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Patterns and drivers of deadwood volume and composition in different forest types of the Austrian natural forest reserves

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ABSTRACT

Deadwood is an important structural feature in forests providing essential resources for various organisms. Both forest management and conservation are increasingly focusing on the integration of deadwood into forest management. Deadwood volume and composition are driven by forest type, stand age, natural tree mortality, tree species composition and harvesting intensity. Here, we used inventory data from 28 unmanaged natural forest reserves (NFR) in Austria to analyse the patterns and drivers of: (i) the volume of standing and lying deadwood, (ii) the diversity of deadwood in different forest types. Eight forest types are located in the investigated NFRs covering a wide range of vegetation types with altitudes of 140–1825 m asl.

The volumes of living wood and deadwood differed markedly between forest types. The average deadwood volume per forest type ranged from 23 m^3 ha^{-1} in larch forests to 109 m^3 ha^{-1} in spruce-fir-beech forests. Likewise, deadwood diversity (species diversity as well as diversity in diameter classes and degree of decomposition) differed significantly among forest types, with the highest deadwood diversity found in beech and spruce forests and the lowest in hardwood floodplain forests, carbonate pine forests and larch forests.

Our results show that volume and composition of deadwood vary greatly among different forest types. Regression models revealed that the availability of deadwood was mainly driven by tree- and stand related factors (e.g. forest type, diameter at breast height and volume of living stand), whereas site-related (e.g. altitude) and climatic factors (e.g. mean annual precipitation) had a minor influence. The variables tree species diversity, aspect and slope showed no significance and were therefore not integrated into the final model.

This study provides insights into deadwood availability and diversity in NFRs on a national scale, providing reference data for unmanaged temperate forests and aiding decision-making in nature conservation and forest management, since NFRs are reference areas for close-to-nature forestry.

1. Introduction

Deadwood, often also named as coarse woody debris (Franklin et al., 2006), is defined as non-living woody biomass not contained in the litter, either standing or lying on the ground […](IPCC, 2006). It is added to forests due to mortality via various processes such as insect outbreaks, forest fire, competition, extreme climatic events (e.g. storms, wind breaks), and tree death at the end of the tree species-specific life cycle (Harmon et al., 1986; Rondeux et al., 2012).

Deadwood contributes to ecosystem functioning and fluxes in forests by changing microclimate (i.e. soil moisture by increasing water storage capacity and increasing nutrient availability (Franklin et al., 2006; Harmon et al., 1986; Maser and Trappe, 1984). Further, deadwood facilitates natural tree regeneration, particularly in forests in cool climates such as temperate mountain or boreal forests (Humphrey et al., 2004; Siitonen et al., 2000; Zielonka, 2006). Moreover, 25% of forest-dwelling species are dependent on deadwood (Siitonen, 2001; Schuck et al., 2004). For instance, deadwood provides essential resources for saproxylic species like wood-decaying fungi (Lassauce et al., 2011), arthropods, bryophytes, and lichens (Lassauce et al., 2011; Rimle et al., 2017; Shorohova and Kapitsa, 2015).

The volume of deadwood has often been used for assessing the conservation value of natural and managed forests (Mönkkönen et al., 2008; Müller and Bütler, 2010; Stokland et al., 2004). While in natural temperate forests, volume of deadwood is impressive (Horák et al., 2016; Rimle et al., 2017; Zielonka, 2006), in silviculturally managed

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forests it is a severely reduced forest component (Fridman and Walheim, 2000; Morrissey et al., 2014). Müller and Bütler (2010) suggest a threshold range of 20–50 m^3 ha^{-1} for deadwood volume, which can be viewed as minimum requirement for European forests. The actual average volumes, however, are much lower with 8 m^3 ha^{-1} in Northern Europe and 20 m^3 ha^{-1} in Central and Western Europe (Forest Europe, 2015). Humphrey et al. (2004) report similar average values of 20 m^3 ha^{-1} for forests of the Northern Alps as does the Austrian Forest Inventory with average values of 20.6 m^3 ha^{-1} for Austrian forests (BFW, 2019) and large standing deadwood being particularly scarce.

Accordingly, in Europe many biota that are dependent on deadwood—particularly species that depend on specific types of deadwood or large amounts of deadwood—have greatly declined in silviculturally used forests and often are reduced to isolated populations in unmanaged forest remnants (Bütler and Lachat, 2009; Lassauce et al., 2011). Nevertheless, especially in regions where long-lasting human influence on forests has only left isolated and small remnants of natural forests it is essential to integrate biodiversity conservation such as deadwood into forest management (Doerfler et al., 2017; Parviainen and Frank, 2003; Shorohova and Kapitsa, 2015).

In recent years, several studies on deadwood volume and composition in European beech (Meyer and Schmidt, 2011), spruce (Rimle et al., 2017; Zielonka, 2006), beech and oak forests (Bölöni et al., 2017; Vandekerkhove et al., 2009) have been published. Often these studies focus on a specific forest type or study area and conclusions beyond are difficult to draw, also with regard to varying survey methodology. There is thus still a need for studies with larger areas of investigation and a consistent survey methodology (Bujoczek et al., 2018). Moreover, many of them concentrate on forests in Scandinavia or the Carpathians, while for many forest types in Central Europe the information on deadwood volume and composition in the forests is still insufficient.

It is known that deadwood volume and composition depend on a variety of factors (e.g. stand age, natural tree mortality, tree species composition), macroclimatic conditions (Přívětivý et al., 2016) and silvicultural forest management (Doerfler et al., 2017). Nevertheless, it has also been pointed out that deadwood volume alone is an insufficient metric for assessing the conservation value and naturalness of forests (Kunttu et al., 2015). Deadwood diversity is important as well due to the varying habitat requirements of different species (Brin et al., 2009).

In Europe, forest reserves have therefore become increasingly important for biodiversity conservation (Bauhus et al., 2009). They also constitute ideal research sites on ecosystem functioning and structure under natural conditions (Korpel, 1995). Analysis of deadwood volume and composition in forest reserves contributes to biodiversity conservation, and provides important data for close-to-nature silviculture (BMNT, 2018). Research in natural forest reserves also helps to deepen the understanding of forest dynamics (Bugmann and Brang, 2009).

The Austrian Natural Forest Reserve (NFR) program was established in 1995 (Frank and Müller, 2003) with the aim of protecting all types of forest communities (Willner and Grabherr, 2007) in each growing region (Kilian et al., 1994). This is primarily intended to conserve and enhance forest biodiversity, as it is an indispensable prerequisite for the sustainable existence of healthy forests that can fulfil their functions. Of the 118 relevant forest communities, 84 are included in the program. Currently, 192 NFRs cover a total area of 8.355 ha and a wide range of ecoregions from the pannonian to the subalpine zone, representing 0.02% of the total forest area of Austria (3.53 million ha) (BMNT, 2019). Before being designated as NFRs, these forests had been used for silviculture, but any usage has ceased afterwards. Generally, NWRs can be regarded as valuable reference areas for ecologically oriented, close-to-nature silviculture.

The aim of the present study was to analyse the patterns and drivers of (i) the volume of standing and lying deadwood, and (ii) the diversity of deadwood in eight different forest types of Austrian NFRs covering a wide range of altitudinal and environmental conditions.

We hypothesise that the amounts of deadwood are higher in deciduous and mixed forests than in coniferous forests with low standing proportion in all forest types; deadwood diversity in terms of species, diameter, decomposition and type varies among forest types being highest in mixed forests. Stand- and tree species-related, climatic and site conditions are expected to have an influence on deadwood volume and proportion, although to different extents: while stand- and tree related conditions are likely to have a greater influence on proportion, site conditions should have a greater influence on volume. We analysed the inventory data from 28 unmanaged natural forest reserves (NFR) in Austria to test these hypotheses. Finally, we discuss the results in the context of forest biodiversity conservation and forest management.

2. Materials and methods

2.1. Study sites

In the NFRs, permanent plots were established with a standardized design and stand inventories were done in intervals of 15 to 20 years. Data on deadwood was collected since 2013. A total of 910 plots in 52 NFRs covering 24 forest types were surveyed. The forest types were classified according to the vegetation maps based on phytosociological classification following Willner and Grabherr (2007). In transition zones between two forest types, the decision was based on the predominant tree species. We included only NFRs with at least 10 plots per forest type and only forest types with a minimum number of 30 plots. Ultimately, the following eight forest types covering a wide range of vegetation types were analysed in 28 NFRs: hardwood floodplain forests (4 NFRs), oak-hornbeam forests (10 NFRs), beech forests (2 NFRs), carbonate pine forests (2 NFRs), spruce-fir-beech forests (6 NFRs), larch forests (1 NFRs), low subalpine spruce forests (2 NFRs) and mire spruce forests (3 NFRs) (Table 1). Data on living stand and deadwood were collected at regular grids of 50x50 m or 100x100 m depending on the size of the area under investigation and was based on an expert decision. A map of the 28 NFRs is provided in Fig. 1.

