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Postfire Phosphorus Enrichment Mitigates Nitrogen Loss in Boreal Forests

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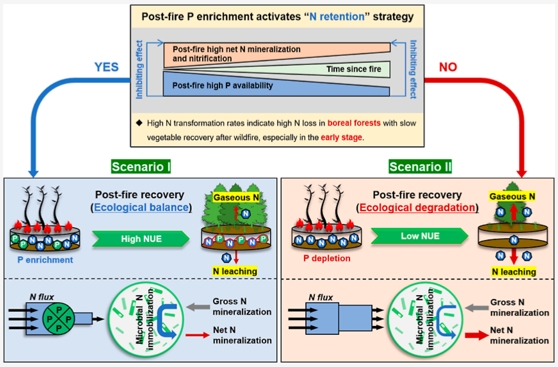
ABSTRACT: Net nitrogen mineralization (N_{min}) and nitrification regulate soil N availability and loss after severe wildfires in boreal forests experiencing slow vegetation recovery. Yet, how microorganisms respond to postfire phosphorus (P) enrichment to alter soil N transformations remains unclear in N-limited boreal forests. Here, we investigated postfire N−P interactions using an intensive regional-scale sampling of 17 boreal forests in the Greater Khingan Mountains (Inner Mongolia-China), a laboratory P-addition incubation, and a continental-scale meta-analysis. We found that postfire soils had an increased risk of N loss by accelerated N_{min} and nitrification along with low plant N demand, especially during the early vegetation recovery period. The postfire N/P imbalance created by P enrichment acts as a "N retention" strategy by inhibiting N_{min} but not nitrification in boreal forests. This strategy is attributed to enhanced microbial N-use efficiency and N immobilization. Importantly, our meta-analysis found that there was a greater risk of N loss in boreal forest soils after fires than in other climatic zones, which was consistent with our results from the 17 soils in the Greater Khingan Mountains. These findings demonstrate that postfire N−P interactions play an essential role in mitigating N limitation and maintaining nutrient balance in boreal forests.



KEYWORDS: *boreal forest, nitrogen limitation, ecological stoichiometry, nutrient cycling, wildfire, nutrient balance*

■ INTRODUCTION

Boreal forests cover ~1.10 billion hectares (27% of total forest area)[1] and provide ~32% (272 ± 23 Pg C) of the global forest carbon sink.[2] Rapid global warming in boreal regions is expected to result in a 111% increase of wildfire frequency in boreal regions by the end of the 21st century, as compared to a 29% increase for global wildfires overall.[3,4] Nitrogen (N) is the most common limiting nutrient in boreal forest ecosystems,[5] and a large portion of the vegetation/soil N stock can be lost to volatilization by severe wildfires, which can aggravate N limitation,[6,7] thereby determining the direction and speed of vegetation recovery after wildfire.[8−10] Therefore, it is crucial to understand postfire N dynamics for predicting vegetation recovery under the expected increase of fire frequency/severity in the rapidly warming climate of boreal forests.

As the rate-limiting step of organic−inorganic N turnover, the net N mineralization rate (N_{min}) is a key process controlling postfire N availability in boreal forests.[11,12] Moreover, the subsequent nitrification process is a key step controlling the amount of nitrate (NO_3^-) leaching and denitrification.[13] Vegetation recovery in boreal forests undergoing stand-replacing fires can take decades or even hundreds of years,[14−16] implying prolonged periods of low biotic N demand. If microorganisms provide more mineral N than can be taken up by plants (i.e., high soil N_{min} and nitrification), the excess N can be lost by denitrification and leaching after forest fires.[17] As such, the response of N_{min} and nitrification to fire will determine the overall relationship between soil N supply and plant N demand,[11,18] thereby dictating whether N is retained versus lost from postfire soils. However, there is no unifying principle concerning the response of N_{min} and nitrification to fire in the boreal forest zone.

Responses of N_{min} and nitrification to fire may reflect distinctions in microbial N requirements across postfire ecological recovery in distinct climate zones, which are closely related to the physiological responses of microorganisms.[19,20] According to ecological stoichiometric theory, microbial N requirement is related to the stoichiometric relationship between microbial biomass and soil nutrient availability (e.g., N/P stoichiometry).[21] Although much of wildfire ash is ephemeral due to removal by wind and water erosion, the

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remaining ash tends to create a postfire "phosphorus (P) enrichment" in forest ecosystems due to P accumulation in ash and the strong adsorption of phosphate to soil minerals.[22−24]

Theoretically, microorganisms preferentially reduce soil N_{min} and nitrification rather than producing/releasing more N-acquiring enzymes to meet their higher postfire N demands owing to fire-induced P enrichment because the production of extracellular enzymes is energy-intensive.[25−28] The stoichiometric ratios of soil microbial biomass (e.g., C/N/P) show a limited range compared to soil nutrient availability, suggesting that the soil microbial biomass composition maintains a state of homeostasis.[29] Therefore, microbial adjustment of N-use efficiency (microbial NUE, ratio of N invested in growth over total N uptake) is an important response to postfire P enrichment, that is, microorganisms retain excess N released through N_{min} and subsequent nitrification according to their metabolic needs.[26,27] However, there is a paucity of rigorous evidence revealing the role of postfire N−P interactions in controlling N_{min} and nitrification, especially in boreal forests.

Herein, we evaluated a stoichiometric hypothesis that soil N_{min} and nitrification are inhibited by postfire P enrichment in boreal forests (H1). To evaluate this hypothesis, we identified changes in postfire soil N and P availability and potential relationships with N_{min} and nitrification in a detailed field study from 17 independent stand-replacing forest fires across a 30 year fire chronosequence in the Greater Khingan Mountains (Inner Mongolia-China). We further posit that microbial NUE plays a vital role in regulating N_{min} and subsequent nitrification as a response to the postfire N/P imbalance (H2). To assess this hypothesis, we applied a P-addition gradient incubation and used a biogeochemical equilibrium model that predicts microbial NUE and ^{15}N isotopic pool dilution techniques that measure gross N transformation rates. Finally, we tested the hypothesis that this "N retention" strategy caused by N−P imbalance is widespread and plays a key role in boreal forest soils undergoing stand-replacing fires (H3). To verify this hypothesis, we conducted a meta-analysis of globally published literature examining soil N_{min} ($n = 377$) and nitrification ($n = 308$) following forest fires. The main objective of the study was to identify the effects of postfire P enrichment on the soil N cycle in boreal forests.

METHODS

Soil Sampling. Based on the forest fire history records of the local forestry bureau in the Greater Khingan Mountains, we selected sites where forest fires occurred in the past 30 years and where critical information such as fire location, fire severity, and prefire vegetation type were clearly recorded. Then, according to the principles of stand-replacing fire, site accessibility, large burned area, and similar vegetation types, 17 independent sites were finally selected. The study sites composed a 30 year postfire chronosequence within a nature reserve that experienced minimal human influence (e.g., prescribed fire, forest thinning, etc.).[30] Figure 2a provides a map of the study sites along with remote sensing derived ecosystem C density from Mao et al. (2019).[31] Each fire site contained paired samples from one unburnt and three burnt locations for a total of 68 total soil sampling sites. According to the historical records and remote sensing images from the State Forestry Administration, we were able to confirm that no fires occurred in the unburnt sites for at least 100 years (1915−2015) before sampling and that the burnt sites all experienced high-severity wildfires between 1985 and 2015. Stand-replacing forest fires (i.e., high-severity wildfires) are here defined as tree mortality rates greater than 70% and shrub, herb, and forest floor mortality/destruction greater than 90%. Each burnt site was similar to its paired unburnt site in terms of microhabitat (e.g., climate, landform, and soil type). Additional information for the Greater Khingan Mountains and 17 sampling sites is shown in Supplementary Methods and Table S1.

In July 2015, we established four 50 m × 50 m plots at each sampling location with a distance of more than 100 m including three burnt plots and one unburnt plot. To reduce soil heterogeneity, five subplots (10 m × 10 m, subsample distance at least 15 m apart) were established and a composite soil sample consisting of at least 10 cores was collected using a soil coring device (core sample distance was >1 m). Soil samples were collected from the organic layer (O horizon) and the top 15 cm of mineral soil (A horizon). For one of the 17 forest locations, we collected only O horizon soils because the thickness of O horizon in this unburnt plot was generally more than 30 cm. Before collecting O horizon soil, we carefully remove all small twigs, roots, fungal hyphae, and charcoal fragments. The collected soil samples were packed in sterile plastic bags, refrigerated, and returned to the laboratory for cold storage. Overall, we obtained a total of 132 soil samples, which included 68 O horizon soils (51 burnt and 17 unburnt) and 64 A horizon soils (48 burnt and 16 unburnt). Fresh soil was passed through a 2 mm screen, and subsamples of the <2 mm fraction were stored at −80 and 4 °C for the analysis of biochemical properties and incubation studies. An additional subsample of soil was air-dried and passed through 2 mm and 0.149 mm sieves for the determination of selected physical and chemical properties.

Assessments of Net N Mineralization and Net Nitrification Rates. The net N mineralization rate and net nitrification rate were calculated as the difference in inorganic N (NO_3^-−N and NH_4^+−N) concentrations extracted with 1 M KCl between the initial state and the end of a 30 day incubation at 20 °C and 60% water holding capacity (WHC).[32] The NO_3^-−N and NH_4^+−N concentrations were analyzed by two-wavelength ultraviolet spectrometry (220 and 275 nm) and the indophenol blue spectrophotometric method (625 nm) on a Microplate System (Synergy H1, BioTek, US), respectively.

