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.


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 (FC), total nitrogen (TN) and nitrate nitrogen (NO3) and increased ammonium nitrogen (NH4) 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 NH4 and NO3 in savanna because of non-significant responses of N mineralization rate (Nmin) to fire. Conversely, fire increased NH4 and decreased NO3 in tropical dry forest, but did not affect NH4 and increased NO3 in tropical moist forest owing to thermal decomposition of soil organic C and increased soil nitrification, respectively. Moreover, NH4 declined and NO3 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.
1 INTRODUCTION

Fire is a common disturbance in terrestrial ecosystems and burns 423 million hectares annually worldwide (Kijowska et al., 2015). Growing studies and remote-sensing data have revealed that fires, including anthropogenic burning related to land conversion, are more prevalent in tropical and sub tropical ecosystems than anywhere else on Earth (Arias-Cano & Chuvieco, 2015; Goharzadeh, 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, 2010; 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 on this (Cotrufo et al., 2007; Dakeishi et al., 2019; 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, volatilization of 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 aboveground biomass are frequently observed in tropics (e.g., Ahlgren et al., 2010; Barbour & Fearnside, 2005; Levick et al., 2010). 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 (CO₂) and N gases, such as the atmospheric pollutants (NOₓ) and ammonia (NH₃), the potent greenhouse gas nitrous oxide (N₂O) and inert dinitrogen gas (N₂) (Cotrufo, 2005; Dannenmann et al., 2015). Moreover, large fractions of burned organic N are converted into heterocyclic N compounds (e.g., pyroles, imidazoles and indoles) and into inorganic forms (ammonium nitrogen [NH₄] and nitrate nitrogen [NO₃]), under low to medium fire intensity (i.e., temperatures c. 200-500°C) (Cotrufo, 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 (Wardle et al., 2003). Therefore, fire can alter below-ground characteristics, such as soil C and N storage, N availability and decomposition activities (Koch et al., 2008; Ellingson et al., 2000; Pellegrini, Hobbs, 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 stocks.

**KEYWORDS**

carbon cycling, experimental duration, fire frequency, meta-analysis, nitrogen cycling, tropical ecosystems, vegetation.
savana and Northwest pastures ahead of the rainy season (Petersen et al., 2014). Conversely, wildfires are uncontrolled and typically start in dry environmental conditions and with high fuel loads; hence, they are often severe (Dally et al., 2013). Although Blair (2015) and Liu et al. (2015) found reductions in soil total carbon (C) and total nitrogen (N) following two types of fires in tropical moist forests, Coe et al. (2013) 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 (Dix et al., 2014). On the other hand, fire-induced declines in plant biomass and leaf litter production decrease above-ground C and N inputs to soils (Petersen, McLaughlin, 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 (Doerner, 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. Coe et al. (2008) found that N pools in topsoil (0-50 cm) were low at sites where fires were frequent (annual burning). In contrast, Coe et al. (2013) showed that fire frequency had no effects on soil C and N in an African savanna. Although Coe 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 (biennial burning) in a wet sclerophyll forest. Few studies have explored post-fire C and N dynamics related to experimental duration, although Petersen et al. (2015), 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 (5–45 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, 2004; Nave et al., 2011; Wan et al., 2011), 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 (Anandakumar, 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 the 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 the effects of soil depth, vegetation type (savana, tropical dry and moist forests) and time since fire on the net-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 NH₄⁺ and NO₃⁻ would differ among vegetation types because of different impacts of vegetation on N uptake and nitrification processes (Wan et al., 2001) and (2) considering the role of experimental duration in shaping both plant inputs and soil decomposition (Petersen, Hibbard, et al., 2000), 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., 2011). 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 index 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 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) (Harshorn
& 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 cli-
mates). 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-digiti-
er.com/) software. Measurements from different locations, eco-
system types, species, soil layers and treatment levels within a single
study were treated as separate observations. The analyses also in-
cluded 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 17 pub-
lished papers, for a total of nine response variables (Supporting
Information Appendix S1). These 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 ammo, NH4+, and NO3−.
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., 2020b). If the soil bulk density was not reported specifically
in a study, it was estimated based on soil texture (USDA Natural
.gov/wps/portal/csrees/detail/survey/office/er50/its/124-n-
rcs144p2_074844) (Pelegri, 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 experi-
mental duration. Soil depth was recorded as the midpoint of each
soil depth interval (Chen et al., 2020b). Across all studies, mineral
soil depths varied from 1 to 76.5 cm. Mineral soil depths were sep-
parated into the surface soil layer (0–5 cm) and deep soil layer
(10–50 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 savannas (Atapanea, 2014). Time since fire (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 ammo, NH4+ and NO3− 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 mortal-
ity 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, 2,000–9,000
and >9,000 kilowatts per metre when it was originally estimated
with heat released per metre of fire front or subjective visual as-
sessment during or after a fire (Butler, et al., 2018). The exper-
imental duration (1–19 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 (Pelegri et al., 2018). Fire frequency is the number of fires per
year (Saywer, 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 transformed (lnRR) and used to estimate the magnitude of the treatment effect:

