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Impact of slope exposure on chemical and microbiological properties of Norway spruce deadwood and underlying soil during early stages of decomposition in the Italian Alps

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ABSTRACT

Mountain forest ecosystems are particularly sensitive to changing environmental conditions that affect the rate of deadwood decay and, thus, also soil carbon turnover and forest productivity. Little is known about how slope exposure and climate influence microbial abundance and activity in general, and wood-inhabiting bacteria during deadwood decomposition in particular. Therefore, a field experiment using open mesocosms was carried out along an altitudinal gradient (from 1200 to 2000 m above sea level) in the Italian Alps to evaluate the impact of exposure (north (N)- vs. south (*S*)-facing sites) on microbial biomass (double stranded DNA, dsDNA); microbial abundance (real-time PCR-based: fungi; dinitrogen reductase, *nifH*; ammonia-monooxygenase, *amoA*); and several hydrolytic enzyme activities involved in the main nutrient cycles during decomposition of *Picea abies* wood blocks (2 × 5 × 5 cm) over a 2-year period. In addition, soil physico-chemical and (micro)biological properties were determined at each site. The cooler, moister and more acidic conditions at north-facing slopes led to an increase in the wood and soil fungal abundance. Furthermore, soil nitrogen-related bacterial functional genes (*nifH* and *amoA*) gave a contrasting response to exposure in terms of abundance: *nifH* (N > S, altitude and decay time-dependent); ammonia-oxidising bacteria (AOB; S > N, altitude and decay time-dependent); ammonia-oxidising archaea (AOA; N > S, only at 2000 m a.s.l.). The AOB and AOA abundance, however, was below the detection limit in the wood blocks. Soil microbial biomass was in general higher at the north-facing slopes, whereas in the wood exposure affected to a lesser extent the microbial biomass. Overall, the exposure-effect on the microbial biomass and abundance as well as for most of the enzymatic activities was altitude- and decay time-dependent.

1. Introduction

Deadwood — the residue of living trees such as stumps, standing and fallen dead trees, fallen branches and coarse woody debris (CWD) (Zhou et al., 2007) — is one of the most important carbon stocks in forest ecosystems (Pan et al., 2011). Deadwood decay rate is determinant for the soil carbon turnover and forest productivity (Zhou et al., 2007). As woody material decays, its structure and chemical composition gradually change over time, which can result in a turnover of the wood-inhabiting microbiota as species are replaced by those better adapted to the substrate according to their biochemical requirements (Rajala et al., 2012). All of these changes can ultimately

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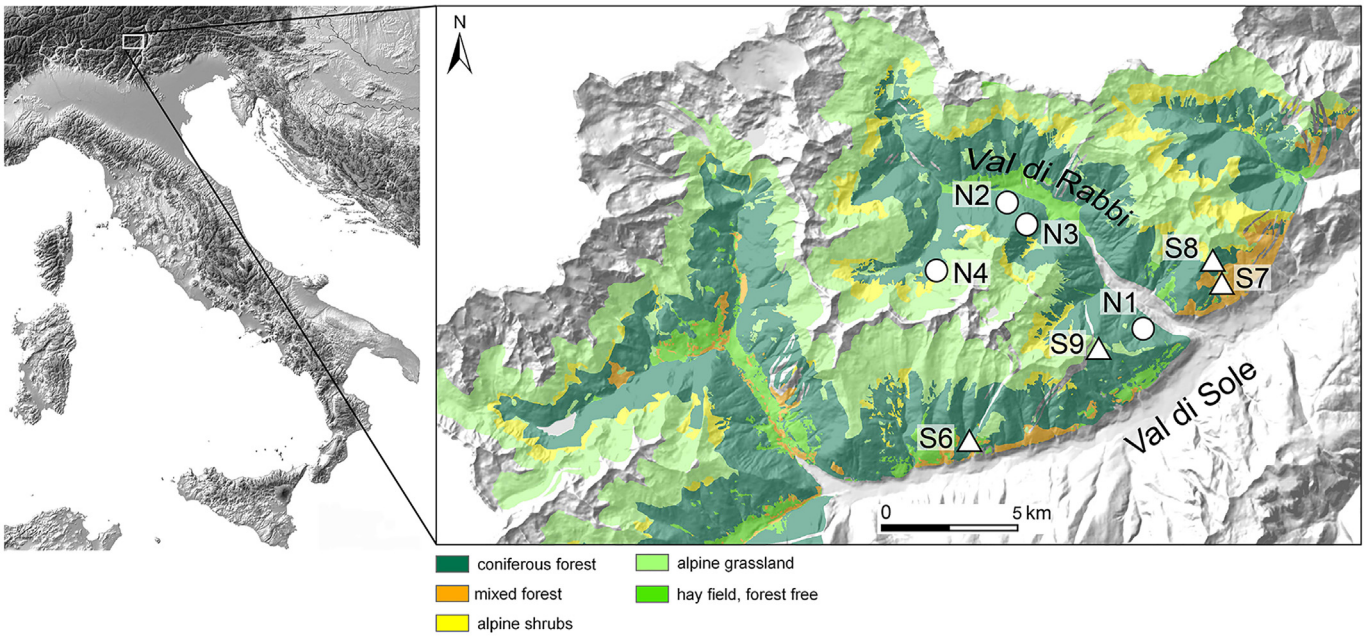

Fig. 1. Overview of the study area (Trentino Alto Adige, Italia) (Egli et al., 2006; Fravolini et al., 2016).

have consequences on the chemical and biological properties of the forest floor, especially the organic soil surface due to the incorporation of decaying woody material over the course of decomposition (Strukelj et al., 2013; Fravolini et al., 2016).

Fungi are considered the primary wood decomposers based on the ability to breakdown complex substrates such as lignin and cellulose, which can comprise 60–75% of wood dry mass (Meier et al., 2010). In particular, white-rot fungi efficiently degrade lignin via oxidative metalloenzymes such as laccases and manganese peroxidases (Valentín et al., 2014; Kielak et al., 2016). During the decay process, the fungal activity may increase the acidic conditions in wood that may result in an adverse environment for the bacterial colonization (Kielak et al., 2016). However, there are indications of both antagonist and beneficial fungal-bacterial interactions occurring in wood as reviewed by Johnston et al. (2016). In line with this, Hoppe et al. (2014) found positive correlations between fungal sporocarps and the richness of *nifH* (dinitrogen reductase) genes in deadwood logs from *Fagus sylvatica* and *Picea abies*. This is in accordance with the pioneering studies from Merrill and Cowling (1966) and Larsen et al. (1978) who suggested that associations with nitrogen-fixing bacteria might enable fungi to overcome their nitrogen deficiencies for vegetative and generative growth. Indeed, nitrogen is a very limited nutrient in early stages of wood decay and can be accumulated over time (Baldrian et al., 2016; Gómez-Brandón et al., 2017; Hu et al., 2017). The role of nitrogen-fixing bacteria is to bind the atmospheric dinitrogen (N_2) into a biologically accessible form (NH_3), and the *nifH* gene is considered the most useful marker to study the distribution and diversity of diazotrophic microorganisms in forest ecosystems (Levy-Booth and Winder, 2010; Levy-Booth et al., 2014).

The biological oxidation from ammonia (NH_3) to nitrite (NO_2^-) is also of great relevance in forest soils (Levy-Booth et al., 2014), as it is the rate-limiting step of the nitrification process. This reaction is carried out by both ammonia-oxidising bacteria (AOB) and archaea (AOA), which can be quantified by the ammonia-monooxygenase (*amoA*) gene (Rotthauwe et al., 1997; Francis et al., 2005; Leininger et al., 2006). Previous studies have suggested that AOB and AOA respond differently to the environmental conditions, with one or the other being more competitive under a given set of conditions, as they belong to separate phylogenetic domains with different cell biochemical and metabolic process (Erguder et al., 2009). Acidity (pH) and the availability of nitrogen forms in wood are the major drivers affecting the abundance of both AOB and AOA communities (Harmon et al., 1986; Cornelissen et al., 2012; Levy-Booth et al., 2014; Ribbons et al., 2016).

Topographic features such as slope aspect largely influence the local climate and the amount of solar irradiation intercept by the slope orientation affecting the soil biogeochemical processes (Ascher et al., 2012; Egli et al., 2016; Bardelli et al., 2017) and deadwood decay dynamics (Petrillo et al., 2015, 2016; Fravolini et al., 2016) in mountain ecosystems. These latter studies highlighted the changes in deadwood chemistry decay dynamics in response to the thermal conditions represented by different exposure along a climosequence approach. However, scarce attention has been paid so far on the influence of slope exposure on the deadwood inhabiting microbiota in terms of microbial abundance and activity and how these microbiological features change over time (during the decay process). Moreover, due to the often-time slow decomposition, deadwood can directly affect the nutrient and microbiota turnover in forest soils through the so-called “proximity effects” (Gonzalez-Polo et al., 2013) To date, few studies have addressed the changes in both deadwood and the forest floor over time from a microbiological viewpoint (van der Wal et al., 2007; Risch et al., 2013). Therefore, a field mesocosm experiment was carried out along an altitudinal gradient in the Italian Alps in order to evaluate the impact of exposure (north- vs. south-facing sites) on the abundance of fungi and nitrogen-related bacterial functional genes (*nifH* and *amoA*) assessed by real-time PCR, during decomposition of *Picea abies* wood blocks (2 × 5 × 5 cm) and the underlying soil (0–5 cm; in direct contact with the wood blocks). Furthermore, several potential enzymatic activities involved in the main nutrient cycles in both *P. abies* wood blocks and the underlying soil were also determined as a function of exposure and over a 2-year observation period.

In the same *in-field* mesocosm study, Fravolini et al. (2016) found that a higher soil moisture and clay content (related to a higher weathering of the soils) along with a lower pH seemed to accelerate wood decay at the north-facing slopes. We therefore hypothesised that: (1) the microbial biomass and activity will be higher at the north- than at the south-facing slopes during *P. abies* deadwood decomposition, and such effects on microbial communities will be altitude- and time-dependent; (2) the abundance of fungal and nitrogen-related bacterial functional genes will be higher at the end of the monitoring study due to the higher release of nutrients with the progressing wood decay.

Table 1
Characteristics of the eight study sites at north- and south-facing slopes (N_{1-4} and S_{6-9}, respectively) in Val di Rabbi (Egli et al., 2006; Petrillo et al., 2015).

Sites	Altitude (m a.s.l.)	Aspect (°N)	Slope (°)	(mm y^{-1})	MAAT (°C)	MAST (°C)	Parent material	Dominating tree species	Land use	Soil classification (WRB)
N_1	1180	340	31	950	5.6	7.3	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Episkeletic Cambisol (Dystric)
S_6	1185	160	31	950	7.6	8.1	Paragneiss debris	*Picea abies*	Ex-coppice, natural forest (ecological forestry)	Episkeleti-Endoleptic Cambisol (Chromi-Dystric)
N_2	1390	0	28	1000	4.6	6.3	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Episkeletic Cambisol (Dystric)
S_7	1400	145	33	1000	6.6	8.7	Paragneiss debris	*Larix decidua*	Natural forest (ecological forestry)	Dystri-Endoskeletic Cambisol
N_3	1620	0	29	1060	3.5	5.8	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Chromi-Endoskeletic Cambisol (Dystric)
S_8	1660	210	33	1060	5.5	6.0	Paragneiss debris	*Picea abies*	Natural forest (ecological forestry)	Skeletic Umbrisol
N_4	1930	20	12	1180	1.4	5.0	Paragneiss debris, Moraine material	*Larix decidua*	Originally used as pasture	Episkeletic Podzol
S_9	1995	160	25	1180	3.4	6.4	Paragneiss debris	*Larix decidua*	Ex-pasture, natural forest (ecological forestry)	Skeletic Umbrisol

MAP = mean annual precipitation, MAAT = mean annual air temperature (Sboarina and Cescatti, 2004); MAST = mean annual soil temperature.

2. Material and methods

2.1. Study area and experimental set-up

The study area is located in Val di Rabbi (Trentino) in the Italian Alps (Fig. 1) where a comprehensive database about soils, topographic and environmental settings already exists (Egli et al., 2006; Fravolini et al., 2016; Bardelli et al., 2017). Eight subalpine sites were selected along an altitudinal gradient from 1200 to 2000 m above sea level (a.s.l.), four sites at north- (N_{1-4}) and other four at south-facing (S_{6-9}) slopes, thereby providing a climosequence (Fig. 1). The altitudes of the sites were selected to be as similar as possible in order to establish a comparison between both slope exposures. A detailed description of the study sites is shown in Table 1.

An *in-field* mesocosm experiment was set up at each study site of the climosequence as described by Fravolini et al. (2016) in order to monitor the early stage of deadwood decomposition as a function of slope exposure and time in i) wood blocks and ii) the uppermost topsoil layer (0–5 cm). Mesocosms (PVC tubes having diameter = 10.2 cm and height = 25 cm) were installed into the natural soil in August 2012, that is one year prior to the addition of the wood blocks of *Picea abies* (L.) Karst, at a distance of > 1 m from large trees and > 0.5 m from the adjacent mesocosms, leaving at the surface a border of about 1 cm. Considering that the size and geometry of deadwood may have a strong influence on the decay processes (Van der Wal et al., 2007), wood blocks from the same *P. abies* tree and with a uniform size (2 × 5 × 5 cm) were placed on the soil surface in each of the mesocosm tubes. Three replicate mesocosms for each time point were installed in each of the eight study sites. The wood blocks and the uppermost topsoil layer (0–5 cm) were collected (with lab-gloves) after 12 (t1; August 2013), 25 (t2; October 2013), 52 (t3; July 2014) and 104 (t4; July 2015) weeks, resulting in a total of 96 samples for each substrate (=8 sites × 4 times × 3 replicates), with three wood blocks kept as controls (t0). Moreover, prior to the placement of the wood blocks into the mesocosms, five soil sub-samples (t0) were collected in the surrounding area of the mesocosm set up at each study site. Wood and soil samples were placed in polyethylene bags and transported in cool-boxes to the laboratory. In the laboratory, the wood blocks were air-dried at room temperature, cut-milled (4 mm; Retsch mill). The soil samples were sieved (< 2 mm) and aliquoted into 50-mL sterile conical centrifuge tubes. The physico-chemical characterisation of the wood and soil samples was done after each sampling time. In addition, an aliquot of the samples was stored at −20 °C for the (micro)biological analyses. These latter analyses were performed at the end of the monitoring period.