Soil and Microbial Characterization. Soil water content was measured as mass loss after drying the soil at 105 °C for 24 h. Soil pH was determined in 1 M KCl suspension (soil/solution = 1:2.5) using a pH meter (FE28, Mettler Toledo, Switzerland). Soil total N content was determined using an elemental analyzer (Vario EL III, Elementar, Germany). While certain forms of soluble organic matter may not be readily available to microorganisms, amino acids and peptides are regarded as biologically active.[33] Thus, we measured soil dissolved organic C (DOC), total dissolved N (TDN), and available P contents. For DOC and TDN, 5 g of fresh soil was mixed with 20 mL of 0.5 M K_2SO_4 in a 50 mL centrifuge tube and shaken for 60 min. The suspension was filtered through a 0.45 μm membrane, and DOC and TDN were determined on an Elementar TOC analyzer (Multi N/C 3100, Analytikjena, Germany). Available P content was extracted with 20 mL of 0.05 M HCl-0.025 M H_2SO_4 solution from 5 g of air-dried soil and measured colorimetrically with the molybdate-ascorbic acid method on a Microplate System at 880 nm. Microbial biomass C (MBC) and N (MBN) contents were determined

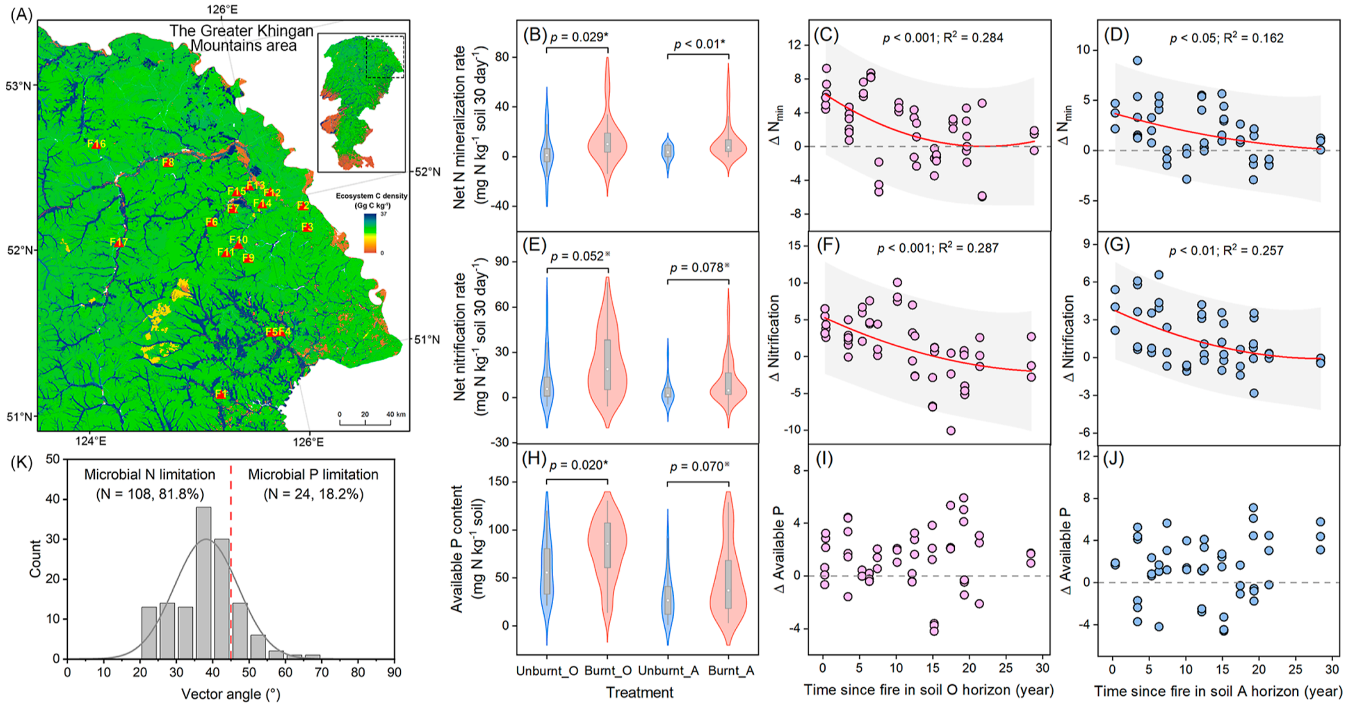

Figure 1. Distribution of 17 independent stand-replacing fires (A), changes of net N mineralization rate ($N_{\min}$) (B–D), net nitrification rate (E–G) and soil available P (H–J), and the distribution of microbial N/P limitation (K) following fire and over recovery time in O and A horizons across 17 forest fires during a 30 year postfire recovery period in the Greater Khingan Mountains of Inner Mongolia (China). The width of the violin represents the number of samples for a specific value. The box and whisker plots provide the 5th, 25th, 75th, and 95th quartiles (interquartile range); white point represents the median value. * and # denote significant difference between unburnt and burnt treatments at $p < 0.05$ and 0.10, respectively. Sample numbers for unburnt (17) and burnt (51) sites in O horizon and unburnt (16) and burnt (48) sites in A horizon. Strong significant regressions at $p < 0.05$ level are shown as solid lines. Insignificant regressions are not shown at $p > 0.10$ level. Δ (delta values) calculated as Normalization(X_{Burnt}) − Normalization(X_{Unburnt}); Normalization(X) = SIGN(X) × SQRT(ABS(X)), where X is the observation value. Vector angle >45° represents microbial P limitation, and vector angle <45° represents microbial N limitation. Microbial P limitation increases with increasing vector angle, whereas microbial N limitation decreases with increasing vector angle.

using chloroform fumigation and calculated using the universal conversion factors of 0.45 for MBC[34] and 0.54 for MBN.[35]

The activities of C-acquiring enzymes [β-1,4-glucosidase (BG) and β-D-cellobiosidase (CBH)], N-acquiring enzymes [β-1,4-*N*-acetylglucosaminidase (NAG) and leucine amino-peptidase (LAP)], and P-acquiring enzymes [acid and alkaline phosphatase (AP)] were determined by a fluorometric method using the substrates labeled with 4-methylumbelliferone (MUB) or 7-amino-4-methylcoumarin (AMC).[36] Prepared plates were incubated in the dark at 20 °C for up to 4 h following substrate addition before measuring fluorescence using a Microplate System with 365 nm excitation and 450 nm emission filters.

Microbial NUE was calculated as follows[27]

$$\text{NUE} = \text{CUE}/(B_{\text{C:N}}/L_{\text{C:N}})$$

$$\text{CUE} = \text{CUE}_{\max}[S_{\text{C:N}}/(S_{\text{C:N}} + K_{\text{N}})]$$

$$S_{\text{C:N}} = (1/\text{EEA}_{\text{C:N}})(B_{\text{C:N}}/L_{\text{C:N}})$$

where $S_{\text{C/N}}$ represents the extent to which the allocation of enzyme activities offsets the disparity between the elemental composition of dissolved resources (DOC/TDN) and the composition of microbial biomass (MBC/MBN). K_{N} is the half-saturation constant and was set to 0.5. $\text{CUE}_{\max}$ is the maximum microbial C-use efficiency and was set to 0.6 based on thermodynamic constraints. $\text{EEA}_{\text{C/N}}$ is the ratio of C- to N-acquiring enzyme activities and was calculated as BG:(NAG + LAP). $B_{\text{C/N}}$ is the microbial biomass C/N ratio and $L_{\text{C/N}}$ is the dissolved organic matter C/N ratio.

This study aimed to determine how soil microorganisms respond to the elemental imbalance after forest fires to control soil N transformations. Therefore, microbial element limitation was assessed by enzyme ratios, which is different from the concept of element limitation at the forest ecosystem level.[25,33,37] To measure the extent of soil microbial N and P limitations, we used vector analysis[37] of the soil enzymatic stoichiometry based on untransformed proportional activities as follows

$$\text{Vector angle }((°) = \text{DEGREES}(\text{ATAN2}(x, y))$$

where x represents the relative activity of C- versus P-acquiring enzymes and is calculated as (BG + CBH)/(BG + CBH + AP), and y represents the relative activity of C- versus N-acquiring enzymes and is calculated as (BG + CBH)/(BG + CBH + NAG + LAP). Vector angles >45° represent microbial P limitation, whereas vector angles <45° represent microbial N limitation. Microbial P limitation increases with increasing vector angle, while microbial N limitation decreases with increasing vector angle.

P-Addition Experiment. We conducted a P-addition gradient experiment to explore whether P enrichment has a linear inhibition on soil N mineralization and nitrification. The physicochemical properties and microbial characteristics of forest soil may be disturbed by wildfire for a long time.[7,23,24,30] To explore the N−P interaction mechanism in postfire soil, we selected burned soil rather than unburnt soil to conduct the P addition experiments. Soil available P contents varied greatly among burnt soils in the Greater Khingan Mountains, ranging from 3 to 130 mg P kg^{-1} soil. The mean increase in available P contents due to fire was 18.4 mg P kg^{-1} soil in O horizons and 20.5 mg P kg^{-1} in A horizons. Overall, available P content did not change with time since fire (Figure 1) but was positively correlated with dissolved organic N content ($p < 0.001$; Figure S1E). This indicates that the N−P interaction driven by postfire P enrichment may exist for a long time in the Greater Khingan Mountains.

Considering the prevalence of N limitation in boreal forests,[5] we selected nine representative soils (OB19, OB22 OB25, OB33, AB3, AB8, AB13, AB19, and AB27) that had microbial N limitation based on vector angles <35° (Table S2). Given the various P adsorption potentials for forest soils, we set the maximum P addition concentration to 80 mg P kg^{-1} soil to simulate the expected range of the postfire natural fire-induced P increment (Figure S2A). The P gradient consisted of nine concentration levels (0, 5, 10, 15, 20, 30, 40, 60, and 80 mg P kg^{-1} soil) with 3 replicates for each soil (9 soils × 9 P levels × 3 replicates = 243 total samples). Further, we use 5 g of soil (dry weight) for each sample and chose to extend the incubation time for N_{min} and nitrification from 30 to 180 days at 20 °C and 60% WHC to amplify N−P interactions.

