143. Jahrgang (2026), Heft 2, S. 151–186

Austrian Journal of Forest Science
Centralblatt für das gesamte Forstwesen

Deadwood quantity, quality and decomposition processes in *Picea abies* L. dominated Natural Forest Reserves in Austria

Totholzmenge, Totholzqualität und Zersetzungsprozesse in Picea abies L. dominierten Naturwaldreservaten in Österreich

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Keywords: Necromass, decay rates, coarse woody debris, conservation, habitat value, carbon, biodiversity, oldgrowth forests, Norway spruce

Schlüsselbegriffe: Nekromasse, Zerfallsgeschwindigkeit, Naturschutz, Habitatqualität, Kohlenstoff, Biodiversität, Urwälder, Gemeine Fichte

Abstract

Forest biodiversity, habitat value and carbon sinks are strongly linked to deadwood quantity (stocks) and quality (decay class). Repeated measurements of unmanaged forests allow to quantify the natural range of deadwood properties for different ecosystems and describe the dynamics over time, which can support recommendations in conservation and carbon management. In our study we repeatedly investigated the growing stock and deadwood conditions in six natural forest reserves (NFR) in Austria using 167 permanent monitoring plots to examine the changes over time. Apart from one, all studied NFR showed constant live tree volume stocks non-significantly changing over 12 years, with a highly variable small tree density, suggesting that these forests are in optimal to climax/terminal phase. Standing deadwood stocks, including stump deadwood, have been increasing in all but one NFR and lying deadwood stocks increased in all but two NFRs. Summarizing measured above ground deadwood and live volume and using deadwood density and carbon fraction data

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from literature suggest that two NFRs are on average accumulating carbon at about +1 tC/ha per year, and two NFRs have decreasing live and dead carbon stocks at -0.2 to -0.4 tC/ha per year. A consistent relationship between time since death (TSD) and decay class (DC) was found across all sites. Based on the relations between TSD and DC, a model for future deadwood volumes in different decay classes in Norway Spruce-dominated forests is made. Recommendations for future research and monitoring in NFR are given.

Zusammenfassung

Biodiversität, Habitatqualität und Kohlenstoffsenken von Wäldern stehen in einem klaren Zusammenhang mit der Totholzmenge (Bestand) und Qualität (Zersetzungsklasse). Wiederholungsaufnahmen in unbewirtschafteten Wäldern ermöglichen es die natürliche Variabilität von Totholz in unterschiedlichen Waldökosystemen zu quantifizieren und die zeitliche Dynamik zu beschreiben, was bei der Erarbeitung von Empfehlungen im Naturschutz- und Kohlenstoffmanagement helfen kann. In dieser Studie haben wir den Lebend- und Totholzbestand in sechs Naturwaldreservaten (NWR) in Österreich, auf Basis von 167 permanenten Monitoringflächen, hinsichtlich dessen Entwicklung über die Zeit untersucht. Bis auf eines zeigten alle NWR einen konstanten Lebendvorrat ohne signifikante Veränderung über einen Zeitraum von 12 Jahren. Die Stammzahl kleiner Bäume variierte stark, was daraufhin hinweist, dass sich diese Wälder in der Optimalphase bzw. Klimax-/Terminalphase befinden. Stehender Totholzvorrat, einschließlich Stocktotholz, hat bis auf einem in allen NWR zugenommen und der liegende Totholzvorrat hat in allen bis auf zwei NWR zugenommen. Der gesamte gemessene Lebend- und Totholzvorrat weist in Kombination mit den aus der Literatur ermittelten Totholzdichte und Kohlenstoffgehalt darauf hin, dass die mittlere Kohlenstoffmenge in zwei NWRs um etwa +1 tC/ha pro Jahr angestiegen ist, während in zwei NWRs die Menge an Lebend- und Totholz-Kohlenstoff um etwa -0.2 bis -0.4 tC/ha pro Jahr gesunken ist. Ein deutlicher Zusammenhang konnte zwischen der Zeit seit dem Absterben (TSD) und dem Zersetzungsgrad (DC) auf allen Flächen beobachtet werden. Aus der Beziehung zwischen TSD und DC wurde ein einfaches Modell entwickelt, um zukünftige Totholzvorräte in subalpinen Fichtenwäldern abzuschätzen. Empfehlungen für die zukünftige Forschung und Monitoring in NWR werden gegeben.

1 Introduction

Upcoming changes in forest policy, public demand for more protected areas and landowner decisions leading to (partial or temporary) abandonment of active forest management will likely lead to changes in tree species composition and forest structures across various forest types in Europe. The amount of deadwood in forests will likely increase due to no or more extensive forest management, by setting-aside forests for conservation or carbon storage purposes, prolonging rotation periods and/or retaining harvest residues on-site. Increases in deadwood stocks can be also expected from increasing frequency and severity of disturbances (Senf and Seidl, 2021), such as bark beetle outbreaks or storm damage, that will likely become more under climate change will lead to an increasing volume of standing and lying deadwood, depending on disturbance agent and salvage-logging. As deadwood is also one of many indicators for "old-growthness" or naturalness (Borghi *et al*., 2023; Lassauce *et al*., 2011; Vandekerkhove *et al*., 2022), this can also impact biodiversity assessments. However, as habitat value and thus biodiversity is linked by rather complex relations with deadwood quantity and quality (Müller *et al*., 2015; Vítková *et al*., 2018), comprehensive information on deadwood and its decomposition is needed to evaluate the consequences of conservation management or extensive forest management.

In Austria, since 1995 almost 200 Natural Forest Reserves (NFR) have been established. An earlier study published in this journal, synthesized data measured in 2009 as part of the project ELENA from five NFRs established between 1997 and 1999 (Ruprecht *et al*., 2012). In this study, we built on that pilot study to understand changes in deadwood quantity and quality and explore possible limits to deadwood volume stocks using repeated observations of unmanaged natural forests dominated by Norway spruce (*Picea abies* L.) due its wide distribution in Europe and important contributions to forest carbon stocks and economic value of European forests (Caudullo *et al*., 2017; FOREST EUROPE, 2020). Norway spruce is still the most widespread tree species in Austria and accounts for almost half of Austrian forest area, despite widespread decline and mortality events (Jandl, 2020). Deadwood volume stocks can be as large or even larger than live tree stocks, depending on development stage, disturbance regimes and decay rates (Harmon *et al*., 2020; Wijas *et al*., 2024). While carbon storage in deadwood decreases as decay progresses (and deadwood density decreases), deadwood volume can represent a considerable carbon storage in forests and increasing deadwood carbon stocks contributed to global temperate and boreal forests being a carbon sink between 1990 and 2020 (Pan *et al*., 2024). For long, live trees have been the focus of carbon assessments, being the primary producers, representing usually the largest carbon component (after organic and mineral soil) and due to easier sampling and biomass estimates, but the importance of dead trees for the forest carbon cycle are becoming more and more acknowledged (Seibold *et al*., 2021; Wijas *et al*., 2024). The contributions of deadwood to forest carbon sink depend on changes in deadwood quantity (stocks) and quality (decay stage, decay class). Deadwood decay class is a potent proxy for amount of dry biomass and carbon stored in 1 m^3 deadwood and can be assessed in the field (Fravolini *et al*., 2018; Öder *et al*., 2021). Increasing deadwood volume stocks will likely be associated with increasing deadwood carbon stocks, unless the deadwood decay classes shift towards more advanced decay stages (Neumann *et al*., 2023). Thus, assessing deadwood quantity and quality over time allows us to track the contributions of deadwood to carbon stocks and habitat value in NFRs in Austria and contrast them to live tree stocks.

The objectives of this study are,

(1) to quantify deadwood quantity and quality, separated by standing and lying deadwood for Norway spruce-dominated NFRs in Austria,
(2) to assess changes in live tree and deadwood volume and carbon in Norway spruce-dominated NFRs in Austria over a period of 12 years, in comparison with literature data from other NFRs, and
(3) to make predictions of deadwood dynamics (i.e., changes in deadwood volume over time) by estimating decay rates using decay classes and time since death for Norway spruce-dominated NFRs in Austria.

2 Methods

We used empirical data sampled in six NFRs (Goldeck n = 30, Hutterwald n = 29, Kronawettgrube n = 19, Krimpenbachkessel n = 25, Laaser Berg n = 21 and Schiffwald n = 43, with a total number of 167 sample plots, each measured two times) representing sub-alpine Spruce forests (*Piceetum*) and montane Spruce-fir forests (*Abietetum*) with an elevation range from 1000 to 1700 m (Fig. A1). We reanalyzed data used by Ruprecht *et al*. (2012) to compare the forest conditions in 2008-10 with those in 2021, representing on average 12 years of continuous monitoring using permanent sample plots. Some of the collected data was reported in student thesis (Götze, 2013; Hardalau, 2022; Huber, 2022; Kasseroler, 2011; Starcevic, 2022; Winter, 2009).

2.1 Live and deadwood volume

We grouped deadwood into 5 cm diameters classes, consistent with the methodology used by (Ruprecht *et al*., 2012) for live trees. We removed standing deadwood with diameter at breast height (DBH) smaller than 5 cm and lying deadwood with mid diameter smaller than 10 cm, to be consistent and results comparable between regions and plots. We calculated stem density, basal area and volume per hectare based on a sample plot size of 300 m² (radius 9.77 m). For lying deadwood, we calculated volume assuming the shape of a cylinder, as mid diameter was measured. If mid diameter or deadwood length was not measurable, we assumed it to be the average of all other lying deadwood pieces in that plot, respectively. If both diameter and length were not measurable (*e.g*. for heavily decomposed pieces or irregular shaped deadwood fragments), we ignored this deadwood piece for volume assessment. For standing deadwood and live trees, we calculated volume using form factors, FF (Eq. 1). Tree height, H, was measured for all standing live and dead trees.

$$V = FF\ DBH^2\ \pi / 4\ H \qquad (1)$$

For standing deadwood, we accounted for changes in stem taper due to crown or stem break by varying FF. For living trees, we calculated FF using the equations of Pollanschütz (1974) also used for the Austrian National Forest Inventory. For standing dead trees with branches still attached to crown, we assumed FF of 0.4, equal to living trees. For standing dead trees without crown, we assumed FF to be 0.7 and for dead stumps and lying deadwood, we assumed FF to be 1, thus having a shape of a cylinder. For lying deadwood, the mid diameter, MD, was used instead of DBH and length, L, instead of H, for calculating volume (Eq. 1). Relations between DBH/ MD and H/L are shown in Figs A2-4. We used mean live and deadwood volume stocks reported by Oettel *et al*. (2020) from low subalpine spruce forests (number plots = 44) and spruce-fir-beech forests (n = 114), to compare our data against literature data on other Austrian NFRs with similar forest types. We note that data on the NFRs reported in Oettel *et al*. (2020) were not included in Ruprecht *et al.* (2012) or this study. We used dry wood density and carbon fraction of live trees to estimate their carbon stocks after Neumann *et al*. (2016). Since there is no published Austrian data available for deadwood density and carbon fraction grouped by the decay classes used here, we used data collected in Switzerland, for similar forest types and management systems (Hararuk *et al*., 2020). We used density and C fraction of "*Picea abies*" for all conifers and "*Fagus sylvatica*" for all broadleaves.

We used histograms (pooling trees into 5-cm classes, consistent with the pilot study) and boxplots to compare changes in stem density and volume stocks of live trees, standing dead and lying dead trees. Kruskal-Wallis tests were used to assess statical differences between measurement times for the six NFRs, as data was non-normally distributed and positively skewed. We calculated differences in two ways,

(1) between mean values of deadwood on plots grouped by NFR and sampling year and
(2) by pair-wise comparing plots with the same ID, to apply greater scrutiny to assessed changes over time.

Option (2) further allowed us to check for significant changes.

2.2 Deadwood decay classes and deadwood dynamics

Information on deadwood decay rates, transition time between decay classes or deadwood residence time (Kruys *et a*l., 2002; Russell *et al*., 2014, 2013; Vrška *et al*., 2015) is required to understand changes in deadwood quantity (volume) and quality (decay class) over time. For the NFRs used in this study, an assessment of the time since death, henceforth abbreviated with TSD, in years of observed deadwood pieces was made on site. Deadwood decay was assessed using a five-class decay classification system (Ruprecht and Vacik, 2009), expanding the four-class system (Albrecht, 1991; Rauh and Schmitt, 1991) with a fifth class for highly decayed, humus-like deadwood with in total five decay classes, henceforth abbreviated with DC (Table 1). We pooled deadwood volume by decay class, to track changes in deadwood quality over time. We linked DC and TSD using regression functions, to check the time needed for state-transitions through the here used DC system, after replacing letters (A-E) with numbers (1-5) to allow fitting regression functions. We checked for non-linear behavior using second-order polynomial functions, in comparison to linear functions. We considered using mixed effects models, but decided to use separate models to demonstrate the effects of region, deadwood type and species on the relations between TSD and DC. By using ordinary least squares, we assume that independent variable (DC) is error-free. We then used the functions linking TSD and DC for estimating changes in deadwood volume over time. We calculated Nagelkerke pseudo-R^2 to assess model performance. All analysis and visualization of results was done using R statistical software (R Development Core Team, 2021).

Table 1: Description of used decay classes (in brackets numerical transformed), translated into English from German, reported in Ruprecht and Vacik, (2009).

Tabelle 1: Beschreibung der verwendeten Zersetzungsklassen (in Klammer der numerisch transformierte Wert), übersetzt in Englisch von Deutsch, überliefert in Ruprecht und Vacik (2009).

Decay class	Description
A (1)	fresh dead, bark still attached on wood, inserted nail cannot be pulled out
B (2)	beginning decay, bark start falling off, inserted nail cannot be pulled out
C (3)	advancing decay, bark partly shed, inserted nail can be pulled out
D (4)	strong decayed, bark mostly shed, wood structure soft but still recognizable
E (5)	humus, wood structure not recognizable

3 Results

3.1 Size variations of deadwood in Spruce-dominated nature forest reserves using two measurement periods

Stem density distributions of live trees averaged for the six NFRs, separated for the first measurement and remeasurement about 12 years later, reveal slight changes for higher diameter classes and more pronounced changes for live trees smaller than 10 cm DBH, especially for Goldeck and Krimpenbachkessel (Fig. 1). For NFR Krimpenbachkessel, we observed gains in live tree density (predominantly driven by the 0-5 cm class), while all other NFRs lost live tree density (see also Table 2).