2.2. Data collection

2.2.1. Living stand

The composition of tree species was systematically determined for

Table 1
Forest types and associated forest associations (according to Willner and Grabherr, 2007).

Forest type	Association	Plots
Beech forest	Galio odorati-Fagetum	9
	Melampyro-Fagetum	5
	Ostryo-Fagetum	17
Carbonate-pine forest	Erico-Pinetum sylvestris	34
Hardwood floodplain forest	Fraxino pannonicae-Ulmetum	50
Larch forest	Rhodothamno-Laricetum	30
Low subalpine spruce forest	Adenostylo glabrae-Piceetum	31
	Calamagrostio villosae-Piceetum	13
Mire spruce forest	Bazzanio-Piceetum	20
	Sphagno-Piceetum	32
Oak-hornbeam forest	Galio sylvatici-Carpinetum	128
	Pseuostellario-Carpinetum	16
	Stellario-Carpinetum	10
Spruce-fir-beech forest	Adenostylo glabrae-Fagetum	14
	Anemono trifoliae-Fagetum	35
	Dentario pentaphylli-Fagetum	13
	Galio odorati-Fagetum	30
	Lonicero alpigenae-Fagetum	12
	Luzulo-Fagetum	10

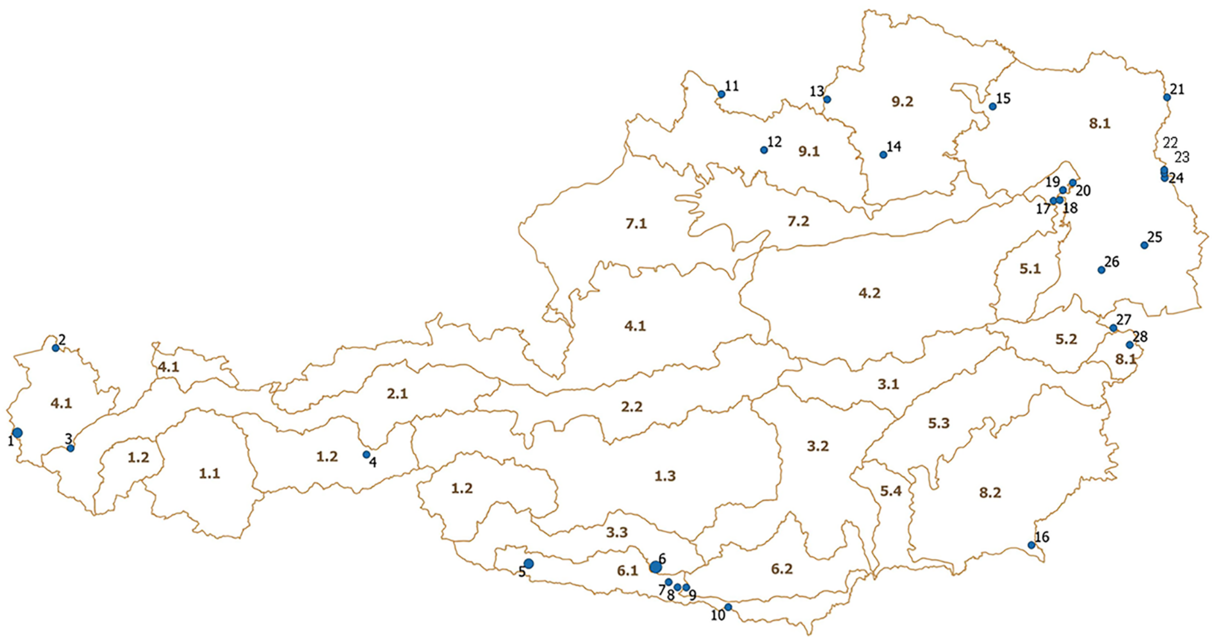

Fig. 1. Map of Austria including the 28 investigated Natural Forest Reserves (NFR) and the regional forest growth regions according to Kilian et al. (1994). Numbers 1–28 refer to the following natural forest reserves:1 Goppaschrofen, 2 Bromatsreute II, 3 Bomatschis, 4 Ebenschlag, 5 Niedergailwald, 6 Koflachgraben, 7 Scharte-Dobratsch, 8 Waben, 9 Warmbad VI, 10 Urwald Selkacher Teil, 11 Spirkenwald-Bayerische Au, 12 Balzplatz, 13 Luxensteinwand, 14 Sandlerau, 15 Sonnholz, 16 Halbenrain, 17 Deutschwald, 18 Johannser Kogel, 19 Steinerne Lahn, 20 Pfaffenberg, 21 Moravka, 22 Alte March, 23 Nani Au, 24 Schleimlackenwiese, 25 Rumwald, 26 Knörzelberg, 27 Lange Leitn, 28 Kreutzer Wald.

the sampling plots within the NFR using Bitterlich's angle count sampling with a fixed angle of sight (1:25, referring to basal area factor of four) to select the trees to be assessed (Bitterlich, 1984, 1948). No threshold was defined for the diameter at breast height (dbh). Tree height, crown height and the position of each tree within the plot (distance and direction) were also measured.

2.2.2. Deadwood

Standing deadwood was recorded on fixed plots with a size of 300 m^2. For each standing dead tree, the species (if identification at species level was not possible, at least classified as deciduous or coniferous), mid-height diameter (mdm) or dbh (mdm if height $<$ 1.3 m and dbh if height $\geq$ 1.3 m), height of the stump or tree and position within the plot were determined.

Lying deadwood was recorded using the line intersect method developed by Warren and Olsen (1964) and improved by Van Wagner (1968). We adapted the methodology used by the Swiss National Forest Inventory (Keller et al., 2013) to four lines of 10 m length for practicability in steep terrain. Starting from the centre of each plot, the intersect lines were placed in northerly, easterly, southerly and westerly directions. Each log crossing the intersect lines was measured. The respective tree species (see description for standing deadwood) and the diameter at the point of intersection was determined.

Generally, deadwood was recorded using a threshold dbh of 10 cm, as indicated in the IPCC guidelines (IPCC, 2006, 1997). For each standing and lying dead tree, the dominant degree of decomposition was determined using 5 classes ranging from 1 (recent death) to 5 (highly decayed deadwood) according to the methodology used by the Swiss National Forest Inventory (Keller et al., 2013) and applied in the Swiss Natural Forest Reserves (Robin and Brang, 2009).

2.3. Data analysis

All statistical analysis and modelling was carried out using the R software package version 3.6.2 (R Core Team, 2019).

2.3.1. Living and deadwood volume

The volume of *living trees* was calculated based on dbh and height measurements using the volume function and form factors for merchantable wood (Kennel, 1973). For the calculation of *standing deadwood* volume, three different categories of standing deadwood (trees, trunks and stumps) were differentiated. Dead trees and trunks were differentiated according to their height(m)/dbh(cm) ratio (if height/dbh $\geq$ 0.3 = dead tree, if height/dbh $<$ 0.3 = trunk) (Doerfler et al., 2017). For *dead trees*, the volume function and form factors for merchantable wood were used in the same way as for the living trees. The volumes of *trunks* and *stumps* (height $<$ 1.3 m) were calculated using the formula for cylindrical shapes. *Lying deadwood* volume was calculated using the formula by Van Wagner (1968):

$$V = \frac{\pi^2 \sum d^2}{8L} \quad (1)$$

where V (m^3) is the volume of deadwood, d (cm) is the diameter of deadwood at the point of intersection and L (m) is the length of intersection lines per plot (in our case 40 m). For average values, the volumes were weighted by NFR. The weighting according to NFR is necessary because the samples are clustered and depend on the respective historical stand development including site-specific characteristics.

2.3.2. Deadwood composition

The diversity of deadwood was analysed with regard to the following four categories, which represent complementary facets of deadwood quality: (1) species, (2) diameter class, (3) degree of decomposition and (4) type of deadwood.

Tree species were determined at genus level. The measured diameter values were separated into three classes: small (diameter $<$ 30.0 cm), medium (30.0 $\geq$ diameter $\leq$ 60.0) and large (diameter $>$ 60.0). The five decomposition classes and the four types of deadwood (tree, trunk, stump and lying) were determined as described in Section 2 (Data collection).

