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ARTICLE

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Fire decreases soil enzyme activities and reorganizes microbially mediated nutrient cycles: A meta-analysis

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Abstract

The biogeochemical signature of fire shapes the functioning of many ecosystems. Fire changes nutrient cycles not only by volatilizing plant material, but also by altering organic matter decomposition, a process regulated by soil extracellular enzyme activities (EEAs). However, our understanding of fire effects on EEAs and their feedbacks to nutrient cycles is incomplete. We conducted a meta-analysis with 301 field studies and found that fire significantly decreased EEAs by ~20%–40%. Fire decreased EEAs by reducing soil microbial biomass and organic matter substrates. Soil nitrogen-acquiring EEA declined alongside decreasing available nitrogen, likely from fire-driven volatilization of nitrogen and decreased microbial activity. Fire decreased soil phosphorus-acquiring EEA but increased available phosphorus, likely from pyro-mineralization of organic phosphorus. These findings suggest that fire suppresses soil microbes and consumes their substrates, thereby slowing microbially mediated nutrient cycles (especially phosphorus) via decreased EEAs. These changes can become increasingly important as fire frequency and severity in many ecosystems continue to shift in response to global change.

KEYWORDS

biogeochemistry, effect size, fire, nitrogen, nutrient cycling, phosphorus, soil extracellular enzymes

INTRODUCTION

Globally, wild and prescribed fires burn 400–520 million hectares of terrestrial ecosystems annually (Lizundia-Loiola et al., 2020), resulting in a widespread combustion of plants that is generally followed by rapid regrowth of surviving plants and/or regeneration of new individuals and species (Keeley, 2009; Tepley et al., 2018). At the same time, fire can directly combust plant biomass, surface litter, and surface-soil organic matter, volatilizing carbon (C) and nitrogen (N) while redepositing phosphorus (P) in the system via pyro-mineralization (Butler et al., 2018; Miesel et al., 2018; Pellegrini et al., 2018; Wan et al., 2001). This biogeochemical signature of fire alters soil nutrient cycles in the postfire environment, which may further influence or regulate the effects of fire on vegetation recovery (Butler et al., 2018). However, the degree to which these nutrient-pool responses are caused directly by fire versus by fire effects on microbial processes remains unclear. Soil extracellular enzymes produced by microbes in particular decompose organic matter of varying complexity and release essential nutrients for plant uptake (Holden et al., 2013; Pellegrini et al., 2020) and as such have an important role in driving biogeochemical nutrient cycling. Therefore, understanding the mechanisms of fire effects on soil extracellular enzyme activities (EEAs) and their linkages to nutrient cycles is critical to understanding postfire ecosystem dynamics and recovery.

There is a broad diversity of soil extracellular enzymes (Burns et al., 2013; Sinsabaugh et al., 2008), but those involved in the hydrolysis of carbohydrates (e.g., cellulose and glucose), organic N (e.g., proteins and chitin) and organic P compounds (e.g., nucleic acids and phospholipids) are particularly crucial for the recovery of nutrient cycling following fires. While plants may also directly release certain enzymes (e.g., phosphatase) in their rhizospheres (e.g., Batterman et al., 2018), extracellular enzymes in bulk soil are mostly produced by free-living microbes to catalyze substrate transformations for energy and nutrient acquisition (Sinsabaugh et al., 2008). However, disturbances may alter substrates and products of the enzyme reaction and impact soil EEAs (Allison et al., 2010; Allison & Vitousek, 2005; Zhou & Staver, 2019). Existing work suggests three major mechanisms for fire to affect soil EEAs, including (1) direct fire impacts on soil microbial populations, (2) volatilization of enzyme substrates, and (3) feedbacks from nutrient availability to enzyme production.

First, fire is a direct threat to the survivorship of soil microbes since heat transferred to soils during fire causes microbial mortality (Hart et al., 2005). Previous meta-analyses demonstrated that fire can decrease soil microbial biomass by 30%–50% (Dooley & Treseder, 2012; Holden & Treseder, 2013); therefore, it is reasonable to hypothesize that fire may lead to an overall reduction in soil EEAs, although contrasting patterns at individual sites have been reported (e.g., Pellegrini et al., 2020). In addition, the direction and magnitude of fire effects on soil microbial biomass depends on fire characteristics (e.g., fire severity and time since the last fire) and vegetation types (Dooley & Treseder, 2012; Holden & Treseder, 2013). For example, wildfires tend to be more severe than prescribed burns, leading to a greater reduction in soil microbial biomass (Dooley & Treseder, 2012). These fire and site characteristics not only affect soil microbial biomass but may also modify responses of soil EEAs to fire.

Second, fire may affect soil EEAs by decreasing the amount of organic matter in soils and by shifting the composition of organic matter inputs. In some extreme cases, severe fire consumes large amounts of organic matter in soils, leading to a long-lasting substrate limitation to microbial population and thereby declining soil EEAs in the postfire environment (e.g., Dove et al., 2020; Ludwig et al., 2018; Waldrop & Harden, 2008). In most cases, fire combusts plant biomass and litter, altering both the quantity and quality of organic matter inputs into soils (Ojima et al., 1994), which substantially shifts the stoichiometry and substrate limitation to soil microbes and their production in enzymes. For example, global syntheses have revealed that fire can deplete surface soil organic carbon (SOC) and total N by ~10%–40% (Dijkstra & Adams, 2015; Pellegrini et al., 2018; Wan et al., 2001), but increase total P marginally by ~5% (Butler et al., 2018). This change in organic matter inputs and stocks may have additional impacts on soil microbial communities beyond the direct effects of fire discussed above (Dooley & Treseder, 2012), amplifying reductions in soil microbial biomass after fires. It is unknown, however, whether these different responses of soil C, N and P storage to fire are mirrored by coupled changes in soil C-, N-, and P-acquiring EEAs.

