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PATTERNS OF DEADWOOD VOLUME AND DYNAMICS IN SLOVENIAN FORESTS
ZNAČILNOSTI IN DINAMIKA ODMRLEGA LESA V SLOVENSKIH GOZDOVIH

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ABSTRACT
Deadwood, and its temporal and spatial variation, plays an important role in several forest ecosystem services. This study demonstrates the assessment of deadwood dynamics using data from Slovenian national forest inventory permanent sampling plots, employing a mass-balance approach. Our results reveal that deadwood volume is a highly variable metric across regions, deadwood types and tree species. Despite the influx of large volumes of new deadwood due to recent natural disturbances, only moderate increases in deadwood volume were observed between 2007 and 2018. This was mainly offset by deadwood losses due to salvage logging and decomposition. The extent of deadwood losses varied considerably by species. We discuss the implications of the calculation method on estimating changes in deadwood volume, compare these findings with existing literature on deadwood and highlight promising areas for future research activities to better understand deadwood dynamics.

Key words: deadwood, carbon, natural disturbances, decomposition

IZVLEČEK
Odmrla lesna biomasa (odmrli les) in njene spremembe v času in prostoru so pomembne z vidika različnih ekosistemskih storitev gozdov. V članku je prikazano, kako je mogoče z uporabo bilančne metode (vnosi, iznosi) in podatkov s trajnih vzorčnih ploskev nacionalne gozdne inventure oceniti dinamiko odmrlega lesa. Rezultati prikazujejo spremenljivost količine odmrlega lesa glede na ekoregije, tipe odmrlega lesa in drevesne vrste. Zmerno povečanje količine odmrlega lesa med letoma 2007 in 2018 je bilo kljub povečanju količin novega odmrlega lesa kot posledice naravnih ujm kompenzirano z zmanjševanjem količin odmrlega lesa, predvsem zaradi povečanih sanitarnih sečenj in razkroja. Opažene izgube odmrlega lesa se precej razlikujejo glede na drevesno vrsto.

Ključne besede: odmrli les, ogljik, naravne motnje, razkroj

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1 INTRODUCTION
1 UVOD

Deadwood, also known as deadwood biomass, coarse woody debris or necromass, is one of the key indicators of sustainable forest management (Forest Europe, 2015). It is an important indicator of biodiversity, acting as a key habitat for many specialized organisms (Lassauce et al., 2011; Lombardi et al., 2016). Deadwood represents one of the five carbon pools in forest ecosystems that are mandatory for Land Use, Land-Use Change and Forestry (LULUCF) reporting, in addition to aboveground woody biomass, belowground woody biomass, litter and soil (Good practice ..., 2003). Additionally, deadwood possesses economic value as a biomass source, primarily for energy purposes, such as harvesting tree stumps (Rahman et al., 2019). The amount of deadwood, its structure (type, dimensions, tree species, etc.) and degree of decomposition are also important (Paletto and Tosi, 2010; Denac and Mihelič, 2015). The degree of decomposition (i.e., extent of decay, changes in chemical composition and loss of density and structural integrity) is important due to its significant correlation with the density and carbon content of deadwood (e.g. Přívětivý and Šamonil, 2021; Neumann et al., 2023b). More advanced decomposition stages have lower density, and thus the degree of decomposition also changes the energy contained in deadwood due to the correlation of energy and carbon content (Barrette et al., 2014; Neumann et al., 2020). Deadwood is also an important habitat for various species (Swift, 1977), with its structure and quantity being important for the habitat function of forest ecosystems (Diaci and Perusek, 2004; Kovac et al., 2020). Although there are suggested thresholds for the amount of deadwood, the definitive quantity and quality required to satisfactorily ensure the habitat function of forest ecosystems remain under debate (Diaci and Perusek, 2004; Kadunc, 2008; Müller and Bütler, 2010).

Broadly defined, deadwood encompasses all non-living woody biomass that is not considered part of the litter, whether standing, lying on the ground or incorporated into the soil, with a diameter of at least 10 cm (Good practice …, 2003; Rondeux et al., 2012; Harmon et al., 2020). Country-specific definitions of deadwood often vary, hindering direct comparison of data between countries. To address this, "bridging functions" have been developed to harmonize the data, such as those for tree volume and growing stock (Gschwantner et al., 2019). Due to its rarity in space and time from a statistical perspective and high spatio-temporal variability, measuring deadwood using the same sampling systems as those used for live trees may yield unreliable estimates (Ritter and Saborowski, 2012; Öder et al., 2021).

According to Slovenian rules of forest protection (Pravilnik o varstvu gozdov, 2009), deadwood consists of dead standing trees, dead lying trees, snags, stumps, coarse woody debris, harvesting residues and other biomass intentionally left in the forest. These rules also prescribe the retention of deadwood to maintain biodiversity and ecosystem health, stipulating that the volume of deadwood in a forest must constitute at least 3% of the growing stock in each forest management unit, considering the risk of outbreaks of harmful organisms, including bark beetles. Furthermore, it requires that deadwood be distributed as evenly as possible and cover all diameter classes, including those larger than 30 cm (Pravilnik o varstvu gozdov, 2009).

Large-scale forests monitoring systems, such as national forest inventories (Tomppo et al., 2010), focus not only on the current state but also on changes and long-term trends in indicators. This includes assessing whether the amount of deadwood in the forest is stable, increasing or decreasing over time, which helps in determining if target values are being approached and estimating the time required to achieve them. Forest management is keen on identifying effective forest management interventions for regulating the quantity and quality of deadwood. For instance, in countries such as Finland, stumps are extracted and primarily used for energy production (Rahman et al., 2019). In other countries, stumps are left in the forest after harvesting due to legal or economic factors (Forest Europe, 2015), and in areas prioritizing protection functions (e.g. against avalanches), stumps are intentionally left with greater heights than the typical cutting height (Leverkus et al., 2021; Caduff et al., 2022). Forest management methods and silvicultural measures can thus play crucial roles in influencing deadwood dynamics in forests (Kadunc, 2008; Meyer and Schmidt, 2011; Nagel et al., 2012; Neumann et al., 2023a).