We also observed notable shifts in the standing dead trees (Fig. 2) and losses in live trees were commonly associated with gains in standing dead trees (with Goldeck being an exception, Table 2). Again, most change we can observe for smaller diameters. Gains in live trees and losses in deadwood density suggest NFRs are predominantly in "early optimal phase" and "regeneration phase" according to literature (Korpel, 1995; Mayer and Neumann, 1981; Zukrigl *et al*., 1963), where the forest are accumulating live tree volumes and growth rates are exceeding mortality. Losses in live trees and gains in deadwood would suggest the analyzed NFRs being in "climax phase" and "decay phase", while losses in both live trees and deadwood would suggest them being in "collapse phase" (see Korpel, 1995; Scherzinger, 1996).

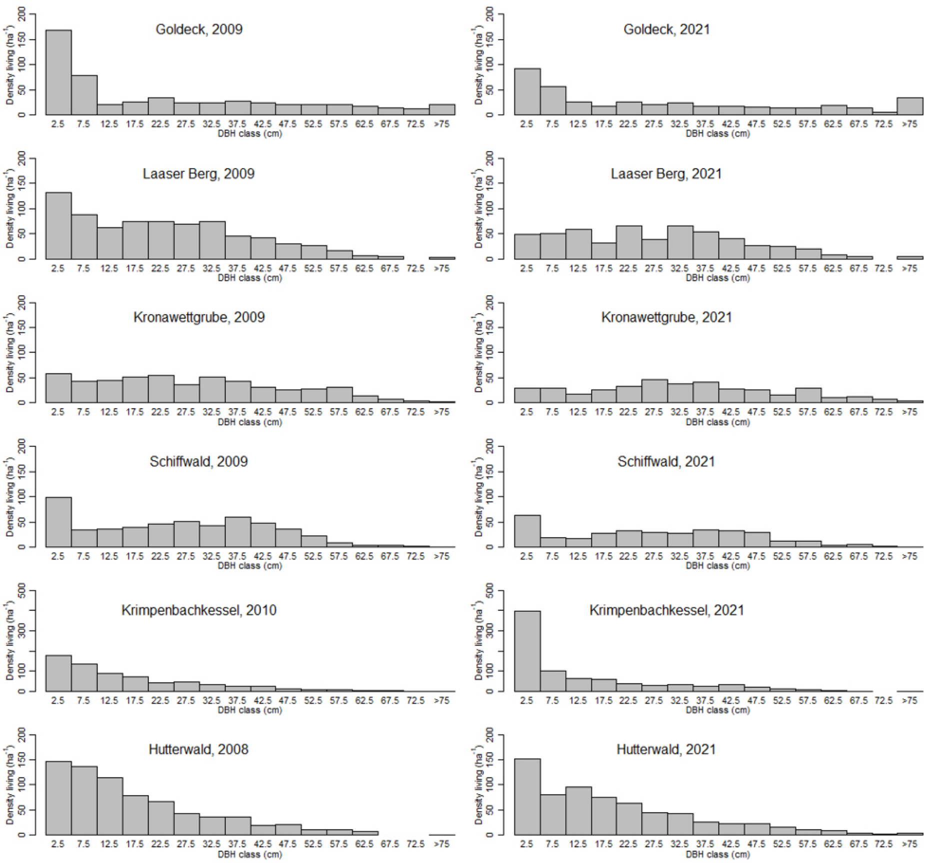

Figure 1: Live tree density (ha-1) versus diameter at breast height (binned into 5-cm classes) for measurements in 2008-2010 with the remeasurements in 2021. We show mean values for each class and for each NFR for 2008-2010 and 2021. Note the different extent of y-axis for Krimpenbachkessel.

Abbildung 1: Stammzahl lebender Bäume (ha-1) versus Brusthöhendurchmesser (gruppiert in 5-cm Klassen) für die Messungen von 2008-10 und die Wiederholungsaufnahmen in 2021. Wir zeigen Mittelwerte für jede Klasse und jedes NWR für 2008-10 und 2021. Bitte die unterschiedliche Y-Achsen für Krimpenbachkessel beachten.

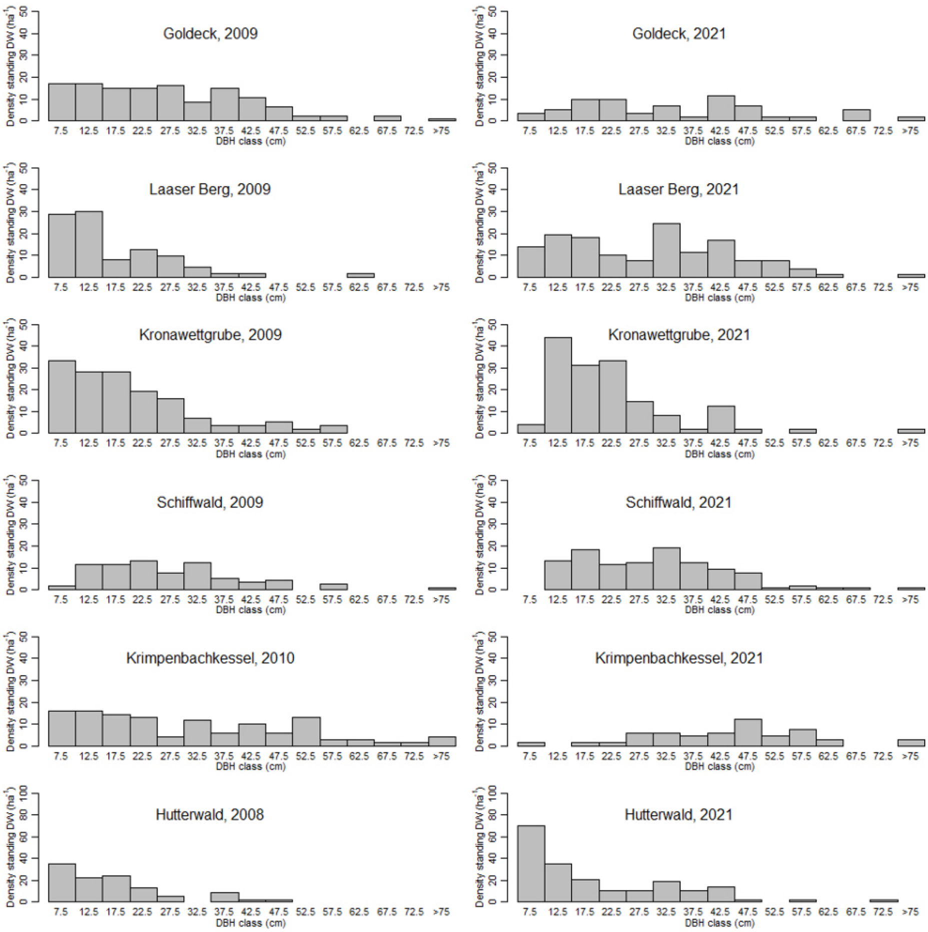

Figure 2: Standing deadwood density (ha-1) versus diameter at breast height (binned into 5-cm classes) for measurements in 2008-2010 with the remeasurements in 2021. For details see Fig. 1. Note the different extent of y-axis for Hutterwald.

Abbildung 2: Anzahl toter stehender Bäume (ha-1) versus Brusthöhendurchmesser (gruppiert in 5-cm Klassen) für die Messungen von 2008-10 und die Wiederholungsaufnahmen in 2021. Für Details verweisen wir auf Abb. 1. Bitte die unterschiedliche Y-Achsen für Hutterwald beachten.

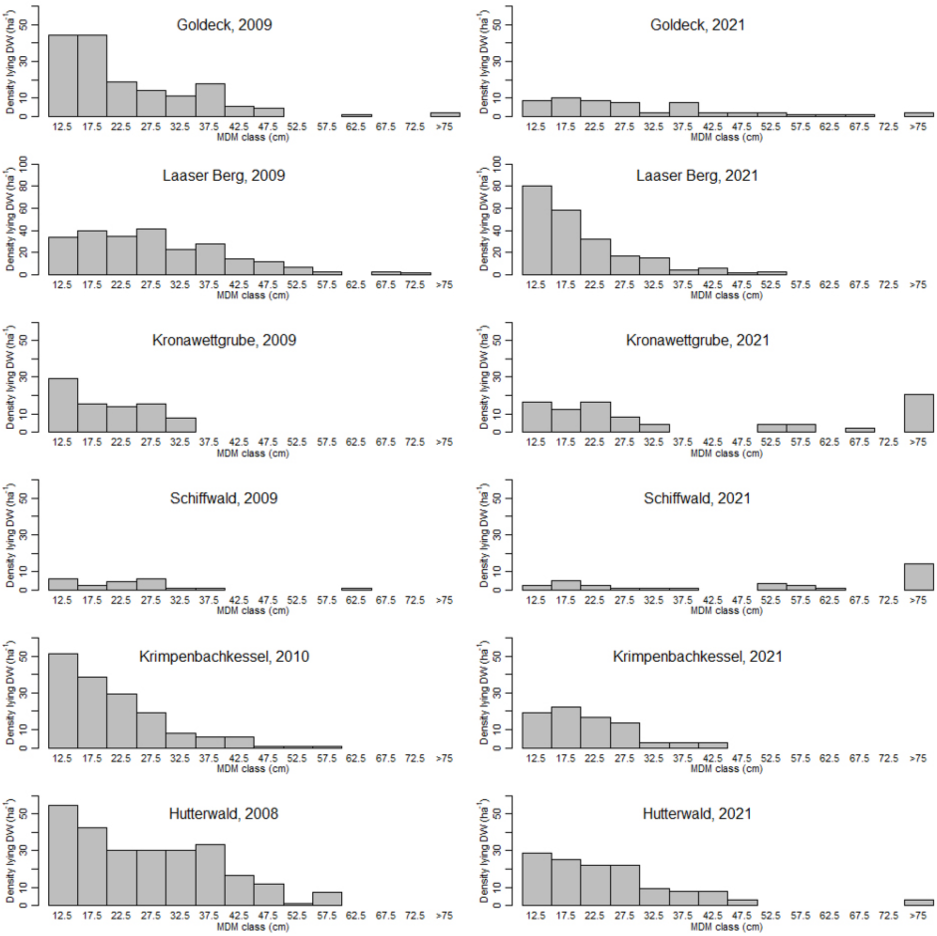

Figure 3: Lying deadwood density (ha-1) versus mid diameter (binned into 5-cm classes) for measurements in 2008-2010 with the remeasurements in 2021. For details see Fig. 1. Note the different extent of y-axis for Laaser Berg.

Abbildung 3: Anzahl toter liegender Bäume (ha-1) versus Mitteldurchmesser (gruppiert in 5-cm Klassen) für die Messungen von 2008-10 und die Wiederholungsaufnahmen in 2021. Für Details verweisen wir auf Abb. 1. Bitte die unterschiedliche Y-Achsen für Laaser Berg beachten.

Table 2: Change in density of live trees, standing deadwood and lying deadwood between 2008-10 and 2021 for all analysed NFRs (Table A1 shows the density per hectare in 2008-10 and 2021). We show sum of all measured trees and trees with diameter >10 cm (consistent size class measured for all groups) and binned into 5-cm classes. Gains are color-coded blue and losses in red. "-" indicates that this diameter class was not surveyed consistently.

Tabelle 2: Veränderungen in Stammzahl lebender Bäume, stehenden und liegenden Totholz zwischen 2008-10 und 2021 für alle analysierten NWR (Tabelle A1 zeigt die Stammzahl pro Hektar 2008-10 und 2021). Wir zeigen die Summen für alle gemessenen Bäume und Totholzstücke, die Summen mit Brusthöhendurchmesser/Mitteldurchmesser > 10 cm (konsistente Größenklasse für die drei Gruppen) und die Werte gruppiert nach 5-cm Klassen. Zunahmen werden blau dargestellt und Abnahmen in Rot. "-" zeigt, dass diese Durchmesserklasse nicht erhoben wurde.

NFR	Component	Change from 2008-10 to 2021 (ha^{-1})																	
		all	>10	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	>75
Goldeck	living	-143	-44	-77	-22	4	-8	-9	-3	-1	-9	-7	-6	-7	-8	1	0	-7	13
	standing	-61	-47	-	-14	-12	-5	-5	-13	-2	-13	1	0	0	0	0	3	0	1
	lying	-107	-107	-	-	-36	-34	-10	-7	-9	-10	-3	-2	2	1	0	1	0	0
Laaser Berg	living	-208	-87	-83	-37	-4	-42	-9	-31	-9	8	-3	-4	-1	3	3	0	0	3
	standing	45	60	-	-14	-11	10	-2	-2	20	10	15	8	8	4	0	0	0	1
	lying	-22	-22	-	-	47	19	-3	-24	-8	-24	-9	-10	-4	-3	0	-3	-1	0
Krona-wettgrube	living	-123	-81	-28	-14	-27	-24	-21	10	-13	-2	-3	0	-11	-2	-2	6	5	3
	standing	7	36	-	-29	16	3	14	-1	1	-1	9	-3	-2	-1	0	0	0	2
	lying	7	7	-		-13	-3	3	-7	-4	0	0	0	4	4	0	2	0	21
Schiffwald	living	-187	-136	-36	-15	-19	-13	-13	-22	-15	-25	-16	-6	-10	2	0	2	0	0
	standing	35	37	-	-2	2	6	-2	5	7	7	6	3	1	-1	1	1	0	0
	lying	13	13	-	-	-4	2	-2	-5	0	0	0	0	4	3	0	0	0	14
Krimpen-bachkessel	living	129	-51	216	-36	-27	-14	-7	-17	-1	0	8	6	3	2	-1	-2	-1	0
	standing	-66	-51	-	-14	-16	-13	-12	2	-6	-1	-4	6	-8	5	0	-1	-1	-1
	lying	-81	-81	-	-	-32	-16	-13	-5	-5	-3	-3	-1	-1	-1	0	0	0	0
Hutterwald	living	-52	-2	6	-55	-18	-3	-2	2	7	-9	3	2	6	0	2	3	2	2
	standing	84	49	-	35	13	-3	-2	5	19	1	12	0	0	2	0	0	2	0
	lying	-129	-129	-	-	-26	-17	-8	-8	-21	-25	-9	-9	-2	-8	0	0	0	3

Changes in stem density by diameters class do not reflect changes in height (length for lying deadwood) and volume. Thus, we next looked into changes in volume (proxy for biomass and carbon stocks, assuming that density of live and dead trees are comparable) over time. Decreasing stem density of live trees larger 10 cm (Fig. 1) observed for all NFRs coincide with constant or decreasing volume stocks of live trees (Fig. 4). We show the mean volume stocks by NFR separated in Table 3. The decrease was not significant, except for NFR Schiffwald, which also had the largest loss in live trees > 10 cm DBH (Table 2). Only in NFR Hutterwald mean live tree volume stocks increased notably over 12 years of remeasurements (see also Table 3). Variation of standing and lying deadwood was clearly skewed and more variable than live tree volume. NFRs Schiffwald, Kronawettgrube and Laaser Berg notably increased in deadwood stocks, while the increase was significant only for Schiffwald and Laaser Berg (Fig. 4). The pair-wise comparison of plots yielded in general similar results than using averages by NFR (Table 3), however for NFR Schiffwald the change was not strongly significant (p 0.01). Only for the lying deadwood in Laaser Berg also the pair-wise comparison confirmed the significant differences from Fig. 4. In summary, carbon stocks in live trees and deadwood were increasing in three NFRs (Goldeck, Hutterwald, Kronawettgrube), with the two latter exhibiting increases > 1 tC/ha per year. NFRs Schiffwald, Laaser Berg and Krimpenbachkessel exhibited decreasing live tree and deadwood carbon, with the two latter showing losses with less than -0.2 tC/ha per year. This calculation ignores potential changes in organic and mineral soil layers, as well as ground vegetation.

