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META ANALYSIS

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Carbon and nitrogen dynamics in tropical ecosystems following fire

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Abstract

Aim: Tropical ecosystems have grown increasingly prone to fire over the last century. However, no consensus has yet emerged regarding the effects of fire disturbances on tropical biogeochemical cycles.

Location: Tropics.

Time period: 1960–2018.

Major taxa studied: Tropical ecosystems: Above- and below-ground carbon (C) and nitrogen (N) dynamics.

Methods: We analysed the impacts of fire on C and N dynamics in tropical ecosystems through a meta-analysis of 1,420 observations from 87 studies.

Results: Fire reduced both above- and below-ground C and N pools, with greater reductions above- than below-ground. Fire decreased soil total carbon (TC), total nitrogen (TN) and nitrate nitrogen (NO_3^-) and increased ammonium nitrogen (NH_4^+) in surface mineral soil layers but did not affect those in deep layers. Fire decreased TC and TN in savanna but did not affect those in tropical dry and moist forests. Fire did not affect NH_4^+ and NO_3^- in savanna because of non-significant responses of N mineralization rate (N_{min}) to fire. Conversely, fire increased NH_4^+ and decreased NO_3^- in tropical dry forest, but did not affect NH_4^+ and increased NO_3^- in tropical moist forest owing to thermal decomposition of soil organic N and increased soil nitrification, respectively. Moreover, NH_4^+ declined and NO_3^- increased initially and then decreased with time after fire. Above- and below-ground response variables to prescribed fire were mediated largely by fire frequency and experimental duration, respectively.

Main conclusions: Our results suggest a high vulnerability of the above-ground C and N pools to fire, whereas the biogeochemical cycles below-ground are of high complexity. Fire effects on below-ground C and N pools, which are highly uncertain and vegetation specific, should be investigated further.

KEYWORDS

carbon cycling, experimental duration, fire frequency, meta-analysis, nitrogen cycling, tropical ecosystems, vegetation

1 | INTRODUCTION

Fire is a common disturbance in terrestrial ecosystems and burns 423 million hectares annually world-wide (Giglio et al., 2018). Ground studies and remote-sensing data have revealed that fires, including anthropogenic burning related to land conversion, are more prevalent in tropical and subtropical ecosystems than anywhere else on Earth (Alonso-Canas & Chuvieco, 2015; Cochrane, 2003). This was confirmed by data (2003–2016) from the Global Fire Atlas (Andela et al., 2019). In addition to being a powerful and instantaneous environmental modifier (Bowman et al., 2009; DeLuca & Sala, 2006), fire can potentially have profound and long-term effects on the biogeochemical and stoichiometric characteristics of plant–soil systems (e.g., DeLuca & Sala, 2006; Toberman et al., 2014), especially the dynamics of carbon (C) and nitrogen (N) in the tropics (Pellegrini et al., 2014). However, no consensus has been reached (Coetsee et al., 2008; Døckersmith et al., 1999; Pellegrini et al., 2015), and it is therefore imperative to synthesize and quantify the effects of fire on C and N dynamics in tropical ecosystems.

Empirical studies have undoubtedly advanced our understanding of C and N dynamics following fire in tropical zones. Research has shown that fire can shift ecosystem C and N cycles through the combustion of plant biomass, volatilizing C and N from organic matter before it can be decomposed and integrated into soils (Pellegrini et al., 2014; van der Werf et al., 2017). Fire-induced reductions in above-ground biomass are frequently observed in tropics (e.g., Asbjornsen et al., 2005; Barbosa & Fearnside, 2005; Levick et al., 2019). During burning, significant amounts of C and N stored in above-ground biomass are oxidized and lost to the atmosphere through volatilization in the form of carbon dioxide (CO_2) and N gases, such as the atmospheric pollutants (NO_x) and ammonia (NH_3), the potent greenhouse gas nitrous oxide (N_2O) and inert dinitrogen gas (N_2) (Certini, 2005; Dannenmann et al., 2018). Moreover, large fractions of burned organic N are converted into heterocyclic N compounds (e.g., pyrroles, imidazoles and indoles) and into inorganic forms [ammonium nitrogen (NH_4^+) and nitrate nitrogen (NO_3^-)], under low to medium fire intensity (i.e., temperatures c. 200–500°C) (Certini, 2005). After the fire, the particulate returns to the soil surface in pyrogenic organic matter (PyOM) and ashes, which may then be lost to wind or water erosion (Wanthongchai et al., 2008). Therefore, fire can alter below-ground characteristics, such as soil C and N storage, N availability and decomposition activities (Cech et al., 2008; Ellingson et al., 2000; Pellegrini, Hobbie, et al., 2020).

Although many studies have been conducted in recent decades, there remains considerable disagreement concerning the potential effects of fire on soil C and N in tropical ecosystems. Recent research has concluded that fire decreases soil-resident C and N owing to reduced organic inputs following fire (Pellegrini et al., 2014). However, other studies have reported that fire enriched soil C by promoting the establishment of more productive plant species and the downward leaching of ash (Boerner et al., 2009; Pellegrini et al., 2018). Not only can fire enrich soil C, but also it invariably enriches soils with "very stable" C (Wolf et al., 2013). A recent article described how global fire emissions (2.2 Pg C/year) were significantly buffered through the generation of pyrogenic C (.26 Pg C/year) (Jones et al., 2019). Moreover, the limited or minor post-fire losses of soil N can be compensated through natural processes, such as N_2 fixation (Cech et al., 2010). For example, repeated fire could change plant communities in favour of N_2-fixing species (Holdo et al., 2012; Pellegrini et al., 2015). Additionally, divergent empirical findings have also been reported regarding the effects of fire on NH_4^+ and NO_3^-, varying among ecosystems, climate conditions, fire regimes and time since fire (Pellegrini, Hobbie, et al., 2020; Wan et al., 2001). Several studies have reported higher rates of net N mineralization (N_{min}) following slash burning in a Mexican dry forest (Døckersmith et al., 1999), whereas others found that fire treatments had no significant influence on the N_{min} in a South African savanna (Coetsee et al., 2008). Fire-derived NH_4^+, either a direct product of combustion or a product of post-fire mineralization activity, is of key importance for the regrowth of plants (Dannenmann et al., 2018). Microbial nitrification, the transformation of NH_4^+ to NO_3^-, thereby opening both leaching and gaseous N-loss pathways by denitrification (a microbial process of reducing NO_3^- and NO_2^- to N_2O and N_2), is a predominant process for N loss (Certini, 2005; Knicker, 2007). Increases in soil NH_4^+ and NO_3^- during the first 2 years after fire in a tropical dry savanna have also been reported (Singh et al., 1991), but Ellingson et al. (2000) observed an increase in soil NH_4^+ and a decrease in soil NO_3^- immediately (0–3 months) after fire in a Mexican tropical dry forest.

