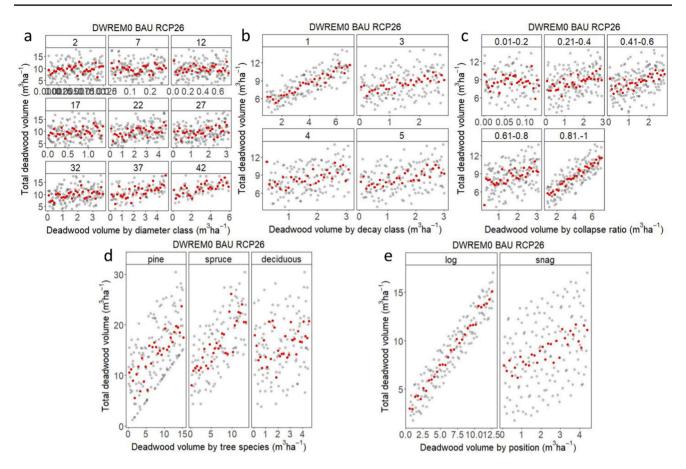


Fig. 7 Relationships between the variability in the simulated values of deadwood volumes, in x axes, of each of the five deadwood characteristics (in the panels: a=9 diameter classes expressed in cm, b=4 decay classes, c=5 collapse classes, d=3 tree species, e=2 deadwood positions), and the predictions of total deadwood (for the Sobol' G function, cf., Puy et al. 2022) in y axes, for one

4 Discussion

4.1 Contribution and impact of sources of uncertainties

The GUSA provides evidence that the large total deadwood uncertainty is mainly determined by the uncertainty in the initial inventory data and the uncertainty in deadwood characteristics estimated from the projections. This agrees with a recent uncertainty analysis of deadwood empirically measured in NFI plots (Campbell et al. 2019). The decomposition model embedded in SIMO overestimates the mean residence time of deadwood in each decay class (Mäkinen et al. 2006), therefore the overall uncertainty in the total deadwood volume may be systematically overestimated.

uncertainty scenario (i.e., no deadwood removal from the forest floor (DWREM0), Business-As-usual management (BAU), GHG concentration scenario=RCP2.6). Red dots represent mean predictions of total deadwood volume and grey dots the predicted uncertainty in its values. The regression model is the polynomial function from Becker and Saltelli (2015)

4.2 Contribution of sources of uncertainties

The analysis on the contributions of single sources of uncertainty revealed that the five deadwood characteristics are not equally important in explaining the total variability in deadwood. In our case study, this variability is more derived from the variability in volumes of deadwood items of different tree species and position on the forest floor and less from the variability in the collapse ratio, decay class, and diameter. This finding reflects the ranking of the impact of these factors on the deadwood decomposition rate found in a global comparative analysis conducted by Harmon et al. (2020). The fact that the total variability in the five deadwood characteristics was smaller than the variability induced by deadwood items of different species is likely explained by an interaction effect between sources of uncertainties,

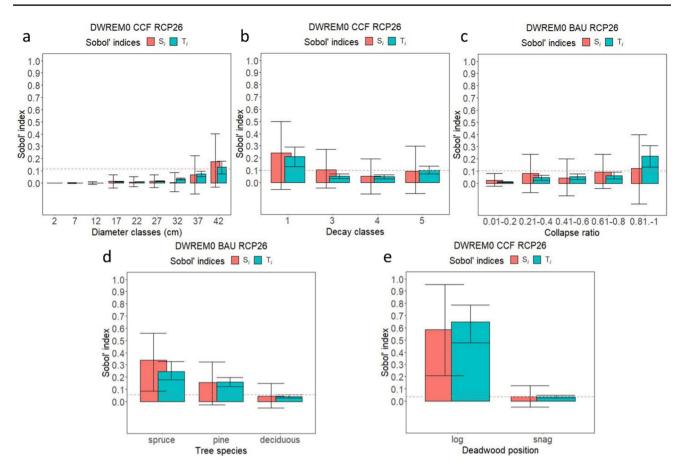


Fig. 8 First (*Si*) and total (*Ti*) order Sobol indices (derived from the Sobol' G function, cf., Puy et al. 2022) of the total deadwood volume uncertainty partitioned by the uncertainty in each of the five deadwood characteristics (in the panels: a=9 diameter classes, b=4 decay classes, c=5 collapse classes, d=3 tree species, e=2 dead-