The diversity of deadwood was calculated using the Shannon Index (H):

Table 2

Explanatory variables (diameter at breast height, tree height, volume of the living stand, volume of deadwood, deadwood proportion of total volume, living species diversity, forest type, elevation, aspect, slope, temperature and precipitation) used for the quasi-binomial logistic regression of the volume and proportion of deadwood in 509 sample plots in 28 NFRs.

Variable	Acronym	Unit	Classification	Range/Categories	Description
Diameter at breast height	dbh_cm	cm	Continuous	0–104.1	Living tree diamaters were measured in cm at breast height
Tree height	h_m	m	Continuous	0–38.6	Living tree heights were measured in m using Vertex III
Volume of the living stand	Vliving	$m^3\ ha^{-1}$	Continuous	0–1742	The living wood volume per plot was calculated using function and form factors for merchantable wood
Volume of deadwood	Vdead	$m^3\ ha^{-1}$	Continuous	0–1,303	The deadwood volume per plot was calculated using function and form factors for merchantable wood for standing dead trees. The volume of tree trunks and stumps was calculated using cylindric formula and the volume of lying deadwood was calculated using the formula by Van Wagner (1968)
Deadwood proportion of total volume	Vdead/(Vdead + Vliving)	–	Categorical	0–1	The deadwood proportion of the total volume (Vdead + Vliving) was calculated by Vdead/total volume
Living species diversity	species_div	–	Categorical	0–1.59	Living species diversity (at genus level) was calculated per plot using Shannon Index
Forest type	foresttype	–	Categorical	beech spruce-fir-beech mire spruce low subalpine spruce oak-hornbeam hardwood-floodplain carbonate-pine larch	The determination of forest types was based on the vegetation classification of Willner and Grabherr (2007)
Elevation	–	m asl	Continuous	140–1825	The elevation of each site was determined in m above sea level using the digital terrain model for Austria with a resolution of 50 m
Aspect	–	°	Continuous	0–359	The aspect of each site was determined in ° using the digital terrain model for Austria with a resolution of 50 m
Slope	–	°	Continuous	0–47	The slope inclination of each site was determined in °using the digital terrain model for Austria with a resolution of 50 m
Temperature	t	°C	Continuous	2.8–10.4	Mean annual temperature was determined in °C using climate data from 1971 to 2000 (Hiebl et al., 2011)
Precipitation	p	mm	Continuous	530–1910	Sum annual precipitation in mm using climate data from 1971 to 2000 (Hiebl et al., 2011)

$$H = -\sum_{i=1-n}^{n} p_i \log_2 p_i \quad (2)$$

where p_i is the proportion of the i^{th} species, diameter class, decay class or type. No diversity is indicated by H = 0. Higher diversity is indicated by higher H-values.

2.3.3. Drivers of deadwood volume and composition

We considered 10 potential drivers for modelling deadwood availability in NFRs and grouped them into tree- and stand-related variables, site variables and climatic variables (Table 2).

Tree-related variables include (I) dbh and (II) height of the living trees, which were averaged per plot. *Stand-related variables* include (III) volume of the living stand - calculated using the volume function and form factors for merchantable wood as described above - , (IV) living species diversity, - calculated using Shannon Index - , and (V) forest type. Both, tree- and stand-related variables were included as general information to describe forest structure.

Site variables include (VI) elevation, (VII) aspect and (VIII) slope. These were determined using the measured GPS coordinates of the plots overlaid with the digital terrain model of Austria using a resolution of 50 m. Aspect was transformed into the continuous variables easterly aspect [sin(aspect/180*π)] and northerly aspect [cos(aspect/180*π)]. Slope angles were converted to the degree of slope [atan(slope/100)]. For the analysis, the inclined surface of each plot was used combining slope and aspect.

(IX) Mean annual temperature and (X) precipitation were taken into consideration as *climatic variables*. For each plot, these variables were derived by overlaying GPS coordinates with climate maps from the period 1971–2000, which were modelled with a grid size of 250 m × 250 m (Hiebl et al., 2011).

For the analysis of the relationship between deadwood volume and composition and the explanatory variables, we tested and compared two models: *model a* for deadwood volume and *model b* for deadwood proportion, calculated as (deadwood volume/(deadwood volume + living volume)). As data was incomplete in a few cases, only 509 of 519 plots were investigated.

We used general linear mixed modells (GLMM) with penalized quasi-likelihood to predict deadwood volume and composition (MASS package with glmmPQL function in R 3.6.2., Ripley et al., 2019). GLMMs were computed with random and fixed effects. The fixed effects for estimating deadwood volume respectively composition was the set of variables defined in the previous steps. Since plot distribution is clustered in NFRs, the number of observations per NFR was considered as random effect to account for autocorrelation. A quasi-poisson distribution ("log") (model a), and a quasi-binomial distribution ("logit") (model b) were applied. Final models were selected by sequentially removing non-significant variables from the full model. The statistical significance of individual predictors was tested using Pearson's chi-squared test with a significance level of < 0.05. Final models include only significant variables. We used predict function on response scale and compared measured with predicted values to check goodness of fit of the models.

3. Results

3.1. Deadwood volume and proportion

A general overview on the dataset and plot results on deadwood per forest type is presented in Fig. 2. Therefore, data was harmonized into ratios (deadwood volume/(deadwood volume + living wood volume) varying from 0 to 1, with ratio = 0 indicating no deadwood and ratio = 1 indicating no living trees. A large number of plots in all forest types show low ratios. However, two plots in mire spruce forests exhibited a very high ratio (ratio = 1) and therewith no living trees, two plots in oak-hornbeam forests and another one in spruce-fir-beech forests exhibited high ratios (ratio > 0.75). The total volume refers to total aboveground biomass (deadwood volume + living wood volume). Total volume was low in the coniferous-dominated forests carbonate pine and larch forests and high in the deciduous-dominated and mixed forests hardwood floodplain forests, oak-hornbeam forests and spruce-fir-beech forests. There are also some plots with outliers in total volume, e.g. in hardwood-floodplain forest, oak-hornbeam forest and mire spruce forest.

Deadwood and living wood volumes varied greatly among the surveyed forest types, with the highest average values found in spruce-fir-beech forest (109 m^3 ha^{-1}) and beech forest (92 m^3 ha^{-1}), and the lowest values found in larch forest (23 m^3 ha^{-1}), and carbonate-pine forests (36 m^3 ha^{-1}) (Table 3). These results confirm our hypothesis that the volumes would be higher in deciduous and mixed forests and lower in coniferous forests. Essentially, the volume of deadwood increased with the living volume of the forest, with two exceptions being hardwood floodplain forest with remarkably low deadwood volumes and beech forest with remarkably high deadwood volumes.

A comparison of the proportionate tree species distribution in deadwood and living wood showed that it is very similar; the main tree species of the living stand are also represented in deadwood (Fig. 3). A noticeable fact is, that the proportion of deadwood from spruce in larch forest is high (70%) compared to its proportion in the living volume (25%).

In all NFRs, deadwood was found as standing (trees, trunks and stumps) and lying elements (Fig. 4). The average standing volume reached a minimum of 5.6 m^3 ha^{-1} in beech forests and a maximum of 34.2 m^3 ha^{-1} in mire spruce forests. Lying deadwood contributed far more to the total deadwood volume in deciduous and mixed forests. Average volumes ranged from 9.9 m^3 ha^{-1} in larch forest to 88.8 m^3 ha^{-1} in spruce-fir-beech forests. The contribution of standing deadwood to the total deadwood volume is on average 31% and generally appears to be significantly higher in coniferous forests (47%) than in deciduous and mixed forests (16%). Standing compared to lying proportion was higher in larch forests and in mire spruce forests, which only partially verified our hypothesis. In general, variation was greater in deciduous and mixed forests than in coniferous forests.

3.2. Deadwood composition

The compositional diversity of deadwood also varied greatly among forest types, with Shannon Index values ranging from 0 to 1.43, 1.10, 1.61 and 1.39 for tree species, diameter classes, decay classes and types, respectively (Fig. 5A-D).

The *species diversity* of deadwood was high in deciduous and mixed forests (spruce-fir-beech forest, beech forest, oak-hornbeam forest) and low in coniferous forests (larch forest, low subalpine spruce forest, mire spruce forest) (Fig. 5A). The one-sided distribution in hardwood floodplain forests and larch forests indicates a large number of plots with deadwood from low species diversity.

The *diameter diversity* was low in carbonate pine forests, hardwood floodplain forests and oak-hornbeam forests, and high in spruce-fir-beech forest, mire spruce forests and low subalpine spruce forest (Fig. 5B). This is indicative of the structural variety between the different forest types, whereby low diameter diversity refers to single-layer forest structures.