Next, we selected two soils from the above nine burnt soils (limited to two soils due to experimental costs) for measurements of microbial biomass N, gross N transformation rate, and microbial NUE. The two soils were selected as NH_4^+-dominated (OB22 soil: NH_4^+−N 79 mg N kg^{-1} soil and NO_3^-−N 9 mg N kg^{-1} soil) and NO_3^--dominated (AB17 soil: NH_4^+−N 2 mg N kg^{-1} soil and NO_3^-−N 88 mg N kg^{-1} soil) end-members of the overall soils (2 soils ×9 P levels ×3 replicates = 54 total samples). Potassium dihydrogen phosphate (KH_2PO_4) was applied as the source of the exogenous P. The KH_2PO_4 was chosen as it has a minimal effect on the overall K^+ background concentration of the burnt soils[38] and it does not appreciably affect the soil pH (Figure S2B).

Assessment of Gross N Transformation Rate. To determine gross N transformation rates, a ^{15}N tracer experiment was conducted using isotope pool dilution techniques (^{15}N-IPD).[39] Briefly, two ^{15}N labeled treatments were designed to increase isotopic enrichment to <10 atom %, i.e., $(^{15}NH_4)_2SO_4$ (98.0 atom %, Spectra and Cambridge Isotope Laboratories, Europe, Radeberg, Germany), and $K^{15}NO_3$ (98.0 atom %, Isotec-Sigma-Aldrich, Vienna, Austria). The samples were incubated for 24 h at 20 °C and 60% WHC. At 1 (T_0) and 24 h (T_1) after ^{15}N addition, the soils (3 replicates for each labeled treatment) were extracted with 1 M KCl (5:1 solution/soil) to determine the concentration and ^{15}N enrichment of NH_4^+−N and NO_3^-−N in the extracts. The ^{15}N abundance of NH_4^+ and NO_3^- was analyzed following published protocols using an isotope ratio mass spectrometer (Delta Plus XP, Thermo Finnigan, Germany). See Supplementary Methods for the calculation of gross N mineralization rate (mg N kg^{-1} dry soil day^{-1}).

Data Collection and Analysis of N_{min} and Nitrification for Meta-Analysis. Literature studies for our meta-analysis were obtained by searching Google Scholar, Web of Science, and CNKI databases using the search terms: TS = [(burn* OR *fire*) AND soil AND forest AND ("nitrogen mineralization" OR "nitrification")]. Articles were selected according to specific criteria outlined in the Supplementary Methods. Based on these criteria, a total of 377 pairs of observations from 67 papers and 308 pairs of observations from 43 papers published before December 2022 were included in this synthesis of soil N_{min} and nitrification, respectively. Then, the response ratios of soil N_{min} and nitrification due to forest fire disturbance were calculated for different categories (e.g., fire severity, vegetation type, and climatic region) (see Supplementary Methods).

Statistical Analyses. All data were checked for normality and homogeneity of variance using the Shapiro−Wilk test and Levene's test, respectively, and sqrt-transformed when necessary. We used a *t*-test to assess differences between burnt versus unburnt soil properties and conducted an ordinary-least-squares regression to evaluate the relationships of soil N transformation parameters with time since fire, soil N−P availability, and P-addition gradient. All statistical analyses were performed using SPSS 22.0. The levels of $p < 0.10$ and $p < 0.05$ were considered weakly and strongly significant, respectively.

RESULTS AND DISCUSSION

High N_{min} and Nitrification Induce Soil N Loss after Wildfire in Boreal Forests. We can acquire a more comprehensive assessment of whether soil N pools are degraded or have potential N loss risk after forest fires by comparing the different N pools. We found that soil total N content significantly decreased by 47.5% in O horizon and 40.5% in A horizon ($p < 0.001$) following severe stand-replacing fires in the Greater Khingan Mountains due to pyrovolatilization of organic matter and reduced plant litter inputs.[24] The total soil N pool generally recovered in O ($p < 0.01$) and A horizons by atmospheric N deposition[8] and biological N fixation[18] during the 30 year recovery period (Figure S3D−F). However, the postfire recovery of the soil total N pool in the Greater Khingan Mountains was slower than the global average (∼10 years),[24] suggesting that boreal forests have potential N limitation risks associated with more frequent fires in the future. In addition to N deposition and biological N fixation as exogenous inputs, N loss is a key factor affecting the recovery rate of the soil N pool after wildfire in boreal forests.

After forest fires, a portion of N from ash and charred organic matter leachates is lost through runoff and wind erosion, regardless of N form.[40] The remaining N leaches to the subsoil horizons,[41−43] where it may be retained by biological uptake and mineral adsorption or lost by gaseous emission (NH_3, N_2O, NO_X, and N_2) and leaching [i.e., dissolved inorganic N (DIN) and dissolved organic N (DON)].[17,18,40,44,45] We found that soil DIN content showed a depletion during postfire recovery in the Greater Khingan Mountains (Figure S3E,F; $R^2 = 0.118$, $p < 0.05$ in O horizon; $R^2 = 0.180$, $p < 0.01$ in A horizon). In contrast, soil DON content gradually increased during postfire recovery (Figure S3H,I; $R^2 = 0.086$, $p < 0.05$ in O horizon; $R^2 = 0.221$, $p < 0.001$ in A horizon). Soil DON gradually replaced DIN as the dominant form of extractable N during postfire recovery. Though plants continue to favor inorganic N forms, conifers commonly invest in ectomycorrhiza to access organic N sources.[46] Thus, we speculate that this shift in the dominant N form may promote the plant availability of N in boreal forests as some boreal forest species can directly utilize DON (e.g., peptides, amino acids) during postfire vegetation recovery.[19]

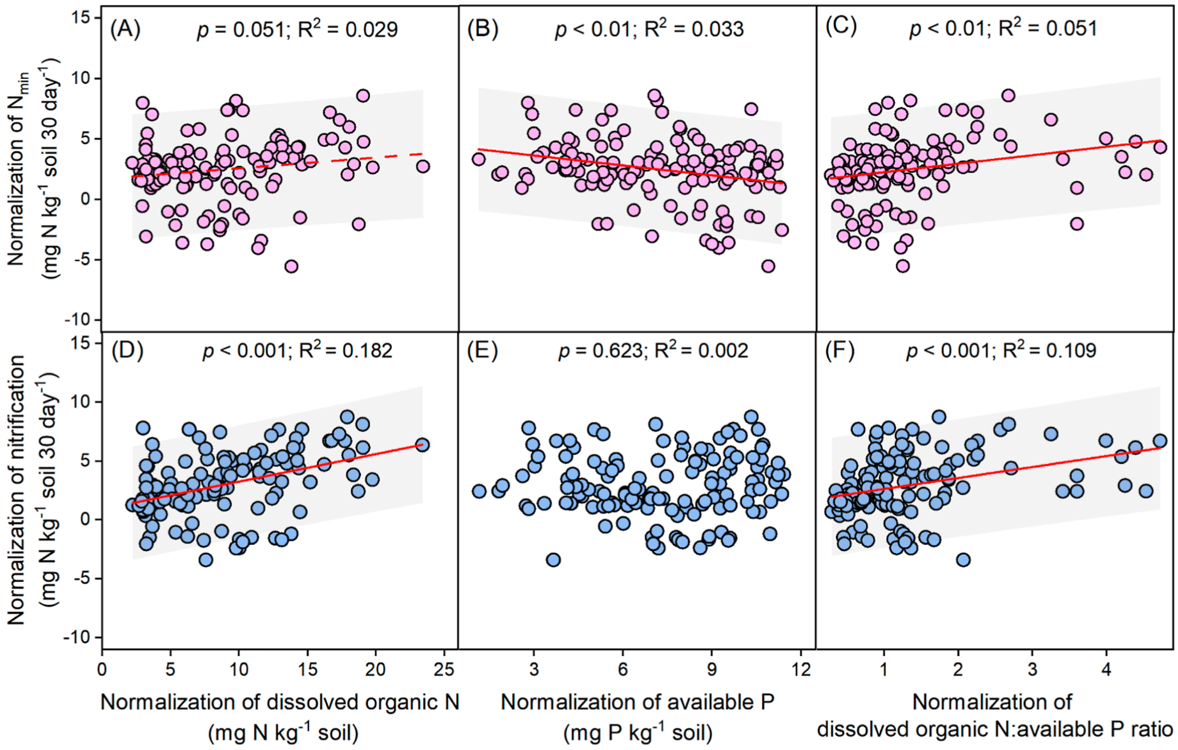

Figure 2. Relationships of soil net N mineralization rate (N_{min}) (A−C) and net nitrification rate (D−F) with dissolved organic N, available P, and their ratios across 17 forest fires in the Greater Khingan Mountains. Strong ($p < 0.05$) and weak ($p < 0.10$) significant regressions are shown as solid and dotted lines, respectively. Insignificant regressions ($p > 0.10$) are not shown. The gray areas represent the 95% confidence intervals (CIs). Data were normalized as Normalization(X) = SIGN(X) × SQRT[ABS(X)], where X is the observation value.

We acknowledge that although soil total and inorganic N stocks were not measured in this study, N stocks are better descriptions of ecosystem development relative to newly burned or undisturbed forests than DIN and DON concentrations that more readily address biological availability.

