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Research article

Spatial trade-offs between ecological and economical sustainability in the boreal production forest

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ABSTRACT

Economically-oriented forestry aims to sustain timber harvest revenues, while ecologically-oriented management supplies suitable habitat for species using deadwood as primary habitat. As these objectives are conflicting, planning for economic and ecological sustainability involves compromise and trade-offs. We analyze the spatial trade-offs between the economic value from timber harvesting and the volume of deadwood in the boreal forest. We assess these trade-offs from three perspectives: (1) landscape characteristics, affected by conservation strategies; (2) forest management promoting either economic or ecological values; (3) uncertainty in inventory errors undermining the estimate of the two sustainability objectives. To reveal the tradeoffs between the forest economic and ecological values we simulated and optimized a production landscape in Finland 30 years into the future accounting for uncertainty in biomass and deadwood inventories. We found that, with a limited reduction in timber harvesting (7%), (i) the amount of deadwood increased more in non-aggregated (45%) than in aggregated (16%) stands, (ii) constraining stands in adjacent areas further increased deadwood (21%) respect to the matrix and (iii) 7% of connected stand area harbored $\geq 20 \text{ m}^3/\text{ha}$ deadwood supporting survival of near-threatened species. Our results demonstrate that the structure of the landscape for biodiversity can be improved with limited economic losses. However, improving habitat configuration requires larger economic losses than only increasing habitat amount, but its ecological benefits are larger both for common and red-listed species. We found that management oriented towards stand aggregation not only creates connected areas with high deadwood of high value biodiversity but also improves the value of the whole matrix by decreasing intensive timber harvesting and energy wood collection. Finally, we found that uncertainties alter the estimate of the potential of the forest landscape to supply deadwood, and this can affect the choice of management actions to allocate over the landscape. To conclude, our results demonstrate the trade-offs between economic forest use and conservation are affected differently by landscape characteristics, forest management and uncertainty in inventory errors. As such these drivers should be considered when optimizing the forest for multiple uses.

1. Introduction

Planning the use of forests requires careful consideration of multiple sustainability goals (Pohjanmies et al., 2017, 2021). Forest management planning involves balancing resource extraction and conservation strategies, which can benefit from the use of multi-objective forest management (Triviño et al., 2017). Economically-oriented forestry aims to maximize timber harvest revenues, or sustained revenues over time (Vierikko et al., 2008). In turn, closer-to-nature forest management

strives to supply suitable habitat for a wide spectrum of biodiversity objectives improving forest conservation value, through the retention of habitat trees and deadwood, and the promotion of structural heterogeneity (Larsen et al., 2022). Planning for economic and ecological sustainability involves compromise and trade-offs, as management maximizing timber revenues conflicts with conservation priorities (Eriksson and Hammer, 2006; Naumov et al., 2018). For instance, harvested timber extracted from the forest would have been available as a habitat for biodiversity, if left to accumulate as deadwood via tree death

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and decomposition (Woodall et al., 2009; Chirici et al., 2011). Ultimately, continued timber extraction can negatively affect the capacity of the forest to meet simultaneously multiple sustainability goals (Mönkkönen et al., 2014).

The three factors that can have a potential effect on these trade-offs are *landscape characteristics*, affected by conservation strategies, *forest management*, promoting either economic or ecological values, and *uncertainty in inventory errors*, undermining the estimate of sustainability objectives.

The *landscape characteristics*, i.e., its (1) structure and (2) configuration can affect the quality of the forest landscape and therefore affect the trade-off between harvested timber and deadwood volume. In fact, in the boreal context, Lassauce et al. (2011) and Bouget et al. (2013) demonstrated that local patterns of biodiversity dependent on deadwood are driven by structure and configuration of the landscape (Janssen et al., 2009). The value of the landscape structure for biodiversity (1) depends on the proportion of stands with high deadwood volume. According to the “habitat amount” effect (Fahrig, 2013), the value of the production landscape for biodiversity increases dramatically beyond a threshold proportion of suitable landscape, at which the accumulation rate of species or individuals strongly increases. This threshold proportion corresponds to the amount of suitable habitat below which landscape fragmentation may affect species persistence (Andrén, 1994; Rybicki and Hanski, 2013). Gustafsson et al. (2012) suggest that the amount of suitable habitat, in terms of proportion of tree retention within a production forest should be above 5–10% to achieve ecological enrichment. However, improving the landscape structure for biodiversity in the production landscape translates into a diminished economic return from timber extraction (Mönkkönen et al., 2014). The value of the landscape configuration for biodiversity (2) depends on the proportion of stands with high deadwood volume that are spatially aggregated. According to the “spillover” effect (Gell and Roberts, 2003), the value of the production forest landscape for biodiversity can be enhanced if suitable patches within the landscape are well connected by forest patches of higher quality (Bouget and Parmain, 2016). This is explained by the fact that a species can increase its presence in the low-quality patches of the production landscape, despite the local low reproductive success and fitness, thanks to the influx of propagules from source populations living in a nearby habitat of higher quality (Shmida and Ellner, 1984). However, the capacity of forest species of recolonizing low-quality habitat depends on their degree of specialization, as observed by Nordén et al. (2013) for wood-inhabiting fungi.

Management oriented towards either economic or ecological values can also affect the availability of deadwood for forest biodiversity (Deuffic and Lyser, 2012; Koskela and Karppinen, 2021) and this may further affect its trade-offs with timber production. Forest owners that are primarily interested in timber production harvest the majority of living tree biomass to obtain timber revenues and collect trees felled by natural mortality for selling or using them for bioenergy production, in both cases removing these resources from the forest. On the other hand, forest owners managing the forest in a closer-to-nature fashion leave more trees to grow and let all the wood to decay naturally on the forest floor after clear-cut (Eräjää et al., 2010). The preference of the forest owner for one of the two strategies is dependent on the price of timber and energy wood which affects the deadwood volume.

Knowledge of *uncertainty* helps to identify the certainty of meeting conservation orientated sustainability goals (Ascough II et al., 2008). The data used for stand-level decision making is based on a model-based approach, i.e., on predicting the required forest characteristics based on a prediction model estimated from sample plot data (e.g., Astrup et al., 2019). The uncertainty of the model parameters is directly proportional to the size of the sample, and this uncertainty propagates to all forest sustainability indicators such as biomass and deadwood. Large inventory errors when predicting the tree basal area and the tree height (for both, % Standard Error (SE) ≤ 20% in laser scanning according to Næsset, 2004) will induce a large uncertainty in the estimate of timber

(Duvemo and Lämås, 2006). Furthermore, the estimate of total deadwood volume is affected by large inventory errors (Root Mean-Square Error ranging between 128% and 203% in commercial forest stands, Maltamo et al., 2014). The inventory errors in forest characteristics can affect the choice of the management plan to apply in the forest to maximize sustainability indicators and the trade-offs among them.

We analyze the trade-offs between forest development and conservation simulating and optimizing a production landscape in the boreal Finland 30 years into the future, with and without spatial aggregation constraints, and finally evaluate the effect of these trade-offs on the species richness of wood-inhabiting fungi, well-recognized indicators of biodiversity dwelling in deadwood.

2. Methods

2.1. Study area

The study area is a typical production forest in the Central Finland region, and it is located mostly in the southern boreal vegetation zone (Fig. 1). It covers 690 ha and consists of 491 adjacent forest stands. The average extension of each stand is about 1 ha (mean ± standard deviation (SD) = 1.4 ± 1.3 ha, range = 0.0–9.8 ha). The average stand age is 45 years (range: 0–125 years). 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%) and downy birch (*B. pubescens*, 1.1%) while other mixed coniferous and deciduous trees represent the remnant 11.7%. While we have no specific information on the past management of the area, the young stand age suggests that the area has been used extensively for production forestry, following an even-aged management that until 2014 was the only legally accepted management system in Finland (Äijälä et al., 2014). Forests in the study area are privately owned and managed with diverse silvicultural options (Kuuluvainen et al., 1996). Thus, the past management has differed from a strict following of management recommendations, e.g., from the economically optimal timing of thinnings and final fellings.

2.2. Inventories, simulation of forest growth and decomposition, management regimes

The stand-level inventory data for our study area were produced, owned, and archived by the Finnish Forest Centre (www.metsakeskus.fi) (https://aineistot.metsaan.fi/avoinmetsatieto/Metsavarakuviot/Maa_kunta) and used as input data in the forest growth simulator. It is based on laser scanning, as is most data collected for stand-level forest management purposes. Initial deadwood characteristics for Central Finland were estimated from the Finnish National Forest Inventory (NFI) estimates for the years 1980–2015 (Korhonen et al., 2020). Deadwood initialization parameters are summarized by tree species, diameter, decay class, position, and years after death (Table 1). The data of the deadwood initialization and simulations are available from the authors upon reasonable request and with permission of the Finnish Forest Centre.