Variation in the effects of fire on soil C and N dynamics among studies can result from differences in soil sampling depth (Hume et al., 2016; Nave et al., 2011), type of fire (Sawyer et al., 2018), vegetation (Liu et al., 2015; Wan et al., 2001) and time since fire (Pellegrini et al., 2015; Xue et al., 2014). Fire usually has a much stronger direct effect on organic matter in exposed surface soils, because deep soils are insulated from all but the most extreme surface fires (Nave et al., 2011). Therefore, surface soil C and N dynamics are more commonly affected by fire than the deep soil layers (Mondal & Sukumar, 2014). Prescribed fires have less severe impacts on soil C and N than wildfires because prescribed fires tend to be initiated in less extreme fuel and weather conditions than wildfires (Sawyer et al., 2018). Prescribed (controlled) fires are usually set to promote germination and improve growth of desired forest species (Certini, 2005) or to remove shrubs and unpalatable species in savanna and refresh pastures ahead of the rainy season (Pellegrini et al., 2014). Conversely, wildfires are uncontrolled and typically start in dry environmental conditions and with high fuel loads; hence, they are often severe (Jolly et al., 2015). Although Blair (2005) and Liu et al. (2015) found reductions in soil total carbon (TC) and total nitrogen (TN) following two types of fires in tropical moist forests, Coetsee et al. (2010) and Liu et al. (2015) showed a minor decrease in soil TC and TN following prescribed fires in savanna and tropical dry forest. These site-specific responses are likely to be attributable to differences in the type of vegetation and soil moisture regime. Soil-resident C and N increased in <1 year following wildfires, and over time, decreased progressively to concentrations that were lower than unburned soil (Xue et al., 2014). On the one hand, fire-induced declines in plant biomass and leaf litter production decrease above-ground C and N inputs to soils (Pellegrini, McLauchlan, et al., 2020). On the other hand, soil erosion increases under heavy rainfall owing to the removal of the vegetation cover and litter, in addition to alteration of the soil surface conditions after fire (Doerr et al., 2000).

Additional factors associated with prescribed fires, including experimental duration (the duration of an experimental design) and fire frequency (the number of fires in an area per unit time), might also influence soil C and N dynamics. Cech et al. (2008) found that N pools in topsoil (0–10 cm) were low at sites where fires were frequent (annual burning). In contrast, Coetsee et al. (2010) showed that fire frequency had no effects on soil C and N in an African savanna. Although Coetsee et al. (2008) found that N availability was not affected by frequent fires (annual burning) in a South African savanna, Liu et al. (2015) observed that it increased with reduced fire frequency (triennial burning) in a wet sclerophyll forest. Few studies have explored post-fire C and N dynamics related to experimental duration, although Pellegrini et al. (2018), using data from 48 sites in savanna grasslands and broadleaf forests, found that fire-initiated losses of soil C and N increased with experimental duration (9–65 years). Much uncertainty remains on the sources of variability contributing to global patterns of post-fire C and N dynamics for prescribed fire. This knowledge gap limits the predictive accuracy of C and N cycling in tropical zones, emphasizing the need to examine C and N dynamics closely following fire in the tropics.

To gain a better understanding of how fire influences C and N dynamics in pan-tropical ecosystems, it is useful to synthesize the disparate results of individual studies. Such a meta-analysis, the subject of this study, enables a comprehensive evaluation of the effects of and can guide fire-management decisions. Although many studies have synthesized the overall effects of fire in temperate regions (Johnson & Curtis, 2001; Nave et al., 2011; Wan et al., 2001), less work on fire C and N dynamics in pan-tropical regions has been reported. Increasing human-dominated fire regimes in tropical regions (Andela et al., 2017) and the contribution of tropical C to global C cycles (Amundson, 2001) suggest that it is essential to understand the general impacts of fire in these regions, especially for prescribed fires. We recognized two types of fires, prescribed fires and wildfires, according to their original description, in order to quantify the effects of fire types on pan-tropical C and N dynamics while identifying the primary sources of variability using a meta-analysis. For prescribed fire only, experimental factors, including experimental duration, fire frequency and time since fire, were tested to determine the most important factors that affected variations in above- and below-ground C and N dynamics. We addressed the following questions:

1. What are effects of soil depth, vegetation type (savanna, tropical dry and moist forests) and time since fire on the fire-derived responses of above- and below-ground C and N dynamics following prescribed fires and wildfires?
2. Which drivers best explain the responses of above- and below-ground C and N dynamics to prescribed fires across the vegetation in tropical ecosystems?

Accordingly, we hypothesized that: (1) the responses of NH_4^+ and NO_3^- would differ among vegetation types because of different impacts of vegetation on N_{min} and nitrification processes (Wan et al., 2001); and (2) considering the role of experimental duration in shaping both plant inputs and soil decomposition (Pellegrini, Hobbie, et al., 2020), experimental duration could regulate the responses of soil C and N to prescribed fires.

