https://doi.org/10.17221/44/2024-JFS

Impacts of management and changed hydrology on soil microbial communities in a floodplain forest

Jiří Volánek[1], Martin Valtera[1], Ladislav Holík[1], Martin Kománek[2], Hana Burdová[3], Josef Trögl[3], Diana Polanská Nebeská[3], Jitka Novotná[4], Pavel Samec[1,5], David Juřička[1]*

[1]*Department of Geology and Soil Science, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic*

[2]*Department of Silviculture, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic*

[3]*Faculty of Environment, Jan Evangelista Purkyně University in Ústí nad Labem, Ústí nad Labem, Czech Republic*

[4]*Czech Geological Survey, Brno, Czech Republic*

[5]*Global Change Research Institute of the Czech Academy of Sciences, Brno, Czech Republic*

**Corresponding author: volanek@gmail.com*

Citation: Volánek J., Valtera M., Holík L., Kománek M., Burdová H., Trögl J., Polanská Nebeská D., Novotná J., Samec P., Juřička D. (2024): Impacts of management and changed hydrology on soil microbial communities in a floodplain forest. J. For. Sci., 70: 574–592.

Abstract: Long-term human activities substantially altered floodplain regions of temperate Europe. Forest management and extensive changes in hydrology greatly affected natural floodplain soil properties, in which microbes play key roles. This study aims to assess the effects of human activities through a gradient of forest management intensity on soil microbial community (SMC), its biomass, activity, and structure. Soil chemical and physical-chemical properties were used to explain the general associations and within-site variation using principal component analysis (PCA), linear regression (LR) and linear mixed-effect regression (LMER) models. It was found that forest management application, regardless of its intensity, led to significant microbial biomass reduction. PCA revealed that microbial biomass, expressed as a sum of phospholipid fatty acids along with recalcitrant carbon fraction (ROC) best explained the variability in data. LR and LMER highlighted that bacteria are affected by floodplain forest management more than fungi, and that bacterial response to pH was highly diversified. Also, pH was identified as the best predictor of SMC structure and activity but not of its size. The study calls for further investigation in SMC interactions with ROC, soil-available Fe and Mn, and the role of redox-active metals in soil organic carbon degradation.

Keywords: enzyme activity; forest management; groundwater mineralisation; microbial community structure; soil microbial biomass

Floodplain forests are recognised as valuable forest ecosystems in lowland regions of central Europe (Brown et al. 1997; Kowalska et al. 2020; Machar et al. 2020). Their ecological importance has long been suppressed by human cultural and economic needs resulting in habitat loss, degradation, trans-

Supported by an internal grant of Mendel University in Brno, project IGA LDF_TP_2019014, and co-funded by the internal grant agency of Jan Evangelista Purkyně University in Ústí nad Labem, project UJEP-IGA-2024-44-007-2.

https://doi.org/10.17221/44/2024-JFS

formation, or fragmentation (Decamps et al. 1988; Wenger et al. 1990; Tockner, Stanford 2002). While naturally providing a wide spectrum of ecosystem services crowned by natural governance of water resources (Pechanec et al. 2017), they have high carbon sequestration capacity with potential for long-term (> 100 years) storage in soil (Sutfin et al. 2016). It was mainly their high production potential driving the change of land use or management implementation in the past (Brown et al. 1997; Tockner, Stanford 2002). Even protected remnants of floodplain forests are now very often affected by large-scale human alterations affecting stand hydrology, species composition and diversity, microclimatic conditions and horizontal and vertical vegetation structure but also cumulating a wide array of knock-on effects manifested in ecosystem processes and functions (Haase, Gläser 2009; Kowalska et al. 2020) such as decreased C storage potential. The extent of deviation from the original state is subject to land use character and intervention nature. Various approaches are used to assess site hemeroby or disturbance and management intensity (Schall, Ammer 2013). While production forests are most often assessed for the presence or absence of common silvicultural practices or treatments (Sarr et al. 2005; Kahl, Bauhus 2014; Suchomel et al. 2020) and such evaluation is widely applied in most national forest inventarisations, forest naturalness assessment, on the other hand, is globally less common (Rondeux, Sanchez 2009; McRoberts et al. 2012), understudied (Kunttu et al. 2015) and reported to lack objective methods (McRoberts et al. 2012). Challenges in comparing unmanaged and managed sites may stem from approach differences, however, mutual evaluation parameters exist (Winter 2012). For instance, the role of downed and standing deadwood (DW) in forest ecosystems is emphasised by a majority of the abovementioned authors. And so, DW volume, as well as variables including its type, size or decay class, are considered critical to ecosystem evaluation. DW represents a substantial pool of gradually released nutrients (Bani et al. 2018; Vítková et al. 2018), an energy substrate, which is distinguished from other inputs by specific chemical structure and persistence to degradation (Vrška et al. 2015). Its recalcitrant nature and long decomposition times guarantee multigenerational continuity for forest ecosystem components (Bauhus et al. 2018). While DW contributes to C input diversity and is considered an important factor of ecosystem stability, recalcitrant C fractions significantly contribute to long-term C sinks (Shi et al. 2023). Soil organic carbon (SOC) species are known to have different thermal stability (Manning et al. 2005), therefore, the content of lignin derivates (phenolic compound content) can be determined by thermally based separation as ROC, often referred to as residual oxidisable C or recalcitrant organic C.

Aboveground and belowground ecosystem components are strongly interconnected, jointly controlling ecosystem processes and properties (Bardgett, Wardle 2010; Fanin, Bertrand 2016). The relationship is often described as intimate, and aboveground occurrences or interventions show rapid and robust responses in the soil microbial community (SMC) (Zak et al. 1994; Moore-Kucera, Dick 2008; Van Der Heijden et al. 2008). SMC play an integral role in organic matter (OM) decomposition and drive most nutrient cycles, therefore long-term changes in their structure, activity, and functions can have retroactive effects on system interconnectedness, complexity, and productivity (Zechmeister-Boltenstern et al. 2015; Richter et al. 2018). Shared reciprocal environmental feedbacks are, however, highly context-dependent and hard to decode, and the results of their interactions can overlap and oscillate between beneficial and detrimental (Wardle et al. 2004). Phospholipid fatty acids (PLFAs), assayed by profiling of fatty acid methyl esters (FAMEs), are commonly used to provide both functional and structural information on microbial communities (Willers et al. 2015). For soils, the approach provides an efficient and robust way of determining microbial community structure and potential shifts in the major metabolic channels (Ramsey et al. 2006). The PLFAs are separated into indicator groups and their ratios. Propotions such as the fungal-to-bacterial ratio (*F*/*B*), the gram-positive/gram-negative bacterial ratio (*G*+/*G*–) and the unsaturation index comparing the abundance of cyclopropyl fatty acids to their precursor fatty acids (cy/pre) are used as environmental indicators of SOC quality, habitat factors or nutritional stress. The method provides a reliable tool for microbial biomass assessment as phospholipids do not accumulate in soil and their decomposition rate is rapid. Moreover, Zhang et al. (2019b) documented that high PLFAs turnover rates are not biomass size-dependent and do not suffer from decomposition lag.

Both plants and soil microorganisms produce extracellular enzymes, serving as biological catalysts, reducing the necessary activation energy for chemical reactions, and breaking down polymers that contain important nutrients or present restrictions to their

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growth (Burns 1982; McDaniel et al. 2013). Soil enzymes are produced in response to substrate availability and microbial demand and their quantity, activity and stability is regulated by various factors including temperature (Alvarez et al. 2018), moisture (Brockett et al. 2012) and OM content quantity and quality (Katsalirou et al. 2010; Song et al. 2012; Raiesi, Beheshti 2015). Enzymes do not accumulate in soil, they interact with microorganisms, soil minerals and soil environment variables once excluded from cells, which eventually leads to their inactivation and loss of their catalytic activity and may contribute to slower degradation of soil organic carbon. Enzymatic activity is also directly influenced by soil pH and most enzymes exhibit high activity at slightly acidic pH depending on soil type and enzyme specificity (Turner 2010; German et al. 2011). The value of pH affects the cation exchange rate with clay minerals, which in turn influences the availability of enzyme cofactors, especially Mn, Fe, and Mg. These cofactors tend to be depleted in acidic soils, which affects the availability of enzyme substrates, i.e. the mobilization and distribution of nutrients in the soil (Curtright, Tiemann 2021).

