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Fire intensity regulates the short-term postfire response of the microbiome in Arctic tundra soil

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ABSTRACT

Arctic tundra fires have been increasing in extent, frequency and intensity and are likely impacting both soil nitrogen (N) and phosphorus (P) cycling and, thus, permafrost ecosystem functioning. However, little is known on the underlying microbial mechanisms, and different fire intensities were neglected so far. To better understand immediate influences of different fire intensities on the soil microbiome involved in nutrient cycling in permafrost-affected soil, we deployed experimental fires with low and high intensity on an Arctic tundra soil on Disko Island, Greenland. Soil sampling took place three days postfire and included an unburned control. Using quantitative real-time PCR, copy numbers of *16S* and *ITS* as well as of 17 genes coding for functional microbial groups catalyzing major steps of N and P turnover were assessed.

We show that fires change the abundance of microbial groups already after three days with fire intensity as key mediating factor. Specifically, low-intensity fire significantly enhanced the abundance of *chiA* mineralizers and ammonia-oxidizing archaea, while other groups were not affected. On the contrary, high-intensity fire decreased the abundance of *chiA* mineralizers and of microbes that fix dinitrogen, indicating a dampening effect on N cycling. Only high-intensity fires enhanced ammonium concentrations (by an order of magnitude). This can be explained by burned plant material and the absence of plant uptake, together with impaired further N processing. Fire with high intensity also decreased *nirK*-type denitrifiers. In contrast, after fire with low intensity there was a trend for a decreased *nosZ* : (*nirK*+*nirS*) ratio, indicating – together with increased nitrate concentrations – an enhanced potential for nitric oxide and nitrous oxide emissions. Concerning P transformation, only *gcd* was affected in the short term which is important for P solubilization.

Changes in gene numbers consistently showed the same contrasting pattern of elevated abundance with low fire intensity and decreased abundance with high fire intensity. Differentiating fire intensities is therefore crucial for further, longer-term studies of fire-induced changes in N and P transformations and potential nutrient-climate feedbacks of permafrost-affected soils.

1. Introduction

Fires are nowadays among the main disturbances in the Arctic where they have been increasing in extent, frequency and intensity in the last decades, in particular with regard to tundra wildfires (Bowman et al., 2009, Hu et al., 2015, Sae-Lim et al., 2019, Holloway et al., 2020, Abbott et al., 2021). Most wildfires in the Artic occur between June and August and their distribution and fire intensity (a measure of heat and duration) depends on warm and dry conditions in late spring to mid-summer, with fire intensity also being correlated with less precipitation and soil

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moisture in the preceding winter and spring (Masrur et al., 2017).

Arctic fires, besides soil carbon (C) (e.g., Mack et al., 2011, Kulmala et al., 2014, Ribeiro-Kumara et al., 2020), potentially also reduce soil nitrogen (N) and phosphorus (P) stocks (Certini, 2005, Knicker, 2007), inducing shifts in nutrient cycling. Therefore, they have been considered to trigger positive feedbacks on climate warming via greenhouse gas (GHG) emissions. Fire oxidizes organic matter, leading to emissions of carbon dioxide (CO_2), nitrogen oxides (NOx), nitrous oxide (N_2O), and dinitrogen (N_2), during combustion (Andreae and Merlet, 2001, Certini, 2005, Mack et al., 2011, Rodríguez et al., 2017). But there are also C and N losses in the postfire months via soil emissions due to changes in soil properties and altered soil biogeochemical processes (Brown et al., 2012, Karhu et al., 2015, Dannenmann et al., 2018, Xu et al., 2021a). For example, fire caused a loss of up to 80% of aboveground N in a forest in boreal Alaska (Boby et al., 2010). Despite such losses, mineral N concentrations were found to increase postfire in topsoils due to pyrogenic organic matter (PyOM) inputs (Xu et al., 2022b) and conversion of organic N mostly to ammonium (NH_4^+) (Levine et al., 1988, Marion et al., 1991, Prieto-Fernández et al., 2004, Karhu et al., 2015).

Similarly, fire can also liberate considerable amounts of organic P through combustion and mineralization due to high temperatures (Gimeno-García et al., 2000, Butler et al., 2018). For example, a moderate fire caused a surplus of available P of 32 mg kg^{-1} dry soil, while a stronger fire (double the amount of biomass as fuel) led to a surplus of 55 mg kg^{-1} dry soil (Gimeno-García et al., 2000). Phosphorus from burned plant material might be deposited in the ash-bed rather than lost to the atmosphere (Arianoutsou and Margaris, 1981). However, P cycling can be affected, for instance acid and alkaline phosphatase activities were lower in a high-intensity burning treatment in Iranian forest one year postfire compared to the control (Pourreza et al., 2014).

Changes of soil microbial gross N turnover due to fire have been studied in temperate ecosystems with the use of ^{15}N pool dilution methods. Fire responses of N cycling and the associated microbiome in Mediterranean systems are very variable and seem to depend on time after fire (Dannenmann et al., 2011, Karhu et al., 2015, Dannenmann et al., 2018) but also fire intensity, e.g., via impacts on C sources (Bárcenas-Moreno and Bååth 2009, Rodríguez et al., 2017). For permafrost regions there is however a lack of data on influences of fire on the soil microbial community. Taş et al. (2014) analyzed postfire C and N cycling in a boreal upland forest soil in Alaska, showing increased potential enzymatic carbohydrate degradation activity, microbial community shifts and changed microbial β-diversity. Microbes catalyzing the galactose metabolism increased while microbes involved in methanogenesis and CH_4 oxidation decreased compared to the control treatment (Taş et al., 2014). In addition, the authors observed increased ammonia (NH_3) and nitrate (NO_3^-) assimilation in contrast to decreased nitric oxide (NO) reduction according to indicator genes (Taş et al., 2014). Very few Arctic studies to date investigated both N and P at the same time (e.g., Xu et al., 2021a) although the availability of different N and P forms is tightly coupled (Mooshammer et al., 2012) and these nutrients are usually limiting in pristine environments but crucial for biota as well as ecosystem functioning (Vitousek et al., 2010, Chen et al., 2018).

In addition, former studies did not differentiate between different fire intensities. Yet it is well known that fire intensities strongly vary according to below- and aboveground biomass fuel availability, plant composition and soil drainage (Walker et al., 2020). While it has been reported that permafrost GHG emissions can differ substantially depending on fire intensity (Sawamoto et al., 2000, Boby et al., 2010, Morishita et al., 2015), the role of different fire intensities for the abundance of microbes catalyzing major processes of nutrient cycling is still unclear. Therefore, the goal of this study was to assess whether fires of different intensity in Arctic tundra would differently impact the soil microbiome on the short-term. By providing such information, we also aimed to provide decision support whether fire intensity treatments should be included in future long-term Arctic fire experiments.

