

The long and short of it: A review of the timescales of how fire affects soils using the pulse-press framework

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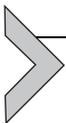
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Abstract

Understanding factors that regulate ecosystem responses to disturbances is a long-standing ecological goal and has been useful in predicting the effects of global change. The response of an ecosystem to a single perturbation does not necessarily predict its response to repeated perturbations—highlighting the ‘pulse’ vs. ‘press’ framework to predict ecosystem responses to single or recurring perturbations, respectively. This framework can help guide hypotheses around how ecosystems may, or may not, respond to changes in disturbance regimes. Here we apply the pulse-press framework to understand fire effects on soils and plant communities. Specifically, we combine a quantitative meta-analysis on the response of soil carbon and nutrients with a literature review of the response of microbial and plant communities. We argue that fire is a

cumulative disturbance driving a 'press' response and can be both coupled and decoupled from the 'pulse' response to a single burn depending on whether the response variable is regulated by the direct effects of heating or the indirect effects of changing plant and microbial communities. Our meta-analysis demonstrates that carbon and nutrient content in mineral soils responded differently because carbon and nitrogen, which are volatilized to the atmosphere in a fire and turn over relatively slowly in soil, are regulated by the long-term losses of plant biomass inputs more so than heating-induced volatilization, and thus change relatively little in a single fire. Contrastingly, the elements calcium, potassium, and phosphorus, which are enriched in ash because of their resistance to volatilization, are regulated by the intermittent pulses into the soil following a fire. A literature review suggests microbial biomass and decomposition activity tended to decline after a single fire because of heat-induced mortality, which was consistent with the effects of repeated burning, likely due to combined effects of repeated heat-induced mortality and lower soil organic matter. Another important 'press' response was how nutrient losses shape the nutrient use strategies of plants (tissue stoichiometry and nutrient acquisition strategy) and how changes in plant strategies influence soil responses. Past studies have generally found that species with low nutrient concentrations in biomass, high nutrient recycling before tissue senescence, and a greater reliance on mycorrhizal symbioses tend to increase in abundance with frequent burning. Many of these traits likely lead to slower decomposition and nutrient availability, but few studies have rigorously linked fire-driven shifts in traits with carbon and nitrogen cycling. The processes we have identified are likely to be especially important in tropical ecosystems, where disturbance by fire is shifting rapidly, attributable to changes in land use and climate. Tropical savannas are some of the most responsive landscapes to altered fire regimes, with large changes in soil carbon and nutrients, suggesting that shifts in fire regimes may change the carbon balance of these ecosystems substantially. We propose that more fire-manipulation experiments are needed in tropical forests, especially in moist forests where plants are not as well adapted to fire.



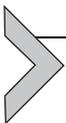
1. Introduction

The response of ecosystems to altered fire regimes will be a key factor determining the trajectory of the global carbon (C) sink ([Andela et al., 2017](#); [van der Werf et al., 2017](#)) and the preservation of biodiversity ([Bond and Parr, 2010](#)). Some of the largest changes in fire regimes are occurring in tropical ecosystems, such as savannas and forests ([Andela et al., 2017](#); [Trumbore et al., 2015](#)), which also play critical roles in the global carbon cycle ([Dixon et al., 1994](#)). Shifts in fire activity caused by changes in land use and climate ([Abatzoglou and Williams, 2016](#); [Andela et al., 2017](#)) are hypothesized to have long-term effects on ecosystem functioning because of the potential for past fires to influence processes like nutrient availability for decades

(Johnstone et al., 2016; Zarin et al., 2005). Such long-lasting effects of fire are hypothesized to emerge through a variety of mechanisms, such as changes in soil carbon and nutrients, microbial communities and plant physiological traits.

The response of soils to fire is complex because the immediate effects of a single fire are not always consistent with the long-term effects of repeated burning. For example, inorganic nitrogen (N) in the mineral soil may increase immediately following a single fire (Wan et al., 2001), but can be significantly depleted with repeated burning as the availability of mineralizable organic matter declines (Guinto et al., 2001; Norris et al., 2013; Pellegrini et al., 2014; Reich et al., 2001). Similarly, plant species colonizing a landscape immediately after a fire can have nutrient-rich tissues, high leaf area, and rapid biomass turnover, while those persisting in frequently burned landscapes often have relatively nutrient poor tissues and long-lived biomass (Cavender-Bares and Reich, 2012; Hoffmann et al., 2012; Pellegrini, 2016). Consequently, the effect of fire on ecosystems that emerges after decadal alterations in fire frequencies may remain undetected when only single burns are examined.

