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Surviving trees and deadwood moderate changes in soil fungal communities and associated functioning after natural forest disturbance and salvage logging

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ABSTRACT

Temperate forests are increasingly subject to natural disturbance by stand replacing windthrows or bark-beetle attacks. Forests are commonly salvage logged after disturbance, whereby substantial parts of biological legacies, such as surviving trees and deadwood, are removed. Despite increasing concerns about the ecological consequences of salvage logging operations, our knowledge on the effects on the soil microbiome and associated functioning remains limited.

Here, we studied soil fungal communities, decomposition processes, and soil organic matter dynamics in 21 intact or disturbed, temperate Norway spruce stands about one decade after they were damaged by windthrow or bark-beetle attacks. Disturbed stands comprised different post-disturbance management, i.e. deadwood retention and salvage logged plots. We used high-throughput sequencing and ergosterol measurements to explore fungal communities and biomass, and enzyme assays to study decomposition processes.

Disturbance shifted soil fungal communities from ectomycorrhizal to saprotrophic dominated assemblages. Fungal biomass declined with decreasing tree abundance after disturbance. Activities of organic matter degrading enzymes declined by ca. 30–80% after disturbance. The relative abundance of ectomycorrhizal fungi was positively related to enzymatic activities. Tree biomass parameters and amounts of deadwood retained were positively related to fungal biomass, certain ectomycorrhizal taxa, and relative ectomycorrhizal fungal abundance among disturbed stands, which, in turn, was associated with higher enzymatic activities.

Our findings demonstrate a significant response of soil fungal communities to natural forest disturbance and salvage logging, with consequences for decomposition and soil organic matter dynamics. We conclude that the

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retention of surviving trees and deadwood as biological legacies attenuated associated changes to a significant extent, highlighting their importance for the preservation of ectomycorrhizal fungi and the maintenance of decomposition processes after disturbance.

1. Introduction

Forest disturbances have increased in extent, frequency, and severity across Europe, with wind and insects representing the major natural disturbance agents (Gardiner et al., 2010; Senf and Seidl, 2020). The timber volume derived from windthrows and bark beetle attacks more than doubled between 1970 and 2010, a trend which is partly attributed to climate change, and further predicted to increase (Seidl et al., 2014b). Stand-replacing disturbance causes an abrupt change in forest composition, structure, and function (Franklin et al., 2002; Meigs and Keeton, 2018). Particularly surviving trees and retained deadwood—so called biological legacies—have been identified as effecting habitat quality and species richness positively (Thom and Seidl, 2015) thus enhancing ecosystem biodiversity and resilience following disturbance (Swanson et al., 2011; Seidl et al., 2014a; Thorn et al., 2017, 2018). However, for economic reasons, and to mitigate further disturbance events (e.g., subsequent insect outbreaks), windthrown and bark-beetle affected forests are commonly salvage logged after disturbance, whereby dead and damaged trees are harvested (Leverkus et al., 2018; Müller et al., 2019). As additional management-induced disturbance (i.e. compound disturbance), salvage logging is argued to have strong and long-lasting negative ecological impacts on forests such as, for instance, a disruption of ecosystem recovery (Lindenmayer et al., 2017; Kleinman et al., 2019). Despite a growing recognition of the effects natural forest disturbance and salvage logging can have aboveground, our understanding about potential impacts on the belowground biome and associated functions is still far from complete (Kleinman et al., 2019).

Fungi are a key group of the soil microbiome in temperate and boreal forests, and their community composition can strongly be affected by forest disturbance. Particularly ectomycorrhizal (EM) fungi have been shown to strongly decrease in abundance following windthrows, bark beetle attacks, forest fires, and harvesting operations, as they rely on the supply of recently fixed carbon (C) from their host trees (Holden et al., 2013; Stursova et al., 2014; Pec et al., 2017; Kohout et al., 2018; Custer et al., 2020; Pérez-Izquierdo et al., 2021; Rodriguez-Ramos et al., 2021). Salvage logging and associated reduction of deadwood may additionally influence soil fungal communities, by, for example, soil disturbance from machinery movement (Hartmann et al., 2012), changes in organic matter input to soil (Bradford et al., 2012; Hotta et al., 2020), or alterations of the microclimate (Walker et al., 2012; Perreault et al., 2021). Deadwood removal can also impair the regeneration of trees after disturbance (Jonášová and Prach, 2004; Macek et al., 2017) which, in turn, might negatively affect EM fungal abundance. Some EM species are strongly associated to deadwood (Tedersoo et al., 2003) or need rotten wood as substrate for the growth of their fruiting bodies (Jones, 2017). The harvest of surviving trees during salvage logging can further amplify the reduction in EM abundance, as shown for bark beetle-affected stands (Rodriguez-Ramos et al., 2021). Similarly, Pérez-Izquierdo et al. (2021) found a stronger negative response of EM fungi to forest fire when salvage logging was applied. These authors consequently suggested that avoiding or reducing the harvest of surviving trees could be a strategy to mitigate the impact of forest disturbance on fungal communities. In addition to the amount of lying deadwood retained, the number of surviving trees may therefore be an important biological legacy determining soil fungal community composition following natural forest disturbance and salvage logging.

A shift in the soil fungal community composition following disturbance can alter C and nitrogen (N) dynamics in forest soils, as fungi are strongly involved in the decomposition of soil organic matter (SOM). Ectomycorrhizal fungi are assumed to be less efficient SOM decomposers than free-living saprotrophic fungi (Lindahl and Tunlid, 2015; Zak et al., 2019). However, a wide range of EM species possess the enzymatic capacity to degrade organic compounds such as cellulose, chitin, and even lignin—most likely to mine SOM for organic N and other nutrients (Bödeker et al., 2014; Kohler et al., 2015; Shah et al., 2016; Nicolás et al., 2019). This function makes EM fungi essential for the nutrient supply of their host trees, ultimately impacting forest growth performance and ecosystem fertility (Read and Perez-Moreno, 2003). In support of this idea, studies from Norway spruce stands showed a coinciding decrease in EM fungal abundance and associated extracellular enzyme activities following clear cut harvest and bark-beetle attacks (Stursova et al., 2014; Kohout et al., 2018). A loss in EM fungi following disturbance might also affect C and N dynamics in forest soils by widening the ecological niche for saprotrophic communities. A released competition between EM fungi and saprotrophs for growth-limiting resources has been suggested to increase SOM decomposition (Gadgil and Gadgil, 1971; Fernandez and Kennedy, 2016). This phenomenon, however, seems to occur mainly in upper soil horizons where organic substrates are less decomposed and richer in energy (Brzostek et al., 2015; Averill and Hawkes, 2016; Fernandez and Kennedy, 2016; Sterkenburg et al., 2018). Attenuation of disturbance-induced reductions in EM fungi by the retention of biological legacies might thus also mitigate effects on SOM decomposition processes (Pérez-Izquierdo et al., 2021). Investigating such feedback mechanisms is key to better predict soil C and N dynamics following natural forest disturbance and salvage logging.

In this study, we investigate how soil fungal communities, enzymatic decay of SOM, and soil C and N pools of Norway spruce stands respond to windthrows and bark beetle attacks, and whether subsequent salvage logging further amplifies a disturbance-induced response. Twenty-one forest plots across the Bavarian Forest National Park were selected covering intact and disturbed stand situations. Half of the disturbed plots were salvage logged after disturbance, while the other half retained affected trees on site, resulting in large quantities of deadwood. We hypothesized that 1) disturbance-induced changes in soil fungal community composition and particularly EM fungal abundance relate to the amounts of biological legacies (i.e. retaining deadwood and surviving trees) retained after disturbance, and 2) disturbance-induced changes in fungal community composition coincide with alterations in enzymatic decay of SOM. Specifically, we discuss whether and how fungal associated changes in enzymatic decay may influence post-disturbance C and N dynamics and organic matter storage in forest soils.

2. Materials and methods

2.1. Site description

The study was conducted in the Bavarian Forest National Park, Germany. Mean annual precipitation ranges from 1300 to 1800 mm, and mean annual temperatures range from 3 to 4 °C. In 2007, the National Park was hit by the extratropical cyclone 'Kyrill' with hurricane-strength winds, followed by severe outbreaks of the bark beetle *Ips typographus* L. in Norway spruce (*Picea abies* (L.) H. Karst) stands—resulting in large areas of stand-replacing disturbance (Senf et al., 2019). In the core zones of the park the accruing dead woody debris was retained on site. In the border zones to neighbouring managed forests, dead woody debris was removed by salvage logging after disturbance using ground-based machines (i.e. forwarders).