2.2. Wood and soil physico-chemical analyses

The fresh and dry weight of the wood blocks was determined to assess the wood mass as a function of progressing decay. In particular, wood (1 g fresh weight, fw) and soil samples (5 g, fw) were oven-dried (105 °C) for 24 h to determine their dry weight. The volatile solids (VS) content was determined from the weight loss following ignition in a muffle furnace (Carbolite, CWF 1000) at 550 °C for 5 h. Total C and N contents were analysed in dried samples, using a CN analyser (TruSpec CHN; LECO, Michigan, U.S.A.). Electrical conductivity (EC) and pH were measured in water extracts (1:20 and 1:10, *w/v* for wood and soil, respectively) using a conductivity meter LF 330 WTW (Weilheim, Germany) and a pH meter Metrohm 744, respectively. For the wood cellulose extraction, 10 mg of powdered samples were weighed in Teflon bags (Leavitt and Danzer, 1993). They were then washed in a 5% NaOH solution, twice at 60 °C, and again three times using a 7% $NaClO_2$ solution and 96% CH_3COOH at 60 °C to ensure the pH was between 4 and 5. Afterwards, the Teflon bags were oven-dried at 50 °C and the cellulose content was determined as the difference between the initial weight and dried samples. The total lignin was determined according to Dence and Lin (1992) based on the extraction of water-soluble compounds. Ultrapure water (80 °C) was added to 1 g of pulverized wood sample and stirred three times for 15 min. After each washing, the samples were centrifuged for 10 min at 4500 rpm, dried in the oven at 80 °C and washed three times with 5 mL of ethanol. They were then centrifuged (10 min at 4500 rpm) and the supernatant was discarded. Thereafter, ethanol was added to the sample and then filtered. The filters were dried overnight at 60 °C. Afterwards, 3 mL of a 72% H_2SO_4 solution were added to 300 mg of the filter cake, stirred, and 84 mL of ultrapure water added and autoclaved for 1 h at 120 °C. This solution was filtered into ceramic crucibles, the liquid evaporated at 110 °C and then the weight of the dry matter in the crucibles was measured (Klason lignin). The acid-soluble lignin (ASL) in the filtrate was determined using an UV-VIS Spectrophotometer. The total lignin was obtained by the sum of the Klason lignin and ASL. Soil ammonium (NH_4^+) and nitrate (NO_3^-) contents were measured in 0.0125 M $CaCl_2$ extracts (Kandeler, 1993a, 1993b). Briefly, 60 mL of 0.0125 M $CaCl_2$ were added to soil samples (5 g, fresh weight, fw), shaken for 1 h at 125 rpm and

filtered. Then, 5 mL of the filtrate were mixed with 2.5 mL of a freshly prepared solution consisting of 0.3 M sodium hydroxide, 0.35 M sodium nitroprusside dehydrate and 4.02 mM sodium salicylate. One mL of 0.1% (*w/v*) dichloroisocyanuric acid sodium salt dehydrates was added to mix. Standard solutions containing 0.0, 1.0, 1.5, 2.0, 2.5 μg N mL^{-1} were prepared and treated the same way as the samples. After 30 min incubation, NH_4^+ was determined spectrophotometrically at 660 nm. NO_3^- content from soil samples was determined after adding 0.4 mL 10% sulphuric acid to two test tubes per sample. Two copper-sulphate covered zinc granules were added to one of the tubes. Standard solution containing 0.0, 0.5, 1.0 and 1.5 μg N mL^{-1} were prepared and treated like the samples. After an overnight incubation, NO_3^- was determined spectrophotometrically at 210 nm. Absorbance values of tubes containing zinc granules were subtracted from their corresponding granule-free tubes. In order to determine total P content, 0.5 g of soil samples (fw) were placed in a backer where 5 mL of H_2SO_4 and 3 mL of H_2O_2 solutions were added to promote the oxidation of soil organic matter. One mL of HF was added and then the breaker was placed on a pre-heated hot plate at 150 °C for 10 min to eliminate excess H_2O_2. Afterwards, distilled water was added to bring the volume of the solution to 50 mL. This solution was mixed, filtered and an aliquot with the clear filtrate was used to determine the total P concentration. For the available P content, 2 g of soil (fw) was placed into a 50 mL flask and 20 mL of extracting solution (0.02 M HCl in 0.03 M NH_4F) were added. Afterwards, the solution was shaken at 200 rpm for 5 min at room temperature, filtered and an aliquot containing the clear filtrate was used to determine the available P. Both the total and available P concentrations in soil samples were measured by the ascorbic acid method (Kuo, 1996) using an UV mini 1240, UV-VIS Spectrophotometer.

2.3. Potential enzyme activities

Seven hydrolytic enzyme activities covering the principal nutrient cycles including: i) C-cycle: β-glucosidase (*gluc*), cellulase (*cell*), xylosidase (*xylo*); ii) N-cycle: chitinase (*chit*), leucine-aminopeptidase (*leu*); and iii) P-cycle: acid and alkaline phosphomonoesterase (*ac*P and *alk*P) were determined from soil and wood samples by using a hetero-molecular exchange procedure (Fornasier and Margon, 2007). An amount of 0.2 g of soil (fw) was placed together with 1.4 mL of 3% lysozyme solution and glass beads in 2-mL microcentrifuge tubes. By mechanical cell-disruption (bead-beating) using a Retsch 400 beating mill at 30 strokes s^{-1} for 3 min, the supernatant containing the desorbed enzymes was extracted and centrifuged at 20,000 g for 5 min. Afterwards, it was dispensed into 384-well white microplate with a specific buffer to fluorometrically quantify the enzymatic activities using 4-methyl-umbelliferyl (MUF). In order to perform the enzymatic multiple assay for the wood samples (0.1 g, fw), the following modifications were necessary: the extraction buffer consisted in a 3% lysozyme solution in 0.1 M NaCl, pH 6.7; and the bead-beating lasted 180 s. After centrifugation, 750 μL of supernatant were taken and diluted with 250 μL of TRIS 50 mM, pH 7.0 buffer. 20 μL of diluted extracts were pipetted in duplicate on 384-well microplates with 40 μL of appropriate buffer in order to determine fluorometrically the different potential enzyme activities by using specific substrates. Each microplate was read 4 times at time intervals of 5–180 min according to the intensity of each enzyme using a Synergy HT microplate reader (BIOTEK). All the measurements were performed in duplicate for each field replicate and the activities were expressed as nanomoles of MUF min^{-1} g^{-1} dry (soil/wood).

2.4. Molecular analyses

2.4.1. Wood and soil microbial biomass index (dsDNA)

Whole community DNA was extracted from wood (0.1 g, fw) and soil (0.2 g, fw) samples by mechanical cell disruption (bead-beating) in presence of a sodium phosphate buffer (0.12 M, pH 8 Na_2HPO_4) according to Fornasier et al. (2014), and *crude* (not purified) double stranded DNA (dsDNA) was directly quantified by using PicoGreen fluorescent dye (Life Technologies).

2.4.2. DNA extraction

Whole community DNA was extracted from wood (0.1 g, fw) and soil (0.2 g, fw) samples and purified by using a commercial kit (FastDNA Kit for Soil, MP-Biomedicals). In the case of wood samples, one ceramic sphere (Lysing Matrix E, MP, Biomedicals) was added to the lysing tubes, so as to guarantee for an accurate cell disruption of the woody tissue. DNA was qualitatively characterised by agarose gel electrophoresis (1 × Tris Acetate-EDTA buffer; 1:10000 EtBr; 0.8% *w/v*; 100 V 60 min) to assess the molecular weight and fragment length distribution in comparison to a DNA Mass Ladder Mix (Fermentas, 80–20,000 bp). The concentration of DNA was assessed using two quantification methods, namely via fluorometric (Quant-iT PicoGreen; specific for dsDNA) and spectrophotometric (Picodrop; DNA absorbance at 260 nm) measurements (Ascher et al., 2009).

2.4.3. Quantitative real-time PCR

Quantitative real-time PCR (qPCR) analysis was performed to determine the 18S rRNA gene copy number of fungi, and the abundance of certain functional genes involved in the N cycle (*nifH* and *amoA*) in the wood and the soil samples. Real-time PCR was conducted in a Rotorgene 6000 Real Time Thermal Cycler (Corbett Research, Sydney, Australia) in combination with the Rotorgene Series Software 1.7. Standard curves were constructed using the purified PCR products of known concentrations of the following pure cultures used as templates: *Fusarium solani* (DSMZ 10696) – fungi; *Azospirillum irakense* (DSMZ 11586) – *nifH* gene; a plasmid containing an *amoA* sequence – ammonia-oxidising bacteria (AOB) and -archaea (AOA). The primer pairs used for qPCR were as follows: FF390/FR1 (fungi; Prévost-Bouré et al., 2011); nifHf/nifHr (*nifH* gene; Töwe et al., 2010); amoA1F/amoA2R (*amoA* gene – AOB; Rotthauwe et al., 1997); and Arch-amoAF/Arch-amoAR (*amoA* gene – AOA; Francis et al., 2005). Stock concentration [gene copies μL^{-1}] was determined via PicoGreen measurement. Ten-fold dilutions ranging from 10^9 to 10^2 copies μL^{-1} were used for the standard curve construction. The reactions were performed in 20-μL assays containing 1 × Sensimix™ SYBR® Hi-rox (Bioline, USA), forward and reverse primers (200 nM each primer), 0.4 mg mL^{-1} BSA, distilled water (RNase/DNase free, Gibco™, UK) and 2 μL of either 1:10 diluted DNA-extract, and ten-fold diluted standard DNA. All the standards and samples were run in duplicate. After an initial denaturation at 95 °C for 10 min, thermal cycling comprised 40 cycles of 15 s at 95 °C, 30 s at 50 °C, 30 s at 72 °C for fungi; 45 s at 95 °C, 45 s at 55 °C, 45 s at 72 °C for *nifH* gene; 25 s at 95 °C, 25 s at 57 °C (AOB) or 53 °C (AOA), followed by 40 s at 72 °C for both AOB and AOA *amoA* gene. To check for product specificity and potential primer dimer formation, runs were completed with a melting analysis starting from 65 °C to 95 °C with temperature increments of 0.25 °C (0.5 °C for *nifH* gene) and a transition rate of 5 s. The purity of the amplified products was checked by the presence of a single band of the expected length on a 1% agarose gel stained with the DNA stain Midori Green (Nippon Genetics, Germany) and visualised by UV-transillumination (Vilber Lourmat Deutschland GmbH).

2.5. Statistical analyses

The effects of exposure (north- vs. south-facing slopes) and time (t0, t1, t2, t3, t4) on wood and soil physico-chemical and microbiological parameters were evaluated using a factorial analysis of variance (ANOVA). The normality and the homogeneity of the data were tested prior to ANOVA using the Shapiro-Wilks and Levene's tests, respectively. Prior to analysis, a log-transformation was necessary for most of the wood and soil physico-chemical and microbiological parameters to meet the requirements for ANOVA. Paired comparisons were done using the Tukey HSD test. A non-parametric test (Kruskal-Wallis test)

Table 2
Physico-chemical properties of wood samples collected in June 2013 (t0; control), in August 2013 (t1; 12 weeks), in October 2013 (t2; 25 weeks); in July 2014 (t3; 52 weeks), in July 2015 (t4; 104 weeks) in the *in-field* mesocosm experiment along the climosequence scenario. The results are shown pairwise, i.e., the couple of north- and south-facing sites at the same elevation (N_1-S_6; 1200 m a.s.l.; N_2-S_7; 1400 m a.s.l.; N_3-S_8; 1600 m a.s.l.; N_4-S_9; 2000 m a.s.l.). Values are means (n = 3) with the standard deviations. Data are expressed on a dry weight basis. Different letters indicate significant differences ($p < 0.05$; ANOVA followed by Tukey post-hoc test) as a function of the time of decay.

