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Research article

Modelling the effects of climate and management on the distribution of deadwood in European forests

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A B S T R A C T

Deadwood is a key old-growth element in European forests and a cornerstone of biodiversity conservation practices in the region, recognized as an important indicator of sustainable forest management. Despite its importance as a legacy element for biodiversity, uncertainties remain on the drivers of deadwood potentials, its spatial distribution in European forests and how it may change in the future due to management and climate change. To fill this gap, we combined a comprehensive deadwood dataset to fit a machine learning and a Bayesian hurdle-lognormal model against multiple environmental and socio-economic predictors. We deployed the models on the gridded predictors to forecast changes in deadwood volumes in Europe under alternative climate (RCP4.5 and RCP8.5) and management scenarios (biodiversity-oriented and production-oriented strategies). Our results show deadwood hotspots in montane forests of central Europe and unmanaged forests in Scandinavia. Future climate conditions may reduce deadwood potentials up to 13% under a mid-century climate, with regional losses amounting to up to 22% in Southern Europe. Nevertheless, changes in management towards more biodiversity-oriented strategies, including an increase in the share of mixed forests and extended rotation lengths, may mitigate this loss to a 4% reduction in deadwood potentials. We conclude that adaptive management can promote deadwood under changing environmental conditions and thereby support habitat maintenance and forest multifunctionality.

1. Introduction

Biodiversity conservation is at the center of contemporary debates on forest stewardship, where the improvement of habitat availability to sustain forest taxa and ecosystem multifunctionality takes a prominent role (Aggestam et al., 2020). Biodiversity is a cornerstone of several forest processes and underlies ecosystem resilience, in the face of changing environmental conditions (Mori et al., 2017; Schuldt et al., 2018). Hence, biodiversity protection became a primary forest management goal and has influenced attitudes towards forest use (Messier et al., 2019) and environmental policies in Europe (Muys et al., 2022).

The interplay between forest resilience and biodiversity conservation are seen as central aspects for the maintenance of forest functions in the future (Mori et al., 2017). In this respect, legacy and old-growth elements are essential to sustain ecosystem functioning (Gustafsson et al., 2020a). Deadwood is a key legacy element and plays a central role in forest ecology and dynamics, and the preservation of forest-dwelling taxa. Schuck et al. (2005) highlight that 20–25% of forest species depend on decaying wood, providing substrate and supporting the maintenance of saproxylic organisms. Saproxylic beetles, for example, are particularly affected by habitat loss. According to the International Union for Conservation of Nature red list, 19.7% of the species in this group are endangered in Europe (Calix et al., 2018). Several studies suggest that larger amounts of deadwood are linked to increased species richness and abundance of saproxylic organisms (e.g. Lassauce et al., 2011; Haeler et al., 2021; Kärvemo et al., 2021). Deadwood volume thresholds of 20–30$m^3 ha^{-1}$ have been suggested as appropriate amounts to sustain these communities and guide management practices in Europe (e.g. Müller and Bütler, 2010), although recent analyses highlight that diversity in deadwood dimensions and decay stages are also essential determinants of species diversity (Müller et al., 2020).

Deadwood also affects forest processes and productivity, being

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particularly important for nutrient cycling, soil carbon accumulation and regeneration dynamics in forest stands (Lombardi et al., 2013; Palviainen and Finér, 2015). Kappes et al. (2007) found deadwood amounts to be positively linked to better soil quality and reduced acidification, although the magnitude of these effects is context dependent (Bauhus et al., 2018). Additionally, deadwood contributes to soil maintenance, helping to stabilize slopes, mitigate soil erosion and reduce water runoff (Merganičová et al., 2012). It must be noted, however, that high deadwood stocks can increase the risk of forest fires, especially in the Mediterranean region (Morán-Ordóñez et al., 2020). Given the crucial role of deadwood in forest functioning and biodiversity conservation, it was identified as a key indicator of sustainable forest management established by the Ministerial Conference on the Protection of Forests in Europe (MCPFE, 2002).

Apart from the crucial role in ecosystem functioning and biodiversity conservation, deadwood is also an important component of the forest carbon balance, contributing to climate mitigation targets related to forest ecosystems (Bai et al., 2023). Deadwood provides temporary carbon storage in forests and can have an important role in the total climate mitigation contribution of forest management (Pukkala, 2018), also affecting soil carbon sequestration and the contribution of afforestation efforts (Liu et al., 2010; Gong et al., 2021). Forest utilization affect inter-tree competition and mortality rates in forest stands (Mazziotta et al., 2014), altering the inputs to the deadwood pool and, consequently, the deadwood stock. Similarly, species composition and its change via forest management exert influence on the deadwood, considering that mortality and decay rates are species-specific (Zell et al., 2009). Decay rates and deadwood amounts are also determined by climatic conditions, particularly by temperature and precipitation regimes (Seibold et al., 2021). Pukkala (2018) found that in boreal forests, low intensity management may lead to improved carbon benefits of forest management, due to the low decay rates, providing equivalent or better carbon storage than wood products in the long term. Current estimates point out that 7% of the total carbon in European forests is stored in the deadwood pool (FOREST EUROPE, 2020) . This highlights the importance of this indicator both to biodiversity and climate commitments. Hence, assessments of the distribution and amounts of deadwood are needed to improve carbon balance estimates of European forests. They are also useful to inform forest modelling activities and monitor habitat quality and forest naturalness.

Recently, sustainable forest management and biodiversity indicators at high resolution have been derived for European forests with the help of increasing availability of data collected from remote sensing and field surveys (e.g. Nabuurs et al., 2019; Sabatini et al., 2018, 2021; Giannetti et al., 2018; Mikkonen et al., 2020). Such developments are important steps to identify high quality habitats and potential target areas for ecosystem restoration and protection. Still, spatially explicit deadwood estimates are largely missing, despite its high ecological importance in forest ecosystems and connection to ecosystem services. Furthermore, analyses on the impacts of changes in forest attributes and climatic conditions on the amount and distribution of deadwood in European forests are lacking. In this context, we aimed to build a model capable of identifying drivers of deadwood amounts across Europe and answer the following research questions: 1 - What are the factors influencing the occurrence of deadwood in European forests? and 2 – How changes in forest management and climate may impact deadwood potential in the future?

To answer these research questions, we built statistical models employing Bayesian inference and boosted regression trees (BRT). We grounded our analysis on the survey conducted by the International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP) network (http://www.icp-forests.org) and the corresponding dataset constructed by Puletti et al. (2019). We used this dataset combined with a series of grided predictors related to biophysical attributes and socio-economic parameters. We then fit the statistical models and evaluated deadwood distribution and amounts in European forests and deployed them to upscale deadwood estimates. Despite limitations on the representation of transient forest dynamics in our model, where climate change and management effects on forest dynamics were proxied by the set of gridded environmental and forest predictors, our results provide valuable information for further analyses and modeling efforts on the effects of management and climate on deadwood distribution in European forests.

2. Methods

To compute drivers of deadwood potentials in Europe, we employed the large-scale biodiversity survey from the ICP forests network, combined with a series of state-of-the-art gridded datasets. We included climatic parameters, terrain characteristics, forest attributes and socio-economic indicators in our analysis. We fitted two alternative models to regress deadwood volumes against the aforementioned predictors. The models were then employed to identify the effect of the different predictors on deadwood amounts, to upscale deadwood predictions and to assess possible effects of changes in climate and forest management characteristics on deadwood potential in European forests (Fig. 1).