Last, fire-induced changes in soil nutrient availability may feed back to EEAs in the postfire environment. Although soil extracellular enzymes catalyze a variety of critical biogeochemical reactions, resource acquisition is the primary function from the microbial perspective (Allison et al., 2010; Allison & Vitousek, 2005), and the rate of extracellular enzyme production may depend upon resource availability (Sinsabaugh et al., 2008; Waldrop et al., 2004; Zhou & Staver, 2019). Thus, microbial regulation of extracellular enzyme production may result in increased or decreased EEAs after fires, depending on direct soil nutrient responses to fire. Importantly, these may differ by nutrient. On the one hand, fire consistently promotes soil available P through heat-induced mineralization of organic P (Butler et al., 2018; Dijkstra & Adams, 2015; Hartshorn et al., 2009). Conversely, despite a pulsed increase in soil available N immediately after fire due to ash deposition (Wan et al., 2001), fire generally has neutral to negative impacts on soil N availability on long-term scales (Guénon et al., 2013; Holden et al., 2013; Wan et al., 2001). Thus, in a relatively P-enriched postfire environment, soil microbes are likely more constrained by N (Jian et al., 2016), which may, in turn, stimulate the production of soil N-acquiring enzymes while suppressing P-acquiring enzymes based on the relative demand of soil microbes (Allison, 2005; Allison & Vitousek, 2005; Burns et al., 2013; Schimel & Weintraub, 2003). If this is the case, fire may differentially affect soil N- and P-acquiring EEAs and their feedbacks to nutrient availability in the postfire environment.

Overall, a comprehensive and quantitative synthesis examining fire effects on soil EEAs is still lacking. Such an analysis may help us to better understand fire-induced changes in soil EEAs and nutrient cycles, particularly in the context of changes in fire frequency and severity driven by land-use change and climate change. To fill this knowledge gap, we conducted a meta-analysis of 301 field studies that measured soil EEAs in both burned and unburned treatments. We aimed to examine directions and magnitudes of fire effects on different functional groups of soil EEAs (e.g., C-, N-, and P-acquiring enzymes); the extent to which characteristics of fires and changes in soil properties (e.g., soil microbial biomass and organic matter) influence and explain responses of soil EEAs to fire; and feedbacks between soil nutrient availability and nutrient-acquiring EEAs in the postfire environment. We hypothesized that fire would lead to an overall reduction in soil EEAs, due primarily to fire-induced declines in soil microbial biomass and organic matter substrates (the first and second mechanisms, above). We also hypothesized that linkages between soil nutrient availability and nutrient-acquiring EEAs might differ between N and P, since loss of soil nitrogen inputs by fire volatilization would suppress N-acquiring EEA via substrate limitation while increased soil P availability through pyro-mineralization of organic P can suppress P-acquiring EEA via microbial down-regulation (the third mechanism above).

MATERIALS AND METHODS

Study selection

We searched the Web of Science database using terms fire* OR burn* AND enzyme AND soil to obtain potential publications for this meta-analysis on 2 December 2020. We used the Preferred Reporting Items for Systematic Reviews and Meta-Analyses protocol to screen and identify publications to be included in this analysis (Appendix S1: Figure S1). Briefly, title, abstract, and methods section of each publication were initially screened for eligibility based on whether the publication included fire impacts on soil EEAs. Eligible publications were further filtered based on whether the publication included at least one field study that examined soil EEAs between burned and unburned plots or treatments (see Appendix S2 for more details on field study identification). Overall, a total of 301 field studies from 85 study sites were extracted from 71 publications (Appendix S2). Geographic locations of the study sites are shown in Appendix S1: Figure S2.

Data collection

For each field study, we recorded site locations (latitude and longitude), climatic variables (mean annual precipitation [MAP] and mean annual temperature [MAT]), vegetation types, soil clay content, soil types, fire types (wildfire or prescribed fire), fire severity (low, moderate, and high), time since the last fire (years), and the number of fire events (e.g., the number of fires that occurred during the timeframe of the study). If these data were not reported, we contacted the corresponding authors for additional information. Otherwise, site latitude and longitude were extracted from Google Maps based on the approximate location reported in the publication; MAT and MAP were extracted from the WorldClim database; and soil clay content was extracted from SoilGrids database (Hengl et al., 2017). We classified vegetation into coniferous forests, deciduous forests, mixed forests, woodlands/shrublands, and savannas/grasslands based on potential different responses to fires (Pellegrini et al., 2018). Though criteria for estimating fire severity may vary among studies, we used the reported fire severity from studies. If a study reported fire severity as "low to moderate" or "moderate to high," we made a conservative decision to use the lower estimate. In some cases, if descriptions on postfire changes in aboveground vegetation and organic matter in soils were reported, we assigned fire severity to these studies based on criteria from Keeley (2009). We classified soil types to orders based on United States Department of Agriculture soil taxonomy (Soil Survey Staff, 1999).