Ludwig et al. (2018) analyzed potential extracellular enzyme activities in the laboratory and found that with increasing fire intensity, activities of β-glucosidase (break down of cellulose to glucose), phenol oxidase (decomposition of lignin), leucine aminopeptidase (degradation of proteins/polypeptides) and acid phosphatase (cleavage of phosphate (PO_4^{3-}) groups from organic molecules) decreased up to 70% and soil respiration by 50% one year after fire. Also from studies in non-Arctic ecosystems one can deviate a decrease of microbial biomass (Mataix-Solera et al., 2009), bacterial diversity (Adkins et al., 2020) and activity (Castaldi and Aragosa, 2002) with increasing fire severity.

Hence, we hypothesized that fire would directly exert negative effects on microbes involved in N and P turnover (therefore visible in the short term) and that negative effects would be stronger after high-intensity fire compared to low-intensity fire. To test this, we set up experimental fires of low and high intensity (resulting in heat loads of 285 and 505 °C minutes, respectively, in the top 2 cm soil during 40 min) in Arctic tundra soil on Disko Island, Greenland, and sampled after three days. The abundance of microbial key players involved in N_2 fixation, P solubilization/transport, N and P mineralization, nitrification and denitrification was assessed using qPCR-based quantification of marker genes.

2. Material and methods

2.1. Study site, experimental design and sampling

The low-Arctic study site at Blæsedalen Valley (69°16′N, 53°27′W; 90 m a.s.l.) is located on Disko Island, Western Greenland, with a mean annual precipitation of 418 mm (1991–2017) and a mean annual temperature of −3 °C (1991–2017) (Zhang et al., 2019). The soil is haplic cryosol with a thin organic layer of 5–10 cm (Blok et al., 2016). It is underlain by discontinuous permafrost with an active layer depth of 1.5 m (Blok et al., 2016). The dry heath tundra ecosystem is dominated by low shrub vegetation of *Betula nana* L., *Salix glauca* L., *Vaccinium uliginosum* L., *Empetrum nigrum* L., *Cassiope tetragona* (L.) D. Don, lichens (*Cetraria islandica* (L.) Ach. and *Stereocaulon paschale* (L.) Hoffm.) and mosses (*Tomentypnum nitens* (Hedw.) Loeske and *Aulacomnium turgidum* (Wahlenb.) Schwägr.) (Xu et al., 2022a). In the study area, wildfires appeared infrequently in the past, but in August 2017 a major fire burned for two weeks in southwestern Greenland (Xu et al., 2021a).

The experiment included three treatments: unburned control (UC), low-intensity fire (LF), high-intensity fire (HF). Per treatment there were five replicates (Fig. 1) of 2 × 2 m and 3.4 ± 0.1 kg dry aboveground biomass m^{-2} each (Xu et al., 2022a) on a northeast-facing slope (5.7°). The study site was selected based on screening of the vegetation coverage and composition being representative to the characteristics of the area (D'Imperio et al., 2017). Side cross effects between treatments were avoided by a distance of at least 2 m between the plots.

The fires were applied on July 30th (2019) with a butane-gas burner. The treatment of LF corresponded to a deployment of the burner for no more than five minutes with an aggregated heat load (integrated area under temperature history trace during 40 min from onset of fire; for the concept of heat loads please compare Burrows, 1999) of 285 °C minutes in the top 0–2 cm soil (max. temperature value 340 °C) and 167 °C minutes in 5 cm soil depth (max. temperature value 60 °C). The HF treatment corresponded to a deployment of the burner for 20 min reaching a heat load of 505 °C minutes in the top 0–2 cm soil (max. temperature value 382 °C) and 214 °C minutes in 5 cm soil depth (max. temperature value 191 °C). Aboveground shrub material was completely burned after application of both fire types. For LF only, burning of cryptogamic and litter cover was patchy.

Three days after the simulated fires, an intact soil core (6 cm diameter, 3.5 cm height) was taken at each plot (0–3.5 cm depth). The sampled soil had very few plant roots. The cores were immediately frozen at −20 °C and remained in that state during subsequent shipping to Helmholtz Munich, Germany.

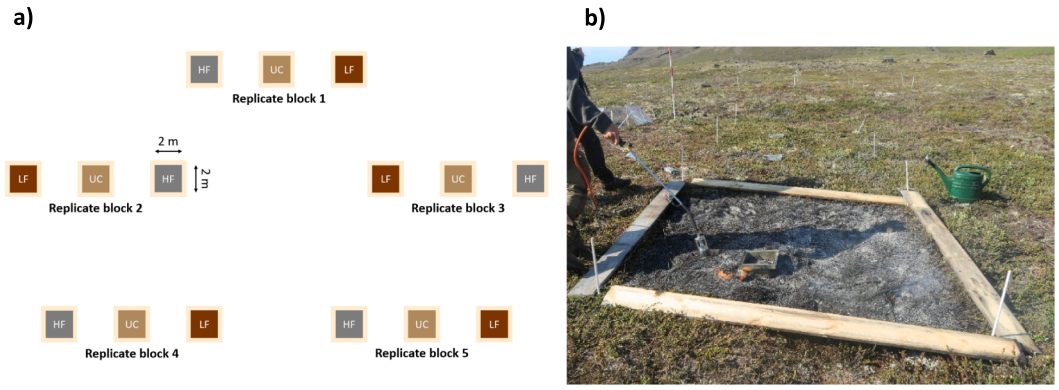

Fig. 1. (a) Plot layout. Five replicate blocks, each containing three plots à 2 × 2 m: unburned control (UC), low-intensity fire treatment (LF), high-intensity fire treatment (HF). (b) Starting the experimental fire with a butane-gas burner in one plot.

2.2. Quantification of marker genes for key processes of N and P cycle via quantitative real-time PCR

Soils for DNA samples were taken with sterile spoons from three different spots of each soil core (ca. 1 g) after removal of the top 0.8–0.9 cm topsoil; 0.1–0.4 g thereof were transferred into an extraction tube. DNA was extracted using the Nuclespin Soil kit (Macherey Nagel with SL1 and SX solution and an elution volume of 30 µL according to manufacturer's instructions). The DNA yield and purity were checked with a spectrophotometer (Nanodrop, PeqLab, Germany). Quantitative real-time polymerase-chain reactions (qPCRs) were conducted following a SYBR-Green®-based approach with a 7300 real-time qPCR machine (Applied Biosystems, Germany). The reaction mix of 25 mL contained 12.5 µL of SYBR Green® (Thermo Fisher Scientific, USA), forward (F) and reverse (R) primers (Metabion, Germany), 0.5 µL BSA (3%, Sigma, Germany), and DEPC-treated water. We included no-template controls and serial dilutions of plasmid DNA containing the PCR products of the respective genes listed in Table S1 to calculate standard curves. To avoid PCR inhibition caused by co-extracted humic substances, the optimal uniform dilution was determined by a pre-experimental dilution series of randomly chosen DNA extracts (data not shown). Then qPCRs were run for the following genes:

- *16S* rRNA gene (proxy for bacteria)
- *ITS* region of the rRNA gene (proxy for fungi)
- Indicator genes for major N turnover processes: *nifH* (biological N fixation); *npr*, *apr* and *chiA* (mineralization); *amoA* (AOA) and *amoA* (AOB) (ammonia oxidization by archaea and bacteria, respectively); *narG*, *nosZ*, *nirK*, *nirS* (denitrification)
- Indicator genes for major P turnover processes: *gcd* (solubilization of mineral-bound P); *phoD*, *phoN*, *appA* and *phnX* (mineralization of organic P); *pitA* (low-affinity transporter for cellular uptake of inorganic P, P_i); *pstS* (high-affinity transporter for cellular uptake of P_i, induced at low P_i concentrations)

For more information on analyzed marker genes, reaction conditions, primers and calibration standards please see Table S1. To confirm the specificity of the SYBR-Green®-quantified amplicons, melting curve analysis and agarose gel were performed after each PCR run. Amplification efficiency (Eff) of the qPCRs was calculated for each gene as $\text{Eff} = 10^{(-1/\text{slope})} - 1$ and was between 84 and 97% regarding the N genes and between 67 and 86% regarding the P genes.