We used SIMO, an open-source decision support system (Rasinmäki et al., 2009), to simulate the future forest states. SIMO produces projections of future stand development based on the initial characteristics of the stand and the forestry operations applied to the stand. Using forest growth models, the forest simulator makes use of the Tapio guidelines (Äijälä et al., 2014) to create a wide range of management regimes using a decision tree (Eyvindson et al., 2021). Management regimes can be created on the basis of the initial conditions of the stand, conducting optional silvicultural treatments, delaying or lengthening harvesting, and removing a variable amount of deadwood from the forest floor. SIMO silvicultural activities include planting, fertilizing, thinning and other tending activities, as well as final harvest, described in detail in Eyvindson et al. (2018). We used market prices to estimate the Net

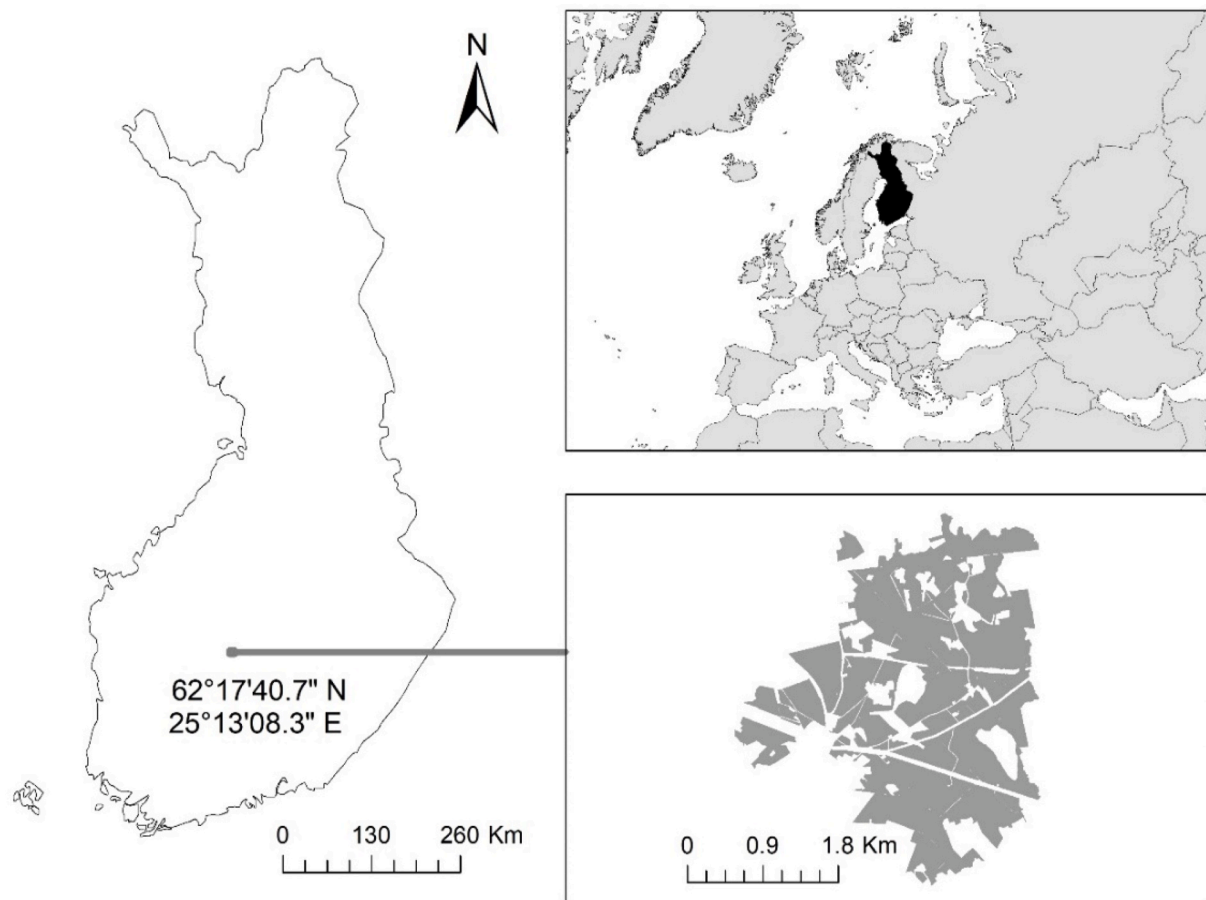


Fig. 1. Locations of the study area in Central Finland and Finland in northern Europe.

Present Value (NPV, in €/ha) of timber harvest revenues at a typical 3% discount rate to measure the landscape economic value from timber harvesting. We incorporated deadwood extraction from natural mortality for household firewood into the NPV calculations, attributing a price of 20 cents per kg of extracted biomass.

The formation of deadwood and its decomposition are projected with SIMO by applying the empirical statistical model developed for Scots pine, Norway spruce and silver birch by Mäkinen et al. (2006). These models are based on data collected from long-term thinning experiments in southern and central Finland. The remaining fraction of deadwood volume is estimated by the model as a Gompertz function of the year after death. The simulations of deadwood were initialized making use of the regional level deadwood characteristics from the Finnish NFI, whose estimates were used as values to spin-up initial deadwood volumes based on a variation of management regimes. We assume that historical management alternatives, as well as natural mortality, are represented in the prevailing deadwood volumes. Specifically, to each stand was randomly assigned a managed regime (either Business as Usual, Continuous Cover Forestry or Set Aside) and a deadwood removal level from the forest floor after clear-cut (either 0%, 40% or 75%). A conceptual model explaining the flow of the deadwood initialization and simulation is represented in Fig. 2. The stands to which was randomly assigned one of the six combinations of management and deadwood removal were then re-simulated for 30 years into the future at 5-year time steps. The 30-year time window is the approximate duration of forest ownership at property level. The 30-year time horizon is also a compromise solution due to the computational times of the simulations. The average volume of deadwood was estimated by the end of the simulation horizon. Each stand was simulated with the same climate change scenario characterized by moderate Greenhouse Gas Emissions

(GHG) consistent with current emission trajectories and policy commitments (i.e., the Representative Concentration Pathway (RCP) 4.5, corresponding to moderate GHG emission reduction, van Vuuren et al., 2011) for the General Circulation Model CanESM2 (von Salzen et al., 2013).

We simulated the forest landscape with alternative management regimes for each stand and selected the ones that could be selected by the forest owner among the ones implemented or considered for application in Finland by government agencies. To allocate the management regimes we used a branching approach applying to each management unit a finite number (maximum 30) of feasible management schedules (Siitonen, 1993). The simulation of the management schedules consists of chains of states and events. Events are natural processes (e.g., ingrowth, growth and mortality of the trees) or human activities (e.g., cuttings, silvicultural treatments like thinning or tree retention, fertilization, deadwood removal). Branches of the simulation are due to several alternative human activities.

2.3. Sources of uncertainty

The uncertainty in biomass production corresponds to plus/minus (\pm) one and two standard deviations (SD) from the mean value in basal area and tree height. SDs were calculated multiplying the values of the z -scores for the normal cumulative distribution (with mean = 0 and SD = 1) by the maximum inventory standard errors for basal area (SE = 20%) and tree height (SE = 20%). The negative and positive deviations from the mean of the uncertainties in basal area and tree height were symmetric. This reflects the Gaussian distribution for these two forest attributes. Instead, the positive and negative deviations from the mean of the uncertainty in deadwood volume were asymmetric, its distribution

Table 1

Summary statistics of NFI estimates for Central Finland of the deadwood parameters used to initialize the simulations. 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.