The amount of deadwood in forests depends on a variety of factors, including forest ownership, forest type, productivity, tree composition, management method, stand age, and rates of mortality or decomposition (e.g. Kahl et al., 2017; Ķēniņa et al., 2022; Oettel et al., 2023; Neumann et al., 2023b). The volume of deadwood in the forest is not static but changes dynamically over time (Kroiher and Oehmichen, 2010; Přívětivý et al., 2018). As trees age and grow, they contribute new deadwood through natural mortality, while deadwood volume decreases due to removals (such as salvage logging) and the process of decomposition and decay. In the absence of major disturbances, the amount of deadwood will eventually stabilize, reaching a steady state governed by background mortality levels. The rate of deadwood decomposition varies depending on factors such as deadwood size, shape, tree species, climatic conditions, contact with the ground and the presence of forest fauna (Kroiher and Oehmichen, 2010; Přívětivý et al., 2018; Oettel et al., 2020; Öder et al., 2021). These factors often differ across regions due to variations in soil, climate, forest communities and social factors, such as management practices or local collection of fuelwood. While some tree species, such as *Quercus petraea*, *Pinus sylvestris* and *Robinia pseudoacacia*, are known for their decay-resistant wood, characterized by a large proportion of decay-resistant heartwood and/or the presence of recalcitrant wood extractives, other species, such as *Fagus sylvatica* and *Picea abies*, are reported to decay more rapidly (Lesar et al., 2008; Harmon et al., 2020).

Over the last decade, Slovenian forests have been repeatedly affected by natural disturbances, including an ice storm in 2014, windthrows between 2017 and 2018, and bark beetle outbreaks from 2015 to 2018, primarily in mountainous and lowland regions, according to national reports (Pregledovalnik …, s.a). Consequently, the average growing stock in Slovenian forests decreased from 333.9 to 329.6 m^3/ha from 2012 to 2018, while deadwood volumes increased from 19.8 to 24.2 m^3/ha in the same period (Skudnik, 2015; Skudnik et al., 2021a, 2021b; Skudnik and Kusar, 2021; Pintar et al., 2022; Kušar and Kovač, 2023). The regional implications of these disturbances and the role of tree species on the observed changes in the structure of Slovenian forests are yet to be fully understood.

The aim of this article is to:

- Present the quantitative and structural characteristics of deadwood in Slovenian forest regions for the years 2007, 2012 and 2018, using national forest inventory data.
- Explore the species-specific dynamics of deadwood volumes in Slovenian forests from 2007 to 2018, using input-output balances.

2 METHODS
2 METODE
2.1 Deadwood measurements by the Slovenian national forest inventory
2.1 Meritve odmrlega lesa pri slovenski nacionalni gozdni inventuri

The data for this study were sourced from the Large-scale Monitoring of Forests and Forest Ecosystems (FFECS) database (Monitoring gozdov ..., s.a.), collected between 2007 and 2018 across a 4 x 4 km systematic grid (Skudnik et al., 2021a, 2021b). The number of concentric permanent sample plots varied during the observation period (724 in 2007; 760 in 2012; 759 in 2018). Measurements were performed according to established methodology (Kovac et al., 2009; Skudnik et al., 2022). Deadwood was categorized into five types: standing deadwood, lying deadwood, stumps, snags and coarse woody debris. Standing deadwood consists of standing dead trees that retain at least parts of their crown. Their volume is calculated in the same way as the volume of living trees. Snags are broken trees without a crown, and their volume is calculated as a wood cylinder. Stumps represent the remains of cut trees with a height lower than 50 cm. Stumps taller than this threshold are classified as snags. Lying deadwood includes dead, uprooted or broken trees on the ground, retaining parts of their crown. Their volume is calculated in the same way as the volume of living trees. Coarse woody debris refers to deadwood fragments lying on the ground. All deadwood types must have a minimum diameter of 10 cm, measured at breast height (1.3 m above ground) for snags and standing trees, and at the larger end for lying deadwood (Kovac et al., 2009; Skudnik et al., 2022).

2.2 Analysis of deadwood dynamics
2.2 Analiza dinamike odmrlega lesa

Forest monitoring data provide deadwood measurements for the years 2007, 2012 and 2018. For our analysis, we selected only those plots in which deadwood measurements were recorded in all three sampling years. Given that individual pieces of deadwood are not marked and their locations are not recorded, tracking changes of single deadwood pieces over time, as is feasible for live trees using a permanent plot design, is not possible (Eastaugh and Hasenauer, 2013; Battipaglia et al., 2020). Here, we propose a method to assess changes in deadwood volume using input-output relationships (mass balance approach) and comparing deadwood gains and losses (Eq. 1). Deadwood gain is new tree mortality and deadwood loss is due to decay or removal. Since gains and losses are equal to or greater 0, changes in deadwood volume can be both positive and negative.

$$\text{change} = \text{gains} - \text{losses} \quad (1)$$

$$\text{change} = \text{deadwood } 2012/2018 - \text{deadwood } 2007/2012 \quad (2)$$

$$\text{losses} = (\text{gains} - \text{change})/\text{period length} \quad (3)$$

When the change in deadwood volume is positive (gains > losses), this indicates an increase in deadwood volume. Conversely, a negative change signifies that losses exceed gains, leading to a decrease in deadwood volume. Although NFI data do not allow for direct quantification of losses, gains can be quantified using tree mortality records from the NFI (i.e., trees that have died and were not removed). Changes in deadwood volumes between two consecutive inventory periods (2012 vs. 2018, 2007 vs. 2012) can also be assessed. By subtracting the calculated gains from the total change, we can estimate deadwood losses in m^3/ha/year, accounting for period lengths of 6 (2012-2018) and 5 years (2007-2012) (Eq. 3). We used both sampling periods in this analysis. We grouped plots according to the dominant tree species, which is the tree species contributing most to basal area, excluding tree species represented in less than 10 plots. For post-stratification, ecoregion geospatial datasets (Kutnar et al., 2002), representing different climatic and edaphic conditions, were used. All analyses were performed using Microsoft Office 365 and R Statistical software (R ..., 2021).