wood positions) for one uncertainty scenarios (no deadwood removal from the forest floor (DWREM0), Continuous Cover Forest management (CCF), GHG concentration scenario=RCP2.6). The horizontal red dashed lines mark the upper limit of the Si indices of the dummy parameter. The vertical error bars are based on standard errors

with errors of opposite sign cancelling each other (Mäkinen et al. 2010).

4.3 Impacts of sources of uncertainties

The evaluation of the impacts of the exclusion of single sources of uncertainties in deadwood characteristics from the overall deadwood uncertainty showed that the uncertainties induced by tree species and deadwood diameter are the two most crucial in altering the estimates of the total deadwood volume, cumulatively contributing the most to the total uncertainty. In a laser-scanning based inventory, this would be possible by moving from predicting the expected deadwood volume for each pixel to identifying each dead log lying in the forest floor separately. Such approach is only possible for the largest logs (> 30 cm) which can be most efficiently located in the forest (Heinaro et al. 2021). Identifying the large logs individually would also reduce a large part of their position error. It can be assumed that the option of locating the largest individual dead trunks will become more and more realistic in the future and have strong implications for tracking resources suitable for biodiversity. For example, knowledge about the position of large logs would improve the decisions also concerning the optimal level of firewood taken from the forests and the allocation of conservation areas in the production landscape (cf., Mazziotta et al. 2023).

Our ranking of the importance of the sources of uncertainty in deadwood volume partly reflects the empirical results of the uncertainty analysis conducted by Campbell et al (2019). They also found that diameter was an important source of uncertainty in the measurement of downed coarse woody debris at plot level while collapse ratio and decay class had minor importance. In our simulations, the large uncertainty in deadwood of large diameter classes likely derived by the initial uncertainty of the large logs. Our analysis confirms that minimizing the error in the inference of certain deadwood characteristics can improve the level of confidence to assess habitat quantity and quality available for species dwelling in deadwood (Tikkanen et al. 2006, 2007; Kouki and Tikkanen 2007). In our study, the initial uncertainty in the deadwood inventory reflects that of the regional NFI, meaning that the assumed uncertainty level is an underestimate for an actual laser-scanning-based forest management inventory. However, as we consider the relative effects of different diameter classes, it does not have an effect on the conclusions.

4.4 Contributions and impacts of uncertainties by scenarios

The GUSA for the scenarios of stakeholders' preferences, management actions, and climate change showed that in some scenarios the prediction of deadwood volumes with certain characteristics could be less certain than in others. The impact of the exclusion of each source of uncertainty was also sensitive to the uncertainty scenario adopted. This means that in some scenarios the error-free inference of certain deadwood characteristics can be more important than in others to reduce the uncertainty in deadwood estimation.

The choice of the forest owners to remove deadwood from the forest floor decreased the variability in deadwood volume. The assessment of the tree species and diameter class was less uncertain when most of the deadwood had been removed from the forest floor, likely because of the selective removal of the less decomposed deadwood logs belonging to the largest diameter classes, all characteristics that caused most of the uncertainty. Behaviour of private forest owners may create bias in the snag/log ratio and NFI deadwood data. Based on the 9th Finnish NFI data, it is suggested that removal of snags and hard deadwood from forests for firewood reduces the number of logs and larger diameter deadwood of advanced decay classes in southern Finland (Tikkanen et al. 2009). A similar north south bias in the snag/log ratio in forest inventory data has been reported in Sweden (Fridman and Walheim 2000).