2 | METHODS

2.1 | Approach

We conducted a meta-analysis to synthesize individual studies according to the generally established methods (Butler et al., 2018; Nave et al., 2011; Wan et al., 2001). The results of appropriate experiments were combined into a common database to estimate the magnitude of treatment effects. Distinct experimental results were expressed using an indexing effect known as a response ratio (*RR*), and its estimated value was averaged across studies (Wan et al., 2001). The *RR* is the ratio of the mean for a measured variable between treatment and control groups. Differences between treatments and controls (burned and unburned) were determined by statistically testing the *RR* significance. Heterogeneity in *RR* was calculated to determine whether all studies shared a common magnitude of the effect of treatment. Differences in *RR* between groups were determined ultimately by grouping the *RR* according to independent variables (e.g., fire type and vegetation type).

2.2 | Data sources and compilation

We searched for peer-reviewed publications (published between 1960 and 2018) relating to the effects of fire on C and N dynamics in tropical ecosystems using the ISI Web of Science and Google Scholar. A number of keyword combinations were used for this search, including "fire" OR "burn" OR "management" AND "nutrient" OR "carbon" OR "nitrogen" OR "C" OR "N" OR "biomass" AND "soil" OR "above-ground" OR "plant" OR "below-ground". The effects of fire on root biomass, reported in only three studies, were not included in our subsequent analyses. Only those studies that met the following criteria were included in this investigation. First, the research must have been conducted in tropical zones, defined as regions that lie between the Tropics of Cancer and Capricorn (23° N–23° S) (Hartshorn & Whitmore, 1999; Santelices, 2007). This included parts of Africa, Asia, Australia, Central America, the Caribbean and South America. Some studies included from locations outside the tropics were those with year-round average temperatures of 18°C or higher (tropical climates). Second, the research must have included control (unburned) and treatment (burned) values for the variables under study. Third, the sample sizes and means for the treatment and control groups must either have been reported directly or could be extracted from figures using the GRAPH DIGITIZER v.2.24 (http://getdata-graph-digitizer.com/) software. Measurements from different locations, ecosystem types, species, soil layers and treatment levels within a single study were treated as separate observations. The analyses also included tropical ecosystems with different fire regimes (fire intensity and frequency; Supporting Information Figures S1 and S2), which were sampled across a range of experimental durations (Figure 1). Our final dataset included 1,420 paired observations from 87 published papers, for a total of nine response variables (Supporting Information Appendix S1). Three above-ground and six below-ground response variables were collected, namely total above-ground biomass (TAGB), carbon (TAGC) and nitrogen (TAGN), TC and TN stocks, microbial biomass carbon (MBC), N_{min}, NH_4^+ and NO_3^-. A list of data sources used in the study is provided in Supporting Information Appendix S2.

The stocks of below-ground C and N were calculated from the soil C and N concentrations and soil bulk density (Chen et al., 2020). If the soil bulk density was not reported specifically in a study, it was estimated based on soil texture (USDA Natural Resources Conservation Service Soils; https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/office/ssr10/tr/?cid=nrcs144p2_074844) (Pellegrini et al., 2018). Study site locations (latitude and longitude) and several independent variables that might affect these response variables were also collected. The independent variables were soil sampling depth, vegetation type, time since fire, fire type, fire intensity, fire frequency and experimental duration. Soil depth was recorded as the midpoint of each soil depth interval (Chen et al., 2020). Across all studies, mineral soil depths varied from 1 to 77.5 cm. Mineral soil depths were separated into the surface soil layer (0–5 cm) and the deep soil layer (>5 cm). The surface soil layer contains the highest concentrations of soil organic matter and is most sensitive to fires. Vegetation types were classified as tropical dry forest, tropical moist forest and savanna (Atangana et al., 2014). Time since fire (the number of months between the time of measurements and the time of last fire) was aggregated into three time periods (0–6, 6–12 and >12 months) for above-ground C and N and soil TC and TN, and into six time periods (0–2, 2–4, 4–6, 6–12, 12–24 and >24 months) for soil MBC, N_{min}, NH_4^+ and NO_3^- according to their immediate response following fire. There are various options, such as energy released from the fire, flame length and rate of spread, and mortality of trees or loss in biodiversity, to quantify fire intensity in fire ecology (Keeley, 2008). In our study, fire intensity was divided into low, moderate and high levels, which were <2,000, 2,000–8,000 and >8,000 kilowatts per metre when it was originally estimated with heat released per metre of fire front or subjective visual assessment during or after a fire (Butler et al., 2018). The experimental duration (1–59 years) is the number of years a particular community experiences repeat fire disturbance and reveals the effects of persistent fire events on dynamics of ecosystem C and N (Pellegrini et al., 2018). Fire frequency is the number of fires per year (Sawyer et al., 2018).

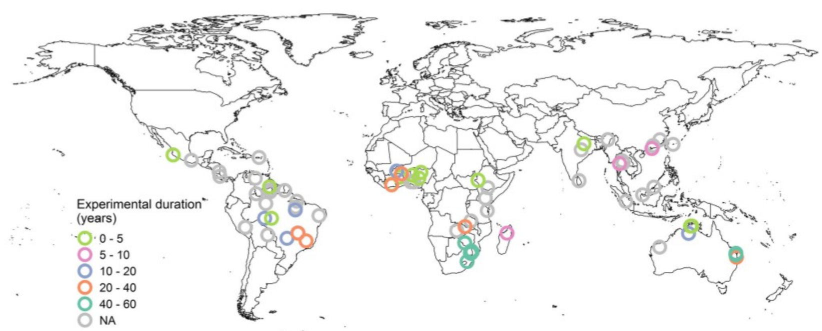

FIGURE 1 Geographical distribution of sites. Coloured circles represent the experimental duration (in years) as indicated in the key. Grey circles indicate that no experimental duration was reported. NA = not applicable

2.3 | Data analysis

For each variable of interest, all datasets were analysed to determine the overall effects of fire. Subsequently, sub-datasets of the various factors that might influence the effects of fire on the response variables were analysed. The *RR* was ln-transformed (ln*RR*) and used to estimate the magnitude of the treatment effect:

$$\ln RR = \ln \left(X_t / X_c \right), \tag{1}$$

where X_t and X_c are means of the treatment (burned) and control (unburned) groups, respectively.