2.1. Data

2.1.1. Deadwood data

To conduct our analysis, we used a comprehensive dataset of deadwood amounts based on the biodiversity survey of the ICP forests network (Bastrup-Birk et al., 2006; Puletti et al., 2019). This survey was conducted from 2006 to 2008 within the framework of the BioSoil project (see Durrant et al., 2011), on 3243 ICP Level I plots, established in a 16×16 km grid and covering 19 European countries (Fig. 2). In the BioSoil project, for each of the points in this grid, 3 circular concentric subplots of 30, 400 and 2000 m^2 were established to assess structural diversity, deadwood and ground vegetation. Deadwood was measured in the 400 m^2 plots across the network, including stems, limbs, branches lying on the ground occurring in the inner subplots 1 and 2 (30 and 400 m^2). The deadwood survey included the quantification of standing and lying dead trees, coarse wood debris (lying deadwood with diameter larger than 10 cm), snags and stumps, as well as the decay stage (5 classes) of all components. Additionally, fine wood debris (diameter <10 cm) amounts was optionally recorded (Bastrup-Birk et al., 2006). Here, we used the total deadwood volume, i.e. the sum of lying and standing deadwood stocks from all decay classes.

Puletti et al. (2019) have extracted, pre-processed and merged the raw deadwood ICP data into a consistent and harmonized deadwood dataset, giving deadwood amounts by class and decay stage in each plot, which was used in this study. Further details can be found in the ICP forests manual (http://icp-forests.net/page/icp-forests-manual) and (Puletti et al., 2019) .

2.1.2. Environmental and socio-economic predictors

To fit the deadwood models, we combined and harmonized field data and remotely sensed data for multiple biophysical and socio-economic parameters (Table 1). We included in the model four classes of predictors, encompassing climate characteristics (precipitation and temperature), terrain features (elevation and slope), several forest attributes (age, biogeographic region, aboveground biomass (AGB), tree density, forest type, mortality rate, disturbance occurrence and vulnerability to natural disturbances) and socio-economic conditions (accessibility, based on the distance to markets, management suitability, protection status, ownership type, forest area per capita, GDP contribution of the forest sector and country). The predictors were retrieved in their native resolution for the deadwood observations and resampled to a 1 km resolution for the predictions at the European level, reprojecting from the LAEA to WGS84 projection system where necessary.

For the tree density predictor (3.5), we converted the total tree density in the grid cell given in the original dataset to tree density per

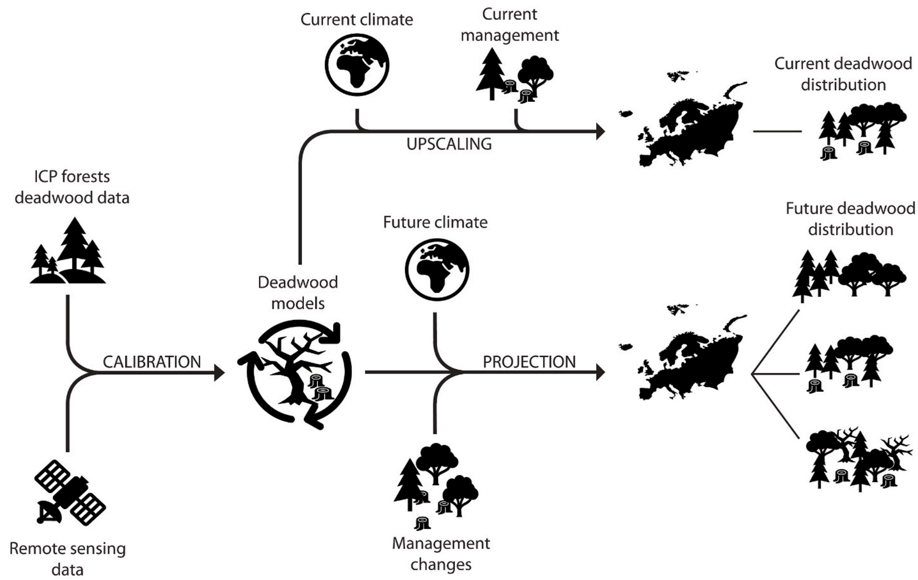

Fig. 1. Overview of the analysis carried out for the assessment of deadwood amounts in Europe. We combined a field survey on deadwood amounts with a series of predictors obtained from remote sensing to fit statistical models and analyze drivers and distribution of deadwood in Europe. The models were then used to upscale current deadwood potentials and evaluate changes due to climate and management.

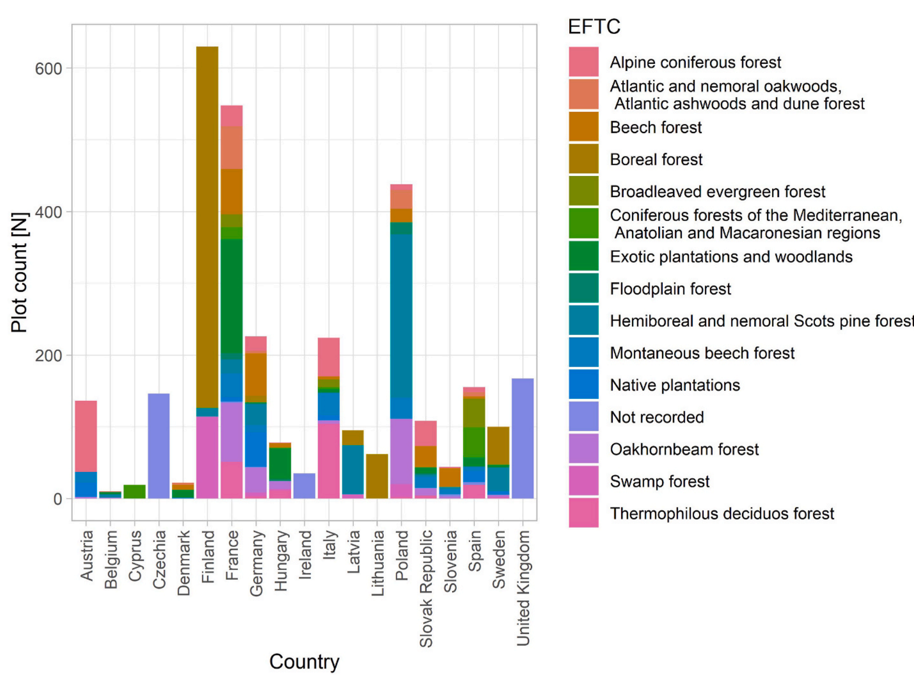

Fig. 2. Distribution of deadwood plots by country and European Forest Type Classification (EFTC) compiled in the deadwood dataset.

hectare of forest, to better capture the stocking and competition level that affects tree mortality and deadwood volume. To this end, we used the forest area map from the Copernicus Land Monitoring Service (https://land.copernicus.eu/), which was also used to produce the protected area layer, retrieved from the World Database on Protected Areas (WDPA) and biogeographical region layers. Furthermore, we conducted forest growth simulations using the r3PG package (Trotsiuk et al., 2020) across Europe to estimate mortality rates under different climate trajectories.

For France, Ireland and Poland, only approximated plot coordinates were available (the seconds component of the coordinates are set to zero due to confidentiality concerns), affecting 555 observations in the dataset. To reduce the error in the extraction of forest attributes in these cases, the seconds component in the coordinates was set to 30", inducing an error of up to approximately 1 km to the plot coordinates. We included in our analysis plots with up to 200 $m^3.ha^{-1}$ of deadwood, based on deadwood volumes naturally occurring in unmanaged forests (Hahn and Christensen, 2005), to better reflect typical deadwood amounts in European forests. Due to the approximation of plot coordinates in these countries, and coverage of the predictors across Europe, some data points had at least one of the predictors with no data. To address this issue, we imputed the missing data applying the MICE R package (Van Buuren and Groothuis-Oudshoorn, 2011) using a random forest method and generating five distinct datasets with the imputed data. The models were then fitted to these multiple datasets. After removing outliers, the final dataset was composed of 2547 data points.

Table 1
Overview of input data.