Sites	Time	Wood mass loss (g)	Wood moisture (%)	pH	Electrical conductivity (μS cm^{-1})	Total C (%)	Cellulose (%)	Total lignin (%)
	t0	22.5 (0.01) **a**	8.2 (2.0) **d**	5.5 (0.1) **ab**	51.7 (6.5) **ab**	49.0 (0.3) **bc**	44.5 (4.5) **ab**	30.7 (1.5) **a**
N_1	t1	22.2 (0.7) **a**	58.9 (0.9) **a**	5.8 (0.03) **a**	16.3 (2.3) **c**	48.8 (0.4) **b**	44.0 (4.7) **ab**	31.7 (0.5) **a**
	t2	21.9 (4.0) **a**	54.2 (2.7) **a**	5.7 (0.1) **a**	24.3 (5.2) **bc**	48.8 (0.2) **b**	46.5 (1.9) **a**	32.2 (1.3) **a**
	t3	21.7 (1.4) **a**	58.4 (7.99) **a**	5.6 (0.05) **a**	15.8 (1.7) **c**	49.4 (0.3) **b**	40.5 (7.3) **ab**	31.3 (0.9) **a**
	t4	21.2 (2.9) **a**	50.6 (15.0) **ab**	5.8 (0.4) **a**	46.5 (13.5) **b**	46.7 (1.2) **c**	41.3 (3.9) **ab**	33.3 (5.9) **a**
S_6	t1	22.0 (1.8) **a**	55.3 (5.5) **a**	5.9 (0.14) **a**	17.7 (3.5) **c**	48.9 (0.1) **b**	46.4 (0.9) **a**	30.6 (1.3) **a**
	t2	22.2 (0.1) **a**	52.3 (11.3) **ab**	5.8 (0.2) **a**	25.5 (4.5) **bc**	49.1 (1.5) **b**	44.4 (2.3) **ab**	30.3 (0.4) **a**
	t3	21.5 (4.5) **a**	54.5 (3.4) **a**	4.5 (0.7) **b**	80.7 (47.0) **a**	51.6 (0.5) **a**	37.9 (3.1) **b**	31.6 (2.6) **a**
	t4	22.8 (1.9) **a**	39.6 (12.5) **b**	5.5 (0.5) **a**	40.5 (9.7) **bc**	46.2 (0.9) **c**	40.5 (2.9) **ab**	31.4 (0.8) **a**
N_2	t1	26.0 (0.01) **a**	51.0 (6.9) **abc**	5.5 (0.1) **ab**	13.8 (1.1) **c**	50.4 (1.0) **a**	43.4 (7.1) **ab**	35.1 (3.1) **a**
	t2	21.1 (1.5) **ab**	62.6 (1.2) **a**	5.4 (0.1) **abc**	13.6 (4.4) **c**	51.8 (0.5) **a**	50.4 (0.9) **a**	33.0 (1.3) **a**
	t3	21.7 (5.5) **ab**	58.2 (6.8) **ab**	5.0 (0.1) **bcd**	10.3 (0.8) **c**	50.5 (1.3) **a**	42.2 (5.3) **ab**	31.1 (1.9) **a**
	t4	21.3 (2.0) **ab**	45.8 (10.5) **abc**	4.6 (0.2) **d**	35.0 (25.8) **bc**	46.4 (1.4) **c**	39.3 (6.0) **b**	30.4 (1.0) **a**
S_7	t1	17.9 (2.9) **b**	44.7 (1.2) **bc**	4.9 (0.9) **cd**	55.0 (45.7) **b**	48.7 (0.2) **abc**	39.5 (6.9) **b**	34.4 (6.5) **a**
	t2	20.3 (0.9) **ab**	50.3 (3.9) **abc**	5.8 (0.01) **a**	30.0 (3.3) **bc**	51.3 (1.0) **a**	48.4 (3.6) **a**	32.8 (1.7) **a**
	t3	20.0 (1.9) **ab**	39.1 (9.8) **c**	5.5 (0.2) **ab**	32.9 (1.6) **bc**	49.7 (0.5) **ab**	37.4 (3.0) **b**	31.8 (1.3) **a**
	t4	23.0 (2.8) **ab**	14.0 (6.3) **d**	4.6 (0.4) **d**	99.2 (33.5) **a**	46.9 (2.3) **bc**	42.9 (3.7) **ab**	34.8 (3.3) **a**
N_3	t1	22.6 (2.9) **a**	61.1 (2.7) **a**	5.4 (0.2) **bc**	17.7 (8.4) **cd**	48.7 (0.3) **c**	46.1 (1.0) **ab**	30.9 (1.8) **a**
	t2	23.0 (4.2) **a**	59.8 (6.8) **ab**	5.6 (0.01) **abc**	9.4 (1.6) **d**	50.1 (0.8) **ab**	46.0 (6.3) **ab**	34.3 (1.7) **a**
	t3	23.8 (0.01) **a**	48.6 (13.2) **bc**	5.2 (0.2) **c**	19.9 (8.5) **c**	49.9 (0.3) **bc**	44.5 (3.7) **ab**	31.6 (2.1) **a**
	t4	21.0 (3.7) **a**	56.4 (4.5) **abc**	5.4 (0.05) **bc**	19.2 (3.8) **c**	47.0 (1.2) **d**	37.2 (3.1) **b**	31.3 (0.7) **a**
S_8	t1	21.3 (1.0) **a**	46.7 (11.4) **c**	5.6 (0.01) **abc**	17.8 (3.0) **cd**	48.6 (0.01) **c**	49.2 (1.9) **a**	35.5 (6.3) **a**
	t2	22.1 (2.8) **a**	55.5 (7.7) **abc**	5.7 (0.01) **ab**	18.9 (3.2) **cd**	51.4 (1.5) **a**	44.3 (1.9) **ab**	29.3 (1.9) **a**
	t3	20.5 (1.7) **a**	61.9 (2.5) **a**	5.9 (0.1) **a**	18.2 (2.6) **cd**	51.4 (0.5) **a**	41.1 (4.3) **ab**	32.0 (1.1) **a**
	t4	23.2 (0.01) **a**	54.5 (3.1) **abc**	5.7 (0.3) **ab**	40.3 (7.2) **b**	48.6 (1.1) **c**	40.8 (4.5) **ab**	32.7 (2.3) **a**
N_4	t1	22.4 (6.2) **a**	54.9 (6.4) **ab**	5.5 (0.1) **a**	10.2 (1.2) **c**	48.5 (0.2) **c**	45.3 (2.8) **a**	33.4 (0.9) **ab**
	t2	21.6 (1.8) **a**	61.0 (2.1) **a**	5.4 (0.2) **a**	14.3 (6.7) **c**	52.2 (0.5) **a**	46.2 (3.0) **a**	33.6 (3.3) **ab**
	t3	16.0 (0.01) **b**	61.0 (2.1) **a**	5.7 (0.3) **a**	22.2 (16.2) **bc**	49.1 (0.1) **bc**	45.9 (2.2) **a**	33.3 (1.4) **ab**
	t4	22.0 (4.6) **a**	44.9 (9.1) **c**	5.4 (0.3) **ab**	17.7 (5.9) **c**	48.4 (2.1) **c**	37.7 (3.3) **bc**	35.1 (0.9) **a**
S_9	t1	19.1 (3.4) **ab**	52.6 (6.4) **abc**	5.7 (0.1) **a**	17.3 (6.0) **c**	48.4 (0.4) **c**	45.4 (2.1) **a**	32.4 (2.1) **ab**
	t2	20.2 (4.2) **ab**	53.8 (6.5) **bc**	5.4 (0.2) **ab**	32.8 (7.6) **bc**	49.5 (0.9) **bc**	46.3 (3.2) **a**	28.7 (0.9) **b**
	t3	21.1 (1.1) **a**	53.7 (6.5) **ab**	5.4 (0.1) **a**	22.3 (7.2) **bc**	48.9 (0.9) **c**	45.5 (2.9) **a**	32.2 (1.2) **ab**
	t4	14.9 (1.1) **b**	12.8 (2.7) **d**	4.8 (0.2) **b**	78.6 (25.8) **a**	51.0 (2.6) **ab**	31.1 (6.7) **c**	35.8 (2.3) **a**

was performed for several wood physico-chemical parameters (moisture, pH) and two enzymatic activities (cellulase and alkaline phosphomonoesterase) that did not meet the normality condition. Associations between the potential enzymatic activities and the main chemical and microbiological variables were explored by Pearson's correlation. These analyses were carried out using the software Statistica 9 (StatSoft, USA).

3. Results

3.1. Wood physico-chemical parameters along the studied climosequence

Wood mass loss was 32% higher at the north- than at the south-facing sites after 12 and 104 weeks at 1400 and 2000 m a.s.l., respectively; whereas no exposure- and time-effect was recorded at the remaining altitudes (Tables 2 and 6). Wood moisture was not significantly affected by the slope exposure, although its levels were 85% higher after 12 weeks, and no further changes were observed until the end of the monitoring period (104 weeks). Slope exposure had a significant impact on the wood pH only at 1600 m a.s.l., being one unit lower at the north- than at the south-facing sites after 52 weeks. Wood EC levels were on average 64% higher at the south- compared to the north-facing sites. This exposure-effect (south > north-facing sites) was also recorded for the wood C content after 52 weeks at 1200 m a.s.l. and independently of the duration of the monitoring at 1600 m a.s.l. Cellulose and total lignin contents were not significantly affected by the slope exposure. The lowest cellulose content was recorded after 104 weeks at both slopes at 1600 and 2000 m a.s.l. However, a significant increase (14%) in lignin amount was observed at 2000 m a.s.l. between 25 and 104 weeks. The N content in the wood blocks was below the detection limit.

3.2. Soil physico-chemical parameters along the studied climosequence

An overview of the soil physico-chemical parameters and the statistical output as a function of slope exposure and time is given in Tables 3 and 6, respectively. Along the altitudinal gradient, soil moisture was on average 34% higher at the north- than at the south-facing sites and significantly varied with time only at the altitude of 2000 m a.s.l., where the lowest moisture level was found after 104 weeks irrespective of the exposure. The VS content was 40% higher at the north- than at the south-facing sites between 1200 and 1600 m a.s.l., whereas no exposure-effect was found at 2000 m a.s.l. The north-facing sites were characterised by higher soil acidity, being soil pH one unit lower than at the comparable south-facing ones. The soil EC levels were 66% higher at the south- than at the north-facing sites after 25 and 52 weeks at 1400 m a.s.l. Soils at the north-facing sites showed, on average, 71% and 48% higher total C and N contents respectively than those from the comparable south-facing ones, regardless of the duration of the monitoring. The soil NH_4^+ content was between 70% and 95% higher at the north- than at the south-facing sites after 12, 25 and 52 weeks along the altitudinal gradient. The soil NO_3^- content was 32% and 60% higher at the south- than at the north-facing sites at 1400 and 1600 m a.s.l. respectively. At these altitudes such exposure effect (south > north-facing sites) was observed irrespective of the duration of the monitoring. In addition, total and available P

Table 3
Physico-chemical properties of the soil samples collected in June 2013 (t0; control), in August 2013 (t1; 12 weeks), in October 2013 (t2; 25 weeks); in July 2014 (t3; 52 weeks), in July 2015 (t4; 104 weeks) in the *in-field* mesocosm experiment along the climosequence scenario. The results are shown pairwise, i.e., the couple of north- and south-facing sites at the same elevation (N_1-S_6; 1200 m a.s.l.; N_2-S_7; 1400 m a.s.l.; N_3-S_8; 1600 m a.s.l.; N_4-S_9; 2000 m a.s.l.). Values are means (n = 3) with the standard deviations. Data are expressed on a dry weight basis. Different letters indicate significant differences ($p < 0.05$; ANOVA followed by Tukey post-hoc test) as a function of the time of decay.