	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	5.1
	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
Average \pm SD			0.026 \pm	0.009 \pm	73 \pm	38 \pm	15.4 \pm	3.7 \pm
			0.005	0.002	15	8	3.2	0.8

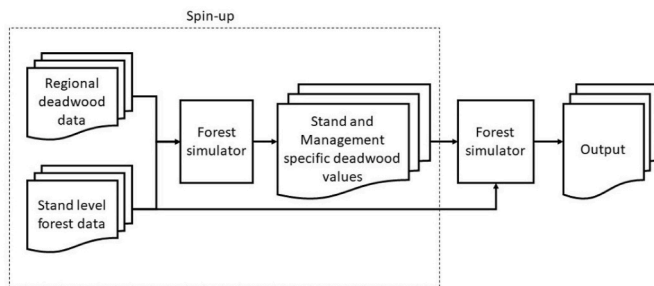


Fig. 2. Flowchart describing the procedure of deadwood initialization and simulation.

having mostly large positive deviations from the mean values. This is because the natural distribution of the deadwood volume in the stands is centered around close to zero m³/ha, as most of the stands have low deadwood volume. Therefore, we assumed that the distribution of the values of deadwood volume followed a log-normal distribution with mean = 0 and SD = 2. Realization of uncertainty in deadwood volume were calculated at 15%, 25%, 45% and 50% of the probability density function of the log-normal distribution, which represents most of the deadwood values. Departures from the mean at each probability level were calculated multiplying the values of the z-scores for the log-normal cumulative distribution by the maximum inventory standard errors for deadwood volume (SE = 200%).

2.4. Optimization problem

To reveal the relationships among the two objectives (i.e., economic value of harvested timber and deadwood volume), we used multi-objective optimization (Miettinen, 1999). We formulated the

bi-objective optimization problem as maximizing the two objectives (objective functions) on the set of all management plans that can be implemented in the landscape. We used bi-objective optimization to analyze the severity of trade-offs between pairs of objectives. Extreme solutions maximize only one objective, while compromise solutions, i.e., single Pareto optimal balanced solutions (sensu Miettinen, 1999), identify management plans that, while guaranteeing the required level of one objective, result in the smallest losses in the other objective from its maximum.

A management plan is defined as a specific combination of the available management regimes across stands. It is impossible to achieve the maximal values for all the objectives simultaneously when there is even a slight conflict among them. Thus, the solution to the optimization problem is a set of Pareto optimal plans. A plan is Pareto optimal if the outcome cannot be improved for any objective without deteriorating at least one of the other objectives. We used the ε -constraint method (Miettinen, 1999) for deriving Pareto optimal solutions. In our study we have set NPV greater than epsilon, from 1.25% of max NPV to 100% (or 99%) of max NPV. The detailed mathematical formulation of the bi-objective optimization problem is reported here:

$$\text{maximize}(f_1(x), \dots, f_n(x))$$

$$\text{subject to } x \in X,$$

Where $(f_1(x), \dots, f_n(x))$ are objective functions and X is the set of alternative management regimes. Here, the objective functions are for timber harvest revenues (NPV) and deadwood volume. The value of each objective function depends on x , i.e., the management regime applied.

Let $s = 1, 2, \dots, m$ be the index of forest stands and $r = 1, 2, \dots, n$ be the index of management regimes. The decision variables x_{sr} are binary variables belonging to $\{0,1\}$.

The set of feasible solutions is defined by:

$$X = \left\{ x = (x_{s,r})_{m \times n} \in \{0, 1\}^{m \times n}; \sum_{r=1}^n x_{s,r} = 1 \text{ for each } s = 1, \dots, m \right\}.$$

Thus, each feasible solution is a management plan where for each forest stand, one of the management regimes is selected.

Any of the two objective functions is defined by the formula:

$$f_i(x) = \sum_{s=1}^m \sum_{r=1}^n c_{sr}^{(i)} x_{sr},$$

Where coefficient $c_{sr}^{(i)}$ is the contribution of the s -th stand to the value of i -th objective in the case where the r -th management regime is selected. In other words, for each forest stand s and each management regime r , the coefficients describe the following outcomes of managing stand s with regime r :

- $c_{sr}^{(1)}$ – timber harvest revenue (NPV) from the stand;
- $c_{sr}^{(2)}$ – deadwood volume from the stand.

Here we employ the following two properties of Pareto optimal solutions to analyze the forest management problem:

- 1) For each Pareto optimal solution x , its corresponding objective function values $y = (y_1, y_2) = (f_1(x), f_2(x))$ characterize the maximum achievement for each of the two objectives under a constraint on the other objective:
 - y_1 is the maximum value of NPV, which can be achieved under the condition that deadwood volume will not drop below ε_2 ;
 - y_2 is the maximum value of deadwood volume, which can be achieved under the condition that the NPV will not drop below ε_1 .
- 2) When sorting all Pareto optimal solutions in an ascending order by one of the two objectives, we always obtain a descending order by the other objective. The 2D-plot of such a sequence of Pareto optimal solutions is called a trade-off curve. Because the set of feasible solutions of our problem is finite, the trade-off curves obtained consist of discrete points. However, in the visualizations of the Pareto optimal solutions we interpolate between finite sets of points to get continuous lines.

The optimization calculations were carried out using Coin-OR's CBC solver (Forrest and Lougee-Heimer, 2005).

2.5. Spatial optimization

To evaluate the effect of landscape structure and configuration on the trade-off between NPV and DW, we formulate a second optimization problem that links the decision from the non-spatial solution to a spatial optimization problem. This problem formulation uses the management decisions from the non-spatial solution, then selects spatially adjacent forest stands that prioritize a second objective function. The objective function of this problem is to maximize the joint production of NPV and DW at a ratio of 20:80:

$$\text{Maximize} \left(\frac{f_1(x)}{f_1(x)^{\text{ideal}} - f_1(x)^{\text{nadir}}} \right) * 0.2 + \left(\frac{f_2(x)}{f_2(x)^{\text{ideal}} - f_2(x)^{\text{nadir}}} \right) * 0.8$$

where the opposite ideal (i.e., constructed by all the optimal objective values) and nadir (i.e., derived from the extreme points in a non-dominated solution set) values of both NPV ($f_1(x)$) and DW ($f_2(x)$) are calculated through separate optimization calculations. An NPV/DW ratio of 20:80 is congruent with the expectations for a production landscape, where not all the adjacent area of suitable habitat patches can be managed to maximize DW.

To prioritize DW in spatially adjacent stands, we used the clique approach (Weintraub and Murray, 2006), where a clique is a predefined

set of two or more stands where each stand in the clique is adjacent to all other stands in the clique. We required that ~50% of the total forest area were assigned to cliques that prioritized DW. This is accomplished through an iterative approach, where we first maximize for non-spatial optimization problem, then select as close to 50% of the forest area to promote DW in cliques. This approach allowed us to explore the economic costs and ecological benefits from spatially aggregating DW resources into adjacent forest stands.

For each solution in the non-spatial Pareto frontier a constraint was added that allowed management in the specific clique to change, according to the objective that maximizes DW. The constraint allowing a change in management for specific cliques is formulated as:

$$\sum_{s \in CL_c} (\hat{x}_{sr^*} x_{sr}) \geq \#CL_c (1 - y_c), \forall c \in CL$$

CL is the set of cliques, with CL_c as a set of stands in the clique c , $\#CL_c$ is the cardinality of clique c (i.e., the number of stands in the clique), y_c is the decision variable to change the management of clique c , \hat{x}_{sr^*} is a parameter, set equal to the decision found in the previous optimization and with r^* being the management regime selected in the non-optimal solution. This constraint requires that the management be not changed between the \hat{x}_{sr^*} and x_{sr} unless $y_c = 1$. This constraint restricts management to be identical to the non-spatial optimal solution if $y_c = 0$, and allows the management to change if $y_c = 1$.

To ensure that some change in management is made in each clique, we applied an additional constraint:

$$\sum_{s \in CL_c} (\hat{x}_{sr^*} x_{sr}) \leq (\#CL_c - 1) y_c, \forall c \in CL$$

this ensures that for each clique that was selected, at a minimum, the management schedule for at least one stand must be different.

An additional constraint limits the area of the cliques with changed management alternatives to be less than or equal to A (a parameter set by the decision maker and corresponding to the area of the cliques):

$$\sum_{c \in CL} y_c a_c \leq A$$

Area restriction: y_c is a binary decision variable to change management of stands within clique c , a_c is the area of c , and A is the total allowable area to be changed. The difference between the solutions is represented by the change in those specific cliques. Finally, the procedure is iterated across the Pareto frontier.

In our study case we evaluated the effect of increasing proportions of adjacent stand area on the Pareto front (area varying from 10% to 50% of the total stand area, Fig. S1 in Appendix A). However, to facilitate the comparison between non-spatial solutions and spatially-aggregated solutions in the Pareto front we compared the non-spatial solutions only with the solutions of the most expensive spatial optimization option, when 50% of the total stand area was adjacent.