The ln*RR* estimates and subsequent inferences in meta-analyses can depend on how individual observations are weighted. In our dataset (Supporting Information Appendix S1), 15 of 87 studies were pseudo-replicated. Weightings based on sampling variance could inflate the "power" of these studies (Zhang et al., 2018). Similar to previous research (Butler et al., 2018; Zhang et al., 2018), ln*RRs* were weighted by replicate number ($n = 1$ for pseudo-replicated studies):

$$W_r = \left(N_c \times N_t \right) / \left(N_c + N_t \right), \tag{2}$$

where W_r is the weight associated with each ln*RR* observation, and N_t and N_c are the numbers of replicates of treatment and control groups, respectively.

Mean effect sizes (mean ln*RR*) and 95% bootstrap confidence intervals (CI) were calculated using the "*rma.mv*" function from the *metafor* package in R v.3.5.1 software (R Development Core Team, 2018) with the maximum likelihood estimation (Chen et al., 2018; Viechtbauer, 2010):

$$\text{Mean}\ln RR = \frac{\sum_i \left(\ln RR_i \times W_{r_i} \right)}{\sum_i W_{r_i}}. \tag{3}$$

In order to identify categorical variables that influenced C and N responses to fire, subgroup analysis was used to examine the effects of fire on above- and below-ground C and N dynamics for different soil sampling depths, vegetation type, time since fire, fire type and fire intensity groups. We conducted the analysis with a mixed-effects model using the "*rma.mv*" function in *metafor* (Viechtbauer, 2010). "Study" and "plot ID" were included as random effects in the model to account for autocorrelation among observations within each "study" and "sample plot". Conventional heterogeneity statistics (*Q*-statistics) were used to test between-group heterogeneity (Q_M) among different subgroups (Ouyang et al., 2018; Wallace et al., 2017). The significance levels ($p < .05$) of the heterogeneity in the mixed-effects model (Q_M) included variation in the ln*RR* values that were explained by these models. These were tested against a chi-square distribution, which was equivalent to calculating the significance level of the slope against a normal distribution. We also transformed the ln*RR* and its corresponding CI to percentage change, to evaluate directly the effects using $\left(e^{\ln RR} - 1 \right) \times 100\%$. Fire was considered to have a significant effect on a variable if the CI of its percentage change did not overlap zero ($p < .05$). Mean ln*RR* values of categorical variables were considered significantly different if their 95% CIs did not overlap with each other.

We performed a mixed-effects meta-regression model in R v.3.5.1 software (R Development Core Team, 2018) to determine the most important factors (continuous variables) that affected variation in above- (TAGC and TAGN) and below-ground (TC, TN, NH_4^+ and NO_3^-) C and N to prescribed fire. For each variable of interest, a full model that controlled for experimental duration (in years), fire frequency (times per year), number of fires, time since fire, and their interactions was fitted. The number of fires was not included in the model because it was positively correlated with experimental duration ($r^2 = .60$; $p < .001$; $n = 485$). All models were examined for deviations from normality. To eliminate non-significant terms, we use the "*dredge*" function of the *MuMIn* package (Bartoń, 2020) based on the Akaike information criterion (AIC) to select the most parsimonious model among all alternatives. The R scripts needed to reproduce the analyses are available as Supporting Information Appendix S3.

3 | RESULTS

3.1 | Effects of fire on above-ground plant biomass

On average, fire decreased TAGB, TAGC and TAGN by 40.3%, 84.2% and 81.2%, respectively ($p < .001$; Figure 2a). Fire-induced decreases in TAGB, TAGC and TAGN were significantly influenced by vegetation types ($p < .05$; Supporting Information Table S1). For example, the decreases in TAGC in response to fire were much higher in savanna than in tropical forests, whereas no significant difference was found between tropical dry and moist forests (Figure 2b). Compared with tropical forest, savanna is more fire-prone owing to widespread herbaceous vegetation, which is non-compact and easily combustible (Russell-Smith et al., 2013). Above-ground plant biomass gradually recovered over time following fire ($p < .001$; Supporting Information Table S1; Figure 2c). For example, the fire-driven losses of TAGB across vegetations declined from 64.2% at 0–6 months to 29.8% and 29.9% at 6–12 and >12 months, respectively, following fire. Wildfires and fires of high intensity showed much stronger impacts on TAGB than prescribed fires and fires of low intensity, respectively (all $p < .05$; Supporting Information Table S1; Figure S3). Wildfires are always more severe (high intensity) than prescribed fires (Sawyer et al., 2018). Moreover, high-intensity fires usually cause loss of the entire above-ground vegetation, resulting in significant post-fire degradation (Alcañiz et al., 2018).