3 RESULTS
3 REZULTATI
3.1 Regional variations of deadwood components in Slovenian forests
3.1 Regionalne razlike v tipih odmrlega lesa v slovenskih gozdovih

Deadwood volume varies greatly across Slovenian forests, with higher values observed in the Alpine and Dinaric regions (Table 1). A comparison of deadwood volume with live volume (growing stock) reveals that the Alpine and in the Sub-Mediterranean regions have deadwood volumes accounting for about 8% of live

Table 1: Results for live tree volume and deadwood volume, including mean, standard deviation (SD), interquartile range (IQR), and the number of plots with deadwood measurements (N) available from the Large-scale Monitoring of Forests and Forest Ecosystems (FFECS), grouped by ecoregions (Kutnar et al., 2002). All plots measured from 2007 to 2018 were included in the analysis. We calculated the ratio of live to dead volume as percentages.

Preglednica 1: Rezultati lesne zaloge živih dreves in odmrlega lesa, srednja vrednost, standardni odklon (SD), interkvartilni razpon (IQR) in število ploskev z meritvami odmrlega lesa (N) na ploskvah Monitoringa gozdov in gozdnih ekosistemov (MGGE), razdeljenih po ekoregijah (Kutnar et al., 2002). Vse ploskve, merjene v obdobju od 2007 do 2018, so bile vključene v analizo. Razmerje med živo lesno biomaso in odmrlim lesom je izražen v %.

Ecoregion	Name	Mean live volume	SD live volume	IQR live volume	Mean dead volume	SD dead volume	IQR dead volume	Ratio dead:live	N
1	Alpine	377	224	278	28	39	32	8%	407
2	Pohorje	479	201	213	22	23	19	5%	150
3	Prepannonian	316	164	183	17	26	17	5%	286
4	Prealpine	337	183	237	18	27	18	5%	373
5	Predinaric	314	157	206	20	23	28	6%	295
6	Dinaric	342	158	222	25	36	24	7%	465
7	Sub-Mediterranean	202	126	179	16	25	19	8%	267

volume, exceeding the target value of 3% (Pravilnik o varstvu gozdov, 2009). This finding suggests that higher live volume does not necessarily correlate with higher deadwood volume. For instance, the Pohorje region, which recorded the highest mean live volume of 479 m^3/ha, ranked third in terms of mean deadwood volume at 22 m^3/ha. Notably, the warmest and driest region, the Sub-Mediterranean region, recorded the lowest stocks of both live and deadwood.

Deadwood volume is highly skewed across all deadwood categories, encompassing both vertical objects such as standing deadwood, snags and stumps, as well as horizontal forms such as lying deadwood and coarse woody debris (Fig. 1). On average, standing dead trees contribute the most to the total deadwood volume, followed by lying deadwood and coarse woody debris. While snags and stumps make important contributions, they account for smaller proportions of the total deadwood volume. Notably, many plots report no deadwood volume across all categories, resulting in a median volume of 0 m^3/ha for all deadwood categories except coarse woody debris. This underscores the heterogenous distribution of deadwood and the sensitivity of reported mean deadwood volumes to single plot observations with large deadwood volumes.

3.2 Deadwood dynamics and the role of tree species

3.2 Dinamika odmrlega lesa in vpliv drevesnih vrst

Fig. 2 illustrates the changes in deadwood volume from 2007 to 2018, confirming national reporting on an increasing deadwood volume over this period (Skudnik et al., 2021b). There was little change in average deadwood volume between 2007 (mean 20.2 m^3/ha, median 11.4 m^3/ha) and 2012 (mean 19.8 m^3/ha, median 10.2 m^3/ha), despite the continuous contribution of new deadwood through mortality (see Table 2, Skudnik et al., 2021a). A notable increase in both median and arithmetic mean deadwood volumes was observed from 2012 to 2018 (mean 24.2 m^3/ha, median 13.6 m^3/ha), suggesting a robust increase in deadwood volume.

Using Equations 1-3, we then estimated deadwood losses from changes in deadwood volumes between consecutive measurements and deadwood gains from new tree mortality. We identified 12 tree species with at least 15 observations each, including many widespread Central European tree species. For all tree species except *Robinia pseudoacacia* and *Acer pseudoplatanus*, deadwood volume increased over time (change > 0). Losses (gains minus change) in m^3/ha/year were largest for *Carpinus betulus*, followed by *Acer pseudoplatanus* and *Picea abies.* The lowest losses in m^3/ha/year were observed for *Pinus sylvestris* and *Ostrya carpinifolia*, with the former known for its durable heartwood (Lesar et al., 2008). When accounting for differences in deadwood volume and expressing losses in percent loss per year, our results suggest the fastest decomposition rates for *Carpinus betulus*, followed by *Robinia pseudoacacia* and *Acer pseudoplatanus* Forest dominated by *Picea abies* have 30% lower deadwood stocks than those dominated by *Fagus sylvatica*, and 55% lower losses in m^3/ha/year, but only 20% lower when expressed as losses in %/year.