From a total of 293 long-term monitoring plots established across the park (Bässler et al., 2010), 21 plots (30 m × 30 m) were selected (Fig. S1) based on comparable disturbance intensities/history, pre-disturbance

stand conditions, geology (gneiss) and soil types (Cambisols). Plots covered three treatments: mature, intact forest stands as control (referred to as 'intact' plots), disturbed areas where deadwood was kept on site ('deadwood retention' plots), and disturbed areas where dead and dying trees and deadwood (except stumps) were removed ('salvage logged' plots; n = 7 each). Both intact and disturbed plots are/were dominated by Norway spruce. Disturbed plots are now characterized by a sparse regeneration of Norway spruce and a dense pioneer ground vegetation dominated by grasses (i.a. *Calamagrostis villosa, Deschampsia flexuosa*).

2.2. Soil sampling, vegetation, and deadwood mapping

At each plot, three subplots (1 m^2) were selected randomly (distance between subplots ≥10 m). In June 2018, one soil core per subplot was taken to a depth of 40 cm using a soil auger (diameter: 8 cm). Soil cores were separated into 4 layers: litter, organic, mineral topsoil and mineral subsoil layers. Mineral subsoil was defined at a depth of 25–40 cm. The soil layers of the 3 subplots were combined to derive one composite sample per soil layer and plot (n = 84; 21 plots × 4 soil layers). Samples were transported to the laboratory in plastic bags under cooled conditions and were immediately processed after arrival.

The percentage surface cover of ground vegetation (grasses and herbs) was determined for each subplot using a 1 × 1 m frame. Living trees and standing deadwood snags were measured within a radius of 1–6 m (depending on tree/snag density) from the subplot centre. Tree species and diameters at breast height (dbh) were determined. Aboveground standing biomass of living trees as well as leaf biomass of trees (t ha^{-1}) were subsequently calculated for each plot using allometric functions (Forrester et al., 2017). Trees with a diameter at breast height ≤10 cm were considered as regenerating trees. Standing (snags), lying (logs), and stump deadwood were determined on a volume-base (m^3 ha^{-1}), using diameter, height, and length. Leaf biomass of ground vegetation was sampled within a 0.5 × 0.5 m frame; total leaf biomass was calculated by multiplication with percentage cover.

2.3. Root biomass and soil carbon and nitrogen stocks

In the laboratory, the total weight of sampled layers was determined (±0.1 mg). Except for litter layers, samples were carefully sieved (2 mm) to separate soil from roots; roots were picked from the sieve and separated into woody fine (diameter ≤2 mm) and coarse roots (d > 2 mm), and grass/herb (ground vegetation) roots (Rewald et al., 2012). Litter layer samples were picked for roots and stones first, and remaining litter material was cut into small pieces and homogenized afterwards. All root samples were carefully rinsed, dried (70 °C, 48 h) and subsequently weighed (±0.1 mg); total stocks were calculated (t ha^{-1}). Additionally, stones and non-soil fractions (e.g. small twigs, pieces of cones) were separated from samples. Moisture content was determined gravimetrically on 10 g (litter) and 20 g (soil) subsamples, respectively. Subsamples were dried (70 °C, 48 h) and weighed (±1 mg); total soil dry weight (excluding stones, g m^{-2}) was determined for each layer. Total C and N concentrations of 300 mg dried subsamples were measured with a TruSpec CN analyser (Leco Corp., St Joseph, MI, USA) (ÖNORM L 1080, 2013); subsamples were ground and homogenized prior to measurements. Total C and N stocks (t ha^{-1}) per soil layer were calculated by multiplying total soil dry weight by C and N concentrations.

2.4. Fungal community analysis

Fungal community analysis followed the protocol described in Gorfer et al. (2021) and Mayer et al. (2021), respectively. Immediately after soil sieving, 0.5 g of homogenized soil was weighed into 1.5 ml LifeGuard Soil Preservation Solution (MO BIO, Carlsbad, CA, USA). For the isolation of DNA, 50% of the suspension was put into wells of a Bead Plate from the PowerSoil-htp 96 Well Soil DNA Kit (MO BIO, Carlsbad, CA, USA). Following centrifugation and removal of the supernatant, the manufacturer's protocol for vacuuming and centrifugation was followed. Cell lysis was performed in a FastPrep-96 bead beater (MP Biomedicals, Santa Ana, CA, USA) twice at 6 m s^{-1} for 45 s with a 1 min break between the two runs. New Bead Solution and Solution C1 were added to the soil pellet after the first extraction to increase recovery of DNA from soil; the full extraction was repeated (Feinstein et al., 2009). Library preparation and Illumina MiSeq sequencing of fungal ITS2-amplicons was performed as described earlier (Keiblinger et al., 2018; Gorfer et al., 2021). For primer details see Supporting Information (Methods S1). Illumina MiSeq PE250 sequencing was conducted at the NGS Unit of the Vienna Biocenter Core Facility GmbH (Vienna, Austria).

The analysis of sequence data followed the protocol outlined in Unterwurzacher et al. (2018) and Gorfer et al. (2021). Initial quality filtering was done with Trimmomatic (v. 0.36) (Bolger et al., 2014), the USEARCH program suite (v. 9.0.2132) (Edgar, 2010) was used for merging forward and reverse reads, chimera detection and removal of underrepresented sequences (<10). VSEARCH (Rognes et al., 2016) was used for clustering and counting sequences per cluster, using a 97% sequence similarity, which is a widely used threshold for the ITS region (e.g. Gorfer et al., 2021) and lies between generally accepted limits for discrimination of species and genera (Vu et al., 2019). Taxonomic affiliation of OTUs was done with the UTAX script against the UNITE database (Kõljalg et al., 2013). Subsequently, additional manual editing of taxonomic affiliations was done to increase phylogenetic accuracy (Hofstetter et al., 2019; Deltedesco et al., 2020; Gorfer et al., 2021). When accurate classification at the genus level was not possible, the closest taxonomic level, to which a clear affiliation was possible, was used instead. Non-fungal sequences were not included in further analyses. Fungal operational taxonomic units (OTUs) were assigned ecological lifestyles/guilds using an in-house database (see Deltedesco et al. (2020); Gorfer et al. (2021); Mayer et al. (2021)). Fungal lifestyles/guilds were grouped into EM fungi, other symbiotic fungi (e.g. species with unspecific mycorrhizal lifestyle or arbuscular mycorrhizal fungi), saprotrophic fungi, potentially plant pathogenic fungi, and unknown lifestyle; grouping was conducted at genus level or closest taxonomic level. For a full list of taxonomic groups see Table S1.

2.5. Fungal biomass

Ergosterol was extracted as described in Rousk and Bååth (2007). In brief, 0.5 g of fresh soil was transferred to test tubes and 5 ml 10% KOH in methanol were added. The samples were sonicated for 15 min, followed by a 90 min heat treatment at 70 °C. After the samples cooled down to room temperature, 1 ml deionized H_2O and 2 ml cyclohexane were added to the test tubes. After vortex mixing for 1 min, the test tubes were centrifuged for 5 min on a table centrifuge at 3000 rpm to separate phases. Thereafter, the cyclohexane was transferred into new tubes. Another 2 ml of cyclohexane were added, and the test tubes were processed as above. The combined cyclohexane phases were evaporated at 40 °C under N_2 to dryness. The samples were then dissolved in 200 μl methanol, heated for 15 min at 40 °C, filtered through a 0.45 μm syringe filter and analysed using HPLC (Hitachi, Tokyo, Japan) and a UV detector (282 nm). Ergosterol concentrations (μg g dry $soil^{-1}$) are used as proxy for fungal biomass (Rousk and Bååth, 2007); ergosterol stocks (mg m^{-2}) per soil layer were calculated by multiplying the total soil dry weight by ergosterol concentrations.

