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River distance, stand basal area, and climatic conditions are the main drivers influencing lying deadwood in riparian forests

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ABSTRACT

Riparian forests are among the most diverse terrestrial ecosystems, yet their biodiversity is increasingly threatened by habitat degradation, climate change, river regulation and invasive species. We investigated deadwood, widely recognized as an indicator for forest biodiversity, in riparian forests of the Mura-Drava-Danube Transboundary Biosphere Reserve. The Biosphere Reserve is a conservation area that spans five countries and three rivers located in south-eastern Europe. In detail, we analyzed the drivers of lying deadwood volume, occurrence and decay related to floodplain type, silvicultural management, and climatic conditions using regression models. Lying deadwood occurrence and volume significantly decreased as distance from the river edge increased, indicating that river dynamics likely play a role in deadwood accumulation in riparian forests. Deadwood volume was also positively influenced by stand basal area, a parameter that can be directly addressed by silvicultural management. Deadwood decay was affected positively by temperature and negatively by precipitation, highlighting the importance of climatic conditions on decay progression. However, in order to draw more accurate conclusions about the drivers and dynamics of deadwood in riparian forests, further monitoring efforts that consider river flooding and flow regime, deadwood transport and saproxylic organism activity in addition to forest management and site conditions, are needed.

1. Introduction

Riparian forests are among the most biodiverse terrestrial ecosystems as well as among the most endangered ones (Richardson et al. 2007; Ellison et al. 2017). These extra-zonal forests have evolved in response to proximity to rivers and in response to river and sediment dynamics, among other factors. They can underlie highly dynamic hydrologic and sediment regimes rapidly responding to changes in environmental conditions at different scales (Decamps 1996; Tabacchi et al. 1998). In addition, riparian areas provide numerous ecosystem services, such as exceptionally high carbon sequestration and water regulation (Dixon et al. 2019). Periodic water supply is a key process for biological exchange, soil moisture, organic matter, dispersal of species, nutrient distribution and deadwood mobilization (Gurnell et al. 1995). Given these conditions and their large share of terrestrial biodiversity, many riparian forests in Europe are thus part of protected areas.

Deadwood contributes to ecosystem functioning and forest fluxes by improving microclimate and increasing nutrient availability (Maser and Trappe 1984; Franklin et al. 2006). Around 20 to 25% of forest-dwelling species are dependent on deadwood, a finding that applies to both temperate and boreal forests in Europe (Siitonen 2001; Grove 2002; Dodelin 2010). Deadwood provides essential resources for saproxylic (deadwood-dependent) species like wood-decaying fungi, arthropods, bryophytes, lichens, birds and bats (e.g. Lassauce et al. 2011; Dittrich et al. 2014; Shorohova and Kapitsa 2014; Rimle et al. 2017). Given its immense biodiversity value, deadwood has received considerable

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attention from researchers and forest managers in recent decades, with some having investigated deadwood quantity and dynamics in riparian forest regions worldwide (e.g. Keeton et al. 2007; Holmes et al. 2010; Pollock and Beechie 2014).

Occurrence, volume, and decay of deadwood in riparian ecosystems are influenced by river and flood dynamics as well as forest management. Deadwood occurrence and volume is generally higher in unmanaged forests than in managed forests, as known from other forest types. Dahlström and Nilsson (2006) provide deadwood volumes of 27 and 68 m^{3}ha^{-1} for managed and unmanaged Swedish riparian forests. Lombardi et al. (2008) as well as Oettel et al. (2020) found comparable values in unmanaged forest reserves of Italy (56 m^{3}ha^{-1}) and Austria (51 m^{3}ha^{-1}), respectively. Slightly lower values (25 to 43 m^{3}ha^{-1}) were reported by Bujoczek et al. (2018) for unmanaged riparian forest reserves in Poland. In old-growth riparian forests, however, much higher deadwood volumes can be expected, as shown by Bobiec (2002) in Białowieża National Park (126 to 160 m^{3}ha^{-1}).

Sources of deadwood along rivers can include mortality and breakage, as well as lateral input from uplands and input from the river channel through flooding and deposition (Harmon et al. 1986). In addition to individual mortality providing a continuous input of deadwood stochastic events such as floods and storms can cause mortality and breakage of riparian trees (Moroni 2006; Harmon 2009) and rapid accumulation of deadwood (Phillips and Park 2009). Previous work shows longer mean residence times (Guyette et al. 2002), while decay rates were faster in river habitats compared to forest habitats (Charles et al. 2022) suggesting somewhat faster decay in floodplain forests through increased humidity.