	Predictor	Description	Resolution	Source
1 Climate (historical)				
1.1	precipitation	Annual precipitation sum [mm]	1 km	WorldClim 2.1
1.2	temperature	Mean annual temperature [degrees C]	1 km	WorldClim 2.1
2Terrain				
2.1	elevation	Elevation [m a.s.l.]	25m	European Environment Agency (2016)
2.2	slope	Slope [DN[b]]	25m	European Environment Agency (2016)
2.3	latitude	Latitude [o]		–
2.4	longitude	Longitude [o]		–
3 Forest attributes				
3.1	Age	Average forest age [years]	1 km	Besnard et al. (2021)
3.2	biogeoregion	Biogeographical region	V[a]	European Environment Agency (2016)
3.3	biomass	Aboveground forest biomass [$tC.ha^{-1}$]	100m	Santoro et al. (2021)
3.4	forest type	Forest type classification	100m	Buchhorn et al. (2020)
3.5	tree density	Tree density per hectare [$N.ha^{-1}$]	1 km	Crowther et al. (2015)
3.6	mortality	Modeled mortality rate [$m^3.ha^{-1}year^{-1}$]	10 km	Authors
3.7	disturbance	Percentage of disturbed forest area in the past 10 years [%]	100m	Senf & Seidl (2021)
3.8	wind	Vulnerability to wind disturbances [% of biomass]	0.25°	(Forzieri et al., 2021)
3.9	fire	Vulnerability to wildfires [% of biomass]		(Forzieri et al., 2021)
3.10	insect	Vulnerability to biotic disturbances [% of biomass]		(Forzieri et al., 2021)
4 Socio-economic				
4.1	access	Travel time to closest market [min]	1 km	Weiss et al. (2018)
4.2	management	Suitability of forest management types	1 km	Hengeveld et al. (2012)
4.3	WDPA	World Database on Protected Areas (WDPA) protection status	V[a]	(EEA)
4.4	ownership	Share of public forests [%]	V[a]	Pulla et al. (2013)
4.5	country	Country	V[a]	–
4.6	Area	Per capita forest area [$ha.inhabitant^{-1}$]	V[a]	EUROSTAT
4.7	GDP	Forest sector contribution to GDP [%]	V[a]	EUROSTAT

[a] - vector files.
[b] - degree = acos (DN/250)*180/π

2.2. Deadwood models

To unveil deadwood drivers and upscale deadwood distribution in European forests, we regressed the deadwood amounts in the deadwood dataset against the gridded predictors described in Table 1. We initially applied a square root transformation to the deadwood amounts to mitigate the skewness of the deadwood distribution and scaled the deadwood amounts and non-categorical predictors according to their range. This dataset was then split between a training and a validation dataset, where the training dataset retained 80% of observations and the validation dataset 20% of the observations.

We compared different modelling approaches, including statistical models (generalized linear regression, generalized additive models, generalized additive mixed effects models and additive mixed effects hurdle-lognormal) and machine learning models (boosted regression trees and random forests). After comparing the outcomes, the mixed effects hurdle lognormal generalize additive model (HL) and the boosted regression trees (BRT) were selected based on the superior performance, in terms of the explained variance and root mean squared error (RMSE) in both validation and training datasets.

2.2.1. Hurdle lognormal model

Given to the occurrence of plots with no deadwood (12%), we selected a generalized additive mixed effects model (Eq .(1) - Eq. (3)) with a hurdle-lognormal response distribution (HL) to simultaneously assess the deadwood amounts, while accounting for the probability of deadwood occurrence (Eq. (1)), where the random effect components referred to the countries in the dataset. The probability of occurrence of deadwood was fitted based on a Bernoulli likelihood (Eq. (2)), while the amount of deadwood was fitted based on a lognormal likelihood (Eq. (3)).

$$deadwood\Big|\pi,\theta \sim \begin{cases} 1-\pi & deadwood = 0 \\ \pi f(deadwood|\theta) & deadwood > 0 \end{cases} \tag{Eq. 1}$$

$$\pi \sim s(temperature) + s(precipitation) + s(biomass) + (1|country) + aGP(lon, lat) \tag{Eq. 2}$$

$$\begin{aligned} f(deadwood|\theta) \sim\ & s(temperature) + s(precipitation) + s(elevation) \\ & + s(slope) + s(age) + s(biomass) + forest\ type \\ & + s(mortality) + s(tree\ density) + s(wind) + s(fire) \\ & + s(access) + s(ownership) + wdpa + (1|country) \\ & + aGP(lon, lat) \end{aligned} \tag{Eq.3}$$

Where: π = probability of deadwood occurrence (Bernoulli likelihood), *deadwood* = deadwood volume [m3. ha^{-1}], θ = coefficients for the deadwood amount model, $f(deadwood|\theta)$ = deadwood amount model (lognormal likelihood), $s(.)$ = smooth functions of the predictors, temperature = yearly average temperature, precipitation = yearly precipitation sum, biomass = aboveground tree biomass, elevation = average elevation, slope = average slope, age = average forest age, forest type = forest type (broadleaved, conifer or mixed), mortality = forest mortality rate, tree density = number of trees per hectare, wind = forest vulnerability to wind damage, fire = forest vulnerability to wildfires, access = forest accessibility in terms of travel time to closest market, ownership = share of public forest ownership, *country* = country where the plot is located, $aGP(lon, lat)$ = approximate gaussian process term on the latitude and longitude.

To avoid overfitting in the HL model, we performed a variable selection using the R package VSURF (Genuer et al., 2015). After running this procedure, we retained for the hurdle component the climate predictors (1.1 and 1.2), the AGB (3.3) and the approximate Gaussian process (aGP) term. For the lognormal component, we retained all variables and the aGP term, except for the management suitability (4.2), disturbance in the previous 10 years (3.6), insect vulnerability (3.10) and biogeographical region (2.2).

We fit the HL model using Bayesian inference using the R package brms (Bürkner, 2017), running three chains for 5000 iterations, which was found sufficient to allow for posterior convergence of all parameters ($\widehat{R} < 1.05$). For the aGP terms, we included 25 basis functions as a compromise between performance and model flexibility.

2.2.2. Machine learning model

For the machine learning variant, we selected the boosted regression trees (BRT) model. We used the same variables selected in the HL model, adding the plot coordinates (latitude and longitude) as predictors (while those were included in the gaussian process term in the HL model). We fitted the boosted tree using the gbm.step function, implemented in the R package dismo (Hijmans et al., 2017). The algorithm was parametrized to allow for increased predictive performance as follows: initial trees = 10, tree complexity = 4, learning rate = 0.01 and bag fraction = 0.5.

2.3. Evaluating changes in management and climate

Based on the models detailed above, we evaluated what would be the effect of possible changes in climate and forest management on the potential availability and distribution of deadwood in European forests (Fig. 3). To this end, we harmonized all the predictors retained in the statistical models (see Table 1) to a 1 km resolution grid and subsequently applied the models to these novel environments. For the HL model, we computed the mean of 1000 posterior draws for each grid cell in the final predictions.

Changes in climate were derived using the downscaled WorldClim 2.1 CMIP6 data with a 2.5-min resolution for different shared socio-economic pathways (SSP) and representative concentration pathways (RCP) combinations. We retrieved the climate parameters used in the models, namely temperature and precipitation, for the periods 2040–2060 and 2080–2100, considering the SSP2 x RCP4.5 and SSP5 x RCP8.5 forcing, from 8 models (BCC-CSM2-MR, CanESM5, CNRM-CM6-1, CNRM-ESM2-1, IPSL-CM6A-LR, MIROC6, MIROC-ES2L and MRI-ESM2-0). These estimates were averaged for each RCP combination and replaced the current temperature and precipitation layers in the models' predictions.

For changes in management, we modified model parameters that reflect current management strategies. Specifically, we tested a biodiversity-oriented scenario targeting to reduce wood utilization and increase rotation lengths, to promote old-growth elements and habitat availability (Management Cons) and a production-oriented scenario with a reduction in rotation lengths, targeted at increasing wood supply (Management Prod). For the conservation-oriented scenario, the forest age was increased by 25 years (Gutsch et al., 2018; Kaipainen et al., 2004) and for the production-oriented scenario, it was decreased by 5–15 years, depending on the current average age (decreased by 5 years for areas where 30 < age <70, 10 years for areas where 70 ≤ age ≤110 and 15 years for areas where age >110). At the same time, we expanded the share of mixed forests in conifer-dominated areas for the conservation-oriented management scenario, according to current adaptation recommendations (e.g. Keenan, 2015; Santopuoli et al., 2021). To this end, we converted grid cells with coniferous forests to mixed forests, with a probability of 0.3. For higher latitudes (>55°), this probability was linearly reduced to 0.1 towards higher latitudes (70°).