In this study, the selected area presents a unique floodplain environment with a well-documented history of human interaction. The aim is to assess the effects of floodplain forest management on soil microbial biomass, activity, and structure, which reflect the chemical and biochemical properties in soil. The study is relevant since SMC are considered a main biological soil fitness indicator and help to better understand the limits of managemental and environmental loading. Additionally, the changed hydrology of the studied area induces possible future scenario conditions of temperate zone alluvial forest salinisation and, therefore, offers valuable insight into the possible SMC response. The hypotheses are (*i*) that microbial biomass will equate resource quantity and will be differentiated by the management-related forest structure, (*ii*) that microbial activity will be differentiated by changes in soil pH and chemistry, (*iii*) that microbial community structure will be adversely affected by micromanagement, and (*iv*) that the changes will be most evident in the structure of bacterial communities.

MATERIAL AND METHODS

Study area. The study area is in the lowlands of southeastern Czechia at elevations of 166–175 m a.s.l. and belongs to one of the warmest regions (average annual mean of 9.8 °C) with relatively low yearly precipitation averages of 563 mm (CHMI 2024). It constituted a large forested riparian inland delta formed by the confluence of three rivers. The history of flooding and human interaction is well documented from the 8th century AD (Demek et al. 1970; Heteša et al. 2004) and the most significant human landscape-level alterations include constructions of regulated draining channels (18th century), artificial river dikes (19th century) and Nové mlýny reservoir cascades (1980's). The status quo comprises a mixed land use alluvial landscape inlaid with a mosaic of softwood and hardwood floodplain forest remnants with various degrees of human alteration in terms of forest management, river flow and ground water regime. The primary objects of protection hitherto are best-preserved stands dominated by ash and oak (*Fraxinus excelsior* L. and *Quercus robur* L.) and willow and alder (*Salix alba* L., *Salix fragilis* auct. and *Alnus glutinosa* L.), even though, in most cases, the hydrology of the stands was severely altered, and both the water inlet and the outlet are regulated. Such measures prevent natural flooding but also limit surface and ground water (GW) draining. The soil, composed of quaternary fluvial sediments (QFS), is underlain by marine Neogene sediments, forming an impenetrable hydrological barrier allowing for aquifer formation in the above-imposed QFS. Accumulated ground water, interacting with the older and deeper sediments, is hence highly mineralised and rich in dissolved solids [bicarbonate (HCO_3^-), sulphate (SO_4^{2-}), Cl^-, Na^+, Ca^{2+}, Mg^{2+}, Fe, and Mn]. The high GW table has a profound effect on soil chemistry and biochemistry and surface water salinisation (Valtera et al. 2021), compositionally resembling saline wetlands of the subtropical zone. According to the world reference base soil nomenclature, predominant soil types of the area are Fluvisols (Eutric and Gleyic), overlapped by Fluvic Gleysols.

Selected sites. Three hardwood floodplain forest stands dominated by common oak (*Quercus robur* L.) were selected to best represent the gradient of forest management intensity (Figure 1). Forest management plans, historical records and site micromanagement (all available in Nožička 1956 and Chalupa 2018) were considered as principal management intensity precursors.

The most important characteristics of the sites are given in Table 1. Bedřich forest (BF), a plantation subjected to a long history of intensive production-driven management, is constituted by an even-aged, 72-year-old common oak monoculture planted in rows. European ash (*Fraxinus excelsior* L.) consti-

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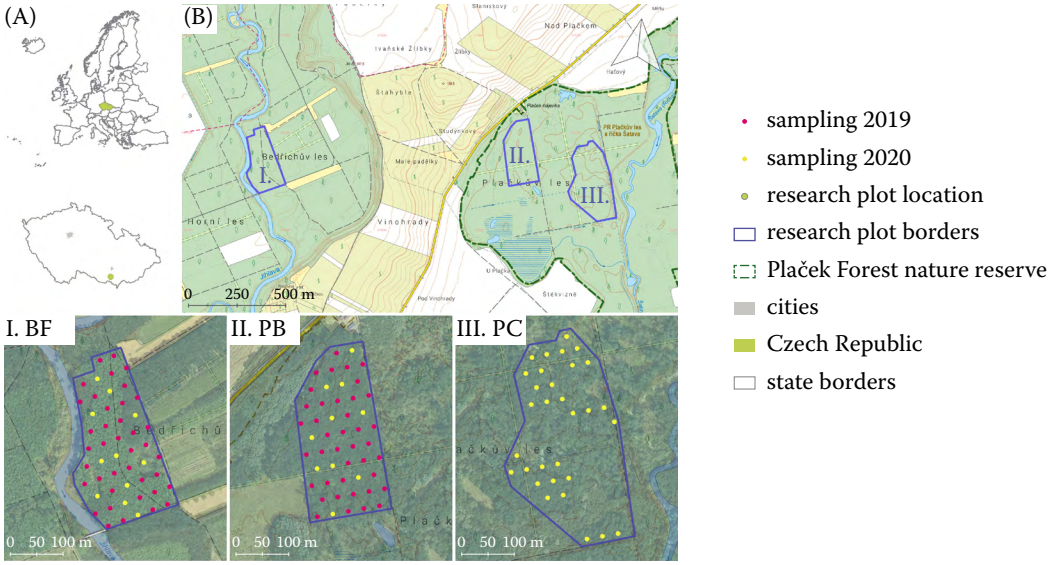

Figure 1. Study area

(A) – international and (B) – regional positions, respectively; I., II., III. – individual localities in detail; I. BF – Bedřich forest; II. PB – Plaček Forest buffer; III. PC – Plaček Forest core zone

tutes 22.5% as shown in Table 1. Thinning residues and wood debris are not retained on site in any form, stumps are removed or chipped. Natural shrub understorey is mostly absent, allowing for the development of a rich herbaceous layer dominated by *Urtica dioica* L. Adjacent to the Jihlava river, the average groundwater level at BF was evidenced in the depth of > 3 m. The soils at BF were classified as Eutric Fluvisols. Plaček Forest (Plačkův les) nature reserve incorporates two additional plots located in its buffer (PB) and core zone (PC). PB is a 140-year-old close-to-nature oak stand (cultural forest) with an admixture of European ash and naturally formed dense understorey dominated by *Sambucus nigra* L., *Swida sanguinea* L. and to a smaller degree *Viburnum opulus* L. Silvicultural interventions in PB are of medium intensity and consist mainly in managed harvest and commercial and pre-commercial thinning regime oriented at the recreation of natural species composition and structure. Stumps, DW or snags cannot be removed during the transition period, post-harvest residues are not to be piled up, and clearcuts are allowed, provided that a minimum amount of 10 seed trees per ha is left on site. PC is also semi-natural, partially managed, over 160 years old oak and ash stand, with diversified species composition and stand architecture due to spontaneous development. Management is focused on natural-state preservation, clearcut logging and DW removal is not permitted, and regeneration is natural (spontaneous). Both the shrub and the herbaceous layers are fully developed, the latter is formed by *Galium aparine* L., *Glechoma hederacea* L., *Impatiens parviflora* DC. and various *Carex* sp. While the ground water table at PB and PC fluctuates between 0.4 m and 0.7 m, PC incorporates more surface water features. The dominant soil types at the sites are Eutric and Gleyic Fluvisols, dependent upon the degree of water logging.

Soil sampling. A GPS-located hexagonal sampling grid, established in our earlier study, was utilised for resampling in May 2020. For detailed information on experimental design see Valtera et al. (2021). Ten plots of the original fifty 2019 plots were selected upon stratification of soil conductivity into deciles at BF and PB, where always one plot of each decile was randomly selected for resampling in 2020. Further 31 plots were added at PC, avoiding waterlogged areas (Figure 1). One composite topsoil sample, collected from 0–10 cm, was assembled at each plot from three subsamples. Subsampling points were spatially distributed in a triangular design, 8 m apart, around each central plot point. Samples were mixed on site, plastic-bagged and refrigerated at 4 °C for transportation, later homogenisation, and fridge storage also at 4 °C (ISO 18400-201:2017).