3.2 Comparing stocks of Norway spruce-dominated nature forest reserves with literature data

Comparing with mean volume stocks reported by Oettel *et al.* (2020) for similar forest types makes it obvious that some NFRs studied here in detail (and not included in the analysis of Oettel *et al*., 2020) are in different development phases, than the NFRs reported in Oettel *et al*. (2020) (henceforth called NFR_Oettel2020). NFR Krimpenbachkessel, the only NFR predominantly representing spruce-fir-beech forests, had considerably lower live tree volume stocks than the spruce-fir-beech NFR_Oettel2020. On the other hand, NFR Goldeck with elevation above 1100 meter and dominated by Norway spruce is a typical subalpine spruce forest, but has mean stocks much larger than live tree volume stocks in subalpine spruce NFR_Oettel2020. A value of 30 m³/ha deadwood is often used as a target for deadwood quantities in forest policy (Müller and Bütler, 2010). Here assumed that out of the 30 m³/ha threshold determined for both lying and standing deadwood for Norway spruce forests 24 m³/ha were lying deadwood and 6 m³/ha standing deadwood, based on separate images in the original literature (Ranius and Jonsson, 2007). Our analysis thus underpins that protected and unmanaged forests may have higher or lower stocks compared to literature reference values, depending on site conditions, development stage and disturbance history, and this extends to both live trees and deadwood. The spatially highly variable nature of deadwood makes assessing changes over time particular challenging.

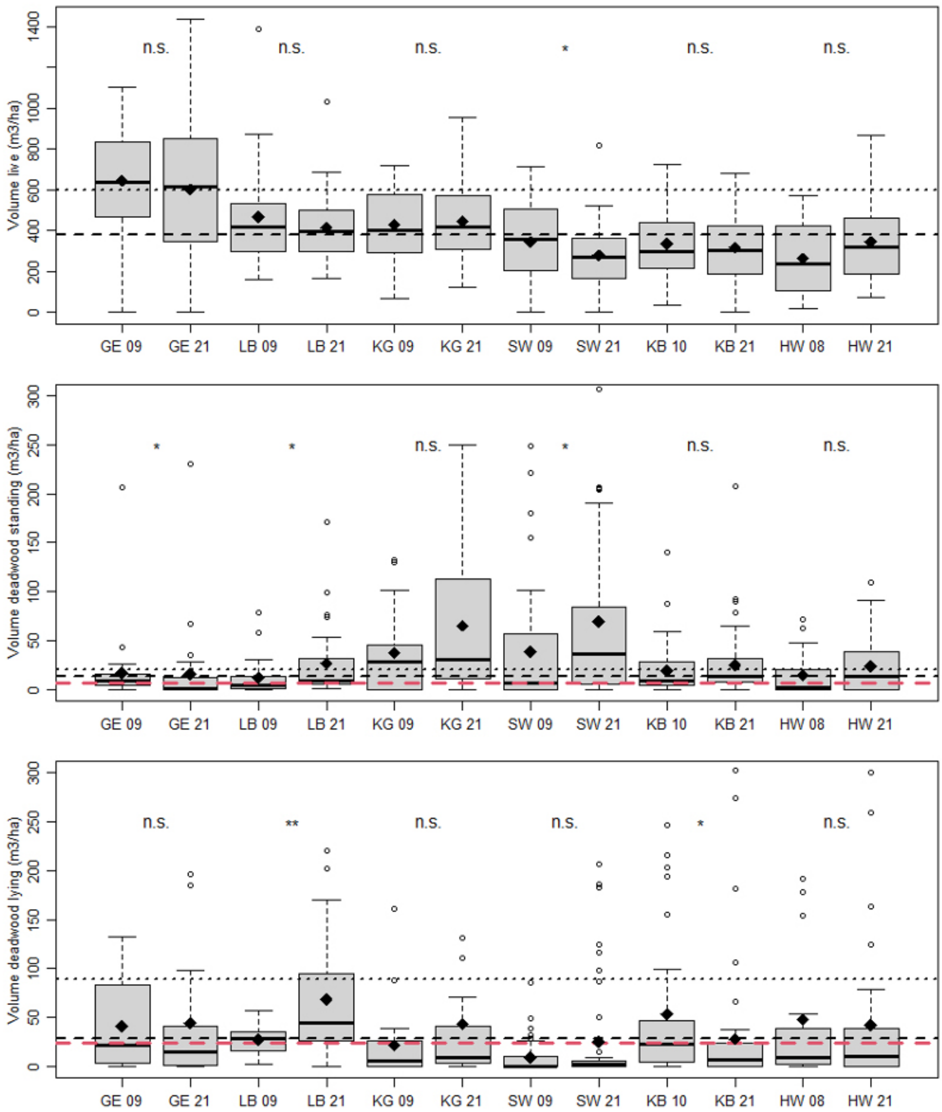

Figure 4: Comparisons of live, standing deadwood and lying deadwood volume of the analysed NFRs (n = 197, for 2008-10 and 2021, respectively). GE stands for Goldeck, LB Laaser Berg, KG Kronawettgrube, SW Schiffwald, KB Krimpenbachkessel and HW Hutterwald. Mean volume stocks (381 m³/ha live stocks, 13 m³/ha standing dead, 28 m3/ha lying dead) from subalpine spruce forests are shown by the dashed horizontal line and from spruce-fir-beech forests (598 m³/ha live stocks, 20 m³/ha standing dead, 89 m³/ha lying dead) by the dotted horizontal line (Oettel et al., 2020). The red dashed lines show 6 m³/ha standing and 24 m³/ha lying deadwood, which sum up to 30 m³/ha after the study of Ranius and Jonsson, (2007), often used as target deadwood quantity in forest policy (Müller and Bütler, 2010). We show results of pair-wise Kruskal-Wallis tests above the boxplots. Boxes represent the median and the 25th and 75th percentile. Diamonds indicate arithmetic means. Whiskers extend to 1.5 of the interquartile range and values outside this range are indicated by circles.

Abbildung 4: Vergleich von Lebendvorrat, stehendem und liegendem Totholzvorrat der analysierten NWR (n = 197, für 2008-10 und 2021, jeweils). GE steht für Goldeck, LB Laaser Berg, KG Kronawettgrube, SW Schiffwald, KB Krimpenbachkessel und HW Hutterwald. Mittlerer Vorrat (381 m3/ha lebend, 13 m3/ha stehend tot, 28 m^3/ha liegend tot) für subalpine Fichtenwälder werden mit strichlierter schwarzer Linie gezeigt und für Fichten-Tannen-Buchen-Wälder (598 m^3/ha lebend, 20 m^3/ha stehend tot, 89 m^3/ha liegend tot) mit gepunkteter schwarzer Linie, nach Oettel *et al.* (2020). Die rote strichlierte Linien zeigen 6 m^3/ha stehendes und 24 m^3/ha liegendes Totholz, in Summe 30 m^3/ha, nach Ranius und Jonsson, (2007), ein häufig verwendeter Zielwert für Totholzmengen in der Waldbewirtschaftung und Waldpolitik (Müller und Butler, 2010). Wir zeigen die Ergebnisse von paar-weisen Kruskal-Wallis Tests oberhalb der Boxplots. Boxplots zeigen Median und 25- und 75-Prozent Perzentile. Rauten zeigen arithmetische Mittel. Whisker gehen bis zum 1.5-fachen des Interquartilabstandes und Werte außerhalb dieses Bereiches werden als Kreise gezeigt.

Table 3: Summary of mean volume and carbon stocks by analysed NFR. We also show their change per year (delta) and the p-value of one-sided t-tests after pair-wise comparing single plots. For details see method section. Increases are highlighted blue, losses in red. Significant differences are in bold font. Sum delta summarized changes in live and dead volume.

Tabelle 3: Zusammung der mittleren Volums- und Kohlenstoffvorräte pro analysierten NWR. Wir zeigen auch die Veränderung pro Jahr (delta) sowie die p-Werte von ein-seitigen t-Tests nach paar-weisem Vergleich von einzelnen Plots. Für Details verweisen wir auf die Methodik. Zunahmen werden blau dargestellt und Abnahmen in Rot. Sum delta summiert die Veränderungen in lebenden und toten Bestand.

	Volume living (m^3/ha)				Volume standing dead (m^3/ha)				Volume lying dead (m^3/ha)				
	2008-10	2021	Delta	p	2008-10	2021	Delta	p	2008-10	2021	Delta	p	Sum delta
Goldeck	644.1	602.7	-3.450	0.266	16.6	15.5	-0.092	0.708	41.1	44.2	0.258	0.838	-3.283
Hutterwald	262.7	344.3	6.800	0.020	14.3	23.5	0.767	0.159	47.4	42.4	-0.417	0.517	7.150
Krimpenbachkessel	334.9	316.7	-1.517	0.514	18.8	24.9	0.508	0.353	53.3	27.8	-2.125	0.069	-3.133
Kronawettgrube	428.8	446.7	1.492	0.724	37.1	65.2	2.342	0.026	21.5	43.6	1.842	0.278	5.675
Laaser Berg	466.6	414.8	-4.317	0.022	11.7	26.5	1.233	0.031	27.3	68.4	3.425	0.002	0.342
Schiffwald	**344.7**	**278.7**	**-5.500**	**<0.001**	38.3	69.5	2.600	0.011	8.9	25.1	1.350	0.152	-1.550
	Carbon living (tC/ha)				Carbon standing dead (tC/ha)				Carbon lying dead (tC/ha)				
	2008-10	2021	Delta	p	2008-10	2021	Delta	p	2008-10	2021	Delta	p	Sum delta
Goldeck	122.8	122.4	-0.033	0.975	1.8	2.5	0.058	0.738	4.5	4.8	0.025	0.836	0.050
Hutterwald	51.7	66.7	1.250	0.024	2.5	3.9	0.117	0.159	6.7	6.4	-0.025	0.567	1.342
Krimpenbachkessel	71.5	68.6	-0.242	0.719	2.2	3.0	0.067	0.353	6.5	4.0	-0.208	0.069	-0.383
Kronawettgrube	77.7	80.9	0.267	0.725	4.1	8.9	0.400	0.026	2.6	5.9	0.275	0.280	0.942
Laaser Berg	90.6	81.3	-0.775	0.030	1.6	2.9	0.108	0.031	**2.8**	**8.1**	**0.442**	**<0.001**	-0.225
Schiffwald	**65.1**	**52.5**	**-1.050**	**<0.001**	2.4	9.8	0.617	0.013	1.1	4.7	0.300	0.169	-0.133

3.3 Deadwood dynamics in Norway spruce-dominated nature forest reserves

Deadwood in forests has not only different diameter and length (volume) and position (standing, lying), but also varying quality, commonly assessed in the field using a decay class system (*e.g.* Harmon *et al.*, 1987; Müller-Using and Bartsch, 2007; Neumann *et al.*, 2023). Decay classes represent differences in wood density, moisture content, carbon fraction and many other important deadwood traits, including habitat value for many different insects (Jomura *et al.*, 2022; Neumann *et al.*, 2023; Shorohova *et al.*, 2016). Since Oettel *et al.*, (2020) did not report decay classes, we compare here our observations with the volume stocks by decay class, assuming every decay class has the same share (20% since five decay classes) using the earlier used mean volume stocks of NFR_Oettel2020. Conceptually trees after their death start in decay class A (see description in table 1) and move through decay class B-E, until they are fragmented, incorporated in the soil or humus layers and thus became unmeasurable using transects or plots. We note, that there are exceptions, such as internal decay of living standing trees or shedding dead decaying large limbs from live trees or variations according to site and microclimatic conditions. Variations in deadwood quality (using decay class as proxy) help assess habitat value and biodiversity in more detail, than only using total deadwood volume stocks.

The NFRs studied here had more deadwood volume in middle decay classes B-D, while fresh and very heavily decayed deadwood volume (decay classes A and E) was more rarely observed, especially at the first measurements in 2008-2010. 12 years of continuous protection resulted in a more balanced deadwood volume distribution especially for lying deadwood, except for decay class E (Fig. 5). We note again the skewness in deadwood volume, which makes it challenging to track changes over time. The absence of standing deadwood with decay class E is not surprising, since advanced decay reduces wood density and makes fragmentation likely (transferring volume into the lying deadwood pool).