Sites	Time	Soil moisture (%)	Volatile solids (%)	pH	Electrical Conductivity (μS cm^{-1})	Total C (%)	Total N (%)	NH_4^+ (mg kg^{-1} dw)	NO_3^- (mg kg^{-1} dw)	Total P (mg kg^{-1} dw)	Available P (mg kg^{-1} dw)
N_1	t0	41.7 (1.6) **a**	30.2 (2.1) **abcd**	5.8 (0.1) **bc**	33.3 (1.5) **cd**	22.4 (1.1) **a**	0.9 (0.01) **a**	43.4 (6.4) **b**	6.6 (1.9) **d**	540.4 (13.6) **abc**	38.4 (1.8) **bc**
	t1	49.8 (7.3) **a**	33.0 (10.7) **abc**	5.7 (0.3) **bcd**	55.5 (11.3) **ab**	21.8 (10.5) **ab**	0.8 (0.3) **ab**	36.3 (4.1) **bc**	49.3 (7.6) **abc**	569.7 (41.0) **abc**	78.3 (36.6) **a**
	t2	43.3 (11.9) **a**	36.9 (20.5) **ab**	5.5 (0.1) **cd**	45.3 (31.0) **bcd**	16.9 (7.3) **abc**	0.9 (0.4) **a**	16.9 (4.1) **bcd**	33.2 (12.1) **bcd**	761.5 (187.0) **a**	75.9 (56.3) **a**
	t3	42.8 (7.8) **a**	22.4 (7.7) **bcd**	5.3 (0.3) **d**	29.1 (4.6) **d**	11.1 (4.3) **abc**	0.3 (0.1) **bc**	22.4 (8.1) **bcd**	59.9 (32.3) **ab**	689.4 (542.5) **ab**	19.7 (5.3) **cd**
	t4	42.5 (16.7) **a**	39.8 (10.4) **a**	5.6 (0.4) **cd**	56.7 (27.7) **ab**	20.2 (67) **abc**	0.8 (0.2) **abc**	99.2 (67.8) **a**	13.7 (4.9) **d**	392.7 (169.3) **bc**	65.6 (6.6) **ab**
S_6	t0	33.6 (0.6) **ab**	14.6 (0.1) **d**	5.8 (0.01) **bc**	33.5 (1.0) **cd**	6.4 (0.2) **bc**	0.3 (0.01) **c**	19.2 (1.5) **bcd**	5.1 (1.1) **d**	363.7 (65.2) **bc**	11.5 (2.5) **cd**
	t1	45.7 (5.6) **a**	22.7 (4.2) **bcd**	6.2 (0.4) **a**	68.6 (25.7) **a**	10.9 (3.1) **abc**	0.6 (0.2) **abc**	2.6 (0.3) **d**	74.2 (2.5) **a**	376.0 (88.4) **bc**	39.7 (17.7) **bc**
	t2	42.9 (16.6) **a**	22.3 (10.4) **bcd**	6.1 (0.2) **ab**	44.7 (22.8) **bcd**	5.6 (2.4) **c**	0.6 (0.6) **abc**	4.9 (0.8) **d**	30.8 (14.9) **cd**	669.2 (193.7) **ab**	66.3 (15.3) **ab**
	t3	35.2 (7.9) **ab**	17.7 (8.5) **cd**	5.8 (0.1) **bc**	49.2 (20.1) **bc**	8.8 (4.8) **abc**	0.5 (0.2) **abc**	26.1 (8.0) **bcd**	25.7 (12.7) **cd**	359.7 (192.6) **bc**	18.8 (9.1) **cd**
	t4	23.2 (2.2) **b**	20.0 (8.7) **cd**	6.4 (0.1) **a**	42.6 (21.2) **bcd**	9.6 (5.4) **abc**	0.5 (0.3) **abc**	14.7 (6.5) **cd**	6.1 (2.0) **d**	243.5 (51.9) **c**	8.5 (0.7) **d**
N_2	t0	64.1 (1.8) **ab**	68.1 (2.3) **abc**	4.4 (0.01) **de**	43.0 (1.7) **d**	37.3 (2.7) **ab**	1.5 (0.2) **ab**	33.7 (2.8) **c**	7.4 (3.2) **d**	506.6 (47.2) **bc**	116.9 (20.0) **abc**
	t1	73.6 (1.4) **a**	81.6 (5.4) **ab**	5.1 (0.2) **c**	51.1 (15.6) **cd**	43.9 (1.8) **a**	1.8 (0.2) **a**	161.6 (95.2) **a**	23.2 (7.2) **cd**	708.3 (105.3) **a**	184.5 (26.6) **a**
	t2	69.5 (7.8) **a**	72.2 (17.1) **abc**	4.8 (0.2) **cd**	42.3 (9.0) **d**	36.3 (10.1) **ab**	1.9 (0.4) **a**	178.0 (29.1) **a**	37.5 (11.6) **abc**	625.0 (43.0) **ab**	134.5 (34.4) **abc**
	t3	72.9 (1.7) **a**	77.2 (12.5) **ab**	4.4 (0.2) **de**	40.8 (10.3) **d**	43.4 (4.4) **a**	1.3 (0.1) **ab**	152.4 (32) **ab**	30.6 (5.3) **bcd**	449.6 (68.0) **c**	96.5 (11.8) **abc**
	t4	56.8 (13.3) **abc**	86.3 (2.6) **a**	4.1 (0.2) **e**	87.0 (25.5) **bcd**	45.8 (1.3) **a**	1.3 (0.02) **ab**	52.0 (31.5) **bc**	24.8 (16.0) **cd**	534.6 (30.3) **bc**	83.3 (22.2) **bc**
S_7	t0	38.6 (0.1) **cd**	33.4 (0.8) **d**	5.7 (0.08) **b**	78.1 (3.8) **bcd**	18.8 (0.8) **bc**	0.8 (0.01) **b**	28.7 (1.9) **c**	7.5 (0.3) **d**	739.7 (76.7) **a**	91.6 (5.3) **abc**
	t1	27.9 (10.9) **de**	24.2 (2.7) **d**	6.2 (0.1) **a**	46.5 (3.1) **cd**	14.4 (3.4) **c**	0.7 (0.2) **b**	18.2 (12.6) **c**	25.5 (11.5) **cd**	534.4 (84.6) **bc**	39.9 (5.2) **c**
	t2	27.4 (7.7) **de**	51.7 (12.9) **bcd**	6.1 (0.3) **ab**	175.7 (8.9) **a**	21.3 (13.4) **bc**	1.2 (0.8) **ab**	27.2 (8.9) **c**	54.3 (1.0) **ab**	773.8 (172.2) **a**	154.1 (94.3) **ab**
	t3	44.2 (6.8) **bcd**	77.2 (12.5) **cd**	5.6 (0.1) **b**	94.6 (17.2) **bc**	26.9 (8.3) **abc**	1.1 (0.3) **ab**	49.3 (15.7) **c**	57.9 (13.0) **a**	742.1 (149.3) **a**	90.3 (11.3) **abc**
	t4	16.5 (1.3) **e**	52.8 (17.9) **bcd**	5.8 (0.2) **ab**	108.6 (29.7) **b**	26.9 (8.3) **abc**	1.2 (0.3) **ab**	27.7 (0.6) **c**	35.2 (9.8) **abc**	546.6 (43.0) **bc**	58.5 (11.8) **bc**
N_3	t0	61.4 (1.0) **abc**	59.4 (5.1) **bcd**	4.6 (0.03) **c**	39.5 (1.9) **c**	33.8 (2.2) **abc**	1.2 (0.1) **bcd**	78.2 (10.7) **cd**	6.3 (0.5) **c**	462.6 (99.2) **abc**	89.8 (6.4) **b**
	t1	69.0 (2.0) **ab**	83.9 (7.5) **a**	5.2 (0.4) **ab**	65.5 (15.2) **bc**	44.8 (4.5) **a**	1.8 (0.3) **ab**	227.4 (118.1) **a**	34.0 (5.4) **bc**	453.7 (124.8) **bc**	128.0 (33.1) **a**
	t2	72.6 (3.8) **a**	80.7 (7.3) **ab**	5.0 (0.2) **abc**	39.0 (10.4) **c**	41.1 (3.5) **ab**	2.1 (0.1) **a**	171.2 (11.2) **ab**	20.8 (6.1) **bc**	673.2 (159.6) **ab**	87.1 (26.6) **b**
	t3	72.3 (3.2) **a**	84.5 (6.7) **a**	4.8 (0.05) **bc**	55.2 (10.8) **bc**	44.8 (2.7) **a**	1.4 (0.04) **abc**	188.9 (69.8) **ab**	56.7 (6.4) **b**	716.8 (80.4) **ab**	66.2 (16.4) **bc**
	t4	68.5 (6.4) **ab**	73.7 (20.4) **abc**	4.8 (0.2) **bc**	42.4 (4.1) **c**	36.5 (9.1) **abc**	1.2 (0.2) **bcd**	135.6 (38.6) **bc**	29.8 (13.0) **bc**	459.9 (79.2) **abc**	94.6 (38.0) **ab**
S_8	t0	33.3 (0.9) **d**	26.5 (0.4) **e**	5.4 (0.2) **a**	30.3 (0.6) **c**	12.8 (1.9) **d**	0.6 (0.1) **d**	10.6 (0.2) **d**	12.6 (0.7) **bc**	462.8 (24.7) **abc**	13.3 (0.4) **d**
	t1	51.8 (15.5) **bcd**	48.5 (17.1) **de**	5.6 (0.1) **a**	52.0 (14.6) **bc**	30.0 (9.4) **bc**	1.3 (0.4) **bcd**	29.1 (23.3) **d**	60.7 (23.6) **b**	538.9 (141.5) **ab**	36.9 (9.2) **cd**
	t2	42.1 (4.4) **cd**	57.5 (18.0) **cd**	5.5 (0.3) **a**	50.7 (22.8) **bc**	28.8 (9.7) **c**	1.3 (0.4) **bcd**	28.9 (16.9) **d**	42.2 (11.2) **bc**	655.1 (76.6) **ab**	67.6 (27.4) **bc**
	t3	55.0 (10.8) **abc**	47.6 (15.9) **de**	5.2 (0.1) **ab**	150.4 (34.0) **a**	25.2 (8.9) **c**	1.2 (0.2) **bcd**	7.3 (1.1) **d**	204.5 (81.3) **a**	747.7 (98.9) **a**	26.8 (12.9) **d**
	t4	45.8 (5.5) **cd**	47.4 (19.0) **de**	5.4 (0.3) **a**	84.3 (48.1) **b**	24.8 (11.3) **cd**	0.9 (0.4) **cd**	55.7 (26.1) **cd**	53.0 (28.6) **bc**	243.9 (25.0) **c**	69.1 (8.3) **bc**
N_4	t0	47.7 (0.6) **ab**	31.3 (0.7) **a**	5.3 (0.1) **cde**	30.3 (1.5) **c**	16.3 (0.6) **a**	1.3 (0.03) **ab**	76.1 (1.9) **abc**	8.6 (4.3) **c**	1374.7 (56.2) **a**	71.1 (7.9) **ab**
	t1	48.7 (5.4) **ab**	28.3 (8.5) **a**	5.7 (0.3) **abc**	23.3 (6.0) **c**	13.7 (2.9) **ab**	1.1 (0.3) **ab**	48.9 (24.1) **cde**	10.7 (2.2) **bc**	1086.6 (185.1) **b**	64.5 (31.1) **abc**
	t2	55.1 (1.5) **a**	30.3 (5.2) **a**	6.1 (0.03) **a**	31.7 (5.7) **bc**	14.8 (2.9) **ab**	1.7 (0.3) **a**	95.4 (32.5) **a**	14.3 (8.2) **bc**	1228.2 (61.8) **ab**	89.2 (22.7) **a**
	t3	53.2 (4.2) **ab**	30.6 (7.3) **a**	5.2 (0.2) **cde**	36.8 (18.7) **bc**	15.0 (4.0) **ab**	1.1 (0.2) **ab**	79.3 (20.8) **ab**	58.4 (18.3) **b**	1277.3 (279.2) **ab**	48.0 (2.2) **bcde**
	t4	33.4 (2.3) **c**	23.3 (4.1) **a**	4.9 (0.3) **e**	49.5 (30.8) **bc**	10.5 (2.0) **b**	0.7 (0.2) **b**	46.5 (5.6) **de**	9.3 (6.7) **c**	311.65 (114.0) **d**	22.9 (3.5) **e**
S_9	t0	28.4 (0.8) **cd**	24.3 (0.3) **a**	5.7 (0.1) **abc**	28.3 (1.5) **c**	13.3 (0.6) **ab**	0.8 (0.1) **b**	31.6 (1.7) **e**	1.8 (1.5) **c**	710.0 (56.2) **c**	25.4 (1.9) **de**
	t1	35.5 (8.6) **c**	24.4 (6.2) **a**	6.1 (0.2) **a**	43.7 (7.2) **bc**	12.4 (4.2) **ab**	0.8 (0.3) **b**	48.3 (11.0) **cde**	24.4 (8.2) **bc**	632.4 (74.6) **c**	63.6 (0.4) **abcd**
	t2	31.9 (10.1) **cd**	27.8 (3.3) **a**	5.9 (0.1) **ab**	37 (10.5) **bc**	10.4 (2.6) **b**	0.7 (0.2) **b**	47.5 (23.5) **cde**	8.2 (8.2) **c**	742.3 (141.1) **c**	40.6 (4.5) **bcde**
	t3	45.8 (3.5) **b**	29.4 (5.2) **a**	5.2 (0.1) **de**	80.1 (15.6) **a**	15.3 (2.7) **a**	1.0 (0.2) **b**	52.2 (13.7) **bcde**	167.9 (86.0) **a**	839.2 (114.7) **c**	29.6 (15.1) **cde**
	t4	23.4 (1.9) **d**	31.5 (3.0) **a**	5.4 (0.2) **bcd**	61.1 (37.0) **ab**	15.5 (3.1) **a**	0.9 (0.1) **b**	62.7 (0.8) **bcd**	7.6 (2.7) **c**	231.1 (43.5) **d**	22.6 (0.3) **e**

Table 4
Microbiological properties of wood samples collected in June 2013 (t0; control), in August 2013 (t1; 12 weeks), in October 2013 (t2; 25 weeks); in July 2014 (t3; 52 weeks), in July 2015 (t4; 104 weeks) in the *in-field* mesocosm experiment along the climosequence scenario. The results are shown pairwise, i.e., the couple of north- and south-facing sites at the same elevation (N_1-S_6; 1200 m a.s.l.; N_2-S_7; 1400 m a.s.l.; N_3-S_8; 1600 m a.s.l.; N_4-S_9; 2000 m a.s.l.). Values are means (n = 3) with the standard deviations. Data are expressed on a dry weight basis. Different letters indicate significant differences ($p < 0.05$; ANOVA followed by Tukey post-hoc test) as a function of the time of decay.