Based on the adjustment of the average age and forest types, we altered the AGB to reflect management changes, based on random forest models. We regressed the AGB against environmental and forest parameters, namely age, temperature, precipitation, elevation, forest type, latitude and longitude. Random forests were found to outperform BRT models to predict aboveground biomass. To calibrate the models we selected one third of the observations in the prediction layers (>1.2 million data points) and used the R package ranger (Wright et al., 2021), applying a maximum tree depth of 20. The models were found to have good adherence to the data, with a R^2 of 0.77. Finally, the new AGB layers were created by employing the fitted models to the current and new environments. Based on the models' predictions, we computed anomalies in AGB between the predicted layers. These anomalies were subsequently added to the current AGB layer. We applied the same procedure to correct AGB estimates for the multiple climate change scenarios tested, i.e. computing AGB anomalies caused by changes in temperature and precipitation.

The changes in parameters related to forest management were initially tested with historical climatic conditions, and subsequently in combination with future climate scenarios, enabling to disentangle marginal effects of climate, management and their interaction on deadwood amounts. In total, we tested six future climate and management scenarios, in addition to the baseline (Table 2).

3. Results

3.1. Factors affecting deadwood amounts and distribution

Deadwood amounts were sensitive to all classes of parameters, including climate, forest structure, terrain, and socio-economic conditions (Fig. 4). The marginal estimates, calculated by maintaining other

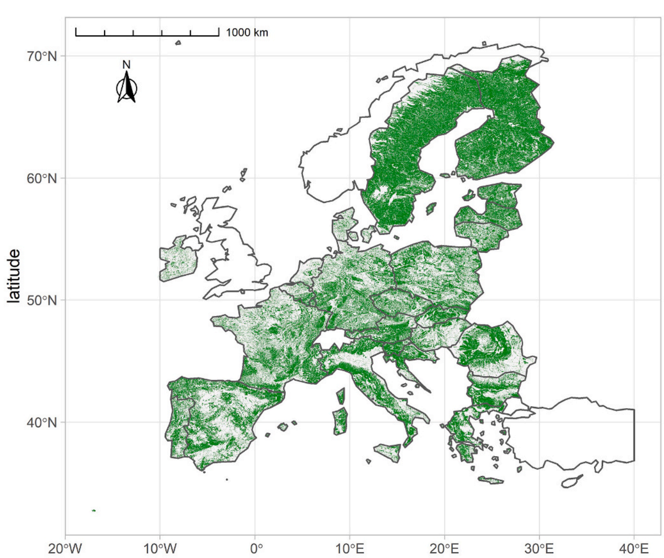

Fig. 3. Study region considered in the analysis. Green areas indicate the occurrence of forest areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Scenario design for deadwood predictions. RCP refers to representative concentration pathways.

Scenario ID	Scenario name	Climate scenario	Management scenario	Climate period
1	baseline	current	current	historical
2	RCP4.5 2050	RCP 4.5	current	2050
3	RCP8.5 2050	RCP 8.5	current	2050
4	RCP4.5 2100	RCP 4.5	current	2100
5	RCP8.5 2100	RCP 8.5	current	2100
6	Management Cons	current	biodiversity-oriented[a]	historical
7	Management Prod	current	production-oriented[b]	historical
8	RCP4.5 2100+ Management Cons	RCP 4.5	biodiversity-oriented[a]	2100
9	RCP8.5 2100+ Management Cons	RCP 8.5	biodiversity-oriented[a]	2100
10	RCP4.5 2100+ Management Prod	RCP 4.5	production-oriented[b]	2100
11	RCP8.5 2100+ Management Prod	RCP 8.5	production-oriented[b]	2100

[a] Biodiversity-oriented management considers a simultaneous increase in forest age and expansion of mixed forest areas, with the corresponding modifications in aboveground biomass.

[b] Production-oriented management refers to a reduction of forest age, representing a decrease in rotation length with the corresponding modifications in aboveground biomass.

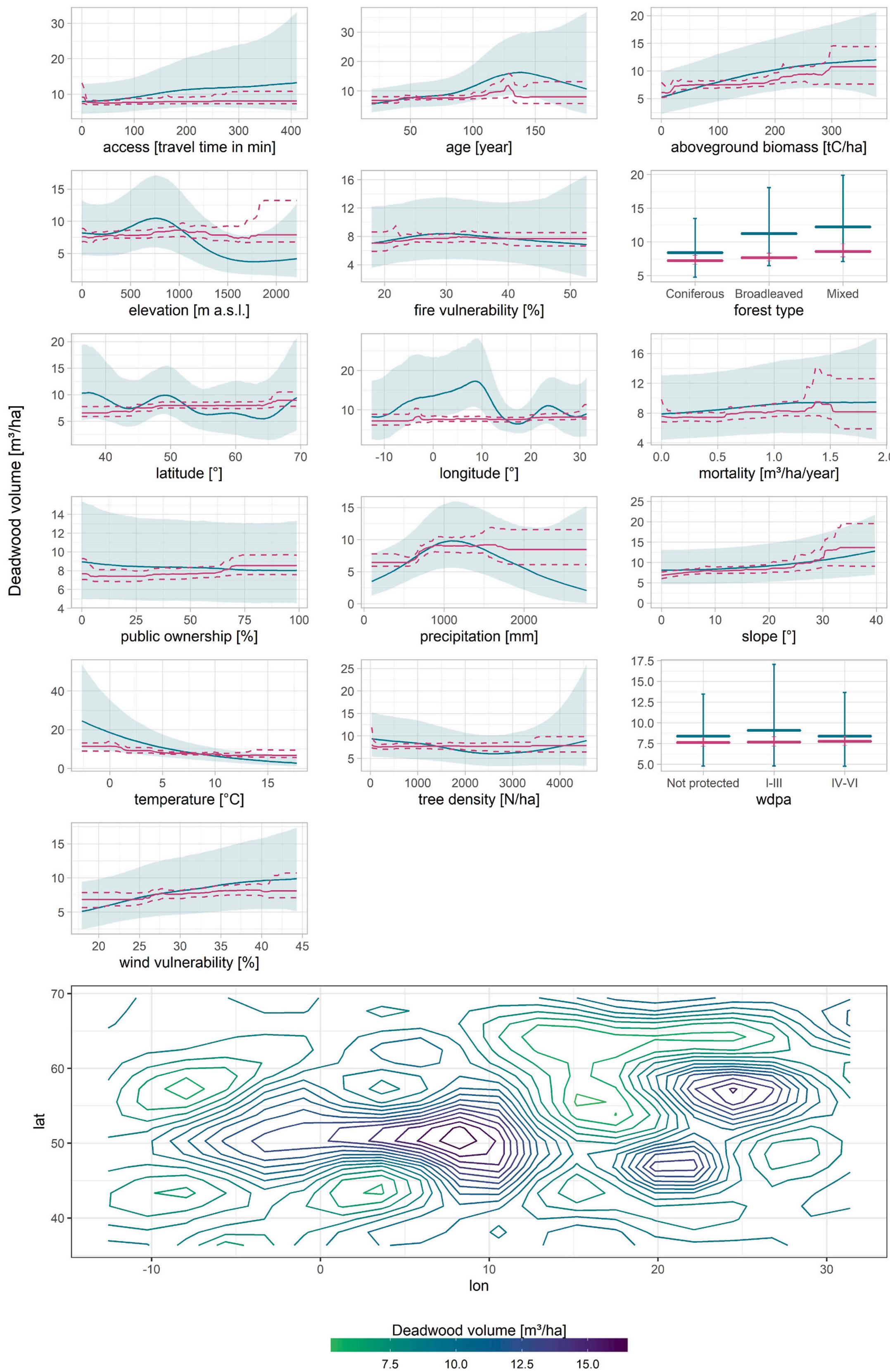

Fig. 4. Marginal effects for the most important deadwood predictors. The upper plots show the marginal effects of each predictor on the deadwood amounts (y axis – natural scale). Green lines and confidence intervals refer to the results of the hurdle-lognormal model, whereas red lines indicate the results of the boosted regression tree model. The dashed red lines refer to the corresponding confidence interval obtained by a bootstrapping procedure. The lower panel shows the marginal effects of the Gaussian process term in the hurdle lognormal model, which shows the spatial effects depending on the latitude and longitude across Europe. FT refers to the forest type and WDPA refers to the World Database on Protected Areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