2.6. Evaluation of the effect of forest management on trade-offs

We evaluated how the management decisions to harvest more or less timber and collect more or less energy wood drive the trade-off between NPV and deadwood volume. We selected two indicators as a measure of forestry intensification in the Pareto optimal set: (1) the change in the proportion of forest area where the allocation of management options maximizes timber harvesting and (2) the change in the forest area where timber is harvested under increasing levels of collection of deadwood deployed in the forest by natural mortality (low, i.e., 5%, intermediate, 40%, or high, 75%). As before, to facilitate the comparison between non-spatial solutions and spatially-aggregated solutions we reported the results on the impact of forest management only for the non-spatial solutions and for one spatial case (proportion of adjacent stand area = 50% of the total forest area).

2.7. Evaluation of the effect of inventory errors on trade-offs

We estimated the uncertainty induced in the Pareto solutions by inventory errors in tree basal area, tree height and deadwood volume. The ensemble of the uncertain solutions represents a ‘Pareto region’ surrounding the Pareto curve (Rebello et al., 2021). To evaluate how much of the total uncertainty of the Pareto region derived from each uncertainty in the three indicators, we recalculated the solutions in the Pareto region by removing in turn one source of uncertainty (i.e., inventory error) at a time with a leave-one-out procedure. This means that we considered that each of the three forest variables were assumed correct, assuming no inventory errors (i.e., the mean values were used, corresponding to the values of the input data). The boundaries of the Pareto region were derived from the random sampling from the Gaussian distribution of simulated inventory errors for basal area and tree height, and from the log-normal distribution for deadwood volume. To simplify these irregular boundaries, we calculated a standard deviation (SD) value for the set of 20 uncertainty values in correspondence of each mean solution of the Pareto curve. In this way, the borders of the spread of the Pareto region were simplified but still representative of the local variability of the solutions. With this technique, it was possible to approximate the irregular point-like spread of the solutions of the Pareto region to a more regular region. As the mean Pareto solutions were not output at regular interval, also the SD values correspondent to the mean solutions were not equally spaced in the Pareto frontier. To evaluate the total extent of the Pareto regions we computed the concave hull polygon (Park and Oh, 2012) from all its borders (i.e., standard deviations from the mean solutions). This operation resulted in a single polygon approximating the area of the Pareto region. The polygon areas represented a measure of the spread of the Pareto region, that we used to evaluate the effect of each source of uncertainty on the total uncertainty induced by all the inventory errors. This was done by calculating the difference between the Pareto region embedding all the three sources of uncertainty and the Pareto region embedding all the sources of uncertainty but one. We reported the results only for the non-spatial solutions,

as the uncertainty in inventory errors was calculated in identical way also in the spatial cases and therefore was not significantly different among the spatial solutions (as reported in Fig. S1 in Appendix A).

2.8. Evaluation of the impact of the trade-offs on forest biodiversity

To evaluate the impact of the trade-offs between timber harvesting and deadwood volume on forest biodiversity dwelling in deadwood, we considered how the changes in deadwood volume induced by the changes in the forest economic value (NPV) affected a well-recognized indicator of biodiversity in deadwood, i.e., the number of species of wood-inhabiting fungi. To do so, we re-calculated, based on the study of Penttilä et al. (2004), the relationship between deadwood volume and richness for all fungal species and only for the species that were evaluated as near-threatened (NT) at the time of the study (Rassi et al., 2001) and applied them to the values of deadwood projected in our landscape for the main Pareto solutions.

3. Results

3.1. Non-spatial and spatial trade-offs between timber production and deadwood volume

We found a clear non-linear relationship between deadwood volume (DW) and economic value from timber harvesting (Net Present Value, NPV) in the set of Pareto optimal solutions (Fig. 3). This reveals that in production landscapes for compromise solutions (i.e., the point nearest to the ideal point on the Pareto curve, NPV = 93% in Fig. 3), it is possible to increase much more the stand DW per hectare respect to the minimum value in the Pareto curve when stands with high DW are not aggregated (i.e., by 45.3% for the non-spatial solution) than when they are aggregated (i.e., only by 16.5% for the spatially aggregated solution in Fig. 3). Finally, in the extreme solution when 60% of the maximum NPV was obtained, the gain in DW respect to the compromise solution was large both for the non-spatial solution (+110% respect to the minimum DW

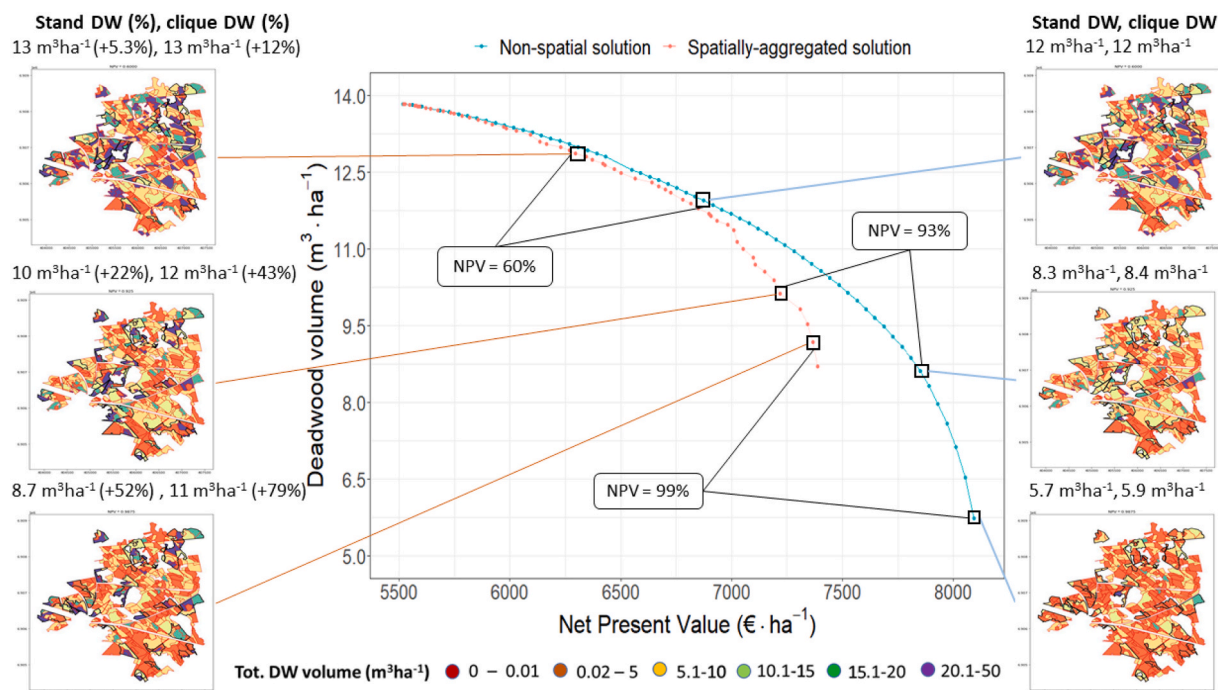


Fig. 3. Comparison of non-spatial (blue dots) and spatial (red dots) Pareto optimal solutions for the economic value from timber harvesting (Net Present Value per hectares in x axis) and the corresponding deadwood volume (DW per ha, in y axis). Maps represent the distribution of deadwood volume per hectare in the stands. Stand deadwood volume per hectare is reported for the whole area and for the clique area, along with percent increases from the respective non-spatial to the spatial solutions. Groups of adjacent stands with marked borders represent areas of spatial aggregation (i.e., cliques).

value, corresponding to a further gain from the compromise solution of +64.8%) and for the spatially-aggregated solution (+45.7% respect to the minimum DW value, +29.2% respect to the compromise solution) (Fig. 3).

The maps representing the distribution of the non-spatial and spatial Pareto optimal solutions (Fig. 3) showed that most of the stands had low DW. In fact, whether or not connectivity among stands was considered, the ranges of DW in the Pareto fronts were between 5.73 and 12.6 m³/ha in the non-spatial solutions and between 8.70 and 13.9 m³/ha in the spatially-aggregated solutions, respectively. This low DW is the result of a very high proportion of the stand area with very low or low DW (depending on the Pareto solutions, area with DW < 10 m³/ha was ranging between 71% and 91%, when DW was close to its maximum value and minimum values, respectively, Table 2), and only few stands retaining instead high DW (depending on the Pareto solutions, area with DW ≥ 10 m³/ha was ranging between 8.8% and 29% and area with DW ≥ 20 m³/ha was ranging between 2.2% and 11.2%, when DW was close to its minimum and maximum values, respectively, Table 2). For the compromise solution (i.e., NPV = 93%), 7% of connected stands 'area harbored ≥ 20 m³/ha deadwood.