Decomposition diversity was high in mire spruce forest and low subalpine spruce forest, beech forest and low in carbonate-pine forests and hardwood floodplain forests. Larch forests and hardwood floodplain forests exhibited an uneven distribution and high variation. In general, the differences among the forest types were low (Fig. 5C).

Type diversity was high in carbonate pine forests and mire spruce forests, and low in hardwood floodplain forests (Fig. 5D). The appearance of specific types of deadwood (lying, standing, broken, stumps) is not related to stand volume of the respective forest type.

Diversity generally varies between forest types, which is consistent with our hypothesis, but it cannot be generalized that diversity is

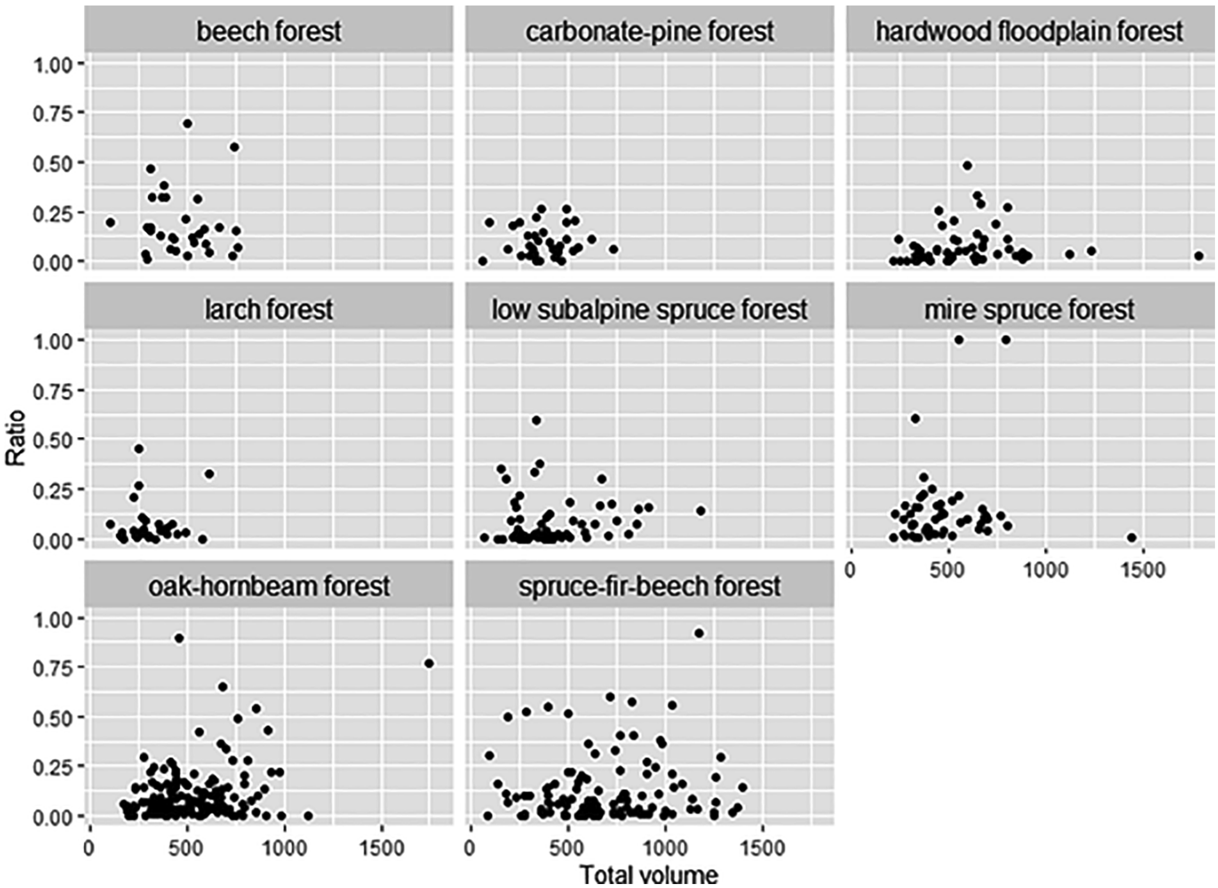

Fig. 2. Deadwood volume (expressed as ratio of deadwood volume to total (i.e. deadwood volume + living wood) volume) per plot for the eight investigated forest types: beech forest (n = 31), carbonate pine forest (n = 35), hardwood floodplain forest (n = 51), larch forest (n = 30), low subalpine forest (n = 49), mire spruce forest (n = 53), oak-hornbeam forest (n = 154) and spruce-fir-beech forest (n = 116).

Table 3
Deadwood and living wood volumes ($m^3\ ha^{-1}$) averaged per forest type including standard errors.

Forest type	Deadwood volume	± Std.error	Living volume	± Std.error
Spruce-fir-beech forest	108.89	± 28.31	597.60	± 51.77
Beech forest	91.9	± 32.76	382.22	± 8.41
Oak-hornbeam forest	63.16	± 12.24	474.88	± 36.65
Mire spruce forest	60.77	± 25.28	384.05	± 37.93
Hardwood floodplain forest	50.68	± 11.66	563.40	± 50.64
Low subalpine spruce forest	41.06	± 12.63	381.11	± 14.76
Carbonate-pine forest	35.77	± 9.43	338.94	± 25.16
Larch forest	23.11	± 0.0	285.98	± 0.0

highest in mixed forests. Combining the four above-discussed facets of deadwood diversity into an integrated indicator, highest diversities were found in spruce-fir-beech forest and mire spruce forest, while the lowest combined diversities appeared in hardwood floodplain forest, carbonate pine forest and larch forest.

3.3. Drivers of deadwood volume and composition

The GLMMs - i.e. models a (deadwood volume) and b (deadwood proportion) - showed that the tree and stand related variables diameter (dbh), the volume of the living stand as well as the forest type, the site-related variable elevation, as well as the climatic variables mean annual precipitation and temperature influence the availability of deadwood to varying extent.

Deadwood volume is strongly influenced by forest type (Table 4). It decreased slightly with increasing annual mean temperature and tree height and increased with increasing dbh ($p < 0.05$).

In addition, we calculated a volume model without considering forest type. A comparison with the volume model including forest type (Table 4) showed that the models are equivalent. The residuals, which indicate the dispersion around the predicted volume, did not differ between the models (*results not shown*).

According to model b, deadwood proportion was mainly influenced by living wood volume and forest type (Table 5). The proportion of deadwood increased slightly with diameter ($p < 0.001$). In addition, it was positively correlated with precipitation. This results only partially confirm our hypothesis that stand- and tree species-related conditions had the greatest influence on deadwood proportion. However, we could not find that the site variables elevation and aspect had a great influence on deadwood volume. For the prediction of deadwood volume also stand- and tree related conditions were found to be the main drivers.

Diagrams for checking the goodness of fit of models a and b are given in Appendix A.