3.2 | Effects of fire on soil C and N

Overall, fire decreased soil TC by 18.9% ($p < .01$; Figure 3a) and decreased soil TN marginally, by 8.7% ($p = .05$; Figure 3e). Although the TC and TN of deep layers were not affected by fire ($p > .05$; Figure 3b,f), it decreased TC by 25.2% ($p < .001$; Figure 3b) and

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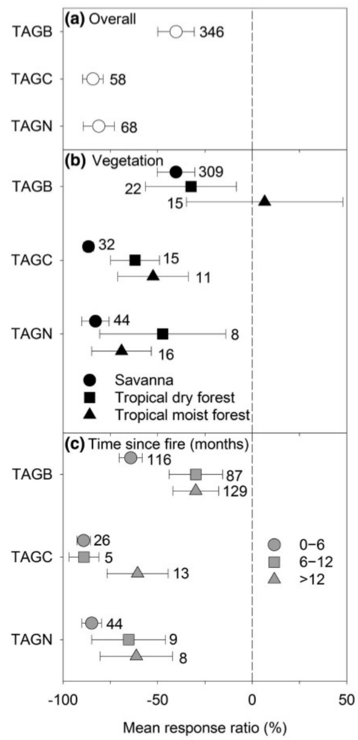

FIGURE 2 Effects of fire on: (a) total above-ground biomass, carbon and nitrogen (TAGB, TAGC and TAGN, respectively); (b) their vegetation type-specific responses (savanna, tropical dry forest and tropical moist forest); and (c) time since fire (in months). Values are means with 95% confidence intervals. Numbers beside each attribute are the number of observations

TN marginally (9.8%) in surface layers (p = .08; Figure 3f). Among vegetation communities, fire decreased TC (p < .001; Figure 3c) and marginally decreased TN in savanna ecosystems (p = .06; Figure 3g), but did not affect TC or TN in either tropical dry or moist forests (p > .05; Figure 3c,g). Across vegetation types, TC did not increase to pre-fire levels even >12 months after fire (p < .01; Figure 3d). Fire had no impact on TN across time-scales (0–6, 6–12 and >12 months) following fire for all vegetations pooled (p > .05; Figure 3h). Fire type and intensity had no significant impacts on soil TC and TN in response to fire (all p > .05; Supporting Information Table S1; Figure S3), probably because the effects of fire might be mediated primarily through vegetation rather than fire type and intensity (Holdo et al., 2012).

3.3 | Effects of fire on MBC, N_{min} and available N

In general, fire had no impact on MBC, N_{min}, NH_4^+ and NO_3^- (p > .05; Figure 4a,e,i,m). In the surface layer, fire did not affect MBC and N_{min} (p > .05; Figure 4b,f); however, it increased NH_4^+ by 21.8% (p < .05; Figure 4j) and decreased NO_3^- marginally, by 22.7% (p = .08; Figure 4n). In the deep soil layer, fire had no impact on N_{min}, NH_4^+ and NO_3^- (p > .05; Figure 4f,j,n); it increased MBC by 49.7% (p < .05; Figure 4b). The responses of N_{min}, NH_4^+ and NO_3^- to fire varied with different vegetation (p < .001; Supporting Information Table S1), although fire had no effects on MBC across the types of vegetation (p > .05; Figure 4c). Fire decreased N_{min} in tropical dry forests and increased N_{min} in tropical moist forests (p < .01) but had no impacts on N_{min} in savannas (p > .05; Figure 4g). Fire had no significant impacts on NH_4^+ and NO_3^- in savannas (all p > .05), increased NH_4^+ and decreased NO_3^- in tropical dry forests (p < .01) and did not affect NH_4^+ and increased NO_3^- in tropical moist forests (p > .05 and p < .05; Figure 4k,o). For the pan-tropics, fire generally had no effect on MBC and N_{min} over time following fire (p > .05; Supporting Information Table S1; Figure 4d,h), although N_{min} was decreased at 2–4 months following fire (p < .05; Figure 4h), perhaps owing to a limited number of observations. In contrast, there was a substantial temporal variability in soil NH_4^+ and NO_3^- after fire (p < .001; Supporting Information Table S1). The NH_4^+ was higher immediately after fire (p < .05; 0–2 and 2–4 months), recovered to pre-fire levels with time (p > .05; 4–6, 6–12 and 12–24 months) and decreased after 24 months (p < .001; >24 months) (Figure 4l). The NO_3^- did not increase during the first 4 months after fire, increased at 4–6 months after fire (p < .05), gradually returned to pre-fire levels at 6–12 months (p > .05) and was reduced at >12 months after fire (p < .05) (Figure 4p).

3.4 | Controls for responses of above- and below-ground C and N to prescribed fire

The response to prescribed fire of above-ground variables (TAGC and TAGN) was mediated by fire frequency, whereas those below-ground (TC, TN, NH_4^+ and NO_3^-) were mediated largely by experimental duration (p < .01; Table 1). Multiple linear regression models showed that fire-induced losses in TAGC and TAGN increased with greater fire frequency (p < .001; Table 1; Figure 5a). Responses of fire-initiated losses of soil TC, TN and available N (NH_4^+ and NO_3^-) increased with increasing experimental duration (p < .01; Table 1; Figure 5b,c). Additionally, our results showed that time since fire might also affect the response of above- and below-ground C and N variables to prescribed fire; particularly those below-ground (Table 1; Figure 5d–f).

4 | DISCUSSION

4.1 | Impacts of fire on above- and below-ground C and N

We observed that, generally, fire decreased both above- and below-ground C and N pools (Figures 2 and 3). The decreases of above-ground

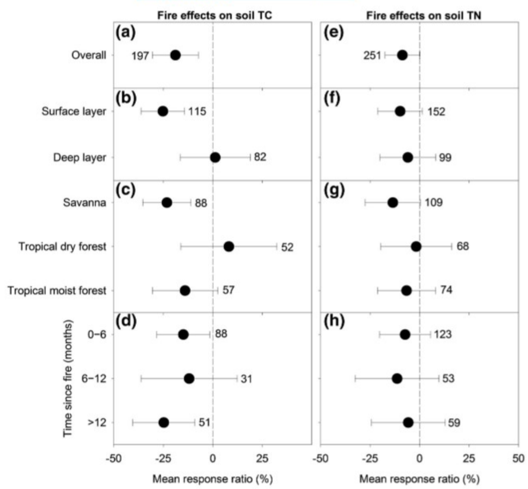

FIGURE 3 Effects of fire on (a–d) soil total carbon (TC) and (e–h) total nitrogen (TN): (a,e) overall dynamics; (b, f) between soil depths; (c,g) among vegetation types; and (d,h) time since fire. Values are means with 95% confidence intervals. Numbers beside each attribute are the number of observations