Differences in deadwood losses due to decay can be also caused by differences in growing stock and deadwood volume, as higher forest productivity may result in more examined potential patterns between live volume and deadwood volume for the 12 tree spe-

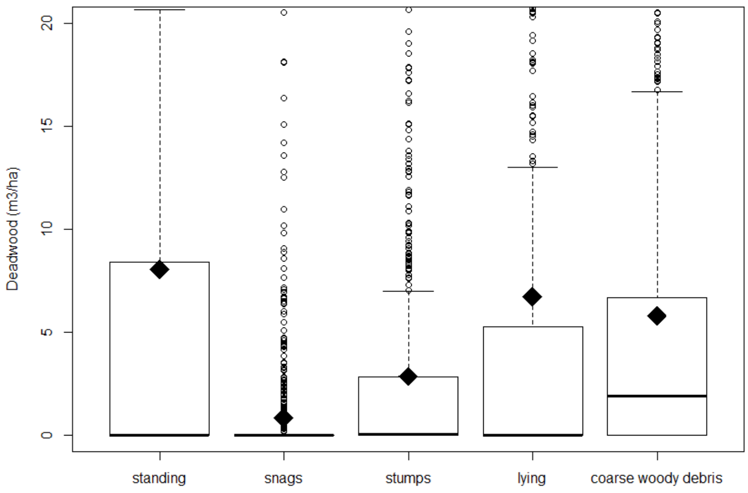

Fig. 1: Deadwood categories assessed by FFECS in 2018. The box represents the median and the 25th and 75th percentiles, the diamond denotes the arithmetic mean, the whiskers extend to 1.5 of the interquartile range and values outside this range are indicated by circles. For clarity, only values up to 20 m^3/ha are displayed, but larger values are included in the boxplots.

Slika 1: Tipi odmrlega lesa, ocenjeni na ploskvah MGGE v letu 2018. Okvir (pravokotnik) ponazarja mediano in 25. ter 75. percentil, diamant prikazuje aritmetično sredino, ročaji segajo do 1,5 interkvartilnega ranga, vrednosti zunaj tega ranga so označene s krogci. Zaradi jasnosti so prikazane samo vrednosti do 20 m^3/ha, višje vrednosti pa so vključene v okvir (pravokotnik).

cies (Fig. 3). A higher live volume was associated with greater deadwood volume, and this relationship was significant ($p < 0.001$, coefficient of determination R^2 0.708). Additionally, a higher deadwood volume correlated with higher deadwood losses, although this relationship was weaker and not statistically significant (p 0.346, R^2 0.089). The relationship between losses as a percentage per year and deadwood volume (not shown) was also not significant.

4 DISCUSSION

4 RAZPRAVA

4.1 Deadwood assessment based on national forest inventory data

4.1 Ocena odmrlega lesa na podlagi podatkov nacionalne gozdne inventure

In national forest inventories, the location of all trees measured on permanent sampling plots is typically known, enabling accurate determination of the status of

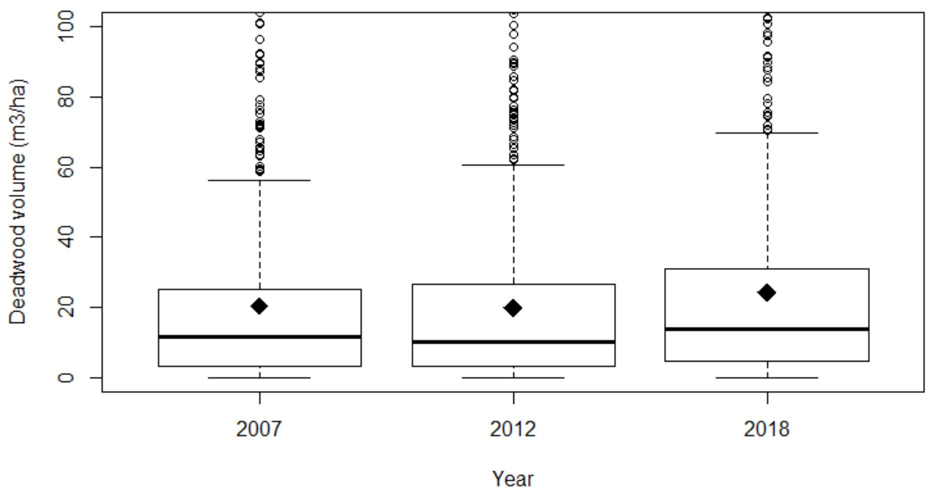

Fig. 2: Changes in deadwood volume from 2007 to 2018. For boxplot details, see the explanation for Fig. 1.

Slika 2: Spremembe v volumnu odmrlega lesa v obdobju 2007–2018. Za razlago simbolike grafikonov glej sliko 1.

Table 2: Deadwood dynamics estimated using a mass-balance approach, grouped by dominant species. The species listed represent the dominant species at the second measurement. 'N' indicates the number of observations (plots measured two times). The last column shows losses relative to deadwood volume at time 1.

Preglednica 2: Ocena dinamike sprememb odmrlega lesa z uporabo bilančne metode, razdeljene po dominantnih drevesnih vrstah. Naštete drevesne vrste predstavljajo dominantno drevesno vrtno na ploskvi pri drugi meritvi. 'N' je število opazovanj (ploskve izmerjene dvakrat). Zadnji stolpec prikazuje izgubo glede na volumen odmrlega lesa v času prve meritve.

Species	N	Deadwood 1 (m^3/ha)	Deadwood 2 (m^3/ha)	Change (m^3/ha/year)	Gains (m^3/ha/year)	Losses (m^3/ha/year)	Losses (%/year)
Fagus sylvatica	505	24.5	25.0	0.11	1.87	1.77	7.2
Picea abies	367	18.9	21.5	0.47	1.60	1.14	6.0
Abies alba	85	29.6	30.1	0.09	0.66	0.57	1.9
Pinus sylvestris	75	12.5	22.8	1.87	2.03	0.16	1.3
Quercus petraea	68	20.5	22.7	0.41	1.45	1.05	5.1
Carpinus betulus	54	18.7	18.9	0.03	2.53	2.50	13.4
Acer pseudoplatanus	35	17.9	16.0	-0.34	1.46	1.80	10.1
Ostrya carpinifolia	35	12.6	17.4	0.88	0.95	0.07	0.6
Pinus nigra	32	11.9	13.1	0.23	1.08	0.85	7.1
Castanea sativa	29	19.3	28.2	1.61	2.67	1.05	5.5
Quercus cerris	24	10.2	12.9	0.49	1.14	0.64	6.3
Robinia pseudoacacia	15	13.9	8.6	-0.97	0.47	1.44	10.4