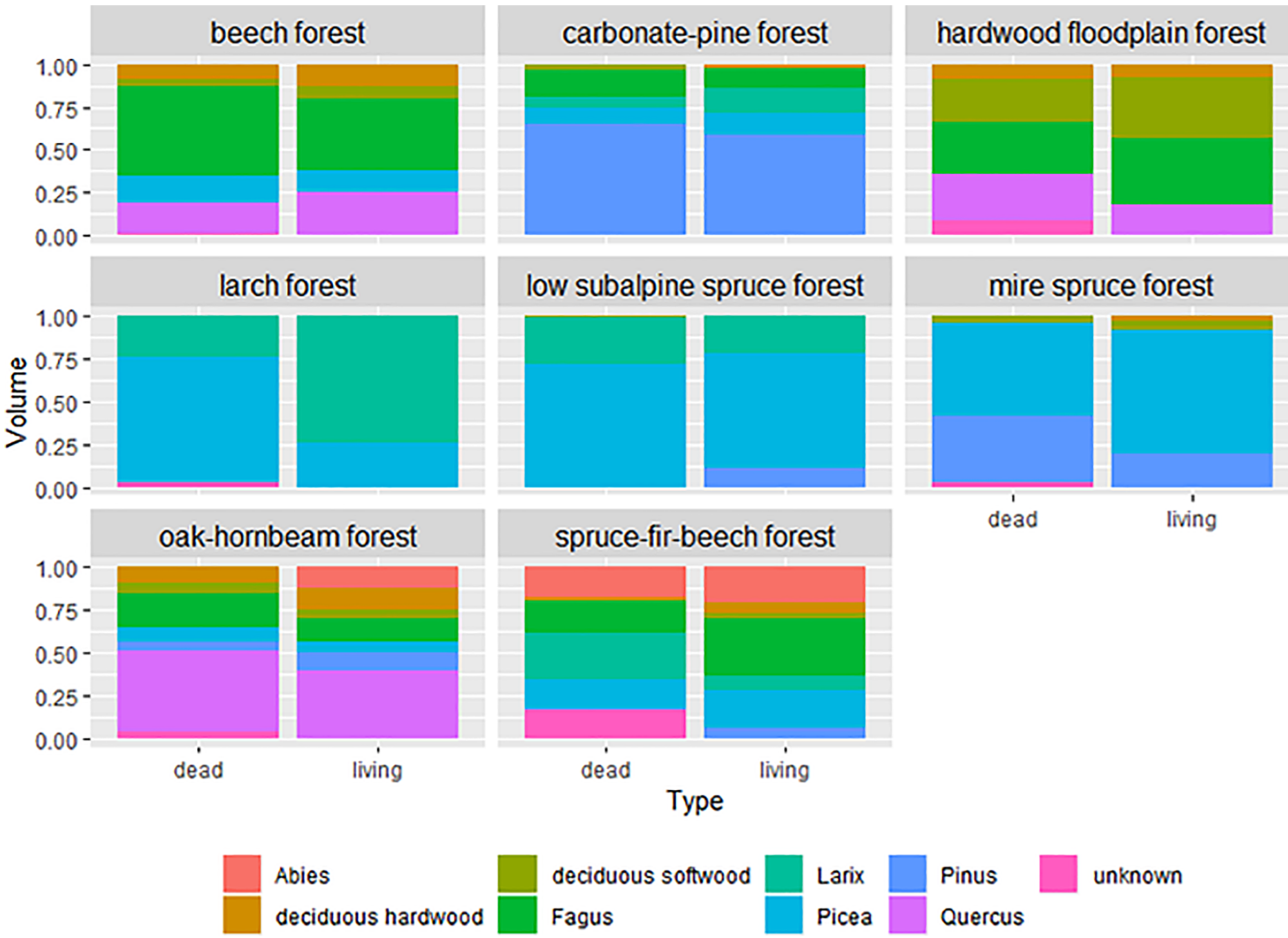

Fig. 3. Tree species proportion in the living and deadwood for the eight investigated forest types. Species were determined at genus level. When this was impossible, deadwood was classified as deciduous or coniferous. If this was likewise impossible, it was classified as unknown.

4. Discussion

4.1. Deadwood volume

We found that deadwood volumes and ratios varied greatly among forest types in Austrian NFRs. Both volume and ratio were highest in deciduous and mixed forests and lower in coniferous forests. Further, variation between plots within individual forest types was also high. The highest average deadwood volumes were measured in spruce-fir-beech forests (109 m^3 ha^{-1}), the lowest in larch forests (23 m^3 ha^{-1}). During the last two decades many studies have been published which investigate deadwood volumes in unmanaged forests all over Europe (Table 6). Deadwood volumes similar to those reported here have been given for beech forests in North-eastern Germany (Oheimb et al., 2007), recently (< 50 years) protected European beech forests (Christensen et al., 2005), and for spruce and pine forests in Scandinavia (Siitonen, 2001). Also, deadwood volumes reported for oak-beech forests in Romania (Petritan et al., 2012) and for European oak-dominated forests (Vandekerkhove et al., 2009) are similar to our average value for oak-hornbeam forests. Our results for dead wood volume in low subalpine spruce forests (41 m^3 ha^{-1}) are considerably lower than the averages of 112 m^3 ha^{-1} found in Swiss NFRs (Rimle et al., 2017) and the averages of 143 m^3 ha^{-1} in subalpine spruce forests of Poland (Bujoczek et al., 2018). One reason for this could be the duration of the abandonment, since the NFR network has existed in Switzerland since 1940 (Rimle et al., 2017) and deadwood measurements in the boreal zone were carried out in primeval forest stands (Shorohova and Kapitsa, 2015). Also our values for spruce-fir-beech forests (109 m^3 ha^{-1}) are markedly lower compared to averages of 327 m^3 ha^{-1} in the Dinaric mountains with old-growth conditions (Keren and Diaci, 2018; Motta et al., 2015, 2011). Our averages for beech forests however notably exceed the reported values for forest reserves from other European countries such as Switzerland (Herrmann et al., 2012), the central Apennines (Persiani et al., 2016) and north-western Germany (Meyer and Schmidt, 2011). Taken together, forests in Austrian NFRs have accumulated rather high volumes of deadwood after c. 20 years of their designation, and these are mostly at our above published average from other European regions. However, it should be noted that measurement methods and threshold values do differ somewhat among different studies.

Our results show that especially in deciduous forests (beech forest, hardwood floodplain forest and spruce-fir-beech forest) lying deadwood accounted for a predominant proportion of the total deadwood (on average 85%) while standing deadwood was only found in low volumes. However, in coniferous forests (carbonate-pine forest, larch forest, mire spruce forest and subalpine spruce forest) standing and lying deadwood were almost equally distributed, with an average proportion of standing deadwood of 47%. These findings confirm the results for protected European beech forests of Christensen et al. (2005), who reported similar proportions of standing deadwood and further described a trend of increasing standing proportion in montane forests. Ganey et al. (2015) also found a positive correlation between standing deadwood and elevation for coniferous forests in Northern Arizona. However, the ratios of the individual forest types reported here differ from other studies, which described higher proportions in protected German beech forests (Meyer and Schmidt, 2011), but lower in Swiss spruce forests reserves (Rimle et al., 2017).

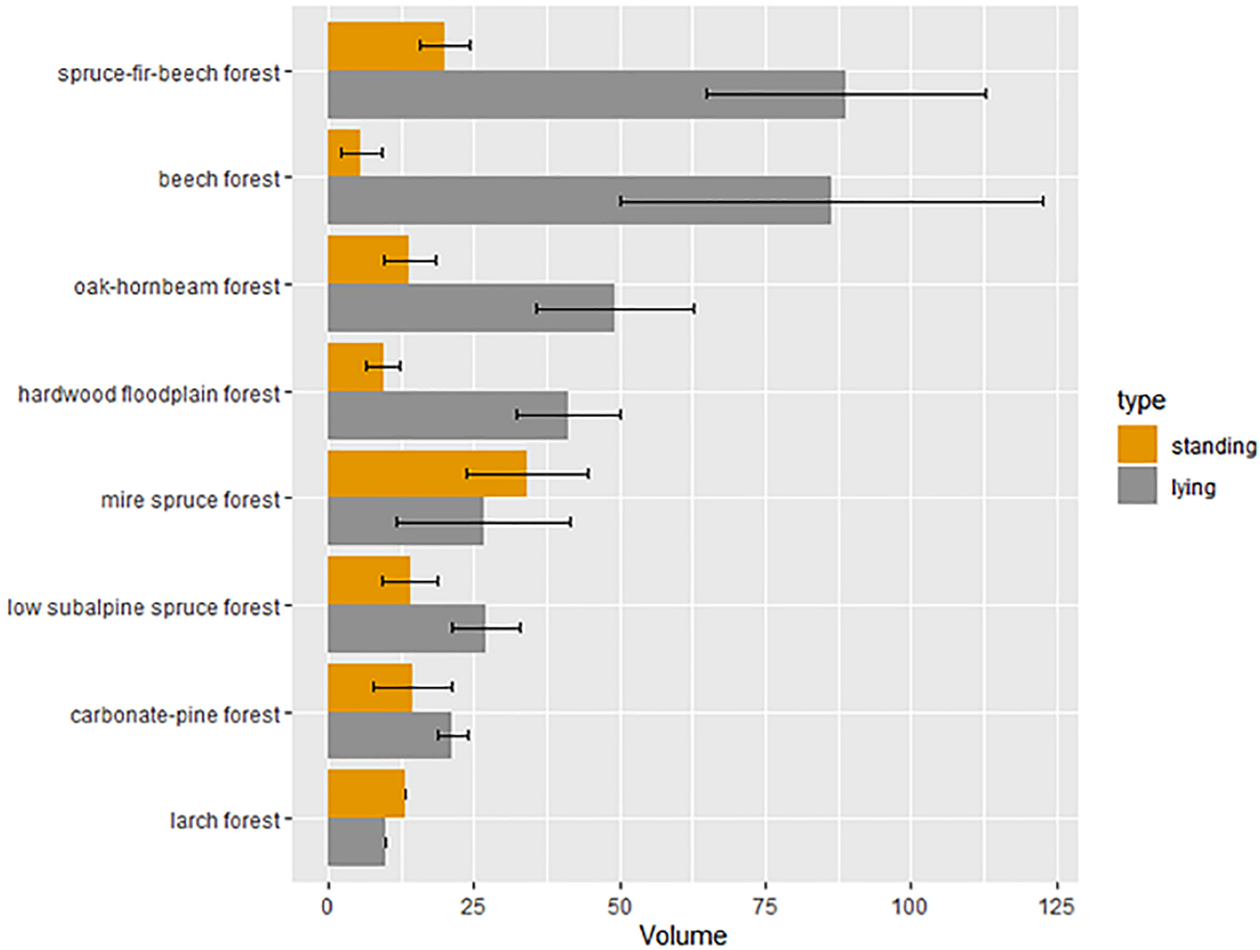

Fig. 4. Lying and standing (trees, trunks and stumps) deadwood volume in m^3 ha^{-1} for the eight investigated forest types. Plot values are weighted per NFR. Error bars denote standard errors.