The variability of deadwood volumes increased with management actions attempting a close to-nature silviculture, likely due to the increased representation of deadwood of large diameter classes at least in the short term (Kuuluvainen et al. 2012). The estimate of deadwood characteristics in stands under CCF was more error-prone compared with stands under other management actions. This is likely due to the presence of deadwood logs of large diameter in CCF, which were created more often by the mortality model in CCF respect to the other two regimes. Under BAU, the predicted volume of deadwood is similar or even higher than the deadwood in CCF (see the "All" case in Table 3). However, this high volume is not available as habitat for biodiversity, as site preparation after clear-cut (e.g., harrowing) and movements of forest machinery destroys coarse woody debris which has been left since the previous tree generation (Hautala et al. 2004). Furthermore, in BAU clear-cutting residues left on the ground contribute deadwood with small diameters and limited variability in decay classes which reduces the total deadwood uncertainty (Kuuluvainen et al. 2012). The amount of tree canopy remaining after timber extraction is larger in CCF than in BAU, and this can affect the quantity of deadwood and its characteristics. This is likely because gaps left following clearcutting operations in BAU management will lead to more solar radiation hitting the surface of the deadwood, leading to potential photodegradation and to warmer and drier conditions either favouring or retarding the decomposition process (Harmon et al. 2020). It must be noticed that the deadwood decomposition model adopted in our simulator has been validated on the material collected from commercial and dense unthinned single-species stands (Mäkinen et al. 2006). Therefore, its application might have some limitations when predicting deadwood volumes in mixed stands managed with CCF and old-growth SA. In our simulations we assumed that BAU, CCF and SA are equally applied in forest management. However, this is not currently the case, with BAU being the dominant management regime in Finland, CCF applied especially in peatlands and SA officially only in state-owned or voluntary nature reserves. However, it is not known how the proportion of these management regimes may change in the future to comply with sustainability goals and pressures to adapt forests to climate change and this represents a large source of uncertainty in forest planning.

Finally, climate change increased the total deadwood volume (see the "All" case in Table 3) but not the variability in its characteristics. This can be related to the increase in the decomposition rate, which reduces the deadwood residence time (Mazziotta et al. 2014; Russell et al. 2014; Ekman et al. 2024). Consequently, it might be more difficult to detect deadwood items with certain characteristics, as their presence on the forest floor is more ephemeral. However, it must be considered that the model parameters for decomposition used in our forest simulator were not dependent on an increase in temperature and process rates, therefore it may well be that the actual representation of deadwood volumes with different characteristics, and their uncertainties, could be different from our projections. Furthermore, our forest simulator did not incorporate forest disturbances (e.g., drought, windstorms, insect and disease outbreaks, wildfires), and the changes in their frequency and magnitude induced by climate change. These extreme events may further alter the inputs into the standing and downed deadwood pools (Russell et al. 2014; Venäläinen et al. 2020).

4.5 Relationships between uncertainties in total deadwood and sensitivity indices

The analysis of the relationships between uncertainties and the sensitivity indices showed that the representation from the simulator of the distribution of the deadwood items can be erroneous, i.e., with a large prediction error. The deadwood items whose distribution is erroneously estimated from the simulator predictions are: logs with large diameters, recently dead trees characterized by low collapse in their volume, coniferous rather than deciduous tree species, and logs rather than snags. On the other hand, at stand level, the large uncertainty is likely explained by the fact that buried logs, as they have already been almost totally decomposed, generally exhibit the lower decomposition rate than snags aboveground, allowing the coexistence of a larger variability in deadwood characteristics (Stokland et al. 2016), especially of large diameter classes and advanced decay stages, whilst the decomposition rate of conifer snags is lower than logs, as the snags of old pines can be very durable (Yatskov et al. 2003). Reducing the initial uncertainty in estimate of deadwood items with these characteristics may help decision makers and forest managers to drastically reduce the uncertainty in the final estimate of the deadwood volume. The higher importance of the classes of deadwood with a larger diameter in affecting deadwood volumes might be explained by the fact that larger trees have larger variability in volume than small trees; the higher importance of coniferous rather than deciduous trees by their larger occurrence in the managed stands. Finally, the larger impact of uncertainty on the early decay classes might be due to a bias in our decomposition model, caused by the low number of observations in the most advanced decomposition stages. In fact, the predictions for the most advanced decomposition phases are extrapolations and, thus, less reliable (Mäkinen et al. 2006).