For quantifying fire effects on EEAs, we recorded means, standard deviations (SD) (or standard errors [SE]), the number of replicates for EEAs measured in unburned and burned treatments from the top-most soil layers. Soil extracellular enzymes were categorized into C-, N-, and P-acquiring enzymes (see Appendix S1: Table S1). Soil C-acquiring enzymes included α-1,4-glucosidase, β-1,4-glucosidase, β-1,4-xylosidase, β-D-cellobiohydrolase, cellulase, invertase, and xylanase; N-acquiring enzymes included β-1,4-N-acetyl-glucosaminidase, asparaginase, leucine aminopeptidase, protease, and urease; and P-acquiring enzymes included both acid and alkaline phosphatase. We also provided information on soil oxidative and S-acquiring enzymes, though these two categories are not discussed in depth here. Where available, we tabulated soil pH, water content, organic C (or matter), total N (TN), total P (TP), available N (or total inorganic N), NH_4^+, NO_3^-, available P, soil microbial biomass carbon (SMBC), and soil microbial biomass nitrogen (SMBN). Following other meta-analyses of fire impacts on soil C and N cycles (e.g., Pellegrini et al., 2018; Wan et al., 2001), soil P cycle (Butler et al., 2018), and soil microbial biomass (e.g., Dooley & Treseder, 2012), we treated different sampling dates after fire within the same publication as separate and independent field studies (Appendix S2). When results were presented graphically, we used WebPlotDigitizer 4.4 to digitize the data (Rohatgi, 2020).

Statistical analysis

We evaluated the effects of fire on soil EEAs using the natural log of the response ratio (lnRR), a metric commonly used in meta-analyses (Hedges et al., 1999)

$$\mathrm{lnRR} = \ln\left(\frac{X_{\mathrm{B}}}{X_{\mathrm{UB}}}\right)$$

where X_{B} and X_{UB} are means of the variable for burned and unburned plots or treatments, respectively. The variance (v) of lnRR is calculated as

$$v = \frac{S_{\mathrm{B}}^2}{N_{\mathrm{B}} \times X_{\mathrm{B}}^2} + \frac{S_{\mathrm{UB}}^2}{N_{\mathrm{UB}} \times X_{\mathrm{UB}}^2}$$

where N_{B} and N_{UB} are numbers of replicates and S_{B} and S_{UB} are SD of means for burned and unburned plots or treatments, respectively.

To test the directions and magnitudes of fire impacts on soil EEAs and other soil parameters (Appendix S1: Figures S3–S5, Tables S2–S4), we used a random-effects model with restricted maximum-likelihood estimation, with effect sizes weighted by the inverse of their variances. The weighted mean effect size was considered significant if the 95% bootstrapped confidence intervals (CIs) with 999 iterations did not overlap zero (Rosenberg et al., 2000). In addition, we calculated the percent change of soil EEAs in response to fire according to $(e^{R+} - 1) \times 100$, where R^{+} is the weighted mean effect size (Rosenberg et al., 2000).

Because soil extracellular enzymes within the same functional group (e.g., C-, N-, and P-acquiring enzymes) generally responded similarly to fire (Appendix S1; Figure S6), we followed other meta-analyses that grouped responses (e.g., Chen et al., 2018): if a field study reported several soil extracellular enzymes belonging to the same functional group (Appendix S1: Table S1), we summed their mean values as overall responses for burned and unburned plots or treatments. The corresponding SD were then calculated following the error propagation method (Chen et al., 2018; Lorber, 1986):

$$\mathrm{SD}^2 = \sum_{i=1}^{n} S_i^2$$

where S_i is the SD for each soil EEA within the same functional group. Following this procedure, the mean effect size for each functional group of the grouped data set was almost identical to that calculated based on the whole data set (Appendix S1: Figure S7 and Table S4). Thus, we proceeded with our meta-analysis using the grouped data set.

The effects of environmental conditions on responses of soil EEAs to fire were examined with a random-effects meta-regression. Environmental conditions (i.e., moderators) comprised categorical variables, including fire type, fire severity, fire events (i.e., single or multiple), vegetation types, and soil types, as well as continuous variables, including time since the last fire, MAP, MAT, latitude (in absolute value), soil pH, soil clay content, SOC (lnRR), and SMBC (lnRR). The amount of heterogeneity (Q_{M}) explained by the moderator is compared to a χ^2 distribution and a Q_{M} with $p < 0.05$ implies that the moderator explains significant differences in the variability in the effect sizes (Rosenberg et al., 2000). Then we analyzed all potential combinations of variables in a mixed-effects meta-regression model to identify essential variables predicting the response of soil C-, N-, and P- acquiring EEAs to fire, using the *glmulti* package (Calcagno & de Mazancourt, 2010). Because latitude was highly correlated with MAT and soil pH was highly correlated with MAP (Appendix S1: Figure S8), we excluded latitude and soil pH in the model to avoid the problem of multicollinearity. In addition, SMBC was considered as a surrogate for soil microbial biomass and SOC for organic matter substrates. Model selection was based on the corrected Akaike information criterion ($\mathrm{AIC_c}$). The relative importance value for each variable was based on the sum of the Akaike weights for models that included the variable. Variables with large Akaike weights will receive high importance values. A cutoff of 0.8 was set to differentiate between essential and nonessential variables (Terrer et al., 2016).