We found that the tree species distribution of the living tree specimens is generally represented in the deadwood volume. While this is not surprising, it still is in contrast to other studies, where certain tree species were over- respectively underrepresented in the deadwood volume (Christensen et al., 2005; Meyer and Schmidt, 2011; Vandekerkhove et al., 2009). Deadwood ratios are relevant in restoration ecology, when determining the realistically achievable amount of deadwood being restored. Our average deadwood to total deadwood and living wood volume ratio of 12% (Fig. 2) is above the reported average of 5% for protected, natural and primeval forests in Poland (Bujoczek et al., 2018). Although it is usual for conditions to vary among the different forest types, our relatively high average shows that rather large amounts of deadwood has accumulated within the short period of abandonment. Deadwood ratios allow conclusions to be drawn on the severity of the events leading to mortality. Generally, selective events such as bark beetle outbreaks that kill one target species (e.g. Norway spruce) and thus exclusively add one species to the deadwood volume seem not to play an important role in Austrian NFRs. This confirms the results of Garbarino et al. (2015) and Vandekerkhove et al. (2009).

4.2. Deadwood diversity

We analysed complementary facets of compositional diversity of deadwood, i.e. tree species composition, degree of decomposition, diameter and type. These different facets of deadwood composition reflect the relevant characteristics of deadwood for dependent species. For instance, while some deadwood dwelling-species are highly specialized on certain tree species, other species are less selective in this regard, but need specific deadwood qualities such as state of decomposition, diameter and type) (e.g. Brin et al., 2009; Gossner et al., 2016; Lassauce et al., 2011; Müller and Bütler, 2010).

We found that different forest types differ profoundly in deadwood diversity. The volume of the respective forest type is not reflected in diversity, which is in contrast to the deadwood diversity index of Kunttu et al. (2015), who concluded that in more productive forests with higher species richness, also deadwood diversity can be higher. His study, however, was conducted in the boreal zone, comparing forest types in similar growing conditions. In contrast, our study is encompassing very diverse climatic conditions.

Decomposition and type diversity were more evenly distributed across forest types and—in contrast to Siitonen (2001)—did not reflect varying deadwood volumes of the forest types. Other studies have reported a lack of correlation between decomposition diversity and site conditions (e.g. Shorohova and Kapitsa, 2015), explaining these results with high continuity and variation of tree mortality. The considerable variation among forest types may be the result of different histories of disturbance and tree mortality as well as different decomposition rates of tree species in general and across climatic gradients (Christensen et al., 2005; Schuck et al., 2004; Shorohova and Kapitsa, 2015).

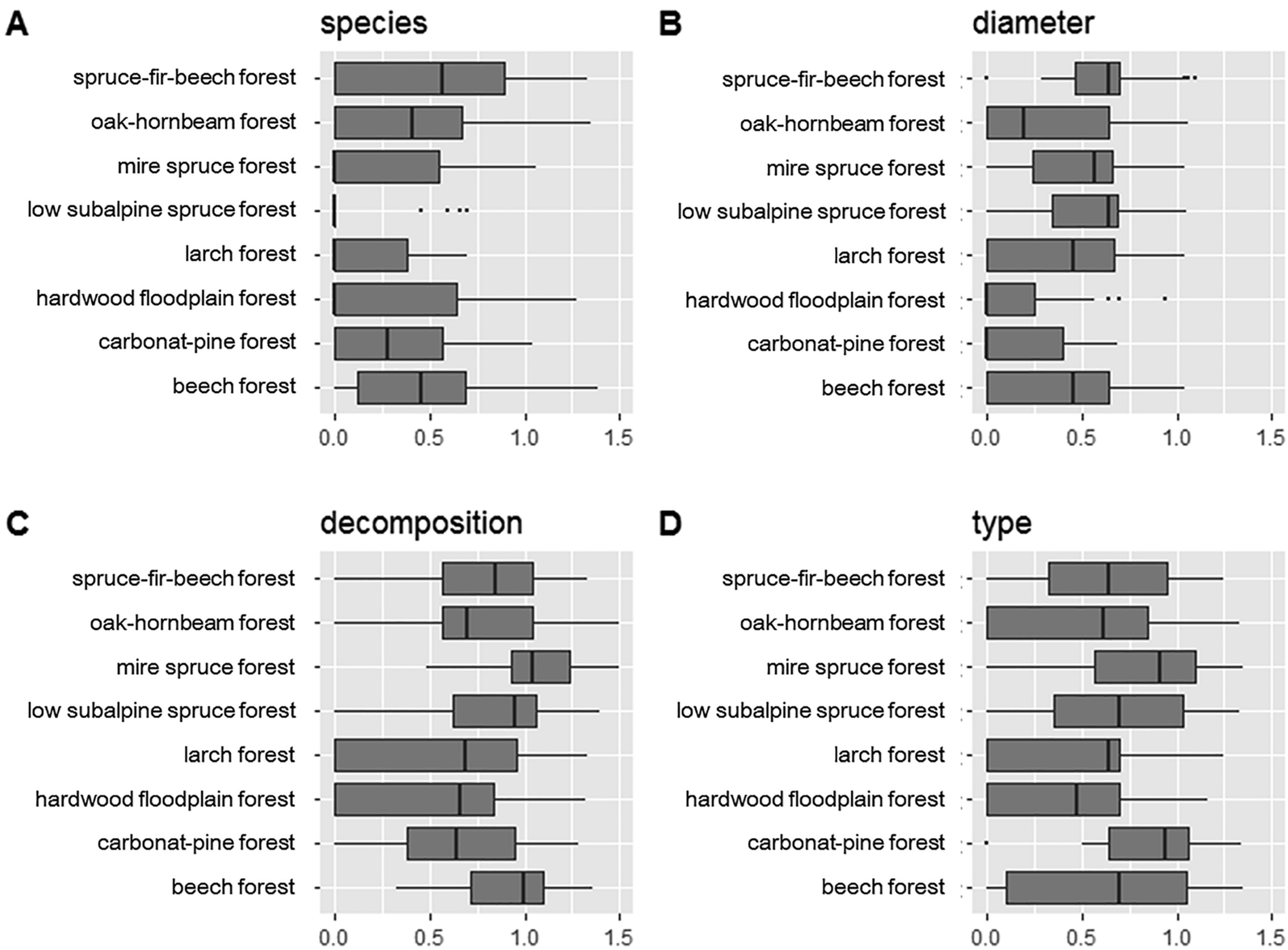

Fig. 5. Compositional diversity of deadwood in the different forest types. Shannon Index values for (A) tree species, (B) dbh classes, (C) decay classes and (D) types.

In summary, highest deadwood diversities were found for mixed beech and spruce forests, and the lowest for floodplain forests and carbonate pine forests. This can be explained by high variation and temporal continuity of mortality under different conditions and influencing factors. Hoppe et al. (2016) defined climatic conditions, like temperature and moisture, as important factors influencing decomposer community and activity. Therefore, decomposition of deciduous tree species progressed rapidly in hardwood-floodplain forest, while it was slow in coniferous dominated carbonate pine forest.

Table 4
Parameter estimates, std. errors, t-, and p values of fixed effects for the prediction of deadwood volume in NFR sites using generalised linear mixed models (error structure = Poisson; link function = log). Only significant explanatory variables occurring in the minimal adequate GLMM were included in the model.