2.3. Extractable soil C, N and P forms

Directly after sampling for DNA analysis the soil cores were thawed, homogenized (including removal of large roots and stones) and 10 g thereof extracted in 50 mL deionized water after shaking for 1 h using a vacuum pump and porcelain funnels with Whatman GF/A filters, and syringe filters with 0.45 µm pore size as a second filtration step as described in Dannenmann et al. (2009). Microbial biomass C, N and PO_4^{3-}-P were obtained using the chloroform fumigation method (no correction factors) as described in Guo et al. (2013) with a fumigation time of 24 h. This approach is based on the differences in extractable dissolved organic carbon (DOC), total dissolved nitrogen (TDN) and PO_4^{3-}-P in control versus chloroform-fumigated soil. Extracts were frozen immediately at −18 °C until analysis. All extracts were sent to the Center for Permafrost in Copenhagen for analysis of NH_4^+-N, NO_3^--N and PO_4^{3-}-P (Tecator 5000 FIAStar, Höganäs, Sweden), as well as DOC and TDN (TOC-TN analyzer, Shimadzu, Kyoto, Japan). By subtracting NH_4^+-N and NO_3^--N from TDN, dissolved organic N (DON) was calculated.

2.4. Soil characteristics

Soil gravimetric water content was determined by drying subsamples at 105 °C until constant weight. Soil pH of 10 g soil in 25 mL deionized water was evaluated using a pH meter station. Also, subsamples of the frozen soil cores were unfrozen and dried at 60 °C. Afterwards they were milled and analyzed with an elemental analyzer coupled to isotope ratio mass spectrometry as described by Liu et al. (2015). Thus, soil organic C (SOC) and total N (TN) concentrations were obtained. Throughout the study region there is carbonate-free basaltic rock of volcanic origin so that carbonates do not occur (Callaghan et al., 2011). Consequently, measured total C resembles SOC.

2.5. Statistical analysis

Analyses were performed in R version 4.1.3 with a 5% significance level. A heatmap was conducted using the R command "heatmap.2" (gplots package) with the qPCR data per g soil fresh weight. Before applying parametric tests, it was assured that data were normally distributed with Shapiro-Wilk tests and that variance was homogenous with Levene's tests. If the data were not normally distributed and/or had non-homogeneous variance, Kruskal-Wallis tests and Wilcoxon Ranks Sum tests were performed, otherwise ANOVAs and t-tests. The p-values were adjusted after the Bonferroni method for testing more than two groups. We referred to trends for results with $0.05 < p < 0.1$. To cope with spatial heterogeneity between the five replicate blocks, i.e. to make the results more robust, they were also normalized for SOC concentrations. The control of different soil properties on gene copy numbers was assessed using stepwise multiple linear regression analysis which was conducted in SPSS version 8.0.

3. Results

3.1. Effects of fire intensity on chemical and bulk biological soil properties

Soil water content and pH (Table S2) did not significantly differ among treatments. The treatment HF showed a significantly higher NH_4^+ concentration than LF (data in μg per g dry soil; Wilcoxon, $p = 0.03$) as well as UC (Wilcoxon, $p < 0.01$) (Fig. 2a). In contrast, there was only a trend for an increase in NO_3^- concentration at LF and HF compared to the control (UC: 0.87 ± 0.21, LF: 1.50 ± 0.14, HF: 1.46 ± 0.51 μg g^{-1} dry soil; ANOVA, $p = 0.08$); PO_4^{3-} concentrations were not significantly larger in the fire treatments. There was a trend for higher DOC concentration at HF compared to LF and control (data in mg per g dry soil; ANOVA, $p = 0.07$; Fig. S1). In terms of microbial biomass C there were no differences among treatments (ANOVA, $p = 0.69$). There were also no differences in TDN (data per g dry soil; Kruskal-Wallis, $p = 0.10$), even less so for microbial biomass N.

DNA yield in ng μL^{-1} was 200 ± 20 for UC, 221 ± 20 for LF and 167 ± 19 for HF. Similarly, gene copy numbers of the *16S* rRNA gene (data per ng DNA) which were used as a proxy for bacterial abundance were larger under LF compared to HF (Wilcoxon, $p = 0.02$) (Fig. 2b). There was a higher *16S*:*ITS* ratio at HF compared to LF (Wilcoxon, $p = 0.05$) (Fig. 2c). This was because gene copy numbers for *ITS* (data per ng DNA) generally indicating fungal abundance showed a trend of a decrease with HF compared to LF and UC (ANOVA, $p = 0.09$; Fig. 2d). The pattern of lower *ITS* abundance with HF than with LF became significant when normalizing for SOC (*t*-test, $p = 0.03$) (Fig. S2a), with SOC being not significantly different between treatments (ANOVA, $p = 0.71$).

3.2. Effects of fire intensity on the abundance of microbiota catalyzing major processes of N and P cycling

Fire intensity generally had a pronounced and consistent effect on the abundance of microbes catalyzing major processes of N and P turnover which was visible in the extracted DNA subjected to qPCR, showing either unchanged or increased gene abundances for the LF treatment and unchanged or decreased abundances for the HF treatment (Fig. 3). Based on the analysis of gene copy numbers per ng DNA, per g dry soil and per g SOC, LF intensity did not affect the abundance of microbes harboring the *nifH, npr, apr, chiA*, bacterial *amoA, narG, nosZ, nirK* and *nirS* genes compared to UC. In contrast, HF significantly reduced the abundance of *nifH* (per g SOC) which is a proxy for N-fixing microbiota (Wilcoxon, $p = 0.02$) (Fig. 4a). The HF treatment also tended to decrease the abundance of a group of ammonifiers harboring the *chiA* gene while with LF, there was a trend for more *chiA* copies compared to the other two treatments (most differing when normalized for g SOC; ANOVA, $p = 0.07$; Fig. 4b). Also the *apr* gene was (statistically insignificantly) increased for LF but not for HF. The ratio *nifH* : (*apr*+*chiA*), providing an index for the relative importance of the N-fixing microbiome vs. the mineralizing microbiome, was thus decreased for LF. The latter was, however, also slightly decreased for HF which is due to the decrease in *nifH* (Fig. 4).