The effects of fire on relationships between soil nutrient-acquiring EEAs (lnRR) and nutrient availability (lnRR) were examined with a random-effects meta-regression. The response of soil available N to fire included those measured as total inorganic N, $\mathrm{NH_4}^{+}$, and $\mathrm{NO_3}^{-}$. If a field study measured both $\mathrm{NH_4}^{+}$, and $\mathrm{NO_3}^{-}$, we summed their mean values as the overall response and calculated the SD based on the error propagation method. Most field studies reported soil available P, though extraction solutions/methods varied, including citric acid, Bray-1 solution, resin membrane, etc. If a field study presented different P fractionations, labile inorganic P was considered as available P. All statistical analyses were performed using the *metafor* package (Viechtbauer, 2010) in R 3.6.1 (R Core Team, 2019).

RESULTS

We found that fire significantly decreased all functional groups of soil EEAs, with mean effect sizes and bootstrapped 95% CIs all less than zero (Figure 1a and

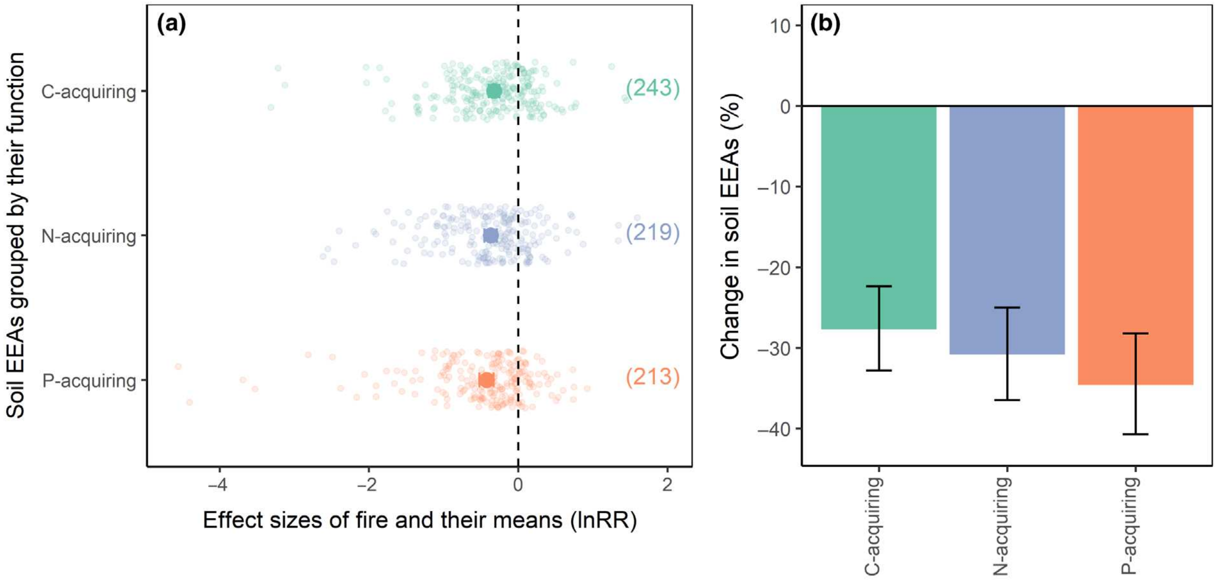

FIGURE 1 Effect sizes and their means (lnRR) of fire impacts on different soil extracellular enzyme activities (EEAs) grouped by (a) their function (C-, N-, and P-acquiring enzymes) and (b) percent changes in soil EEAs in response to fire. A negative mean effect size indicates that the burned site had lower soil EEAs compared to the unburned site. The bars around the mean indicate 95% bootstrapped confidence intervals (CIs). Fire effects were considered significant where the CIs did not overlap zero. In panel (a), confidence intervals are shown but some are too narrow to be visible; numerical values are given in Appendix S1: Table S4. The number of observations for each functional group of soil EEA is indicated in parentheses.

Appendix S1: Figures S3a and S4). The activities of soil C-, N-, and P-acquiring enzymes were decreased by 27.7% (22.4%–32.8%), 30.8% (25.0%–36.5%), and 34.6% (28.2%–40.7%), respectively (Figure 1b). In addition, fire significantly decreased SMBC (−25.3%), SMBN (−23.4%), SOC (−7.6%), and soil water content (−12.4%), but increased soil available P (+76.1%) and pH (+6.9%) (Appendix S1: Figure S5).

Fire effects on soil EEAs varied with characteristics of fire and site. Wildfires had stronger negative effects on all soil EEAs than prescribed fires (Figure 2a). Fire severity increased responses of all soil EEAs to fire, with high-severity fires causing the strongest negative effects compared to low- and moderate-intensity fires (Figure 2b). Sites experiencing multiple fires had stronger negative effect sizes of soil C- and N-acquiring EEAs than those experiencing a single fire, while the opposite pattern was found for soil P-acquiring EEA (Figure 2c). Surprisingly, the effects of fire on soil EEAs did not change substantially with time since the last fire (Appendix S1: Table S5 and Figure S9). The effect sizes of fire on soil C-acquiring EEA increased with increasing mean annual rainfall (Appendix S1: Table S5). Only responses of soil C-acquiring EEA to fire significantly differed among vegetation types, with grasslands having a relatively less negative effect size compared to woodland and forest ecosystems (Figure 2d). The effects of fire on all soil EEAs differed significantly among soil types (Figure 2e).

However, when all variables were considered, a model selection analysis revealed that only fire-induced changes in SMBC and SOC were consistently essential for predicting responses of soil C-, N-, and P-acquiring EEAs to fire (Figure 3a–c). Effect sizes of fire on soil C-, N-, and P-acquiring EEAs were all significantly and positively related to those of SMBC (lnRR) and SOC (lnRR) (Figure 3d–i). Other important variables for predicting responses of soil C-acquiring EEA to fire included soil type and fire severity (Figure 3a) and fire severity for predicting responses of soil N-acquiring EEA (Figure 3b).