\[ \text{lnRR} = \ln \left( \frac{X_i}{X_j} \right) \]

where \( X_i \) and \( X_j \) are means of the treatment (burned) and control (unburned) groups, respectively.

The lnRR estimates and subsequent inferences in meta-analyses can depend on how individual observations are weighted. In our dataset (Supporting Information Appendix S1), 15 of 67 studies were pseudo-replicated. Weightings based on sampling variance could inflate the "power" of these studies (Zhang et al., 2013). Similar to previous research (Butler et al., 2010; Zhang et al., 2013), lnRRs were weighted by replicate number (\( n = 1 \) for pseudo-replicated studies):

\[ W_i = \frac{N_i}{N_i + N_j} \]

where \( W_i \) is the weight associated with each lnRR observation, and \( N_i \) and \( N_j \) are the numbers of replicates of treatment and control groups, respectively.

Mean effect sizes (mean lnRR) and 95% bootstrap confidence intervals (CI) were calculated using the "meta" function from the metafor package in R v3.5.1 software (R Development Core Team, 2008) with the maximum likelihood estimation (Chen et al., 2013; Viechtbauer, 2010):

\[ \text{MeanlnRR} = \frac{\sum (\text{lnRR} \times W_i)}{\sum W_i} \]

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 "meta" 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 (I²-statistics) were used to test between-group heterogeneity (I²) among different subgroups (Hoxey et al., 2016; Wallace et al., 2017). The significance level (\( p < 0.05 \)) of the heterogeneity in the mixed-effects model (\( Q_m \)) included variation in the lnRR values that were explained by these models. These were tested against a ch-squared distribution, which was equivalent to calculating the significance level of the slope against a normal distribution. We also transformed the lnRR and its corresponding CI to percentage change, to evaluate directly the effects using \( (e^{\text{lnRR}} - 1) \times 100\% \). Fire was considered to have a significant effect on a variable if the CI of its percentage change did not overlap zero (\( p < 0.05 \)). Mean lnRR 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 v3.5.1 software (R Development Core Team, 2008) to determine the most important factors (continuous variables) that affected variation in above- (TAGB and TAGN) and below-ground (TC, TN, NH₄, and NO₃) C and N in prescribed fires. 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 (\( p = 0.60 \); \( n = 46 \)). All models were examined for deviations from normality. To eliminate non-significant terms, we used the "update" function of the MuMIn package (Bartoň, 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, TACC and TAN by 40.2%, 94.2% and 81.2%, respectively, \( p < 0.001 \); Figure 2a). Fire-induced decreases in TAGB, TACC and TAN were significantly influenced by vegetation types \( p < 0.05 \) (Supporting Information Table S1). For example, the decreases in TACC in response to fire were much higher in savannas than in tropical forests, whereas no significant difference was found between tropical dry and moist forests (Figure 3a). 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 \( p < 0.001 \) (Supporting Information Table S1; Figure 2a). For example, the fire-driven losses of TAGB across vegetation 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 low intensity showed much stronger impacts on TAGB than prescribed fires and fires of low intensity, respectively \( p < 0.05 \); 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 (Akaiš et al., 2018).