2.6. Enzyme activities

Potential activities of six hydrolytic enzymes (nmol g^{-1} dry soil h^{-1}) involved in the breakdown of SOM (Nannipieri et al., 2018) were estimated using the microplate fluorometric assay according to Marx et al. (2001), DeForest (2009), and German et al. (2011). We evaluated the activities of β-glucosidase (BG), β-xylosidase (XYL) and cellobiohydrolase (CEL), leucine-aminopeptidase (LAP),

N-acetyl-β-D-glucosaminidase (NAG) and acid phosphatase (AP). Amino-methyl-coumarin (AMC) was the substrate basis for LAP, while methyl-umbelliferone (MU) was the substrate basis for all other hydrolytic enzymes. All substrates were purchased from Sigma Aldrich (Missouri, USA). Optimal substrate concentrations and incubation times for BG (0.5 mM), XYL (1 mM), CEL (0.3 mM), LAP (1 mM), NAG (1 mM) and AP (2 mM) were evaluated in advance, whereby substrate concentrations ranging between 0.1 and 4 mM and incubation times between 60 and 240 min were tested (data not shown). In brief, 0.5 g of fresh soil were suspended in 50 ml of a 100 mM sodium acetate buffer, pH 4.5, and homogenized for 1 min in a sonication bath. Aliquots of 200 μl were pipetted under constant stirring into black 96-well microplates, with four technical replicates for each sample. 50 μl substrate (dissolved in buffer solution) were added to each well and horizontally shaken for 30 s to mix with the sample suspension. Four standard solutions with concentrations between 10 and 250 μM were prepared for MU-based substrates (NAG, BG, XYL, CEL, AP); two standard curves with concentrations of 20 μM and 50 μM were used for AMC-based substrates (LAP). The well plates were covered with a cohesive plastic film and incubated in the dark at 20 °C for 120 min (AP) and 180 min (LAP, NAG, BG, XYL, CEL), respectively. Fluorescence was measured using an EnSpire multiplate reader (PerkinElmer, Waltham, MA, USA) with an excitation of 365 nm and an emission of 450 nm, at 20 and 100 flashes. Soil quenching was evaluated for each soil sample individually using the slope quotient of the standard curves (50 μM for both AMC and MU) in buffer and soil slurry, respectively.

Phenol oxidase (POX; nmol g^{-1} dry soil h^{-1}) was measured using 3,4-Dihydroxy-L-phenylalanine (L-DOPA) as substrate (Sigma Aldrich, Missouri, USA). In brief, 900 μl of soil suspension (or 900 μl of buffer solution for blanks to control for background absorbance) were mixed with an equivalent amount of a 10 mM L-DOPA solution (prepared in 100 mM sodium acetate buffer, pH 4.5), horizontally shaken at 500 rpm for 10 min and centrifuged at 5000 rpm for 5 min. Immediately after, 250 μl of this suspension were transferred into a clear 96-well plate with threefold repetition. Plates were incubated in the dark at 20 °C for ~6 h. Absorbance at 450 nm was measured using a multiplate reader (as above) twice: immediately after transfer, and after incubation. The extinction coefficient used for determining the POX activity was 7.9 μmol^{-1} (Bach et al., 2013) and the activity was calculated as the difference between before and after incubation.

We wish do draw to attention that fluorometric assay measurements represent potential enzymatic activities and may not reflect actual *in-situ* enzymatic activities (Nannipieri et al., 2018). However, the method has a long history in soil biochemistry and several studies have successfully used it to assess decomposition processes and fungal functioning in forest soils (Sinsabaugh et al., 2005; Kyaschenko et al., 2017; Mayer et al., 2021).

2.7. Carbon mineralization, and dissolved carbon and nitrogen, nitrate, ammonium, and pH

For C mineralization measurements, fresh litter/soil (litter layer: 20 g, organic layer: 50 g, mineral top- and subsoil: 100 g) was filled in steel cylinders at field bulk density after sieving/cutting (Kutsch et al., 2010). After an equilibration time of ~3 days, cylinders were put in 2 l plastic jars connected to an infrared gas analyser (SBA-4, PP Systems International Inc., Amesbury, MA, USA). Carbon mineralization rates were determined as CO_2 efflux of each sample over a measurement period of 6 min. Carbon mineralization rates (μg CO_2-C g^{-1} dry soil h^{-1}) were determined at 20 °C. Details of the measurement system can be found in Mayer et al. (2017).

Dissolved organic C (DOC) and dissolved N (DN) were determined on fresh, homogenized subsamples (litter: 3 g, soil: 5 g). Samples were shaken in 25 ml of 0.5 M K_2SO_4 for 1 h, then centrifuged and filtered (using cellulose acetate Whatman filter); soil extracts were subsequently analysed with a Shimadzu TOC-L analyser (Shimadzu Corp., Kyoto, Japan). Soil nitrate and soil ammonium concentrations were measured on 5 g of fresh soil shaken in 50 ml of 1 M KCl for 2 h. Soil extracts were subsequently filtered (as above), and nitrate was determined photometrically (540 nm) using vanadium (III) as reductant (Miranda et al., 2001), while ammonium was determined photometrically (660 nm) using the indophenol blue method (Rhine et al., 1998). DOC, DN, nitrate and ammonium concentrations (μg g^{-1} dry soil) were calculated per gram dry soil. Soil pH in H_2O (4:1 extracts v/v) was determined for fresh soil samples with a pH meter.

2.8. Statistical analysis

Statistical analysis and plotting was conducted in R (R Core Team, 2017). Differences between intact and disturbed plots were evaluated using one-way analysis of variance (ANOVA) and post-hoc Tukey tests. Data were log transformed in case criteria for ANOVA were not met. Canonical correspondence analysis (CCA; *cca* function in the R package 'vegan' (Oksanen et al., 2016)) was used to investigate fungal community composition among intact and disturbed plots and different soil layers and to determine the effects of tree and deadwood legacies on the soil fungal community composition at salvage logged and deadwood retention plots (Paliy and Shankar, 2016). Standing biomass of trees, tree fine root biomass, number of regenerating trees, and volume of standing and lying deadwood, and volume of stumps were used as respective indicator variables. The significances of the variables were tested by means of Monte Carlo permutation tests (n = 999). Based on the CCA, a variance partitioning analysis (*varpart* function in the R package 'vegan' (Oksanen et al., 2016)) was used to determine the relative contribution of component sources of variation (i.e. standing biomass of trees, tree fine root biomass, number of regenerating as 'tree variables'; volume of standing and lying deadwood, and volume of stumps as 'deadwood variables') in shaping soil fungal community composition. Additional CCA's were used to test how much of the total variation was explained by the single variables. The CCA's were based on 166 and 135 taxonomic groups (OTUs) that occurred on $\geq$ 3 plots. Relationship between potential enzymatic activities and relative abundances of EM and saprotrophic fungi were analysed by means of linear regression models; linear regression modelling was done for all plots and separately for disturbed and intact plots. Tree and deadwood variables were also linearly related to relative abundances of EM and saprotrophic fungi, ergosterol, and soil C and N stocks. Throughout the manuscript, means and 1SE are given; level of significance for statistical analyses was set at $P < 0.05$.

3. Results

3.1. Biomass, deadwood, and ground vegetation cover

Total standing biomass as well as leaf biomass of trees were significantly greater at intact plots while leaf biomass of ground vegetation was significantly greater at disturbed plots; no differences were found between deadwood retention and salvage logged plots (Table 1). The number of regenerating trees was significantly greater at deadwood retention plots when compared to intact plots. The amounts of lying, standing, and total deadwood were significantly greater at plots with deadwood retention. No differences in stump deadwood were found among intact and disturbed plots. Grass root biomass and cover of ground vegetation was significantly greater in disturbed plots when compared to intact plots, while the opposite pattern was found for woody roots (Table 1).

3.2. Fungal guilds, fungal biomass, and community composition

Among all plots, EM and saprotrophic fungi were dominating the fungal community. Intact plots were dominated by EM fungi (Fig. 1a)—having a relative abundance between 60 and 74%. Relative EM

Table 1
Vegetation cover, aboveground biomass, and deadwood, and belowground parameters of intact and disturbed (deadwood retained or salvage logged) forest stands in the Bavarian Forest National Park. Different letters indicate significant ($P < 0.05$) differences between treatments (mean ± SE; n = 7). Abbreviations: diameter at breast height (dbh).