Considering the slow vegetation recovery of boreal forests after severe wildfire, soil DON supply is more synchronous with plant N demand than soil DIN during postfire recovery. This is common in undisturbed snow-dominated ecosystems where N export occurs in early spring before plant nutrient uptake ramps up,[47] and the pattern is more obvious after fire disturbance. Importantly, soluble N (i.e., DIN and DON) has high biological activity and a high risk of loss from forest soils after fires due to its high mobility.[48] Given the limited rainfall (<500 mm) and winter frozen soils in boreal regions, N loss by leaching may be limited, whereas gaseous emissions are deemed an important N loss mechanism in boreal forest ecosystems.[17,49]

Soil N_{min}, as a key step in organic−inorganic N turnover, was accelerated by 314% in O horizons ($p = 0.029$) and 260% in A horizons ($p < 0.01$) following fire, especially in the early stage (Figure 1B). Subsequently, soil nitrification rate, which determines the potential for leaching and denitrification by producing NO_3^-−N,[13] was increased by 93% in O horizons ($p = 0.052$) and 165% in A horizons ($p < 0.078$) following fire, particularly in the early stage (Figure 1E). Meanwhile, we found that N_{min} and nitrification gradually returned to prefire conditions in soil O and A horizons in boreal forests of the Greater Khingan Mountains ($p < 0.05$) (Figure 1C,D,F,G). Clearly, the early postfire excess DIN supply from high N_{min} and nitrification is highly suspectable to losses from NO_3^-−N leaching and gaseous emissions.

Postfire P Enrichment Inhibited Soil N_{min} but Not Nitrification. Faced with the high N loss risks in boreal forests after wildfire, it is important to identify the key factors controlling postfire soil N transformations (e.g., N_{min} and nitrification) that attenuate N losses. Soil pH was negatively correlated with N_{min} and positively correlated with nitrification (Figure S1A,B). These opposing trends imply that the positive effect of pH on soil N retention may be offset due to differences in the optimal pH values of the microorganisms and their enzymes involved in these two processes.[12,13] Moreover, soil N transformations should be regulated in part by elemental imbalances between microorganism nutrient requirements and the soil nutrient resources (e.g., N/P stoichiometry).[21,28] We found that the DON: available P ratio was significantly related to N_{min} and nitrification ($p < 0.01$ and $p < 0.001$, respectively; Figure 2C,F), which supports the ecological stoichiometric theory. Specifically, soil N_{min} had positive and negative correlations with DON ($R^2 = 0.029$, $p = 0.05$) and available P content ($R^2 = 0.033$, $p < 0.01$) across the 17 postfire forest sites in the Greater Khingan Mountains, respectively (Figure 2A,B). Soil nitrification showed a positive relationship with DON ($R^2 = 0.182$, $p < 0.001$) (Figure 2D). This implies that soil N_{min} was regulated jointly by N and P availability, while nitrification was regulated only by N availability.

Soil available P content was enhanced by 33.9% in O horizons ($p = 0.020$) and 59.1% in A horizons ($p = 0.070$) across the 17 forests following stand-replacing fires (Figure 1H). As P is not readily volatilized during a forest fire,[50] it generally increases in the residual ash of the postfire soil.[51] This ash could increase soil pH,[38] thereby reducing the amount of iron- and aluminum-bound P in acidic soils and thus increasing P availability[52] (Figure S1C). P enrichment in

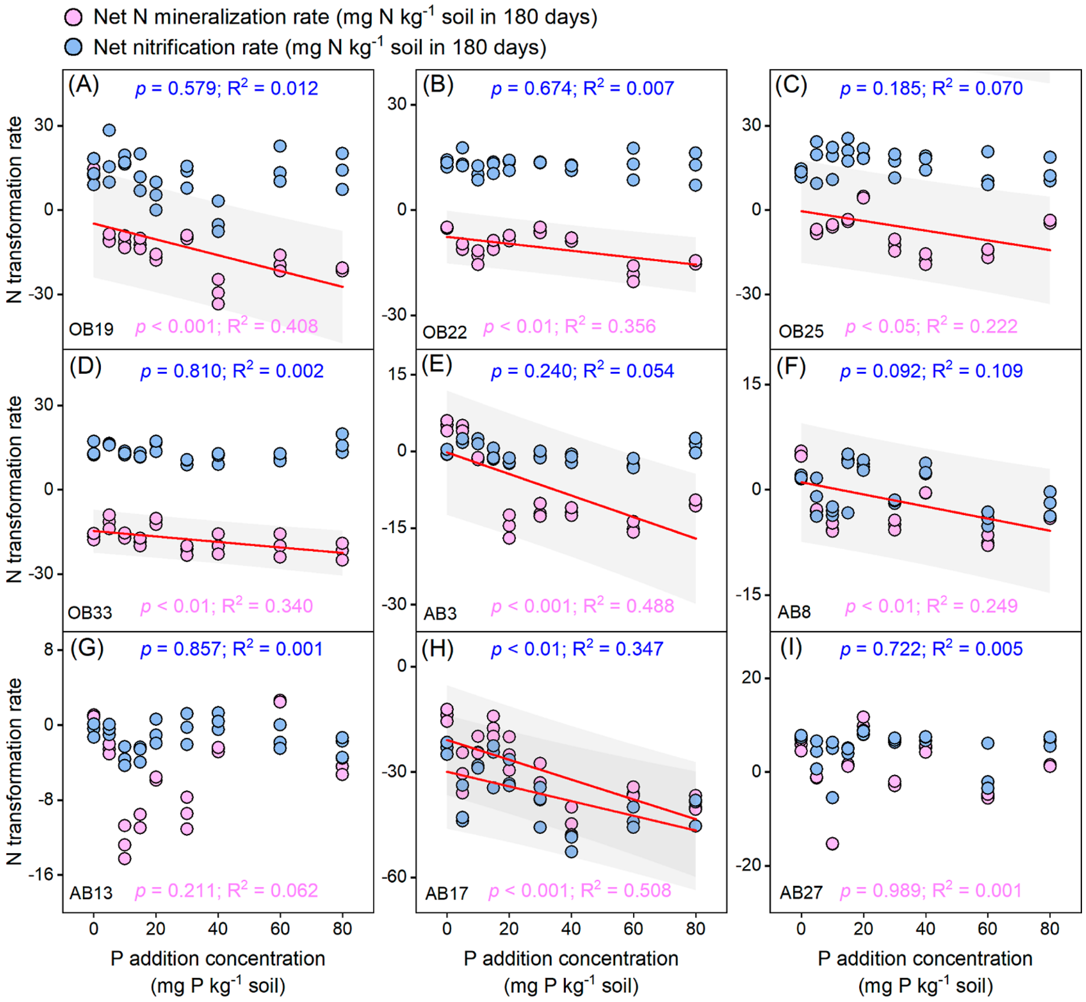

Figure 3. Net N mineralization rate (pink circle) and net nitrification rate (blue circle) of 9 N-limited soils (based on enzyme ratio) from the Greater Khingan Mountains during a 180 day incubation as a function of P-addition rate. Significant linear regressions ($p < 0.05$) are shown as solid lines; insignificant linear regressions ($p > 0.05$) are not shown. The gray areas represent the 95% CIs.

both O and A horizons persisted for at least three decades following fires in the Greater Khingan Mountains (Figure 1I,J) but was especially prominent during the earlier recovery stages having a lower N/P ratio (Figure S3N,O). In the face of stoichiometric imbalance, microorganisms will choose to increase the intake of limiting elements to maintain their homeostasis,[28,29,53] suggesting that this postfire P enrichment could enhance biotic N demand and tighten the soil N cycle,[53−56] which would act to alleviate N losses. This infers that the postfire inhibition effects of the N/P imbalance on N_{min} resulting from soil P enrichment could preserve N in N-limited boreal forests.

To directly assess whether N/P imbalance resulting from P enrichment inhibits soil N_{min} in boreal forests, we selected nine burnt soils with severe microbial N limitation (based on enzyme ratios) and applied a P-addition gradient experiment for each soil. With different soil banding properties (e.g., pH, organic matter, and metals),[52,57] the P addition gradient experiments showed variable responses of P availability among the nine soils after the 180 day incubation (Figure S2). Regardless of the available P increment, soil N_{min} linearly declined with increasing amounts of added P (Figure 3; $p < 0.05$; 7 of 9 soils). Although two soils did not display a linear relationship between N_{min} and P addition, soil N_{min} generally decreased when comparing P addition treatments with the treatment having no P addition ($p < 0.05$). By contrast, the inhibition of soil nitrification by P addition was only shown in a NO_3^-−N-dominated soil (Figure 3). This experiment provides compelling evidence that postfire P enrichment can inhibit soil N_{min} but not nitrification in boreal forests.