predictors at their average values, produced by both modelling approaches (BRT and HL) displayed agreement on the effects of the predictors considered, with most BRT marginals contained in the confidence interval of the HL outputs. Additionally, both modelling approaches had a similar performance on the training and validation data. The hurdle lognormal model displayed a Bayesian-R^2 of 0.32, while the BRT model showed a pseudo-R^2 of 0.31. We observed a similar RMSE for both models in the training data (4.8 $m^3.ha^{-1}$), while the HL model showed superior performance on the validation data (5.4 and 4.8 $m^3.ha^{-1}$ for BRT and HL – for details see the supplementary material).

Temperature and precipitation displayed important implications for deadwood amounts, with opposing effects on the estimates. Deadwood increased with increasing precipitation up to approximately 1000 mm/year and decreasing temperatures. The latter effect corresponds with the decreasing deadwood decay rates and a deadwood volume gradient from Mediterranean to temperate forests. Considering the terrain features, deadwood amounts consistently increase with slopes. Similarly, higher elevations (up to 1000 m) were associated with higher deadwood amounts, while forests in subalpine altitudinal zones displayed lower deadwood amounts than montane forests.

Deadwood amounts increased with aboveground biomass, indicating that more densely stocked forests store higher amounts of deadwood. Similarly, deadwood was found to increase with average forest age up to approximately 150 years old, whereas tree density had the opposite effect, as higher tree density is indicative of younger forests and typically conifer-dominated areas. Higher AGB indicate more intensive tree competition in fully stocked areas, leading to increased deadwood inputs. Conifer-dominated areas showed lower deadwood amounts compared to broadleaved dominated areas and mixed forests, whereas the latter forest types were found to have similar deadwood potentials. This is likely arising from the differences in managament intensity among the species groups, where conifer-dominated forests typically display higher intensity, as well as diverse mortality and decay rates among the forest types. Forests displaying higher vulnerability to disturbances, especially wind, also displayed increased deadwood amounts.

The protection status of forest was also associated with deadwood potentials and areas under strict protection (WDPA categories I-III) displayed the highest deadwood amounts, whereas areas under other protection classes (WDPA categories IV-VI) had similar deadwood amounts to unprotected areas. The protection status is closely related to management intensity, harvesting rates and biodiversity-friendly management practices (e.g. longer rotation ages and lower thinning intensities), promoting deadwood. Similarly, less accessible forests (located at longer travel times to the markets) displayed more deadwood, potentially due to lower management intensity, given the decreased road network density and higher harvesting costs. The ownership had only a modest effect on deadwood amounts, with opposing trends for the different modelling approaches.

We deployed the fitted deadwood models to upscale deadwood amounts at the country level, using the layers of predictors corresponding to the current forest and climatic conditions (Fig. 5). The average deadwood amount predicted by our model amounted to 10.7 $m^3.ha^{-1}$ for the reference period of data collection (2005–2008). In agreement with the effects of the predictors considered, high deadwood stocks were observed in montane forests of central Europe and the Carpathians. These regions are associated with higher productivity and increased competition, as well as higher deadwood stocks in undisturbed forests, compared to Mediterranean and Boreal ecosystems. Additionally, remote forests in northern Finland and Sweden were found to house large amounts of deadwood, compared to managed boreal forests, as a result of the reduced forest utilization and lower decay rates. Conversely, the Mediterranean forests of Spain and Portugal displayed the lowest deadwood potentials, in the face of the lower growth rates and management practices towards reducing susceptibility to wildfire occurrence.

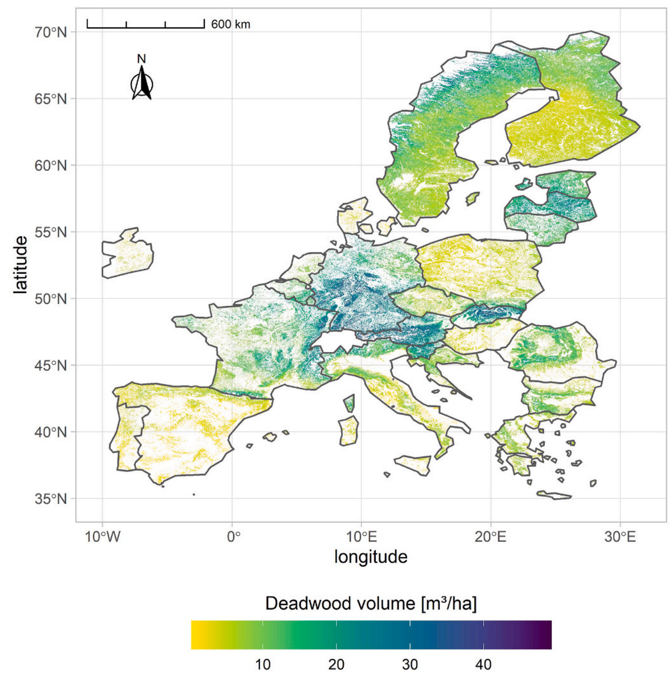

Fig. 5. Deadwood distribution over Europe, obtained by averaged model predictions.

We compared the model predictions at the country level with observed data from ICP forests and the data reported by Forest Europe (Table 3). The modeled deadwood at the country level is expressed as the average between the BRT and HL models. In countries with good data availability, such as Finland, the discrepancies between modeled

Table 3
Comparison of average deadwood volume (m^3ha^{-1}) with observed data from the Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP) network and reported data from the Ministerial Conference on the Protection of Forests in Europe for 2005 and 2010 (FOREST EUROPE, 2015).

Country	Forest Europe 2005 deadwood volume [m^3ha^{-1}]	Forest Europe 2010 deadwood volume [m^3ha^{-1}]	ICP (2006–2008) deadwood volume [m^3ha^{-1}]	Modeled deadwood volume [m^3ha^{-1}]
Austria	17.4	20.3	23.7	24.6
Belgium	7	7.3	17.5	13.4
Bulgaria	–	–	–	8.5
Croatia	–	14	–	8.4
Czechia	11.6	11.6	9.8	8.8
Denmark	4.9	5.1	6.2	3.5
Estonia	12.5	14.6	–	14.2
Finland	5.7	5.7	7.1	6.1
France	–	–	22.3	13.2
Germany	11.5	15	29.6	22.5
Greece	–	–	–	6.9
Hungary	–	–	9.7	4.8
Ireland	6.6	6.3	6.1	5.4
Italy	8.7	9.1	14.9	8.0
Latvia	17.7	17.7	26.4	19.1
Lithuania	23	23	17.7	12.7
Luxembourg	–	–	–	13.4
Netherlands	8.1	9.8	–	8.6
Poland	–	5.6	9.9	5.4
Portugal	2.8	–	–	3.5
Romania	–	–	–	10.1
Slovakia	26.2	26.2	27.3	23.2
Slovenia	17	19.1	33.1	19.6
Spain	–	4.6[a]	5.6	3.4
Sweden	7.9	8.2	24.4	10.2

[a] Value retrieved from Alberdi et al. (2020) based on NFI data.

and reported deadwood stocks were minor and there was a good agreement across datasets. We observed major discrepancies in the reported data for central European countries, depending on the source considered (e.g. Belgium and Germany). Nevertheless, model estimates in these areas remained within the boundaries of both data sources. Moreover, model estimates for Mediterranean forests, with lower deadwood stocks, displayed a close match with the Forest Europe reported data. In general, we obtained a correlation ranging between 0.8 and 0.9 at the country aggregates between the reported and modeled data.