Concerning microbial nitrifiers harboring the *amoA* gene, significant differences were detected among the three treatments in archaeal *amoA* (AOA) gene copies (Fig. 4c). There were more archaeal *amoA* copies per g dry soil for LF compared to the control (Wilcoxon, $p = 0.05$) and to HF (Wilcoxon, $p < 0.01$; Fig. S3a). Thus, we found elevated nitrifier gene

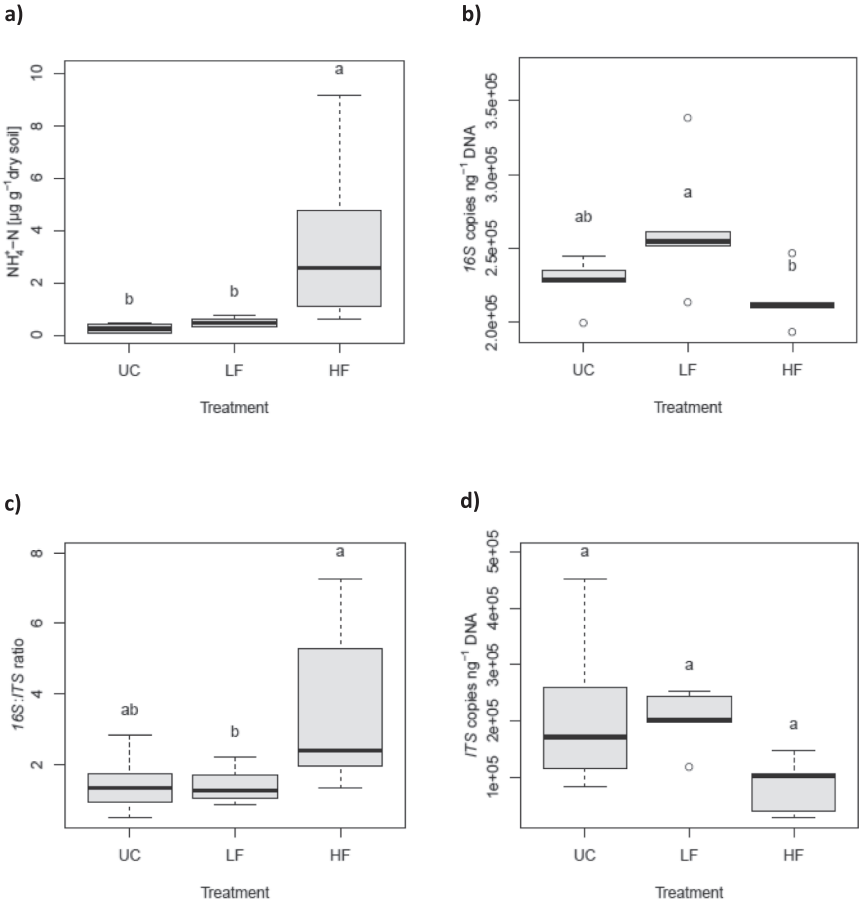

Fig. 2. (a) Ammonium (NH_4^+-N) concentration [μg/g dry soil], (b) *16S* gene copies [ng^{-1} DNA], (c) *16S:ITS* ratio and (d) *ITS* gene copies [ng^{-1} DNA] of unburned control (UC), low-intensity fire (LF) and high-intensity fire (HF) shown in boxplots. Letters show significance of differences according to Wilcoxon Ranks Sum tests.

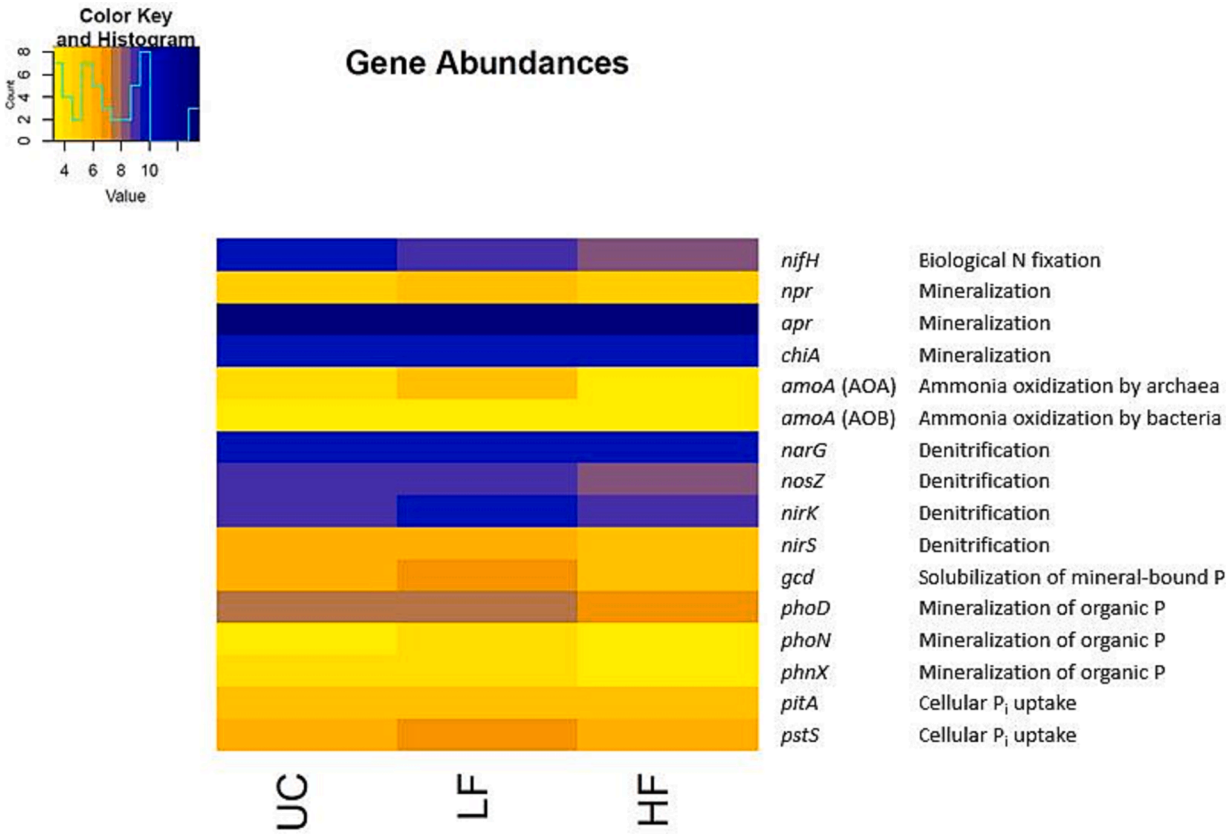

Fig. 3. Gene abundances [g^{-1} fresh soil] in logarithmic scale of successfully measured functional genes (except *appA*, coding for phytase which mineralizes organic P, because there were often only <5 copies μL^{-1}) involved in N and P cycle of unburned control (UC), low-intensity fire (LF) and high-intensity fire (HF) shown in a heatmap. Relatively low to relatively high abundances are decoded in yellow to blue. Color differences do not infer statistical significance.

numbers where there was lower NH_4^+ concentration. Concerning the abundance of microbial denitrifiers, there were less *nirK* copies (data per g SOC; Fig. 4d) in HF compared to UC (Wilcoxon, $p = 0.03$) and LF (Wilcoxon, $p = 0.03$). The ratio *nosZ* : (*nirK*+*nirS*) shows N_2O reduction (to N_2) relative to NO_2^- reduction (to NO). This relative N_2O reduction tended to increase for the HF plots (ANOVA, $p = 0.08$).