Here, we evaluate the factors that determine the response of soils from short- to long-term changes in fire regimes, through combining pulse-press and hierarchical response frameworks. To accomplish this, we review the literature on how fire impacts soils (both carbon and nutrient content and microbial communities) by contrasting the data from the effects of a single fire with those of repeated burning. To test the hierarchical scales at which fire effects emerge, we explore how plant and microbial communities respond to fire and how their compensatory responses lead to potential changes in soil nutrient cycling. Our aim is to provide a better understanding of how fire affects soils and why the effects of single fires may sometimes differ from those of repeated burning. To accomplish this aim, we combine a quantitative meta-analysis on the response of soil carbon and nutrients with a literature review of the response of microbial and plant communities. We first take a global approach to explore the applicability of these frameworks and then explicitly discuss the relevance to tropical ecosystems.



2. The pulse-press framework

The effect of burning on ecosystems can potentially be conceptualized using the pulse-press framework, which has been developed to reconcile the different effects of a discrete ‘pulse’ change in resource supply with the

continued ‘press’ of chronic changes in resource supply (Ives, 1995; Ives and Carpenter, 2007). This framework has been applied to many topics such as flooding in streams (Lake, 2000), precipitation and drought in terrestrial ecosystems (Sala et al., 2012; Schwinning et al., 2004), and eutrophication in aquatic systems (Ives and Carpenter, 2007). With drought, for example, the ‘pulse’ effects are determined by intraseasonal dynamics of how individual rainfall events affect ecosystems; the ‘press’ effects focus on interseasonal dynamics of how longer-term changes in rainfall across multiple growing seasons affect ecosystems (Schwinning and Sala, 2004). The response to ‘pulse’ declines in precipitation is not always predictive of the ‘press’ declines due to prolonged changes in precipitation (Schwinning and Sala, 2004). For example, different timescales of physiological responses (rapid enzyme production vs. slow biomass production) can result in a short change in rainfall eliciting a change in these rapid response variables, while a prolonged change induces shifts in slower response variables, such as plant community biomass and composition (Harris et al., 2018).

Similar analogies exist for fire. For example, in tropical savannas, plant communities can rapidly regrow and resprout after a single fire (Hoffmann et al., 2009), but repeated burning changes community composition by limiting the ability of juvenile plants to become adults, suppressing woody plant abundance and biomass over decades of repeated burning (Higgins et al., 2007; Moreira, 2000). The effects of single vs. repeated fires on belowground properties may also differ because a single fire may result in pulsed increases due to leaching of ash into soils (which would occur on daily to annual timescales) whereas repeated burning may result in losses due to lower aboveground plant biomass inputs into soils due to repeated combustion (which would occur on decadal timescales) (Fig. 1). In ecosystems with intense canopy wildfires that can directly combust soil organic matter, such as in boreal forests, the pulse and press effects may converge because organic matter losses from soils occur in both scenarios of single and repeated burns (Johnson and Curtis, 2001; Nave et al., 2011; Walker et al., 2019). Yet in many ecosystems that experience surface fires, such as tropical savannas and forests, soil responses can be determined by changes in plant communities on decadal timescales, as either succession when fire is excluded or slow losses of biomass and changing plant composition when fires recur (Higgins et al., 2007; Moreira, 2000). As a result of declining plant biomass inputs, soil organic matter can decline (e.g. in tropical savannas (Coetsee et al., 2010, Pellegrini et al., 2015)).

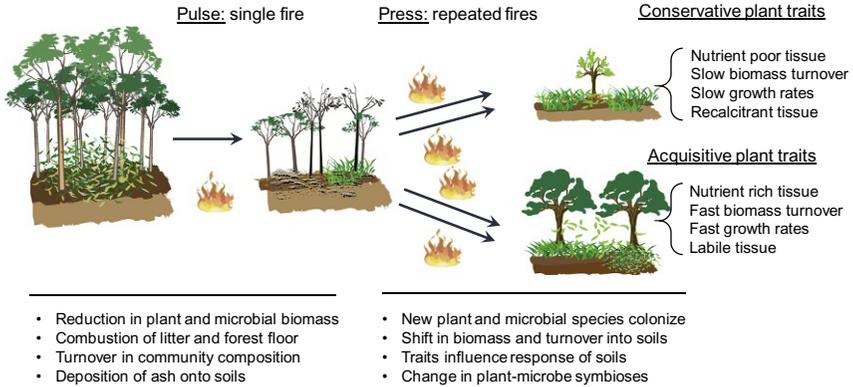
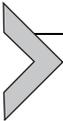


Fig. 1 Hypothesized conceptual schematic illustrating the potential responses of the ecosystem to alterations in burning. A single surface fire tends to reduce plant and microbial biomass as well as combust biomass in live plants (in wood and leaves) and the forest floor and litter layers (Kauffman et al., 1994). Elements that are not volatilized can be redeposited as ash that can be leached into the soils. Species with traits allowing them to resist mortality or re-grow rapidly after fire increase in abundance. Repeated burning restricts the turnover of aboveground biomass into the soils and reduces microbial activity (Metcalfe et al., 2018; Pellegrini et al., 2014), which can reduce soil nutrients (Guinto et al., 2001). Changes in the plant community can shift plant functional traits (Higgins et al., 2012), which generally group plant species into two broad 'strategies' of species that are conservative because they grow slowly and have nutrient poor and recalcitrant tissue and low biomass turnover (top scenario) (Wigley et al., 2016) or acquisitive because they grow quickly, have nutrient rich and labile tissue, and rapid biomass turnover (bottom scenario) (Pellegrini, 2016).