3.2. Effects of changes in forest management and climate

3.2.1. Climate effects

Climate change might have important implications for the potential deadwood stock in European forests (Fig. 6). We observed a majorly negative association of future climatic conditions with deadwood potentials in the region, except for some managed forest areas in southern Finland and Sweden. These regions displayed an increase in deadwood potentials, given the predicted increase in aboveground biomass and deadwood input, due to more favorable climate conditions for forest growth. Under midcentury climatic conditions, our model points to a deadwood potential loss of 11 and 13% for the RCP4.5 and RCP8.5, respectively. These estimates, however, disregard transient changes in deadwood inputs due to higher mortality rates under climate change, which may temporarily increase deadwood availability. It must be noted that typical forest types and growth rates under warmer and drier climatic conditions, and the corresponding management changes, may lead to a reduction in deadwood potentials. Deadwood losses were also heterogeneously distributed across forest types and regions (Table 4), where the largest impacts were observed under RCP8.5, especially in forests in Southern Europe, with losses up to 15.5%.

Considering climatic conditions at the end of the century (2100), the same patterns observed by midcentury were amplified and losses of

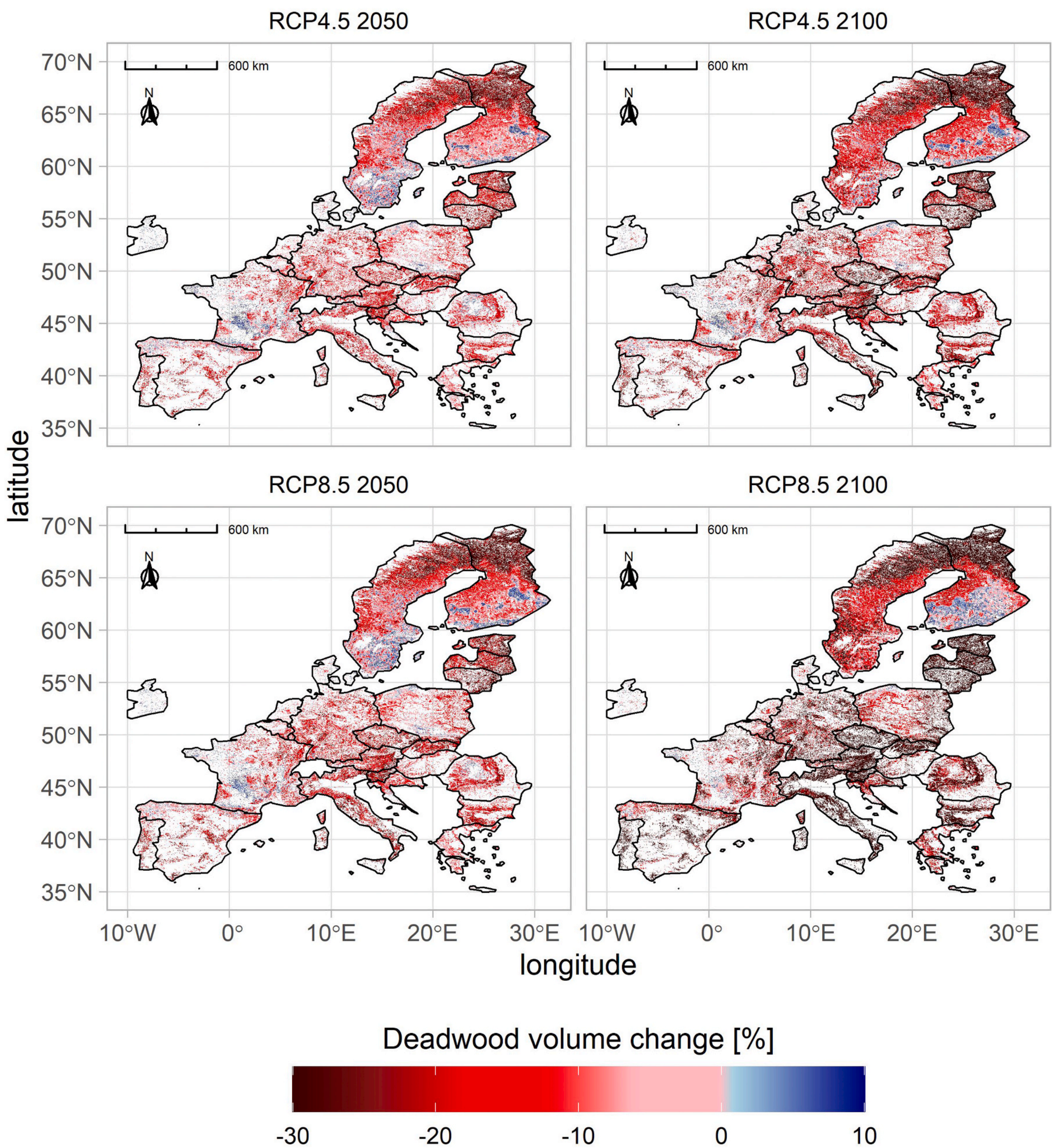

Fig. 6. Relative changes (% change compared to the current climate deadwood volume) in deadwood potentials under different climate trajectories and the corresponding time periods (2050 and 2100). RCP refers to Representative Concentration Pathways.

Table 4
Regional effect of climate on deadwood distribution. The table shows the relative changes in deadwood among climate scenarios [in % compared to current climate], aggregated over five European regions (following the State of Europe's Forests regions).

Region	RCP4.5 2050 change in deadwood potential [%]	RCP8.5 2050 change in deadwood potential [%]	RCP4.5 2100 change in deadwood potential [%]	RCP8.5 2100 change in deadwood potential [%]
North	−11.5	−12.8	−15.6	−19.5
Central-west	−8.5	−10.9	−14.2	−22.0
Central-east	−10.0	−12.4	−15.1	−25.8
South-west	−11.7	−15.5	−17.3	−31.5
South-east	−10.6	−13.6	−16.3	−25.5
EU	−10.5	−12.7	−15.4	−23.2

deadwood potential amounted to 15.4 and 23.2% for RCP4.5 and RCP8.5, respectively. This represents changes of up to −15.8 to 18.4 $m^3.ha^{-1}$ at the grid cell level, where the largest reductions occurred in montane forests of central Europe and the Carpathians. Regions with deadwood potential gains remained stable for RCP4.5, with increases up to 7.7 $m^3.ha^{-1}$, since temperature and precipitation changes stabilized after 2050. Conversely, deadwood potentials reduced for the more extreme climate scenario (RCP8.5), due to the loss of carbon stocks under more extreme conditions. When looking at the regional patterns, forests in southern Europe remained severely affected, with losses up to 31.5%. Central European forests were also severely affected, with losses up to 25.8% under RCP8.5.

3.2.2. Management effects

Forest management changes and the corresponding alterations in forest attributes can impact deadwood amounts and distribution across European forests (Fig. 7). The increase in average forest age by 25 years, representing an extension of rotation lengths, with the simultaneous expansion of mixed forests replacing conifer-dominated areas, led to an increase in the deadwood potentials by 17% on average (Table 5). Conversely, management intensification, with a reduction in forest age caused a decrease in deadwood potentials by 4%, potentially reflecting a less intensive inter-tree competition and exposure to other disturbance events.