Concerning the microbiome involved in P turnover we did not find any significant differences in the tested genes between the treatments except for microbes harboring *gcd*. The *gcd* numbers of HF were significantly lower than the *gcd* numbers of UC (data per g SOC; Wilcoxon, $p = 0.05$; Fig. 4e). Moreover, the *gcd* gene showed a trend for more *gcd* copies at LF than at HF (Wilcoxon, $p = 0.08$).

To explore drivers of the functional groups of microbes under investigation across the sampled plots ($n = 5$), the data were also subjected to stepwise linear regression which led to modeled equations showing different dependencies for microbes harboring the *nifH, chiA, nirK* and *gcd* genes (Table 1). Common controls of the three N turnover genes were a negative control by DOC (or microbial biomass C) and a positive control by PO_4^{3-} (or microbial biomass PO_4^{3-}). Nitrogen-mineralizing microbes (based on the abundance of the *chiA* gene) were further correlated with NH_4^+ which is the end product of the mineralizing process. There was no significant influence of soil water content or pH on gene copy numbers.

4. Discussion

In the frame of this study we reveal a consistent pattern of lowered gene abundance with high-intensity fire (HF) but an unchanged or elevated gene abundance with low-intensity fire (LF), suggesting that fire intensity is a crucial regulator of postfire microbial functioning especially with regard to N (Fig. 5). Interestingly, these patterns were persistent or even more pronounced when gene abundance was normalized by SOC content, thereby taking into account the potential effect of soil heterogeneity. Abundance of genes (DNA level) involved in N cycling provides information on the presence of microorganisms but not necessarily on their activity, the latter being related to gene expression (mRNA level). This might be particularly true for the diverse group of denitrifiers with their metabolic alternatives (Chen et al., 2015), while in the case of nitrifier gene abundance close relationships with gross nitrification rates have been observed (e.g. Dannenmann et al., 2016, Wang et al., 2016), probably due to their limited metabolic alternatives.

4.1. Promoting effects of fires with low intensity

First of all, there was no detectable NH_4^+ increase in the LF treatment (Fig. 2a), indicating either that low-intensity fire did not cause much combustion to NH_4^+, or that the NH_4^+ was immediately nitrified or immobilized. Also in Xu et al.'s (2021a) low-intensity fire experiment on Disko Island, soil NH_4^+ was only 0.01 mg kg^{-1} dry soil three weeks after the weak fire. However, after two years, it was 3.5 mg kg^{-1} dry soil (compared to 0.9 mg kg^{-1} dry soil in the unburned control) (Xu et al., 2021a). It can be concluded that both in Xu et al.'s (2021a,b) and in this study the low fire intensities did no trigger high NH_4^+ concentrations in the short term. However, they can be elevated in the longer term, suggesting altered postfire biogeochemical N cycling that we are only starting to explore in this study.

From the abundances of *16S* and *ITS*, total microbial biomass can be approximated. The increased *16S* and *ITS* numbers in low-intensity fire plots thus give a hint that by LF, microbial biomass was not decreased but rather increased in abundance (Fig. 2b,d), possibly triggering more depolymerization of proteins to DON and more ammonification of DON