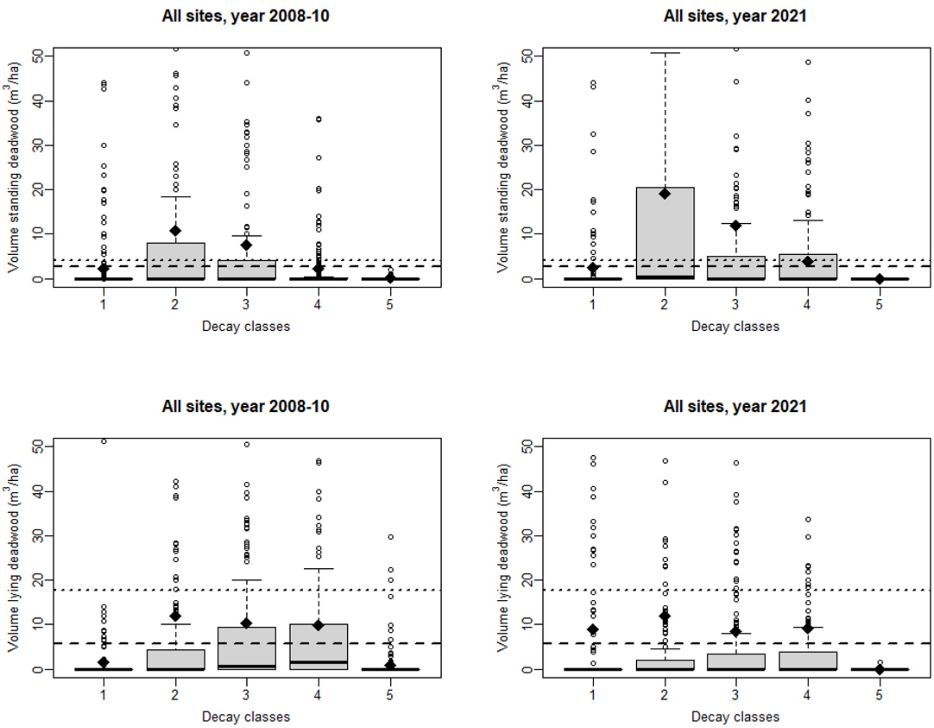

Figure 5: Volume stocks by decay classes for all analyzed NFRs. The images are grouped by measurement year (column) and deadwood type (rows). For description of decay classes, see table 1. Horizontal lines delineate 20% of mean stocks reported in Oettel et al., (2020), assuming even distribution of deadwood volume in the five decay classes. For description of line font and boxplots, see caption of Fig. 4.

Abbildung 5: Totholzvorrat nach Zersetzungsklassen für alle analysierten NWRs. Die Abbildungen sind gruppiert nach Messjahr (Spalten) und Totholztyp (Reihen). Für eine Beschreibung der Zersetzungsklassen verweisen wir auf Tabelle 1. Horizontale Linien zeigen 20% der mittleren Vorräte, nach Oettel *et al*. (2020), unter der Annahme einer gleichmäßigen Verteilung von Totholzvorräten in den fünf Zersetzungsklassen. Für Details zur Darstellung verweisen wir auf Abb. 4.

We analyzed many functions relating TSD and DC for lying and standing deadwood, by species, elevation and/or size class (Fig. 6, A6-A10). We found no conspicuous differences of TSD by NFRs, but note that NFRs Schiffwald, Laaser Berg and Kronawettgrube had somewhat smaller slopes and thus faster decay (Fig. A5). There were also no significant differences of functions relating TSD and DC between lying and standing deadwood using deadwood type as dummy variable in linear regression functions ($p = 0.172$), owing to the large variation of TSD in the single DCs (Fig. 6). We also found no significant influence of species on functions relating TSD and DC (see also Figs A8-A9) nor clear non-linear relationships (Fig. 6). Grouping by elevation (pooled into

200 m classes) did not reveal clear patterns (Fig. A10). The variation of TSD was large especially for decay classes B-D (equivalent to 2-4 in Fig. 6) ranging from <5 to >40 years. For standing deadwood a second order polynomial function improved pseudo-R^2 (coefficient of determination) by 0.003 compared to the linear trend function. Linear functions without intercept had similar pseudo-R^2 than functions with intercept, but better captured observed TSD for lower DC.

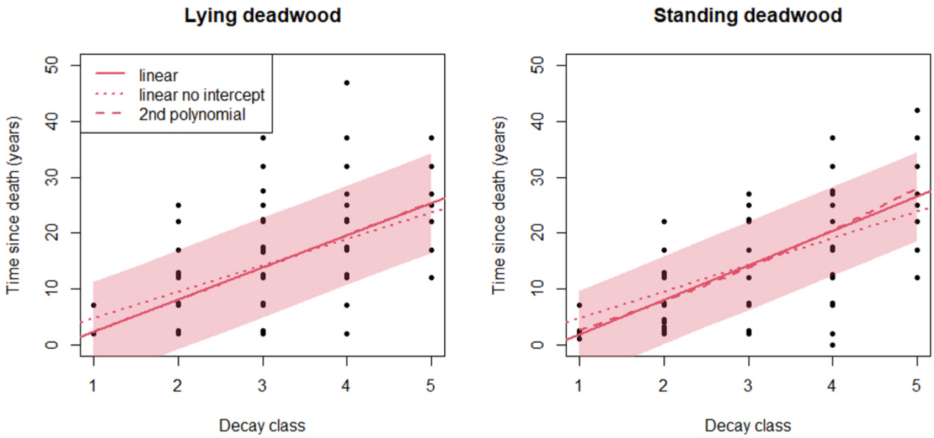

Figure 6: Decay class, DC, versus time since death, TSD, separated for lying and standing deadwood (all tree species, including deadwood pieces where species could not be identified). The solid lines represent linear trend functions, for lying deadwood TSD = -3.50 + 5.78 DC, pseudo-R^2 0.563 and for standing deadwood TSD = -4.42 + 6.19 DC, pseudo-R^2 0.591. The dotted line is the linear trend function without intercept (TSD = 4.745 DC, pseudo-R^2 0.568 and TSD = 4.763 DC, pseudo-R^2 0.557). The dashed line is the second-order trend curve and the second-order polynomials term was only significant for standing deadwood (TSD = -1.731 + 4.024 DC + 0.387 DC^2, pseudo-R^2 0.594). The shading the 90% prediction intervals.

Abbildung 6: Zersetzungsklasse, DC, versus Zeit seit Absterben, TSD, separat für liegendes Totholz und stehendes Totholz (alle Baumarten, inklusive Totholzstücke deren Baumart nicht sicher identifiziert werden konnte). Die durchgezogene Line zeigt Trendgeraden: TSD = -3.50 + 5.78 DC, Bestimmtheitsmaß R^2 0.563 and TSD = -4.42 + 6.19 DC, R^2 0.591. Der schraffierte Bereich ist das 90% Prognoseintervall. Die strichlierte Linie ist die quadratische Trendfunktion, wobei der Polynomsterm zweiten Grades nur für stehendes Totholz signifikant war (TSD = -1.731 + 4.024 DC + 0.387 DC^2, R^2 0.594).

We decided to use a linear trend function without intercept pooling all tree species and deadwood types for estimating the time needed to pass from one decay class to the next higher decay class, which is on average 5 years, rounded to integer (TSD = 4.754 DC or DC = TSD / 4.754, pseudo-R^2 0.564). Our reasons include

(1) the large variation of TSD by DC (also within NFRs, see Fig. A6),
(2) small differences of functions fitted for separate deadwood types (Figs 6, A6-A9) and
(3) rare mixed tree species, accounting for 15% of all observed deadwood pieces.

63% were identified as Norway spruce and for the remaining 22% of observed deadwood pieces, species could not be determined. Assuming the share of Norway spruce among unidentifiable deadwood pieces is similar to that of identifiable pieces (86%), result in about 82% of all deadwood pieces originating from Norway spruce trees.

4 Discussion

4.1 Dynamic rather than static NFRs

To enhance the biodiversity condition of coniferous forest in Austria related to deadwood it is important to gain knowledge on reference values derived from unmanaged forests under natural conditions. A key objective for establishing natural reserves in Austria was to maintain forest biodiversity and provide a reference for discussions on threshold values for sustainable forest management (Frank and Müller, 2003). Few studies have investigated forest dynamics of strictly unmanaged Norway spruce subalpine forests. However, as Norway spruce mortality is expected to increase in the future due to climate change related bark-beetle outbreaks, storms and droughts (Štraus and Bončina, 2025), it is important to understand natural forest dynamics under the past climatic conditions to design close-to-nature management approaches for the future. In this context the findings of our study can support this discussion as it revealed dynamical changes over time of the studied NFRs, under formal protection since 1997-1999 (Ruprecht *et al*., 2012), based on permanent monitoring plots. This has implications on carbon storage as well as habitat value of these forests. Apart from one, all studied NFR showed constant live tree volume stocks non-significantly changing over 12 years, suggesting that these forests are in optimal to climax/terminal phase (Korpel, 1995; Mayer and Neumann, 1981), based on the measurement of the monitoring plots. Only NFR Schiffwald show indications being in early decay phase, since live stocks are significantly declining and standing deadwood stocks are significantly increasing. Our data on live and dead stocks suggest that NFR Hutterwald and Kronawettgrube are a carbon sink, while Krimpenbachkessel, Laaser Berg and Schiffwald are a carbon source and for Goldeck losses in live carbon are compensated by gains in deadwood. We note that this assessment is based on live trees and deadwood only and based on the available monitoring plots ignoring changes in carbon pools in the soil. More NFRs may be become a C source in the near future, due to higher temperatures and changing disturbance regimes, identified as main drivers for C losses in unmanaged mountain forests (Albrich *et al*., 2022). Currently the studied NFRs have similar carbon stocks than other Norway spruce-dominated protected forests in Austria (Oettel *et al*., 2020). Only Goldeck despite representing a typical Spruce-dominated montane forests (see Fig. A1), has considerably higher live stocks (due to higher basal area), more similar to Spruce-fir-beech forests based on literature data.

Various insects and lichens have a strong preference for sun-exposed stumps and snags (Thorn *et al*., 2017; Vogel *et al*., 2021). For maintaining biodiversity related to deadwood it is therefore important to keep a good balance between standing and lying deadwood compartments (Rahman *et al*., 2008). The size distributions of live trees reported in Ruprecht *et al*. (2012) were in general similar to that of dead standing and dead lying trees reported here and smaller sized trees were more numerous than larger-sized trees. Small tree density was more variable over time, pointing towards them being more affected by competition and/or browsing compared to larger trees in the upper canopy. In NFR Krimpenbachkessel, a pronounced increase in stem density of live trees smaller than 5 cm DBH, compensated for losses in stem density of larger trees (Kasseroler, 2011) and resulted in a general increase of live tree density over 12 years. Stem density of trees >10 cm DBH was decreasing for all NFRs, albeit at different rates. The number of large trees >75 cm DBH was increasing for all NFRs, with likely positive outcomes for organisms associated with large, old and habitat-bearing trees and old-growth conditions. Larger trees also tend to have more tree-related microhabitats, such as cavities, cracks or dead branches (Larrieu *et al*., 2018).

Deadwood volume measured in 2021 accounted for on average about 20% of mean live tree volume and thus a somewhat higher share than at the first measurement of 10-20% (Götze, 2013; Kasseroler, 2011; Ruprecht *et al*., 2012; Winter, 2009). Thus since 2008 in the studied NFRs the habitat value for saproxylic organisms, depending on deadwood (Müller *et al*., 2020), most likely has increased. Standing and lying deadwood stocks have been increasing for all NFRs (except for lying deadwood in NFR Krimpenbachkessel). Such changes in deadwood volume stocks are the result of the mass balance of deadwood input and deadwood losses (Kušar and Neumann, 2024). Compared to the results of Oettel *et al.* (2020), which revealed an average deadwood volume of 41.06 m³/ha for low subalpine spruce forests in Austria, the average deadwood amounts in this study are higher. However, as indicated by Nilsson et al. (2002) on many forest sites 30-50 m³/ha of standing deadwood and about 100 m³/ha of lying deadwood were probably very plausible amounts before European forests were subjected to human exploitation. In this context the average deadwood amounts observed in the NFRs are still low, with some exceptions indicating the possible ranges. Also the amount of lying deadwood typically predominates in unmanaged forests (Rimle *et al*., 2017; Vacek *et al.*, 2015), but the time passed by since no management activities have been observed in the NFRs, might be still too short for a larger accumulation of lying deadwood (Kürsten, 2015; Parigger, 2021; Steininger, 2017). The monitored period of in total 30 years might be still too short to draw conclusions about the general natural dynamics in the forest and there may be other possible trajectories in natural development of these forests (Vacik *et al*., 2009).

4.2 Estimating deadwood dynamics using functions relating TSD and DC

In this study we were able to derive mean transition or residence time of deadwood in decay classes using the fitted models of time since death (TSD) and decay class (DC). We found no notable deviations between deadwood type, species, elevation and NFR in TSD and DC relations, presumably due to simple field assessments of TSD. The relationships between TSD and DC were linear and non-linear functions did not improve considerably the explained variation and were subject to multi-collinearity (VIF > 30). We note that determining TSD accurately is challenging and may require time-demanding and costly techniques, such as dendrochronology or radiocarbon dating (Petrillo *et al*., 2016). Keeping the above in mind, the consistent relationship of TSD and DC, across sites, field crews and species is remarkable. It was unexpected to see no clear species-specific effect in the relations of TSD and DC, as literature points towards species and associated resistance of wood to decay (due to heartwood, extractives or other decay-inhibiting factors) can explain variation in deadwood decay rates, unexplained by site conditions (*e.g.* Edelmann *et al*., 2023; Harmon *et al*., 2020). Literature also suggest that deadwood decay slows as air temperature decreases (Harmon *et al*., 2020; Seibold *et al*., 2021), which is not supported by the results of this study, using elevation as proxy, which is commonly negatively correlated with temperature in Austria.

Until more detailed empirical data on deadwood decay is available for Austria, for instance using in-situ deadwood experiments (Edelmann et al., 2023; Seibold et al., 2021), we can use the relations of TSD and DC put forth by this study for estimating future deadwood volumes in Norway Spruce forests. This is important for anticipating potential changes in habitat value of saproxylic organisms as well as the carbon storage in deadwood. Table 4 summarizes a small analysis, where we used the deadwood volume stocks measurements 12 years apart, separated by DC and the average transition time of 5 years for a deadwood piece in shift to the next higher DC (see results section). We considered three scenarios,

(1) no deadwood input,
(2) deadwood input into DC 1 and
(3) deadwood input into DC1 and DC2.

For (1) the simulated deadwood stocks fit quite well the volume stocks in DC 4, but underestimate DC 1-3 (Table 3). For (2) and 5 m^3/ha per year – a typical volume growth rate of mountain forests, assuming steady-state volume stocks and volume growth to be equal to tree mortality - the deadwood input after 12 years, would be in total 60 m^3/ha. Scenario (2) much better capture DC1-4 stocks, but still underestimate observed stocks in DC2 and DC3. Scenario (3) with 2.5 m^3/ha added to DC1 and 2.5 m^3/ha added to DC2 each year reproduced the pattern of observed stocks increasing from DC1 to DC3 to DC2.

Table 4: Observed deadwood stocks by decay class based on this study (highlighted red) and simply calculated estimates of deadwood stocks using relations of TSD and DC (highlighted green) and assuming (1) no input and (2) input of new deadwood at 5 m³/ha per year.