Deadwood assessment. DW quantity and quality was evaluated according to Janík et al. (2019). Snags (standing DW) and logs (fallen DW) were evaluated for diameter at breast height (*DBH*), snag height, log length and diameters, decay class and species. Decay classes

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Table 1. Site characteristics

Forest name	Bedřich forest (BF)	Plaček Forest (PB)	Plaček Forest (PC)
Site classification	plantation	nature reserve buffer zone	nature reserve core zone
GPS	48°56'31.6"N, 16°34'16.3"E	48°56'39.8"N, 16°35'20.0"E	48°56'33.4"N, 16°35'41.3"E
Forest type	production forest	cultural forest	natural forest
Management intensity	high	medium	low
Stand structure complexity	low	medium	high
Forest site typology	Ulmeto-Quercetum alluvialis	Ulmeto-Quercetum alluvialis	Ulmeto-Quercetum alluvialis
Water table depth (m)	> 3	0.4–0.8	0.4–0.6
Species mix – oak/ash/other (%)	77.1/22.5/0.4	85.4/13.5/1.1	71.1/26.4/2.5
Area (ha)	3.3	4.7	4.8
Age (years)	66	142	153
Trees (pcs·ha^{-1})	310	225	214
Basal area (m^2·ha^{-1})	32.1	41.8	37.3
Tree above ground biomass (m^3·ha^{-1})	381.7	620.0	548.4
Mean tree height (m)	32.1	27.0	26.6
Mean tree diameter (cm)	35.2	40.7	38.8
Stocking (%)	90	110	100
Deadwood count (pcs·ha^{-1})	10	83	136
Deadwood volume (m^3·ha^{-1})	2.2	26.4	99.2
Snag count (pcs·ha^{-1})	0	5	10
Snag volume (m^3·ha^{-1})	0	8.7	29.9
Total aboveground biomass (m^3·ha^{-1})	383.9	655.1	677.5

were assigned values 1–5, where 1 is recently fallen wood with intact bark and branches, 2 is still mostly sound wood but may have some bark loss and minor decay, 3 is moderately decayed wood (softer, structure is starting to break down), 4 is heavily decayed wood (soft and easily broken apart) and 5 is fully decomposed and integrated into soil (only remnants visible). Smalian's formula (Goulding 1979) was used to quantify the volume (V), as expressed by Equation (1):

$$V = \frac{B + S}{2} \times L \quad (1)$$

where:

V – volume (m^3);

B – cross-sectional area at the large end of the log (m^2);

S – cross-sectional area at the small end of the log (m^2);

L – long length (m).

Laboratory analyses. Selected chemical and biochemical soil properties, considered as independent variables, were assessed according to methods presented in Table 2. The C/N was calculated as the ratio of organic carbon (OC) and total nitrogen (TN). The microbial quotient (*MiQ*) was calculated as the proportion of substrate-induced respiration to soil organic C (*SIR*/OC) and the metabolic quotient (*MeQ*) was calculated as the proportion of basal respiration to microbial C biomass (BR/C_{mic}).

PLFAs and the extracellular enzyme activities, considered dependent variables, were analysed according to ISO/TS 29843-2 and Bárta et al. (2014), respectively. In short, total lipids were extracted from the soil by a mixture of methanol, chloroform, and phosphate buffer (0.05 mol·L^{-1}, pH 7, ratio 2 : 1 : 0.8) and separated on polar silica SPE (solid phase extraction) columns to fractions. Polar lipids were methanolised by a mixture of methanol and KOH. FAMEs were determined by gas chromatography-mass spectrometry (GC-MS). Total microbial PLFA (total PLFA) was determined as the sum of all FAMEs between 10 : 0 and 20 : 0 methyl ester retention times. Biomass of microbial groups was discriminated using indicator fatty acids, i.e. fungal biomass (*F*) by con-

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Table 2. Chemical and biochemical soil properties (independent variables), their units, abbreviations and methods used for determination

Soil property		Abbreviation	Principle	Reference
Soil water content (%)		*w*	gravimetry, constant weight drying	ISO 17892-1:2014
Carbon fractions ($g \cdot kg^{-1}$)	total C	TC	temperature C fractionation by dry combustion, infra-red detector, where OC is measured at 400 °C, ROC at 600 °C, IC at 900 °C, and TC is the summation of OC, ROC, and IC	DIN 19539:2016-12; SoliTOC (Elementar, Germany)
	total organic C	OC		
	total inorganic C	IC		
	total residual oxidisable C	ROC		
Total nitrogen, total sulphur ($g \cdot kg^{-1}$)		TN TS	dry combustion, thermal conductivity detector	Vario MACRO cube (Elementar, Germany)
Plant-available phosphorus ($mg \cdot kg^{-1}$)		P	Mehlich 3, inductively coupled plasma-based spectrometry	Mehlich 1984; Cade-Menun et al. 2018
Total H_2O extractable Na^+ ($mg \cdot kg^{-1}$)		Na	flame emission spectrometry	ISO 9964
Total H_2O extractable Cl^- ($mg \cdot kg^{-1}$)		Cl	coulometry – adsorbable organically bound halogens	ISO 9562
Total H_2O-extractable SO_4^{2-} ($mg \cdot kg^{-1}$)		SO_4	isotachophoresis	Zbíral et al. 2011
Plant-available Mn ($mg \cdot kg^{-1}$)		Mn	Mehlich 3, atomic absorption spectrometry	Mehlich 1984; ISO 5961
Plant-available Fe ($mg \cdot kg^{-1}$)		Fe	Mehlich 3, atomic absorption spectrometry	Mehlich 1984; ISO 12020
Soil reaction (H_2O)		pH	potentiometry	ISO 10390
Electrical conductivity ($\mu S \cdot cm^{-1}$)		*EC*	conductivity	ISO 11265
Microbial-carbon biomass ($g \cdot kg^{-1}$)		C_{mic}	chloroform-fumigation K_2SO_4 extraction, spectrophotometry	ISO 14240-2; Zbíral et al. 2011
Substrate-induced respiration ($\mu g\ CO_2 \cdot g^{-1} \cdot h^{-1}$)		*SIR*	titration	ISO 16072
Basal respiration ($\mu g\ CO_2 \cdot g^{-1} \cdot h^{-1}$)		*BR*	titration	ISO 16072

centrations of 18:2ω6,9; bacterial biomass (*B*) by sum of i14:0, i15:0, a15:0, 16:1ω7t, 16:1ω9, 16:1ω7, 18:1ω7, 10Me-16:0, i17:0, a17:0, cy17:0, 17:0, 10Me-17:0, 10Me-18:0, cy19:0; biomass of gram-positive bacteria (*G*+) by sum of i14:0, i15:0, a15:0, i17:0, a17:0; biomass of gram-negative bacteria (*G*–) by sum of cy17:0, cy19:0, 18:1ω7; and biomass of actinobacteria (*ACT*) by sum of 10Me-16:0, 10Me-17:0, and 10Me-18:0. Residual bacterial biomass is referred to as unspecific identification group (*UnsB*). Nutrition indicator (*NuStr*) was calculated as the ratio of cyclopropylated fatty acids (cy17:0 + cy19:0) to their metabolic precursors (16:1ω7 + 18:1ω7), see Equation (2):

$$NuStr = \frac{\text{cy17:0} + \text{cy19:0}}{\text{16:1}\omega7 + \text{18:1}\omega7} \quad (2)$$

Measured values were recalculated to dry weight of soil. Fluorometric tests utilising black 96-well plates according to Bárta et al. (2014) were used for extracellular enzyme activity evaluation. All hydrolytic enzyme activities were determined in 200 µL of soil suspension, to which 50 µL of methylumbelliferyl was added for β-glucosidase (BGL), arylsulphatase (sulphatase, SUL), phosphomonoestherase (phosphatase, PHO), and N-acetyl-glucosaminidase (chitinase, NAG) determination and 50 µL of 7-aminomethyl-4-coumarin was used for the determination of leucine-aminopeptidase (LAP), alanine-aminopeptidase (AAP), and tyrosine-aminopeptidase (TAP). Fluorescence was quantified at 360 nm excitation wavelength and 465 nm emission wavelength. Oxidative enzyme activities of peroxidase (PER) and phenoloxidase (PHE)

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were measured using L-DOPA (l-3,4-dihydroxyphenylalanine). 20 µL of 0.3% H_2O_2 (*v*/*v*) was added to the L-DOPA solution to determine the activity. Absorbance was measured at 450 nm (Bárta et al. 2014). Catalase activity was measured volumetrically as O_2 production from H_2O_2 dissociation according to Gömöryová et al. (2011).