Although deadwood is of high importance to river functioning (e.g. Harmon et al. 1986; Stokland et al. 2012; Gurnell et al. 2020), and preserving deadwood along rivers has been shown to be particularly important (e.g. Tabacchi and Planty-Tabacchi 2003; Steiger et al. 2005; Keeton et al. 2007), less attention has been paid to deadwood and species composition in riparian forests so far (Tabacchi and Planty-Tabacchi 2003; Lininger et al. 2017; Wohl et al. 2019). To contribute to the understanding of riparian forest dynamics, our study focuses on hardwood and softwood riparian forest types in the Mura-Drava-Danube Transboundary Biosphere Reserve (TBR), the largest riverine protected area in Europe with differing silvicultural management. While bioclimatic conditions (Sallmannshofer et al. 2021) and the role of biotic threats (de Groot et al. 2022) have been studied for the TBR, little information is available on important biodiversity indicators such as deadwood. We aim to elucidate the main drivers of deadwood occurrence, volume and decay in riparian forests of the TBR. Therefore, we address following questions: What are factors that significantly influence (1) occurrence, (2) volume, and (3) decay stage of deadwood in riparian forests as a function of floodplain type, silvicultural management, and climatic conditions? We hypothesize that the occurrence of deadwood is influenced by floodplain type, being higher in proximity to the river and lower with increasing distance. The volume of lying deadwood is expected to be higher in extensively managed forests than in intensively managed forests, and decay processes are likely to be accelerated by moist-warm climatic conditions.

2. Methods

2.1. Study area

The TBR encompasses riparian forest ecosystems in Austria, Slovenia, Hungary, Croatia and Serbia in south-eastern Europe (Fig. 1) and stretches along three major European rivers (Mura, Drava, and Danube). Forests cover about 27% (2250 km^2) of the TBR (in the core zone it is 61%) and the most commonly occurring tree species are pedunculate oak (*Quercus robur* L.), European ash (*Fraxinus excelsior* L.), narrow-leaved ash (*Fraxinus angustifolia* Vahl), black alder (*Alnus glutinosa* (L.) Gaertn), black poplar (*Populus nigra* L.), field elm (*Ulmus laevis* L.), and European white elm (*Ulmus minor* L.) (Sallmannshofer et al. 2021). Based on the flood regime and the presence and abundance of the above-mentioned tree species, two forest types can be distinguished: ‘hardwood floodplain forest’ (FFH-type 91F0) and ‘softwood floodplain forest’ (FFH-type 91E0) (Drescher et al. 2014). Additionally, a ‘transition zone’ between these two types (Nagy 2022) and ‘other’ forest types were differentiated. The latter comprises forests that are not dominated by the above-listed riparian tree species and therefore cannot be assigned to floodplain forests.

The number of sample sites per country was proportional to the area of TBR in the respective country. GIS orthophoto and river edge analysis in QGIS (v. 2.18.16) from Bing satellite images was used to randomly determine 47 forest transects (Austria: 7, Slovenia: 6, Hungary: 11, Croatia: 13, Serbia:10) with their axes orthogonal to the respective river, with a minimum width of 20 m and a minimum length of 300 m (de Groot et al. 2022). If the criteria were not met, transects were re-located up- or down-stream to the closest position meeting the defined criteria. Additionally, extended transects were planned in each of the five

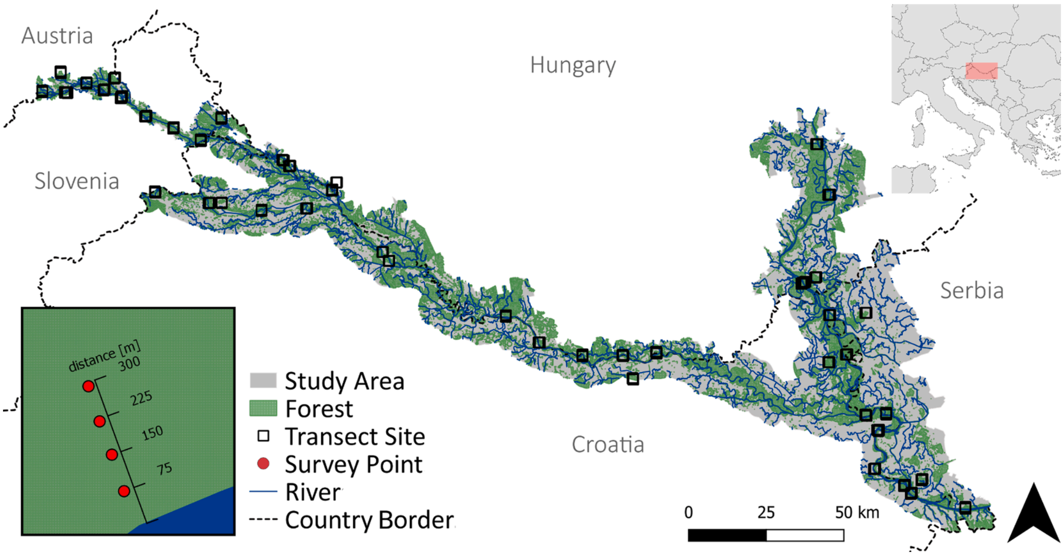

Fig. 1. The Mura-Drava-Danube Transboundary Biosphere Reserve is located in Europe along the rivers Danube, Mura and Drava in Austria, Slovenia, Croatia, Hungary, and Serbia.