5 Conclusions

Our study confirms that stakeholders' decisions, management actions, and climate change can alter the distribution of the frequency classes of deadwood volumes in the forest. The forest owners' decision to leave or remove deadwood from the forest floor respectively increased and reduced the availability of deadwood in the landscape for forest-dwelling species (Koskela and Karppinen 2020). This decision was certainly the one that affected the most the availability of deadwood on the forest floor and the certainty of its estimation. When the forest management followed a decreasing gradient of forest intensification, from mainstream evenaged forestry to single tree selection harvest, to closer-tonature development, the deadwood volume increased consistently (Pohjanmies et al. 2021). Deadwood accumulated more in forest stands under high-end (RCP8.5) climate scenarios triggered by a higher forest growth (Creutzburg et al. 2017; Blattert et al. 2020) but also the likelihood of erroneous estimates.

To summarize, a reduction of the uncertainty of selected deadwood characteristics is instrumental in reducing the uncertainty in deadwood volume estimation from projections and in aligning the level of certainty in the assessment of the deadwood volume to the elevated level of certainty already achieved in biomass estimation. Better modelling of the deadwood decomposition pathway can be achieved by reducing the sources of uncertainty in the inventory of various deadwood pools (Russell et al. 2014). In our case study, the uncertainty and sensitivity analysis were successful in ranking the factors propagating errors in the inferences of deadwood and helped to identify a strategy for minimizing uncertainty in the estimation of deadwood characteristics. Deadwood has the capacity to supply several forest ecosystem services, including regulating services, for its capacity of climate regulation by storing carbon (Stokland et al. 2016) and maintenance services, for its capacity to create habitat for forest biodiversity (CICES, Common International Classification of Ecosystem Services, Haines-Young and Potschin 2018; NCP, Nature's Contributions to People, Díaz et al. 2018). The capacity of deadwood to supply these services in the long term is continuously changing in a forest landscape modified by stakeholders' preferences, management actions, and climate change. These scenarios are expected to have large impacts on the capacity of the forest to produce deadwood. In this context, the estimation of the uncertainty in deadwood levels under the scenarios developed in our study can help decision makers to evaluate the risk of decreasing its value for biodiversity conservation and climate change mitigation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00477-023-02655-2.

Author contributions AM and KE conceived the study. AM and KE performed the simulations. AM performed the GUSA analyses. AM and KE led the writing of the manuscript. AM, KE, AK, IDPL and O-PT interpreted the results and participated in writing the paper.

Funding Open access funding provided by Natural Resources Institute Finland. AM, KE and IDPL received funding from Kungl. Skogs- och Lantbruksakademiens, Tandem Forest Values 2017 (project MAIN-TAIN 01). AM, KE and AK received funding from the Academy of Finland Flagship Forest-Human–Machine Interplay—Building Resilience, Redefining Value Networks and Enabling Meaningful Experiences (UNITE) 337653.

Declarations

Competing interests No potential conflict of interest was reported by the author(s).