Data analyses. Data were analysed using R Studio (Version 4.2.1, 2020). Principal component analysis (PCA) and Pearson's linear pairwise correlations (PLPC) were used to explore the data, examine variability among data and accent main dependences regarding soil microbial community biomass, activity, and structure. The data were Box-Cox transformed and scaled to unit variance and zero mean prior to analysis. The soil chemical and physical-chemical properties (independent variables) were used to explain the within-site variation in soil enzymatic activity and microbial community composition using simple linear regression (LR) and linear mixed-effect regression (LMER) models. For each model, a single explanatory variable was used as the fixed effect in LR or LMER model. The study site was used as the factor variable in LM and as the random effect in LMER. The significances of random and fixed effects were tested separately using the likelihood test; if the random or fixed effects were not significant, a simple LR model was fitted instead, and the *t*-test was used to assess the significance of the model. If both the fixed and random effects were significant, a LMER model was applied. The unadjusted R^2 or the marginal R^2 (R^2_m) were calculated for each LR or LMER model, respectively. Consequently, the *F*-value criterion was used to select among the competing models of each dependent variable. All statistics were considered significant at $P < 0.05$.

RESULTS

Deadwood. Assessed for entire plots and recalculated to ha, DW of all identified volume and decay classes confirmed the assumption of increasing DW biomass removal along the management intensity gradient. The lowest DW count and volume were identified at BF and the highest at the partially managed PC ($10 < 83 < 136$ pcs·ha^{-1} and $2.2 < 26.4 < 99.2$ m^3·ha^{-1}, see Table 1). The count and volume of snags followed the same trend being the lowest at BF and the highest at PC ($0 < 5 < 10$ pcs·ha^{-1} and $0 < 8.7 < 29.9$ m^3·ha^{-1}). The initial stage of DW decomposition, decay class 1 (DC1), was the most represented at all sites in terms of volume and count. DW volume progressively decreased as the decomposition class increased. Decay classes 4 and 5 were absent at all sites. Comparable counts of DW in DC1 at PB and PC, however, constituted very different volumes, highlighting the difference in DW dimensions and its origin (mostly fallen and delimbed post-harvest debris at PB *vs* whole trees at PC). Detailed DW results are presented in Figure S1A, B in the Electronic Supplementary Material (ESM).

General associations across sites. PCA showed good differentiation along the hypothesised management intensity gradient (Figure 2). BF and PC were clearly separated by the factor loadings of PC1, whereas PC3 contributed to the separation of PB from the other two and provided a clear distinction among the studied plots (Figure 3). 71.64% of the dataset variance was explained by the first three PC's (32.12%, 26.12%, and 13.4%, respectively). Variables with the highest positive factor loading coefficients associated with PC1 included total PLFA biomass (0.51), ROC (0.33), Na (0.33), SO_4 (0.30), and PHO (0.27). PC1 was negatively loaded by Mn (–0.23) and P (–0.17). Factor loadings positively associated with PC2 were aminopeptidase activities (LAP, TAP, and AAP) 0.54, 0.5, and 0.45, respectively, and ROC (0.19), while negatively associated were SUL and PHO (–0.17 and –0.12). PC3 was almost exclusively defined by a strong positive loading of available P (0.75).

PLPC matrix, combining Pearson's correlation coefficient *r* and the *P*-value, can be found in Figure S2 in the ESM. Briefly, soil microbial biomass indices (C_{mic}, *SIR*, and total PLFA) were positively correlated with OC. Moderate correlations of total PLFA were obtained with both *SIR* and C_{mic} denoting mutual complementarity amongst soil microbial biomass attributes. Good differentiation of the pH values along the management gradient (5.61 ± 0.59 at PC, 5.81 ± 0.7 at PB, and 6.25 ± 0.28 at BF) was reflected in relative microbial abundance and enzymatic activity. The dominant role of soil reaction was forecasted by significant positive associations with *ACT*, *G+*/*G–*, *UnsB* and all aminopeptidases and by significant negative associations with *G–*, *NuStr*, PHO, and SUL. Besides pH, strong positive associations were detected between PHE and Fe, PHE and ROC, *G+*/*G–* and all aminopeptidases, *ACT* and *UnsB*; however, no significant relationship was found for *G+*. Also, *F* was positively harmonised with SO_4 and *G–* with SUL and PHO. Negative associations were found between *ACT* and SUL, PHO and *G–*. *UnsB*, lacking specific fatty acid indicators, showed simi-

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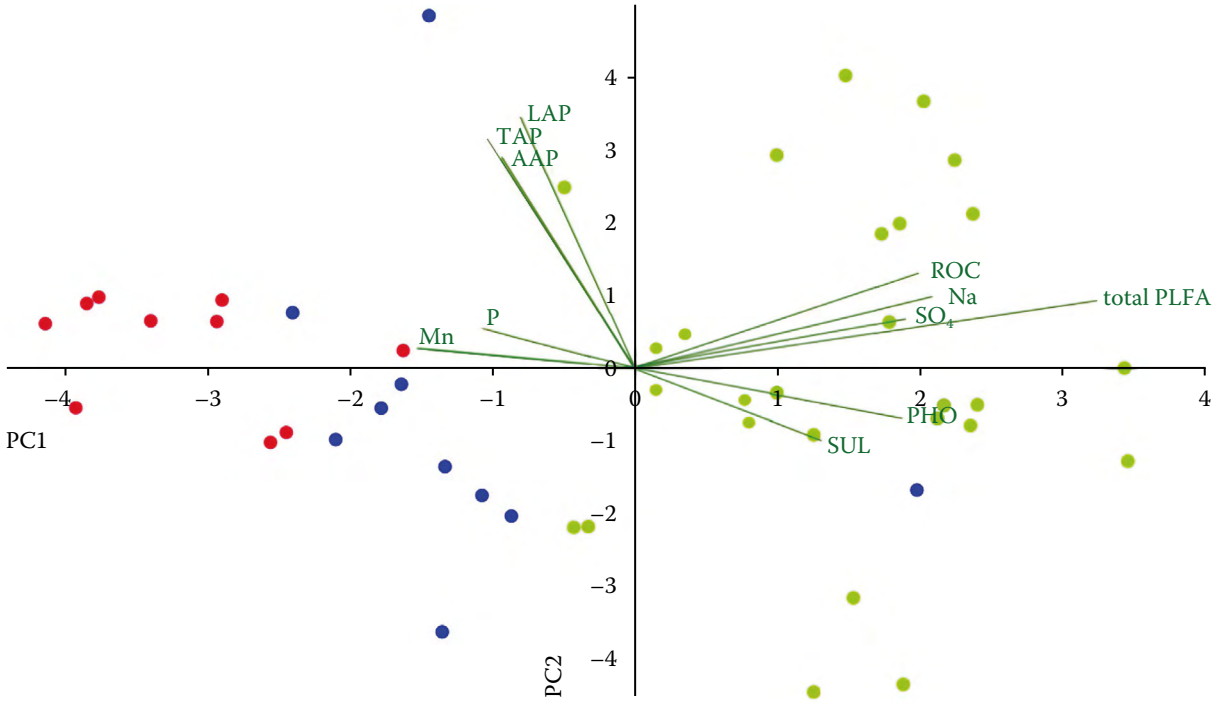

Figure 2. Master data principal component analysis (PCA)

Dots – sampling points: red – BF (Bedřich forest), blue – PB (Plaček Forest buffer), light green – PC (Plaček Forest core zone); vectors – factor loadings; axes (PC) – principal component; AAP – alanine-aminopeptidase; LAP – leucine-aminopeptidase; PHO – phosphomonoestherase; total PLFA – total biomass of microbial phospholipid fatty acids; ROC – residual oxidisable carbon; SUL – arylsulphatase; TAP – tyrosine-aminopeptidase

lar profile traits as *ACT*. PLPC revealed that Mn was negatively associated with a majority of chemical and biochemical soil properties (all except pH and P) and can significantly control OM degradative and transformative processes.