3.2 Effects of fire on soil C and N

Overall, fire decreased soil TC by 18.9% \( p < 0.01 \); Figure 3a) and decreased soil TN marginally, by 8.7% \( p = 0.05 \); Figure 3a). Although the TC and TN of deep layers were not affected by fire \( p > 0.05 \); Figure 3b), it decreased TC by 25.2% \( p < 0.001 \); Figure 3b) and
3.3 Effects of fire on MBC, \( N_{\text{min}} \), and available N

In general, fire had no impact on MBC, \( N_{\text{min}} \), \( \text{NH}_4^+ \), or \( \text{NO}_3^- \) (p > .05; Figure 4a). In the surface layer, fire did affect MBC, and \( N_{\text{min}} \) (p > .05; Figure 4b), however. It increased \( \text{NH}_4^+ \) by 21.6% (p < .05; Figure 4c) and decreased \( \text{NO}_3^- \) marginally by 22.7% (p < .05; Figure 4d). In the deep soil layer, fire had no impact on \( N_{\text{min}} \), \( \text{NH}_4^+ \), or \( \text{NO}_3^- \) (p > .05; Figure 4e). It increased MBC by 49.7% (p < .05; Figure 4f). The responses of \( N_{\text{min}} \), \( \text{NH}_4^+ \), and \( \text{NO}_3^- \) to fire scaled with different vegetation (p < .001; Supporting Information Table S1), although fire had no effects on MBC across the types of vegetation (p > .05; Figure 4g). Finally, fire decreased \( N_{\text{min}} \) in tropical dry forests and increased \( N_{\text{min}} \) in tropical moist forests (p < .01) but had no impacts on \( N_{\text{min}} \) in savannas (p > .05; Figure 4h). Fire had no significant impacts on \( \text{NH}_4^+ \) and \( \text{NO}_3^- \) in savannas (p > .05), increased \( \text{NH}_4^+ \) and decreased \( \text{NO}_3^- \) in tropical dry forests (p < .01), and did not affect \( \text{NH}_4^+ \) and increased \( \text{NO}_3^- \) in tropical moist forests (p > .05 and p < .05; Figure 4i). For the pan-tropics, fire generally had no effect on MBC and \( N_{\text{min}} \) over time following fire (p > .05; Supporting Information Table S1). Figure 4j, although \( N_{\text{min}} \) was decreased at 2–4 months following fire (p < .05; Figure 4k), perhaps owing to a limited number of observations. In contrast, there was a substantial temporal variability in soil \( \text{NH}_4^+ \) and \( \text{NO}_3^- \) after fire (p < .001; Supporting Information Table S1). The \( \text{NH}_4^+ \) was higher immediately after fire (p < .05; 0–2 and 2–4 months), recovered to pre-fire levels with time (p > .05; 0–2, 2–4, 6–12, and 12–24 months) and decreased after 24 months (p < .001; 0–24 months) (Figure 4l). The \( \text{NO}_3^- \) 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 12–24 months after fire (p < .05; Figure 4m).