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are

included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

- Äijälä O, Koistinen A, Sved J, Vanhatalo K, Väisänen P (2014) Metsänhoidon suositukset. [The good practice guidance to forestry, (in Finnish)]. Metsäkustannus Oy, Forestry Development Centre Tapio, Helsinki
- Blattert C, Lemm R, Thürig E et al (2020) Long-term impacts of increased timber harvests on ecosystem services and biodiversity: a scenario study based on national forest inventory data. Ecosyst Serv 45:101150. https://doi.org/10.1016/j.ecoser.2020.101150
- Campbell JL, Green MB, Yanai RD et al (2019) Estimating uncertainty in the volume and carbon storage of downed coarse woody debris. Ecol Appl 29:e01844–e01844. https://doi.org/10.1002/eap.1844
- Carstensen J, Lindegarth M (2016) Confidence in ecological indicators: a framework for quantifying uncertainty components from monitoring data. Ecol Ind 67:306–317. https://doi.org/10.1016/j. ecolind.2016.03.002
- Chirici G, McRoberts RE, Winter S et al (2012) National forest inventory contributions to forest biodiversity monitoring. For Sci 58:257–268. https://doi.org/10.5849/forsci.12-003
- Creutzburg MK, Scheller RM, Lucash MS et al (2017) Forest management scenarios in a changing climate: trade-offs between carbon, timber, and old forest. Ecol Appl 27:503–518. https://doi.org/10. 1002/eap.1460
- Deuffic P, Lyser S (2012) Biodiversity or bioenergy: is deadwood conservation an environmental issue for French forest owners? Can J For Res 42:1491–1502. https://doi.org/10.1139/x2012-073
- Díaz S, Pascual U, Stenseke M et al (2018) Assessing nature's contributions to people. Science 359:270–272. https://doi.org/10.1126/ science.aap8826
- Ekman E, Triviño M, Blattert C, Mazziotta A, Potterf M, Eyvindson K (2024) Disentangling the effects of management and climate change on habitat suitability for saproxylic species in boreal forests. J for Res 35(1):34. https://doi.org/10.1007/ s11676-023-01678-3
- Eyvindson K, Repo A, Mönkkönen M (2018) Mitigating forest biodiversity and ecosystem service losses in the era of bio-based economy. Forest Policy Econ 92:119–127. https://doi.org/10. 1016/j.forpol.2018.04.009
- FFC (2021) Finnish forest centre, open forest information. Available from www.metsakeskus.fi/fi/avoin-metsa-ja-luontotieto/metsatieto aineistot/metsavaratiedot
- Fridman J, Walheim M (2000) Amount, structure, and dynamics of dead wood on managed forestland in Sweden. For Ecol Manag 131:23–36. https://doi.org/10.1016/s0378-1127(99)00208-x
- Gibb H, Ball JP, Johansson T et al (2005) Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. Scand J for Res 20:213–222. https://doi.org/10. 1080/02827580510008392
- Haines-Young R, Potschin-Young M (2018) Revision of the common international classification for ecosystem services (CICES V5.1): a policy brief. One Ecosyst 3:e27108. https://doi.org/10.3897/ oneeco.3.e27108
- Harmon ME, Fasth BG, Yatskov M et al (2020) Release of coarse woody detritus-related carbon: a synthesis across forest biomes. Carbon Balance Manag 15:1–1. https://doi.org/10.1186/ s13021-019-0136-6