Sites	Time	Microbial biomass index (μg dsDNA g^{-1} wood)	Fungi (gene copy number g^{-1} wood)	*nif*H gene (gene copy number g^{-1} wood)
	t0	1.4 (0.2) **c**	3.12×10^9 (1.67×10^9) **bc**	8.77×10^6 (1.37×10^6) **c**
N_1	t1	6.5 (2.1) **bc**	7.75×10^9 (3.56×10^9) **ab**	3.77×10^7 (8.69×10^6) **bc**
	t2	12.1 (4.3) **abc**	9.39×10^9 (2.56×10^9) **a**	3.90×10^7 (1.85×10^7) **bc**
	t3	13.7 (6.6) **ab**	1.42×10^9 (1.20×10^8) **c**	8.95×10^7 (7.38×10^7) **a**
	t4	18.8 (1.2) **a**	4.56×10^9 (4.96×10^9) **abc**	3.99×10^7 (3.03×10^7) **bc**
S_6	t1	10.9 (8.1) **abc**	3.03×10^9 (1.51×10^9) **bc**	3.70×10^7 (1.27×10^7) **bc**
	t2	8.5 (1.2) **abc**	7.30×10^9 (5.37×10^9) **ab**	7.46×10^7 (3.78×10^7) **ab**
	t3	14.6 (1.9) **ab**	1.37×10^9 (1.08×10^9) **c**	2.02×10^7 (3.56×10^6) **c**
	t4	16.6 (0.1) **ab**	4.09×10^9 (2.86×10^9) **bc**	3.18×10^7 (7.21×10^6) **bc**
N_2	t1	5.1 (1.3) **c**	1.35×10^{10} (6.21×10^9) **ab**	1.97×10^6 (1.76×10^6) **b**
	t2	13.1 (3.4) **ab**	2.42×10^{10} (1.38×10^{10}) **a**	1.25×10^7 (9.86×10^6) **b**
	t3	10.9 (2.9) **abc**	2.15×10^9 (4.72×10^8) **b**	9.76×10^6 (7.10×10^6) **b**
	t4	17.5 (3.5) **ab**	1.79×10^{10} (1.00×10^{10}) **ab**	9.04×10^6 (5.16×10^6) **b**
S_7	t1	6.8 (0.9) **bc**	3.86×10^9 (3.00×10^9) **b**	1.55×10^6 (1.77×10^6) **b**
	t2	14.2 (0.9) **ab**	4.78×10^9 (2.43×10^9) **b**	7.82×10^6 (5.83×10^6) **b**
	t3	10.0 (1.1) **abc**	4.51×10^8 (3.96×10^8) **b**	1.35×10^6 (1.78×10^6) **b**
	t4	27.5 (4.2) **a**	1.22×10^{10} (6.38×10^9) **ab**	5.28×10^7 (1.45×10^7) **a**
N_3	t1	9.5 (4.0) **b**	3.80×10^{10} (2.60×10^{10}) **bc**	7.58×10^7 (3.55×10^7) **ab**
	t2	6.1 (1.1) **bc**	3.95×10^{10} (1.96×10^{10}) **bc**	4.07×10^7 (1.79×10^7) **bc**
	t3	12.1 (0.5) **b**	1.30×10^9 (1.82×10^9) **c**	5.32×10^7 (2.32×10^7) **bc**
	t4	26.1 (2.7) **a**	1.09×10^{11} (1.75×10^{10}) **ab**	4.03×10^7 (1.39×10^7) **bc**
S_8	t1	7.0 (1.1) **bc**	1.43×10^9 (1.87×10^9) **c**	3.75×10^7 (1.57×10^7) **bc**
	t2	9.6 (0.9) **b**	2.42×10^{10} (1.43×10^{10}) **c**	9.10×10^7 (4.14×10^7) **ab**
	t3	9.2 (1.0) **b**	1.66×10^9 (6.88×10^8) **c**	7.67×10^7 (3.09×10^7) **ab**
	t4	23.0 (4.7) **a**	1.15×10^{11} (1.32×10^{11}) **a**	1.29×10^8 (8.71×10^7) **a**
N_4	t1	6.4 (0.9) **bc**	1.07×10^{11} (6.84×10^{10}) **abc**	3.91×10^8 (1.19×10^8) **bc**
	t2	8.2 (1.6) **bc**	1.55×10^{11} (3.32×10^{10}) **ab**	6.68×10^8 (4.42×10^8) **abc**
	t3	13.0 (2.0) **abc**	1.81×10^{11} (1.29×10^{11}) **ab**	1.03×10^9 (1.25×10^9) **ab**
	t4	31.6 (15.3) **a**	1.92×10^{11} (8.47×10^{10}) **ab**	1.28×10^9 (2.86×10^8) **a**
S_9	t1	8.1 (0.9) **bc**	7.80×10^{10} (4.51×10^{10}) **bc**	4.59×10^8 (4.51×10^8) **bc**
	t2	11.4 (3.2) **bc**	1.61×10^{11} (3.39×10^{10}) **ab**	4.10×10^8 (2.17×10^8) **bc**
	t3	12.7 (2.4) **abc**	1.17×10^{11} (1.18×10^{10}) **abc**	4.27×10^7 (2.97×10^7) **c**
	t4	22.8 (13.7) **ab**	1.04×10^{11} (1.19×10^{11}) **a**	4.60×10^7 (2.03×10^7) **c**

contents were, on average, 44% and 79% higher at the north- than at the south-facing slopes along the altitudinal gradient, respectively.

3.3. Wood (micro)biological parameters along the studied climosequence

Wood microbial biomass (dsDNA) was 37% higher at the south- than at the north-facing slopes after 104 weeks at 1400 m a.s.l., whereas no exposure effects were found for the other altitudes (Tables 4 and 6). Moreover, dsDNA contents were found, on average, 94% higher after 104 weeks compared to the beginning of the experiment (Table 4). Wood fungal abundance was 60% higher at the north- than at the south-facing sites at 1400 m a.s.l. irrespective of the time, and similarly after 12 weeks at 1600 m a.s.l. (Table 4). At both slopes fungi were, on average, 77% higher after 25 weeks, followed by a decrease after 52 weeks and a subsequent increase at the end of the trial between 1200 and 1600 m a.s.l. (Table 4). The *nifH* gene abundance in the wood blocks was 96% higher at the north- than at the south-facing sites after 52 and 104 weeks at 2000 m a.s.l. No exposure-effects were recorded for the other altitudes (Table 4). Furthermore, the *nifH* gene copy numbers were, on average, 65% higher after 12 weeks at the north- and the south-facing slopes, and remained mostly stable thereafter, except for the south-facing sites at 1400 and 2000 m a.s.l. (Table 4). A significant positive correlation between fungal and *nifH* gene abundances was observed in *P. abies* wood blocks at the north-facing slopes along the altitudinal gradient (*12 weeks*: $R = 0.669$, $p < 0.05$; *25 weeks*: $R = 0.664$, $p < 0.05$; *52 weeks*: $R = 0.943$, $p < 0.001$; *104 weeks*: $R = 0.729$, $p < 0.01$). Such a correlation was also found at the south-facing sites after 12 weeks ($R = 0.947$, $p < 0.001$) and 25 weeks ($R = 0.771$, $p < 0.01$). Both *amo*A bacterial and archaeal abundances were below the detection limit for all of the study sites (*data not shown*).

The β-glucosidase and xylosidase activities were 50% and 44% higher, respectively, at the south-facing sites at 1600 m a.s.l.; whereas the opposite trend (north > south-facing sites) was recorded at 1400 and 2000 m a.s.l. after 104 weeks (Fig. 2A & C). A pronounced increase in these two enzyme activities was observed after 104 weeks at both slopes at 1200 m a.s.l., and at the north-facing slope at 1400 and 2000 m a.s.l. Overall, the highest cellulase (Fig. 2B) and chitinase (Fig. 3A) activities were generally observed after 104 weeks at both slopes along the climosequence scenario. Leucine-aminopeptidase activity was not significantly affected by the slope exposure; however, it was 90% higher after 25 weeks, followed by a decrease after 52 weeks and a subsequent increase at the end of the trial between 1200 and 1600 m a.s.l. (Fig. 3B). Acid phosphomonoesterase was, on average, 43% higher at the north- than at the south-facing sites after 104 weeks along the altitudinal gradient, except for 1400 m a.s.l. (Fig. 3C). Alkaline phosphomonoesterase activity was 86% higher at the south- than at the north-facing site at 1600 m a.s.l. regardless of the sampling time (Fig. 3D). However, no exposure-effect was observed for the remaining altitudes (Fig. 3D).

3.4. Soil (micro)biological properties along the studied climosequence

Soil microbial biomass, assessed as double strand DNA (dsDNA), was 55% and 95% higher at the north- than at the south-facing sites after 25 and 104 weeks (respectively) at 1200 m a.s.l. (Tables 5 and 6). This exposure-effect (north- > south-facing sites) was also observed

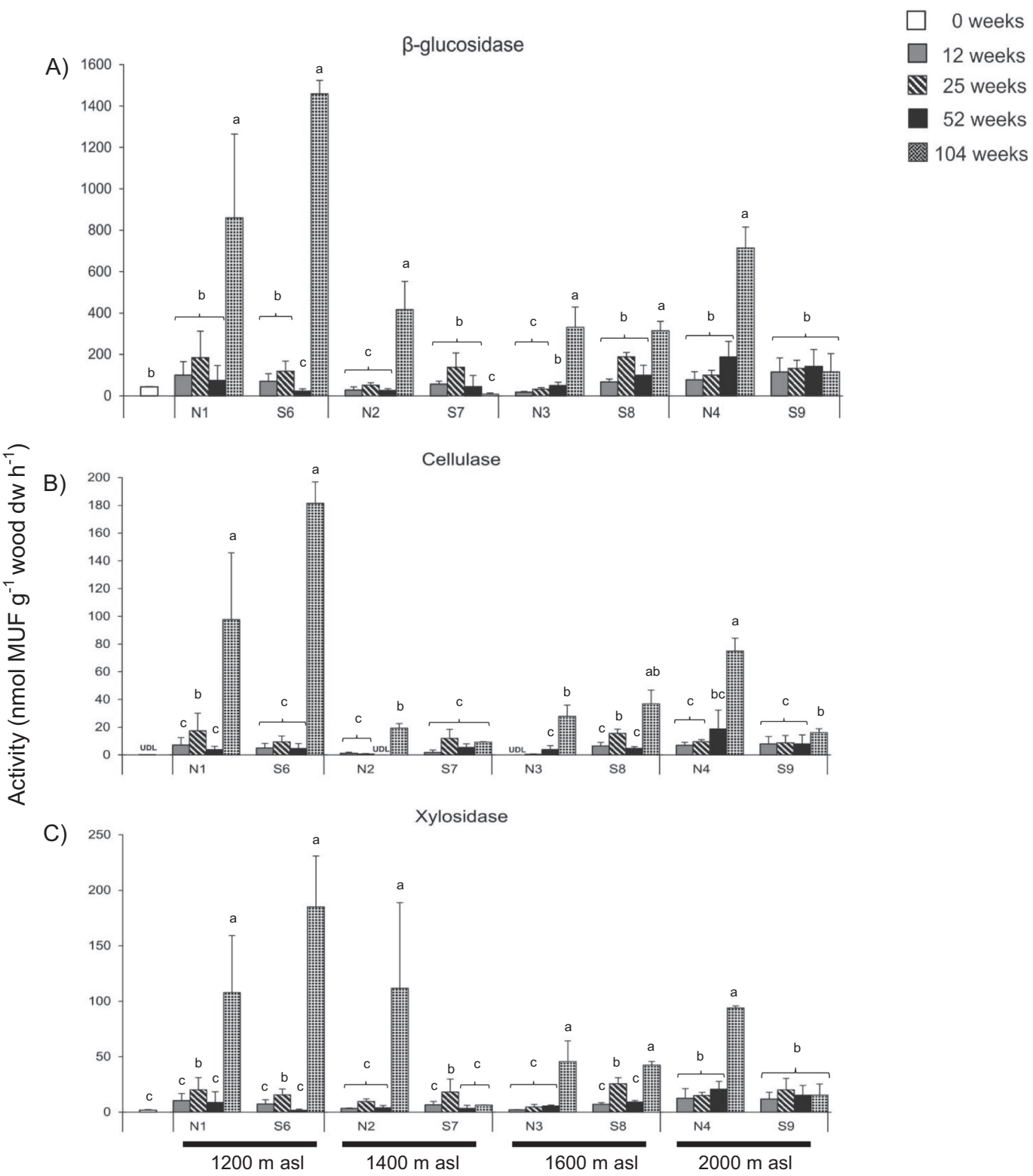

Fig. 2. Potential activities of β-glucosidase (A), cellulase (B), xylosidase (C) of the wood samples collected in June 2013 (0 weeks = start of the decay), in August 2013 (12 weeks), in October 2013 (25 weeks), in July 2014 (52 weeks), and in July 2015 (104 weeks) in the *in-field* mesocosm experiment within the climosequence scenario. The results are shown pairwise, i.e., the couples of north- and south-facing sites (N_1-S_6; N_2-S_7; N_3-S_8; N_4-S_9) at comparable elevation (1200 m; 1400 m; 1600 m; 2000 m above sea level). Values are means (n = 3) with the standard deviations. Different letters indicate significant differences ($p < 0.05$; ANOVA followed by Tukey post hoc test) as a function of the time of decay.