The aggregation of high DW values significantly increased towards extreme Pareto solutions when NPV was close to maximum (i.e., NPV = 99% in Fig. 3). For these Pareto solutions, the stand DW was much higher (+52% but +79% in adjacent stands) than the corresponding DW in the non-spatially aggregated solution (Fig. 3). Instead, the stand DW was limited for Pareto solutions corresponding to lower DW. For the compromise solutions, when NPV was 93% of the total, the stand DW was 22% higher than in the non-spatial solution (but +43% in adjacent stands), and when 60% of the maximum NPV was obtained, the DW aggregation was much lower, just +5.3% (but +12% in adjacent stands) (Fig. 3).

Table 2

Stand area for each class of deadwood volumes (DW, m³/ha) represented in the maps in Fig. 3 for non-spatial and spatial Pareto optimal solutions. Clique areas and their percentages respect to the total clique area are reported in parentheses.

Percentage of maximum NPV	DW (m ³ ha ⁻¹)	Non-spatial solutions		Spatial solutions	
		Total area = 683.6 ha (clique area = 309.1 ha)	% Total area (%) (clique area)	Total area = 683.6 ha (clique area = 309.1 ha)	% Total area (%) (clique area)
NPV = 60%	0-<5	359.1 (162.9)	52.5 (52.7)	352.2 (156)	51.5 (50.5)
	5-<10	144 (70.1)	21.1 (22.7)	136.1 (62.2)	19.9 (20.1)
	10-<15	81.5 (32.3)	11.9 (10.5)	81.3 (32.1)	11.9 (10.4)
	15-<20	31.6 (15.6)	4.6 (5)	37.5 (21.5)	5.5 (7)
	20-<30	30.7 (16.2)	4.5 (5.2)	34.2 (19.7)	5 (6.4)
	30-<40	20.2 (6.5)	2.9 (2.1)	25.1 (11.4)	3.7 (3.7)
	≥40	16.5 (5.5)	2.4 (1.8)	17.2 (6.2)	2.5 (2)
NPV = 93%	0-<5	433.9 (197)	63.5 (63.7)	400.6 (181.4)	58.6 (58.7)
	5-<10	136.5 (68.4)	20 (22.1)	135.6 (60.1)	19.8 (19.5)
	10-<15	59.1 (23.8)	8.6 (7.7)	66.7 (27.6)	9.8 (8.9)
	15-<20	24.1 (9.7)	3.5 (3.1)	30.9 (16.8)	4.5 (5.4)
	20-<30	16.7 (3.9)	2.4 (1.3)	23.3 (9.8)	3.4 (3.2)
	30-<40	7.4 (4)	1.1 (1.3)	15.5 (9.6)	2.3 (3.1)
	≥40	5.8 (2.3)	0.9 (0.7)	11 (3.7)	1.6 (1.2)
NPV = 99%	0-<5	521.2 (242.6)	76.2 (78.5)	452.3 (207.5)	66.2 (67.1)
	5-<10	102.3 (39.8)	15 (12.9)	108.8 (42.3)	15.9 (13.7)
	10-<15	37.2 (15.2)	5.4 (4.9)	57.3 (23.1)	8.4 (7.5)
	15-<20	8 (3.9)	1.2 (1.3)	25.6 (16.8)	3.8 (5.4)
	20-<30	8.1 (4.3)	1.2 (1.4)	16.9 (10)	2.5 (3.2)
	30-<40	2.7 (1.5)	0.4 (0.5)	12.3 (6.1)	1.8 (2)
	≥40	4.1 (1.8)	0.6 (0.6)	10.3 (3.4)	1.5 (1.1)

3.2. Effect of forest management on trade-offs

When the forest landscape was managed with high intensity forestry (NPV = 99% in the top panel of Fig. 4), in the non-spatial solutions almost 90% of the forest area was treated with NPV maximization >0.9 and almost 10% of the area was treated with NPV maximization between >0.8 and 0.9. Instead, in a compromise solution (NPV = 93% in the central panel of Fig. 4), the proportion of the forest area managed with NPV maximization >0.9 decreased to about 60% while the proportion of forest area with lower but still high NPV maximization values increased. Specifically, NPV maximization between >0.8 and 0.9 increased to 25% of the total and NPV maximization between >0.7 and 0.8 increased to about 5% of the total. Finally, when NPV was close to minimum (i.e., NPV = 60% in the bottom panel of Fig. 4), the proportion the forest area managed with very high (>0.9) and high (between >0.8 and 0.9) NPV maximization decreased, being close to 25%, while the proportion the forest area managed with >0.7 and 0.8 NPV maximization increased to 15% of the total. On the other hand, the proportion of forest area treated with low (between >0 and 0.3) and intermediate-high NPV maximization (between >0.4 and 0.7) increased approaching levels of 5–10% (Fig. 4). The spatial aggregation of stands with high DW significantly affected the proportion of area allocated to NPV maximization classes closer to maximum NPV, for which in the spatially-aggregated solutions the proportion of area allocated to high NPV maximization was significantly lower than in the non-spatial solutions, while it was significantly higher for low levels of NPV maximization (Fig. 4).

When the forest landscape had low economic value (left-hand side of Fig. 5, NPV ranging between from 6500 €/ha to 7000 €/ha), all the forest area allocated to timber extraction was entirely treated with low (5%) removal of DW from the forest floor. Instead, moving towards maximum NPV (right-hand side of Fig. 5, >7000 €/ha), most (almost 75%) of the forest area allocated to timber extraction was treated with high (75%) removal of DW from the forest floor, but the rest of the area (about 25–30%) was instead still treated by low (5%) and intermediate (40%) DW removal (Fig. 5). The spatial aggregation of stands with high DW significantly affected the area allocated to timber extraction only close to maximum NPV, for which in the spatially-aggregated solutions (pale dots) the area allocated for timber extraction was significantly lower for intermediate (40%) and high (75%) level of DW removal (Fig. 5) but significantly higher for low (5%) level of DW removal (Fig. 5) respect to the non-aggregated solutions (bright dots of the respective colors).

3.3. Effect of uncertainty on trade-offs

The total uncertainty of the Pareto optimal solutions decreased with the removal of single sources of uncertainty. Specifically, the removal of inventory errors from DW increased the area of the Pareto region by 29.6% where all the three sources of uncertainty were accounted for, while the removal of basal area and tree height decreased the area of 2.21% and 7.75%, respectively (Fig. 6). This means that accounting for DW errors in the Pareto solutions reduces the most uncertainty, while accounting for tree height and basal area increases the total uncertainty. While the Pareto curves where DW uncertainty was removed did not diverge from the pattern observed when all the uncertainties were accounted for, the Pareto curve where the uncertainty in tree height was removed increased the estimates of DW for a defined NPV, while oppositely the Pareto curve where the uncertainty in basal area was removed slightly decreased the estimates of DW for a defined NPV (Fig. 6).

3.4. Relationship between deadwood volume and species richness of wood-inhabiting fungi

In the Finnish study of Penttilä et al. (2004), plots of 4-ha with increasing DW hosted an increasing number of species of wood-inhabiting fungi (species richness) (Fig. S2). A landscape NPV