- Hautala H, Jalonen J, Laaka-Lindberg S, Vanha-Majamaa I (2004) Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodivers Conserv 13:1541–1554. https://doi.org/10.1023/b:bioc.0000021327.43783. a9
- Heinaro E, Tanhuanpää T, Yrttimaa T et al (2021) Airborne laser scanning reveals large tree trunks on forest floor. For Ecol Manage 491:119225. https://doi.org/10.1016/j.foreco.2021.119225
- Heinonen T, Pukkala T, Mehtätalo L et al (2017) Scenario analyses for the effects of harvesting intensity on development of forest resources, timber supply, carbon balance and biodiversity of finnish forestry. Forest Policy Econ 80:80–98. https://doi.org/10. 1016/j.forpol.2017.03.011
- Hynynen J, Ojansuu R, Hökkä H et al (2002) Models for predicting stand development in MELA system. finnish forest research institute. Res Papers 83:1–116
- Hynynen J, Salminen H, Ahtikoski A et al (2015) Long-term impacts of forest management on biomass supply and forest resource development: a scenario analysis for Finland. Eur J Forest Res 134:415–431. https://doi.org/10.1007/s10342-014-0860-0
- Junninen K, Komonen A (2011) Conservation ecology of boreal polypores: a review. Biol Cons 144:1779. https://doi.org/10.1016/j. biocon.2011.04.013
- Juutinen A, Kurttila M, Pohjanmies T et al (2021) Forest owners' preferences for contract-based management to enhance environmental values versus timber production. Forest Policy Econ 132:102587. https://doi.org/10.1016/j.forpol.2021.102587
- Kellomäki S, Peltola H, Nuutinen T et al (2008) Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Philos Trans R Soc Lond B Biol Sci 363:2341–2351. https://doi.org/10.1098/rstb.2007.2204
- Korhonen KT, Ihalainen A, Kuusela S, Punttila P, Salminen O, Syrjänen K (2020) Metsien monimuotoisuudelle merkittävien rakennepiirteiden muutokset Suomessa vuosina 1980–2015. Metsätieteen Aikakauskirja. 10198:1–26. https://doi.org/10.14214/ma. 10198
- Koskela T, Karppinen H (2020) Forest owners' willingness to implement measures to safeguard biodiversity: values, attitudes, ecological worldview and forest ownership objectives. Small-Scale Forest 20:11–37. https://doi.org/10.1007/s11842-020-09454-5
- Kouki J, Tikkanen O-P (2007) Uhanalaisten Lahopuulajien Elinympäristöjen Turvaaminen Suojelualueilla ja Talousmetsissä: Kustannustehokkuus ja Ekologiset, Ekonomiset Sekä Sosiaaliset Vaikutukset Kitsin Seudulla Lieksassa. Ympäristöministeriö, Helsinki, 104 s pp. https://helda.helsinki.fi/handle/10138/38413
- Kuuluvainen T, Tahvonen O, Aakala T (2012) Even-aged and unevenaged forest management in boreal Fennoscandia: a review. Ambio 41:720–737. https://doi.org/10.1007/s13280-012-0289-y
- Kuuluvainen J, Karppinen H, Ovaskainen V (1996) Landowner objectives and nonindustrial private timber supply. Forest Sci 42:300– 309. https://academic.oup.com/forestscience/article/42/3/300/ 4626935
- Lagerwall G, Kiker G, Muñoz-Carpena R, Wang N (2014) Global uncertainty and sensitivity analysis of a spatially distributed ecological model. Ecol Model 275:22–30. https://doi.org/10.1016/j. ecolmodel.2013.12.010
- Lappi J, Pukkala T (2020) Analyzing ingrowth using zero-inflated negative binomial models. Silva Fennica. https://doi.org/10.14214/ sf.10370
- Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol Ind 11:1027–1039. https://doi.org/10.1016/j.ecolind.2011. 02.004