Meanwhile, fire-induced changes in soil available N were significantly and positively correlated with responses of soil N-acquiring EEA to fire (Figure 4a). However, fire significantly increased soil available P (Appendix S1: Figure S5) but suppressed soil P-acquiring EEA (Figure 1), resulting in a significant negative relationship between fire-induced changes in soil available P and responses of soil P-acquiring EEA to fire (Figure 4b).

DISCUSSION

Our meta-analysis provides robust evidence that fire can decrease soil EEAs by ~20%–40%, but the magnitude of changes depended on EEA functional group (i.e., soil C-, N-, and P-acquiring EEAs) (Figure 1). Though characteristics of fire and site modified responses of soil EEAs to fire

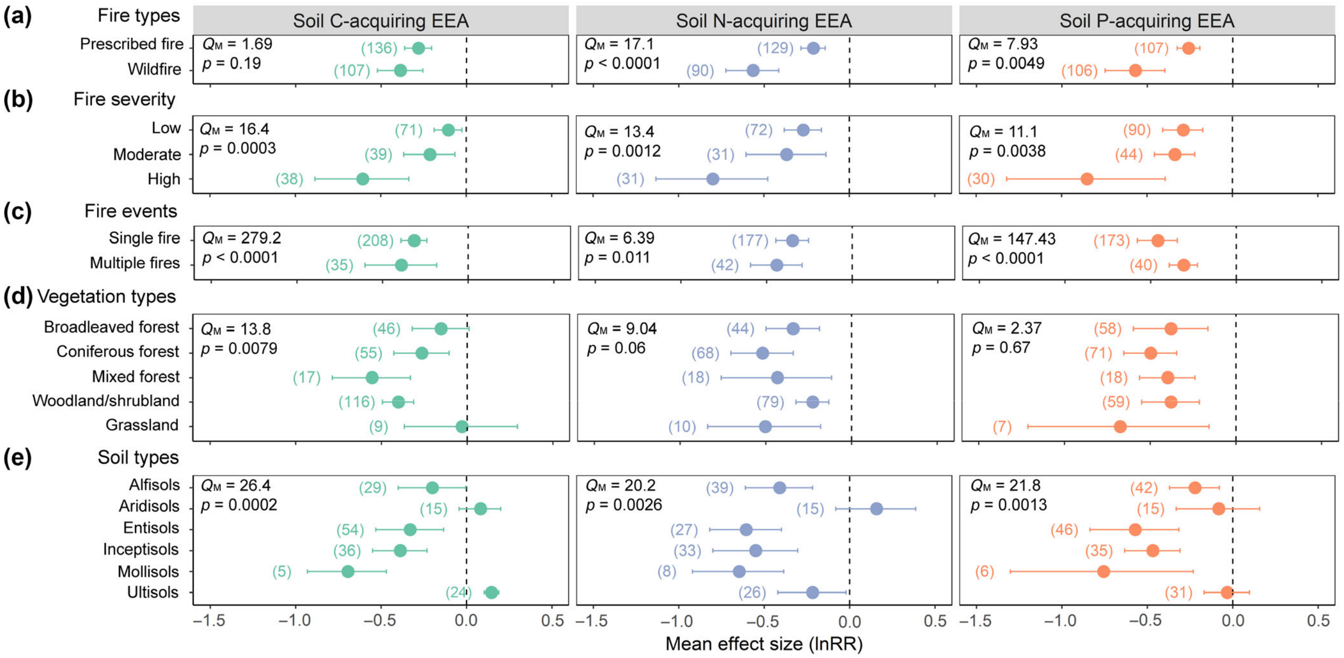

FIGURE 2 Fire effects on soil C-, N- and P-acquiring extracellular enzyme activities (EEAs) with observations categorized based on (a) fire types, (b) fire severity, (c) number of fire events, (d) vegetation types, and (e) soil types. Values are mean effect sizes, with a negative value indicating that the burned site had lower soil EEA compared to the unburned site. The bars around the mean indicate 95% bootstrapped confidence intervals (CIs). Fire effects were considered significant where the CIs did not overlap zero. The number of observations for each category is indicated in parentheses. Q_M represents heterogeneity of effect sizes explained by the respective moderator, with a larger Q_M indicating greater explained variance. A Q_M with $p < 0.05$ implies that the moderator explains a significant amount of the variability in the effect sizes.

(Figure 2 and Appendix S1: Table S5), fire impacts on soil EEAs were predominately driven by fire-induced reductions in soil microbial biomass and organic matter substrates (Figure 3). Meanwhile, soil N availability and N-acquiring EEAs were positively correlated, while soil P availability and P-acquiring EEA were negatively correlated in the postfire environment (Figure 4). On the one hand, soil N availability decreased alongside decreasing N-acquiring EEA, likely because fire volatilizes N and decreases N substrates upon which N-acquiring EEA can act, thereby slowing N decomposition for N releasing. By contrast, soil available P increased but P-acquiring EEA decreased, likely because fire pyro-mineralizes organic P to inorganic forms, which may suppress P-acquiring EEA via microbial down-regulation. Together, these findings suggest that fire disrupts N and P cycles via divergent physical pathways (volatilization vs. pyro-mineralization). Microbially mediated decomposition also slowed, potentially further shifting ecosystems toward N limitation as a result of N losses and the increase of available P in the post fire environment.