Despite the pervasive positive impacts of increased forest age and expansion of mixed forests on deadwood potentials, the management impacts varied regionally, with gains ranging from 14.5 to 22.9% in Northern and South-western Europe, respectively. The largest increases in deadwood potential, in absolute terms, were observed in deadwood-

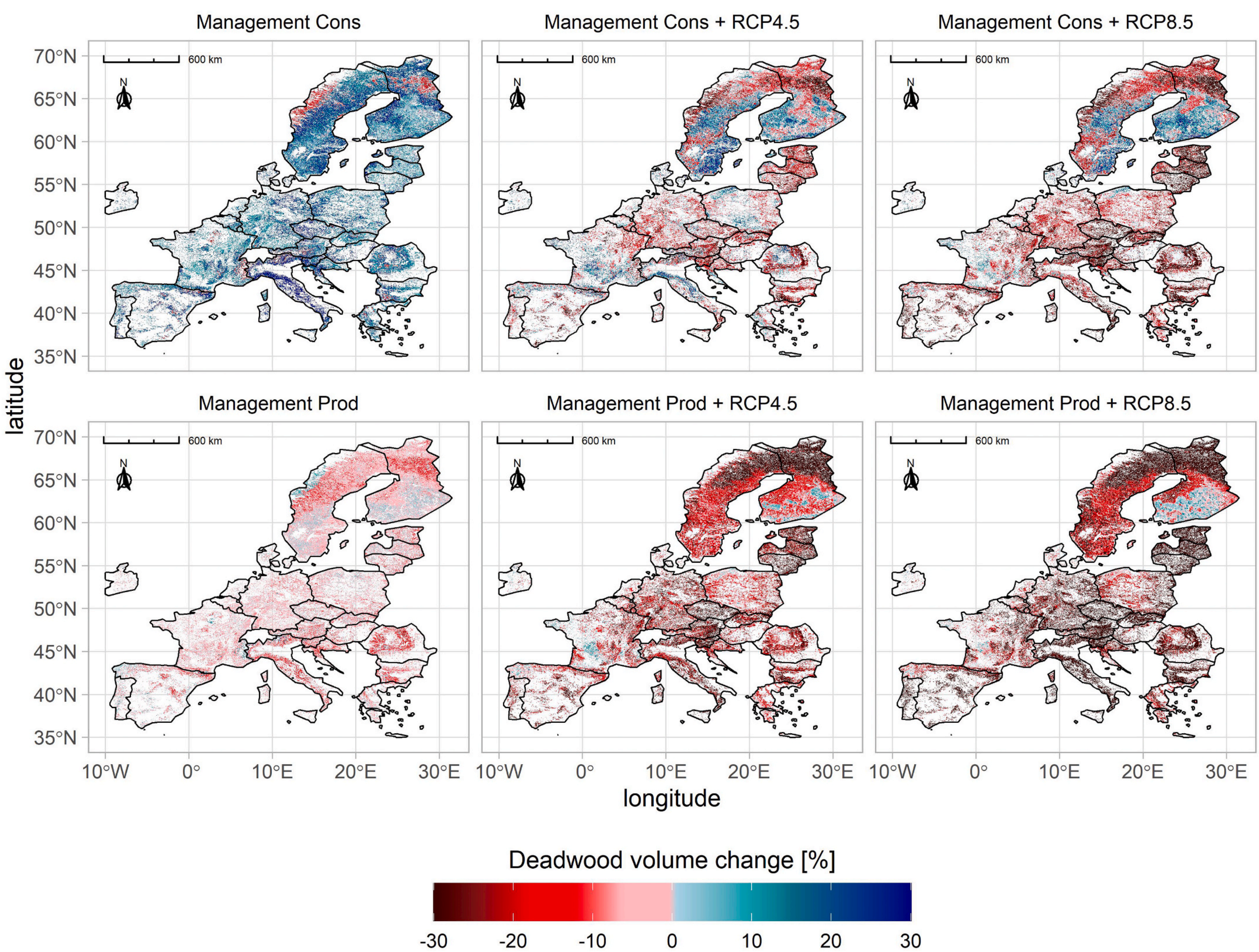

Fig. 7. Relative changes (% change compared to the current climate deadwood volume) in deadwood potentials under biodiversity-oriented (Management Cons) and production-oriented (Management Prod) management strategies for current and future climate (RCP4.5 and RCP8.5). RCP refers to Representative Concentration Pathways.

Table 5
Regional effect of climate on deadwood distribution. The table shows the relative changes in deadwood among management and climate scenarios (in % compared to current climate and management), aggregated over five European regions (following the State of Europe's Forests regions).

Region	Management Cons	Management Prod	RCP4.5 2100 + Management Cons	RCP8.5 2100 + Management Cons	RCP4.5 2100 + Management Prod	RCP8.5 2100 + Management Prod
North	14.5	−3.6	−1.7	−6.2	−18.4	−22.1
Central-west	15.7	−3.9	−4.3	−13.8	−17.4	−24.6
Central-east	18.5	−5.2	−5.0	−18.8	−18.8	−28.3
South-west	22.9	−4.4	−4.4	−21.9	−20.1	−33.4
South-east	16.9	−5.2	−11.1	−22.0	−19.4	−27.7
EU	16.8	−4.2	−3.9	−13.3	−18.5	−25.6

rich montane forests of central Europe and the Carpathians, where the current average forest ages neighbor 80–90 years old. Hence, increases in rotation length in these areas fall into the range where the reported marginal impacts of forest age on deadwood are largest (see Fig. 4). These changes in management caused a decrease in deadwood potential in a few cases, including montane forests in northern Finland and Sweden. This behavior likely arises from the negative influence of ages above 125 years on deadwood amounts, since forests in these areas are amongst the oldest in the age dataset used in our analysis. Considering the production-oriented management, negative effects were largest in Eastern Europe (5.2% decrease in potentials) and smallest in Northern Europe (3.6% reduction).

When the effect of management was combined with climate change, the conservation-oriented strategy dampened the negative influence of higher temperatures and lower precipitation, especially in Northern and South-western Europe. This management strategy was able to mitigate deadwood loss to 3.9% compared to the baseline scenario for RCP4.5 and 13.3% for RCP8.5. For the production-oriented management, deadwood potentials were reduced by 18.5 and 25.6 % for RCPs 4.5 and 8.5 (end of the century climate), respectively (Fig. 7). Management changes showed a stronger influence on Boreal forests, where conservation-oriented management enhanced the positive association of future climate with deadwood potential in managed areas, leading to higher potentials compared to scenarios where only future climate conditions were considered.

4. Discussion

Our results show that deadwood is unevenly distributed across European forests and is closely related to climatic conditions and forest attributes. Moreover, future climatic conditions and changes in forest management have the potential to substantially modify deadwood potential and its distribution. Climate impacts were predominantly negative on deadwood potentials, with the exception of managed forest areas in southern Finland and Sweden (c.f., Mazziotta et al., 2022). Conversely, changes in forest management may buffer negative climate impacts and improve deadwood potentials in European forests.

4.1. Factors affecting deadwood amounts

Our results are in line with previous local analyses of deadwood potential in European forests. We obtained Bayesian and pseudo – R^2 estimates neighboring 0.32. This is in line with previous studies assessing deadwood drivers in Europe. Bujoczek et al. (2021) reported similar performance for their deadwood models in managed forests and forest reserves (ranging from 0.2 to 0.27). Crecente-Campo et al. (2016) reported R^2 values ranging from 0.15 to 0.17 for deadwood models in Spain. These are also comparable to models developed for other ecological indicators such as tree microhabitats (Kozák et al., 2023).

Climatic parameters, specifically mean annual temperature and total annual precipitation were determinants of the availability of deadwood in European forests. Climatic conditions are closely related to the productive capacity of forest ecosystems, affecting inter-tree competition and deadwood inputs, as well as the decomposition rates of deadwood stocks (Mazziotta et al., 2014). Mediterranean forests, in hotter and drier climates, show lower productivity and management aimed at preventing wildfires employed in these areas can further reduce deadwood stocks (e.g. Vilén and Fernandes, 2011). Our results also point to higher deadwood potentials in older and more densely stocked forests. Biomass accumulation over time and the associated competition for resources may increase deadwood inputs and stocks by accelerating self-thinning (Jonsson et al., 2016). Older forests are also linked to deadwood-rich forest reserves or unmanaged forest areas, which display substantially higher deadwood stocks, compared to managed forests (Paillet et al., 2015; Meyer and Schmidt, 2011).