Site variability. A significant differentiation of total PLFA absolute abundance and all its individual constituents was detected between managed and unmanaged sites. The consistent pattern in absolute PLFAs indicator group quantities was defined by significantly higher values in PC compared to BF and PB (Figure 4). At the same time, no significant differences among PLFAs indicator groups were found between the BF and PB – the plantation and the buffer. The fun-

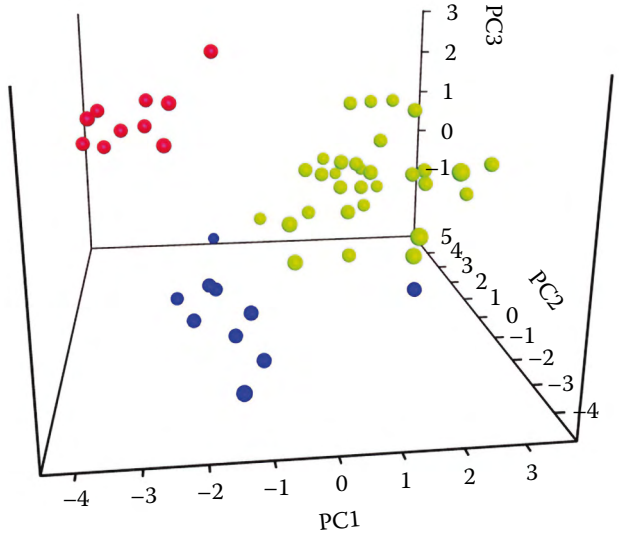

Figure 3. 3D principal component analysis (PCA)

Dots – sampling points: red – BF (Bedřich forest), blue – PB (Plaček Forest buffer), light green – PC (Plaček Forest core zone); axes (PC) – principal component

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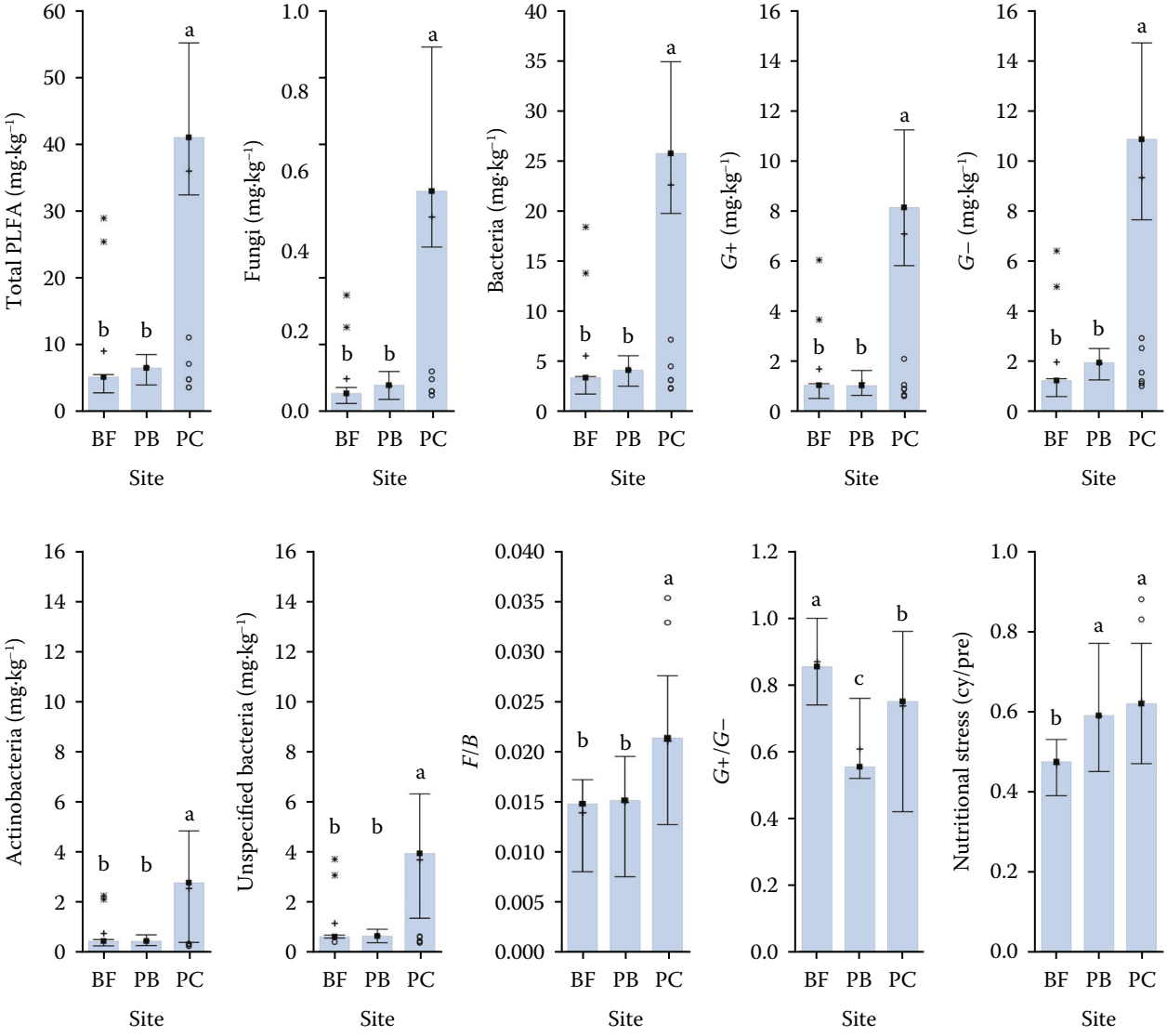

Figure 4. Absolute abundance of total PLFA, its identifier groups and their relevant ratios

Blue bars, black squares – average values; whiskers – 95% confidence intervals; lines – means; points – outliers; stars – extremes; a–c – significant differences between sites at $P = 0.05$ (Tukey's test); total PLFA – total biomass of microbial phospholipid fatty acids; BF – Bedřich forest; PB – Plaček Forest buffer; PC – Plaček Forest core zone; *G*+ – biomass of gram-positive bacteria; *G*– – biomass of gram-negative bacteria; *F*/*B* – fungal-to-bacterial ratio; cy/pre – ratio of cyclopropyl fatty acids to their precursor fatty acids

gal-to-bacterial ratio also shares this uniform trend denoting proportionally higher fungal biomass at PC. On the other hand, the *G*+/*G*– detected significant differences among all sites and, regardless of the management intensity gradient, increased from the buffer across the core zone to the plantation. Nevertheless, the absolute abundance of *G*– was larger than that of *G*+ at all sites.

Significant differences among forest stands were found in BGL, PHE, PER, PHO, SUL, and NAG activities (Figure 5). None of the enzyme activities strictly follow the observed effect of management intensity; however, PHO, SUL, and NAG were significantly higher in the nature reserve core zone, following the trend set by total PLFA and its identifier groups. On the other hand, the activities of OM and C compound degrading enzymes (BGL, PHE, PER, and NAG) adhered to the trend set by *G*+/*G*– being significantly higher in the plantation and core zone over the buffer.