3. The hierarchical response framework

Theory suggests that pulse effects can scale to press effects through a hierarchical response framework via shifts in individual traits and species composition (Smith et al., 2009). Here we apply such a framework through the lens of plant-soil interactions (Bardgett et al., 2013); as repeated burning changes nutrient availability, plants and microbes may respond by shifting how they use and acquire nutrients (e.g., tissue stoichiometry and symbioses) (Fig. 2). In turn, changes in the physiological traits and composition of plants and microbes may further influence the rate at which nutrients become available through decomposition (Hobbie, 1992, 2015) (Fig. 2). Empirical studies have demonstrated that fire can change plant traits relevant to carbon and nutrient turnover in soils (Cavender-Bares and Reich, 2012;

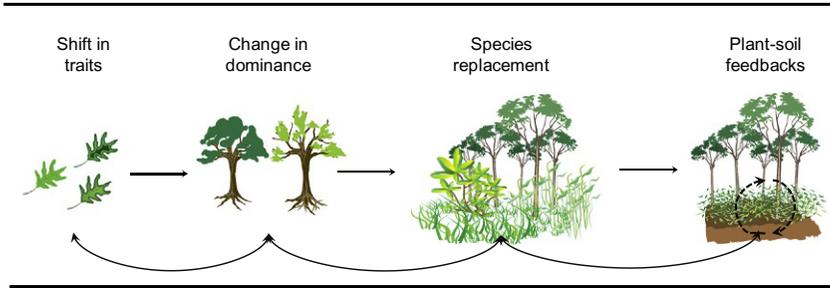
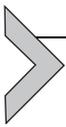


Fig. 2 Conceptual schematic of response hierarchies to changes in fire. The responses scale from shifts in traits, to turnover in the dominant species, to immigration of new species and loss of existing species in the ecosystem, to the restructuring of plant soil feedbacks. The arrows indicate that fire-driven changes emerge over the course of years to decades, but the key theme is that fire can alter the physiology of the plant community at these different scales, and that changes in certain physiological traits can influence soil biogeochemistry. Consequently, the observed changes in soil biogeochemistry may partly be due to the response of plant traits.

Dantas et al., 2013a; Hoffmann et al., 2005). For example, species favoured by fire can invest in resource acquisition such as N fixation (Newland and DeLuca, 2000) or have high nutrient resorption, thick and long-lived leaves, low tissue nutrient content, and high C:N ratios (Maracahipes et al., 2018; Pellegrini, 2016; Wigley et al., 2016), which can influence decomposition (Norris et al., 2013).

The response of plant communities may help explain the pulse vs. press effects on soils because the turnover of the plant community tends to be larger under prolonged changes in fire regimes. Plant communities can recover to pre-fire states after a single fire, even if it takes several decades (Clement and Touffet, 1990; Hanes, 1971); however, changes in fire frequency or intensity tends to alter plant species composition over the course of several years to decades (Glitzenstein et al., 2012; Lewis and Debuse, 2012; Peterson and Reich, 2001). Given that the press response of the plant community to fire is different from the pulse response, repeated burning may have distinct effects on the physiological traits of the plant community that could influence soil C and nutrient storage and turnover.



4. The pulse response: single fire events

4.1 Changes in elemental concentrations in soils

Elemental losses during fire are regulated by the heat of the fire combined with the physical properties of the elements and their compounds.

Combustion usually occurs around 650°C, which is above the temperature that volatilization begins to take place for carbon (C) and nitrogen (N) (200°C) and sulfur (S) (375°C). Potassium (K) and phosphorus (P) have slightly higher thresholds of 774°C, whereas magnesium (Mg) and calcium (Ca) have even higher thresholds of 1107°C and 1484°C, respectively (Hosking, 1938; Raison et al., 1985; Tiedemann, 1987). These temperature thresholds relative to the intensity of the fire determine whether elements in combusted biomass are volatilized to the atmosphere vs. pyromineralized into simpler compounds and retained in the remaining ash and char after the fire (Raison et al., 1985; Seiler and Crutzen, 1980). Over longer timescales, the 'fate' of the elements remaining in the system can be highly variable as they can be lost via erosion and runoff or taken up by regrowing plants and microbes and/or sorbed to minerals (DeBano and Conrad, 1978; Raison et al., 1985; Seiler and Crutzen, 1980). One hypothesis is that fire leads to belowground enrichment of elements with higher volatilization thresholds than combustion (K, P, Mg, and Ca) because they are redistributed from being stored in aboveground plant biomass into ash that is transported into the mineral soil (Butler et al., 2017). Carbon and N, on the other hand, are hypothesized to be lost from soils either through direct combustion of organic matter or a reduction in plant biomass inputs (Pellegrini et al., 2015).