	Intact	Deadwood retention	Salvage logged
Vegetation cover			
Grasses and herbs (%)	14.5 ± 9.5 **a**	51.2 ± 9.5 **b**	56.2 ± 11.5 **b**
Aboveground biomass parameters			
Total standing biomass trees (t ha^{-1})	379.1 ± 21.9 **a**	39.9 ± 10.8 **b**	18.1 ± 7.5 **b**
Regenerating trees (n ha^{-1})	379 ± 118 **a**	4290 ± 2931 **b**	813 ± 236 **ab**
Leaf biomass trees (t ha^{-1})	79.1 ± 7.6 **b**	15.2 ± 3.3 **a**	7.2 ± 2.8 **a**
Leaf biomass grasses and herbs (t ha^{-1})	0.39 ± 0.25 **a**	1.37 ± 0.25 **b**	1.50 ± 0.30 **b**
Deadwood parameters			
Total deadwood (m^3 ha^{-1})	15.4 ± 6.2 **a**	180.1 ± 58.1**b**	39.3 ± 6.1 **a**
Standing deadwood, snags (m^3 ha^{-1})	1.1 ± 1.1 **a**	66.2 ± 22.8 **b**	0±0**a**
Lying deadwood, logs (m^3 ha^{-1})	0 ± 0 **a**	92.7 ± 46.3**b**	11.2 ± 5.8 **a**
Stumps (m^3 ha^{-1})	14.3 ± 6.3 **a**	21.1 ± 5.9 **a**	28.0 ± 4.2 **a**
Belowground parameters			
Total woody root biomass (t ha^{-1})	10.1 ± 1.0 **a**	3.1 ± 1.6 **b**	2.7 ± 1.4 **b**
Woody coarse root biomass (t ha^{-1})	4.5 ± 0.8 **a**	1.5 ± 0.8 **b**	1.0 ± 0.6 **b**
Woody fine root biomass (t ha^{-1})	5.60 ± 0.58 **a**	1.63 ± 0.78 **b**	1.62 ± 0.84 **b**
Grass/herb root biomass (t ha^{-1})	0.26 ± 0.14 **a**	5.13 ± 1.41 **b**	6.77 ± 1.54 **b**

abundance was significantly lower in disturbed plots apart from in the organic layer, where relative EM abundance was similar among intact and deadwood retention plots. Ectomycorrhizal relative abundance did not differ among deadwood retention and salvage logged plots.

Saprotrophic fungi possessed higher relative abundances at disturbed plots compared to intact stands (Fig. 1b); deadwood retention plots showed relative abundances between 39 and 57%, and salvage logged plots between 38 and 48%, respectively. Saprotrophic fungal abundance did not differ among disturbed plots (Fig. 1b). Relative abundance of saprotrophic fungi differed significantly in litter, organic soil, and mineral topsoil layers when comparing intact and salvage logged plots. When comparing intact and deadwood retention plots, these differences were only significant in the litter, and mineral subsoil layers (Fig. 1b). Relative abundances of potential plant pathogenic and other symbiotic fungi were ≤5% across treatments (Fig. S2). Relative abundances of plant pathogenic fungi were higher in the litter and organic layer when comparing salvage logged to intact plots. Relative abundance of other symbiotic fungi differed in all layers, except mineral subsoil when comparing salvage logged to intact plots; salvage logged plots had a higher relative abundance of other symbiotic fungi when compared to deadwood retention plots in the litter and mineral topsoil layers. Ergosterol stocks (i.e. fungal biomass) along the soil profile did not differ between treatments (Fig. 1c).

Canonical correspondence analysis confirmed a disturbance-induced shift in fungal community composition (Fig. 2a). Both, treatment and soil layer were significant variables. The first and second CCA axes explained 5.6 and 4.4% of the variance, respectively. Intact plots clearly separate from deadwood retention and salvage logged plots (CCA axis 1). The litter layer separates from the organic and mineral soil layers (CCA axis 2). Ectomycorrhizal fungi from the genera Russula, Clavulina, Amanita, Lactifluus, and Imleria were clearly associated with organic and mineral topsoil layers of intact plots. Ectomycorrhizal fungi from the genera Inocybe, Lactarius, and Telephora were also present at disturbed plots. Saprotrophic fungi from the genera Podila, Linnemannia, and Mycena were more associated with the litter- and organic soil layers of the disturbed plots. The mineral soil layers were dominated by saprotrophic fungal communities, with fungi from the genus Mortierella being more abundant under disturbed conditions.

Canonical correspondence analysis showed a strong influence of tree and deadwood variables on the soil fungal community composition among salvage logged and deadwood retention plots (Fig. 2b). The first and second CCA axes explained 6.07 and 4.56% of the variance, respectively. All variables of the final model were highly significant, except for lying deadwood which can be related to the strong positive correlation between lying deadwood and number of regenerating trees. Ectomycorrhizal fungi from the genera *Clavulina* and *Inocybe* were positively correlated with standing tree biomass and woody fine root biomass. EM fungi from the genera *Amphinema*, *Amanita*, and *Tomentella* were positively correlated with standing and lying deadwood and the number of regenerating trees, respectively. Stump volume was negatively correlated with most EM taxa. Variation partitioning revealed tree and deadwood variables to explain 1.7 and 2.0% of the fungal community composition, respectively (Fig. 2b, inset). Most of the variation (4%) was explained by the shared effect of tree and deadwood variables. Canonical correspondence analysis of single variables showed standing tree biomass, woody fine root biomass, number of regenerating trees, lying deadwood, standing deadwood, and stumps to explain 4.75, 3.67, 5.68, 5.61, 4.14, and 5.16% of the total variance of the fungal community among disturbed plots.

3.3. Enzyme activities and carbon mineralization

Activities of glucosidase and phosphatase were significantly reduced in litter and organic soil layers when comparing intact and disturbed plots (Fig. 3a,f). Also in the mineral topsoil, salvaged logged plots featured a lower glucosidase activity than intact plots. Activities of cellobiohydrolase, xylosidase, and N-acetylglucosaminidase were significantly reduced in organic soil layers when comparing intact and disturbed plots (Fig. 3b,c,e). Activities of leucine-aminopeptidase were significantly reduced in organic soil layers when comparing intact and salvage-logged plots (Fig. 3d). Phenol oxidase activity was significantly higher in litter layer of deadwood retention plots when compared to salvage logged plots, but no differences were present when compared to intact plots (Fig. 3g). Activities of phenol oxidase were lower in the organic layer of deadwood retention plots than in intact plots. Carbon mineralization rates did not differ among intact and disturbed plots (Fig. 3h).

3.4. Dissolved organic carbon and nitrogen, nitrate, ammonium, pH, and carbon and nitrogen stocks

Dissolved organic C concentrations were significantly greater in the organic soil layer of disturbed plots compared to intact plots; differences in other layers were not significant (Fig. 4a). Dissolved N concentrations in organic soil layer were significantly greater in salvage logged plots when compared to intact plots (Fig. 4b). DOC and DN concentrations in the litter and mineral soil layers did not differ between treatments. Nitrate concentrations were significantly greater in organic soil layers of deadwood retention and salvage logged plots as compared to intact plots (Fig. 4c). In the litter layer, significant differences between nitrate concentrations were found between intact and deadwood retention plots. Ammonium levels did not differ between treatments at any soil layer (Fig. 4d). Soil pH in litter and organic soil layers was significantly higher at disturbed plots when compared to intact plots (Fig. 4e). Soil C stocks of the litter layer were significant lower at salvage logged plots, but soil N stocks were similar when compared to intact plots (Fig. 4f and g). No difference in soil C and N stocks of the litter layer was found between deadwood retention and intact plots. Soil C and N stocks of organic and mineral soil layers did not differ between treatments. Soil C