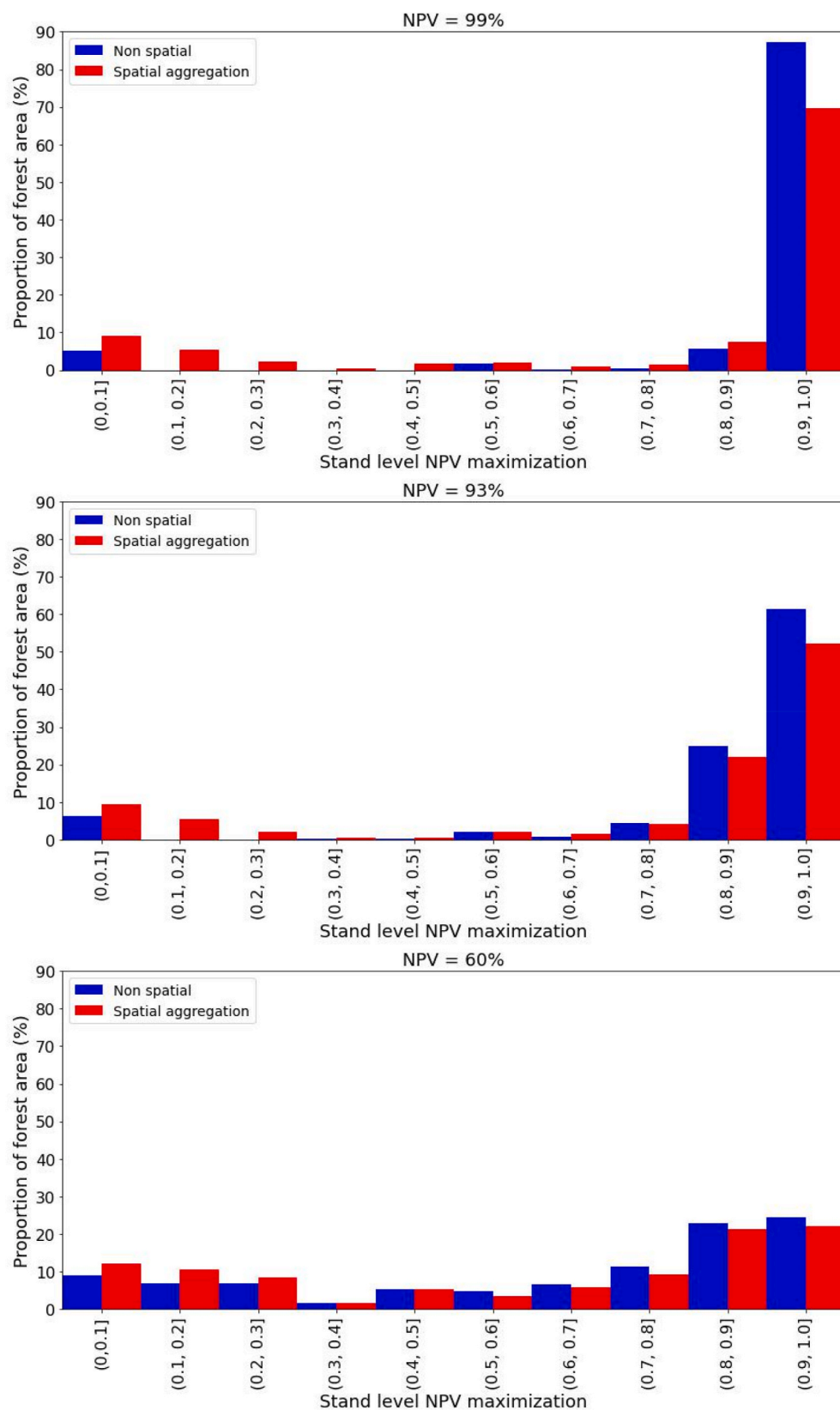


Fig. 4. Comparison of non-spatial (red) and spatial (blue) Pareto optimal solutions for the changes in the proportion of area allocated to timber extraction (in y-axis) with increasing economic value from timber harvesting (stand level NPV maximization in x axis).

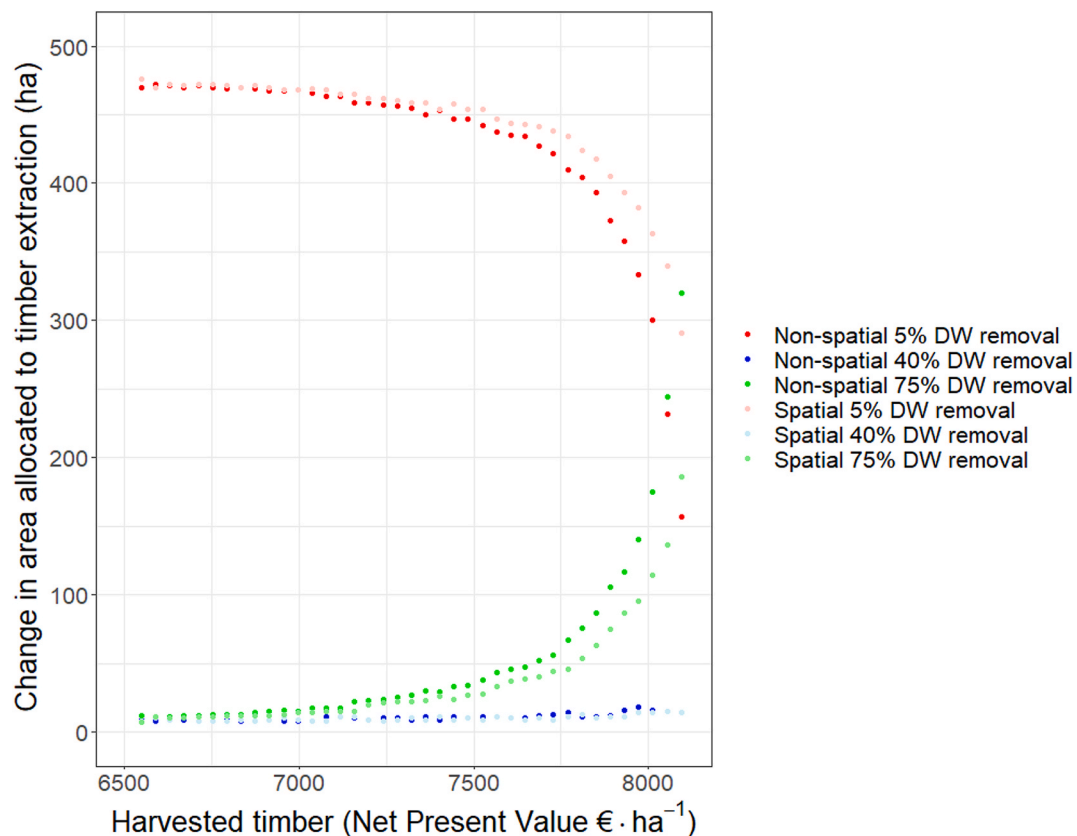


Fig. 5. Comparison of non-spatial (bright-colored points) and spatial (pale-colored points) Pareto optimal solutions for the change in the proportion of area allocated to timber extraction (in y-axis) with increasing economic value from timber harvesting (NPV in x axis) for three proportions of deadwood removed by stakeholders (low, i.e., 5%, intermediate, i.e., 40%, and high, 75% DW removal).

close to maximum (i.e., NPV = 99%) corresponded to an average of 8.7 m³/ha of DW in the spatially-aggregated solutions (Fig. 3), being able to support 28% (median value, with 95% percentile range: 19–43%) of the total polypore species, according to Penttilä et al. (2004) data (Figs. S2 and S3), with slightly higher figures for stands aggregated in cliques (Fig. S5). For this extreme solution, in the spatially aggregated solution 5.8% of the stand area had more than 20 m³/ha DW (Table 2), already being able to support the presence of NT species in the production landscape (Figs. S2, S4, S6). The compromise solution (i.e., NPV = 93%) brought the average DW to 10 m³/ha in the spatially aggregated solution (Figs. 3), and 7.3% of the area had more than 20 m³/ha DW (Table 2). Finally, A landscape NPV close to minimum (i.e., NPV = 60%) in the spatially aggregated solution brought to 13 m³/ha the average DW (Fig. 3), being able to support 32% (median value, with 95% percentile range: 20–47%) of the total polypore species, and 11.2% of the stand area had more than 20 m³/ha DW (Table 2), which increased the proportion of stands able to host more than one NT species (Figs. S4 and S6). The spatially-aggregated solutions were characterized by higher values of species richness across the forest landscape both for the total species (Fig. S3, Fig. S5) and for NT species (Fig. S4, Fig. S6) than non-spatial solutions.

4. Discussion

4.1. Trade-offs between timber production and deadwood volume and impact on biodiversity

The results of our study revealed that landscape structure (“habitat amount” effect) and configuration (“spillover” effect) sensibly affect the trade-off between the economic value from timber and deadwood availability for forest biodiversity.

The “habitat amount” effect on the trade-off was verified by our Pareto curves that showed that, in our study area, it was possible to improve the landscape structure, represented by the amount of deadwood volume available as habitat for biodiversity (by 45% in non-aggregated stands and by 16% in aggregated stands), with a limited reduction in the economic value (7%) obtained reducing timber harvesting (as already observed in other simulation studies, Mönkkönen et al., 2014 and Eggers et al., 2022). This increase brought only to a limited increase (+2%) in the median species richness (Figs. S3 and S5). This evidence supports the suggestions from Gustafsson et al. (2012) that an ecological enrichment in the forest structure can be achieved just converting a small fraction of the production landscape into a landscape with a structure more suitable as habitat for biodiversity. However, our Pareto curves also showed that a defined reduction in economic value from timber harvesting determines a much lower gain in deadwood volume in aggregated than in non-aggregated stands. In other words, improving both the landscape structure (i.e., increasing deadwood volume) and configuration (i.e., increasing connectivity among stands with high deadwood volume) requires larger economic losses (i.e., decrease in NPV) than improving landscape structure alone. This is in contrast with recent findings from Augustynczyk et al. (2018) that instead concluded that the allocation of deadwood “islands” in the production forest landscape would impose only a marginal reduction (<1%) to the NPV. In the specific case larger benefits for biodiversity could be achieved implementing closer-to-nature management aiming to retain more deadwood in the forest either via set-aside (functional segregation) or incorporating conservation measures within production-oriented forests (functional integration) (Larsen et al., 2022).