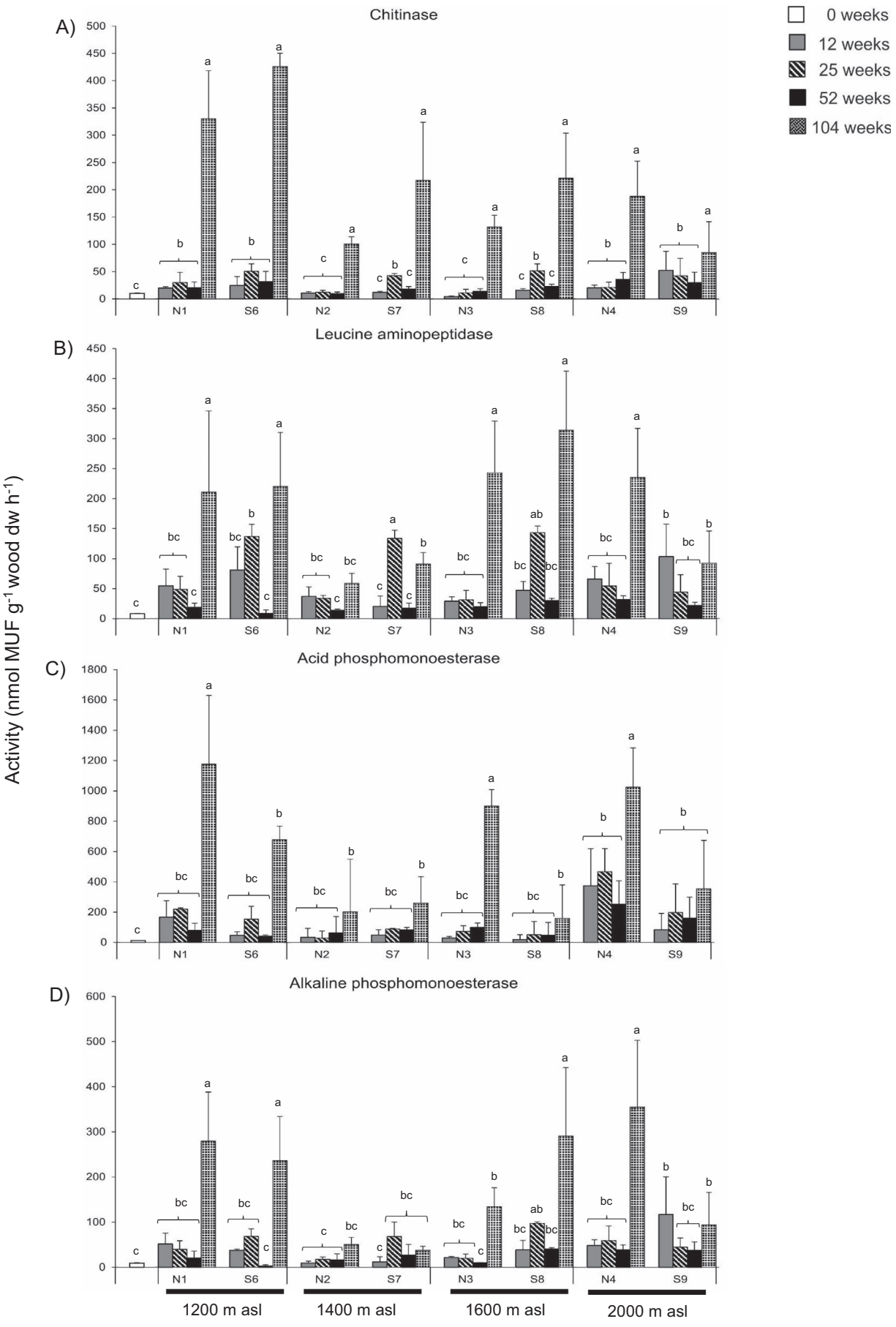

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Fig. 3. Potential activities of chitinase (A), leucine aminopeptidase (B), acid phosphomonoesterase (C), alkaline phosphomonoesterase (D) of the wood samples collected in June 2013 (0 weeks = start of the decay), in August 2013 (12 weeks), in October 2013 (25 weeks), in July 2014 (52 weeks), and in July 2015 (104 weeks) in the *in-field* mesocosm experiment within the climosequence scenario. The results are shown pairwise, i.e., the couples of north- and south-facing sites (N_1-S_6; N_2-S_7; N_3-S_8; N_4-S_9) at comparable elevation (1200 m; 1400 m; 1600 m; 2000 m above sea level). Values are means (n = 3) with the standard deviations. Different letters indicate significant differences ($p < 0.05$; ANOVA followed by Tukey post hoc test) as a function of the time of decay.

after 12 and 25 weeks at 1400 m a.s.l.; after 52 weeks at 1600 m a.s.l.; and generally at 2000 m a.s.l. (Table 5). A similar exposure-effect was found for the soil fungal abundance assessed by qPCR (Table 5). The *nifH* gene copy number was 63% higher at the north- than at the south-facing sites at 1600 m a.s.l. throughout the monitoring period. This exposure effect (north- > south-facing sites) was also observed at the beginning of the trial and after 52 weeks at 1400 and 2000 m a.s.l., respectively (Table 5). The *amo*A bacterial abundance was, on average, 73% higher at the south- than at the north-facing sites along the altitudinal gradient, except for 1200 m a.s.l. (no exposure-effect; Table 5). The *amo*A archaeal abundance was in general below the detection limit, except at the north-facing site at 2000 m a.s.l. (*data not shown*).

The β-glucosidase activity was, on average, 40% higher at the south- than at the north-facing slopes (Fig. 4A) and the cellulase activity showed a similar behaviour (Fig. 4B). Xylosidase activity was 64% higher at the north- than at the south-facing slopes after 25 and 104 weeks at 1200 m a.s.l., while the opposite trend (south > north-facing sites) was observed after 52 weeks at this altitude (1200 m a.s.l.), and after 12 weeks at 1400 and 1600 m a.s.l. No significant exposure-effect was observed at 2000 m a.s.l. (Fig. 4C). Chitinase showed 58% higher activity at the south- than at the north-facing sites at 1600 m a.s.l. after 12 weeks; whereas no exposure effect was observed at the remaining altitudes (Fig. 5A). Nonetheless, leucine-aminopeptidase activity was, on average 54% higher at the north- than at the south-facing sites over time along the altitudinal gradient, except for the time point of 104 weeks at 1600 and 2000 m a.s.l. (no exposure-effect) (Fig. 5B). Slope exposure also affected significantly the acid phosphomonoesterase activity, showing 73% higher levels at the south- than at the north-facing slopes after 12 and 52 weeks at 1400 m a.s.l. likewise observed at the beginning of the monitoring at 1600 m a.s.l. (Fig. 5C). A similar exposure effect (south > north-facing sites) was found for the soil alkaline phosphomonoesterase activity (Fig. 5D).

Table 5
Microbiological properties of soil samples collected in June 2013 (t0; control), in August 2013 (t1; 12 weeks), in October 2013 (t2; 25 weeks); in July 2014 (t3; 52 weeks), in July 2015 (t4; 104 weeks) in the *in-field* mesocosm experiment along the climosequence scenario. The results are shown pairwise, i.e., the couple of north- and south-facing sites at the same elevation (N_1-S_6; 1200 m a.s.l.; N_2-S_7; 1400 m a.s.l.; N_3-S_8; 1600 m a.s.l.; N_4-S_9; 2000 m a.s.l.). Values are means (n = 3) with the standard deviations. Data are expressed on a dry weight basis. Different letters indicate significant differences ($p < 0.05$; ANOVA followed by Tukey post-hoc test) as a function of the time of decay.

Sites	Time	Microbial biomass index (μg dsDNA g^{-1} soil)	Fungi (gene copy number g^{-1} soil)	*nif*H gene (gene copy number g^{-1} soil)	*amo*A-AOB gene (gene copy number g^{-1} soil)
N_1	t0	140.0 (12.4) **a**	9.45×10^8 (7.45×10^8) **cd**	1.57×10^8 (7.94×10^7) **bc**	2.32×10^6 (1.44×10^6) **c**
	t1	101.7 (18.1) **abc**	2.03×10^9 (1.10×10^9) **ab**	2.73×10^8 (2.49×10^7) **a**	7.43×10^7 (1.70×10^7) **ab**
	t2	157.9 (49.9) **a**	1.65×10^9 (5.00×10^8) **bc**	1.60×10^8 (8.33×10^7) **bc**	4.77×10^7 (3.59×10^7) **bc**
	t3	55.8 (21.2) **bc**	2.74×10^9 (6.36×10^8) **a**	2.08×10^8 (2.70×10^7) **ab**	1.23×10^8 (6.30×10^7) **a**
	t4	160.3 (4.8) **a**	5.51×10^8 (4.74×10^8) **d**	1.64×10^7 (8.74×10^6) **d**	1.90×10^7 (1.32×10^7) **c**
S_6	t0	94.2 (13.4) **abc**	5.88×10^8 (1.17×10^8) **d**	1.03×10^8 (7.57×10^6) **c**	1.98×10^6 (7.08×10^5) **c**
	t1	112.2 (25.5) **ab**	1.31×10^9 (2.22×10^8) **bcd**	2.12×10^8 (3.32×10^7) **ab**	1.09×10^8 (4.57×10^7) **a**
	t2	70.6 (17.7) **bc**	1.11×10^9 (2.98×10^8) **bcd**	1.61×10^8 (6.15×10^7) **bc**	3.11×10^7 (1.34×10^7) **bc**
	t3	39.4 (12.5) **c**	1.57×10^9 (6.32×10^8) **bc**	1.73×10^8 (2.20×10^7) **bc**	4.87×10^7 (3.85×10^7) **bc**
	t4	62.2 (29.9) **bc**	3.78×10^8 (6.40×10^7) **d**	2.04×10^7 (7.09×10^6) **d**	6.25×10^6 (5.03×10^5) **c**
N_2	t0	229.9 (11.0) **ab**	8.33×10^8 (2.95×10^8) **bc**	8.46×10^7 (2.33×10^7) **ab**	1.48×10^6 (1.26×10^6) **b**
	t1	344.0 (88.1) **a**	1.20×10^9 (3.73×10^8) **ab**	5.17×10^7 (4.01×10^7) **abc**	2.17×10^6 (2.79×10^6) **b**
	t2	342.4 (55.5) **a**	8.43×10^8 (1.74×10^7) **bc**	9.53×10^7 (2.95×10^7) **a**	5.95×10^5 (3.95×10^5) **b**
	t3	185.2 (18.4) **bc**	1.53×10^9 (1.55×10^8) **a**	8.32×10^7 (1.02×10^7) **ab**	3.99×10^6 (1.10×10^6) **b**
	t4	189.0 (52.4) **bc**	5.01×10^8 (2.28×10^8) **cd**	3.37×10^7 (1.82×10^7) **abc**	5.46×10^6 (2.96×10^6) **b**
S_7	t0	156.5 (23.9) **bc**	4.24×10^8 (5.90×10^7) **d**	6.40×10^6 (3.47×10^6) **c**	1.05×10^7 (1.33×10^6) **ab**
	t1	83.4 (28.5) **c**	3.55×10^8 (1.02×10^8) **d**	5.09×10^7 (1.63×10^7) **abc**	2.73×10^7 (1.34×10^7) **ab**
	t2	143.7 (49.5) **bc**	4.26×10^8 (1.64×10^8) **d**	1.96×10^7 (1.95×10^7) **bc**	3.31×10^7 (6.07×10^6) **ab**
	t3	196.1 (12.0) **bc**	4.05×10^8 (8.55×10^7) **d**	1.08×10^7 (8.90×10^6) **c**	8.72×10^7 (7.43×10^7) **ab**
	t4	186.6 (28.7) **bc**	6.56×10^8 (3.93×10^8) **cd**	2.23×10^7 (5.20×10^6) **bc**	1.09×10^8 (8.24×10^7) **a**
N_3	t0	242.1 (11.8) **ab**	3.11×10^9 (1.16×10^9) **ab**	1.52×10^9 (3.07×10^8) **a**	2.56×10^6 (1.12×10^6) **b**
	t1	218.7 (41.0) **b**	3.13×10^9 (8.44×10^8) **ab**	1.29×10^9 (2.81×10^8) **a**	6.83×10^7 (7.92×10^7) **a**
	t2	182.0 (79.2) **bc**	1.34×10^9 (1.60×10^9) **bc**	4.35×10^8 (3.03×10^8) **b**	6.62×10^6 (1.04×10^6) **b**
	t3	381.1 (19.7) **a**	4.53×10^9 (2.89×10^9) **a**	3.47×10^8 (1.80×10^8) **bc**	8.05×10^5 (8.23×10^5) **b**
	t4	186.2 (16.7) **bc**	7.79×10^8 (1.29×10^8) **c**	5.44×10^7 (1.54×10^7) **cd**	4.11×10^7 (3.69×10^7) **ab**
S_8	t0	115.8 (5.1) **bc**	1.35×10^9 (8.40×10^8) **bc**	5.59×10^8 (1.06×10^8) **b**	1.39×10^7 (1.59×10^6) **ab**
	t1	201.1 (55.6) **bc**	2.36×10^9 (8.72×10^8) **abc**	5.11×10^8 (6.43×10^7) **b**	6.82×10^7 (5.00×10^7) **a**
	t2	208.2 (97.6) **bc**	1.82×10^9 (4.51×10^8) **bc**	1.22×10^8 (2.18×10^7) **cd**	2.13×10^7 (3.39×10^6) **ab**
	t3	192.3 (29.0) **bc**	1.96×10^9 (1.13×10^9) **bc**	1.28×10^8 (4.88×10^7) **cd**	4.16×10^7 (2.52×10^7) **ab**
	t4	71.0 (29.9) **c**	6.63×10^8 (5.85×10^8) **c**	2.20×10^7 (8.51×10^6) **d**	3.66×10^7 (1.83×10^7) **ab**
N_4	t0	214.0 (8.8) **ab**	1.12×10^9 (3.34×10^8) **ab**	5.58×10^8 (4.25×10^8) **a**	3.84×10^6 (2.76×10^6) **b**
	t1	242.8 (30.8) **a**	1.06×10^9 (7.17×10^8) **ab**	3.33×10^8 (1.20×10^8) **ab**	5.02×10^6 (5.48×10^6) **b**
	t2	235.1 (56.8) **a**	5.58×10^8 (2.18×10^8) **ab**	3.58×10^8 (3.47×10^8) **ab**	1.00×10^7 (7.38×10^6) **b**
	t3	247.0 (123.6) **a**	1.32×10^9 (7.94×10^8) **a**	7.86×10^8 (4.02×10^8) **a**	2.89×10^7 (3.05×10^7) **b**
	t4	118.5 (14.7) **ab**	3.38×10^8 (4.24×10^7) **b**	4.33×10^8 (2.27×10^8) **ab**	3.10×10^6 (2.56×10^6) **b**
S_9	t0	135.9 (15.0) **ab**	7.62×10^8 (5.79×10^7) **ab**	3.83×10^8 (1.45×10^8) **ab**	4.89×10^5 (1.30×10^5) **b**
	t1	85.9 (35.9) **b**	1.13×10^9 (1.80×10^8) **ab**	6.18×10^8 (3.42×10^8) **a**	4.39×10^7 (3.97×10^7) **b**
	t2	194.6 (43.0) **ab**	7.21×10^8 (2.85×10^7) **ab**	4.02×10^8 (1.73×10^8) **ab**	1.94×10^7 (2.90×10^7) **b**
	t3	209.9 (16.6) **ab**	1.41×10^9 (4.53×10^8) **a**	9.12×10^7 (6.96×10^7) **b**	3.52×10^8 (2.24×10^8) **a**
	t4	137.1 (11.5) **ab**	1.23×10^9 (1.03×10^9) **a**	5.45×10^7 (5.75×10^7) **b**	3.18×10^7 (1.35×10^7) **b**

Table 6
Statistical output of the soil and wood physico-chemical and microbiological parameters as a function of slope exposure (N vs S) and time of decay between the couples of north- and south-facing sites at the same elevation (N_1-S_6; 1200 m a.s.l.; N_2-S_7; 1400 m a.s.l.; N_3-S_8; 1600 m a.s.l.; N_4-S_9; 2000 m a.s.l.).