Tabelle 4: Beobachtete Totholzvorräte pro Zersetzungsklasse (rot unterlegt) und einfache berechnete Schätzwerte für Totholzvorräte mittels Beziehung zwischen TSD und DC (grün unterlegt), unter den Annahmen (1) kein Input von Totholz und (2) Input von neuen Totholz im Ausmaß von 5 m³/ha pro Jahr.

	Standing and lying deadwood stocks (m³/ha)				
	DC 1	DC 2	DC 3	DC 4	DC 5
2009 observed	4.5	25.2	20.2	13.5	0.7
2021 observed	16.9	40.4	27.1	16.5	0.0
2021 estimated, no input	0.0	0.0	2.3	14.9	22.7
2021 estimated, input 5 m³/ha per yr in DC1	25.0	25.0	12.3	14.9	22.7
2021 estimated, input 2.5 m³/ha per yr in DC1 and 2.5 m³/ha per yr in DC12	12.5	25.0	19.8	14.9	22.7

This estimation neglects deadwood volume loss associated with decay, such as bark shedding or faster decay of sapwood, varying climate conditions as well as the usual irregular deadwood input through tree mortality. Alternative approaches could include empirical determined probability for a deadwood piece to move from one DC to the next (Kruys *et al*., 2002; Russell *et al*., 2013) or mechanistic decay models considering site conditions and deadwood properties (Didion *et al*., 2014; Hararuk *et al*., 2020; Harmon *et al*., 2020). The poor performance for strongly decayed deadwood (DC 5) may be associated to

(1) methodological reasons making it difficult for field crews to detect it separated from soil layers, due to partial cover by soil, litter, other deadwood or ground vegetation,
(2) its rather ephemeral nature, as it may disintegrate under pressure of a fallen log, footsteps or rockfall and/or
(3) poorly defined TSD of deadwood with DC 5 due to the current low number of available observations.

Deadwood with advanced decay may need different sampling such as *in-situ* density determination of density (Ondrejka *et al*., 2020), freezing samples before extraction or additional DCs (Holeksa, 2001; Merganičová and Merganič, 2010) to more accurately describe its conditions. Further work can focus on incorporating the relations between TSD and DC in forest ecosystem and tree growth models (Thurnher et al., 2011), decision support tools (Vacik and Lexer, 2014), refine the assumptions using actual deadwood inputs measured using remote sensing (Senf and Seidl, 2021) or estimated tree mortality (Monserud and Sterba, 1999).

In summary, a permanent monitoring system in protected forests such as the Natural Forest Reserve system in Austria offers many insights into forest dynamics that temporary inventories cannot provide, including carbon stocks and habitat value (Frank and Müller, 2003). While time-demanding and labor-intensive to maintain, re-measuring permanent monitoring plots once in 10 years may be a good trade-off of incurred costs and gained information. Remeasurements periods greater than 10 years may come at the risk of losing plot and tree identification material, such as poles and tags, and miss important changes of the forest development stages in temperate forests.

Acknowledgements

We thank the landowners, that made their forest properties available for the Natural Forest Reserve (NFR) program and made this research possible. Without the continuing support and collaboration with Dipl.-Ing. Georg Frank from Austrian Research Centre for Forests (BFW) long-term maintenance of the NFR system would have been impossible. We acknowledge Dipl.-Ing. Dr. Mathias Leiter for his help with data analysis and data harmonization and Dipl.-Ing. Ambros Berger for statistical advice. We are grateful for the help with field work and data entry by Michael Götze, Alexander Schara, Matthias Kasseroler, Johannes Zorzi, Dimitrios Manousidis, Johannes Huber, Darius George Hardalau, Ajdin Starcevic and Herwig Ruprecht. Support was provided by the Erasmus Mundus Joint Master Degree program Master of Science in European Forestry (ID: 101239159). This research was funded in whole or in part by the Austrian Science Fund (FWF) 10.55776/PAT6986524.

References

Albrecht, L., 1991. Die Bedeutung des toten Holzes im Wald. Forstwissenschaftliches Cent. 110, 106–113. https://doi.org/10.1007/BF02741245

Albrich, K., Seidl, R., Rammer, W., Thom, D., 2022. From sink to source: changing climate and disturbance regimes could tip the 21st century carbon balance of an unmanaged mountain forest landscape. For. An Int. J. For. Res. 1–11. https://doi.org/10.1093/forestry/cpac022

Borghi, C., Francini, S., McRoberts, R.E., Parisi, F., Lombardi, F., Nocentini, S., Maltoni, A., Travaglini, D., Chirici, G., 2023. Country-wide assessment of biodiversity, naturalness and old-growth status using national forest inventory data, European Journal of Forest Research. Springer Berlin Heidelberg. https://doi.org/10.1007/s10342-023-01620-6

Caudullo, G., Welk, E., San-Miguel-Ayanz, J., 2017. Chorological maps for the main European woody species. Data Br. 12, 662–666. https://doi.org/10.1016/j.dib.2017.05.007

Didion, M., Frey, B., Rogiers, N., Thürig, E., 2014. Validating tree litter decomposition in the Yasso07 carbon model. Ecol. Modell. 291, 58–68. https://doi.org/10.1016/j.ecolmodel.2014.07.028

Edelmann, P., Weisser, W.W., Ambarlı, D., Bässler, C., Buscot, F., Hofrichter, M., Hoppe, B., Kellner, H., Minnich, C., Moll, J., Persoh, D., Seibold, S., Seilwinder, C., Schulze, E.D., Wöllauer, S., Borken, W., 2023. Regional variation in deadwood decay of 13 tree species: Effects of climate, soil and forest structure. For. Ecol. Manage. 541. https://doi.org/10.1016/j.foreco.2023.121094

FOREST EUROPE, 2020. State of Europe's Forests 2015. Ministerial Conference on the Protection of Forests in Europe - FOREST EUROPE Liaison Unit Bratislava.

Frank, G., Müller, F., 2003. Voluntary approaches in protection of forests in Austria. Environ. Sci. Policy 6, 261–269. https://doi.org/10.1016/S1462-9011(03)00046-7

Fravolini, G., Tognetti, R., Lombardi, F., Egli, M., Ascher-Jenull, J., Arfaioli, P., Bardelli, T., Cherubini, P., Marchetti, M., 2018. Quantifying decay progression of deadwood in Mediterranean mountain forests. For. Ecol. Manage. 408, 228–237. https://doi.org/10.1016/j.foreco.2017.10.031

Götze, M., 2013. Waldbauliche Analyse des Naturwaldreservates Hutterwald. University of Natural Resources and Life Sciences, Vienna.

Hararuk, O., Kurz, W.A., Didion, M., 2020. Dynamics of dead wood decay in Swiss forests. For. Ecosyst. 7. https://doi.org/10.1186/s40663-020-00248-x

Hardalau, D.G., 2022. Comparative assessment of natural regeneration across natural forest reserves in Austria. University of Natural Resources and Life Sciences, Vienna.

Harmon, M.E., Cromack Jr., K., Smith, B.G., 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Can. J. For. Res. 17, 1265–1272. https://doi.org/10.1139/x87-196

Harmon, M.E., Fasth, B.G., Yatskov, M., Kastendick, D., Rock, J., Woodall, C.W., 2020. Release of coarse woody detritus-related carbon: A synthesis across forest biomes. Carbon Balance Manag. 15, 1–21. https://doi.org/10.1186/s13021-019-0136-6

Holeksa, J., 2001. Coarse woody debris in a Carpathian subalpine spruce forest. Forstwissenschaftliches Cent. 120, 256–270. https://doi.org/10.1007/bf02796097

Huber, J., 2022. Charakterisierung der Waldentwicklung im Naturwaldreservat Laaser Berg. University of Natural Resources and Life Sciences, Vienna.

Jandl, R., 2020. Climate-induced challenges of Norway spruce in Northern Austria. Trees, For. People 1, 100008. https://doi.org/10.1016/j.tfp.2020.100008

Jomura, M., Yoshida, R., Michalčíková, L., Tláskal, V., Baldrian, P., 2022. Factors controlling dead wood decomposition in an old-growth temperate forest in central Europe. J. Fungi 8, 673. https://doi.org/10.3390/jof8070673

Kasseroler, M., 2011. Vergleichende Analyse der Naturverjüngung in unbewirtschafteten und bewirtschafteten Gebirgswäldern am Beispiel des NRW Krimpenbachkessel, Salzatal. University of Natural Resources and Life Sciences, Vienna.

Korpel, S., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.

Kruys, N., Jonsson, B.G., Ståhl, G., 2002. A stage-based matrix model for decay-class dynamics of woody debris. Ecol. Appl. 12, 773–781. https://doi.org/10.1890/1051-0761(2002)012[0773:ASBMMF]2.0.CO;2

Kürsten, M., 2015. Waldbauliche Analyse des Naturwaldreservats Stoissen in den Leoganger Steinbergen. University of Natural Resources and Life Sciences, Vienna.

Kušar, G., Neumann, M., 2024. Patterns of deadwood volume and dynamics in Slovenian forests. Acta Silvae Ligni 133, 1–12. https://doi.org/10.20315/ASetL.133.1

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B., Vandekerkhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. Ecol. Indic. 84, 194–207. https://doi.org/10.1016/j.ecolind.2017.08.051

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol. Indic. 11, 1027–1039. https://doi.org/10.1016/j.ecolind.2011.02.004

Mayer, H., Neumann, M., 1981. Stand structure and dynamics in the virgin forests of Rothwald/Lower Austria and in Čorkova Uvala/Croatia. Forstwissenschaftliches Cent. 100. https://doi.org/10.1007/BF02640624

Merganičová, K., Merganič, J., 2010. Coarse woody debris carbon stocks in natural spruce forests of Babia hora. J. For. Sci. 56, 397–405. https://doi.org/10.17221/11/2010-jfs

Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. For. Ecol. Manage. 113, 109–123. https://doi.org/10.1016/S0378-1127(98)00419-8

Müller-Using, S., Bartsch, N., 2007. Totholz im Elementhaushalt eines Buchenbestandes. Forstarchiv 78, 12–23.

Müller, J., Boch, S., Blaser, S., Fischer, M., Prati, D., 2015. Effects of forest management on bryophyte communities on deadwood. Nov. Hedwigia 100, 423–438. https://doi.org/10.1127/nova_hedwigia/2015/0242

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: A baseline for management recommendations in European forests. Eur. J. For. Res. 129, 981–992. https://doi.org/10.1007/s10342-010-0400-5

Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, J., Weiß, I., Baldrian, P., Tláskal, V., Thorn, S., 2020. Primary determinants of communities in deadwood vary among taxa but are regionally consistent. Oikos 129, 1579–1588. https://doi.org/10.1111/oik.07335

Neumann, M., Echeverria, S., Hasenauer, H., 2023. A simple concept for estimating deadwood carbon in forests. Carbon Manag. 14, 1–12. https://doi.org/10.1080/17583004.2023.2197762

Neumann, M., Moreno, A., Mues, V., Härkönen, S., Mura, M., Bouriaud, O., Lang, M., Achten, W.M.J., Thivolle-Cazat, A., Bronisz, K., Merganič, J., Decuyper, M., Alberdi, I., Astrup, R., Mohren, F., Hasenauer, H., 2016. Comparison of carbon estimation methods for European forests. For. Ecol. Manage. 361, 397–420. https://doi.org/10.1016/j.foreco.2015.11.016

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusiński, G., Ranius, T., 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. For. Ecol. Manage. 161, 189–204. https://doi.org/10.1016/S0378-1127(01)00480-7

Öder, V., Petritan, A.M., Schellenberg, J., Bergmeier, E., Walentowski, H., 2021. Patterns and drivers of deadwood quantity and variation in mid-latitude deciduous forests. For. Ecol. Manage. 487, 118977. https://doi.org/10.1016/j.foreco.2021.118977

Oettel, J., Lapin, K., Kindermann, G., Steiner, H., Schweinzer, K.-M., Frank, G., Essl, F., 2020. Patterns and drivers of deadwood volume and composition in different forest types of the Austrian natural forest reserves. For. Ecol. Manage. 463, 118016. https://doi.org/10.1016/j.foreco.2020.118016

Ondrejka, V., Gergeľ, T., Bucha, T., Pástor, M., 2020. Innovative methods of non-destructive evaluation of log quality. Cent. Eur. For. J. 66, 11. https://doi.org/10.2478/forj-2020-0021

Pan, Y., Birdsey, R.A., Phillips, O.L., Houghton, R.A., Fang, J., Kauppi, P.E., Keith, H., Kurz, W.A., Ito, A., Lewis, S.L., 2024. The enduring world forest carbon sink. Nature 631. https://doi.org/10.1038/s41586-024-07602-x

Parigger, P., 2021. Analyse der Walddynamik im Naturwaldreservat Niedergailwald, Kärnten. University of Natural Resources and Life Sciences, Vienna.

Petrillo, M., Cherubini, P., Fravolini, G., Marchetti, M., Ascher-Jenull, J., Schärer, M., Synal, H.A., Bertoldi, D., Camin, F., Larcher, R., Egli, M., 2016. Time since death and decay rate constants of Norway spruce and European larch deadwood in subalpine forests determined using dendrochronology and radiocarbon dating. Biogeosciences 13, 1537–1552. https://doi.org/10.5194/bg-13-1537-2016

Pollanschütz, J., 1974. Formzahlfunktionen der Hauptbaumarten Österreichs. Informationsd. Forstl. Bundesversuchsanstalt Wien 153, 341–343.

R Development Core Team, 2021. R: A language and environment for statistical computing. R Found. Stat. Comput. Vienna, Austria.

Rahman, M.M., Frank, G., Ruprecht, H., Vacik, H., 2008. Structure of coarse woody debris in Lange-Leitn Natural Forest Reserve, Austria. J. For. Sci. 54, 161–169. https://doi.org/10.17221/3102-jfs

Ranius, T., Jonsson, M., 2007. Theoretical expectations for thresholds in the relationship between number of wood-living species and amount of coarse woody debris: A study case in spruce forests. J. Nat. Conserv. 15, 120–130. https://doi.org/10.1016/j.jnc.2007.02.001

Rauh, J., Schmitt, M., 1991. Methodik und Ergebnisse der Totholzforschung in Naturwaldreservaten. Forstwissenschaftliches Cent. 110, 114–127. https://doi.org/10.1007/BF02741246

Rimle, A., Heiri, C., Bugmann, H., 2017. Deadwood in Norway spruce dominated mountain forest reserves is characterized by large dimensions and advanced decomposition stages. For. Ecol. Manage. 404, 174–183. https://doi.org/10.1016/j.foreco.2017.08.036

Ruprecht, H., Vacik, H., 2009. Aufnahmeschlüssel für die Erhebung in Naturwaldreservaten für das Projekt „ ELENA ".