countries in order to allow sampling in forests more distant to the rivers. Therefore, eleven of the largest forest complexes extending beyond TBR borders were selected and transects extended for an additional 300 m into these forests to include potential historic riparian forests that may have been cut off from streams over time (de Groot et al. 2022). Sample plots were set up every 75 m along all transects, resulting in 322 sample plots covering a gradient of forest communities which were summarized into softwood, transition and hardwood forests.

2.2. Data sampling

Both, living and dead standing trees were recorded on each sample plot using Bitterlich's angle count sampling method with a fixed angle of sight (1:25, basal area factor of four) to select the trees for assessment (Bitterlich 1948, 1984). Lying deadwood was sampled using the line intersect method developed by Warren and Olsen (1964) and improved by Van Wagner (1968). From the center of each sample plot two intersect lines of 37.5 m were placed along the transect. Every piece of dead wood with a minimum diameter of 70 mm crossing the intersect line was measured. The respective tree species, diameter at point of intersection (mm), length (cm) and dominant stage of decay were recorded. Decay stages were distinguished in four categories from (1) recent to (4) decomposed (see Table 1) using an adapted version of the Swiss National Forest Inventory method (Keller et al. 2013). Accordingly, decay stages were classified using a "knife test", which estimates the dominant stage of decay based on how easy a blade enters deadwood. The following four classes were distinguished: (1) recent – recently died tree, blade does not easily enter wood; (2) ongoing – blade easily enters wood in fiber direction, but not against it; (3) progressed – blade easily enters wood in and against fiber direction, wood structure is still remaining; (4) decomposed – blade easily enters wood in and against fiber direction, wood structure is barely recognizable.

At each sample plot the floodplain type was categorized as: softwood, or hardwood floodplain forest, transition zone, or other forest

Table 1

Dependent and independent variables used for the models of the occurrence, volume and decay stages of lying deadwood in the case study area of the Mura-Drava-Danube Transboundary Biosphere Reserve.

Variable		Acronym	Unit	Classification	Range/categories	Description
dependent variables						
deadwood occurrence		occ	–	categorical	(0) no deadwood (1) deadwood	binary variable for deadwood occurrence per sample plot
deadwood volume		vol	m^3/ha	continuous	0.7–990.0	estimation of deadwood volume per sample plot
deadwood decay stage		decay	–	categorical (ordered)	recent, ongoing, progressed, decomposed	deadwood decay stage. This predictor was estimated for a larger dataset per sampled piece
independent variables						
site	country	ctry	–	categorical	Austria (AT), Croatia (HR), Hungary (HU), Serbia (RS), Slovenia (SI)	country (considered as a potential random effect variable)
	floodplain type	fpt	–	categorical (ordered)	softwood, transition, hardwood, other	floodplain type aggregated by angle-count plot
	river	riv	–	categorical	Danube, Drava, Mura, Extension	river (considered as a potential random effect variable)
	transect id	trns	–	categorical	37 transects	transect id (considered as a potential random effect variable)
	elevation	elev	m (asl)	continuous	79.5–329.66	elevation of the angle-count plot
	distance	dist	m	continuous	12.55–591.38	minimum distance of angle-count plot to the river
	topsoil easily available water capacity	eawct	–	categorical (ordered)	low, medium, high, very high	topsoil easily available water capacity by transect. In the source dataset it was coded as follows: low < 100 mm/m, medium 100–140 mm/m, high 140–190 mm/m, very high > 190 mm/m
	subsoil easily available water capacity	eawcs	–	categorical (ordered)	very low, low, medium, high, very high	subsoil easily available water capacity by transect. In the source dataset it was coded as follows: very low: 0 mm/m, low < 100 mm/m, medium 100–140 mm/m, high 140–190 mm/m, very high > 190 mm/m. (ordered categorical: very low < low < medium < high < very high)
silviculture	management type	mnt	–	categorical (ordered)	nature-like, uneven-aged, even-aged, intensively managed	management type aggregated by angle-count plot. The data was coded in nature-like forest, uneven-aged forest, even aged forests, intensively managed forest (coppice, biomass and timber plantations)
	horizontal structure	hrz	–	categorical (ordered)	congested, closed, broken, open, gappy, grouped/cohorted	horizontal structure aggregated by angle-count plot
	mean basal area	ba	m^2	continuous	0.004–2.157	mean basal area by angle-count plot
	species richness	spr	–	categorical (ordered)	1, 2, 3, 4, 5	species richness aggregated by angle-count plot. The source data was coded into 1–7, but values > 5 were very rare, so they were conflated with 5
	tree competition	comp	–	categorical (ordered)	dominant, co-dominant, intermediate, suppressed	tree competition aggregated by angle-count plot
climate	mean annual temperature	mat	°C	continuous	9.61–11.72	mean annual temperature (1985-2014by transect
	mean warmest month temperature	mwmt	°C	continuous	19.90–22.11	mean warmest month temperature (July 1985–2014) by transect
	annual precipitation sum	aps	mm	continuous	538.6–2132.4	annual precipitation sum (1985–2014) by transect
	mean summer precipitation	msp	mm	continuous	59.02–130.17	mean summer precipitation (June-August 1985–2014) by transect
	annual heat-moisture index	ahm	–	continuous	232.0–493.0	annual heat moisture (1985–2014) by transect
	summer heat moisture index	shm	–	continuous	156.70–371.7	summer heat moisture (June-August 1985–2013) by transect