a tree of interest in two consecutive measurements with the following possible outcomes: a new tree (ingrowth), a dead tree (mortality), a felled tree (removal) and a tree that is still alive and present in both measurements (survivor). Using the classical form of the control sampling method, we can calculate states and changes. However, assessing deadwood presents a challenge because the precise location and associated identification of each piece of deadwood cannot always be accurately determined. Consequently, we cannot observe the dynamics at the level of individual deadwood pieces but can monitor the sampling plot values for different deadwood types. Such estimates of deadwood dynamics provide less detailed information than estimates of the dynamics of live trees (growing stock, increment, fellings, growth, mortality). The "mass balance approach" method, using-input output relations employed in this study, allows for the calculation of net changes in deadwood and can be applied to other forest inventory systems measuring deadwood (Tomppo et al., 2010; Rondeux et al., 2012). Despite the obvious methodological constraints, such as the correct identification of tree species or classification of deadwood types, the mass balance approach can still offer valuable insights into deadwood dynamics.

4.2 Deadwood quantity and regional distribution

4.2 Količina odmrlega lesa in njena regionalna porazdelitev

The variation in deadwood volume across Slovenian forests is considerable, ranging on average from 16 m^3/ha in the Sub-Mediterranean region to 28 m^3/ha in the Alpine region. The largest stocks of living trees are in the Pohorje (average 479 m^3/ha) and Alpine (average 377 m^3/ha) regions, and the lowest are in the Sub-Mediterranean region (average 202 m^3/ha). Available literature on montane beech/mixed beech-fir-spruce forest reserves in Slovenia reports live volumes ranging from 525 to 813 m^3/ha and deadwood volumes from 92 to 552 m^3/ha (Christensen et al., 2005). In the "Rajhenav" virgin fir-beech forest remnant, the live volume was 799 m^3/ha and the deadwood volume was 138 m^3/ha (Boncina, 2000). Notably, in our study, the ratio of dead to living biomass is highest in the Alpine and Sub-Mediterranean regions (8%) and lowest at 5% in the Pohorje region. This indicates that, contrary to expectations, a higher live volume does not necessarily correlate with a higher deadwood volume. A similar result was also observed in Austrian forest reserves (Oettel et al., 2020). According to the Slovenia Forest Service's 2022 estimates (Poročilo Zavoda za gozdove ..., 2023), the average deadwood volume is 21.3 m^3/ha (excluding stumps and branches), and the ratio of dead to live biomass is 7%. The highest deadwood volumes are found in the Bled forest management region (Alpine region), at 39.7 m^3/ha (9.6%), and in Tolmin (Alpine and Dinaric regions), at 31.9 m^3/ha (13.1%). The lowest values are in Sežana (Sub-Mediterranean region) at 14.5 m^3/ha (8.7%), Maribor (Pohorje and Prepanonian region) at 14.3 m^3/ha (3.9%), Kočevje (Dinaric region) at 14

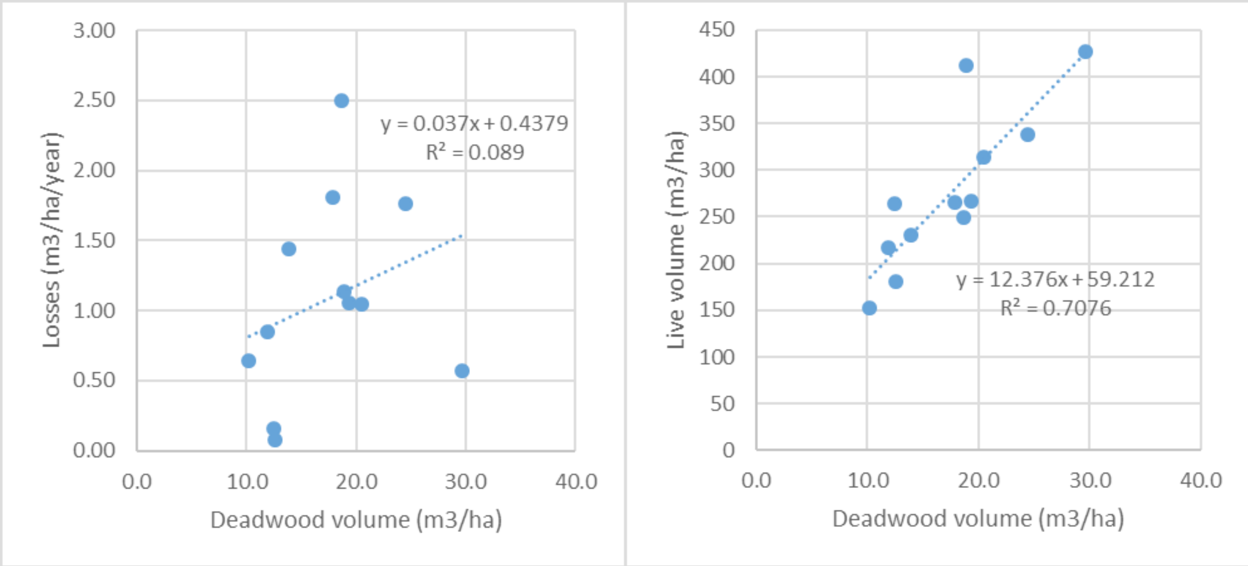

Fig. 3: Relationship between deadwood volume and deadwood loses (left) and relationship between deadwood volume and live volume (right). Linear trend functions were added to illustrate the respective relationships.