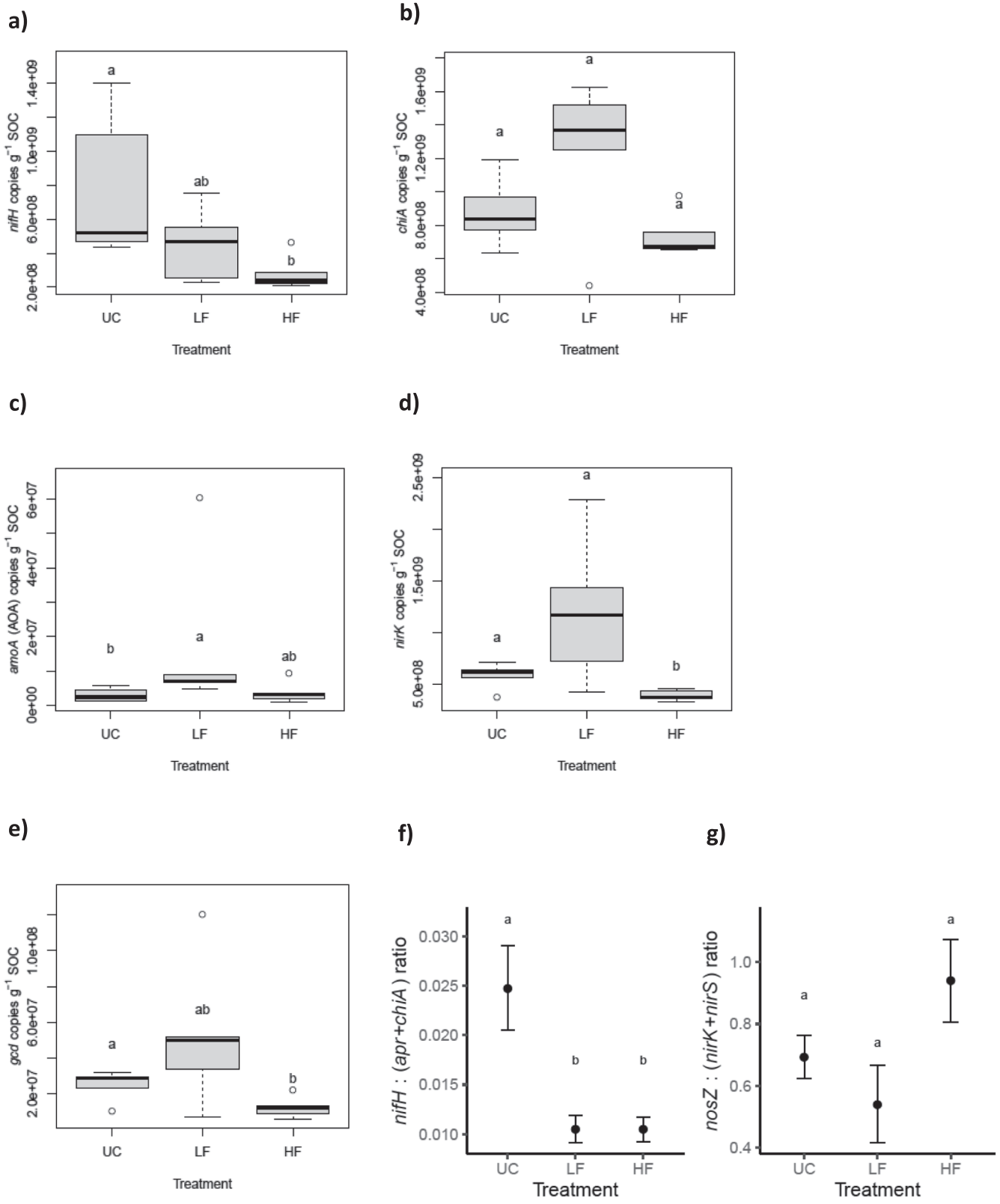

Fig. 4. (a) *nifH* gene copies [g^{-1} SOC], (b) *chiA* gene copies [g^{-1} SOC], (c) *amoA* (AOA) gene copies [g^{-1} SOC], (d) *nirK* gene copies [g^{-1} SOC] and (e) *gcd* gene copies [g^{-1} SOC] of unburned control (UC), low-intensity fire (LF) and high-intensity fire (HF) shown in boxplots. (f) *nifH* : (*apr*+*chiA*) ratio and g) *nosZ* : (*nirK*+*nirS*) ratio of UC, LF and HF shown in barplots (error bars are standard errors). Letters show significance of differences according to Wilcoxon Ranks Sum tests.

Table 1
Stepwise linear regression for gene copy numbers of *nifH*, *chiA*, *nirK* and *gcd* including the variables *16S* [ng^{-1} DNA], *ITS* [ng^{-1} DNA], TDN [mg N g^{-1} dry soil], microbial biomass N (MBN) [mg N g^{-1} dry soil], NH_4^+-N [µg/g dry soil], NO_3^--N [µg/g dry soil], DON [mg N g^{-1} dry soil], DOC [mg C g^{-1} dry soil], microbial biomass C (MBC) [mg C g^{-1} dry soil], PO_4^{3-}-P [µg/g dry soil], microbial biomass PO_4^{3-}-P ($MBPO_4^{3-}$-P) [µg/g dry soil].

Gene copies [ng^{-1} DNA]	Equation	*p*-value	Adj. R^2
nifH	925 × MBDOC	0.000	0.70
	−2292 × DOC	0.001	
	+936	0.003	
chiA	1497 × PO_4^{3-}-P	0.001	0.61
	−2440 × DOC	0.003	
	123 × NH_4^+-N	0.035	
	+2272	0.000	
nirK	3002 × $MBPO_4^{3-}$-P	0.000	0.70
	−915 × MBDOC	0.001	
	1039 PO_4^{3-}-P	0.027	
	+1980	0.000	
gcd	0.001 × *16S*	0.000	0.72
	−176	0.001	

(Suttner and Alef, 1988, Ali et al., 2021, Ramm et al., 2022). The numbers of functional genes in LF were not significantly lower than in the control in the case of all tested N turnover genes. This shows that microbes survived the few days after the fire in 0–3.5 cm soil depth. The abundance of mineralizing microbes even tended to be higher at LF which could best be seen by the low ratio of genes for ammonia generation via N fixation and genes for ammonia generation via mineralization (*nifH* : (*apr*+*chiA*) ratio; Fig. 4f). The mineralization gene *chiA* coding for chitinase was more abundant in soils of LF treatments although there was less DOC than at HF (Fig. S1) which serves as a labile C energy source. The stepwise linear regression revealed *chiA* to be in fact negatively correlated with DOC (Table 1). This could indicate a relatively high consumption of DOC by heterotrophic microbial N turnover processes, i.e., that rather *chiA* is regulating DOC than vice versa. Probably this is also possible because chitin not only provides monomeric organic N but also usable polymeric organic C which can serve as a source of additional labile C for heterotrophic processes (Cohen-Kupiec and Chet, 1998).

Under LF it seems like additional NH_4^+ or NH_3 is transformed into NO_3^- pretty fast (Fig. 2, Fig. S1), which is in line with the observed

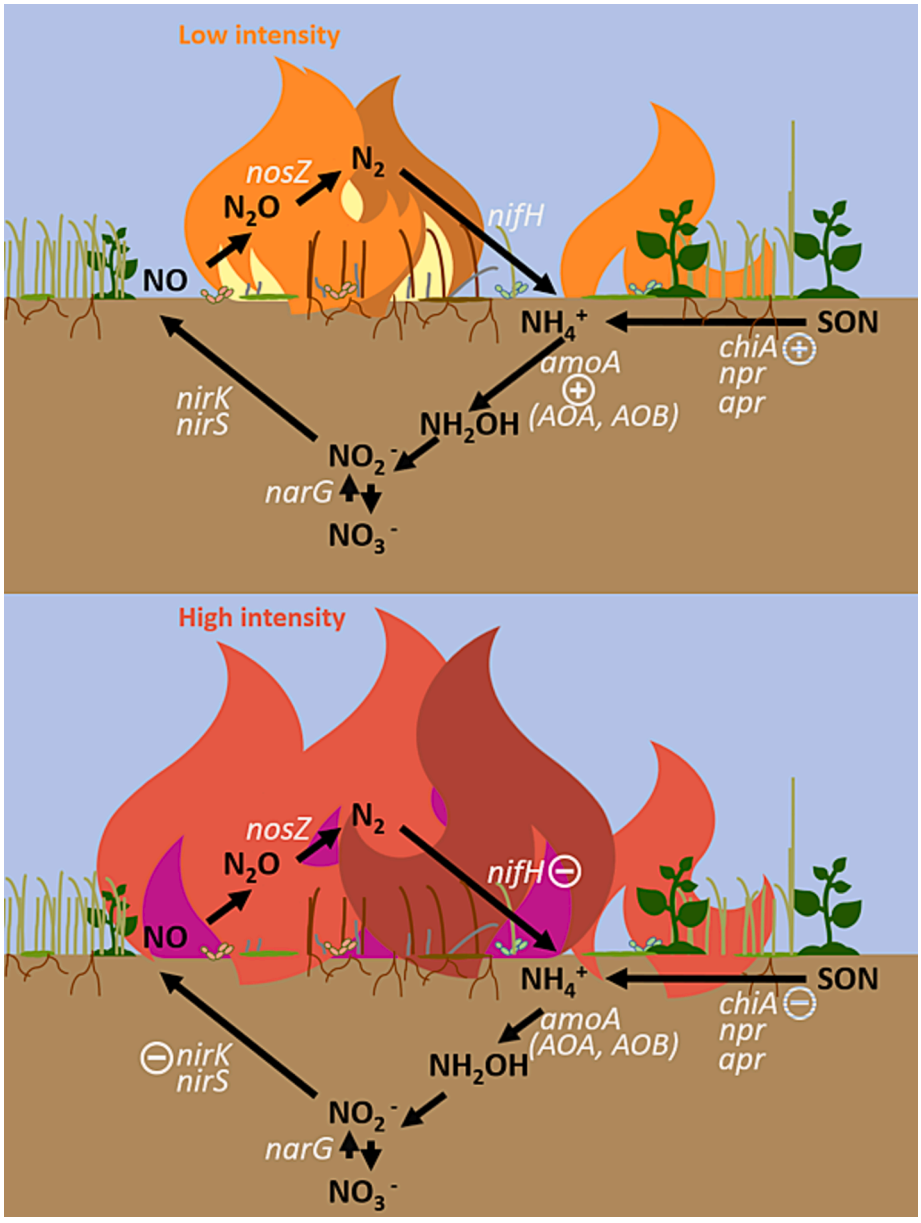

Fig. 5. Synthesis of observed gene abundances (three days postfire) catalyzing N turnover within the soil-atmosphere interface including grass and herbaceous vegetation and lichens/mosses. Note that the listed genes are not complete, there are often more genes involved in a step. Genes are shown in white. The N turnover of SON to NH_4^+, of NH_4^+ to hydroxylamine (NH_2OH), NO_2^- and NO_3^-, and of NO_3^- to NO_2^-, NO, N_2O and N_2, is shown in black. Plus and minus signs show significant differences in gene abundances (compared to the control) under low-intensity (top) and high-intensity (bottom) fire. Dashed signs show a trend with 0.05 < p-value < 0.1.