type. Further, four forest management types were distinguished following the categorization of Duncker et al. (2012); corresponding categories in parentheses: nature-like forest (passive), which follow a natural development, are maintained as ecologically valuable habitats, and show no evidence of direct management intervention such as cut tree stumps; uneven-aged forest (low), i.e. continuous-cover forestry that mimic natural processes, such as leaving deadwood and promoting natural regeneration; even-aged forest (medium and high) managed for economic reasons with trees of one age class and considering moderately to low ecological value; and intensively managed forest (intensive) considering no ecological value, including plantations for biomass and timber production. The horizontal structure was derived from the canopy cover indicating light availability and competition in six classes following Steiner et al. (2019) and ranging from (1) congested to (6) cohorted. For describing site characteristics, the distance from each sample plot to the river edge was measured (hereafter: river distance). Additionally, for each transect, mean temperature during vegetation season and sum of precipitation during vegetation season were calculated from the ECLIPS-2.0 dataset (Chakraborty et al. 2020). Easily available water capacities were considered for both, topsoil and subsoil. A detailed description of variables is provided in Table 1.

2.3. Data analysis

In total, the dataset consisted of 1,291 lying deadwood observations on 322 sample plots along 47 transects. Standing deadwood was not included in the analysis due to a very low number of observations ($n = 24$). The volume of lying deadwood was calculated using the formula by Van Wagner (1968) based on the diameter at the point of intersection and the length of the intersect per plot (here: 75 m). We considered 19 potential predictors for modelling lying deadwood occurrence, volume, as well as decay stages, and grouped them to site, management, and climate-related variables (see Table 1). Country, floodplain type, river, transect ID, elevation, river distance, as well as topsoil and subsoil easily available water capacities were tested as site-related variables. Silvicultural management parameters include management type, horizontal structure, mean basal area, tree competition, and species richness. Mean annual temperature, mean warmest month temperature, annual precipitation sum, mean summer precipitation, as well as annual and summer heat moisture index derived from the ECLIPS-2.0 dataset (Chakraborty et al. 2020) were taken into consideration as climate-related variables.

First, independent variables were tested for normality and transformed with the natural logarithm (ln) to approximate normality where required. Data was aggregated by sample plot (see variable description in Table 1). We modelled lying deadwood occurrence using a generalized linear model (GLM) with a binomial error distribution and logit link function. To model deadwood volume we used a GLM with a gaussian distribution and ln-transformed the dependent variable. Decay stages of deadwood were modelled using an ordinal regression without aggregating the data by sample plot to avoid information loss. Both, occurrence and volume models were tested for spatial autocorrelation with the Moran's I test, and the transect included as random effect in case of spatial autocorrelation (deadwood volume model: observed Moran's I on residuals: -0.12, $p = 0.09$). In the next step, we excluded variable combinations with high multicollinearity (generalized standard-error inflation factor (GSIF) < 5; GSIF definition cf. Fox and Monette (1992). Categorical variables were excluded if no significant relationship was inferred from most of the levels. To select the final models, we tested subsets of predictors potentially affecting the respective dependent variable, followed an information theoretic approach and ranked them according to the conditional Akaike Information Criterion (AICc). All categorical variables with ordered levels were coded based on successive differences (R package MASS, function "contr.sdif"; Venables and Ripley 2002).

All data analyses and modelling were conducted using R version 4.1.0 (R Core Team 2021) and the packages MASS (proportional odds ordinal regression, function "polr", Venables and Ripley 2002; Ripley et al. 2019), lme4 (linear mixed-effects model, Bates et al. 2021), MuMIn (model selection and ranking by AICs, Barton 2020).

3. Results

3.1. Lying deadwood occurrence

Consistent with our expectations, lying deadwood occurred more frequently in nature-like (78% of respective sample plots) and uneven-aged forests (74%) than in even-aged (64%) and intensively managed forests (49%). It was recorded more often in sample plots close to the river edge than in those farther away (0–75 m: 93% of sample plots with lying deadwood occurrence, 75–150 m: 67%, 150–225 m: 79%, 225–300 m: 72%).