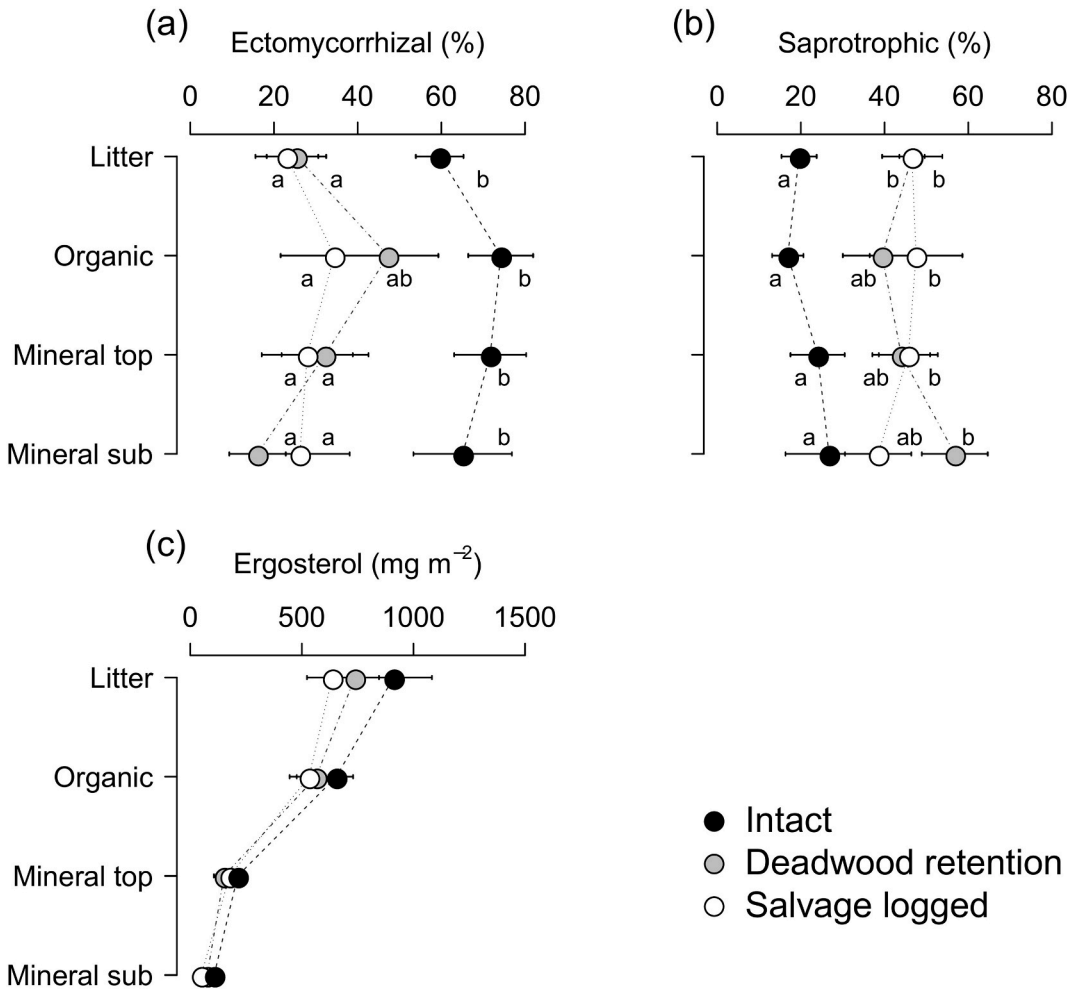

Fig. 1. Relative abundance of ectomycorrhizal (a) and saprotrophic (b) fungi, and ergosterol stocks (c) in litter, organic, mineral topsoil, and mineral subsoil layers of intact forest stands (black), disturbed plots where deadwood retained on site (grey), and salvage logged plots (white) in the Bavarian Forest National Park. Different letters indicate significant ($P < 0.05$) differences between treatments (mean ± 1 SE).

to N ratios did not differ among treatments (Fig. 4h).

3.5. *Relations between fungal guilds, fungal biomass, enzyme activities and biological legacies*

Activities of hydrolytic enzymes were positively related to relative abundances of EM fungi in most of the soil horizons among all plots (Fig. 5a). No significant relation was found for phenol oxidase. When analysing only the disturbed plots (Fig. 5b), glucosidase, cellobiohydrolase, xylosidase, and leucine-aminopeptidase in the organic layer and N-acetylglucosaminidase in litter and mineral soil horizons were positively related with EM relative abundances. The relationship between enzyme activities and relative abundance of saprotrophic fungi showed opposite patterns in most of the horizons (Fig. 5c and d). When analysing the intact plots separately (Fig. S3), acid phosphatase in the litter layer, and glucosidase and leucine-aminopeptidase in the mineral topsoil were positively related with EM relative abundances; glucosidase, leucine-aminopeptidase, and xylosidase were negatively related to relative abundance of saprotrophic fungi. A positive relation between relative abundance of other symbiotic fungi and xylosidase and phenol oxidase was found in the litter and organic layer, respectively (Fig. S4).

Relative abundance of EM fungi was positively related to standing biomass of trees and woody fine roots among all plots (Fig. 6a) and among disturbed plots only (Fig. 6b), respectively. For the latter, however, relations were only significant for litter and mineral topsoil layers. Relative EM fungal abundance in litter, organic, and mineral topsoil layers was negatively related to stump volume and to grass root biomass in mineral topsoil layers. Relative abundance of saprotrophic fungi was negatively related to tree variables, while no significant relations were found when related to deadwood variables (Fig. 6c and d). Ergosterol was strongly positively related to woody fine roots and negatively related to stump volume (Fig. 6e). At disturbed plots, ergosterol was also positively related to standing biomass of trees, number of regenerating trees, and lying deadwood (Fig. 6f).

4. Discussion

Here, we investigated soil fungal communities in a windthrow and bark beetle affected landscape roughly one decade after stand-replacing disturbance events, followed by salvage logging operations at half of the disturbed sites. We explore whether biological legacies (i.e. retaining deadwood, surviving trees) attenuate disturbance related changes in the soil fungal community composition, and relate community changes to soil C and N dynamics including enzymatic decay of SOM.

Generally, we found a strong decrease in the relative EM fungal abundance from intact to both disturbance categories (Figs. 1a and 2a). This can be related to the vast reduction of mature host trees after stand-replacing disturbance and corresponds to results of earlier studies conducted after bark beetle outbreaks (Stursova et al., 2014; Treu et al., 2014; Pec et al., 2017; Rodriguez-Ramos et al., 2021), windthrow

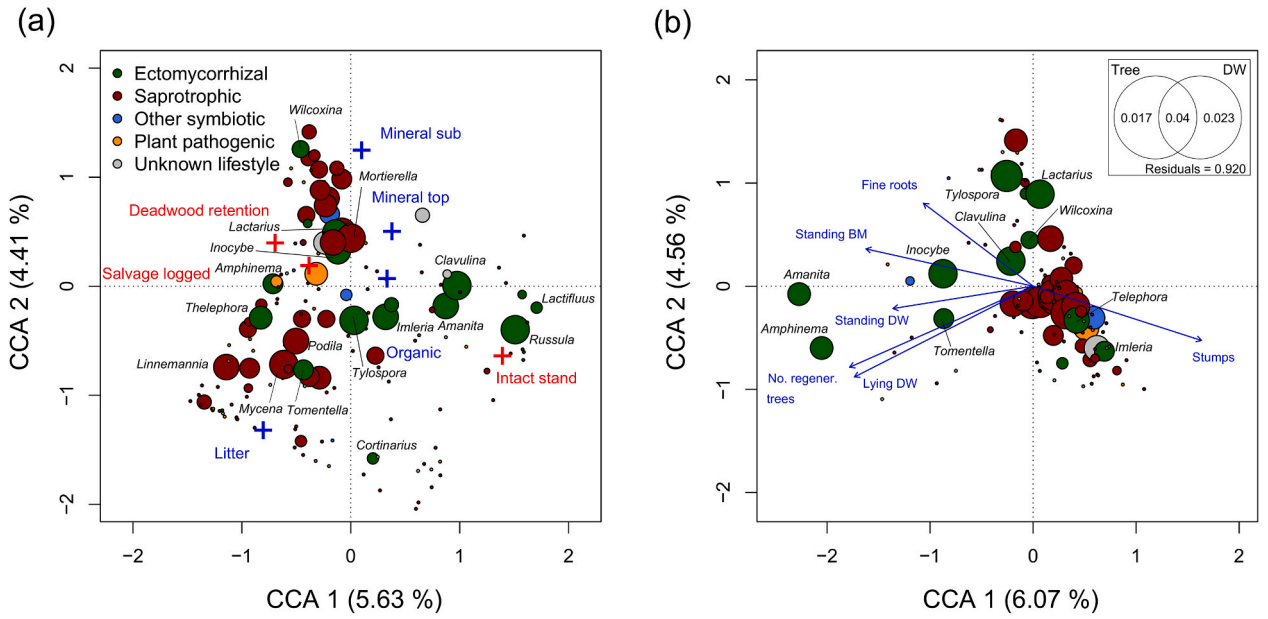

Fig. 2. Patterns of variation of soil fungal communities analysed by canonical correspondence analysis (CCA). (a) Fungal communities of intact and disturbed (deadwood retention and salvage logged plots) forest stands in the Bavarian Forest National Park as explained by soil layer and treatment variables, and (b) fungal communities of disturbed plots as explained by tree- and deadwood variables. The significances of variables were tested by means of Monte Carlo permutation tests (n = 999). The plot inset shows variance partitioning analysis for tree- and deadwood variables. The CCA's are based on fungal taxonomic groups present at ≥3 sampling plots. Taxonomic grouping occurred at genus level or closest taxonomic level. For a full list of taxonomic groups see Table S1. Groups were assigned color-coded fungal lifestyles/guilds; symbol size gives an indication for relative abundance. To improve readability, only most abundant taxonomic groups are displayed. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(Vašutová et al., 2018; Veselá et al., 2019), forest fire (Holden et al., 2013; Custer et al., 2020; Pérez-Izquierdo et al., 2021) or clear-cut harvest (Kyaschenko et al., 2017; Kohout et al., 2018). A disturbance-related decrease in EM fungal abundance was evident throughout the investigated soil profile down to a depth of 40 cm, with organic and mineral topsoil layers of intact and salvage logged plots possessing largest contrasts (Fig. 1a). The relative abundance of EM fungi declined from 67% in intact stands to 28% at salvage logged plots. Particularly affected were late-successional EM taxa from the genera *Russula*, *Amanita*, and *Lactifluus* (Fig. 2a), a finding that is in good agreement with forest chronosequence studies from Scandinavia (Wallander et al., 2010; Kyaschenko et al., 2017). Concomitant with the lower EM fungal abundance, the relative abundance of saprotrophic fungi was significantly greater following disturbance (Fig. 1b). Although the decrease in ergosterol stocks from control to deadwood retention and finally salvage logged plots was statistically not significant (Fig. 1c), a strong positive correlation between ergosterol stocks and woody fine root biomass was found (Fig. 6e). This suggests that not only fungal community composition has changed after disturbance and salvage logging, but also that fungal biomass declined along with a decreasing tree abundance.