- Le Saout S, Hoffmann M, Shi Y et al (2013) Protected areas and effective biodiversity conservation. Science 342:803–805. https://doi. org/10.1126/science.1239268
- Mäkinen H, Hynynen J, Siitonen J, Sievänen R (2006) predicting the decomposition of *Scots Pine*, Norway spruce, and birch stems in Finland. Ecol Appl 16:1865–1879. https://doi.org/10.1890/1051-0761(2006)016[1865:ptdosp]2.0.co;2
- Mäkinen A, Kangas A, Mehtätalo L (2010) Correlations, distributions, and trends in forest inventory errors and their effects on forest planning. Can J for Res 40:1386–1396. https://doi.org/10.1139/ x10-057
- Maltamo M, Packalen P, Kangas A (2021) From comprehensive field inventories to remotely sensed wall-to-wall stand attribute data—a brief history of management inventories in the Nordic countries. Can J for Res 51:257–266. https://doi.org/10.1139/cjfr-2020-0322
- Maltamo M, Næsset E, Vauhkonen J (2014) Forestry applications of airborne laser scanning. Concepts and case studies. Manag Forest Ecosyst 27:460. https://doi.org/10.1007/978-94-017-8663-8
- Matala J, Ojansuu R, Peltola H et al (2005) Introducing effects of temperature and CO_2 elevation on tree growth into a statistical growth and yield model. Ecol Model 181:173–190. https://doi.org/10.1016/j.ecolmodel.2004.06.030
- Matala J, Ojansuu R, Peltola H et al (2006) Modelling the response of tree growth to temperature and CO_2 elevation as related to the fertility and current temperature sum of a site. Ecol Model 199:39–52. https://doi.org/10.1016/j.ecolmodel.2006.06.009
- Mazziotta A, Mönkkönen M, Strandman H et al (2014) Modeling the effects of climate change and management on the dead wood dynamics in boreal forest plantations. Eur J Forest Res 133:405–421. https://doi.org/10.1007/s10342-013-0773-3
- Mazziotta A, Triviño M, Tikkanen O-P et al (2016) Habitat associations drive species vulnerability to climate change in boreal forests. Clim Change 135:585–595. https://doi.org/10.1007/ s10584-015-1591-z
- Mazziotta A, Borges P, Kangas A et al (2023) Spatial trade-offs between ecological and economical sustainability in the boreal production forest. J Environ Manage 330:117144. https://doi. org/10.1016/j.jenvman.2022.117144
- McCarthy BC, Bailey RR (1994) Distribution and abundance of coarse woody debris in a managed forest landscape of the central Appalachians. Can J for Res 24:1317–1329. https://doi.org/ 10.1139/x94-172
- McCarthy DP, Donald PF, Scharlemann JPW et al (2012) Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. Science 338:946–949. https://doi.org/10.1126/science.1229803
- Mönkkönen M, Juutinen A, Mazziotta A et al (2014) Spatially dynamic forest management to sustain biodiversity and economic returns. J Environ Manag 134:80–89. https://doi.org/10. 1016/j.jenvman.2013.12.021
- Næsset E (2004) Accuracy of forest inventory using airborne laser scanning: evaluating the first nordic full-scale operational project. Scand J for Res 19:554–557. https://doi.org/10.1080/02827 580410019544
- Pesonen A (2011) Comparison of field inventory methods and use of airborne laser scanning for assessing coarse woody debris. Dissertationes Forestales. https://doi.org/10.14214/df.113
- Pohjanmies T, Triviño M, Le Tortorec E et al (2017) Impacts of forestry on boreal forests: an ecosystem services perspective. Ambio 46:743–755. https://doi.org/10.1007/s13280-017-0919-5
- Pohjanmies T, Eyvindson K, Triviño M et al (2021) Forest multifunctionality is not resilient to intensive forestry. Eur J Forest Res 140:537–549. https://doi.org/10.1007/s10342-020-01348-7
- Pukkala T, Lähde E, Laiho O (2013) Species Interactions in the dynamics of even—and uneven-aged boreal forests. J Sustain for 32:371–403. https://doi.org/10.1080/10549811.2013.770766