The binomial model revealed the variables annual heat-moisture index (*ahm,* $p = 0.02$) and the river distance (ln*(dist),* $p < 0.01$) as significant drivers of lying deadwood occurrence (Table 2, Fig. 2). Management type (*mnt*) was of minor importance but its inclusion in the final model led to a better model fit compared to a further reduced model (likelihood ratio test of models with and without management type as variable, $p = 0.03$).

3.2. Lying deadwood volume

Lying deadwood volumes ranged from 0.7 m^3ha^{-1} to 990.3 m^3ha^{-1} in the TBR, with highest average amounts in softwood floodplain forests (94.3 ± 16.1 m^3ha^{-1}), followed by the transition zone (79.5 ± 18.6 m^3ha^{-1}) and hardwood floodplain forests (55.0 ± 24.8 m^3ha^{-1}). In areas not belonging to these categories, i.e. category 'other', the lowest volumes were recorded (21.1 ± 9.4 m^3ha^{-1}). The floodplain type, however, was not a significant variable and therefore excluded from the final log-linear regression model. The most important predictors instead were basal area (ln*(ba),* $p = 0.02$), river distance (ln*(dist),* $p < 0.01$) and mean annual temperature (*mat,* $p = 0.02$) (Table 3). In detail, lying deadwood volume decreased significantly with increasing river distance, and increased as mean annual temperature and basal area increased (Fig. 3).

3.3. Lying deadwood decay

Among different floodplain types, we were not able to detect a significant decay pattern of lying deadwood, yet a minor variation in decay stage distribution was observed. While, recent decay stages dominated the transition zone (49% of deadwood) and other forest types (56%), recent (36%) together with ongoing (40%) decay stages were mainly found in hardwood floodplain forests. In contrast, deadwood of ongoing (30%) and progressed (36%) decay dominated in softwood floodplain forests. Overall, the share of decomposed deadwood was very low, with 6% in softwood floodplain forests and 5% in hardwood floodplain forests.

Deadwood decay was modelled as a dependent variable with three

Table 2

Parameter estimates, standard errors, t and p values of effects for the predictions of lying deadwood occurrence in the study area of the Mura-Drava-Danube Transboundary Biosphere Reserve using the most parsimonious binomial model (link function = logit).

Variable	Category Differences	Estimate	Std. Error	t Value	p Value
ahm		0.006	0.003	2.247	0.025
ln(dist)		−0.969	0.257	−3.773	<0.01
mnt	uneven - natural	0.505	0.571	0.885	0.376
	even - uneven	−0.825	0.478	−1.725	0.084
	intensive - even	−0.907	0.481	−1.885	0.059

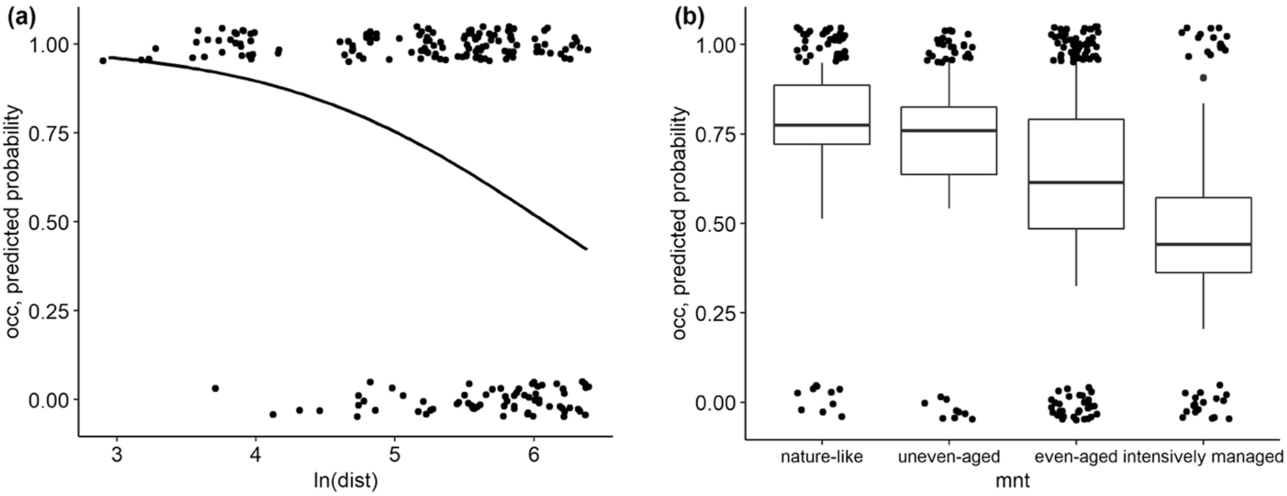

Fig. 2. (a) Predicted probability of deadwood occurrence vs. natural logarithm of minimum distance of angle-count plot to river edge (ln*(dist)*) based on logistic regression. (b) Predicted probability of deadwood occurrence vs. management type (*mnt*). The black points show the presences and absences of deadwood.