Variables	Categories	Estimate	Std.Error	t value	p value
Elevation	elevation^2	−2.36E−06	0.000	−1.899	0.058
Forest type	beech forest	25.284	9.183	2.753	0.061
	carbonate-pine forest	24.545	9.175	2.675	0.077
	hardwood floodplain forest	25.106	9.086	2.763	0.011
	larch forest	21.676	8.419	2.574	0.016
	low subalpine spruce forest	22.664	8.313	2.726	0.012
	montane spruce forest	24.139	8.911	2.709	0.012
	oak-hornbeam forest	25.258	9.153	2.760	0.006
	spruce-fir-beech forest	25.395	9.101	2.791	0.006
Diameter at breast height (dbh)	dbh_cm	0.073	0.024	2.978	0.003
	dbh_cm^2	−5.00E−04	0.000	−2.398	0.017
Tree height	h_m	−0.328	0.056	−5.826	< 0.001
	h_m^2	6.47E−03	0.001	5.911	< 0.001
Volume	Vliving	−1.00E−03	0.001	−3.076	0.002
Temperature	t	−3.770	1.821	−2.071	0.038
	t^2	0.186	0.094	1.983	0.048

Table 5
Parameter estimates, std. errors, t-, and p values of fixed effects for the prediction of deadwood proportion in NFR sites using generalised linear mixed models (error structure = quasi-binomial; link function = logit). Only significant explanatory variables occurring in the minimal adequate GLMM were included in the model.

Variables	Categories	Estimate	Std.Error	t value	p value
Forest type	beech forest	−2.288	0.455	−5.031	< 0.001
	carbonate-pine forest	−2.896	0.627	−4.621	< 0.001
	hardwood floodplain forest	−2.391	0.412	−5.797	< 0.001
	larch forest	−4.126	0.799	−5.164	< 0.001
	low subalpine spruce forest	−3.702	0.741	−4.994	< 0.001
	montane spruce forest	−3.250	0.468	−6.947	< 0.001
	oak-hornbeam forest	−2.558	0.333	−7.716	< 0.001
	spruce-fir-beech forest	−2.994	0.628	−4.761	< 0.001
diameter at breast height (dbh)	dbh_cm	0.015	0.005	3.238	0.001
Volume	Vliving	−0.002	0.000	−6.559	< 0.001
	1/Vlivingˆ2	4.69 E+03	1.34 E+03	3.493	< 0.001
Precipitation	pˆ2	−4.80 E−07	0.000	2.068	0.039

4.3. Drivers for deadwood volume and composition

We analysed the underlying drivers that influence absolute volume of deadwood in different forest types, as well as the proportion of deadwood relative to total aboveground wood biomass. The GLMMs show that tree- and stand-related variables primarily as well as site variables and climatic variables affect both, deadwood volume and proportion. Forest type and mean annual temperature, were the best predictors for deadwood volume (Table 4), while the best predictors for deadwood proportion were volume of the living stand and forest type (Table 5).

Obviously, tree- and stand-related variables such as forest type and volume of the living stand influence deadwood volume as well as proportion. The comparison of the volume models with and without forest type showed, however, that an equally valid prediction is possible using less input variables, such as dbh, tree height and living volume. This is consistent with the results of Larrieu et al. (2014), who found no differences in patterns of deadwood availability in deciduous or coniferous forests. Other studies in turn show significant differences in the amount of deadwood depending on forest type (Lombardi et al., 2012; Saniga and Schütz, 2002). Living tree species diversity had no significant influence on deadwood volume and proportion and thus, was not included in the GLMMs, in contrast to Meyer and Schmidt (2011) and Laarmann et al. (2009).

Table 6
List of studies concerning deadwood volume in various European forest types during the last 20 years (2000–2019).

Forest type	Region/Country	Deadwood volume (m^3 ha^{-1})	Comment	References
Boreal coniferous forest	Northern Europe	59	northern boreal coniferous	Hahn and Christensen (2004)
Boreal pine forest	Scandinavia	20–120	boreal forest	Siitonen (2001)
Boreal spruce and pine forest	Northwestern Russia	132 ± 9		Shorohova and Kapitsa (2015)
Boreal spruce forest	Russia and Finland	41–170		Aakala (2010)
Boreal spruce forest	Finland	15–30		Ylisirniö et al. (2009)
Spruce forest	Finland	111 (70–184)	Southern Finland	Siitonen et al. (2000)
Spruce forest	Poland	191	Western Carpathians	Zielonka (2006)
Spruce forest	Switzerland	112 ± 30	NFR	Rimle et al. (2017)
Spruce forest	Poland	143	subalpine zone	Bujoczek et al. (2018)
Mountain mixed forest	Central Europe	216		Hahn and Christensen (2004)
Spruce-fir-beech forest	Bosnia and Herzegovina	327–387	old-growth forest Dinaric mountains	Keren and Diaci (2018)
Spruce-fir-beech forest	Bosnia and Herzegovina	327 (88–578)	Dinaric mountains	Motta et al. (2011)
Spruce-fir-beech forest	Bosnia and Herzegovina	327–420	Dinaric mountains	Motta et al. (2015)
Beech-fir forest	Poland	224	montane zone	Bujoczek et al. (2018)
Fir forest	Italy	17	fir dominated	Lombardi et al. (2012)
Mixed forests	Switzerland	119 ± 11	NFR	Bütler and Lachat (2009)
Beech-dominated forest	Switzerland	69	selected NFR	Herrmann et al. (2012)
Beech forest	Europe	130 ± 103		Christensen et al. (2005)
Beech forest	North-western and central Europe	86 ± 10	beech dominated	Vandekerkhove et al. (2009)
Beech forest	Germany	8–57	Lower Saxony	Meyer and Schmidt (2011)
Beech forest	Germany	94	North-eastern Germany	Oheimb et al. (2007)
Beech forest	Czech Republik	170–242	Kronose Nationalpark (two plots)	Vacek et al. (2015)
Beech forest	Czech Republic	48	Central Bohemia	Bilek et al. (2011)
Beech forest	Ukraine	163 ± 8	Carpathians	Hobi et al. (2015)
Beech forest	Italy	143	beech dominated	Lombardi et al., 2012
Beech forest	Italy	14–89	Central Apennines	Persiani et al. (2016)
Oak-beech forest	Romania	75 (13–161)	pure beech	Petritan et al. (2012)
	Runcu-Grosi Nationalpark	135 (29–325)	beech dominated	
		134 (32–296)	sessile oak dominated	
Oak forest	North-western and central Europe	52 ± 7	oak dominated	Vandekerkhove et al. (2009)
Oak forest	Hungary	45		Bölöni et al. (2017)
Oak forest	Austria	107	NFR Lange Leitn	Rahman et al. (2008)
Oak forest (holm oak)	Italy	44	Central Apennines	Persiani et al. (2016)
Oak-hornbeam and riparian forest	Poland	104		Bujoczek et al. (2018)
Deciduous forest	Poland, Bialowieza NP	87–187	Tilio Carpinetum	Bobiec (2002)
Riparian forest	Poland, Bialowieza NP	126–160	Circaeo-Alentum	Bobiec (2002)

Climatic variables only had a minor influence, such as temperature on deadwood volume. It was negatively correlated to deadwood volume—in contrast to Shorohova and Kapitsa (2015), who observed a linear increase in deadwood volume with increasing temperature for boreal spruce forest whereas our study covered a wide range of forest types and environmental conditions. Rimle et al. (2017) suggested that slower decay rates in mountain reserves due to colder climate increase deadwood in higher altitudes. This is in line with the results of Přívětivý et al. (2016), who also reported on longer retention time of deadwood in colder climate. Also the higher proportion of slowly decomposing coniferous species in montane forests might affect the decomposition process (Harmon et al., 1986). Additionally, Bujoczek et al. (2018) argued differences between montane and lowland altitudes with greater shares of spruce which is susceptible to barkbeetle infestation. Precipitation was included for predicting deadwood proportion, hence with minor influence, while it did not affect deadwood volume in our study. However, from other studies it is known that high precipitation increases deadwood volumes, as this impairs the tree stability. Prolonged precipitation increases soil moisture, which affects root anchoring, so that wind throws often occur on wet soils (Mitchell, 2013). In addition, precipitation and an increased moisture influence wood fungal activity (Büntgen et al., 2012; Srivastava et al., 2014), which can accelerate the process of tree mortality.

Our results show that both deadwood volume and proportion are not correlated with slope and aspect. Hence, from other studies we know that deadwood amounts are likely to be higher in south-facing slopes, due to slower decomposition and low moisture and nutrient availability (Rubino and McCarthy, 2003); additionally south-exposed sites are more susceptible to heat stress and bark beetles.