The effects of socio-economic and forest structural parameters found in our analysis are also in line with the literature. Alberdi et al. (2020) analyzed deadwood stocks using a comprehensive dataset provided by the Spanish National Forest Inventory and employing generalized additive linear models. The authors also found a positive impact of the forest protection status on deadwood amounts, while the specific protection category had a smaller influence on deadwood. A positive influence of the stand stocking was also observed, as well as a reduction in deadwood for higher temperatures and lower precipitation. Oettel et al. (2020) reported decreasing deadwood amounts with increasing temperature and the converse for precipitation in Austrian natural forest reserves. The authors, however, highlight that deadwood amounts were more influenced by the forest type and standing volume than terrain and climatic conditions. The strong influence of climate found in our results might be related to the higher gradient in climatic conditions encompassed by the ICP network. Bujoczek et al. (2021) developed deadwood models based on climatic conditions, pollution, terrain and local conditions, including socioeconomic factors for forests in Poland, using the ICP database and national forest inventory data. The authors found increasing deadwood volumes with forest age and standing volume, while tree density had a negative influence on deadwood amounts. Moreover, similar to our results, protected areas displayed higher deadwood amounts, especially for forests under strict protection.

4.2. Effects of changes in management and climate

Future climate scenarios led to a reduction in deadwood potentials, apart from managed forest areas in southern/mid Finland and Sweden, where temperature-limited ecosystems may benefit from increasing temperatures and longer vegetation periods (Lindner et al., 2010; Kalliokoski et al., 2018). Hence, the net effect of changing environmental conditions on deadwood potentials will depend on the rate of increase in deadwood inputs and changes decomposition rates. Chagnon et al. (2022) conducted a meta-analysis on climate change impacts on the time since death of coarse woody debris and reported a reduction in the deadwood residence time with climate change. The authors highlight, however, that increased tree mortality can counterbalance the increase in decomposition rates. Löfroth et al. (2023) also point to the context dependency of climate change effects on deadwood, where decomposition rates are likely increasing in temperature-limited regions, while increase in disturbance activity leads to higher deadwood input. Disturbances may also shift forest age classes towards young stands and reduce the share of large diameter deadwood (Löfroth et al., 2023). Ekman et al. (2024) and (Mazziotta et al., 2014) report increases in deadwood volumes for Finland, due to the predicted increase in forest productivity in the region. We emphasize that our results reflect deadwood potentials under stable conditions in relation to climate and management. Hence, it disregards the transition period to the new vegetation state and reflects current management practices in terms of the share of deadwood removals.

Similar to climate impacts, we observed important implications of forest management to deadwood potentials. Our results show that less intensive (biodiversity-oriented) management, with an increase in average forest age and the related aboveground biomass had in general a positive influence on deadwood potentials. This is in agreement with other studies in Europe (Alberdi et al., 2020; Doerfler et al., 2017; Oettel et al., 2023; Paletto et al., 2014; Siitonen et al., 2000; Vandekerkhove et al., 2009). For example, Oettel et al. (2023) also highlights that management is an important driver of deadwood dynamics, finding higher persistent times for snags in extensively managed forests, compared to areas subject to intensive forest management in Austria. Paletto et al. (2014) reported higher deadwood amounts in multifunctional and extensively managed oak-dominated forests in Italy. Similar patterns were reported by Alberdi et al. (2020), analyzing deadwood distribution in Spanish forests. The authors found larger deadwood stock both in unmanaged or extensively managed forests and mixed forests.

Apart from the direct management impacts on deadwood potentials, historical management practices and deadwood utilization also contribute to the current distribution of forest types and deadwood-dependent organisms, especially influencing their regional variation. For example, Mediterranean forests have a long history of forest use and overexploitation, compared to other regions of Europe (Marchetti, 2005; Lassauce et al., 2011), contributing to the deadwood spatial distribution gradients found in our analysis.

Given the negative impacts of forest management intensification on saproxylic organisms, the increase in rotation lengths and the promotion of deadwood quantity and quality have been identified as important management measures to improve habitats for biodiversity conservation in Europe (Oettel and Lapin, 2021). These management actions, however, might generate trade-offs with wood production and other ecosystem services in managed forest areas. In particular, the use of forest residues and deadwood for bioenergy is an important component of climate mitigation portfolios, which may cause deadwood habitat loss (Repo et al., 2020). At the same time, the increase in rotation lengths might increase forest exposure to natural disturbances. Hence, a balance between risk management and habitat maintenance must be considered, to improve forest multifunctionality and sustain the provisioning of multiple ecosystem services in the future (e.g. Blattert et al., 2022; Mönkkönen et al., 2014; Härtl and Knoke, 2019). Moreover, the reduction in management intensity is associated with opportunity costs, and such actions might require financial incentives to forest owners, such as the implementation of payment for ecosystem services schemes (Gustafsson et al., 2020b).

4.3. Limitations

While the modelling of deadwood amounts may provide a useful indication of its spatial distribution in Europe, some limitations in our analysis must be noted. The varying sampling intensity within and among countries poses a limitation of model estimates in regions with few plots (e.g. Ireland and Belgium). Similarly, a low share of the plots is located in protected areas. Hence, it is recommended that future efforts to assess deadwood volumes in Europe include additional deadwood surveys, such as results from national forest inventories and field experiments. This can contribute to better constrain and inform deadwood models and shed light on the interactions between deadwood drivers and different forest types. Furthermore, the inclusion of datasets with repeated measurements would allow to better capture the implications of local conditions and the legacy of past management practices.

We proxied the effects of management and climate based on changes of forest attributes and predictors relevant to the assessment of deadwood amounts. The models applied do not consider the effects of increasing atmospheric CO_2, changes in disturbance regimes and transition towards different forest types on deadwood potentials. Detailed deadwood dynamics under future conditions, including changes in atmospheric CO_2 and nitrogen deposition, can be assessed by mechanistic forest models in future studies (e.g. Sperlich et al., 2020; Gutsch et al., 2018). We highlight, however, that our estimates can provide valuable data for the initialization of deadwood stocks in such models. Furthermore, more detailed models can better capture the deadwood inputs and decomposition rates at the species level, as well as include the effect of residue removal on deadwood dynamics, which may have substantial impacts on deadwood stocks in European forests.

5. Conclusions

Deadwood is among the most important legacy elements in European forests, providing substrate to a large share of endangered species in the region. Climate change and forest management may affect forest dynamics and the availability of deadwood for saproxylic organisms in the future. Hence, these interactions need to be addressed in the planning of biodiversity conservation policies and management strategies. Our results show that climate, forest structural parameters and socio-economic conditions mediate deadwood potentials in European forests. Specifically, climate change may reduce deadwood potential in European forests, due to changes in temperature and precipitation, and the related changes in forest composition. Similarly, forest management have important implications to the future availability of deadwood. Production-oriented management, with decrease in rotation lengths, may further enhance this effect. Conversely, biodiversity-oriented management can buffer the negative influence of future climate conditions, by the implementation of changes compatible with current adaptive management recommendations, including the increase in the share of mixed forests and increase in rotation length. These management changes, however, need to be carefully considered and balanced against other forest goals and risk management, as well as supported by adequate compensation schemes. We conclude that adaptive management actions will be crucial for maintaining deadwood in forest landscapes under changing environmental conditions and for supporting forest resilience and multifunctionality.

CRediT authorship contribution statement

Andrey L.D. Augustynczik: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Mykola Gusti:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Fulvio di Fulvio:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Pekka Lauri:** Writing – review & editing, Writing – original draft, Conceptualization. **Nicklas Forsell:** Writing – review & editing, Writing – original draft, Conceptualization. **Petr Havlík:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data is openly available in the github reporsitory https://github.com/andreyaugustynczik/Deadwood_distribution_Europe

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.120382.

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