Our results support the hypothesis that fire decreases soil EEAs because of postfire declines in soil microbial biomass and organic matter substrates. Fire-induced changes in SMBC and SOC were consistent in predicting fire effects on soil C-, N-, and P-acquiring EEAs (Figure 3). Soil extracellular enzymes are primarily produced by living microbes for resource acquisition and their activities generally reflect the overall active status of soil microbes, which is sensitive to environmental disturbances (Allison et al., 2010; Allison & Vitousek, 2005). Fire may exert negative effects on soil microbial biomass and therefore EEAs through both direct short-term and indirect long-term mechanisms (Dooley & Treseder, 2012). During a fire, direct heat transfer to soils can cause microbial mortality. The lack of reported data on soil temperatures during fire constrains our ability to test this direct effect of fire on soil microbial biomass in this meta-analysis; however, many other studies have shown that fire can increase surface soil temperature to more than 100°C (e.g., Campbell et al., 1995), which is lethal to soil microbes (Dooley & Treseder, 2012). In addition, soil temperatures during fire that exceed 70°C can cause many extracellular enzymes to become less active or completely inactive (Saa et al., 1993; Tabatabai & Bremner, 1970; Thenabadu & Dharmakeerthi, 1996), potentially triggering a short-term decrease in soil EEAs.

Indirectly, declines in soil microbial biomass and EEAs following fires may be related to losses of organic matter substrates (Figure 3), as both the growth of soil microbes and the production of soil extracellular enzymes are generally substrate limited (Allison, 2005; Burns et al., 2013).