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, \( \text{NH}_4^+ \), and \( \text{NO}_3^- \)) 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 \( \text{NH}_4^+ \) and \( \text{NO}_3^- \) increased with increasing experimental duration (p < .01; Table 1; Figure 5b). Additionall, our results showed that time since fire might also affect the responses 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 decrease of above-ground
FIGURE 3  Effects of fire on (a–d) soil total carbon (TC) and (e–h) total nitrogen (TN). (a,G) 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 (NMin); (i–l) ammonium nitrogen (NH₄⁺); and (m–p) nitrate nitrogen (NO₃⁻) 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.
C and N pools were much higher than those of below-ground pools, similar to previous studies (Balbi et al., 2009; Cech et al., 2012; Carboni 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 C pool with biotic 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 3a). 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 (0–20, 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 layers 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 Booth 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, d). Savanna vegetation is mainly herbaceous and easily combustible, which increases the quality of the fuel load (more grass) and the percentage of fuel consumed (Nardello 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 (Emerson et al., 1997; Pellegrini et al., 2016). Interestingly, and consistent with the results of Vermo et al. (2019), we found that the soil TC did not increase even in 12 months following fire (Figure 3b). 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 values required by the microbial decomposers for N mineralization (Chacón & DeZeeuw, 2007). Therefore, microbes might mineralize losses of soil TN by immobilizing inorganic N (NH₄⁺ and NO₃⁻) more efficiently owing to higher microbial N demand (Chacón & DeZeeuw, 2007; Manconi 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; Krueger, 2007).

### 4.2 Impacts of fire on available N

There were no non-significant changes in soil NH₄⁺ and NO₃⁻ following fire (Figure 4). These non-significant changes were in agreement with the findings of other studies that fire has significant influences on soil NH₄⁺ and NO₃⁻ (Ellison et al., 2009; Richards et al., 2012; Singh et al., 1991). There are various processes of the N cycle related to NH₄⁺ and NO₃⁻ following fire, and the magnitude of these processes can differ among sites, explaining the

### 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

<table>
<thead>
<tr>
<th>Trait</th>
<th>Factor</th>
<th>df</th>
<th>F</th>
<th>p-value</th>
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</thead>
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<tr>
<td>Above-ground</td>
<td>TAOC</td>
<td>1</td>
<td>39.46</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Time since fire</td>
<td>1</td>
<td>4.09</td>
<td>0.04</td>
</tr>
<tr>
<td>Above-ground</td>
<td>TAGN</td>
<td>1</td>
<td>35.96</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Time since fire</td>
<td>1</td>
<td>2.83</td>
<td>0.11</td>
</tr>
<tr>
<td>Below-ground</td>
<td>TC</td>
<td>1</td>
<td>6.67</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>Experimental duration</td>
<td>1</td>
<td>4.49</td>
<td>0.04</td>
</tr>
<tr>
<td>Below-ground</td>
<td>TN</td>
<td>1</td>
<td>7.41</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>Experimental duration</td>
<td>1</td>
<td>4.66</td>
<td>0.03</td>
</tr>
<tr>
<td>Below-ground</td>
<td>NH₄⁺</td>
<td>1</td>
<td>22.29</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Experimental duration</td>
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<td>8.15</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Below-ground</td>
<td>NO₃⁻</td>
<td>1</td>
<td>62.45</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Note: Bold values indicate p < 0.05.