We next selected two soils having a high NH_4^+−N to NO_3^-−N ratio ("NH_4^+-dominated soil", OB22) and a low NH_4^+−N to NO_3^-−N ratio ("NO_3^--dominated soil", AB17) from the nine soils utilized in the P addition trials for further investigation of N−P interactions. We found that microbial biomass N/C ratios, where microbial biomass C content was regarded as live microbial biomass, increased at higher levels of P addition in both soils (Figure 4A,C; Pearson's $r = 0.499$ in NH_4^+-dominated soil and 0.631 in NO_3^--dominated soil; $p < 0.01$). This implies that postfire P enrichment increased microbial N immobilization. In addition, microbial NUE increased at higher P addition levels in both the NH_4^+-dominated soil (Pearson's r = 0.433; $p < 0.05$) and NO_3^--dominated soil ($r = 0.693$; $p < 0.001$) (Figure 4B,D). High NUE indicates that microorganisms effectively assimilate/immobilize N and release only a small part of the N back to the soil environment as DIN (i.e., low N_{min}).[27] In the NH_4^+-dominated soil, the gross N mineralization rate ($r = 0.570$, $p <$

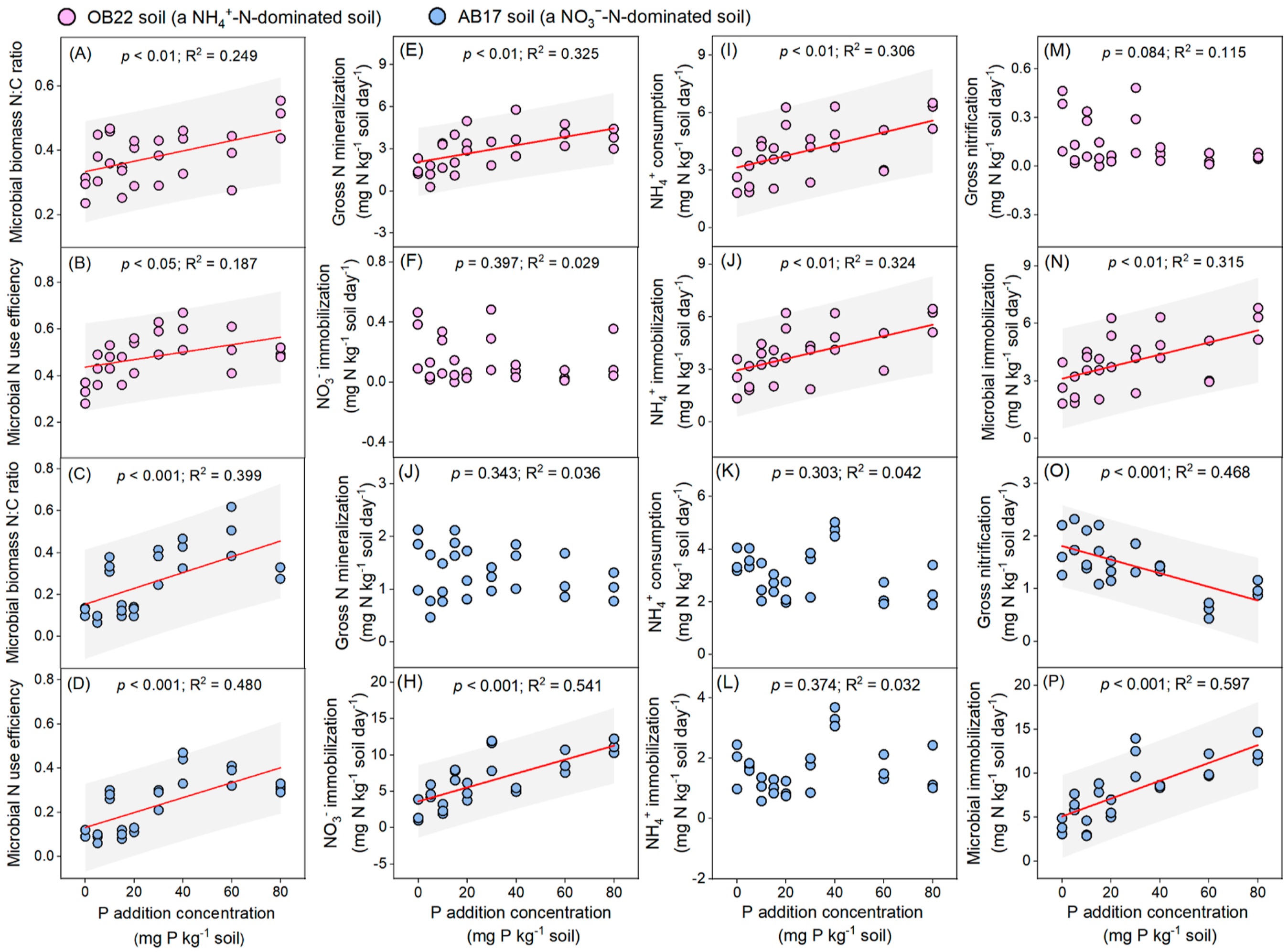

Figure 4. Soil gross N transformation rate, microbial biomass N/C ratios, and microbial NUE of a NH_4^+−N-dominated soil (OB22 soil, pink circle) and a NO_3^-−N-dominated soil (AB17 soil, blue circle) in the Greater Khingan Mountains during the 180 day incubation as a function of P addition rate. The background value of inorganic N pool in NH_4^+−N-dominated soil was 79 mg NH_4^+−N kg^{-1} soil and 9 mg NO_3^-−N kg^{-1} soil, and in NO_3^-−N-dominated soils was 2 mg NH_4^+−N kg^{-1} soil and 88 mg NO_3^-−N kg^{-1} soil. Significant linear regressions ($p < 0.05$) are shown as solid lines; insignificant linear regressions ($p > 0.05$) are not shown. The gray areas represent the 95% CIs.

0.01) and NH_4^+ immobilization rate ($r = 0.569$, $p < 0.01$) increased at higher P levels (Figure 4E,J). In the NO_3^--dominated soil, the gross nitrification rate and NO_3^- immobilization rate showed negative ($r = -0.684$, $p < 0.001$) and positive ($r = 0.735$, $p < 0.001$) relationships with added P levels, respectively (Figure 4O,H). These findings are consistent with the hypothesis that soil microorganisms enhance NUE by promoting microbial N immobilization in response to postfire N/P imbalance. This strategy is an effective mechanism for microorganisms to cope with soil N losses under postfire P enrichment in N-limited boreal forests (79.9% of sampling sites were N-limited in the Greater Khingan Mountains) (Figure 1K).[28,54,58,59] Overall, these results provide a plausible explanation for how boreal forests conserve the soil N pool to limit ecological degradation after severe fire disturbance.

Ecological Significance of Soil N−P Interactions for Postfire Recovery in Global Forests. To investigate the response of soil N_{min} and nitrification to forest fires on the continental scale, we conducted a global meta-analysis of 377 and 308 pairs of observations, respectively (see Supplementary Methods). Coniferous forests (based on vegetation type) and boreal areas (based on climatic zone) showed high response ratios to forest fires both in terms of N_{min} and nitrification than other types (N_{min} in coniferous forests: mean response ratio [MRR] = 0.064 [95% bias-corrected CIs: −0.318 to +0.445], N_{min} in boreal areas: MRR = 0.597 [−0.056 to +1.250]), nitrification in coniferous forests: MRR = 0.471 [+0.261 to +0.691], nitrification in boreal areas: MRR = 0.250 [+0.017 to +0.448] (Figure 5). Nitrification and N_{min} were positively correlated with latitude (absolute value), negatively correlated with MAT and soil pH, and had no correlation with MAP and time since fire (Figure S4, $p < 0.05$). These results were consistent with our observations in the Greater Khingan Mountains having a boreal forest dominated by *Larix gmelina*, acidic soil (pH = 5.5), cold climate (<0 °C), and high latitude (>50 °C) (Figure 2).

In boreal regions, plant N resorption efficiency is high,[60] resulting in a low leaf N/P ratio.[61] Differences in leaf N/P ratios usually correspond to differences in the litter N/P ratios, with soil microorganisms acquiring more P than N from litter.[28] Moreover, given the age of soil substrates, N is typically the dominant limiting nutrient in younger and less leached soils, such as boreal regions.[28,48,62] These phenomena illustrate a tightening of the soil N cycle in mature forests of boreal regions (regarded as a "conservative N cycle"). Following a