Slika 3: Razmerje med volumnom odmrlega lesa in izgubami odmrlega lesa (levo) in razmerje med volumnom odmrlega lesa in volumnom žive lesne biomase po drevesnih vrstah (desno). Funkciji linearnega trenda sta bili dodani za prikaz razmerja.

m^3/ha (4.2%) and Slovenj Gradec (Pohorje region) at 13.6 m^3/ha (3.6%). In Austrian forest reserves, without active forest management, more productive stands generate more live wood and deadwood, yet the ratio between live and dead wood remained relatively constant. Including management information is expected to help distinguish the effects of productivity from those of management. Regional differences in deadwood accumulation are also likely driven by variations in annual mean temperature, mainly due to elevation, with temperature being a strong driver of deadwood decay (Harmon et al., 2020). Moreover, more productive forests may experience higher temperatures and increased rainfall, which in turn can accelerate deadwood decomposition.

4.3 Deadwood structure

4.3 Struktura odmrlega lesa

Standing dead trees account for the largest portion of the total deadwood volume (33%), followed by lying deadwood (28%) and coarse woody debris (24%). Stumps (12%) and snags (3%) contribute smaller but important shares. Nevertheless, numerous plots – and consequently forest stands – have no measurable deadwood volume in certain components. For example, the median value for all deadwood components, excluding coarse woody debris, is 0 m^3/ha. This fact highlights the heterogeneous spatial distribution of deadwood in forests (particularly with regard to entire standing and lying dead trees) and illustrates the sensitivity of reported mean deadwood volumes to observations in plots with substantial deadwood. Strategies to address this heterogeneity and the large variation in deadwood include (1) increasing the number of observations (plots), (2) enlarging the sample area per plot and/or (3) integrating other monitoring systems, such as aerial and terrestrial remote sensing (e.g. Marchi et al., 2018; Sebald et al., 2021). Inventory systems that represent both deadwood-rich and deadwood-poor parts of forests in an unbiased way are imperative for the accurate and reliable monitoring of deadwood.

4.4 Role of natural disturbances and tree species on deadwood dynamics

4.4 Vpliv naravnih motenj in drevesnih vrst na dinamiko odmrlega lesa

Deadwood dynamics are influenced by various factors, including tree species, decomposition rates, ownership, forest types and forest management practices (Vítková et al., 2018; Harmon et al., 2020; Oettel et al., 2022). In Slovenia, despite a continuous influx of new deadwood due to mortality, the average deadwood volume remained largely constant between 2007 and 2012, and mean deadwood volume even decreased by 0.4 m^3/ha over five years. However, an increase in both the median and arithmetic mean deadwood volumes was observed between 2012 and 2018. This rise was largely attributable to natural disturbances, such as the 2014 ice storm, bark beetle outbreaks from 2015 to 2017 and windthrow events in 2017.

For all analyzed tree species, except for *Robinia pseudoacacia* and *Acer pseudoplatanus*, the volume of deadwood increased over time. The largest losses were recorded for *Carpinus betulus*, *Acer pseudoplatanus* and *Fagus sylvatica*, while *Pinus sylvestris* and *Ostrya carpinifolia*, known for their durable heartwood, exhibited the smallest losses (Lesar et al., 2008). The initial volume of deadwood and its stage of decay are important for understanding differences in deadwood losses, as greater exposure to decomposition agents leads to increased mass loss. Our results indicate that the decomposition rate of *Fagus sylvatica* (loss 7.2%/year) is 20% faster than that of *Picea abies* (6.0%/year), despite the larger wood density of *Fagus sylvatica*. This is presumably due to the susceptibility of beech wood to decomposing insects and fungi (Kahl et al., 2017; Herrmann and Bauhus, 2018). It is important to note that differences in deadwood decay stages may explain variations in deadwood loss, as deadwood in more advanced stages of decay is more likely to collapse and thus become unmeasurable using transects and sample plots.

Our study revealed a significant positive correlation between live volume and deadwood volume, suggesting that higher productivity may contribute to higher deadwood stocks. However, regional differences, possibly due to management practices, do exist. The correlation between deadwood volume and deadwood losses is weak and non-significant when using relative losses in percent per year. This indicates that deadwood volume (without information on species, decay stage and management status) is a poor indicator of deadwood losses, as both deadwood volume and resistance of wood to decay determine the amount of deadwood loss.

Deadwood losses can occur through decomposition (mineralization or fragmentation) or the collection of deadwood for fuel (i.e., salvage logging). Deadwood is often collected as fuel until it reaches a certain stage of decomposition; once it is well decayed, it is left in the forest. Given that 77% of Slovenian forests are privately owned, often in small holdings, the majority of forest owners in Slovenia do not actively engage in forest management (Slovenia Forest Service, 2023). This suggests that forest ownership could be a key factor in explaining the observed variations in deadwood volume, through differences in fuelwood collection practices. For instance, forests that are actively managed for sawlog production are likely to accumulate little large-sized deadwood but may have substantial pools of harvest residues and small-sized timber, especially when thinning material is left on the site. Conversely, forests where fuelwood collection is practiced may exhibit deadwood loss even after disturbance events have occurred and deadwood has been measured by a forest inventory.

5 CONCLUSIONS

5 ZAKLJUČKI

We present here insights into deadwood dynamics using national forest inventory data. Despite the large variation in deadwood volume, the complexities of deadwood decomposition and methodological constraints, key information can still be derived from forest inventories employing permanent plot designs. At an average deadwood loss rate of 1 m^3/ha/year, approximately 10 years would be required for 10 m^3/ha of deadwood to decompose completely (a 100% loss), assuming that decay is linear and proportional to initial volume. With an observed average deadwood volume loss of 6% per year, assuming linear decay, 60% of the initial volume would be lost after a certain period ($V_{i+1}=V_i\,(1\text{-}k)$), whereas exponential decay would result in a 50% loss ($V_{i+1}=V_i\,e^{-kt}$), where k is the loss rate in %/year and V_i is the deadwood volume at time i. Further research should explore the non-linearity of deadwood decay and quantify carbon stored in forest soil as organic carbon from deadwood. The species-specific decomposition patterns identified in this study could be further verified with *in-situ* and/or laboratory decay experiments. Developing a reliable and robust decay class system (e.g. AnnMüller-Using and Bartsch, 2009; Tobin et al., 2021; Neumann et al., 2023a) can aid in quantifying mass and density losses in deadwood and thereby complement such decay experiments.