Other factors we did not take into account here, contribute to the accumulation of deadwood. From previous studies, we know, that disturbances (Brassard and Chen, 2008; Christensen et al., 2005; Matteo Garbarino et al., 2015; Siitonen, 2001), stand age (Doerfler et al., 2017; Vandekerkhove et al., 2009) and time of abandonment (non-intervention of forest management) (Christensen et al., 2005; Vandekerkhove et al., 2009) are very important variables affecting deadwood availability in non-managed forests. As our study is limited to a single survey of deadwood in NFRs, we did not analyse the temporal trajectory of deadwood accumulation and residence time. In order to improve our understanding of temporal dynamics of deadwood accumulation, the diverse and often interrelated causes of tree mortality should be investigated further. In particular, there is a severe lack of studies concerning the continuity patterns (persistence) and spatial distribution of deadwood (Larrieu et al., 2014; Rimle et al., 2017) as well as its properties such as diversity (type of deadwood, dimensions, degree of decomposition). The spatial distribution of deadwood with large diameters is particularly important for deadwood-dependent species with limited dispersal capabilities and long development phases. A continuous availability of deadwood at a given site is essential for the survival of such species (Larrieu et al., 2014; Parisi et al., 2016; Ylisirniö et al., 2009). Thus far, however, only very few studies have investigated the spatial continuity of deadwood (e.g. Rimle et al., 2017; Ylisirniö et al., 2009).

The Austrian NFR program has been established only few decades ago and therefore our study covers a limited period of time. In addition, the various NFR sites differ greatly in historical silvicultural land-use. Nevertheless, our results show attributes usually associated with old-growth forests, such as remarkably high lying deadwood volumes and wide decomposition class distribution (e.g. Bauhus et al., 2009; Keeton, 2006). The observed values are similar to other studies in unmanaged forests in Europe and clearly exceed the values for managed forests. They provide reference values for forest managers and owners who are confronted with substantial uncertainties how best to improve the biodiversity value of their forests. Our findings can be used for the elaboration and specification of biodiversity strategies and guidelines for sustainable forest management aimed at increasing deadwood qualities in order to create suitable habitats for saproxylic species.

Future studies should therefore focus on the separate prediction of standing and lying deadwood in natural forests, as the habitat requirements of specialized and therefore often threatened species can vary greatly. Separate predictions could provide more detailed information for forest managers necessary to increase habitat availability. Active accumulation of deadwood in managed forests has been stated as a valuable tool to increase habitat availability (Doerfler et al., 2017), however, more precise information and guidance for forest management with regard to different forest types is needed. In this context, reliable information from protected forests (such as NFRs) is needed (Bugmann and Brang, 2009). Deadwood volume thresholds as reference values for biodiversity or forest naturalness should be applied specifically to forest types and considering site properties. Even then, variation within forest types remains high, as our results show.

5. Conclusions

This study gives an overview of patterns and drivers of deadwood volume and composition in eight forest types within the Austrian NFRs. Deadwood volumes differ a lot among forest types, highest average deadwood volumes were found in spruce-fir-beech forests (109 m^3 ha^{-1}), and lowest in larch forests (23 m^3 ha^{-1}). In general, our values correspond to the published averages from other European regions. This shows that after a relatively short period of abandonment, a considerable amount of deadwood–similar to old-growth forests–can be achieved. Deadwood is apparently a structural feature that seems to regenerate rapidly after cessation of management. Probably for this reason, too, deadwood volume is often used as an indicator for biodiversity or forest naturalness. However, this only applies to the comparison of deadwood volumes between forest stands of the same forest type.

The compositional diversity in terms of species, diameter classes, decomposition classes and types differed greatly among forest types, highest diversities were found in beech forests, and spruce-fir-beech forests whereas lowest diversities were found in floodplain forests and carbonate pine forests. The variation in diversities is based on forest type and tree species related attributes. As diversity of deadwood is strongly linked to biodiversity and certain species depend on a high structural diversity to meet their life history requirements, shaping the compositional structure in deadwood in managed forests should be addressed.

The underlying drivers that influence deadwood volume as well as the proportion of deadwood are tree- and stand-related variables, site variables and climatic variables. Forest type, tree diameter, and volume of the living stand influence both, volume and proportion of deadwood. However, according to our study, there are also drivers that differ depending on whether volume or proportion of deadwood is investigated. For example, mean annual temperature seems to influence volume, but not proportion, whereas precipitation influences proportion, but not volume. Dealing with the processes that influence deadwood occurrence is important when aiming to increase the amount of deadwood and therefore is of valuable information for forest management and nature conservation. Finally, deadwood proportion, which is directly related to the total aboveground wood biomass, should be considered as an additional forest biodiversity indicator.

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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Appendix A

(See Figs. A1 and A2).

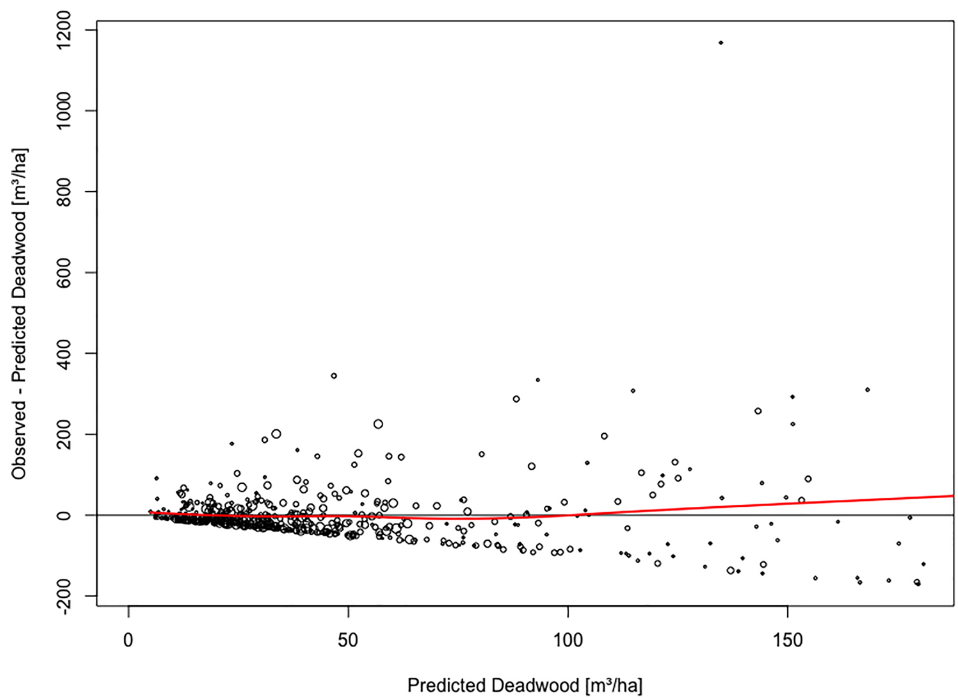

Fig. A1. Comparison of measured with predicted values for deadwood volume (model a) to check goodness of fit.

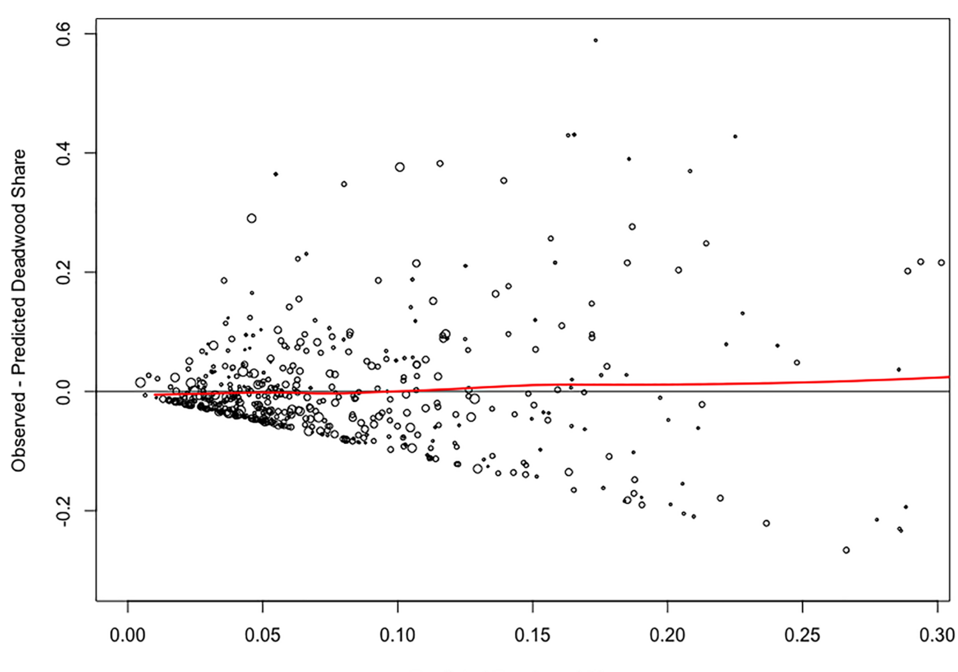

Fig. A2. Comparison of measured with predicted values for deadwood proportion (model b) to check goodness of fit.

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