Overall, relative abundances of EM and saprotrophic fungi were similar when comparing salvage logged to deadwood retention plots (Fig. 1a and b), suggesting a management-independent response of fungal communities to disturbance. However, in line with hypothesis 1, we found evidence that disturbance-induced changes in soil fungal communities, as well as fungal biomass, were related to the amounts of biological legacies that were retained among disturbed plots. Certain EM fungal groups, particularly from the genera *Amanita*, *Amphinema*, *Tomentella*, and *Inocybe,* possessed a higher relative abundance when both, the amounts of deadwood and standing tree biomass were high (Fig. 2b). This may be related to a higher number of regenerating trees under the presence of deadwood (Fig. 2b, Table 1). Deadwood legacies are known to encompass enhanced tree regeneration, with lying logs creating favourable microhabitats and reducing herbivory pressure by natural fencing (Ulanova, 2000; Jonášová and Prach, 2008; Taeroe et al., 2019). Higher relative abundances of certain EM fungal groups under the presence of deadwood might also be related to the absence of soil disturbance from machinery movement after timber harvesting (Hartmann et al., 2012) or to a moderating effect of deadwood on soil temperature and moisture (Walker et al., 2012). Further, relative EM fungal abundance in the litter and top mineral soil horizons was positively related to tree root biomass and standing tree biomass (Fig. 6a and b), suggesting a positive effect of surviving trees *per se* (Luoma et al., 2006; Jones, 2017; Sterkenburg et al., 2019). Finally, we observed a positive relation between ergosterol stocks and standing tree biomass, number of regenerating trees, and woody fine root biomass among the disturbed plots (Fig. 6f). These findings are in line with those from a recent study conducted in bark-beetle infested lodgepole pine stands, where surviving trees maintained relative EM fungal abundance and ergosterol stocks close to undisturbed levels (Rodriguez-Ramos et al., 2021). We therefore suggest that deadwood legacies potentially stabilize EM fungal communities and fungal biomass after disturbance by promoting tree regeneration, and, together with surviving trees, create refugia facilitating the recolonization of tree roots by EM fungi. Mitigation of disturbance induced losses in EM fungi by biological legacies may thus be an important factor enhancing ecosystem recovery and tree growth performance following windthrow and bark-beetle attacks.

In line with hypothesis 2, we found support that post-disturbance shifts in fungal community composition coincide with alterations in enzymatic decay of SOM. In both, litter and organic soil layers, the post-disturbance activities of most hydrolytic enzymes were significantly lower (−31 to −81%) when compared to intact plots (Fig. 3a–f). Thus, we did not find evidence for an increase in SOM decomposition in upper soil horizons after disturbance, although EM constraints on saprotrophic communities were likely reduced at the disturbed plots (Gadgil and Gadgil, 1975; Fernandez and Kennedy, 2016). Instead, we found a strong positive relation between most enzyme activities and the relative abundance of EM fungi (Fig. 5a), similar to other studies conducted after bark-beetle outbreaks and clearcutting (Stursova et al., 2014; Kohout

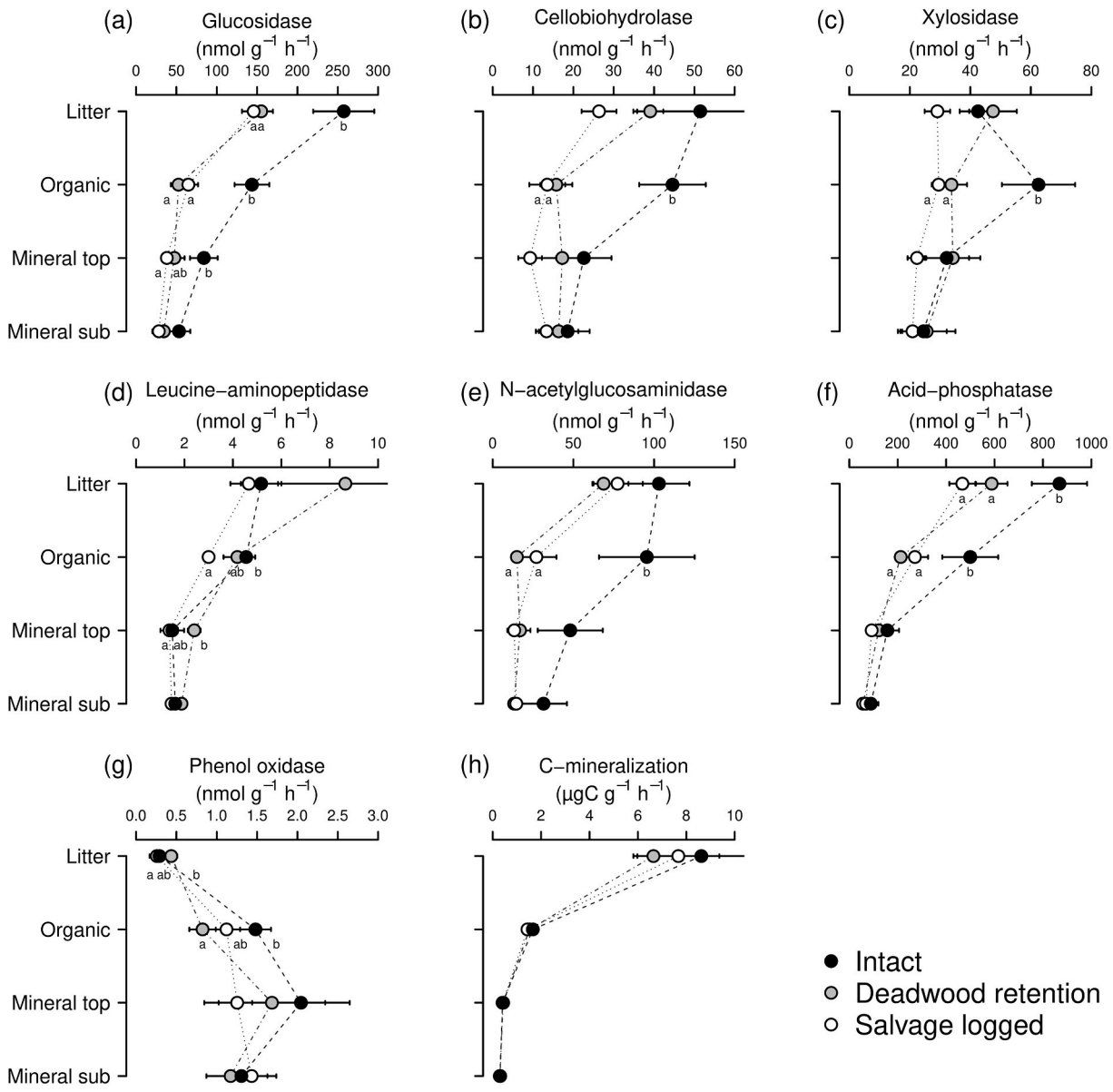

Fig. 3. Potential activities of hydrolytic enzymes (a–f), phenol oxidase (g), and carbon mineralization rates (h) in litter, organic, mineral topsoil, and mineral subsoil layers of intact forest stands (black), disturbed plots where deadwood retained on site (grey), and salvage logged plots (white) in the Bavarian Forest National Park. Different letters indicate significant ($P < 0.05$) differences between treatments (mean ± 1 SE).

et al., 2018). This finding suggests EM fungi to play an important role in SOM decomposition at the studied sites, potentially related to a reduced stimulation of saprotrophic decomposers and/or a direct involvement of EM fungi in SOM decomposition, likely due to N-mining (Shah et al., 2016; Frey, 2019; Zak et al., 2019). Although EM fungi possess a lower enzymatic repertoire compared to saprotrophic fungi, they have considerable hydrolytic abilities to decompose organic substrates, particularly those derived from microbial detritus (Kohler et al., 2015; Martin et al., 2016; Nicolás et al., 2019; Miyauchi et al., 2020). Whether EM use these abilities to mine SOM for N only, or to access additional C for metabolism, remains, however, unclear (Nicolás et al., 2019; Zak et al., 2019). The importance of EM fungi for SOM decomposition was further supported by the finding that activities of several enzymes were positively related to relative EM fungal abundances, even when analysed separately for disturbed and intact plots (Fig. 5b, Fig. S3). These results finally suggest biological legacies not only to moderate disturbance induced losses in EM fungi, but also to maintain functions associated with their presence.