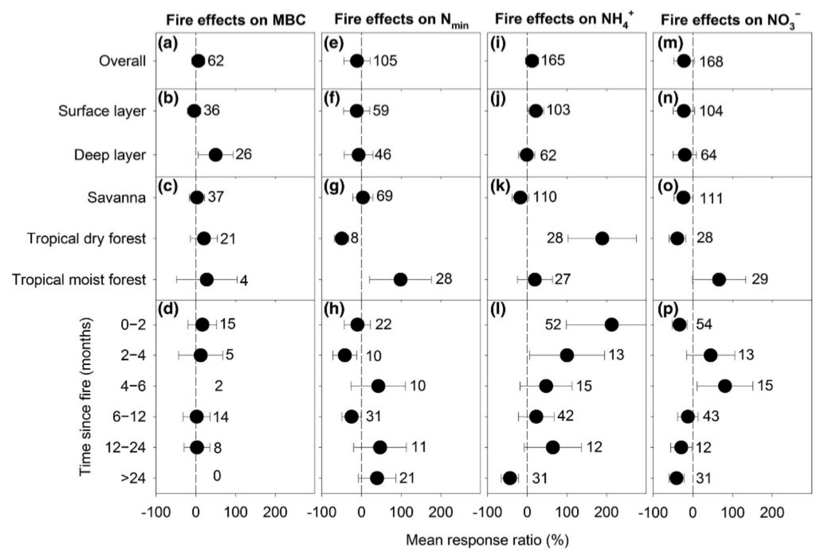

FIGURE 4 Effects of fire on: (a–d) soil microbial biomass carbon (MBC); (e–h) net nitrogen mineralization rate (N_{min}); (i–l) ammonium nitrogen (NH_4^+); and (m–p) nitrate nitrogen (NO_3^-), showing: (a,e,i,m) overall dynamics; (b,f,j,n) effects between soil depths; (c,g,k,o) among vegetation types; and (d,h,l,p) times since fire. Values are means with 95% confidence intervals. Numbers beside each attribute are the number of observations. The results for the data with sample size fewer than four are not presented

TABLE 1 Controls on the variation in the responses (natural logarithmic response ratio) of the above- and below-ground C and N variables to prescribed fire

	Traits	Factor	d.f.	*F*	*p*-value
Above-ground	TAGC	Fire frequency	1	39.46	**<.001**
		Time since fire	1	4.08	.06
	TAGN	Fire frequency	1	35.96	**<.001**
		Time since fire	1	2.83	.11
Below-ground	TC	Experimental duration	1	6.67	**.008**
		Time since fire	1	4.49	**.04**
	TN	Experimental duration	1	7.41	**.01**
		Time since fire	1	4.66	**.03**
	NH_4^+	Experimental duration	1	29.28	**<.001**
		Time since fire	1	81.53	**<.001**
	NO_3^-	Experimental duration	1	62.45	**<.001**

Note.: Bold values indicate $p < .05$.

Abbreviations: NH_4^+, ammonium nitrogen; NO_3^-, nitrate nitrogen; TAGC, total above-ground carbon; TAGN, total above-ground nitrogen; TC, soil total carbon; TN, soil total nitrogen.

C and N pools were much higher than those of below-ground pools, similar to previous studies (Blair, 2005; Cech et al., 2008; Coetsee et al., 2010; Holdo et al., 2012; Pellegrini et al., 2014). Previous studies have shown that despite large fire-induced C and N losses from plant biomass, part of the burned organic matter will return to the soil with pyrogenic organic matter and ashes, offsetting the losses of soil C and N (Dannenmann et al., 2018; Jones et al., 2019).

Although there were no losses of TC and TN in the deep soil layer following fire, we found that fire decreased TC and marginally decreased TN in the surface soil layer (Figure 3b,f). To assess whether our results were biased by the coarsely defined soil layers, we conducted the same analyses for alternative soil depth categories (Supporting Information Figure S4). We found that fire decreased the soil TC in the uppermost soil layer (0–5 cm) but not in the other soil depth ranges (5–20, 20–40, 40–60 and >60 cm), which corroborates our initial results. It has been reported that fire-induced losses of TC and TN in surface layer soils might be attributed to their exposed position in the soil profile, which makes them vulnerable to direct combustion, volatilization and post-fire erosion (Sawyer et al., 2018). Conversely, based on a study by Stoof et al. (2011), the thermal insulation capacity of soils, protecting soils from temperatures >100°C until deep soils are dry, might have been responsible for the negligible changes in C and N pools in the deep soils.

The effects of fire on soil TC and TN varied with vegetation type, with decreases observed in TC and TN in savanna ecosystems, but no changes in tropical dry and moist forests (Figure 3c,g). Savanna vegetation is mainly herbaceous and easily combustible, which increases the quality of the fuel load (more grass) and the percentage of fuel consumed (Nardoto et al., 2006). Conversely, tropical forests generally accumulate C and N in the soil, whereas savanna ecosystems do not (Pellegrini et al., 2014). Therefore, one of the major reasons that why fire did not significantly affect soil TC and TN in tropical forests is that fire-induced losses in total soil C and N were relatively small compared with the total amount of C and N stocks within a certain sampling depth (Eswaran et al., 1993; Pellegrini et al., 2016). Interestingly, and consistent with the results of Verma et al. (2019), we found that the soil TC did not increase even >12 months following fire (Figure 3d), which suggested strongly that soil C accumulation is a long-term process. However, the non-significant responses of soil TN to fire did not change with time since fire (Figure 3h). Previous research has suggested that fire increases C:N ratios in litter owing to stoichiometric changes in corresponding living plant biomass and/or to stoichiometric shifts in C and N resorption before leaf abscission (Toberman et al., 2014). The increased C:N ratios in initial litter were higher than the value required by the microbial decomposers for N mineralization (Chacón & Dezzeo, 2007). Therefore, microbes might minimize losses of soil TN by immobilizing the inorganic N (NH_4^+ and NO_3^-) more efficiently owing to higher microbial N demand (Chacón & Dezzeo, 2007; Manzoni et al., 2008). Moreover, this might also have been attributable to fire causing the formation of char-derived heterocyclic N compounds that are highly recalcitrant to biotic and abiotic decomposition (Jones et al., 2019; Knicker, 2007).