Table 3
Parameter estimates, standard errors, t, and p values of effects for the predictions of lying deadwood volume in the study area of the Mura-Drava-Danube Transboundary Biosphere Reserve using the most parsimonious log-linear regression model.

Variable	Effect	Estimate	Std.Error	t Value	p Value
ln(ba)	fixed	0.291	0.128	2.282	0.022
ln(distance)	fixed	−0.589	0.133	−4.425	<0.01
mat	fixed	0.677	0.293	2.305	0.021
trns	random	0.737			

categories considering each surveyed piece of deadwood without aggregating the data to plot-level. The climatic variables annual precipitation sum (ln*(aps)*) and mean warmest month temperature (*mwmt*) were both significant ($p < 0.01$) (Table 4, Fig. 4). Other predictors of decay were horizontal structure (*hrz*), with open canopy structures showing a significant effect on decay ($p < 0.02$), and management type (*mnt*), with even-aged and intensively managed forests being significant ($p < 0.01$). A summary of regression results is provided in Table 4.

4. Discussion

Our study is one of few investigating the patterns of lying deadwood in south-eastern European riparian forests and providing insights into deadwood dynamics considering floodplain type, silvicultural management and climatic conditions. The results revealed that occurrence and volume of lying deadwood were both influenced by river distance. Following our expectations, lying deadwood occurred more frequently at sites without or with extensive silvicultural management, where nature-like or near natural forest development was possible. A moist, warm climate and an open canopy structure fostered deadwood decay and significantly predicted advanced stages of decay.

In accordance with our hypothesis, river distance was the main driver for lying deadwood occurrence and an important factor for deadwood volume in riparian forests. Deadwood accumulated primarily close to the river edge, likely due to water transport and deposition following flood events. Similar observations have been made by Hassan et al. (2005) in small streams in the Pacific Northwest of North America, Komonen et al. (2008) in lakeside riparian forests in eastern Finland, and Dahlström and Nilsson (2006) in boreal riparian forests in Sweden. The latter further argue that regularly flooded deadwood decays more

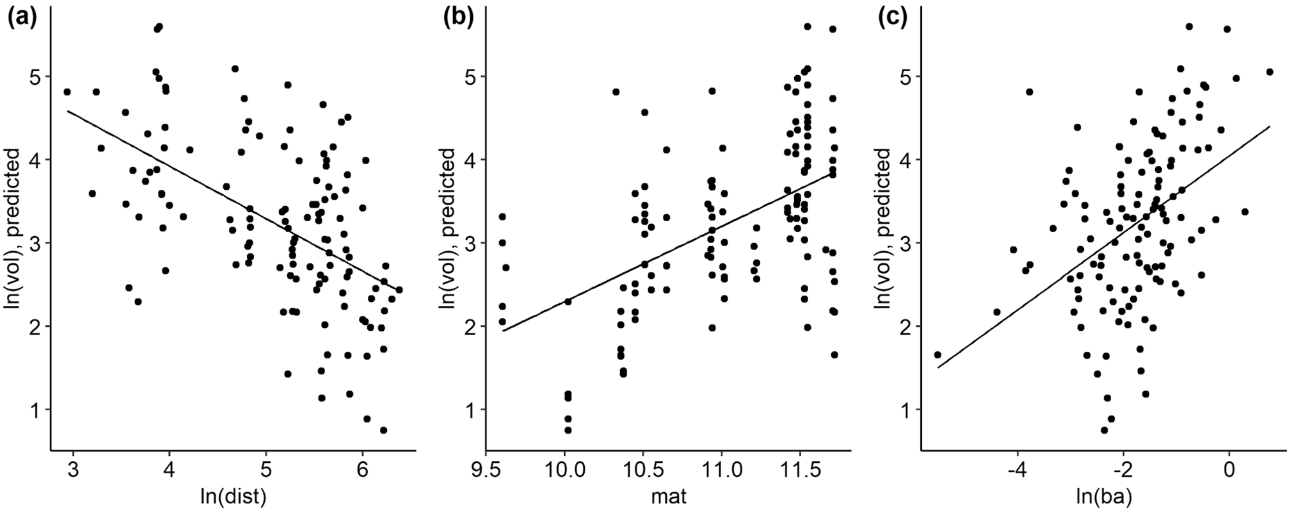

Fig. 3. (a) Predicted natural logarithm of deadwood volume (ln*(vol)*) vs. natural logarithm of minimum distance of sample plot to river edge. (b) Predicted natural logarithm of deadwood volume (ln*(vol)*) vs. mean annual temperature (*mat*, °C). Points in both plots represent volumes calculated for each sample plot for observed data.