The “spillover” effect on the trade-off was verified by our findings that, with a limited reduction in the economic value (7%), stands constrained in adjacent areas increased more (+21%) their deadwood

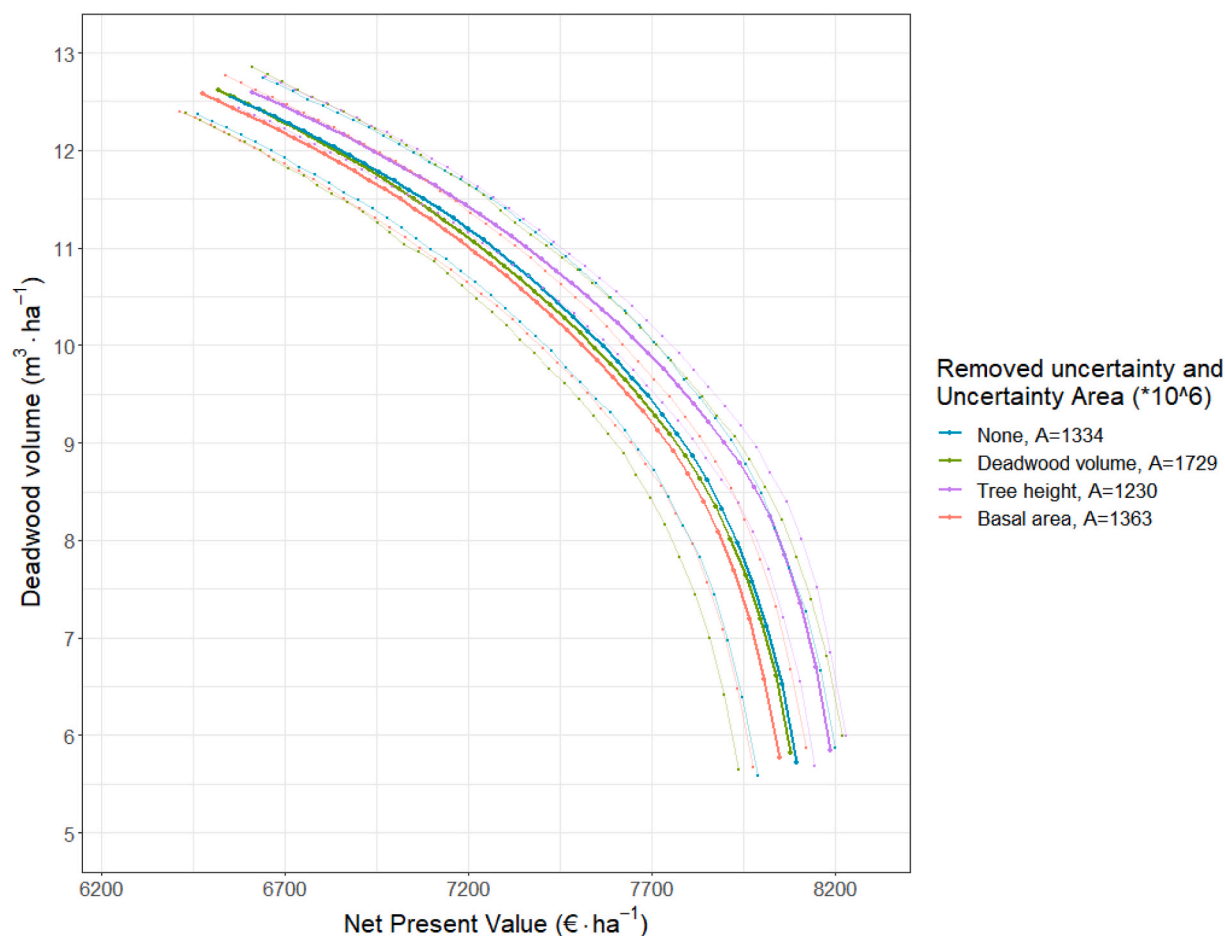


Fig. 6. Comparison between Pareto regions for non-spatial Pareto optimal solutions between economic value from timber harvesting (i.e., Net Present Value per hectare in x axis) and the corresponding deadwood volume (per hectare, in y axis) given the removal of a single source of uncertainty. Means (solid lines) and standard deviations (dotted lines) are represented in different colors when all the sources of uncertainty are considered (“none”) and when in turn one source of uncertainty is removed. Uncertainties derive from combined inventory errors in tree basal area, tree height and deadwood volume. The uncertainty area, i.e., the area of each Pareto region comprised between lower and higher standard deviations, is reported in relative NPV x DW units.

volume than non-aggregated stands, and consequently the former stands increased more their richness than the latter (Figs. S3–S6). This confirmation complies with the findings from Bouget et al. (2016), who uncovered the enhanced value for deadwood-associated biodiversity of suitable well-connected forest habitat patches within the production landscape.

Indeed, we have demonstrated that improving both the structure and configuration of the landscape is beneficial for biodiversity because aggregated forest stands have higher habitat value than isolated stands (Bouget et al., 2016), even though at the same costs stand aggregation could secure less total habitat area over the forest landscape (Bouget et al., 2016). On the other hand, recent research has shown that conserving the cheapest low-quality land has the smallest contribution to connectivity of habitat patches (Mozelewski et al., 2022). Hence, even though a higher number of isolated stands with small deadwood volume could support several isolated species populations in the short term, it could be more cost-effective for the long-term viability of a specialized group of species like wood-inhabiting fungi to preserve a lower number of well-connected forest stands with higher deadwood volume (Nordén et al., 2013).

We found that the overall quality of our forest landscape for red-listed (near-threatened) deadwood biodiversity was low irrespectively of the economic value derived from the timber harvested from the landscape. In fact, when landscape NPV was close to maximum (i.e., for the compromise solution, where NPV = 93% in Fig. 3), most (93%) of our stands’ area showed a DW lower than 20 m³/ha, but 7% of the total

aggregated stand area reached or surpassed this biological threshold important for the survival of red-listed wood inhabiting fungi (Penttilä et al., 2004). Penttilä et al. (2004), did not find NT species in managed forests (age < 120 years) with less than 20 m³/ha of DW, while some observations of NT species were made from managed forests with DW 20–40 m³/ha (just two NT species over a total of 11 NT species). Even though the addition of new species to the local species pool starts to level off already when the DW approaches 46 m³/ha, DW must be at least 100 m³/ha to support more than 50% of the total species pool and a high

Table 3

Prediction of the number of all and near-threatened (NT) species of wood-inhabiting fungi with increasing proportion of the total deadwood volume per hectare according to the equations in Fig. S2 derived from plot values from Penttilä et al. (2004).

Volume (m ³ /ha)	% Total Deadwood volume	All species (Total = 85)	% All species	NT species (Total = 11)	% NT species
1.9	1	16	18.4	0	0.0
9.3	5	27	31.9	0	2.0
18.5	10	32	37.6	1	5.7
46.3	25	38	45.3	2	16.8
92.6	50	43	51.0	4	35.3
138.9	75	46	54.4	6	53.7
176.0	95	48	56.4	8	68.5
183.4	99	48	56.7	8	71.5
185.2	100	48	56.8	8	72.2

number of NT species (about one third of the total NT species) (Table 3, Fig. S2). However, a DW of 100 m³/ha occurs only in old-growth forests. In our data, none of the forests harbored above 50 m³/ha and even the ones close to that were represented in a small fraction of the stands.

It must be considered that the 85 polypore species comprised in Penttilä's study represents the richness that can be achieved in mesic *Myrtillus*-type (MT; *sensu* Cajander, 1949) spruce-dominated forests of one landscape (stands situated within an area of ca. 35 × 80 km and mostly on state-owned land). On the other hand, our landscape covered a wider range of forest types including more (e.g., OMT, *Oxalis-Myrtillus* type) and less (e.g., VT, *Vaccinium* type) fertile soils for which the maximum deadwood volume would be less close or closer to the natural value than MT, and consequently host less or more red-listed species in the same volume.