Ruprecht, H., Vacik, H., Steiner, H., Frank, G., 2012. ELENA – a methodological approach for the long term monitoring of natural regeneration in natural forest reserves dominated by Norway Spruce (Vaccinio-Piceetea). Austrian J. For. Sci. 129, 67–105.

Russell, M.B., Woodall, C.W., Fraver, S., D'Amato, A.W., 2013. Estimates of downed woody debris decay class transitions for forests across the eastern United States. Ecol. Modell. 251, 22–31. https://doi.org/10.1016/j.ecolmodel.2012.12.012

Russell, M.B., Woodall, C.W., Fraver, S., D'Amato, A.W., Domke, G.M., Skog, K.E., 2014. Residence Times and Decay Rates of Downed Woody Debris Biomass/Carbon in Eastern US Forests. Ecosystems 17, 765–777. https://doi.org/10.1007/s10021-014-9757-5

Scherzinger, W., 1996. Naturschutz im Wald: Qualitätsziele einer dynamischen Waldentwicklung (Praktischer Naturschutz). Verlag Eugen Ulmer.

Seibold, S., Rammer, W., Hothorn, T., Seidl, R., Ulyshen, M.D., Lorz, J., Cadotte, M.W., Lindenmayer, D.B., Adhikari, Y.P., Aragón, R., Bae, S., Baldrian, P., Barimani Varandi, H., Barlow, J., Bässler, C., Beauchêne, J., Berenguer, E., Bergamin, R.S., Birkemoe, T., Boros, G., Brandl, R., Brustel, H., Burton, P.J., Cakpo-Tossou, Y.T., Castro, J., Cateau, E., Cobb, T.P., Farwig, N., Fernández, R.D., Firn, J., Gan, K.S., González, G., Gossner, M.M., Habel, J.C., Hébert, C., Heibl, C., Heikkala, O., Hemp, A., Hemp, C., Hjältén, J., Hotes, S., Kouki, J., Lachat, T., Liu, J., Liu, Y., Luo, Y.H., Macandog, D.M., Martina, P.E., Mukul, S.A., Nachin, B., Nisbet, K., O'Halloran, J., Oxbrough, A., Pandey, J.N., Pavlíček, T., Pawson, S.M., Rakotondranary, J.S., Ramanamanjato, J.B., Rossi, L., Schmidl, J., Schulze, M., Seaton, S., Stone, M.J., Stork, N.E., Suran, B., Sverdrup-Thygeson, A., Thorn, S., Thyagarajan, G., Wardlaw, T.J., Weisser, W.W., Yoon, S., Zhang, N., Müller, J., 2021. The contribution of insects to global forest deadwood decomposition. Nature 597, 77–81. https://doi.org/10.1038/s41586-021-03740-8

Senf, C., Seidl, R., 2021. Mapping the forest disturbance regimes of Europe. Nat. Sustain. 4, 63–70. https://doi.org/10.1038/s41893-020-00609-y

Shorohova, E., Kapitsa, E., Kazartsev, I., Romashkin, I., Polevoi, A., Kushnevskaya, H., 2016. Tree species traits are the predominant control on the decomposition rate of tree log bark in a mesic old-growth boreal forest. For. Ecol. Manage. 377, 36–45. https://doi.org/10.1016/j.foreco.2016.06.036

Starcevic, A., 2022. Forest dynamics of the natural forest reserve Schiffwald. University of Natural Resources and Life Sciences, Vienna.

Steininger, B., 2017. Beschreibung der Waldentwicklung im Naturwaldreservat Luxensteinwand. University of Natural Resources and Life Sciences, Vienna.

Štraus, H., Bončina, A., 2025. The vulnerability of four main tree species in European forests to seven natural disturbance agents: lessons from Slovenia. Eur. J. For. Res. 267–282. https://doi.org/10.1007/s10342-024-01754-1

Thorn, S., Bässler, C., Svoboda, M., Müller, J., 2017. Effects of natural disturbances and salvage logging on biodiversity – Lessons from the Bohemian Forest. For. Ecol. Manage. 388, 113–119. https://doi.org/10.1016/j.foreco.2016.06.006

Thurnher, C., Klopf, M., Hasenauer, H., 2011. Forests in transition: a harvesting model for uneven-aged mixed species forests in Austria. Forestry 84, 517–526. https://doi.org/10.1093/forestry/cpr021

Vacek, S., Vacek, Z., Bílek, L., Hejcmanová, P., Štícha, V., Remeš, J., 2015. The dynamics and structure of dead wood in natural spruce-beech forest stand – a 40 year case study in the Krkonoše national park. Dendrobiology 73, 21–32. https://doi.org/10.12657/denbio.073.003

Vacik, H., Lexer, M.J., 2014. Past, current and future drivers for the development of decision support systems in forest management. Scand. J. For. Res. 29, 2–19. https://doi.org/10.1080/02827581.2013.830768

Vacik, H., Rahman, M.M., Ruprecht, H., Frank, G., 2009. Dynamics and structural changes of an oak dominated Natural forest reserve in Austria. Bot. Helv. 119, 23–29. https://doi.org/10.1007/s00035-009-0053-5

Vandekerkhove, K., Meyer, P., Kirchmeir, H., Piovesan, G., Hirschmugl, M., Larrieu, L., Kozàk, D., Mikolas, M., Nagel, T., Schmitt, C., Blumröder, J., 2022. Old-growth criteria and indicators for beech forests (Fageta).

Vítková, L., Bače, R., Kjučukov, P., Svoboda, M., 2018. Deadwood management in Central European forests: Key considerations for practical implementation. For. Ecol. Manage. 429, 394–405. https://doi.org/10.1016/j.foreco.2018.07.034

Vogel, S., Bussler, H., Finnberg, S., Müller, J., Stengel, E., Thorn, S., 2021. Diversity and conservation of saproxylic beetles in 42 European tree species: an experimental approach using early successional stages of branches. Insect Conserv. Divers. 14, 132–143. https://doi.org/10.1111/icad.12442

Vrška, T., Přívětivý, T., Janík, D., Unar, P., Šamonil, P., Král, K., 2015. Deadwood residence time in alluvial hardwood temperate forests - A key aspect of biodiversity conservation. For. Ecol. Manage. 357, 33–41. https://doi.org/10.1016/j.foreco.2015.08.006

Wijas, B.J., Allison, S.D., Austin, A.T., Cornwell, W.K., Cornelissen, J.H.C., Eggleton, P., Fraver, S., Ooi, M.K.J., Powell, J.R., Woodall, C.W., Zanne, A.E., 2024. The Role of Deadwood in the Carbon Cycle: Implications for Models, Forest Management, and Future Climates. Annu. Rev. Ecol. Evol. Syst. 133–155. https://doi.org/10.1146/annurev-ecolsys-110421-102327

Winter, M.B., 2009. Protection efficiency and regeneration preconditions of Norway Spruce (*Picea Abies* (L.) Karst.) in the upper montane mountain forest oft he natural forest reserve Goldeck in Carinthia. University of Natural Resources and Life Sciences, Vienna.

Zukrigl, K., Eckhart, G., Nather, J., 1963. Standortskundliche und waldbauliche Untersuchungen im Urwaldresten der niederösterreichischen Kalkalpen. Mitteilungen der Forstl. Bundesversuchsanstalt Mariabrunn 62, 278.

Appendix

Table A1: Stem density of live trees, standing deadwood and lying deadwood in 2008-10 and 2021 for all analysed NFRs. We show sum of all measured trees and trees with diameter >10 cm (consistent size class measured for all groups) and binned into 5-cm classes. "-" indicates that this diameter class was not surveyed consistently.

Tabelle A1: Stammzahl lebender Bäume, stehenden und liegenden Totholz zwischen 2008-10 und 2021 für alle analysierten NWR. Wir zeigen die Summen für alle gemessenen Bäume und Totholzstücke, die Summen mit Brusthöhendurchmesser/Mitteldurchmesser > 10 cm (konsistente Größenklasse für die drei Gruppen) und die Werte gruppiert nach 5-cm Klassen. "-" zeigt, dass diese Durchmesserklasse nicht erhoben wurde.

NFR	Component	Stem density in 2008-10 (ha^{-1})																	
		all	>10	2,5	7,5	12,5	17,5	22,5	27,5	32,5	37,5	42,5	47,5	52,5	57,5	62,5	67,5	72,5	>75
Goldeck	living	552	307	168	78	21	26	34	24	24	27	23	21	21	21	18	13	12	20
	standing	129	112	-	17	17	15	15	16	9	15	11	6	2	2	0	2	0	1
	lying	164	164	-	-	44	44	19	14	11	18	6	4	0	0	1	0	0	2
Laaser Berg	living	751	532	132	87	63	74	74	69	74	46	42	31	27	17	6	5	0	3
	standing	98	70	-	29	30	8	13	10	5	2	2	0	0	0	2	0	0	0
	lying	238	238	-	-	33	40	35	41	23	28	14	12	6	3	0	3	1	0
Krona-wettgrube	living	528	426	58	44	46	51	54	37	51	44	32	26	28	32	14	7	4	2
	standing	149	116	-	33	28	28	19	16	7	4	4	5	2	4	0	0	0	0
	lying	82	82	-	-	29	16	14	16	8	0	0	0	0	0	0	0	0	0
Schiffwald	living	534	401	99	34	36	40	45	51	43	60	48	36	23	10	4	4	2	1
	standing	74	73	-	2	12	12	13	8	13	5	3	4	0	3	0	0	0	1
	lying	23	23	-	-	6	3	5	6	1	1	0	0	0	0	1	0	0	0
Krimpen-bachkessel	living	682	367	179	136	88	73	43	45	32	25	25	13	8	6	5	3	1	1
	standing	123	107	-	16	16	14	13	4	12	6	10	6	13	3	3	1	1	4
	lying	162	162	-	-	52	38	29	19	8	6	6	1	1	1	0	0	0	0
Hutterwald	living	725	444	146	136	115	79	67	43	36	36	20	21	10	10	7	0	0	1
	standing	113	78	-	35	22	24	13	6	0	9	2	2	0	0	0	0	0	0
	lying	259	259	-	-	55	42	30	30	30	33	17	12	2	8	0	0	0	0
		Stem density in 2021 (ha^{-1})																	
Goldeck	living	409	262	91	56	26	18	26	21	23	18	17	16	14	13	19	13	6	33
	standing	68	65	-	3	5	10	10	3	7	2	12	7	2	2	0	5	0	2
	lying	58	58	-	-	9	10	9	8	2	8	2	2	2	1	1	1	0	2
Laaser Berg	living	544	445	49	50	59	32	65	38	65	54	40	27	26	19	9	5	0	5
	standing	144	129	-	14	19	18	10	8	24	12	17	8	8	4	1	0	0	1
	lying	217	217	-	-	81	58	32	17	15	4	6	1	3	0	0	0	0	0
Krona-wettgrube	living	405	345	30	30	18	27	33	47	38	42	28	27	17	30	12	13	8	5
	standing	156	152	-	4	44	31	33	15	8	2	13	2	0	2	0	0	0	2
	lying	90	90	-	-	17	13	17	8	4	0	0	0	4	4	0	2	0	21
Schiffwald	living	347	265	63	19	17	27	32	29	27	35	33	30	13	12	4	6	1	1
	standing	110	110	-	0	13	18	11	12	19	12	10	8	1	2	1	1	0	1
	lying	36	36	-	-	3	5	3	1	1	1	0	0	4	3	1	0	0	14
Krimpen-bachkessel	living	811	315	396	100	61	59	36	28	31	25	33	19	11	8	4	1	0	1
	standing	58	56	-	2	0	2	2	6	6	5	6	12	5	8	3	0	0	3
	lying	81	81	-	-	19	22	17	14	3	3	3	0	0	0	0	0	0	0
Hutterwald	living	674	441	152	80	97	76	64	45	43	26	23	23	16	10	9	3	2	3
	standing	196	126	-	70	35	21	11	11	19	11	14	2	0	2	0	0	2	0
	lying	130	130	-	-	29	25	22	22	10	8	8	3	0	0	0	0	0	3

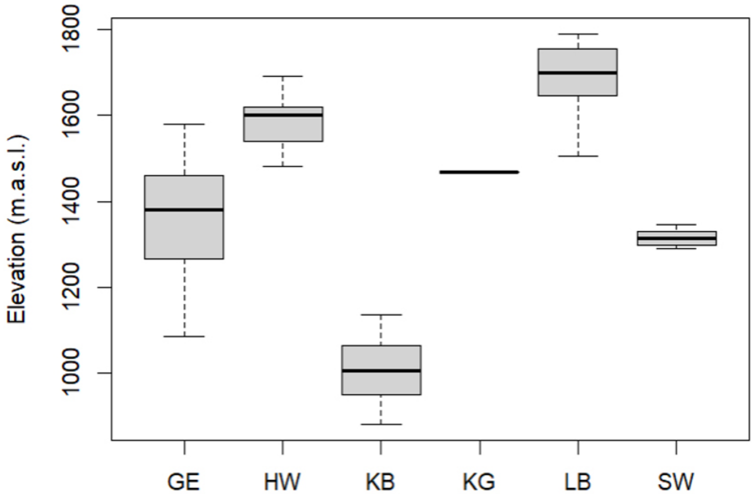

Figure A1: Elevation in meters above sea level of the monitoring plots grouped by the six NFRs. Boxes represent the median and the 25th and 75th percentile. Whiskers extend to 1.5 of the interquartile range and values outside this range are indicated by circles. For abbreviations see caption of Fig. 4.

Abbildung A1: Seehöhe in Meter über Meeresniveau der Monitoringflächen, gruppiert nach den sechs NWRs. Boxplots zeigen Median und 25- und 75-Prozent Perzentile. Whisker gehen bis zum 1.5-fachen des Interquartilabstandes und Werte außerhalb dieses Bereiches werden als Kreise gezeigt. Für Abkürzungen verweisen wir auf Abb. 4.