Table 4
Parameter estimates, standard errors, t and p values for predictors (for categorical variables: for category differences of predictors) for deadwood decay stage differences using the most parsimonious proportional odds logistic regression.

Variable	Category Differences	Estimate	Std. Error	t Value	p Value
dependent variables					
decay	recent|ongoing	5.626	3.77	1.492	0.136
	ongoing|progressed	7.08	3.772	1.877	0.061
	progressed|decomposed	9.586	3.779	2.536	0.011
predictors					
eawct	medium - low	0.407	0.21	1.937	0.053
	high - medium	−0.436	0.219	−1.996	0.046
hrz	closed - congested	−0.502	0.222	−2.265	0.024
	broken - closed	−0.374	0.152	−2.46	0.014
	open - broken	−0.377	0.249	−1.516	0.129
	gappy - open	1.08	0.341	3.163	0.002
	grouped - gappy	−0.531	0.396	−1.343	0.179
ln(aps)		−0.76	0.178	−4.259	<0.01
mnt	uneven - natural	−0.376	0.203	−1.856	0.063
	even - uneven	−0.775	0.195	−3.974	<0.01
	intensive - even	0.728	0.199	3.654	<0.01
mwmt		0.556	0.155	3.593	<0.01

slowly and is thus available for longer. In contrast, decay of deadwood without regular flooding appears to progress more rapidly (Harmon et al. 2000; Stokland et al. 2012). This finding could not be confirmed by our study. The predominantly advanced decay stages found in the softwood forest appear to be the result of less silvicultural activities, tree species-specific wood properties (Harmon et al. 1986; Bond-Lamberty and Gower 2008; Ulyshen 2016) and, accordingly, faster decay (Weedon et al. 2009; Petrillo et al. 2016).

Average lying deadwood volumes in all forest types were higher than the current European averages for managed forests ranging from 8 to 20 m^3ha^{-1} (Forest Europe 2015) and were consistent with published values for riparian forest reserves in Austria (Oettel et al. 2020) and Italy (Lombardi et al. 2008). Moreover, the deadwood amounts reported here exceed the threshold of 20 to 50 m^3ha^{-1} proposed by Müller and Bütler (2010), which allows the majority of deadwood-associated species to persist. Volume of lying deadwood increased with basal area, indicating that higher total forest biomass results in more deadwood. A trend, that has been frequently observed in unmanaged or old-growth riparian forests (e.g. Garbarino et al. 2015; Keren and Diaci 2018; Oettel et al. 2020), but also in managed forests. Ferguson and Archibald (2002) have shown that the living tree basal area is closely related to the dead tree basal area in boreal forests of northwestern Ontario.

Given that basal area is influenced by silvicultural management, more extensive and nature-oriented management practices with reduced harvesting activities are recommended for deadwood promotion (Pötzelsberger et al.; Bauhus et al. 2009). Our findings pointed in the same direction, showing a higher probability of lying deadwood occurrence in nature-like and uneven-aged forests than in even-aged and intensively managed forests. Management type can be used as a proxy for management intensity, with even-aged and intensively managed stands likely to be harvested more frequently and intensively, limiting the accumulation of deadwood. This is in line with Dahlström and Nilsson (2006), who found about three times the amount of deadwood in old-growth riparian forests compared to managed riparian forests in Sweden. The general trend of decreasing deadwood amount with increasing management intensity has been well studied and documented in other forest types as well, such as oak forests (Bölöni et al. 2017), beech forests (Nagel et al. 2017), or mountain forests dominated by beech and silver fir (Lombardi et al. 2012).

Forest horizontal structure, which is also strongly affected by management and linked to biodiversity (Lombardi et al. 2012; Parisi et al. 2016), was an important predictor of decay stage. Our results revealed a predominance of freshly decaying deadwood in even-aged forests with more advanced decaying deadwood in uneven and natural forests. Intensive silvicultural management practices leading to even-aged forests increases forest vulnerability to abiotic and biotic threats, resulting in regular input of fresh deadwood (Aakala 2010; Seidl et al. 2011). In the TBR, this vulnerability is exacerbated by lowland site factors, including high temperatures and regular flooding events (de Groot et al. 2022).

The strongest predictors of the decay stages of lying deadwood, however, were the climatic variables. Mean warmest month temperatures showed a positive relationship to decay and the sum of annual precipitation a negative one. Many studies confirm that decay of deadwood accelerates with rising temperatures (e.g. Merganiov et al. 2012; Garbarino et al. 2015; Pietsch et al. 2019). Precipitation, on the contrary, shows an ambivalent trend by negatively affecting decay under cool conditions and positively affecting it under warm conditions (Seibold et al. 2021). The predictors presented here demonstrate the importance of climatic conditions for deadwood decay, leading to an overall strong influence at high temperatures and high humidity, explaining the low occurrence of highly decayed deadwood in the TBR. A trend that has also been observed by Harmon et al. (1986).