6 SUMMARY

6 POVZETEK

Namen članka je na podlagi podatkov slovenske nacionalne gozdne inventure (NGI) prikazati količinske in strukturne značilnosti odmrlega lesa v slovenskih gozdovih v letih 2007, 2012 in 2018 ter raziskati drevesno vrstno specifično dinamiko odmrlega lesa slovenskih gozdov v letih 2007–2018 z bilančno metodo (vnosi, iznosi).

Odmrl les je pomemben kazalec trajnostnega gospodarjenja z gozdovi in ekosistemskih storitev gozdov. Je indikator biodiverzitete in ključni habitat za različne specialistične vrste. Je tudi eno od petih skladišč ogljika (nadzemna lesna biomasa, podzemna lesna biomasa, odmrli les, opad in tla), o katerih so države obvezne poročati v sektorju LULUCF. Odmrl les ima lahko tudi ekonomsko vrednost kot vir biomase za energetske namene (npr. drevesni panji). Za različne ekosistemske storitve pa ni pomembna samo količina, marveč tudi struktura odmrlega lesa (tip, dimenzije, drevesne vrste) in stopnja razkrojenosti. Stopnja razkrojenosti je pomembna zaradi povezave z gostoto lesa in vsebnostjo ogljika, ki se s stopnjo razkrojenosti

manjša. Količina odmrlega lesa v gozdovih je odvisna od različnih dejavnikov, vključno z lastništvom gozda, gozdnim tipom, produktivnostjo, drevesno vrstno sestavo, načinom gospodarjenja, starostjo sestoja, mortaliteto ali hitrostjo razkroja. Količina odmrlega lesa v gozdu se dinamično spreminja. Drevesa z odmiranjem povečujejo količine odmrlega lesa. Količina odmrlega lesa se zmanjšuje z odstranjevanjem iz gozda (npr. sanitarna sečnja sušic) in razkrojem/razpadom. Hitrost razkroja odmrlega lesa je odvisna od velikosti kosa, njegove oblike, drevesne vrste, podnebnih razmer, stika s tlemi in razširjenosti gozdne favne. Nekatere drevesne vrste imajo odpornejši les zaradi črnjave, ki je odporna proti razpadanju, in/ali pojavljanja drugih počasneje razgradljivih snovi v lesu (npr. hrast graden, rdeči bor ali robinija), les drugih vrst (npr. bukev ali jelka) pa se hitreje razkraja in propada. Brez večjih naravnih motenj v gozdu količina odmrlega lesa sčasoma doseže stabilno stanje.

Vsi podatki, uporabljeni v tej raziskavi, so iz podatkovne baze slovenske NGI, zbranih na trajnih vzorčnih ploskvah v letih 2007, 2012 in 2018 na sistematični vzorčni mreži 4 x 4 km. Odmrl les je razdeljen na pet tipov: stoječi odmrl les (sušice), ležeči odmrl les (podrtice), panji (štori), štrclji in večji lesni kosi. Za primerjavo sprememb odmrlega lesa smo uporabili bilančno metodo in primerjali vnose in iznose odmrlega lesa.

K vnosu odmrlega lesa prištevamo povečanje zaradi mortalitete dreves, k iznosu odmrlega lesa pa zmanjšanje zaradi razkroja ali odstranitve. Takšne ocene sprememb količine odmrlega lesa so sicer manj zanesljive, kot npr. ocene sprememb na drevesni ravni, kjer lahko za vsako inventarizirano drevo ocenimo volumen, prirastek, posek, rast in mortaliteto. Bilančna metoda z uporabo vnosov in iznosov, ki se uporablja v tej študiji, omogoča izračun neto sprememb količine odmrlega lesa in jo je mogoče uporabiti tudi pri drugih inventarizacijah odmrlega lesa. Kljub metodološkim omejitvam, kot je npr. nezanesljiva identifikacija drevesne vrste pri bolj razkrojenih kosih, bilančna metoda omogoča dober vpogled v dinamiko odmrlega lesa. Ker so vnosi in iznosi lahko enaki ali večji od 0, so lahko spremembe pozitivne in negativne. Kadar je sprememba pozitivna (vnosi > iznosi), se količina odmrlega lesa na trajni vzorčni ploskvi povečuje. Kadar je sprememba negativna, pa iznosi presegajo vnose in količina odmrlega lesa se zmanjšuje. Medtem ko na ravni trajnih vzorčnih ploskve ne moremo količinsko opredeliti iznosov, lahko količinsko opredelimo vnose z uporabo podatka o mortaliteti dreves. Gre za drevesa, ki so v zadnjem inventurnem obdobju odmrla in niso bila odstranjena s površine trajne vzorčne ploskve. Dinamiko odmrlega lesa smo dobili s primerjavo količin odmrlega lesa med dvema zaporednima obdobjema nacionalne gozdne inventure (2012–2018, 2007–2012). Če odštejemo vnose od iznosov, lahko ocenimo zmanjšanje odmrlega lesa v m^3/ha/leto, pri čemer ustrezno upoštevamo inventurni periodi 6 (2012–2018) oziroma 5 let (2007–2012). Za potrebe analize po drevesnih vrstah smo trajne vzorčne ploskve združili glede na prevladujočo drevesno vrsto v temeljnici. Drevesnih vrste, ki se pojavljajo na manj kot 10 trajnih vzorčnih ploskvah, nismo upoštevali v analizi. Za poststratifikacijo smo uporabili razdelitev na ekoregije, ki se razlikujejo glede na klimatske in rastiščne razmere.