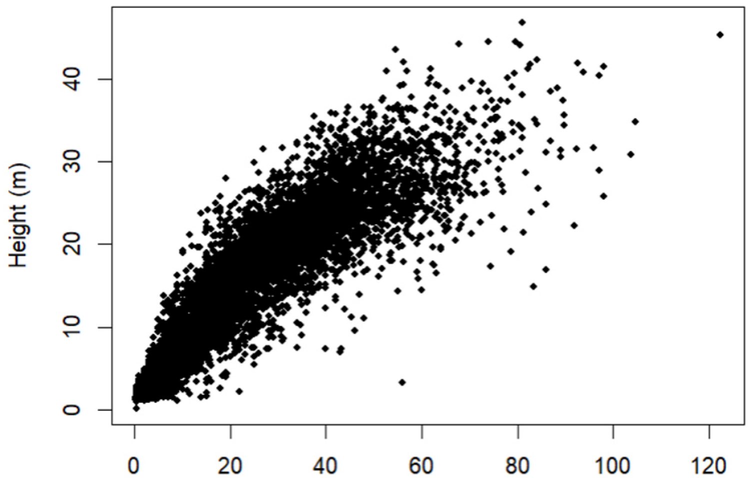

Figure A2: Diameter at breast height versus tree height for all measured live trees.

Abbildung A2: Brusthöhendurchmesser versus Baumhöhe aller gemessener lebender Bäume.

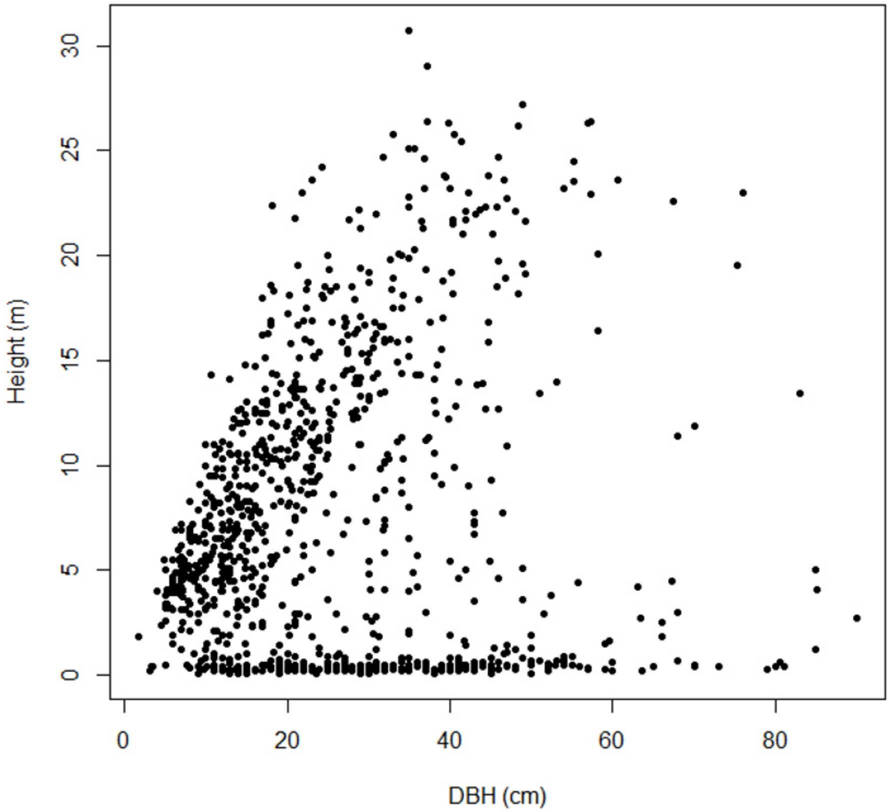

Figure A3: Diameter at breast height versus tree height for all measured standing dead trees, including dead stumps.

Abbildung A3: Brusthöhendurchmesser versus Baumhöhe aller gemessener toter Bäume, inklusive Stocktotholz.

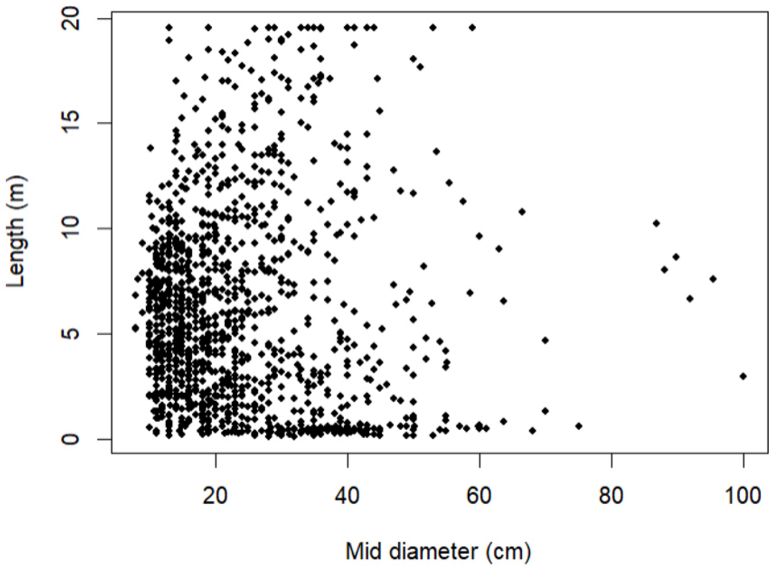

Figure A4: Mid diameter versus length for all measured lying dead trees. Length was limited to 19.5 m due to size of sample plot.

Abbildung A4: Mitteldurchmesser versus Länge von liegenden Totholz. Länge ist limitiert auf 19.5 m aufgrund der Größe des Probekreises.

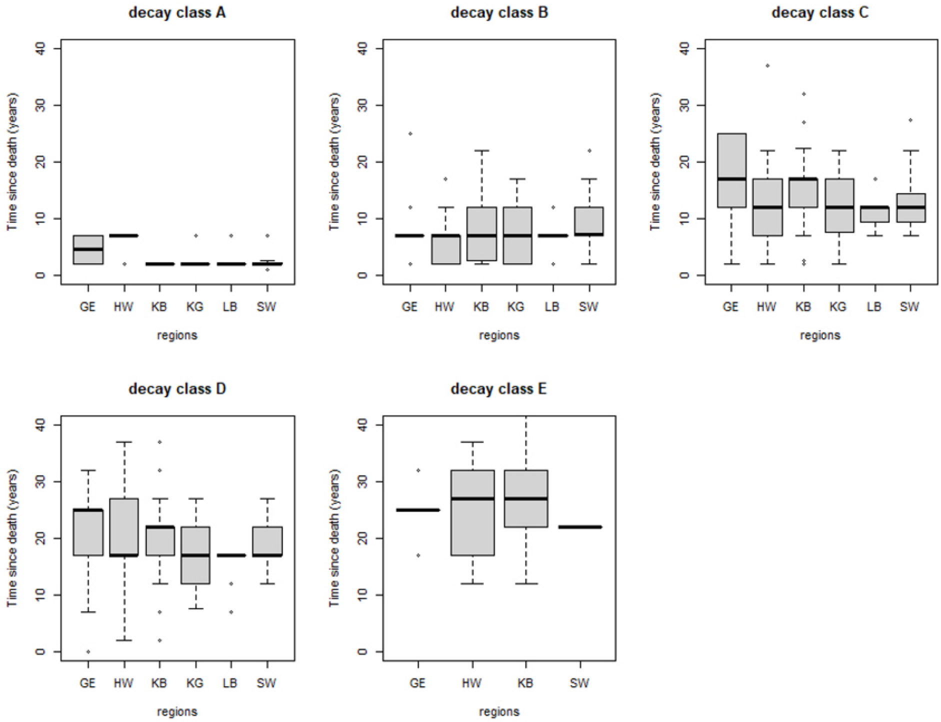

Figure A5: Time since death grouped by NFRs and decay class. For details on display see caption of Fig. A1. No significant difference between NFRs (representing different site conditions) were detected. Decay class 5 was not observed in NFR Hutterwald and Kronawettgrube.

Abbildung A5: Zeit seit Absterben gruppiert nach NWRs und Zersetzungsklasse. Für Details zur Darstellung verweisen wir auf Abb. A1. Keine signifikanten Unterschiede zwischen NWRs (repräsentieren unterschiedliche Standortsbedingungen) konnten beobachtet werden. Zersetzungsklasse 5 wurde auf NWR Hutterwald und Kronawettgrube nicht beobachtet.

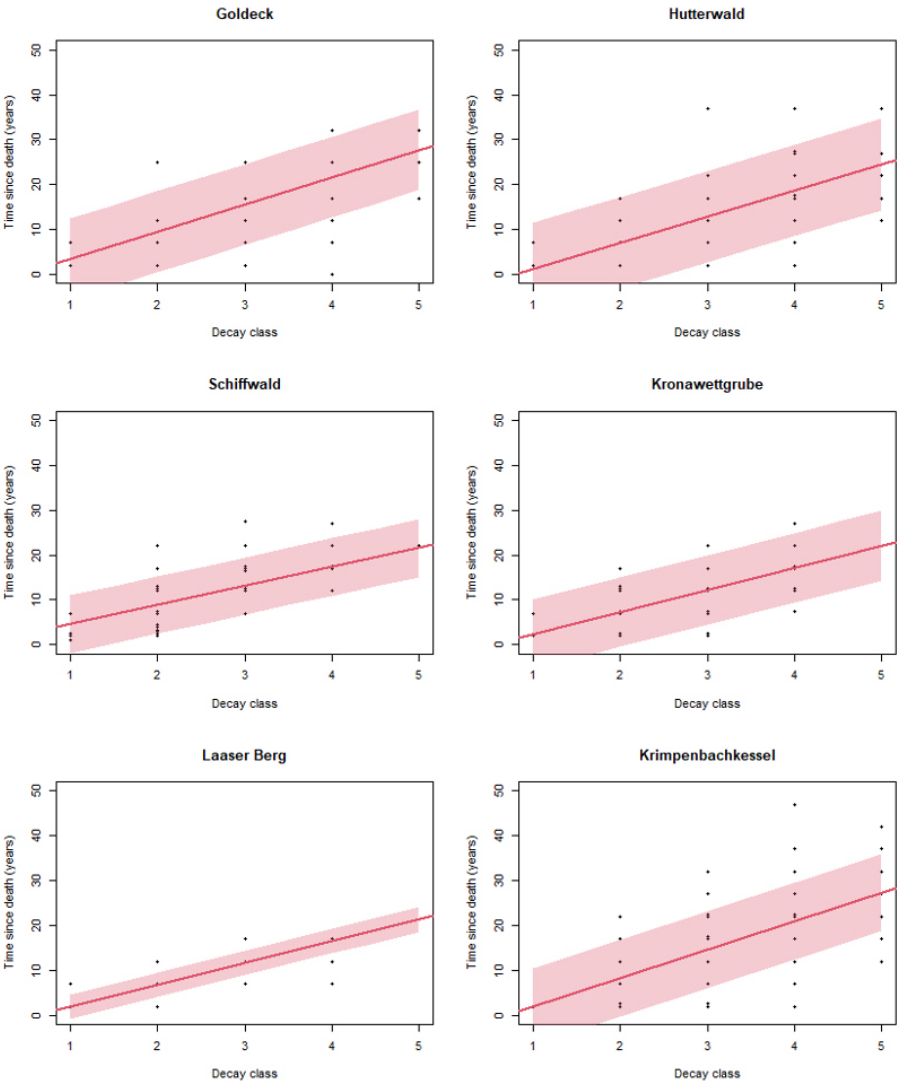

Figure A6: Relations between TSD and DC by NFR for lying and standing deadwood. The solid lines represent linear trend curves: TSD = -2.68 + 6.09 DC, coefficient of determination R^2 0.552 (Goldeck), TSD = -4.450 + 5.80 DC, R^2 0.439 (Hutterwald), TSD = 0.341+ 4.247 DC, R^2 0.438 (Schiffwald), TSD = -2.73 + 4.97 DC, R2 0.426 (Kronawettgrube), TSD = -2.99 + 4.87 DC, R^2 0.932 (Laaser Berg) and TSD = -4.502 + 6.357 DC, R^2 0.537 (Krimpenbachkessel). The shading the 90% prediction intervals.

Abbildung A6: Beziehungen zwischen TSD und DC pro NWR für liegendes und stehendes Totholz. Die durchgezogenen Linien zeigen Trendgeraden: TSD = -2.68 + 6.09 DC, Bestimmtheitsmaß R^2 0.552 (Goldeck), TSD = -4.450 + 5.80 DC, R^2 0.439 (Hutterwald), TSD = 0.341+ 4.247 DC, R^2 0.438 (Schiffwald), TSD = -2.73 + 4.97 DC, R^2 0.426 (Kronawettgrube), TSD = -2.99 + 4.87 DC, R^2 0.932 (Laaser Berg) und TSD = -4.502 + 6.357 DC, R^2 0.537 (Krimpenbachkessel). Der schraffierte Bereich ist das 90% Prognoseintervall.