The low quality of our landscape for deadwood biodiversity derives from the fact that, at the beginning of our simulations, the initial deadwood conditions represented a production landscape mostly managed for timber production. Additionally, a 30 years' planning horizon period was not long enough time to significantly increase the amount of deadwood in the forest. The relationship between deadwood volume and richness of wood-inhabiting fungi estimated from Penttilä et al. (2004) shows that the minimum achievable economic value of the landscape (NPV = 60% of the total) can assure that 11% of the total stand area harbor at least 20 m³/ha of DW or more available both for common and Near Threatened wood-inhabiting fungi. The availability of a minimum deadwood quantity is a biological threshold, an important requirement to ensure the presence of a species in the forest stand (Müller and Bütler, 2010; Junninen and Komonen, 2011). Once this minimum requirement is satisfied, it is possible to consider the improvement in the species fitness at landscape level deriving from stand connectivity. When the minimum threshold volume of deadwood is available, increased stand connectivity may assure the species long-term persistence in the forest landscape favoring its dispersal between suitable forest patches (Hanski and Ovaskainen, 2000). Our results demonstrate that the quality of the forest landscape for wood-inhabiting fungi can be improved by improving both its structure and configuration. The increase in DW between the spatial and non-spatial solutions becomes larger the more landscape total DW decreases. This means that the role of habitat spatial arrangement becomes more important as habitat total amount decreases because of compounding negative effects of habitat loss and habitat fragmentation (Fahrig, 2003). Past research has shown that the structure of the forest landscape, i.e., the availability of deadwood as habitat for biodiversity, can be improved either directly or indirectly. Directly, alleviating the negative impact of timber extraction reducing resources in the forest, for example excluding thinning extending the forest rotation time (García-Gonzalo et al., 2007; Alam et al., 2008) or leaving deadwood on the forest floor after clearcutting (Ehnström, 2001). Indirectly, offsetting biodiversity loss due to harvesting through compensation measures, for example via forest restoration (Halme et al., 2013), retention of single trees (Gustafsson et al., 2020) or setting-aside the whole stand (Mazziotta et al., 2014). Catastrophic events like large storms may locally increase the amount of deadwood in the forest by favoring bark beetles' attacks (Eriksson et al., 2007), but the simulation of these events was beyond the scope of our study. Finally, the configuration of the landscape, i.e., how deadwood is distributed in the forest stands, can be improved via high level landscape planning allocating measures of protection and ecological restoration (e.g., deadwood creation, Koivula and Vanha-Majamaa, 2020) aiming to increase connectivity of suitable patches in the managed landscape (Nordén et al., 2013).

4.2. Effect of forest management on trade-offs and impact on biodiversity

Deadwood volume decreased in the forest landscape because of the intensification of forestry, i.e., with an increase in the proportion of the area allocated to obtain high revenues (NPV) from timber harvesting,

and with high (75%) levels of deadwood removal, while it increased because of less intensive timber harvesting and low (5%) deadwood removal. In other words, an increase in deadwood in the forest landscape was supported both by low intensity forestry and the limitation of energy wood collection. Conversely, deadwood decreased under a regime of high-intensity forestry and high deadwood collection. An intermediate (40%) level of deadwood removal did not prioritize either deadwood volume or timber.

From our findings it is clear that management can maximize economic revenues with a combination of high timber harvesting rates and the collection of a high proportion of deadwood from the forest floor. The trade-off in the use of wood as habitat for biodiversity and as timber and energy wood is modulated by the interest of the forest owner either for nature conservation or for economic revenues (Deuffic and Lyser, 2012). The decision of the forest owner of leaving wood to rotten on the forest floor as biodiversity habitat or of either harvesting timber and collecting residues for energy wood can be driven by the price of timber and energy wood which vary over the years (for example, energy wood price in Finland ranged between 20 €/m³ and 30 €/m³ across years 2014–2021, Vaahtera et al., 2021). The forest owners' decision to let the trees grow or harvest them favors or hampers their future decay, while the decision to leave or collect deadwood from the forest floor increases and directly reduces the availability of deadwood in the landscape for forest-dwelling species (Koskela and Karppinen, 2021). As the highest collection of energy wood takes place when harvesting rate is already high, this can potentially generate further negative impacts for deadwood biodiversity (Rudolphi and Gustafsson, 2005).

Increasing the economic value (NPV) with the constraint of increasing deadwood volume in some adjacent stands permitted leaving a larger area subject to less intensive forestry and to low (5%) deadwood removal, consequently reducing the forest area subject to strong harvesting and intermediate (40%) and high deadwood removal (75%). Management accounting for the connectivity of stands with high deadwood volumes can be operationalized through a zonation in the production of the resources in the forest landscape, or "land sparing," where timber and biodiversity are prioritized in different stands (Kärkkäinen et al., 2020). While a few aggregated stands would be managed to support higher habitat values, the rest would be utilized to co-produce timber and energy wood (Tittler et al., 2012). On the other hand, with no stand aggregation there would be a "land sharing," where all the stands can produce both habitat and provisioning services but at lower levels.

4.3. Effect of uncertainty on trade-offs and impact on biodiversity

In our study area, we found that accounting for the uncertainty from various sources affected the trade-offs between the forest economic and ecological value. This corroborates the evidence that taking account of uncertainty in model parameters in optimization is crucial to quantify their reliability (Bortz et al., 2017). If the distribution of the uncertain values is wider than the original distribution, positive optimization bias in the Pareto front will result (i.e., assuming the errors to follow formula: $y_{erroneous} = y_{true} + \epsilon$) and negative optimization bias if it is narrower than the original distribution (i.e., assuming the error to follow similar formula as regression model errors: $y_{true} = y_{predicted} + \epsilon$) (Kangas and Kangas, 1999). The uncertainty in deadwood volume was the source of uncertainty that stabilized the most the Pareto curve. This implies that to calculate a realistic measure of the potential value of the landscape for deadwood-dependent biodiversity given its economic value, it is crucial to account for the uncertainties in deadwood volume. Even though basal area and tree height had a smaller impact on the total uncertainty than deadwood, the value of the landscape for biodiversity was either underestimated and overestimated, respectively, when their uncertainty was not accounted for, and this can significantly affect the decision making process over the landscape (c.f., Wei and Murray, 2015). In fact, for a certain decrease in the economic value of the forest landscape the

estimates of deadwood could be smaller or higher accounting also for the uncertainty in basal area and tree height, and this is likely to have important consequences for the choice of the management actions to allocate in the landscape to favor either economic development or nature conservation (Balint et al., 2011).

5. Conclusions

Our results demonstrate that the trade-offs between forest development and conservation are differently affected by landscape characteristics, forest management and uncertainty in inventory errors. However, these three factors do not have the same importance in modifying the Pareto curves. Likely a large uncertainty in the sampling error has the largest impact on the trade-offs, as their exclusion or inclusion in optimization either underestimate or overestimate the value of the forest landscape for biodiversity, while spatially-aggregated solutions are different from non-spatial solutions only in certain segments of the Pareto curve but not in others. For example, a progressive decrease in the landscape economic value resulted in a non-linear increase in its ecological value. Taking management decisions to harvest timber more intensively and to collect a smaller or larger fractions of deadwood from the forest floor is strictly dependent on the degree to which the economic value of the landscape is maximized, and this can still be affected by the choice to aggregate stands in deadwood “islands.” As we showed with wood-inhabiting fungi, such a treatment is beneficial for forest species. This aggregation of suitable landscape elements to increase their value for biodiversity is not new, and has shown to be successful in Southern, Central (“Îlots de senescence”, Mason et al., 2016) and Northern European forests (Woodland Key Habitats, Timonen et al., 2010). However, now there is a lack of evidence to evaluate the importance of landscape components for wood-inhabiting fungi. We do see efforts to approach this at a landscape level, for example the ongoing review from Undin et al. (2022). Our study uses wood-inhabiting fungi as an example species group to exemplify the range of impacts that drivers of forest intensification can have on biodiversity. Our results highlight the importance of these three drivers when managing forests for multiple uses, allowing stakeholders to make more target-oriented choices in forest planning.

Credit author statement

AM and KE designed the study; AM and KE performed the research; AM and KE contributed new simulations; AM analysed the data and led the writing of the manuscript; AM, PB, AK, PH and KE interpreted the results and participated in writing the paper.

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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

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2022.117144>.

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