Lesna zaloga v slovenskih gozdovih se je od leta 2012 do 2018 v povprečju zmanjšala s 333,9 na 329,6 m^3/ha, količina odmrlega lesa pa se je v istem času povečala z 19,8 na 24,2 m^3/ha. Variabilnost količine odmrlega lesa v slovenskih gozdovih je velika, vrednosti se gibljejo od povprečno 16 m^3/ha v Submediteranski regiji do povprečno 28 m^3/ha v Alpski regiji. Največja lesna zaloga je v Pohorski (povprečno 479 m^3/ha) in Alpski (povprečno 377 m^3/ha) regiji, najmanjša pa v Submediteranski regiji (povprečno 202 m^3/ha). Primerjava volumna odmrlega lesa z lesno zalogo pokaže, da je v Alpskem in Submediteranskem območju količina odmrlega lesa okoli 8 % lesne zaloge. To nakazuje, da višja lesna zaloga ni nujno povezana z višjo količino odmrlega lesa, saj je bila na Pohorju zabeležena največja povprečna lesna zaloga s 479 m^3/ha, s povprečno količino odmrlega lesa 22 m^3/ha pa je bila ta regija tretja glede na količino odmrlega lesa. Omeniti velja, da je imela Submediteranska regija, ki je najtoplejša in najbolj suha, najmanjšo lesno zalogo in količino odmrlega lesa. Regionalne razlike v akumulaciji odmrlega lesa so lahko odsev spremenljivih letnih povprečnih temperature predvsem zaradi nadmorske višine, saj temperatura vpliva na hitrost razkroja odmrlega lesa. Gozdovi so lahko produktivnejši zaradi višjih temperatur in več padavin, kar lahko posledično poveča razgradnjo odmrlega lesa v njih.

K skupni količini odmrlega lesa največ prispevajo stoječa odmrla drevesa s 33 %, sledijo ležeča odmrla drevesa (28 %) in večji lesni kosi (24 %). Pomemben, a majhen delež skupne količine odmrlega lesa imajo panji (12 %) in štrclji (3 %). Na mnogih trajnih vzorčnih ploskvah ni bilo odkritega odmrlega lesa, kar potrjuje heterogenost njegove porazdelitve v prostoru in posledično nezanesljivost statistične ocene. Zanesljivost ocene lahko izboljšamo s (1) povečanjem števila opazovanj (trajnih vzorčnih ploskev), (2) povečanjem vzorčne površine na ploskev in/ali (3) kombinacijami z drugimi sistemi spremljanja, vključno s tehnikami daljinskega zaznavanja. Za natančno in zanesljivo spremljanje količine odmrlega lesa je nujna uporaba inventurne metode, ki nepristransko upošteva z odmrlim lesom bogate in revne dele gozdov.

Povprečna količina odmrlega lesa se je med letoma 2007 (povprečje 20,2 m^3/ha, mediana 11,4 m^3/ha) in 2012 (povprečje 19,8 m^3/ha, mediana 10,2 m^3/ha) kljub stalnemu vnosu novega odmrlega lesa prek mortalitete le malo spremenila. Tako mediana kot aritmetična sredina sta se od leta 2012 do 2018 povečali (povprečje 24,2 m^3/ha, mediana 13,6 m^3/ha), kar kaže na močno povečanje količine odmrlega lesa v tem obdobju. Slovenske gozdove so v zadnjem desetletju večkrat prizadele naravne ujme, vključno z žledolomom (2014), vetrolomom (2017–2018) in podlubniki (2015–2018), predvsem v gorskih in nižinskih predelih. Pri vseh drevesnih vrstah, z izjemo robinije in gorskega javorja, se je količina odmrlega lesa sčasoma povečala (sprememba > 0). Iznosi (vnos minus spremembe) v m^3/ha/leto so bili največji pri belem gabru, sledita gorski javor in navadna jelka. Najmanjši iznosi v m^3/ha/leto so bili opaženi pri rdečem boru in črnem gabru. Če upoštevamo razlike v količini odmrlega lesa in izrazimo iznose v odstotkih iznosov na leto, rezultati kažejo na najhitrejšo razgradnjo belega gabra, sledita robinija in gorski javor. Gozdovi, v katerih prevladuje smreka, imajo 30 % nižje količine odmrlega lesa kot bukovi gozdovi in 55 % manjše iznose v m^3/ha/leto, vendar le 20 % manjše iznose v %/leto. Začetna količina odmrlega lesa in njegova stopnja razkrojenosti sta pomembni za razumevanje razlik v iznosih odmrlega lesa, saj več odmrlega lesa, izpostavljenega razgradnji, povzroči večje zmanjšanje. Naši rezultati kažejo, da je razkrojenost bukve (izguba 7,2 %/leto) za 20 % hitrejša kot pri smreki (6,0 %/leto), kljub večji gostoti bukovega lesa. To je verjetno posledica večje občutljivosti bukovega lesa za razkrojne žuželke in glive. Ugotavljamo, da lahko stopnje razkrojenosti odmrlega lesa pojasnijo razlike v iznosih odmrlega lesa, saj obstaja večja verjetnost, da bo bolj razkrojen odmrl les prej postal nemerljiv s transekti in vzorčnimi ploskvami.

Razlike v iznosih odmrlega lesa zaradi razpadanja lahko povzročijo tudi razlike v lesni zalogi in količini odmrlega lesa, saj lahko večja produktivnost gozda povzroči več odmrlega lesa in je več odmrlega lesa izpostavljenega organizmom, ki razgrajujejo les. Tako smo preverili, ali obstajajo značilnosti povezane z lesno zalogo in količino odmrlega lesa za 12 drevesnih vrst. Večja lesna zaloga je povezana z več odmrlega lesa in ta povezava je značilna ($p < 0,001$, koeficient determinacije R^2 0,708). Večja količina odmrlega lesa je povezana tudi z večjimi izgubami odmrlega lesa, čeprav je bilo razmerje šibkejše in statistično neznačilno (p 0,346, R^2 0,089). Razmerje med iznosi v odstotkih na leto in količino odmrlega lesa ni bilo statistično značilno.

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