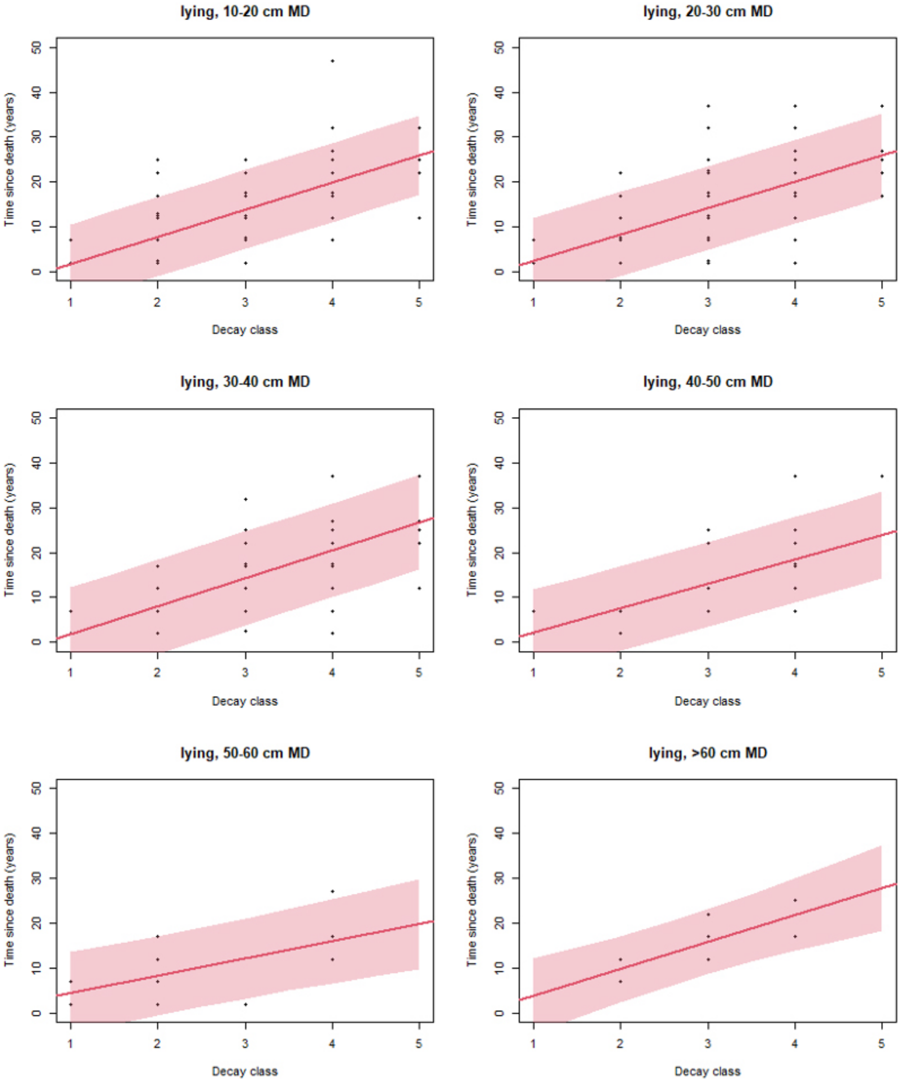

Figure A7: Relations between TSD and DC by size class for lying deadwood. For details we refer to Fig. A6. TSD = -4.29 + 6.05 DC, R^2 0.592 (10-20 cm mid diameter), TSD = -3.31 + 5.84 DC, R^2 0.521 (20-30 cm mid diameter), TSD = -4.54 + 6.26 DC, R^2 0.558 (30-40 cm mid diameter), TSD = -3.30 + 5.43 DC, R^2 0.575 (40-50 cm mid diameter), TSD = 0.59+ 3.84 DC, R^2 0.401 (50-60 cm mid diameter), TSD = -2.29 + 6.04 DC, R^2 0.655 (>60 cm mid diameter).

Abbildung A7: Beziehungen zwischen TSD und DC pro Stärkeklasse für liegendes Totholz. Für Details verweisen wir auf Abb. A6. TSD = -4.29 + 6.05 DC, R^2 0.592 (10-20 cm Mitteldurchmesser), TSD = -3.31 + 5.84 DC, R^2 0.521 (20-30 cm Mitteldurchmesser), TSD = -4.54 + 6.26 DC, R^2 0.558 (30-40 cm Mitteldurchmesser), TSD = -3.30 + 5.43 DC, R^2 0.575 (40-50 cm Mitteldurchmesser), TSD = 0.59+ 3.84 DC, R^2 0.401 (50-60 cm Mitteldurchmesser), TSD = -2.29 + 6.04 DC, R^2 0.655 (>60 cm Mitteldurchmesser).

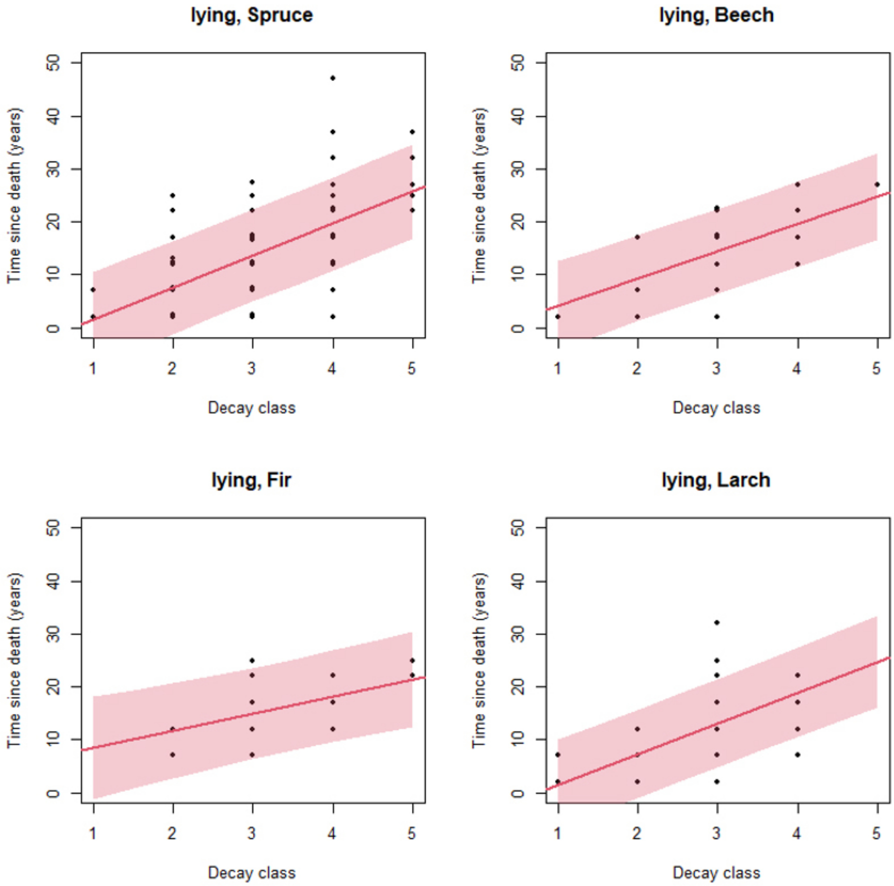

Figure A8: Relations between TSD and DC by species for lying deadwood. For details we refer to Fig. A6. TSD = -4.38 + 6.01 DC, R^2 0.582 (Norway spruce), TSD = -0.89 + 5.12 DC, R^2 0.428 (European beech), TSD = -5.26 + 3.23 DC, R^2 0.256 (Silver fir) and TSD = -4.21 + 5.79 DC, R^2 0.607 (European larch).

Abbildung A8: Beziehungen zwischen TSD und DC nach Baumart für liegendes Totholz. Für Details verweisen wir auf Abb. A6. TSD = -4.38 + 6.01 DC, R^2 0.582 (Gemeine Fichte), TSD = -0.89 + 5.12 DC, R^2 0.428 (Rotbuche), TSD = -5.26 + 3.23 DC, R^2 0.256 (Weißtanne) und TSD = -4.21 + 5.79 DC, R^2 0.607 (Europäische Lärche).

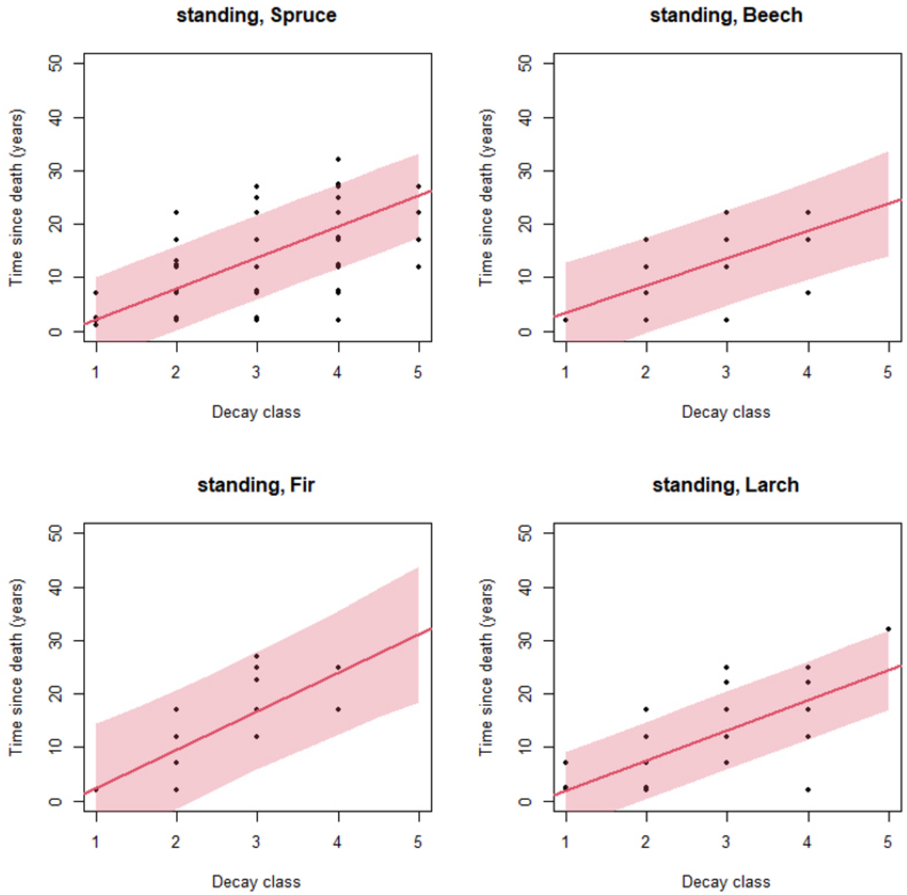

Figure A9: Relations between TSD and DC by species for standing deadwood. For details we refer to Fig. A6. TSD = -3.51 + 5.78 DC, R^2 0.512 (Norway spruce), TSD = -1.53 + 5.07 DC, R^2 0.479 (European beech), TSD = -4.66 + 7.16 DC, R^2 0.472 (Silver fir) and TSD = -3.71 + 5.64 DC, R^2 0.570 (European larch).

Abbildung A9: Beziehungen zwischen TSD und DC nach Baumart für stehendes Totholz. Für Details verweisen wir auf Abb. A6. TSD = -3.51 + 5.78 DC, R^2 0.512 (Gemeine Fichte), TSD = -1.53 + 5.07 DC, R^2 0.479 (Rotbuche), TSD = -4.66 + 7.16 DC, R^2 0.472 (Weißtanne) und TSD = -3.71 + 5.64 DC, R^2 0.570 (Europäische Lärche).

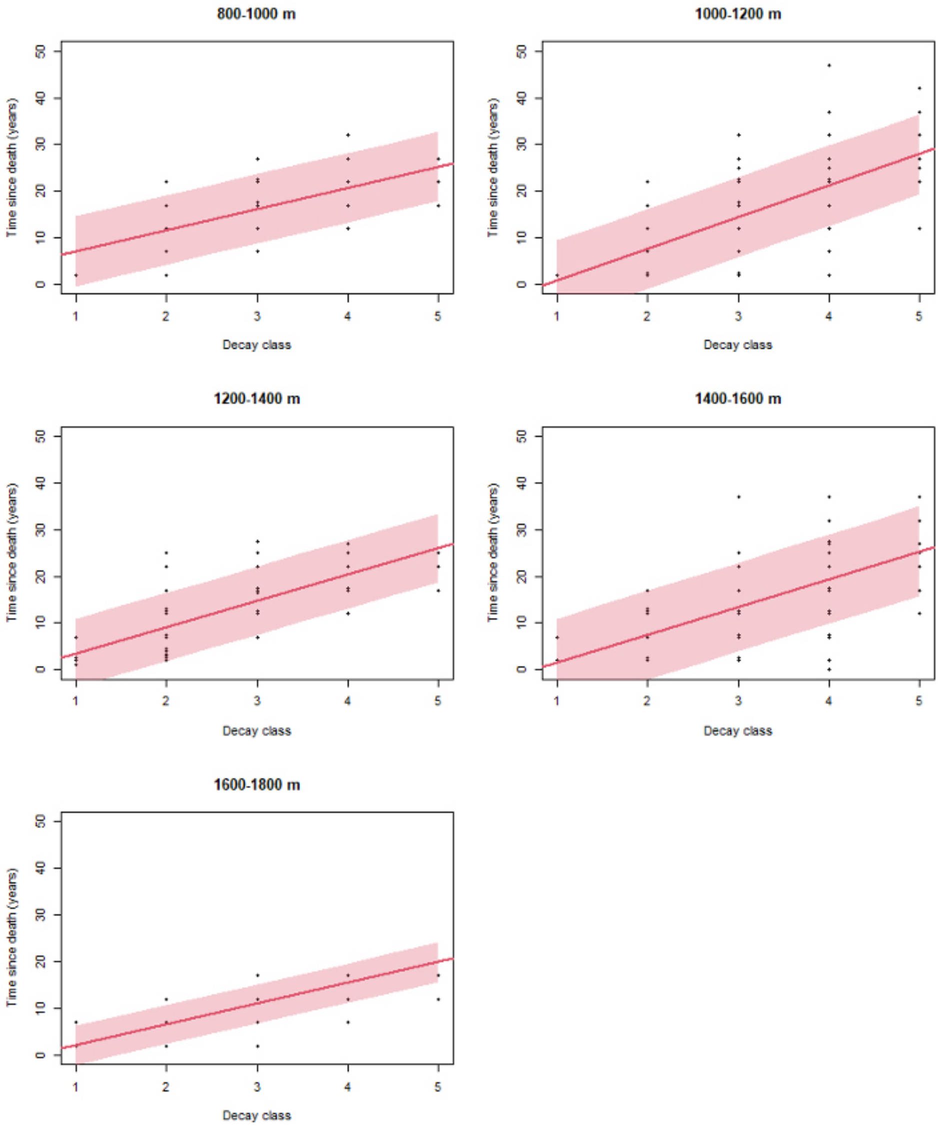

Figure A10: Relations between TSD and DC by elevation for standing and lying deadwood. For details we refer to Fig. A6. TSD = 2.667 + 4.516 DC, R^2 0.429 (800-1000 m), TSD = -5.907 + 6.764 DC, R^2 0.564 (1000-1200 m), TSD = -2.084 + 5.627 DC, R^2 0.599 (1200-1400 m), TSD = -4.574 + 5.995 DC, R^2 0.487 (1400-1600 m), TSD = -2.442 + 4.467 DC, R^2 0.827 (1600-1800 m).

Abbildung A10: Beziehungen zwischen TSD und DC nach Seehöhenklasse für stehendes und liegendes Totholz. Für Details verweisen wir auf Abb. A6. TSD = 2.667 + 4.516 DC, R^2 0.429 (800-1000 m), TSD = -5.907 + 6.764 DC, R^2 0.564 (1000-1200 m), TSD = -2.084 + 5.627 DC, R^2 0.599 (1200-1400 m), TSD = -4.574 + 5.995 DC, R^2 0.487 (1400-1600 m), TSD = -2.442 + 4.467 DC, R^2 0.827 (1600-1800 m).