The site effect. The variability in total PLFA data was best explained by the difference between individ-

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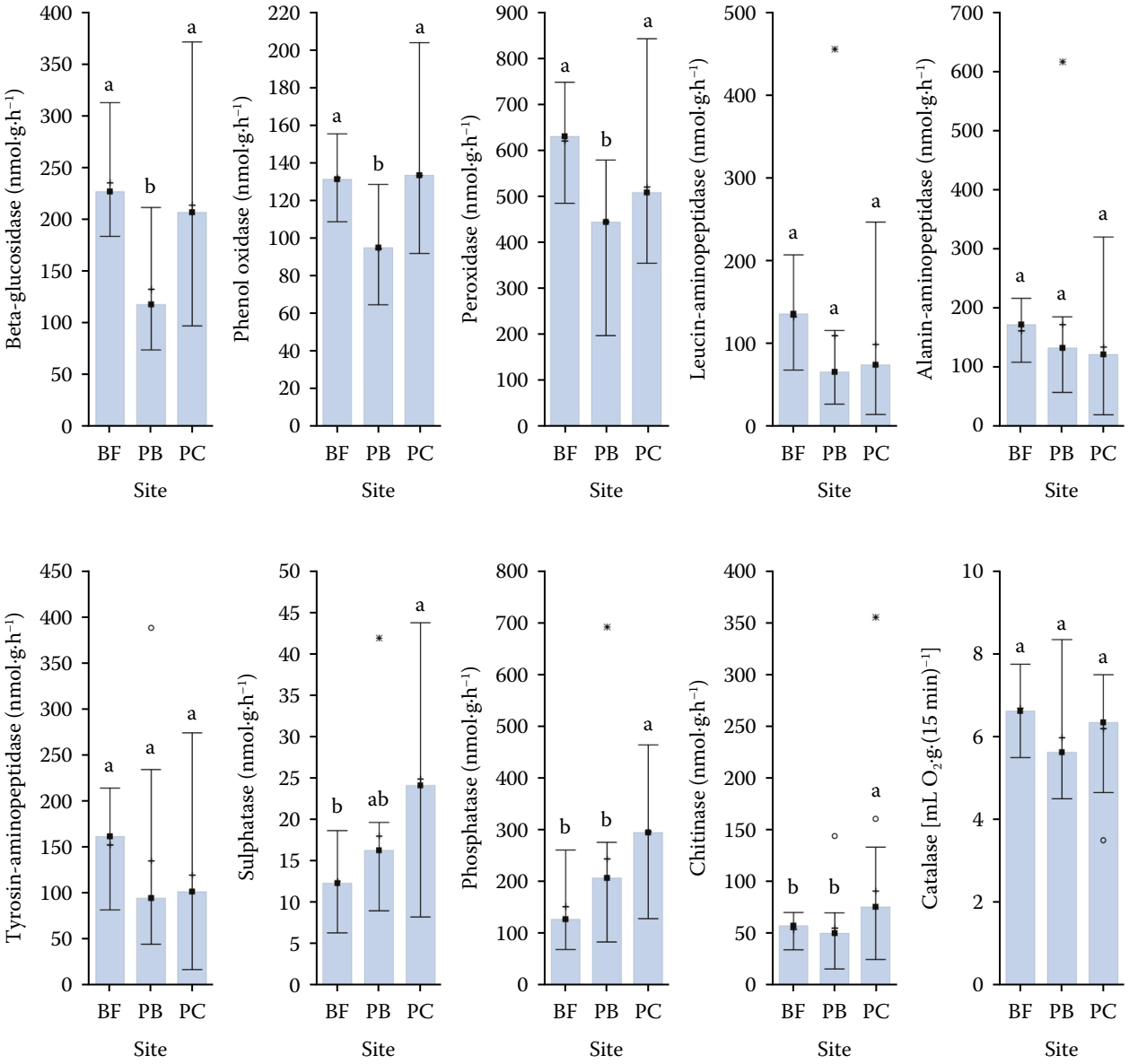

Figure 5. Soil enzyme activities

Blue bars, black squares – average values; whiskers – 95% confidence intervals; lines – means; points – outliers; stars – extremes; a, b – significant differences between sites at $P = 0.05$ (Tukey's test); BF – Bedřich forest; PB – Plaček Forest buffer; PC – Plaček Forest core zone

ual sites (Figure 6). On the other hand, most individual PLFAs group relative abundances and their associated ratios were best predicted by pH except for *F* and *G+*. In detail, positive associations of pH and the response variables (as shown in PLPC, Figure S2 in the ESM) were differentiated by site effect in *G+*/*G–* and *UnsB*, where mixed-effect models significantly strengthened the quality of corresponding LR models. The strong negative association of pH with fungi and *G–* was also accentuated by a significant site effect. The best-fit models for *ACT* and *NuStr* were determined by pH in LRs. Most notably, significant site effects were also confirmed for otherwise negative associations of *G+* with Fe (best model), and SO_4 and ROC. The best model for Fungi was LR with SO_4.

The dominant effect of pH was also confirmed for enzymatic activity (Figure 7) and can be divided into three groups: positive, negative and no effect. Aminopeptidase activities did not differ between sites, and LR's were the best-fit models. On the other hand, the activities of PER, PHO, and SUL varied among the sites, and LMERs confirmed the negative

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PLFA	site	IC	OC	ROC	C/N	TN	TS	P	Fe	Mn	SO_4	pH
ACT	0.26	0.18*	n.s.	n.s.	n.s.	0.12	0.10*	0.11	n.s.	0.12	n.s.	**0.60**
F	0.38	n.s.	0.22	n.s.	n.s.	n.s.	0.10	n.s.	0.20	n.s.	**0.40**	0.11*
G+	0.25	n.s.	n.s.	0.10*	n.s.	n.s.	n.s.	0.15	**0.16***	n.s.	0.13*	0.09*
G–	0.42	0.10*	n.s.	n.s.	n.s.	0.22	n.s.	0.34	n.s.	0.16	n.s.	**0.42***
G+/G–	0.36	0.13	n.s.	n.s.	n.s.	0.08	n.s.	0.31	n.s.	0.13	n.s.	**0.30***
UnsB	0.43	0.18*	0.08*	n.s.	0.07*	0.20	0.12*	0.30	n.s.	0.15	0.07*	**0.35***
NuStr	0.36	0.09	0.20	n.s.	n.s.	0.24	n.s.	0.16	n.s.	0.40	0.11	**0.72**
total PLFA	**0.51**	n.s.	0.38	0.14	0.24	0.09	0.23	n.s.	0.06*	0.14	0.21	n.s.

Figure 6. The proportion of variance (R^2) explained by site (factor variable) and soil properties (continuous variables) in linear and linear mixed-effect regression models of the phospholipid fatty acids (PLFAs) data

*Marginal R^2 of a mixed-effect regression model; bold – the best prediction model; colours – the strength and direction of a relationship (blue for positive); IC – inorganic carbon; OC – organic carbon; ROC – residual oxidisable carbon; TN – total nitrogen; TS – total sulphur; *ACT* – biomass of actinobacteria; *F* – fungal biomass; *G+* – biomass of gram-positive bacteria; *G–* – biomass of gram-negative bacteria; *UnsB* – residual bacterial biomass of unspecific identification groups; *NuStr* – utrition indicator; total PLFA – total biomass of microbial phospholipid fatty acids; n.s. – insignificant models ($P \geq 0.05$)

enzyme activity	site	IC	OC	ROC	C/N	TN	TS	P	Fe	Mn	SO_4	pH
AAP	n.s.	0.22	n.s.	n.s.	0.11	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**0.77**
LAP	n.s.	0.35	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.09	n.s.	**0.84**
TAP	n.s.	0.24	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.08	n.s.	**0.87**
BGL	0.31	0.12	n.s.	n.s.	0.08	n.s.	n.s.	**0.19**	n.s.	n.s.	n.s.	n.s.
NAG	0.22	n.s.	0.13	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**0.19**	n.s.
PER	0.21	n.s.	n.s.	n.s.	n.s.	0.15	0.08	0.16	0.22*	0.12*	n.s.	**0.16***
PHE	0.32	0.08*	n.s.	0.34*	0.11*	n.s.	0.09*	0.16	**0.61***	0.17*	0.24*	n.s.
PHO	0.34	n.s.	0.33	0.13	0.04*	0.19	0.15	n.s.	0.14	0.25	0.28	**0.29***
SUL	0.35	n.s.	0.22	n.s.	n.s.	0.26	n.s.	n.s.	n.s.	0.17	0.13	**0.56***
CAT	n.s.	**0.31**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.27	n.s.	0.19

Figure 7. The proportion of variance (R^2) explained by site (factor variable) and soil properties (continuous variables) in linear and linear mixed-effect regression models of the enzyme-activity data

*Marginal R^2 of a mixed-effect regression model; bold – the best prediction model; colours – the strength and direction of a relationship (blue for positive); IC – inorganic carbon; OC – organic carbon; ROC – residual oxidisable carbon; TN – total nitrogen; TS – total sulphur; AAP – alanine-aminopeptidase; LAP – leucine-aminopeptidase; TAP – tyrosine-aminopeptidase; BGL – β-glucosidase; NAG – N-acetyl-glucosaminidase (chitinase); PER – peroxidase; PHE – phenoloxidase; PHO – phosphomonoestherase; SUL – arylsulphatase; CAT – catalase; n.s. – insignificant models ($P \geq 0.05$)

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and significant site effect of pH for these enzymes. Mn and Fe also explain a high proportion of the variance among sites in PER.