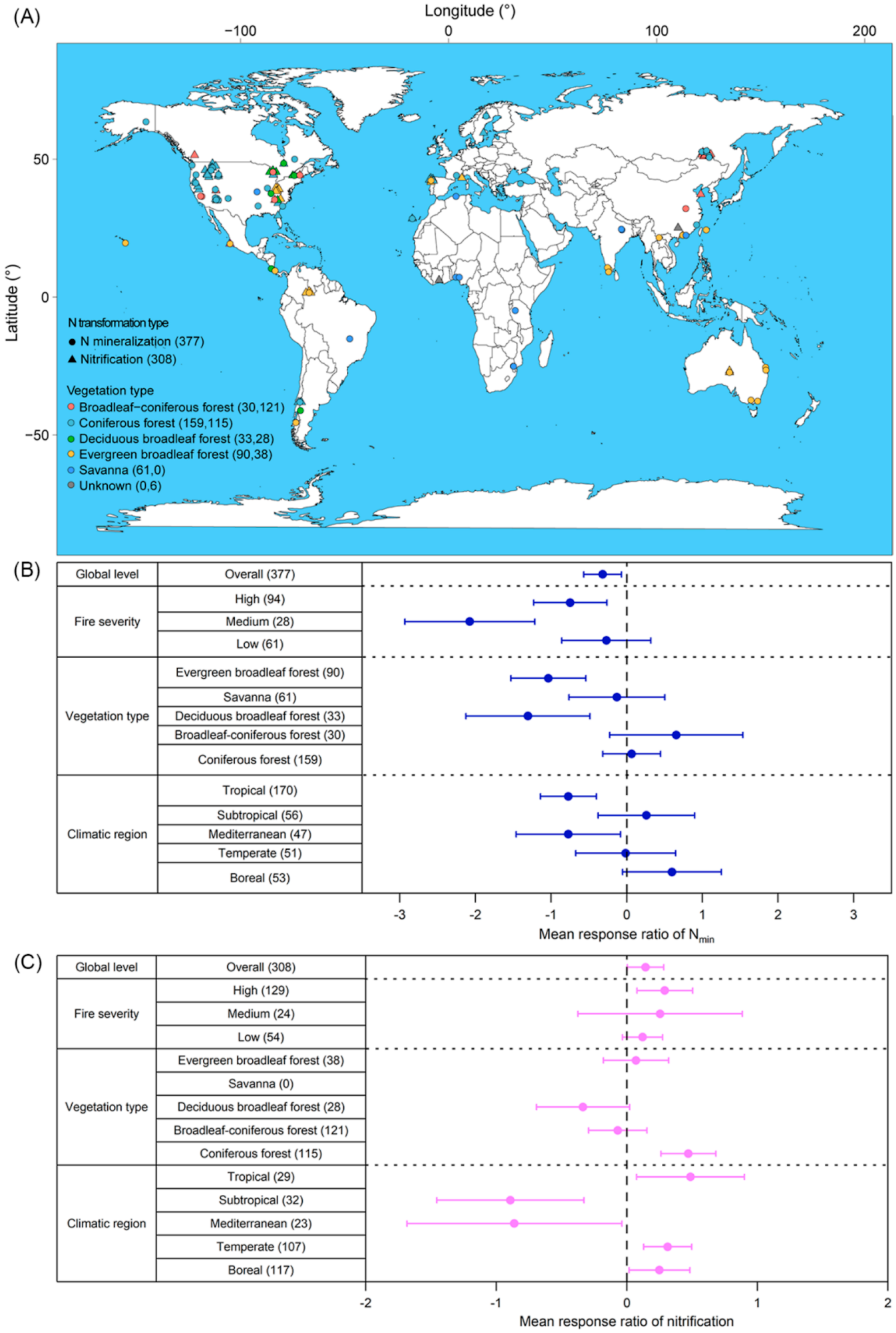

Figure 5. Global map showing the location of studies included in the meta-analysis (A) and the effect size of global forest fires on soil net nitrogen mineralization rate (N_{min}) (B) and nitrification rate (C). Numbers in parentheses denote the number of observations for N_{min} and nitrification. Error bars represent 95% CIs. Significant responses ($p < 0.05$) are recognized if the 95% CI does not overlap with zero. Broadleaf-coniferous forest is a transitional type between deciduous broadleaf forest and coniferous forest, which means that the forest in the study area is mainly composed of these two types of vegetation.

forest fire, soil N losses by microbial metabolism and/or leaching are limited by low temperature (e.g., frozen soils) due to the low water viscosity[63] and membrane permeability[61] in boreal regions. Further, N competition between microorganisms and the slowly recovering plant community is weakened (regarded as an "open N cycle").[16] Therefore, fires cause forest soils in boreal regions to change from a "conservative" to a more "open" N cycle, which drives an

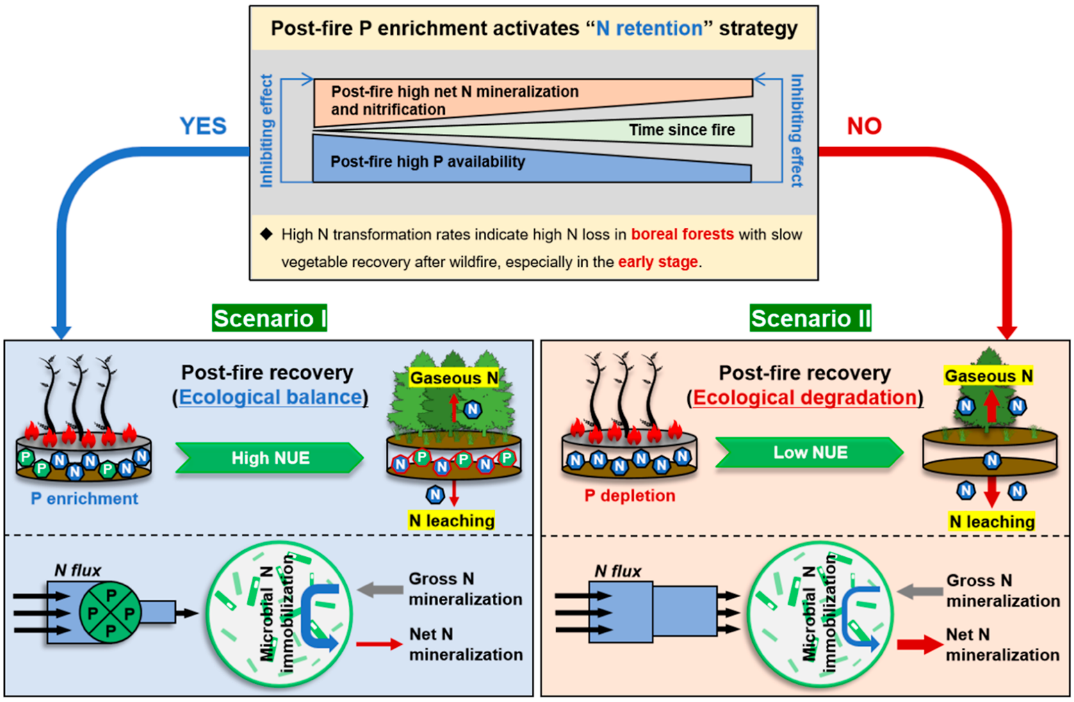

Figure 6. Conceptual diagram of soil N transformations as regulated by P availability after boreal forest fires. A long-term "fire N fertilization effect", caused by burnt organic matter and increased postfire soil $N_{\min}$ and nitrification, appears in boreal forests until plant biomass and N demand increase substantially. In P-enriched environments, microorganisms will retain labile N forms by changing the mineralization-immobilization turnover, which is conducive to maintaining an ecological nutrient balance, a mechanism we term the "N retention strategy". In P-depleted environments, microorganisms will not activate this "N retention strategy", resulting in enhanced N leaching and gaseous N emission. The persistence of postfire P enrichment implies that the "N retention strategy" may be particularly important for N-limited boreal forests, especially in the early succession.

increase in postfire soil $N_{\min}$ and nitrification. In sum, these results corroborate that fire stimulation of the N cycle is a distinctive feature of boreal forests. These results fully support that there is a general phenomenon of a greater risk of N loss after fires in boreal forests. This may also explain why boreal forest ecosystems often appear to be N limited, along with low N fixation and weak weathering reported in previous studies.[5,60,61] Hence, recurrent wildfires may be a key component contributing to the phenomenon of N limitation in boreal forests.

Our meta-analysis found that enhanced soil available P content is a universal phenomenon following forest fires on the continental scale ([MRR] = +0.473 [CIs: +0.366 to +0.588]) (Figure S5A). Notably, boreal forests generally showed strong P-enrichment following high-severity fires (Figure S5A), especially in the earlier stages of recovery (Figure S5D). Moreover, we found that Inceptisols (MMR = 0.980 [0.699 to 1.261]) and Spodosols (MMR = 0.919 [0.609 to 1.229]) showed the largest increase across major soil types (Figure S5C). Inceptisols generally exhibit only moderate degrees of soil weathering and development.[64] The low degree of weathering results in low background levels of available P and is therefore more responsive to the input of ash-derived P. Spodosols formed from intensive weathering/leaching processes that strip organic matter combined with aluminum and iron from the surface soil and deposit them in the subsoil.[64] The limited metal ions in the topsoil reduce the immobilization of ash-P and increase P availability. Notably, these two soil types are widely distributed in the Greater Khingan Mountains and throughout other northern regions[65] (Figure S5B).

In conclusion, the fire-induced increase in soil $N_{\min}$ and nitrification contributes to the N asynchrony between the microbial supply and plant demand, thereby enhancing N losses in boreal forests especially in the early recovery stages.[16] The increase in size, frequency, and severity of wildfires in the rapidly warming boreal region will likely amplify the leakage of N and hinder natural vegetation recovery.[66−69] Therefore, we posit that $N_{\min}$ inhibition by postfire P enrichment is an important mechanism to conserve N following wildfires in boreal forest ecosystems. Although P availability had little effect on nitrification (Figure S1D), soil $N_{\min}$ directly controls the main substrate source of nitrification;[13] hence, P availability also indirectly regulates the nitrification process. Soil N conservation mechanisms will be important for maintaining net primary productivity and ecosystem carbon storage in the face of the global increasing risk of severe forest fires in the future[23] (Figure 6).

■ ASSOCIATED CONTENT

Data Availability Statement

The data that support the findings of this study are available from the corresponding authors upon request.

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.est.4c01662.

Site description of the Greater Khingan Mountains; calculation of gross N transformation rate; data collection and analysis of $N_{\min}$ and nitrification for meta-analysis; data collection and analysis of available P in meta-analysis; relationships between soil N transformation rates and pH across 17 forest fires; soil available P content and pH of the nine N-limited soils in the P-addition gradient experiment; changes of soil pH and soil N and P pools across 17 forest fires during a 30 year postfire recovery; linear relationships between continuous variables associated with site and fire history characteristics and the response ratio for soil N transformation rates in meta-analysis; effect sizes of fire on soil available P content in meta-analysis; description of the study sites for the 17 forest ecosystems; and basic properties of the nine microbial N-limited soils in the P-addition gradient experiment (PDF)

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Author Contributions

J.X. got the funding, developed the original idea, and designed the study. H.S. conducted the laboratory experiments, statistical analyses, and wrote the first draft. J.X., Z.D., D.T., and R.A.D. edited the paper. Q.Z. provided technical guidance for N transformation rate. W.-q.S. collected soil samples.

Notes

The authors declare no competing financial interest.

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REFERENCES

(1) FAO. *Global Forest Resources Assessment 2020-Key Findings*; FAO: Rome, 2020..