	Exposure								Time								Exposure × Time							
	N_1-S_6		N_2-S_7		N_3-S_8		N_4-S_9		N_1-S_6		N_2-S_7		N_3-S_8		N_4-S_9		N_1-S_6		N_2-S_7		N_3-S_8		N_4-S_9	
SOIL	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Moisture	**5.12**	*	**21.01**	***	**18.79**	***	**64.74**	***	2.08	ns	3.71	ns	4.79	ns	**14.84**	***	0.83	ns	na	na	na	na	2.61	ns
Volatile solids	**14.13**	**	**82.04**	***	**39.38**	***	0.49	ns	1.23	ns	**3.05**	*	**3.64**	*	0.49	ns	0.50	ns	2.37	ns	0.29	ns	1.92	ns
pH	**26.96**	***	**440.14**	***	**53.50**	***	**9.74**	**	**3.35**	*	**19.72**	***	**4.79**	**	**25.48**	***	1.91	ns	2.79	ns	1.18	ns	**4.44**	**
EC	0.36	ns	**61.27**	***	1.44	ns	**7.62**	*	1.89	ns	**10.57**	***	**7.06**	**	**3.18**	*	0.71	ns	**11.03**	***	**3.08**	*	1.73	ns
Total C	**28.14**	***	**59.98**	***	**36.39**	***	0.40	ns	1.57	ns	1.93	ns	**3.59**	*	1.06	ns	1.25	ns	0.99	ns	0.51	ns	2.49	ns
Total N	**6.27**	*	**21.01**	***	**25.43**	***	**21.34**	***	1.37	ns	1.36	ns	**8.99**	***	2.56	ns	1.40	ns	2.44	ns	1.59	ns	**6.88**	**
NH_4^+	**89.89**	***	**55.88**	***	**127.43**	***	**10.88**	**	**17.33**	***	**6.03**	**	**4.17**	*	1.79	ns	**12.49**	***	**6.32**	**	**3.32**	*	**3.93**	*
NO_3^-	2.29	ns	**11.12**	**	**30.44**	***	0.72	ns	**29.51**	***	**17.04**	***	**35.18**	***	**17.52**	***	**3.46**	*	2.11	ns	0.89	ns	**4.12**	*
Total P	**7.22**	*	**9.01**	**	0.41	ns	**77.32**	***	**3.49**	*	2.25	ns	**14.26**	***	**37.15**	***	0.23	ns	**5.99**	**	1.95	ns	**3.88**	*
Available P	**31.83**	***	**17.43**	***	**41.05**	***	**28.35**	***	**12.93**	***	**4.33**	*	**3.94**	*	**17.99**	***	**7.19**	***	**7.32**	***	**3.26**	*	**6.01**	**
dsDNA	**29.86**	***	**43.63**	***	**23.08**	***	**11.02**	**	**9.08**	***	1.23	ns	**8.55**	***	**4.17**	*	**5.64**	**	**12.42**	***	**4.91**	**	2.68	ns
Fungi	**8.16**	**	**33.81**	***	1.15	ns	2.65	ns	**8.69**	***	1.14	ns	**3.88**	*	2.59	ns	0.67	ns	**4.33**	*	1.25	ns	1.56	ns
*nif*H	3.12	ns	**23.76**	***	**42.03**	***	**5.54**	*	**20.83**	***	1.34	ns	**64.33**	***	1.49	ns	0.68	ns	**3.99**	*	0.04	ns	**4.06**	*
AOB	4.16	ns	**139.44**	***	**6.02**	*	**5.52**	*	**43.15**	***	**8.26**	***	**3.90**	*	**7.66**	***	1.68	ns	1.58	ns	1.04	ns	**3.89**	*
gluc	2.74	ns	**26.69**	***	**17.13**	***	**4.66**	*	**3.20**	*	2.66	ns	**6.72**	**	1.33	ns	**8.40**	***	**8.65**	***	**11.07**	***	1.70	ns
cell	0.02	ns	**8.78**	**	**10.29**	**	1.78	ns	2.86	ns	1.06	ns	**6.34**	**	1.01	ns	**4.97**	**	**3.40**	*	**8.93**	***	**3.05**	*
xylo	0.73	ns	**14.87**	***	**9.57**	**	1.51	ns	**4.08**	*	**4.02**	*	**4.86**	**	1.98	ns	**14.58**	***	**15.65**	***	**12.39**	***	1.36	ns
chit	1.03	ns	5.84	ns	**9.85**	*	0.06	ns	3.19	ns	0.38	ns	**6.69**	**	1.95	ns	1.63	ns	1.29	ns	1.76	ns	1.23	ns
leu	**45.79**	***	**9.32**	**	**10.85**	**	**93.75**	***	**6.11**	**	0.99	ns	**12.41**	***	**5.62**	**	**4.09**	*	**6.86**	**	0.56	ns	**9.14**	***
*ac*P	2.39	ns	**7.26**	*	2.97	ns	0.48	ns	2.12	ns	1.54	ns	2.76	ns	1.92	ns	**8.63**	***	**10.78**	***	**3.17**	*	2.57	ns
*alk*P	0.34	ns	**35.35**	***	**29.19**	***	**4.38**	*	**3.35**	*	1.86	ns	2.28	ns	**4.37**	*	0.69	ns	**9.57**	***	2.13	ns	**3.33**	*
WOOD	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Mass loss	0.12	ns	4.14	ns	0.62	ns	1.46	ns	0.11	ns	0.69	ns	0.08	ns	1.87	ns	0.16	ns	**3.73**	*	1.20	ns	**3.14**	*
Moisture	0.14	ns	0.26	ns	0.87	ns	0.03	ns	**16.44**	**	**19.41**	***	**15.06**	**	**20.15**	***	na	na	na	na	na	na	na	na
pH	0.08	ns	0.14	ns	**25.27**	***	3.30	ns	**10.79**	*	**14.56**	**	1.25	ns	**5.92**	**	na	na	na	na	**5.61**	**	**3.47**	*
EC	**6.82**	*	**39.25**	***	**9.70**	**	**21.20**	***	**12.50**	***	**11.25**	***	**24.36**	***	**13.84**	***	**6.91**	**	2.68	ns	**3.25**	*	**4.34**	*
Total C	2.7	ns	1.40	ns	**9.0**	**	0.01	ns	**25.03**	***	**16.14**	***	**15.45**	***	**11.39**	*	**3.13**	*	0.83	ns	1.7	ns	na	na
Cellulose	0.16	ns	0.57	ns	0.05	ns	0.11	ns	2.44	ns	**3.27**	*	**3.57**	*	**12.63**	*	0.32	ns	0.66	ns	0.80	ns	na	na
Total Lignin	0.40	ns	0.61	ns	0.02	ns	3.84	ns	0.70	ns	1.75	ns	0.60	ns	**6.33**	**	na	na	1.04	ns	**3.08**	*	2.22	ns
dsDNA	0.02	ns	**7.74**	*	1.03	ns	0.02	ns	**16.46**	***	**69.61**	***	**126.51**	***	**27.39**	***	1.02	ns	**5.25**	**	**3.51**	*	0.98	ns
Fungi	1.21	ns	**17.53**	***	**4.44**	*	0.16	ns	**4.56**	**	**14.81**	***	**22.95**	***	**5.63**	**	0.56	ns	2.14	ns	**5.35**	**	0.29	ns
*nif*H	0.85	ns	0.44	ns	3.03	ns	**21.46**	***	**14.39**	***	**9.19**	***	**20.77**	***	**25.07**	***	**3.66**	*	**4.15**	*	**3.28**	*	**6.06**	**
gluc	0.34	ns	0.42	ns	**70.28**	***	**4.80**	*	**20.93**	***	**2.96**	*	**76.89**	***	**12.89**	***	na	na	**3.75**	*	**16.23**	***	**6.83**	**
cell	0.01	ns	**11.26**	**	**4.14**	*	0.01	ns	**99.75**	***	**46.46**	***	**18.07**	**	**21.07**	***	0.72	ns	**5.05**	**	na	na	na	na
xylo	1.71	ns	0.01	ns	**45.82**	***	**5.65**	*	**55.77**	***	**22.38**	***	**110.48**	***	**28.33**	***	2.08	ns	na	na	**11.69**	***	**5.39**	**
chit	1.09	ns	**11.88**	**	**56.11**	***	0.01	ns	**18.21**	***	**19.69**	***	**105.63**	***	**12.32**	***	0.49	ns	**3.57**	*	**7.84**	***	1.98	ns
leu	0.02	ns	0.90	ns	3.28	ns	1.21	ns	**48.26**	***	**18.07**	***	**27.47**	***	**20.31**	***	1.79	ns	**3.83**	*	2.59	ns	1.15	ns
*ac*P	1.27	ns	**7.50**	*	**10.22**	**	**11.30**	**	2.23	ns	0.39	ns	1.07	ns	**6.79**	**	0.19	ns	0.51	ns	0.87	ns	1.25	ns
*alk*P	1.09	ns	**8.16**	*	**3.64**	*	1.20	ns	**31.59**	***	**11.50**	***	**21.34**	***	**22.69**	***	**3.73**	*	2.15	ns	na	na	**3.08**	*

pH (pH H_2O), EC (Electrical conductivity), NH_4^+ (Ammonium content), NO_3^- (Nitrate content), dsDNA (soil and wood microbial biomass index), Fungi (18S rRNA gene copy number), *nif*H (Bacterial *nif*H gene copy number), AOB (Bacterial *amo*A gene copy number), *gluc* (β-glucosidase), *cell* (cellulase), *xylo* (xylosidase), *chit* (chitinase), *leu* (leucine aminopeptidase), *ac*P (acid phosphomonoesterase), *alk*P (alkaline phosphomonoesterase).

na (not available due to Kruskal-Wallis test); ns (no significant); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