The variability in PHE activity data was best explained by the Fe LMER model (best model), but also well-fitted ROC and SO_4 data. The activities of PER, PHE, PHO, and SUL were negatively affected by Mn.

DISCUSSION

Microbial biomass. Microbial communities are primarily limited by C resources (Wardle 1992), therefore, under equable conditions, their biomass constitutes an aliquot of SOC. We were consistent with the works of many (e.g. Hackl et al. 2005; Wu et al. 2009; Hu et al. 2014; Smith, Paul 2017) in confirming that microbial biomass expressed as total PLFA was correlated with total content of SOC and TC (total carbon) and, that total SOC stock was an important indicator of microbial biomass. Our findings showed that total PLFA well reflected the differences among sites and, at the same time, best explained the variability in data. Data variability among sites may be due to forest management intensification, and the main argument in that sense could subsist the water regime alterations caused by management application. Rinklebe and Langer (2008) showed that surface flooding, responsible for redox conditions in soil, is usually associated with strong soil microbial community response, observable in the decline of *SIR*, PLFA biomass, and microbial quotient. They also stated that floodplain forest soils were distinctive in elevated SOC levels exactly due to epiaquic moisture regimes defined by inundation length. The absence of seasonal surface flooding, responsible for the alternation of oxy-redox conditions in topsoil, can lead to the acceleration of oxidative processes. We assume that at PB and PC, surface flooding could have been partially substituted by high groundwater level fluctuation and the introduction of surface water features (ponds, channels, and bogs). Rinklebe and Langer (2006, 2008) used the microbial quotient to satisfactorily determine the restrictive character of floodplain soils. Applying the same approach, we did not detect any significant differences in *SIR*/SOC among sites (data not shown). As Guo and Gifford (2002) indicated, a prolonged absence of flooding can lead to the loss of SOC as well as variability and heterogeneity of organic C pools (Samaritani et al 2011). Nevertheless, the same outcomes can be attributed to specific silvicultural practices and, as pointed out by Valtera et al. (2021), the effect of forest management and changed hydrology may be hard to disassociate. Not all silvicultural interventions may have a strictly negative effect on SOC stocks. Mayer et al. (2020), in their review, accentuate biomass removal as the key and proportional aspect to reducing SOC stocks, which can be consequently manifested in microbial biomass decrease (Chang et al. 2017). Likewise, retaining wood and DW in forest stands can have a positive effect on SOC (Błońska et al. 2019) and hence microbial biomass (Nazari et al. 2023).

The mixed-effect model detected a contrasting response of total PLFA and *G+* to Fe availability, which suggests localised Fe deficiency or variable utilisation among sites. Alternatively, the sites could be differentiated due to waterlogged redox conditions, under which electron acceptors, such as iron oxides, play a crucial role in regulating SOC mineralisation (Li et al. 2021). However, the related underlying mechanisms are still poorly explored, and the available Fe and microbial biomass relationship calls for further investigation.

In this study, total PLFAs content and all its determinative groups were several-fold higher at the unmanaged nature reserve core zone, which supports our hypothesis that forest management negatively affects microbial biomass and all its components. However, no clear gradual downward trend along the management intensity scale was evidenced and no significant difference was detected between BF and PB (unlike in C_{mic} and *SIR*). Based on our results, we theorise that distinct separation of the unmanaged site is caused by the accumulation of knock-on effects connected to numerous impacts. We support our claim with the findings of Liu et al. (2019) who found that OC, *w*, ROC, and *RBA* (ratio of breast-height basal area of coniferous trees to that of broad-leaved tree species) were the main driving factors of soil microbial biomass changes. Similarly to their findings, we would like to think that the application of specific managemental practices such as biomass removal, DW micromanagement, water draining and stand architecture alteration led to drastic microbial biomass decreases in PB and BF. Most importantly, we conclude that adverse effects must not be thought of as a summation of individual factors, but rather their multiplicands.

Microbial activity. The pH value drives soil microbial activity (Hackl et al. 2005; Sinsabaugh et al. 2008; Cao et al. 2016) and is closely connected with the capacity of soils to store and supply nutrients. However, pH cannot be considered an independent regu-

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lator of microbial life, and its contribution is mostly indirect (Waldrop et al. 2017). Changes in pH have environmental and anthropogenic drivers (Lladó et al. 2018). Local variability of forest soil pH is often explained by physicochemical gradients created on the level of individual trees (Lavoie et al. 2012), quality and quantity of litter inputs (including DW) regulated through species composition and primary production (Scheibe et al. 2015), rhizodeposition and root biomass (Jones et al. 2004) or changes in water balance (Slessarev et al. 2016). Nevertheless, all the above-mentioned can be influenced by forest management. Malik et al. (2018) offer in-depth explanations on how pH increase caused by land use intensification affects soil microbial metabolic processes and consider a pH threshold of ~6.2 for acid reaction soils as critical to carbon loss through increased decomposition. In this study, pH (H_2O) was well associated with the management intensity gradient, which could explain the decreasing OC content towards BF. Malik et al. (2018) also found that the loss of soil OC due to increased management intensity in near-neutral pH led to decreased microbial biomass and reduced growth efficiency, which was, in turn, related to tradeoffs with stress alleviation and resource acquisition (not confirmed by our study). Additionally, Curtin et al. (1998) found that even though soil OM mineralisation rates are often considered unresponsive to soil reaction, a pH increase from ~5.7 to ~7.3 more than doubles N and C mineralisation.

Each enzyme has a distinct pH and temperature optimum towards which its activity increases (Błońska et al. 2019). Microorganisms have relatively low control over extracellular enzyme kinetics, and so, to deal with local soil environment variability, produce isoenzymes with diverse kinetic and thermodynamic parameters (Khalili et al. 2011). In this study, all essayed aminopeptidases provided tight positive correlations with pH across all sites suggesting uniform dynamics, most probably related to higher bacterial N demands. Puissant et al. (2019) determined the LAP optimum at pH 7.2, which explains activity increase along the management intensity gradient linked with a pH increase. Similarly to Uwituze et al. (2022), negative correlations between pH and SUL and PHO (pH optima between pH 4 and 5.7) were found together with significant site effects suggesting varied enzymatic dynamics along the pH and management gradient. Moreover, Moghimian et al. (2017) found a negative effect of timber extraction on the activity of SUL and PHO. In this study, no direct relationship or site effect was detected for BGL, which agrees with Zhou et al. (2020), who found no effect of forest management practices on extracellular C-degrading enzymes (C-hydrolases). However, overlaying enzyme activities and microbial community ordination matrices showed that BGL was likely *G*+-associated (Figure S3 in the ESM). A significant site effect was observed in lignolytic enzyme activities of PER and PHE known to be substrate non-specific agents playing a key role in the breakdown of polyphenolic compounds. Purahong et al. (2014) confirmed that lignin decomposition is one of the limiting steps in plant litter degradation and oxidases are the key mediator; however, they did not find any statistically significant differences in PHE activity among stands with various forest management practices. Contrarily, Zhou et al. (2020) found in their meta-analysis that the activity of PER will be increased by biomass extraction, while the activity of PHE will stay unaffected. Most notably, Carreiro et al. (2000) reported enhanced oxidative enzyme activity under soil management practices associated with soil organic C loss. None of the abovementioned seems of direct relevance to this study. This study demonstrated that PER activity is linked to N and S mineralisation and P availability (not OC), while being differentiated by Fe, Mn, and pH across sites. Thus, it can be associated with higher turnover rates and increased bacterial demand for soil OM. Contrary to the findings of Sinsabaugh et al. (2008), a negative relationship with pH was found in this work. The PHE relationship with pH was found insignificant but was positively correlated with and differentiated by ROC and Fe, confirming recalcitrant C compound and available Fe affiliation. In this study, the PHE activity was higher at BF and PC, suggesting comparable demand for recalcitrant C sources and rate of complex SOC mineralisation, yet the sites were differentiated by the PHE Fe utilisation. This could be related to changes in redox conditions reflected in Fe and Mn oxidation states affecting their availability and enzyme formation. Several studies (Van Bodebom et al. 2005; Liu et al. 2019) reported that the presence of ferrous iron (Fe^{2+}) in a hypoxic environment enhances PHE activity and effectivity. Moreover, Jia et al. (2023) showed how soil wetting and drying (Fe latch and Fe gate activation) can progressively drive the rejuvenation of Fe oxides and simultaneously affect the activity of PHE. Redox-active metals, including Mn and Fe, catalyse abiotic nonspecific oxidation of SOC through Fenton-like, hydrogen peroxide-catalysed oxidative radical production