Higher dissolved N and nitrate concentrations (+62 to +538%) indicate a reduced N uptake by plants, but also a stimulation of bacterial-dominated inorganic N cycling processes (e.g. nitrification) on disturbed plots. The increased soil pH values across disturbed plots might also be indicative for a higher net formation of mineral N, as shown earlier (Smolander et al., 1998). This assumption would further correspond to the findings of a meta-analysis showing increased nitrification rates following clear cut harvest in temperate and boreal forests (Jerabkova et al., 2011). Therefore, we speculate that a fungal decline with decreasing tree abundance and potentially reduced EM mining for organic N may have opened a niche for bacteria, thereby favouring inorganic N cycling processes after disturbance. A surplus of inorganic N renders it also likely that saprotrophs are less dependent on SOM-bound organic N (Craine et al., 2007; Ramirez et al., 2012). In addition, C inputs from large grass/herb root biomass pools may represent a readily available source of labile C (as indicated by higher DOC concentrations, Fig. 4a) (Solly et al., 2014; Pausch and Kuzyakov, 2018), thereby also reducing the saprotrophic demand for SOM-bound C. Together, this

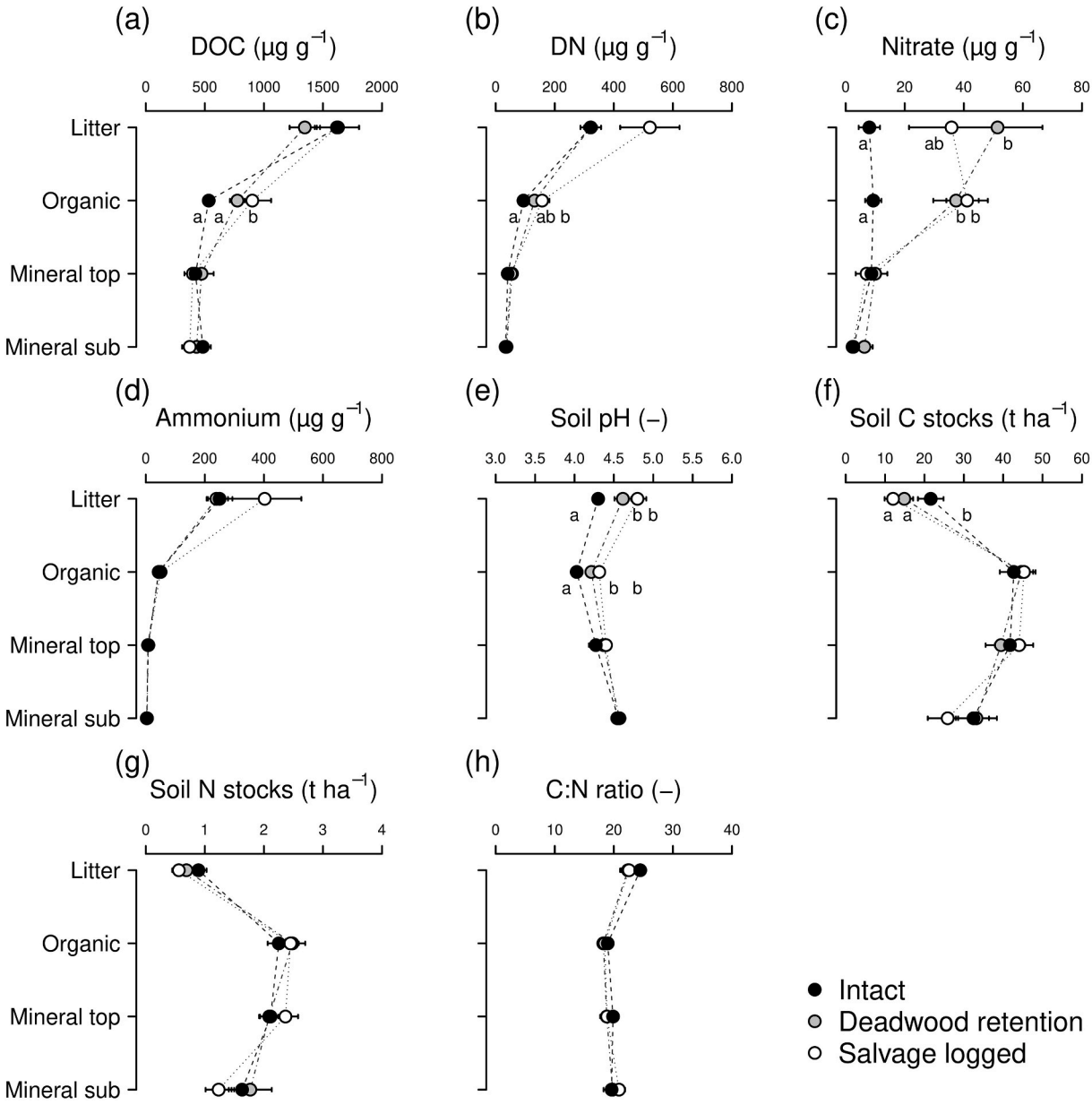

Fig. 4. Dissolved organic carbon (a), dissolved nitrogen (b), nitrate (c), ammonium (d), soil pH (e), soil carbon (f) and nitrogen stocks (g), and carbon to nitrogen ratios (h) in litter, organic, mineral topsoil, and mineral subsoil layers of intact forest stands (black), disturbed plots where deadwood retained on site (grey), and salvage logged plots (white) in the Bavarian Forest National Park. Different letters indicate significant ($P < 0.05$) differences between treatments (mean ± 1 SE).

might explain that C-mineralization rates were similar when comparing disturbed and intact plots (Fig. 3h), while activities of SOM degrading enzymes nevertheless decreased.

Soil C and N stocks can decrease after forest disturbance if SOM decomposition rates exceed organic matter input rates (Christophel et al., 2015; Mayer et al., 2017). A meta-analysis on the effects of clear cutting showed that soil C storage strongly declined within the first ten years after harvest, followed by a phase of recovery between ten to twenty years after harvest (Achat et al., 2015). Here, roughly a decade after stand-replacing disturbance, only the litter layer C stocks of the salvage logged plots were significantly lower when compared to the disturbed plots, while for all other horizons the C and N stocks were similar among treatments (Fig. 4f and g). As soil C and N stocks of litter and organic soil horizons were positively related to grass root biomass among disturbed plots (Fig. S5), it seems plausible that above- and belowground organic matter input from an abundant ground vegetation may have compensated for a decline in tree litter input (Table 1), thereby maintaining C and N storage close to pre-disturbance levels. This assumption would be in line with the findings from a windthrow site in the Tatra mountains (Don et al., 2012). In addition, we hypothesize that a reduced enzymatic decay of SOM may be an important factor favouring the recovery and maintenance of soil C and N stocks after disturbance. This hypothesis would be supported by the findings of a study from subarctic birch stands, where a decrease in decomposition was suggested to be a prime cause for unchanged soil C stocks after forest disturbance by insects (Sandén et al., 2020). Interestingly, no differences in soil C and N stocks were found when comparing deadwood retention to salvage logged plots as shown by others (Bradford et al., 2012; Hotta et al., 2020). Further, no significant relations between C and N stocks and biological legacy variables were found among disturbed plots (Fig. S5). However, this might change in later stages post-disturbance, particularly when snags begin to break down and decaying deadwood logs get incorporated into soil (Hotta et al., 2020).