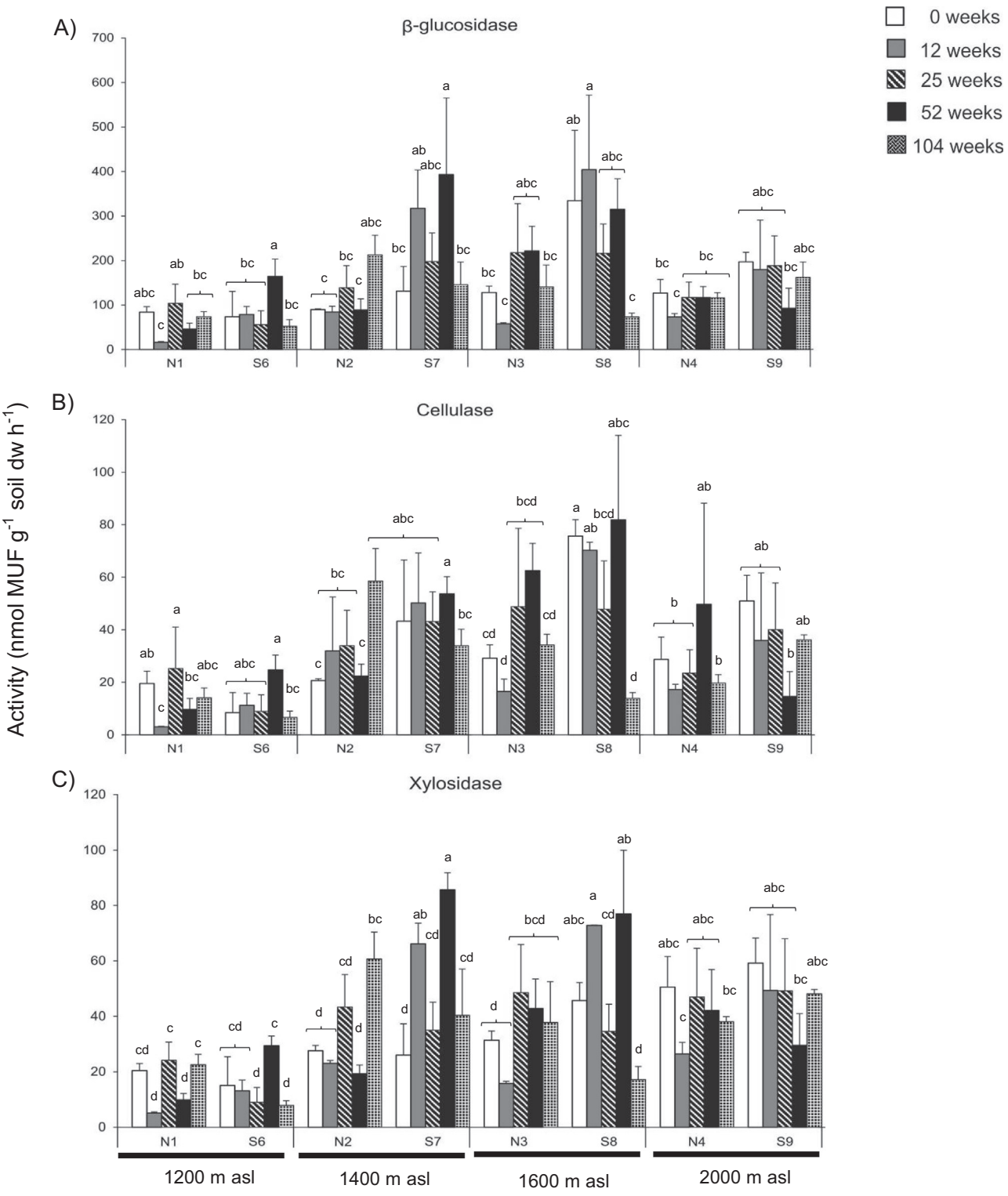
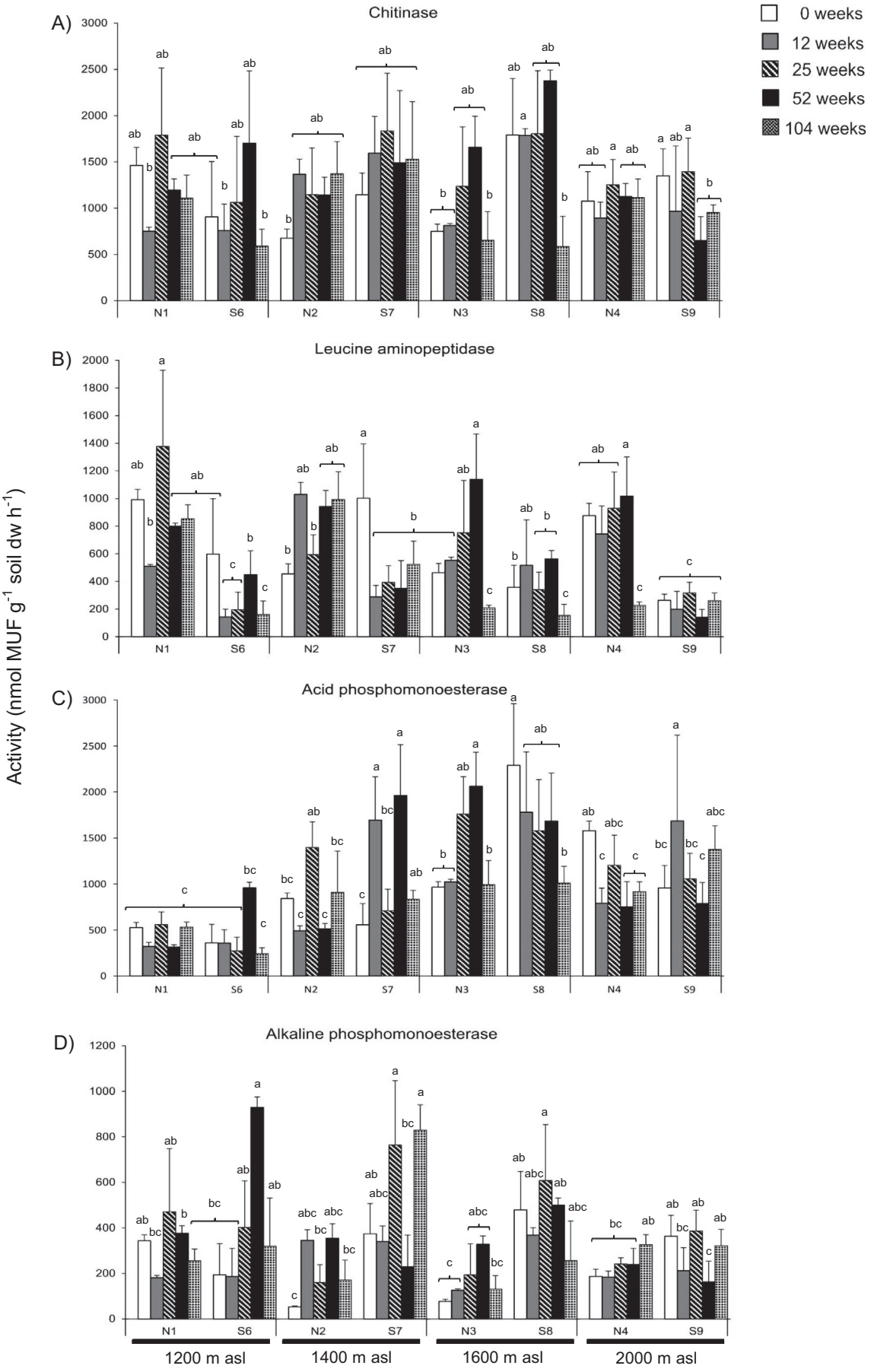


Fig. 4. Potential activities of β-glucosidase (A), cellulase (B), xylosidase (C) of the soil samples collected in June 2013 (0 weeks = start of the decay), in August 2013 (12 weeks), in October 2013 (25 weeks), in July 2014 (52 weeks), and in July 2015 (104 weeks) in the *in-field* mesocosm experiment within the climosequence scenario. The results are shown pairwise, i.e., the couples of north- and south-facing sites (N_1-S_6; N_2-S_7; N_3-S_8; N_4-S_9) at comparable elevation (1200 m; 1400 m; 1600 m; 2000 m above sea level). Values are means (n = 3) with the standard deviations. Different letters indicate significant differences ($p < 0.05$; ANOVA followed by Tukey post hoc test) as a function of the time of decay.

4. Discussion

In agreement with previous studies performed in the same study area (Egli et al., 2006, 2009; Fravolini et al., 2016; Bardelli et al., 2017), the soils located at the north-facing slope were more acidic, moister and richer in OM content compared to those at the south-facing slope. The lower pH and higher moisture levels recorded at the northern slope led to favourable conditions especially for the fungal deadwood decomposers. Indeed, as revealed by real-time PCR, fungi were more abundant in the *P. abies* wood blocks at the north-facing



(caption on next page)

Fig. 5. Potential activities of chitinase (A), leucine aminopeptidase (B), acid phosphomonoesterase (C), alkaline phosphomonoesterase (D) of the soil samples collected in June 2013 (0 weeks = start of the decay), in August 2013 (12 weeks), in October 2013 (25 weeks), in July 2014 (52 weeks), and in July 2015 (104 weeks) in the *in-field* mesocosm experiment within the climosequence scenario. The results are shown pairwise, i.e., the couples of north- and south-facing sites (N_1-S_6; N_2-S_7; N_3-S_8; N_4-S_9) at comparable elevation (1200 m; 1400 m; 1600 m; 2000 m above sea level). Values are means (n = 3) with the standard deviations. Different letters indicate significant differences ($p < 0.05$; ANOVA followed by Tukey post hoc test) as a function of the time of decay.

slopes, even though this exposure-effect (north > south-facing slopes) was altitude- and time-dependent. This is in agreement with Fravolini et al. (2016) who observed faster decay rates of *P. abies* deadwood at the north-facing sites under the same experimental conditions. Moreover, a higher fungal and *nifH* abundances were detected in general at the end of the monitoring experiment (i.e., after 104 weeks), corroborating our second hypothesis. This was probably due to an increase in the availability of micro- and macronutrients required for microbial growth as wood decay progresses (Gonzalez-Polo et al., 2013; Gómez-Brandón et al., 2017). This could explain why a decrease in cellulose content was recorded over time regardless the slope exposure, which is in agreement with previous studies (Bűtler et al., 2007; Fravolini et al., 2016; Gómez-Brandón et al., 2017). Nevertheless, no time-differences were found for lignin concentration, except at 2000 m a.s.l. Specifically, at this altitude the amount of lignin increased with progressing wood decay probably due to its slower degradation and therefore passive enrichment in deadwood (Petrillo et al., 2015, 2016; Gómez-Brandón et al., 2017).

Furthermore, we found a positive and strong correlation between fungi and *nifH* gene in terms of abundance along the climosequence scenario, which suggests the occurrence of complex fungal-bacterial interactions within decaying deadwood. Accordingly, Gómez-Brandón et al. (2017) also observed a strong relationship between both fungi and *nifH* gene (qPCR-based) in *P. abies* coarse woody debris at different stages of natural decay in the same Italian Alpine setting (5 decay class study). Nevertheless, it is still necessary to unravel the exact identity and underling the mechanisms of such associations as pointed out by Johnston et al. (2016).

Similarly to wood, a higher fungal abundance was also detected in the underlying soil at the northern slopes; likewise, higher *nifH* gene copy numbers along with higher soil moisture and OM levels were recorded compared to the corresponding south-facing sites. Previous studies (Thompson and Vitousek, 2006; Levy-Booth and Winder, 2010; Levy-Booth et al., 2014) suggested that higher contents of C and N in the forest floor could increase the abundance of the soil diazotrophic communities, leading to an enhanced N-fixation. Furthermore, the soil fungal communities are generally linked to the N-fixation by promoting N translocation across the forest floor through mycelial networks (Rinne et al., 2017). This could be a plausible explanation of why both the soil *nifH* gene and fungal abundances were more pronounced at the north-facing slopes, although this exposure-effect was altitude- and time-dependent.

Carbon is one of the main energy sources for microorganisms that largely influence their activity, while N is rather a limiting nutrient for microbial growth (Nannipieri et al., 2003, 2017). While deadwood, especially in the early decay stages, is N-limited with C/N ratios ranging from about 350 to 800, there is evidence about increasing N contents as wood decay progresses (Rajala et al., 2012; Gómez-Brandón et al., 2017). In our study, the total N content and the abundance of both ammonia-oxidising bacteria and archaea from *P. abies* wood blocks were below the detection limit during the 2-year observation period, which might be ascribed to the short duration of the experimental set-up. Indeed, Laiho and Prescott (1999) observed little changes in N concentrations in deadwood logs of *P. glauca* and *P. engelmannii* in a longer-term study (14 years) in the Canadian Rocky Mountains of Alberta.

Previous studies have reported soil pH and N mineral sources (NH_4^+, NO_3^-) as the major drivers of niche differentiation between AOA vs. AOB communities in forest soils (Szukics et al., 2012; Levy-Booth et al., 2014). Generally, higher abundances of archaeal *amoA* genes have been found in acidic environments exhibiting low substrate availability and low temperatures (Qin et al., 2013; Stempfhuber et al., 2014). This could explain why this microbial group was more abundant in the soils of north-facing slopes at the highest altitude (2000 m a.s.l.). In contrast, we found higher soil bacterial *amoA* abundance at the south-facing slopes (except for 1200 m a.s.l.) that are characterised by lower acidic conditions and a higher NO_3^- content.

The thermal signal (north- vs. south-facing sites) was dependent on the altitude and time of decay for most of the enzymatic activities involved in the C-cycle (i.e., β-glucosidase, cellulase and xylosidase). These enzymes are closely linked to fungi which have a relevant role in the degradation of biopolymers such as cellulose and hemicellulose (Makoi and Ndakidemi, 2008; López-Mondéjar et al., 2016). Moreover, an increase in the C-related enzyme activities in the *P. abies* wood blocks was accompanied by an increase in wood fungal abundance (qPCR) and microbial biomass (using dsDNA) at the end of the monitoring; suggesting a higher activity of the wood-inhabiting fungi at this stage of decay (Gonzalez-Polo et al., 2013; Pastorelli et al., 2017).

Moisture and OM levels have been shown as major determinants on the activity of soil enzymes (Makoi and Ndakidemi, 2008; Štursová and Baldrian, 2011). However, in our study the previously-mentioned enzymes related to the C-cycle showed a higher activity in soils collected at the south-facing slopes (altitude- and time-dependent), despite higher soil moisture and OM content along with a higher microbial biomass was in general recorded at north exposure. In addition, the north-facing sites were characterised by a higher leucine-aminopeptidase activity regardless of the sampling time. Koch et al. (2007) stated that potential amino-peptidase activities (leucine and tyrosine) had almost constant temperature dependence over 0–30 °C in Alpine areas. This suggests that polypeptide decay can be less sensitive to changes in temperature and even be favoured at lower temperatures as it had occurred in this study. In case of *P. abies* wood blocks, leucine-aminopeptidase activity was not affected by exposure, probably due to N limitation.

Acid and alkaline phosphomonoesterases have a relevant role in P cycling in forest ecosystems, mainly where P availability may limit plant productivity (Salazar et al., 2011). In the *P. abies* wood blocks, we found higher acid and alkaline phosphomonoesterase activities at the north-and at the south-facing slopes respectively, which is probably related to the differences in acidity between both slopes (Egli et al., 2006). Nonetheless, both enzymes showed a higher activity in soils from the south-facing slopes than in those from the comparable north-facing sites at 1400 and 1600 m a.s.l. A plausible explanation could rely on the lower P availability found at South exposure, indicating that an increase in P-acquiring enzyme activities would be expected in case of P deficiency (Fraser et al., 2015). Overall, our first hypothesis is partially corroborated because higher levels of soil microbial biomass were recorded at the north-facing slope. However, exposure affected the wood microbial biomass to a lesser extent than expected. Enzyme-specific exposure effects were found in both the *P. abies* wood blocks and the underlying soil along the climosequence.

5. Conclusion

Our 2-year mesocosm experiment provided evidence that climate effects, i.e., different thermal and moisture conditions due to different exposure, largely affect the decay of *P. abies* wood blocks and the underlying soil in terms of microbial biomass, activity and abundance. In

the *P. abies* wood blocks, the fungal and *nifH* gene abundances together with the microbial biomass showed higher levels at the end of the monitoring period. The cooler, moister and more acidic conditions at the north-facing slopes gave rise to an increase in the soil fungal abundance. The soil nitrogen-related bacterial functional genes (*nifH* and *amoA*), however, responded differently to exposure in terms of abundance: *nifH* (N > S, altitude and decay time-dependent); AOB (S > N, altitude and decay time-dependent); AOA (N > S, only at 2000 m a.s.l.). Furthermore, the impact of exposure was in general enzyme-specific, altitude- and decay time-dependent for both the wood and the underlying soil. Overall, our findings provide insights into the involved microbiota during the dynamic process of deadwood decomposition, thus contributing to unravel the complex picture of soil forest ecosystem in conjunction with climate.

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