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(Naughton et al. 2023). Unfortunately, their contribution to biotic and, specifically, abiotic SOC degradation is not yet fully apprehended and, as shown in this study, calls for further investigation.

Microbial community structure. Forest management, independent of its extent, significantly decreased the absolute abundance of microbial biomass and all individual PLFAs identifier groups. The pattern was mirrored in the *F*/*B* ratio, which was significantly higher at the unmanaged plot. Many authors (Fang et al. 2017; Parladé et al. 2017; Jörgensen et al. 2022) documented that fungal biomass decreases with the introduction or intensification of forest management, but Bapiri et al. (2010) showed that bacterial communities can be affected by perturbations even more. Plausible supporting evidence to that statement relevant in the studied setting can be found in Guo and Gong (2024), who demonstrated that fungal community is in a strong relationship with tree species and bacterial community with soil carbon. Uniform species composition and steep gradient in SOC can, therefore, plausibly rationalise observed shifts in fungal and bacterial communities.

Fungi are often found to act as a mediator for bacterial growth, and so an increase in fungal biomass is followed by an increase in bacteria (Agnihotri et al. 2023). Contrarily, we found strong negative correlation between the two groups proposing significant specialisation of microbial communities across a wide ecological spectrum. While fungal biomass was subordinal to an increase in most chemical soil properties (except pH and available Mn), bacterial response was diversified, yet mostly reciprocal, and manifested reverse metabolic strategy and resource utilisation. Such polarity differentiated the community structure along the environmental spectrum to, on the one hand, conditions favouring fungal-based communities linked with lower rates of decomposition and nitrogen mineralisation and on the other, bacteria-controlled communities with higher turnover rates, higher N demands and lower C use efficiency, which corresponds with the findings of Waring et al. (2013). This study showed that the reciprocity amongst the microbial community groups, associated with characteristic enzyme sets (Figure S3 in the ESM), was best explained by soil pH. Blagodatskaya and Anderson (1998) documented that a pH increase from 3 to 6 significantly decreased the *F*/*B* ratio and that high pH favoured bacterial over fungal biomass, and Kaiser et al. (2016) found soil pH to be the best predictor for bacterial community structure, diversity, and function.

Regarding *G*+/*G*–, we found, that all stands were *G*– dominated, which is typical for broadleaved forest stands (Hiiesalu et al. 2017), and the ratio significantly increased in the order of PB < PC < BF. *G*– are known to be more dependent on plant biomass and root exudate C inputs, while *G*+ have lower nutritional specificity and utilise a wider and more complex resource gamut (Fanin et al. 2019), especially under a high N availability (Orwin et al. 2018). In this study, *G*+ were associated with BGL activity, while *G*– showed no enzyme associations (Figure S3 in the ESM), suggesting that bacterial groups are associated with different C sources and show a contrasting relationship to soil organic matter (SOM) complexity, as described in Fanin et al. (2015). Differences in energy acquisition often lead to a discrimination of bacteria into opportunistic copiotrophs (*G*–) and stress-resistant oligotrophs (*G*+), playing contrasting functional roles in SOM decomposition (Kramer, Gleixner 2008) and, in that sense, they can be considered a good indicator of site energy limitation assessment. Based on the findings of Fanin et al. (2019), who documented that the removal of shrubs and tree roots significantly increased the *G*+/*G*–, we suggest that bacterial communities were differentiated by above-ground biomass, net primary production and root activity. PB comprises the most developed understorey, complex vertical structure, highest stocking, and herb-shrub-tree derived root biomass, which was decreased in BC (slightly older stand with a higher proportion of DW) and almost absent in BF. Although high production rates embrace higher nutritional demands, PB displayed medial nutritional stress, and the unsaturation index (cy/pre) is comparable to PC. Holík et al. (2019) noted that the *G*–, closely linked with the nutritional (cy/pre) indicator, well determines decreased growth potential based on nutrient limitations. At closer examination, available P could potentially become the limit of growth at PB. We also noted that as the share of *G*– in the microbial community proportionally decreased with pH, the proportion of *ACT* and *UnsB* increased. *ACT* are known to provide a wide array of functions and services to plants mirroring fungal and bacterial behaviour (Yadav et al. 2021), which involves the production of a wide spectrum of growth-promoting compounds and metabolites. Moreover, several *ACT* provide nutrients to plants, particularly phosphates and Fe. In agriculture, *ACT* are discussed as microbial fertilisers and inoculants (Boukhatem et al. 2022) and even Fe reducers under oxic and

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pH-neutral conditions (Zhang et al. 2019a). In our study, the pattern in *ACT* (strong positive relationship with pH, IC (inorganic carbon), P, Mn, but also *G+*/*G–* and all aminopeptidases) was extended to *UnsB* and the two could play major roles in nutrient provision differentiation among sites, notably P, which was negatively associated with *G–*. The pronounced site effect along the pH/management gradient proposed the existence of diversified bacterial guilds regarding the *G–* and *UnsB*. The fact that especially the *UnsB* may be a highly diversified group of specialists is documented by the group differentiation across sites in relation to IC, OC, C/N, TS (total sulphur), SO_4 as well as the already mentioned pH. The *G+* and Fe association was highly differentiated among the sites, being positive at BF, neutral at PB and negative at PC, suggesting that Fe availability in soils could become a good indicator of *G+* abundance; however, such a wider environmental context is highly complex and calls for further investigation.

CONCLUSION

Our study presents an insight into a unique floodplain environment altered by gradual land-use intensification. It is focused on understanding the effects of forest management practices on soil health and ecosystem functioning and provides new findings on how changes in soil properties affect SMC biomass, activity, and structure. Three sites, comprising a plantation, a cultural forest and a nature reserve, were well differentiated in regards to soil microbial community and soil organic carbon and the results offer several key findings: (*i*) microbial biomass is the best indicator of forest management; (*ii*) forest management application, regardless of its intensity, leads to a significant microbial biomass reduction; (*iii*) bacterial communities are affected by floodplain forest management to a larger degree than fungal; (*iv*) unmanaged sites favour fungal-based communities linked with lower rates of decomposition and nitrogen mineralisation and managed bacteria-controlled communities with higher turnover rates, higher N demands and lower C use efficiency; and, most importantly, (*v*) pH is the most important driver of SMC structure and activity but not of its overall size. The SMC associations are complex, and their responses to soil properties and environmental conditions are often ambiguous, highlighting the importance of understanding microbial dynamics in forest ecosystems for effective management strategies, especially in times of changing climate. The work underscores the importance of further research on SMC interactions with ROC, available Fe and Mn, as well as the role of redox-active metals in soil organic carbon degradation, and highlights the significance of surface flooding in floodplain environments.

Acknowledgement: We are grateful to Josef Klein and Lesy České republiky, s. p. (Forests of the Czech Republic, a state enterprise), for providing information and support and for enabling research in the area.

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Received: June 28, 2024
Accepted: October 2, 2024
Published online: November 20, 2024