4.2 | Impacts of fire on available N

There were non-significant changes in soil NH_4^+ and NO_3^- following fire (Figure 4i,m). These non-significant changes were in disagreement with the findings of other studies that fires have significant influences on soil NH_4^+ and NO_3^- (Ellingson et al., 2000; Richards et al., 2012; Singh et al., 1991). There are various processes of the N cycle relating to NH_4^+ and NO_3^- following fire, and the magnitude of these processes can differ among sites, explaining the

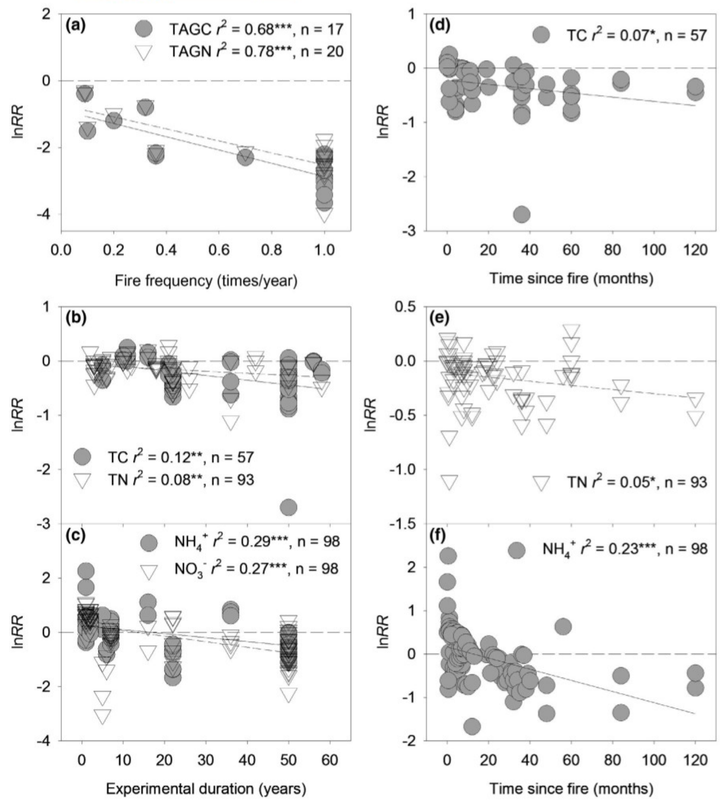

FIGURE 5 Natural logarithmic response ratios (ln*RR*) of the above- and below-ground C and N variables in relationship to fire frequency (expressed as times per year), experimental duration (in years) and time since fire (in months) under prescribed fires. *$p < .05$. **$p < .01$. ***$p < .001$. NH_4^+ = ammonium nitrogen; NO_3^- = nitrate nitrogen; TAGC = total above-ground carbon; TAGN = total above-ground nitrogen; TC = soil total carbon; TN = soil total nitrogen

different results in different studies. For example, fire can enrich NH_4^+ by promoting the thermal decomposition of organic N and post-fire ammonification owing to altered soil microclimate, temperature, pH and microbial activities (Certini, 2005; Stirling et al., 2019). Conversely, fire can decrease NH_4^+, because nitrifying bacteria, which oxidize NH_4^+ to NO_3^-, are stimulated by fire, thereby opening both leaching and gaseous N-loss pathways (Andersson et al., 2004). Our results support the finding by Wan et al. (2001) that fire increased NH_4^+ and marginally decreased NO_3^- in surface layers, but had no impact on available N in deep soil layers (Figure 4j,n). Given that surface soils are typically exposed to ground fires, whereas deep soils are insulated from them, combustion imparts much stronger effects on the thermal decomposition of organic matter and leaching loss pathway in surface layers (Nave et al., 2011), which leads to increased NH_4^+ and marginally decreased NO_3^-. Interestingly, fire increased MBC in deep soil layers (Figure 4b). A previous study has revealed that post-fire increases in labile C and downward movement into deep soil layers benefit microbial growth and lead to increased MBC (Michelsen et al., 2004).

Our analyses suggest that the effects of fire on available N differed among vegetation types. Specifically, fire did not affect NH_4^+ and NO_3^- in savannas; it increased NH_4^+ and decreased NO_3^- in tropical dry forests; and it had no significant impacts NH_4^+ but increased NO_3^- in tropical moist forests (Figure 4k,o). The dominance of post-fire processes of the N cycle relating to NH_4^+ and NO_3^- can vary among vegetation types and soil moisture regimes (Pellegrini, Hobbie, et al., 2020; Wan et al., 2001). The non-significant responses of NH_4^+ and NO_3^- to fire in savannas might result from the finding that fire has no impacts on the post-fire mineralization activity (Supporting Information Figure S5a), which is supported by non-significant responses of MBC and N_{min} to fire (Figure 4c,g). The post-fire increases in NH_4^+ in the tropical dry forests, consistent with a study by Ellingson et al. (2000) in a Mexican tropical dry forest, are the result of thermal decomposition of soil organic N, protein hydrolysis and destructive distillation of organic N, whereas the decreased NO_3^- following fire is attributable to volatilization of the soil NO_3^- pools with a long duration of fire treatment at temperatures >200°C (Supporting Information Figure S5b). In contrast, tropical moist forests rapidly recycle nutrients owing to high temperature and the availability of moisture (Vitousek & Sanford, 1986). The fire-derived NH_4^+ may be largely assimilated by plants and soil microbes for regrowth (Butler et al., 2018; Pellegrini et al., 2014), leading to the non-significant responses of NH_4^+ to fire in the tropical moist forests (Supporting Information Figure S5c). Moreover, increases in NO_3^- in the tropical moist forests are likely to be caused by increased nitrification rates following fire (Andersson et al., 2004; Ilstedt et al., 2003). The post-fire regeneration of nitrifiers and favourable conditions for nitrification, such as raised soil temperature and moisture, would contribute to increased nitrification rates (Wan et al., 2001). Our results regarding the vegetation-specific responses of inorganic N to fire suggest the necessity for appropriate fire-management programmes in different tropical ecosystems.