Abbreviations: NH₄⁺, ammonium-nitrogen; NO₃⁻, nitrate-nitrogen; TAOC, total above-ground carbon; TAGN, total above-ground nitrogen; TC, total soil carbon; TN, total soil 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 (Czertli, 2005; Stirling et al., 2015). 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 (Anderson et al., 2004). Our results support the finding by Wan et al. (2003) 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 4a,b). 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 N-loss pathways 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 NH₄⁺ and NO₃⁻ in savannas. It increased NH₄⁺ and decreased NO₃⁻ in tropical dry forest and it had no significant impacts on NH₄⁺ but increased NO₃⁻ in tropical moist forests (Figure 4a). The dominance of post-fire processes of the N cycle related to NH₄⁺ and NO₃⁻ can vary among vegetation types and soil moisture regimes (Pelletier et al., 2020). The non-significant response of NH₄⁺ and NO₃⁻ 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 Nmin to fire (Figure 4c). The post-fire increase in NH₄⁺ in the tropical dry forest, consistent with a study by Eliasson et al. (2009) in a Mexican tropical dry forest, are the result of thermal decomposition of soil organic N, protein hydrolysis and degradative distillation of organic N, whereas the decreased NO₃⁻ following fire is attributable to immobilization of the soil NO₃⁻ 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 higher temperatures and the availability of moisture (Vitousek & Sanford, 1994). The fire-derived NH₄⁺ may be largely assimilated by plants and soil microbes for regrowth (Barlow et al., 2018). Pelletier et al. (2014), leading to the non-significant responses of NH₄⁺ to fire in the tropical moist forests (Supporting Information Figure S5a). Moreover, increases in NH₄⁺ in the tropical moist forest are likely to be caused by increased mineralization rates following fire (Eliasson et al., 2009; Liston et al., 2003). The post-fire regeneration of nitri- fiers and favorable conditions for nitrification, such as raised soil temperature and moisture, would contribute to increased mineralization rates (Wan et al., 2003). 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 responses patterns of available soil NH₄⁺ and NO₃⁻ to fire identified in our meta-analysis were similar to those found by Wan et al. (2003). Specifically, fire increased soil NH₄⁺ and NO₃⁻ and the response of NO₃⁻ to fire lagged behind that of NH₄⁺ during the first few months following fire (Figure 4d). Furthermore, the responses of both NH₄⁺ and NO₃⁻ to fire generally shifted from increases to decreases with time since fire (Figure 4d). 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 (Eliasson et al., 2009). Leaching losses (Eliasson et al., 2008), microbial immobilization, and assimilation by plants and microbes (Kaye et al., 1999).

4.3 | Response regulators of above- and belowground 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 belowground (TC, TN, NH₄⁺ and NO₃⁻) variables to prescribed fires, respectively, in tropical ecosystems (Table 1, Figure S5a–c). In accordance with the results of Pelletier et al. (2018), we found that the negative effects of fire on TC and TN 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 microorganisms through the removal of accumulated litter (Idso & Knapp, 1993), enhanced availability of NH₄⁺, which is of key importance for plant growth (Hart et al., 2005), and increased efficiency of nutrient uptake by plants and establishment of more productive plant species (Boerner et al., 2009; Eakin et al., 2013; Pelletier et al., 2018). However, above-ground biomass (hence TAGC and TAN) is easily burned and can be consumed completely by fire (Adljanen et al., 2005). For example, we found that annual burning consumed 94.4% of TAGC and 91.8% of TAN (Figure 4a). With increased experimental duration, sequential fires consumed ever more soil TC and TN and increased the imbalance between production and consumption for available N (NH₄⁺ and NO₃⁻). The increased combustion of soil organic matter by fire over a longer-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., N₂O) might be an important pathway for TN losses from soil (Eliasson et al., 2018), which are supported by a fire-induced decline in NH₄⁺ and NO₃⁻ after 240 months (Figure 4b). 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 (Batjes et al., 2014; Valor et al., 2018), which is supported by reduced negative effects of fire on TACB with time since fire (Figure 2b).

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 (Batjes et al., 2010; Delucia & Sala, 2006). Impacts 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 (Hanson et al., 2020). Models that simulate burnt area and fires are increasingly being included in dynamic global vegetation models (Hanson et al., 2010). Our general findings here can also serve as a benchmark for vegetation-fire models, or modelers 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 higher 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 surface layers, but not in tropical dry and moist forests, owing to the highly combustible fuel load in savannas. Fire did not affect N\textsubscript{2}O and NO\textsubscript{3} in savannas, increased NH\textsubscript{4} and decreased NO\textsubscript{3} in tropical dry forests, and had no impacts on NO\textsubscript{2} but positive effects on NO\textsubscript{2} 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 vegetation, 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.K. and Y.L. conceived the idea. D.J. collected and analyzed the data with help from X.K., C.X., C.C., C.J. and W.Y.H.C. X.K. and D.J. wrote the paper with input from all authors.

DATA ACCESSIBILITY STATEMENT

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

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SUPPORTING INFORMATION
Additional supporting information may be found in the online version of the article at the publisher’s website.