(2) Pan, Y.; Birdsey, R. A.; Fang, J.; Houghton, R.; Kauppi, P. E.; Kurz, W. A.; Phillips, O. L.; Shvidenko, A.; Lewis, S. L.; Canadell, J. G.; Ciais, P.; Jackson, R. B.; Pacala, S. W.; McGuire, A. D.; Piao, S.; Rautiainen, A.; Sitch, S.; Hayes, D. A large and persistent carbon sink in the world's forests. *Science* **2011**, *333*, 988−993.

(3) Markon, C. J.; Trainor, S. F.; Chapin, F. S. *The United States National Climate Assessment-Alaska Technical Regional Report: U.S. Geological Survey Circular 1379*, 2012.

(4) Senande-Rivera, M.; Insua-Costa, D.; Miguez-Macho, G. Spatial and temporal expansion of global wildland fire activity in response to climate change. *Nat. Commun.* **2022**, *13*, 1208.

(5) Du, E.; Terrer, C.; Pellegrini, A. F. A.; Ahlström, A.; van Lissa, C. J.; Zhao, X.; Xia, N.; Wu, X.; Jackson, R. B. Global patterns of terrestrial nitrogen and phosphorus limitation. *Nat. Geosci.* **2020**, *13*, 221−226.

(6) Toberman, H.; Chen, C.; Lewis, T.; Elser, J. J. High-frequency fire alters C: N: P stoichiometry in forest litter. *Global Change Biol.* **2014**, *20*, 2321−2331.

(7) Zhou, Y.; Biro, A.; Wong, M. Y.; Batterman, S. A.; Staver, A. C. Fire decreases soil enzyme activities and reorganizes microbially mediated nutrient cycles: A meta-analysis. *Ecology* **2022**, *103*, No. e3807.

(8) Pellegrini, A. F.; Hoffmann, W. A.; Franco, A. C. Carbon accumulation and nitrogen pool recovery during transitions from savanna to forest in central Brazil. *Ecology* **2014**, *95*, 342−352.

(9) Klupar, I.; Rocha, A. V.; Rastetter, E. B. Alleviation of nutrient co-limitation induces regime shifts in post-fire community composition and productivity in Arctic tundra. *Global Change Biol.* **2021**, *27*, 3324−3335.

(10) Pellegrini, A. F. A.; Anderegg, L.; Pinto-Ledezma, J. N.; Cavender-Bares, J.; Hobbie, S. E.; Reich, P. B. Consistent physiological, ecological and evolutionary effects of fire regime on conservative leaf economics strategies in plant communities. *Ecol. Lett.* **2023**, *26*, 597−608.

(11) Elrys, A. S.; Ali, A.; Zhang, H.; Cheng, Y.; Zhang, J.; Cai, Z. C.; Muller, C.; Chang, S. X. Patterns and drivers of global gross nitrogen mineralization in soils. *Global Change Biol.* **2021**, *27*, 5950−5962.

(12) Li, Z.; Tian, D.; Wang, B.; Wang, J.; Wang, S.; Chen, H. Y. H.; Xu, X.; Wang, C.; He, N.; Niu, S. Microbes drive global soil nitrogen mineralization and availability. *Global Change Biol.* **2019**, *25*, 1078−1088.

(13) Li, Z.; Zeng, Z.; Tian, D.; Wang, J.; Fu, Z.; Zhang, F.; Zhang, R.; Chen, W.; Luo, Y.; Niu, S. Global patterns and controlling factors of soil nitrification rate. *Global Change Biol.* **2020**, *26*, 4147−4157.

(14) Wieder, R. K.; Scott, K. D.; Kamminga, K.; Vile, M. A.; Vitt, D. H.; Bone, T.; Xu, B. I. N.; Benscoter, B. W.; Bhatti, J. S. Postfire carbon balance in boreal bogs of Alberta, Canada. *Global Change Biol.* **2009**, *15*, 63−81.

(15) Goulden, M. L.; McMillan, A. M. S.; Winston, G. C.; Rocha, A. V.; Manies, K. L.; Harden, J. W.; Bond-Lamberty, B. P. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biol.* **2011**, *17*, 855−871.

(16) Wang, J. A.; Baccini, A.; Farina, M.; Randerson, J. T.; Friedl, M. A. Disturbance suppresses the aboveground carbon sink in North American boreal forests. *Nat. Clim. Change* **2021**, *11*, 435−441.

(17) Dannenmann, M.; Diaz-Pines, E.; Kitzler, B.; Karhu, K.; Tejedor, J.; Ambus, P.; Parra, A.; Sanchez-Martin, L.; Resco, V.; Ramirez, D. A.; Povoas-Guimaraes, L.; Willibald, G.; Gasche, R.; Zechmeister-Boltenstern, S.; Kraus, D.; Castaldi, S.; Vallejo, A.; Rubio, A.; Moreno, J. M.; Butterbach-Bahl, K. Postfire nitrogen balance of Mediterranean shrublands: Direct combustion losses versus gaseous and leaching losses from the postfire soil mineral nitrogen flush. *Global Change Biol.* **2018**, *24*, 4505−4520.

(18) Turner, M. G.; Smithwick, E. A. H.; Metzger, K. L.; Tinker, D. B.; Romme, W. H. Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone Ecosystem. *Proc. Natl. Acad. Sci. U.S.A.* **2007**, *104*, 4782−4789.

(19) LeDuc, S. D.; Rothstein, D. E. Plant-available organic and mineral nitrogen shift in dominance with forest stand age. *Ecology* **2010**, *91*, 708−720.

(20) Chen, L.; Liu, L.; Mao, C.; Qin, S.; Wang, J.; Liu, F.; Blagodatsky, S.; Yang, G.; Zhang, Q.; Zhang, D.; Yu, J.; Yang, Y. Nitrogen availability regulates topsoil carbon dynamics after permafrost thaw by altering microbial metabolic efficiency. *Nat. Commun.* **2018**, *9*, 3951.

(21) Sterner, R. W.; Elser, J. J. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*; Princeton University Press: Princeton, NJ, USA, 2002.

(22) Butler, O. M.; Elser, J. J.; Lewis, T.; Mackey, B.; Chen, C. The phosphorus-rich signature of fire in the soil-plant system: A global meta-analysis. *Ecol. Lett.* **2018**, *21*, 335−344.

(23) Pellegrini, A. F. A.; Ahlstrom, A.; Hobbie, S. E.; Reich, P. B.; Nieradzik, L. P.; Staver, A. C.; Scharenbroch, B. C.; Jumpponen, A.; Anderegg, W. R. L.; Randerson, J. T.; Jackson, R. B. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* **2018**, *553*, 194−198.

(24) Li, J.; Pei, J.; Liu, J.; Wu, J.; Li, B.; Fang, C.; Nie, M. Spatiotemporal variability of fire effects on soil carbon and nitrogen: A global meta-analysis. *Global Change Biol.* **2021**, *27*, 4196−4206.

(25) Sinsabaugh, R. L.; Hill, B. H.; Follstad Shah, J. J. Ecoenzymatic stoichiometry of microbial organic nutrient acquisition in soil and sediment. *Nature* **2009**, *462*, 795−798.

(26) Mooshammer, M.; Wanek, W.; Zechmeister-Boltenstern, S.; Richter, A. Stoichiometric imbalances between terrestrial decomposer communities and their resources: Mechanisms and implications of microbial adaptations to their resources. *Front. Microbiol.* **2014**, *5*, 22.

(27) Mooshammer, M.; Wanek, W.; Hammerle, I.; Fuchslueger, L.; Hofhansl, F.; Knoltsch, A.; Schnecker, J.; Takriti, M.; Watzka, M.; Wild, B.; Keiblinger, K. M.; Zechmeister-Boltenstern, S.; Richter, A. Adjustment of microbial nitrogen use efficiency to carbon:nitrogen imbalances regulates soil nitrogen cycling. *Nat. Commun.* **2014**, *5*, 3694.

(28) Zechmeister-Boltenstern, S.; Keiblinger, K. M.; Mooshammer, M.; Peñuelas, J.; Richter, A.; Sardans, J.; Wanek, W. The application of ecological stoichiometry to plant-microbial-soil organic matter transformations. *Ecol. Monogr.* **2015**, *85*, 133−155.

(29) Cleveland, C. C.; Liptzin, D. C:N:P stoichiometry in soil: Is there a "Redfield ratio" for the microbial biomass? *Biogeochemistry* **2007**, *85*, 235−252.

(30) Su, W.-q.; Tang, C.; Lin, J.; Yu, M.; Dai, Z.; Luo, Y.; Li, Y.; Xu, J. Recovery patterns of soil bacterial and fungal communities in Chinese boreal forests along a fire chronosequence. *Sci. Total Environ.* **2022**, *805*, 150372.

(31) Mao, D.; He, X.; Wang, Z.; Tian, Y.; Xiang, H.; Yu, H.; Man, W.; Jia, M.; Ren, C.; Zheng, H. Diverse policies leading to contrasting impacts on land cover and ecosystem services in Northeast China. *J. Cleaner Prod.* **2019**, *240*, 117961.

(32) Shen, H.; Zhang, Q.; Zhang, X.; Jiang, X.; Zhu, S.; Chen, A.; Wu, Z.; Xiong, Z. In situ effects of biochar field-aged for six years on net N mineralization in paddy soil. *Soil Tillage Res.* **2021**, *205*, 104766.

(33) Shen, H.; Zhang, Q.; Zhu, S.; Duan, P.; Zhang, X.; Wu, Z.; Xiong, Z. Organic substitutions aggravated microbial nitrogen limitation and decreased nitrogen-cycling gene abundances in a three-year greenhouse vegetable field. *J. Environ. Manage.* **2021**, *288*, 112379.

(34) Vance, E. D.; Brookes, P. C.; Jenkinson, D. S. An extraction method for measuring soil microbial biomass-C. *Soil Biol. Biochem.* **1987**, *19*, 703−707.