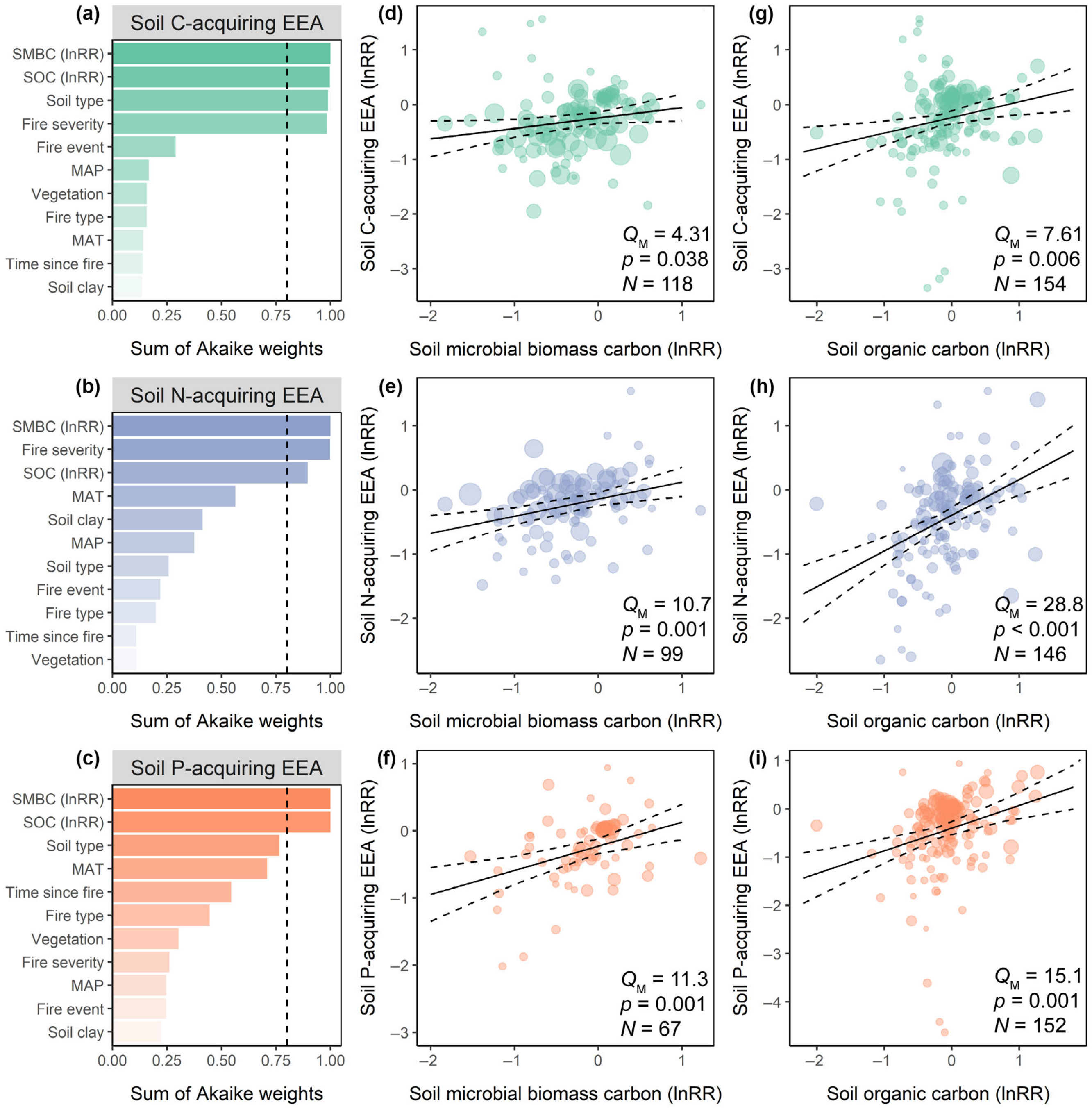

FIGURE 3 (a–c) Model-averaged variable importance for predicting fire impacts on soil C-, N-, and P-acquiring extracellular enzyme activities (EEAs) and their response to changes in (d–f) soil microbial biomass carbon and (g–i) soil organic carbon. Importance is based on the sum of Akaike weights derived from a model selection analysis using corrected Akaike's information criteria corrected for sample size (AIC_c). A cutoff of 0.8 (black dashed line) is set to differentiate between essential and nonessential variables for (a–c). MAP, mean annual rainfall; MAT, mean annual temperature; SMBC (lnRR), effect sizes of soil microbial biomass carbon; SOC (lnRR), effect sizes of soil organic carbon. For meta-regressions, a Q_M with $p < 0.05$ implies that the moderator explains a significant amount of the variability in the effect sizes. Dashed lines indicate the 95% confident intervals. Larger points indicate study outcomes that contributed a greater overall weight in meta-regressions.

Fire usually decreases the quantity and quality of organic matter inputs into soils (Pellegrini et al., 2020), which may lead to long-lasting substrate limitation and therefore suppress microbial biomass and EEAs in the postfire environment (Dooley & Treseder, 2012; Pellegrini et al., 2020). Here, we found that a declining trend in EEAs persisted even a number of years after fire (Appendix S1: Figure S9), which suggests that substrate limitation likely contributed to declines, even if fire had direct impacts on microbial populations immediately following a fire.

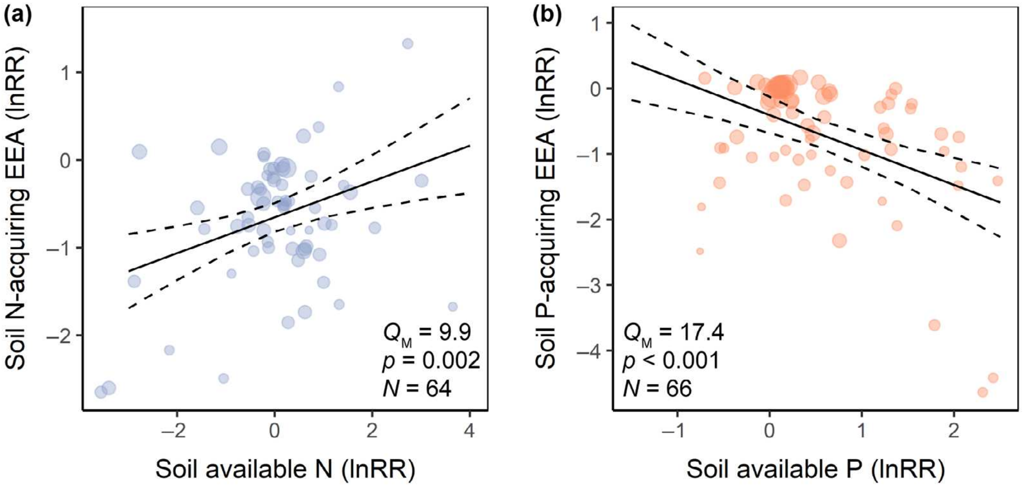

FIGURE 4 Fire effects on soil available N versus fire effects on soil N-acquiring extracellular enzyme activity (EEA) (a) and fire effects on soil available P versus fire effects on soil P-acquiring EEA (b). Dashed lines indicate the 95% confident intervals. Q_M represents heterogeneity of effect sizes explained by the respective moderator. A Q_M with $p < 0.05$ implies that the moderator explains a significant amount of the variability in the effect sizes. Larger points indicate study outcomes that contributed a greater overall weight in meta-regressions, and darker shading reflects overlapping points.

Generally, our results support the idea that both mechanisms are operating (Figure 3a–c). For example, wildfires exerted stronger negative effects on soil EEAs compared to prescribed fires (Figure 2a), potentially because wildfires usually burn at higher temperatures relative to prescribed fires (e.g., Certini, 2005; Nesmith et al., 2011). Within this meta-analysis, 38% of wildfires were reported as high severity while only 12% of prescribed fires were reported as high severity. High-severity wildfires therefore lead to momentary but greater reductions in soil microbial biomass, and consuming larger amounts of organic matter that has long-lasting influences on soil microbial biomass (Dooley & Treseder, 2012) and thereby having stronger negative effects on EEAs (Figure 2b). Likewise, repeated fires generally lead to greater declines in soil microbial biomass and organic matter substrates compared to a single fire (Dooley & Treseder, 2012; Pellegrini et al., 2018). However, we suggest a degree of caution in interpreting EEAs in response to single versus multiple fires since long-term studies in systems with repeated fires were not well represented in this meta-analysis.