- Puy A, Piano SL, Saltelli A, Levin SA (2022) Sensobol: an R package to compute variance-based sensitivity indices. J Stat Softw. https://doi.org/10.18637/jss.v102.i05
- Rasinmäki J, Mäkinen A, Kalliovirta J (2009) SIMO: An adaptable simulation framework for multiscale forest resource data. Comput Electron Agric 66:76–84. https://doi.org/10.1016/j.compag. 2008.12.007
- Riffell S, Verschuyl J, Miller D, Wigley TB (2011) Biofuel harvests, coarse woody debris, and biodiversity—a meta-analysis. For Ecol Manag 261:878–887. https://doi.org/10.1016/j.foreco. 2010.12.021
- Rondeux J, Sanchez C (2010) Review of indicators and field methods for monitoring biodiversity within national forest inventories. Core variable: deadwood. Environ Monit Assess 164:617–630. https://doi.org/10.1007/s10661-009-0917-6
- Russell MB, Woodall CW, D'Amato AW et al (2014) Technical note: linking climate change and downed woody debris decomposition across forests of the eastern United States. Biogeosciences 11:6417–6425. https://doi.org/10.5194/bg-11-6417-2014
- Saltelli A, Annoni P, Azzini I et al (2010) Variance based sensitivity analysis of model output. Design and estimator for the total sensitivity index. Comput Phys Commun 181:259–270. https://doi. org/10.1016/j.cpc.2009.09.018
- Saltelli A, Tarantola S, Campolongo F, Ratto M (2004) Sensitivity analysis in practice. Wiley, London
- Saltelli A, Ratto M, Andres T et al (2008) Global sensitivity analysis. The primer. Wiley, London. https://doi.org/10.1002/9780470725 184
- Shorohova E, Kapitsa E (2014) Influence of the substrate and ecosystem attributes on the decomposition rates of coarse woody debris in European boreal forests. For Ecol Manag 315:173–184. https:// doi.org/10.1016/j.foreco.2013.12.025
- Siitonen J (2001) Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecol Bull 49:11–42
- Sobol IM (2001) Global sensitivity indices for nonlinear mathematical models and their Monte Carlo estimates. Math Comput Simul 55:271–280. https://doi.org/10.1016/s0378-4754(00)00270-6
- Sobol IM (1993) Sensitivity analysis for non-linear mathematical models. Math Model Comput Exp 1:407–414
- Stokland JN, Woodall CW, Fridman J, Ståhl G (2016) Burial of downed deadwood is strongly affected by log attributes, forest ground vegetation, edaphic conditions, and climate zones. Can J for Res 46:1451–1457. https://doi.org/10.1139/cjfr-2015-0461
- Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press, Cambridge
- Tikkanen O-P, Heinonen T, Kouki J, Matero J (2007) Habitat suitability models of saproxylic red-listed boreal forest species in long-term matrix management: cost-effective measures for multispecies conservation. Biol Cons 140:359–372. https://doi.org/10. 1016/j.biocon.2007.08.020
- Tikkanen O-P, Punttila P, Heikkilä R (2009) Species-area relationships of red-listed species in old boreal forests: a large-scale data analysis. Divers Distrib 15:852–862. https://doi.org/10.1111/j. 1472-4642.2009.00590.x
- Tikkanen O-P, Martikainen P, Hyvärinen E, Junninen K, Kouki J (2006) Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. Annal Zoologici Fennici 43:373–383. https://www.annzool.net/PDF/anzf43/ anzf43-373.pdf
- Triviño M, Pohjanmies T, Mazziotta A et al (2016) Optimizing management to enhance multifunctionality in a boreal forest landscape. J Appl Ecol 54:61–70. https://doi.org/10.1111/1365-2664. 12790
- Triviño M, Potterf M, Tijerín J et al (2023) Enhancing resilience of boreal forests through management under global change:

a review. Curr Landsc Ecol Rep. https://doi.org/10.1007/ s40823-023-00088-9

- van Vuuren DP, Edmonds J, Kainuma M et al (2011) The representative concentration pathways: an overview. Clim Change 109:5–31. https://doi.org/10.1007/s10584-011-0148-z
- Venäläinen A, Lehtonen I, Laapas M et al (2020) Climate change induces multiple risks to boreal forests and forestry in Finland: a literature review. Glob Chang Biol 26:4178–4196. https://doi. org/10.1111/gcb.15183
- von Salzen K, Scinocca JF, McFarlane NA et al (2013) The Canadian fourth generation atmospheric global climate model (CanAM4). Part I: representation of physical processes. Atmos Ocean 51:104– 125. https://doi.org/10.1080/07055900.2012.755610
- Woodall CW, Rondeux J, Verkerk PJ, Ståhl G (2009) Estimating dead wood during national forest inventories: a review of inventory methodologies and suggestions for harmonization. Environ Manag 44:624–631. https://doi.org/10.1007/s00267-009-9358-9
- Yatskov M, Harmon ME, Krankina ON (2003) A chronosequence of wood decomposition in the boreal forests of Russia. Can J for Res 33:1211–1226. https://doi.org/10.1139/x03-033

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.