The temporal response patterns of available soil N (NH_4^+ and NO_3^-) to fire identified in our meta-analysis were similar to those found by Wan et al. (2001). Specifically, fire increased soil NH_4^+ and NO_3^-, and the response of NO_3^- to fire lagged behind that of NH_4^+ during the first few months following fire (Figure 4l,p). Furthermore, the responses of both NH_4^+ and NO_3^- to fire generally shifted from increases to decreases with time since fire (Figure 4l,p). These decreases, which were consistent with the findings of Xue et al. (2014), might be attributable to erosion of the nutrient-rich ash layers through runoff and wind (Ellingson et al., 2000), leaching losses (Dannenmann et al., 2018), microbial immobilization, and assimilation by plants and microbes (Kaye et al., 1999).

4.3 | Response regulators of above- and below-ground C and N to prescribed fire

Overall, our results demonstrated that fire frequency and experimental duration regulated the responses of above- (TAGC and TAGN) and below-ground (TC, TN, NH_4^+ and NO_3^-) variables to prescribed fires, respectively, in tropical ecosystems (Table 1; Figure 5a–c). In accordance with the results of Pellegrini et al. (2018), we found that the negative effects of fire on TAGC and TAGN increased with higher fire frequency, simply because of above-ground plant effects. Above-ground productivity usually increases after a fire owing to the improvement in microclimates through the removal of accumulated litter (Briggs & Knapp, 1995), enhanced availability of NH_4^+, which is of key importance for plant regrowth (Hart et al., 2005; Ludwig et al., 2018), and increased efficiency of nutrient use by plants and establishment of more productive plant species (Boerner et al., 2009; Exbrayat et al., 2018; Pellegrini et al., 2018). However, above-ground biomass (hence TAGC and TAGN) is easily burned and can be consumed completely by fire (Asbjornsen et al., 2005). For example, we found that annual burning consumed 94.4% of TAGC and 91.8% of TAGN (Figure 5a). With increased experimental duration, sequential fires consumed ever more soil TC and TN and increased the imbalance between production and consumption for available N (NH_4^+ and NO_3^-). The increased combustion of soil organic matter by fire over a long-term sequence of fire events coupled with the slow accumulation of soil C following fire (Figure 3d) can be responsible for higher TC losses. With greater time since fire, inorganic N leaching and gaseous N loss (e.g., N_2O) might be an important pathway for TN losses from soil (Dannenmann et al., 2018), which are supported by a fire-induced decline in NH_4^+ and NO_3^- after 24 months (Figure 4l,p). Furthermore, the increased loss of available N with greater experimental duration might be attributable to the fact that the consumption of available N exceeds its production, through the promotion of above-ground plant growth following fire (Battipaglia et al., 2014; Valor et al., 2018), which is supported by reduced negative effects of fire on TAGB with time since fire (Figure 2c).

4.4 | Implications for fire-enabled vegetation models

Fire is a crucial ecological process, which affects vegetation structure, biodiversity and biogeochemical cycles in all vegetated ecosystems (Butler et al., 2018; DeLuca & Sala, 2006). Improved projections of fires and their impacts on ecosystem properties will support a wide range of global environmental change assessments and the development of strategies for sustainable management of terrestrial resources (Hantson et al., 2020). Modules that simulate burnt area and fire emissions are increasingly being included in dynamic global vegetation models (Hantson et al., 2016). Our general findings here can also serve as a benchmark for vegetation-fire models, or modellers might use the detailed site data that we collected to evaluate models against results from particular sites.

4.5 | Conclusions

In conclusion, our results showed that the negative effects of fire on above-ground C and N were much higher than those below-ground, suggesting high vulnerability of the above-ground C and N pools. The effects of fire on below-ground C and N varied for different soil layers and vegetation types in the tropics. Soil TC, TN and available N were affected by fire in surface layers but not in deep layers, because deep soils are insulated from all but the most extreme surface fires. Fire decreased TC and marginally reduced TN in savannas, but not in tropical dry and moist forests, owing to the easily combustible fuel load in savannas. Fire did not affect NH_4^+ and NO_3^- in savannas, increased NH_4^+ and decreased NO_3^- in tropical dry forests, and had no impacts on NH_4^+ but positive effects on NO_3^- in tropical moist forests. Different responses of C and N dynamics to fire in different soil layers across vegetation types indicate high complexity of the biogeochemical cycles below-ground. Moreover, fire frequency and experimental duration were found to have negative impacts on the responses of above- and below-ground variables to prescribed fire in tropical ecosystems. Despite consistent negative effects of fire on above-ground C and N dynamics across vegetations, our results overall suggest that the responses of below-ground C and N dynamics to fire are highly uncertain and vegetation dependent, which requires further investigation.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

All authors contributed intellectual input and assistance toward the preparation of this manuscript. X.X. and Y.L. conceived the idea. D.J. collected and analysed the data with help from X.X., C. X., C.C., C.J. and H.Y.H.C. X.X. and D.J. wrote the paper with input from all authors.

DATA ACCESSIBILITY STATEMENT

This study contains published data detailed in the Supporting Information (Appendix S1).

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BIOSKETCH

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SUPPORTING INFORMATION

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