Our results also support the hypothesis that feedbacks between soil nutrient availability and nutrient-acquiring EEAs differ between N and P in the postfire environment (Figure 4). However, evaluating how fire-induced changes in soil nutrient availability may feed back to EEAs requires deeper examination. We found some differences among types of EEAs in their responses to fire, ranging from 20% to 40% depending on their functional groups (Figure 1), but EEAs nonetheless consistently declined across all enzyme types. This consistent decrease is somewhat surprising, given large differences in how soil available nutrients respond to fire. Consistent with past work, we found that fire had neutral to negative effects on soil available N, especially once the short pulse immediately following fires had dissipated (Appendix S1: Figure S5) (Dijkstra & Adams, 2015; Wan et al., 2001), but significantly increased soil available P (Appendix S1: Figure S5) (Butler et al., 2018). If nutrient availability causes microbes to up or down regulate extracellular enzyme production and activities, then we might expect N-acquiring enzymes to be overproduced relative to P-acquiring enzymes in the postfire environment. If, instead, EEAs are responsible for high nutrient availability, we might find consistently positive associations between nutrient availability and EEAs. Instead, we find that all EEAs decrease, irrespective of changes in associated nutrient availability. Moreover, N-acquiring EEAs are positively related to N availability in soil, whereas P-acquiring EEAs are negatively correlated with P availability. This suggests that EEAs are not primarily responsible for postfire changes in soil nutrient availability. Rather, heat-induced mineralization of organic P increases soil available P (Butler et al., 2018; Dijkstra & Adams, 2015; Saa et al., 1993) as much as 76%. This occurs concurrent with fire volatilizing N, shifting the system toward N limitation by reducing organic N substrates upon which N-acquiring EEAs can act, such that microbes become N-substrate limited. Therefore, these fire effects appear to slow microbial decomposition in the postfire environment, reducing microbial biomass and enzyme activity and shifting the system stoichiometry and nutrient limitation.

Further inference is speculative, there is evidence suggesting the possibility that soil microbes have different demands for different nutrients in the postfire environment. We found that soil P-acquiring EEAs decreased more than soil C- and N-acquiring EEAs (Figure 1), even though organic P, the substrate for soil P-acquiring EEA, does not decrease in response to fire (Butler et al., 2018). Firstly, increased soil available P (from pyro-mineralization) may alleviate microbial P demand and thereby suppress soil microbial production of P-acquiring enzymes, since enzyme synthesis is an energy demanding process (Allison & Vitousek, 2005; Burns et al., 2013; Schimel & Weintraub, 2003). Second, greater soil P availability may increase soil microbial demands for other elements such as C and N (Allison et al., 2010), stimulating the production of C- and N-acquiring enzymes (Ajwa et al., 1999; Allison et al., 2010; Chen et al., 2017). Thus, soil available N might be still derived primarily from microbial mineralization of organic N. In contrast, the postfire P cycle may be strongly uncoupled from microbially mediated decomposition, suggesting that a dramatic increase in available P from pyro-mineralization can substantially slow microbial recycling of P. However, further site-specific work is necessary to disentangle these processes.

However, results from this meta-analysis are limited to the studies we included in our meta-analysis (Appendix S2). Most of the studies are from woodlands and forests in the Northern Hemisphere that examined relatively short responses of soil EEAs to a single fire; it is unclear if fire effects on soil EEAs extends to grass-dominated ecosystems that experience long-term repeated fires. Though frequent fires in grasslands and savannas generally lead to substantial losses of soil C (Pellegrini et al., 2018), they may have selected for fire-tolerant microbes over time (Dooley & Treseder, 2012). Therefore, we predict that frequent fires in grassland and savanna ecosystems might decrease soil EEAs but that the magnitude of the reduction might depend on the extent to which soil microbes adapt to frequent fires. Furthermore, long-term frequent fires can lead to a decline in soil N pools and to relatively low N availability, if N inputs from N fixation and deposition are not high enough to offset volatilization losses (Pellegrini et al., 2018; Schafer & Mack, 2018). For this reason, we predict that declines in soil N-acquiring EEAs would correspond with decreases in soil available N even under frequent fires occurring over the long term. Though initial enrichment of soil P pools is common after the first decade of frequent burning (Pellegrini et al., 2018), long-term frequent recurrence of fire can potentially lead to a depletion of soil P from enhanced erosion and leaching (Wanthongchai et al., 2008). Since external P inputs are extremely low, this depletion of P may accelerate internal P cycling and potentially strengthen the production of soil P-acquiring enzymes, a pattern opposite to that of a single fire at short time scale. Additional studies in grass-dominated ecosystems with long-term frequent fires are critical for improving our understanding of how fires affect soil EEAs and microbially mediated decomposition at the global scale.

CONCLUSIONS

In summary, our meta-analysis reveals the sensitivity of soil EEAs to fire. We show that substantial decreases in soil EEAs in response to fire are primarily driven by fire-induced reductions in soil microbial biomass and organic matter substrates. The relationship between nutrient availability and EEAs differs strongly depending on the nutrient, however. Fire effects on soil N availability decreased alongside decreasing N-acquiring EEA, but fire instead increased P availability through pyro-mineralization of organic P, thereby slowing enzymatic decomposition of organic P in the postfire environment. Additionally, our results highlight the need for further studies in unrepresented ecosystems (e.g., grasslands and savannas) and regions that may have different biogeochemical responses to fires compared to well-represented forest ecosystems and for further long-term and continuous monitoring of fire impacts on soil EEAs and nutrient cycle processes to tease apart the direct and indirect effects of fires. Long-term studies can also shed light on how fire-induced changes in decomposition environment influence long-term C cycling, especially the slow-turnover C pools. Overall, our findings illustrate the large magnitude of fire effects on soil nutrients and on decomposition processes, with significant implications for ecosystem dynamics under anticipated changes in fire frequency and severity.

AUTHOR CONTRIBUTIONS

Yong Zhou and A. Carla Staver conceived this study; Yong Zhou collected and analyzed the data and wrote the first draft, with input from A. Carla Staver; all authors contributed to the interpretation of results and the writing of the manuscript.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Zhou et al., 2022) associated with this paper are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.931zcrjn6.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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