(35) Joergensen, R. G.; Mueller, T. The fumigation-extraction method to estimate soil microbial biomass: Calibration of the k(EN) value. *Soil Biol. Biochem.* **1996**, *28*, 33−37.

(36) Alster, C. J.; German, D. P.; Lu, Y.; Allison, S. D. Microbial enzymatic responses to drought and to nitrogen addition in a southern California grassland. *Soil Biol. Biochem.* **2013**, *64*, 68−79.

(37) Moorhead, D. L.; Sinsabaugh, R. L.; Hill, B. H.; Weintraub, M. N. Vector analysis of ecoenzyme activities reveal constraints on coupled C, N and P dynamics. *Soil Biol. Biochem.* **2016**, *93*, 1−7.

(38) James, J. A.; Kern, C. C.; Miesel, J. R. Legacy effects of prescribed fire season and frequency on soil properties in a Pinus resinosa forest in northern Minnesota. *For. Ecol. Manage.* **2018**, *415−416*, 47−57.

(39) Mao, C.; Kou, D.; Chen, L.; Qin, S.; Zhang, D.; Peng, Y.; Yang, Y. Permafrost nitrogen status and its determinants on the Tibetan Plateau. *Global Change Biol.* **2020**, *26*, 5290−5302.

(40) Abbott, B. W.; Rocha, A. V.; Shogren, A.; Zarnetske, J. P.; Iannucci, F.; Bowden, W. B.; Bratsman, S. P.; Patch, L.; Watts, R.; Fulweber, R.; Frei, R. J.; Huebner, A. M.; Ludwig, S. M.; Carling, G. T.; O'Donnell, J. A. Tundra wildfire triggers sustained lateral nutrient loss in Alaskan Arctic. *Global Change Biol.* **2021**, *27*, 1408−1430.

(41) Wan, S. Q.; Hui, D. F.; Luo, Y. Q. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: A meta-analysis. *Ecol. Appl.* **2001**, *11*, 1349−1365.

(42) Mora, J. L.; Girona−García, A.; Martí−Dalmau, C.; Ortiz−Perpiñá, J. O.; Armas-Herrera, C. M.; Badía−Villas, D. Changes in pools of organic matter and major elements in the soil following prescribed pastoral burning in the central Pyrenees. *Geoderma* **2021**, *402*, 115169.

(43) Sánchez-García, C.; Santín, C.; Doerr, S. H.; Strydom, T.; Urbanek, E. Wildland fire ash enhances short-term CO_2 flux from soil in a Southern African savannah. *Soil Biol. Biochem.* **2021**, *160*, 108334.

(44) Karhu, K.; Dannenmann, M.; Kitzler, B.; Díaz-Pinés, E.; Tejedor, J.; Ramírez, D. A.; Parra, A.; Resco de Dios, V.; Moreno, J. M.; Rubio, A.; Guimaraes-Povoas, L.; Zechmeister-Boltenstern, S.; Butterbach-Bahl, K.; Ambus, P. Fire increases the risk of higher soil N_2O emissions from Mediterranean Macchia ecosystems. *Soil Biol. Biochem.* **2015**, *82*, 44−51.

(45) Fernández-Fernández, M.; Rütting, T.; González-Prieto, S. Effects of a high-severity wildfire and post-fire straw mulching on gross nitrogen dynamics in Mediterranean shrubland soil. *Geoderma* **2017**, *305*, 328−335.

(46) Hogberg, M. N.; Hogberg, P.; Wallander, H.; Nilsson, L.-O. Carbon-nitrogen relations of ectomycorrhizal mycelium across a natural nitrogen supply gradient in boreal forest. *New Phytol.* **2021**, *232*, 1839−1848.

(47) Song, Y.; Zou, Y.; Wang, G.; Yu, X. Altered soil carbon and nitrogen cycles due to the freeze-thaw effect: A meta-analysis. *Soil Biol. Biochem.* **2017**, *109*, 35−49.

(48) Hedin, L. O.; Vitousek, P. M.; Matson, P. A. Nutrient losses over four million years of tropical forest development. *Ecology* **2003**, *84*, 2231−2255.

(49) Fang, Y.; Koba, K.; Makabe, A.; Takahashi, C.; Zhu, W.; Hayashi, T.; Hokari, A. A.; Urakawa, R.; Bai, E.; Houlton, B. Z.; Xi, D.; Zhang, S.; Matsushita, K.; Tu, Y.; Liu, D.; Zhu, F.; Wang, Z.; Zhou, G.; Chen, D.; Makita, T.; Toda, H.; Liu, X.; Chen, Q.; Zhang, D.; Li, Y.; Yoh, M. Microbial denitrification dominates nitrate losses from forest ecosystems. *Proc. Natl. Acad. Sci. U.S.A.* **2015**, *112*, 1470−1474.

https://doi.org/10.1021/acs.est.4c01662

(50) Raison, R. J.; Khanna, P. K.; Woods, P. V. Mechanisms of element transfer to the atmosphere during vegetation fires. *Can. J. For. Res.* **1985**, *15*, 132−140.

(51) Galang, M. A.; Markewitz, D.; Morris, L. A. Soil phosphorus transformations under forest burning and laboratory heat treatments. *Geoderma* **2010**, *155*, 401−408.

(52) Wang, Y.-P.; Huang, Y.; Augusto, L.; Goll, D. S.; Helfenstein, J.; Hou, E. Toward a global model for soil inorganic phosphorus dynamics: Dependence of exchange kinetics and soil bioavailability on soil physicochemical properties. *Global Biogeochem. Cycles* **2022**, *36*, No. e2021GB007061.

(53) Wang, R.; Bicharanloo, B.; Hou, E.; Jiang, Y.; Dijkstra, F. A. Phosphorus supply increases nitrogen transformation rates and retention in soil: A global meta-analysis. *Earth's Future* **2022**, *10*, No. e2021EF002479.

(54) Blanes, M. C.; Emmett, B. A.; Viñegla, B.; Carreira, J. A. Alleviation of P limitation makes tree roots competitive for N against microbes in a N-saturated conifer forest: A test through P fertilization and ^{15}N labelling. *Soil Biol. Biochem.* **2012**, *48*, 51−59.

(55) Chen, H.; Gurmesa, G. A.; Zhang, W.; Zhu, X.; Zheng, M.; Mao, Q.; Zhang, T.; Mo, J. Nitrogen saturation in humid tropical forests after 6 years of nitrogen and phosphorus addition: Hypothesis testing. *Funct. Ecol.* **2015**, *30*, 305−313.

(56) Mehnaz, K. R.; Keitel, C.; Dijkstra, F. A. Phosphorus availability and plants alter soil nitrogen retention and loss. *Sci. Total Environ.* **2019**, *671*, 786−794.

(57) Schaller, J.; Tischer, A.; Struyf, E.; Bremer, M.; Belmonte, D. U.; Potthast, K. Fire enhances phosphorus availability in topsoils depending on binding properties. *Ecology* **2015**, *96*, 1598−1606.

(58) Wei, X.; Hu, Y.; Peng, P.; Zhu, Z.; Atere, C. T.; O'Donnell, A. G.; Wu, J.; Ge, T. Effect of P stoichiometry on the abundance of nitrogen-cycle genes in phosphorus-limited paddy soil. *Biol. Fertil. Soils* **2017**, *53*, 767−776.

(59) He, M.; Dijkstra, F. A. Phosphorus addition enhances loss of nitrogen in a phosphorus-poor soil. *Soil Biol. Biochem.* **2015**, *82*, 99−106.

(60) Brant, A. N.; Chen, H. Y. H. Patterns and mechanisms of nutrient resorption in plants. *Crit. Rev. Plant Sci.* **2015**, *34*, 471−486.

(61) Reich, P. B.; Oleksyn, J. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl. Acad. Sci. U.S.A.* **2004**, *101*, 11001−11006.

(62) Chadwick, O. A.; Derry, L. A.; Vitousek, P. M.; Huebert, B. J.; Hedin, L. O. Changing sources of nutrients during four million years of ecosystem development. *Nature* **1999**, *397*, 491−497.

(63) Gao, H.; Shao, M. Effects of temperature changes on soil hydraulic properties. *Soil Tillage Res.* **2015**, *153*, 145−154.

(64) U.S. DEPARTMENT OF AGRICULTURE. https://www.nrcs.usda.gov/resources/education-and-teaching-materials/the-twelve-orders-of-soil-taxonomy (accessed April 15, 2024).

(65) FAO SOILS PORTAL. https://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/ (accessed April 15, 2024).

(66) Hoy, E. E.; Turetsky, M. R.; Kasischke, E. S. More frequent burning increases vulnerability of Alaskan boreal black spruce forests. *Environ. Res. Lett.* **2016**, *11*, 095001.

(67) Stralberg, D.; Wang, X.; Parisien, M.-A.; Robinne, F.-N.; Sólymos, P.; Mahon, C. L.; Nielsen, S. E.; Bayne, E. M. Wildfire-mediated vegetation change in boreal forests of Alberta, Canada. *Ecosphere* **2018**, *9*, No. e02156.

(68) Whitman, E.; Parisien, M.-A.; Thompson, D.; Flannigan, M. Topoedaphic and forest controls on post-fire vegetation assemblies are modified by fire history and burn severity in the northwestern Canadian boreal forest. *Forests* **2018**, *9*, 151.

(69) Zhao, Z.; Li, W.; Ciais, P.; Santoro, M.; Cartus, O.; Peng, S.; Yin, Y.; Yue, C.; Yang, H.; Yu, L.; Zhu, L.; Wang, J. Fire enhances forest degradation within forest edge zones in Africa. *Nat. Geosci.* **2021**, *14*, 479−483.