Taken together, our study provides evidence for a profound change

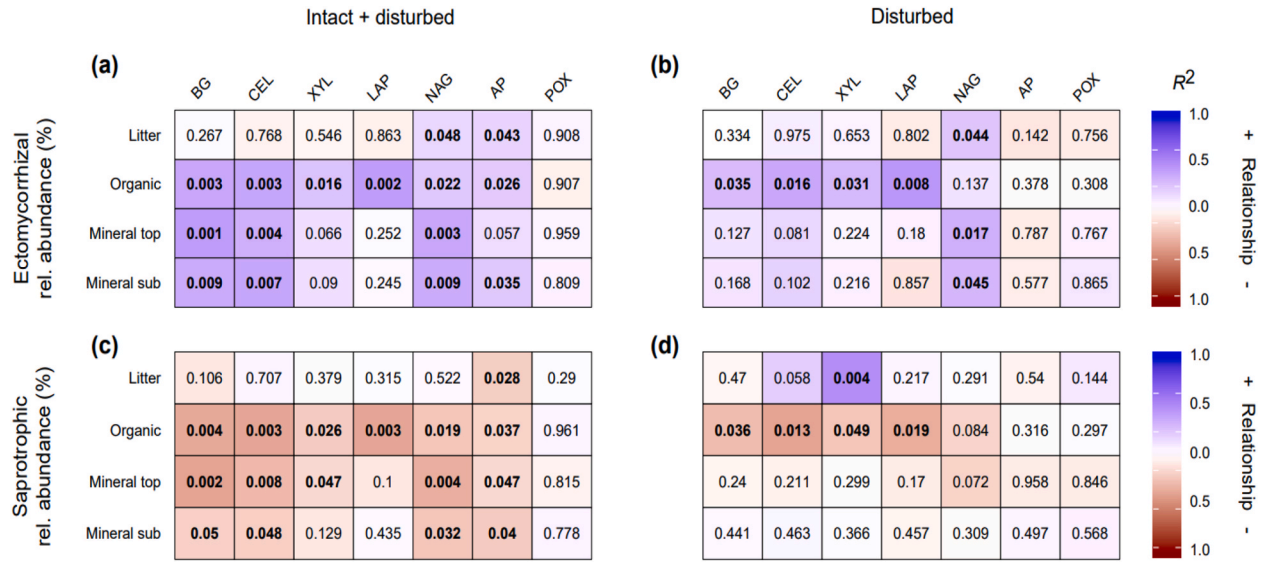

Fig. 5. Heatmaps of linear regression models between relative abundance (%) of ectomycorrhizal and saprotrophic fungi and potential soil enzymatic activities (nmol g^{-1} h^{-1}) in litter, organic, mineral topsoil, and mineral subsoil layers among intact and disturbed plots (a,c) and disturbed plots only (b,d) in the Bavarian Forest National Park. P-values are given, and significant ($P < 0.05$) relations are indicated in bold. Colour intensity of heatmaps indicates R^2 values and different colours indicate positive (blue) and negative (red) relationships, respectively. Abbreviations: BG, β-glucosidase; CEL, cellobiohydrolase; XYL, β-xylosidase; POX, phenol oxidase; LAP, leucine-aminopeptidase; NAG, N-acetyl-β-D-glucosaminidase; AP, acid phosphatase. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

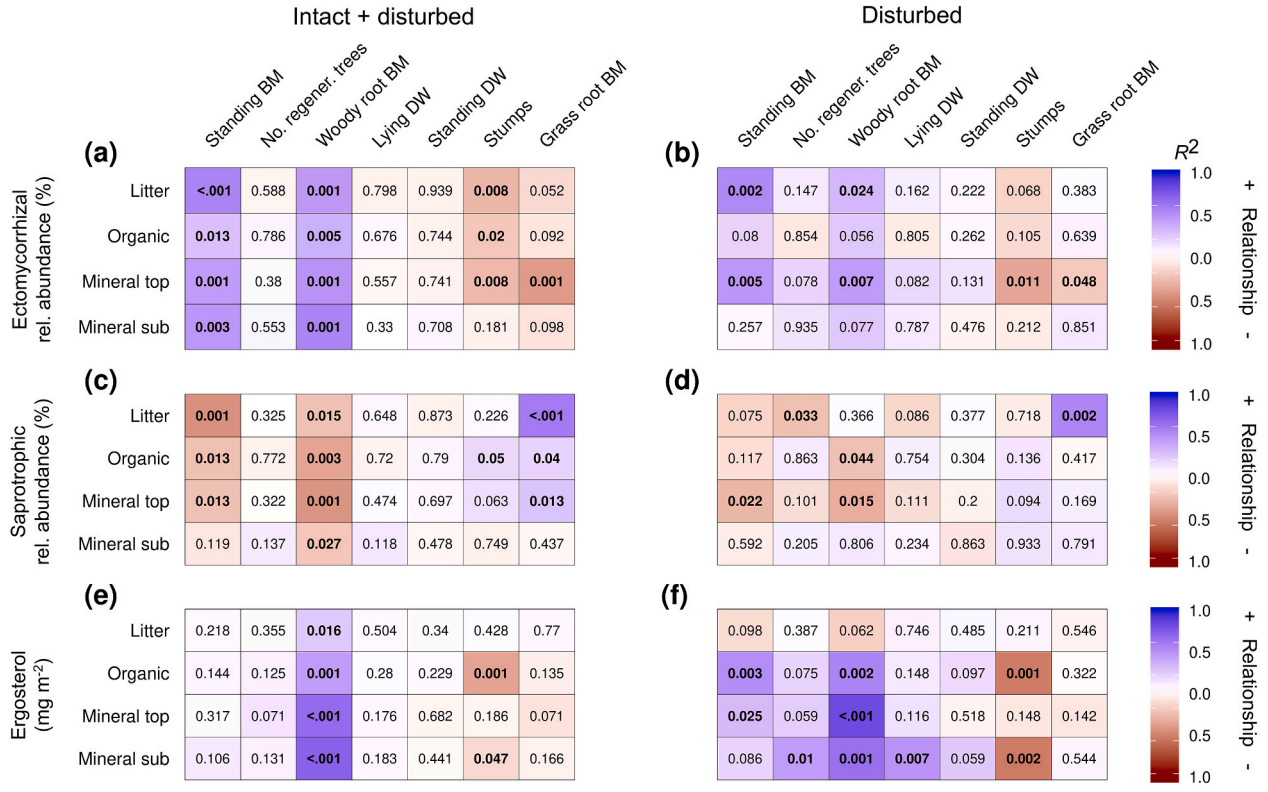

Fig. 6. Heatmaps of linear regression models between relative abundance (%) of ectomycorrhizal-, saprotrophic fungi, and ergosterol stocks in litter, organic, mineral topsoil, and mineral subsoil layers, and tree and deadwood variables, and grass root biomass at intact and disturbed plots (a,c,e) and disturbed plots only (b, d,f) in the Bavarian Forest National Park. P-values are given, and significant ($P < 0.05$) relations are indicated in bold. Colour intensity of heatmaps indicates R^2 values and different colours indicate positive (blue) and negative (red) relationships, respectively. Abbreviations: BM, biomass; DW, deadwood. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

in soil fungal communities after stand-replacing disturbance by windthrow and bark beetle attacks and subsequent salvage logging, with communities shifting from EM to saprotrophic dominated fungal assemblages. Moreover, we could show fungal biomass to decline with decreasing tree abundance. Fungal guild shifts were further accompanied with a decrease in the enzymatic decay of SOM, which we speculate

to favour a recovery of soil C and N stocks at the disturbed plots. However, surviving trees and an enhanced tree regeneration under the presence of deadwood attenuated disturbance-induced changes in EM fungal communities, fungal biomass, and fungal-associated enzymatic decay. We therefore conclude that the retention of biological legacies is not only important for the conservation of fungal communities after forest disturbance, but also for the maintenance of decomposition processes and soil C and N dynamics in forest soils.

Author contribution

MM, CR, and DLG designed the study. MM and CR conducted field work and laboratory analyses. MG, ED, and HB performed fungal community analyses. CB, LS, and JM provided test site information and supported field work. BR supported laboratory analyses. MM and CR wrote the first draft of the manuscript and all authors contributed to later versions of the manuscript and to data interpretation.

Data accessibility

Data is deposited at the National Park Bavarian Forest and is available on request via https://www.nationalpark-bayerischer-wald.bayern.de/english/research. Sequencing and associated data have been deposited at NCBI BioProject PRJNA675197, BioSamples SAMN17015429-SAMN17015502 and GenBank accession numbers MW237871-MW238183.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108558.

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