positive reaction of archaeal *amoA* abundance to LF. The *amoA* gene constitutively codes for ammonia oxidation. Its increase at LF could be due to a change in plant–microbe competition in favor of the microbes that survived in contrast to mostly dead plants and that can feed on increased levels of produced NH_4^+. In a study in Australia, it was found that AOA was mainly correlated to NO_3^- concentration and DOC (Long et al., 2014). Here, the linear regression showed no correlation with any tested variable for archaeal *amoA*, but we also only detected a slight increase in NO_3^-, and DOC was unchanged at LF compared to the control. Long et al. (2014) report that not the archaeal but rather the bacterial *amoA* gene (AOB) increased in abundance when subjected to biennial burning compared to the unburned control and there were changes in the distribution of AOA and AOB. After few days up to ca. 200 days in soil impacted by a fire that produced considerable amounts of ash, the pH might increase due to the high cation content of ash (Jensen et al., 2001, Karhu et al., 2015). This can increase the *amoA* (AOB): *amoA* (AOA) ratio in favor of AOB which is mostly found at neutral pH while AOA prefer slightly acidic pH (Gubry-Rangin et al., 2017, Sanders et al., 2019, Fiencke et al., 2022).

Recurring to NH_4^+, here its concentration remained low although mineralization was promoted by the LF, which can be explained with high NH_4^+ consumption in the form of immobilization and nitrification. The increase in soil NO_3^- at LF shows some fire-induced net nitrification. However, in an earlier sampling in the same area, Xu et al. (2021a,b) measured besides four times more NH_4^+ also five times more PO_4^{3-} and 14 times more NO_3^- two years after applying a low-intensity fire of seven minutes with 60 °C soil temperature (2 cm depth). Consequently, also postfire concentration changes of NO_3^- in the Arctic tundra might occur rather due to more long-term changes of soil biogeochemical cycles rather than directly and immediately affected by fire, because nitrifiers need to recover and/or use the NH_4^+ for growth (Dannenmann et al., 2018).

Concerning PO_4^{3-}, we found very low *appA* gene abundances (Fig. S4) which might show a lack of microbes that mineralize organic P to PO_4^{3-} via phytases. However, LF tended to have more *gcd* than the control which can mean another fitness boost for microbes and indirectly for plants in response to low-intensity fire. The *gcd* is coding for the periplasmic quinoprotein glucose dehydrogenase which catalyzes D-glucose and ubiquinone to D-glucono-1,5-lactone and ubiquinol and is thus important for solubilization of inorganic (mineral-bound) P (Babu-Khan et al., 1995) which is mainly dependent on the efflux of protons and organic anions via oxidation of glucose and other aldose sugars (Cleton-Jansen et al., 1990, Bergkemper et al., 2016). Phosphorus-solubilizing bacteria are abundant in P-poor soils, and high *gcd* abundances are usually associated with limited soluble PO_4^{3-} (as we observed) while its expression is downregulated by available P (Zeng et al., 2016, Pastore et al., 2020). The indicated increased *gcd* abundance could explain how in the longer term after low-intensity fires PO_4^{3-} concentrations might increase as observed, e.g., by Xu et al. (2021a,b) and Hermesdorf et al. (2022).

High NO_3^- concentrations can overall result in more NO_3^- and NO_2^- reduction than N_2O reduction, thereby promoting the importance of N_2O in denitrification product stoichiometry (Butterbach-Bahl et al., 2013). Also in our study, the observed higher NO_3^- concentrations in LF compared to the control (Fig. S1) might have resulted in more NO_3^- and NO_2^- reduction than N_2O reduction (Fig. 5), visible in the decreased *nosZ* : (*nirK*+*nirS*) ratio (Fig. 4g). Studies in the temperate region have found fire-induced increases in soil N_2O emissions (Fierro and Castaldi, 2011, Karhu et al. 2015). For Arctic fires, data are however scarce. Emissions of N_2O and CO_2 increased three-fold in plots burned with low intensity compared to unburned plots at wet conditions in the study by Xu et al. (2021a,b). In view of the highly uncertain relationships between denitrifier gene abundance and actual fluxes (e.g. Chen et al., 2015), future fire studies in Arctic ecosystems should link microbial abundance with gene expression/enzyme activity or gross N turnover as well as N gas flux measurements. According to our marker gene data, low fire intensity maintained or promoted microbial groups which can be explained by less competition and more nutrients for the remaining microbiome, e.g. released from plants (De Marco et al., 2005). Also N and P retention in microbial biomass can be increased after a low-intensity fire (Xu et al., 2022a), which is why a quantification of gross immobilization is of high interest.

4.2. Deteriorating effects of fires with high fire intensity

In contrast to LF, HF immediately decreased microbes harboring certain genes. The ratio of genes involved in ammonia generation via N fixation and genes involved in ammonia generation via mineralization (Fig. 4f) decreased at HF compared to UC (Wilcoxon, $p < 0.01$) due to diminished abundance of *nifH* genes (Fig. 4a). Thus biological N fixation (BNF) activity could be hampered by HF (Fig. 3) – although for proving activities, RNA analyses are needed. The *nifH* gene occurs both in free-living and in symbiotic N-fixing organisms (Raymond et al., 2004), but as there are few plant species which are in symbiosis with N_2 fixers in the experimental area (only *Dryas* sp. in low abundance, no legumes; Per Ambus, pers. commun.), here *nifH* should mostly relate to BNF by free-living bacteria or bacteria associated with lichens and mosses. These were a very vulnerable group according to our study. A finding of impaired BNF after intense fires might have far-reaching consequences. As BNF is the decisive N input pathways into pristine soils in the sub-Arctic and Arctic (Ramm et al., 2022), the circumpolar increase of strong fires might diminish availability of fresh N that is usually taken up by plants, or immobilized or further transformed by microbes. When compared to LF, HF also decreased gene numbers of *amoA* (AOA) (Fig. S3a). While LF boosted ammonia oxidation, HF thus limited it. The missing nitrification step, together with burned plant material and no plant uptake, might explain the observed accumulation of NH_4^+ (Fig. 2). Also soil NO_2^- concentration should be measured in the future in connection with *nxr* (nitrite oxidoreductase) gene abundance analysis, because cells often release NO_2^- in response to stress (Graham et al., 2007).