The constant supply of fresh deadwood in riparian forests could also

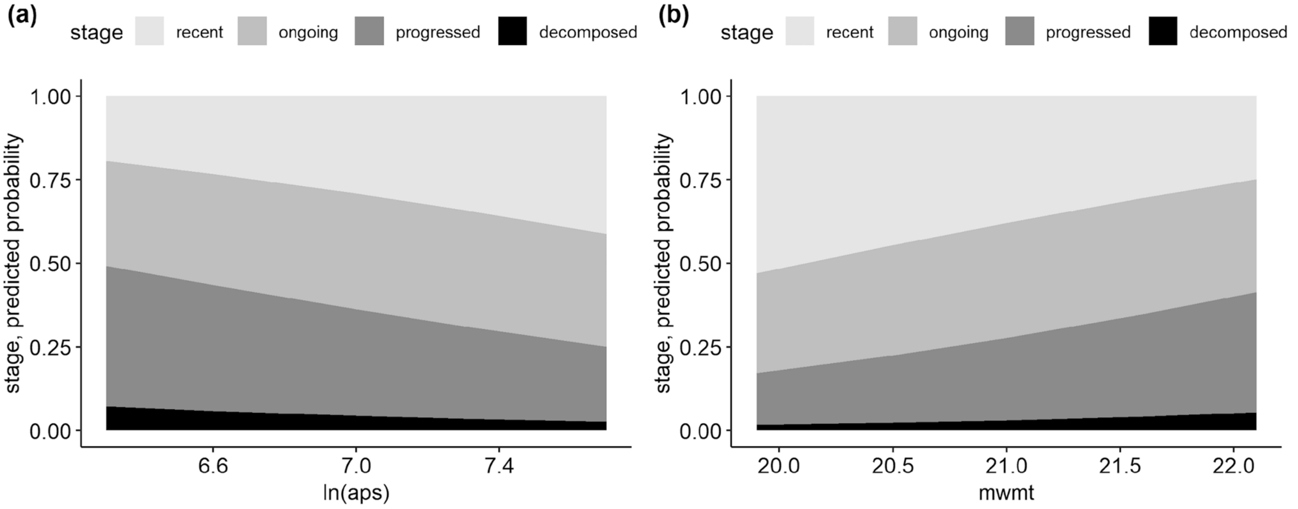

Fig. 4. (a) Predicted decay stage (*stage*) vs. natural logarithm of annual precipitation sum (ln(*aps*), mm). (b) Predicted decay stage (*stage*) vs. mean warmest month temperature (*mwmt*, °C).

be due to a decline in tree population observed in recent decades (Rivers 2019). Stressed trees are hosts for non-native tree pest species enabling their spread and establishment, especially those that are becoming invasive and pose major challenges due to their unpredictability (Lapin et al. 2021). Consequently, almost all tree species in the TBR and in central as well as south-eastern European riparian forests are currently threatened by various pests, diseases or invasive plants (de Groot et al. 2022). The proportion of ash species (*Fraxinus excelsior* and *Fraxinus angustifolia*) has declined in recent decades due ash dieback (*Hymenoscyphus fraxineus*), oak species are facing a complex of factors causing oak decline, and alder species are harmed by *Phytophthora alni*, *Armillaria* sp. and *Neonectria* sp. causing extreme dieback in certain areas (de Groot et al. 2021). With climate change progressing as currently projected, major changes are expected for riparian forest ecosystems in Europe, such as changes in hydrological conditions, an increasing number of abiotic and biotic threats, and progressive tree mortality leading to changes in tree species composition.

5. Conclusion

Our study of lying deadwood in the Mura-Drava-Danube Transboundary Biosphere Reserve –a protected area across five different countries and three rivers – provides valuable insights into the riparian forest deadwood dynamics. The variability of deadwood volume was remarkably high, ranging from 0.7 m^3ha^{-1} to 990.3 m^3ha^{-1}. We have shown that distance to river edge is significantly correlated to deadwood occurrence and volume. This suggests that the role of river dynamics in deadwood transport should be further explored since its role in deadwood occurrence and volume has not yet been considered in this study. Not surprisingly, stand basal area, which is strongly linked to forest management practice, was the main driver of deadwood volume. Increasing the amount of deadwood in all stages of decay should be pursued in managed forests, as it fulfills various ecosystem functions and supports biodiversity in riparian forest areas. The temporal availability and development of deadwood in riparian forests in the face of climate change requires further monitoring and research efforts considering local site conditions, related saproxylic activity, and river dynamics to allow for model improvements. This will help develop more precise models on different forest types and support understanding of habitat development and underlying cause-effect relationships.

Uncited references.

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.

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