Nutrient concentrations typically increase with fire intensity (Kennard and Gholz, 2001, Ludwig et al., 2018). In line with that, free NH_4^+-N in the soil increased drastically (factor twelve) after the application of fire with high intensity (UC: 0.3 ± 0.1, LF: 0.5 ± 0.1, HF: 3.6 ± 1.6 mg kg^{-1} dry soil). Grogan et al. (2000) suggest production of new NH_4^+ via postfire mineralization within six days after a major wildfire, however this might not have happened in this study in the limited time (three days) between fire and sampling. In soil of HF there were 3.3 mg more of NH_4^+-N than in soil of UC so that the assumption of a postfire biogeochemical mechanism would require a relatively high net mineralization rate (please compare Xu et al., 2021b) of 1.1 mg NH_4-N kg^{-1} dry soil d^{-1}. In contrast, genes associated with N mineralization were decreased in HF compared to LF (*apr*, *chiA*). It is thus more plausible to relate the surplus in NH_4^+ to denaturation of proteins, dieback of soil microbes together with impaired plant N uptake after fire (Andersson et al., 2004, Kulmala et al., 2014, Dannenmann et al., 2018). Compared with LF, ammonia oxidizers (archaea) are negatively affected by HF (Fig. 4c) and thus NH_4^+ is not transformed a lot into NO_3^- so that there is even rather less NO_3^- at HF compared to LF (Fig. S1) although there is much more NH_4^+ at HF.

The elevated NH_4^+ concentration of HF treatments supports postfire regrowth of primary producers as well as of recovering microbes if it persists on longer time scales of months to years, which has been observed in a range of ecosystems in the temperate and tropical zones (Grogan et al., 2000, Jensen et al., 2001, Andersson et al., 2004, Dannenmann et al., 2018). In this sense, it seems possible that diverging fire intensity effects on soil nutrient concentrations and microbial nutrient turnover persist on longer time scales as well, e.g., if the observed HF-induced decline in nitrifiers persists over longer time scales, or plant recovery takes longer after HF compared to LF.

While LF did not affect the denitrification gene *nirK* (processing NO_2^-

to NO), HF reduced it. Therefore also the *nirK*:*nirS* ratio was lower for HF than for LF (Wilcoxon, $p = 0.03$) although HF also showed rather less *nirS* (*t*-test, $p = 0.14$; Fig. S5a). The *nosZ* gene (coding for the reduction of N_2O to N_2) numbers did not change significantly with the applied fires. However, the ratio of *nosZ* : (*nirK*+*nirS*) (Fig. 4g) tended to increase for the HF plots, suggesting that more N_2 than N_2O could be expected. However, at HF, all denitrifiers were strongly reduced, so the *nosZ* : (*nirK*+*nirS*) ratio might be misleading as an indicator of total net N_2O emissions. Still, these data provide evidence that permafrost postfire soil emissions might strongly depend on fire intensity, as Boby et al. (2010) describe for C emissions.

Concerning P-processing genes, the observed gene abundance patterns suggest that the microbiome involved in P turnover was less impacted by fire in the short term compared to N. The gene numbers in the HF and LF treatments were not significantly lower than in the control in the case of the tested P turnover genes with one exception. The *gcd* gene had reduced numbers at HF compared to the control so that there was presumably a fitness decrease at HF. However, it must be considered that P often is correlated to the microbial biomass and here we might prevailingly have seen a strong control by bacterial numbers (*16S*; Table 1) which were lower in the HF treatment.

At the HF treatment, according to *16S* data, bacteria were reduced in numbers per ng DNA (Fig. 2b) – despite the fact that HF showed the lowest total DNA weight among the three treatments. As *16S* is part of the total DNA weight, a reduction per ng DNA means that a non-bacterial group of genes must have increased, for example archaea that we did not measure or eukaryotic microbes (but not fungi). Still, lower numbers of bacteria further confirm that strong fires are likely to be detrimental and cause degradation of previously intact soil and its microbiome. Finally, the decrease in *ITS* and the higher *16S*:*ITS* ratio (Fig. S2c, d) of HF plots compared to LF plots show a well-known negative impact of fire on fungi (e.g., Waldrop and Harden, 2008, Bárcenas-Moreno and Bååth, 2009, Mataix-Solera et al., 2009, Nelson et al., 2022) and a community shift towards bacteria as found before in Mediterranean soil (e.g., Rutigliano et al., 2007). Already Klopatek et al. (1988) found that vesicular–arbuscular mycorrhizae were reduced depending on temperatures during fire: Soil temperatures (5 cm depth) below 50 °C caused moderate, temperatures of 50–60 °C significant and temperatures of 80–90 °C even higher losses of mycorrhizae while above these temperatures they were erased. This seems to be driven by how much mycorrhizal host plant biomass (especially roots) survives the fire (Neary et al., 1999) and how much char is left behind which sorbs phenols and thus affects mycorrhizal germination and growth (Knicker, 2007). If fungal biomass decreases due to fire and there is low soil moisture (especially non-permafrost soils within the Arctic) there can be decreased heterotrophic SOC decomposition which hampers nutrient cycling (Waldrop and Harden, 2008, Holden et al., 2013).

All in all, our results are in line with previous research showing that high-intensity fire causes mainly combustion of vegetation and soil OM, while with low- or moderate-intensity fire vegetation biomass is largely converted into still more or less bioavailable pyrogenic organic material and ash (Certini, 2005, Mack et al., 2011, Bird et al., 2015, Xu et al., 2021a). Long-term data will have a high ecological relevance. Arctic ecosystems exposed to fire might either quickly recover and reach an original nutrient and microbial state, or be changed for the long term. Also, longer-term data on abundances of key functional enzyme genes involved in P turnover might reveal significant fire impacts dependent on fire intensity as well as indirect influences imposed by the changes within the N cycle.

5. Conclusions

Short-term fire effects on the soil microbiome as reported here show the immediate regulation of the turnover and potential postfire loss or retention of fire-derived nutrients, with impacts on long-term responses. Surprisingly, the low-intensity fire after three days had either maintained or even promoted the abundance of the microbiome catalyzing the main processes of N and P turnover, which contradicted our hypothesis of gradual deteriorating fire effects on the microbiome increasing with fire intensity. In contrast, HF triggered the expected short-term decline of the soil microbiome, so that fire intensity was most decisive in directing the short-term fire impact on the soil microbiome. Therefore, we stress the importance to differentiate between different types of fires in future field and modelling studies targeted to predict the responses of microbial nutrient turnover including GHGs to fire. Data on fire intensity are thus highly relevant in order to correctly predict impacts of fires in the northern latitude which makes the use of satellite data insufficient that show relative fire intensities during a certain time based on pixels but regularly do not include high temporal resolution (down to minutes) as well as surface and soil temperatures during fires.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

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