Synthesis studies have found that concentrations of C and N can be enriched multiple years after a fire (Johnson and Curtis, 2001), reduced in particular ecosystems and after intense wildfires (Nave et al., 2011; Wang et al., 2012), or change relatively little beneath the top few centimeters of soil (Wan et al., 2001). For example, Wan et al. (2001) synthesized data from 87 studies across many ecosystems and concluded that total C and N concentrations in mineral soils are relatively insensitive to fire, except in the top few centimetres where direct combustion may be occurring. In contrast, Nave et al. (2011) synthesized data from 57 studies in temperate forests and found fire depleted mineral soil C and N concentrations but not stocks because of a concurrent increase in bulk density. In both studies, wildfires (which they interpreted to have higher intensities than prescribed fires because wildfires often occur in drier and/or windier conditions) tended to have larger negative effects on mineral soil concentrations. Consequently, losses are sensitive to the intensity of burning because fire intensity correlates with combustion of organic matter from the mineral horizon (Baird et al., 1999). Nonetheless, for many surface fires, which are usually low in intensity, mineral soil C and N do not change much in a single fire.

The pulse response of other nutrients, such as P and cations, differs from C and N. Several studies have shown that single fires tend to enrich soil P concentrations (Butler et al., 2018). Changes in soil cations are also apparent, but to our knowledge there has yet to be a meta-analysis of how single fires can affect cations (although see Pellegrini et al., 2018 for an analysis of long-term effects of repeated burning). Consequently, to evaluate the effect of fire on Ca concentrations (given that it has a higher temperature threshold), we compiled data from several sites ($n=21$) included in the other meta-analyses for comparability (Wan et al., 2001) and tested for effects using mixed-effects models weighting the contribution of studies by their variance and replication as is standard in other meta-analysis approaches (Hedges et al., 1999; Pellegrini et al., 2018) (see Supplementary Table S1 in the online version at <https://doi.org/10.1016/bs.aecr.2020.01.010>). We found that soil Ca tended to be enriched after a single fire (+59%, $P < 0.0001$), and that the enrichment increased with the time since fire (time since fire effect, $Q_M = 11.08$, $P < 0.001$). The temporal trends suggest that the redistribution of Ca into soil pools continues to occur over multiple years.

Comparing across elements, the volatilization thresholds of elements can be important in determining the pulse response of a single fire. Elements with higher thresholds are not lost to the atmosphere and thus are redistributed from ash into soils relatively rapidly; in contrast, elements with low thresholds tend to change relatively little in the soils because despite large aboveground losses mineral soils tend to not reach sufficiently high temperatures for volatilization to occur.

Unfortunately, most studies are in temperate ecosystems, especially temperate forests. It is likely that the response of the different elements to single fires are similar in tropical ecosystems, given that physical properties of the elements determine their potential volatility. For example, the slash and burn fires in tropical forests tend to support conclusions of C and N in aboveground biomass being volatilized to the atmosphere in a fire (Kauffman et al., 1993).

4.2 Changes in microbial communities

Understanding the pulse response of microbial communities holds promise for improving our ability to predict how fire influences soil C and nutrient turnover and availability. Multiple syntheses have evaluated the effect of single fires on soil microbial communities, which suggest fire can (i) suppress fungi, especially ectomycorrhizal types, more than bacteria (Dove and Hart,

2017), (ii) reduce microbial biomass (Dooley and Treseder, 2012; Pressler et al., 2018), and (iii) change decomposition activity (Wan et al., 2001; Wang et al., 2012), particularly after high intensity wildfires (Dooley and Treseder, 2012; Wang et al., 2012).

The implications of changes in microbial community composition and abundance can be assessed through measurements of heterotrophic respiration and N mineralization rates. For example, respiration can decline immediately following a fire, often attributed to reduced microbial abundance rather than substrate availability, but respiration can also increase, potentially due to an increase in soluble sugars (DeLuca and Zouhar, 2000, Pietikäinen and Fritze, 1995). Mineralization of organic N behaves in similarly complex ways, as there tends to be an increase in nitrification rates from a few days to months following fire. The increase in nitrification is hypothesized to be due to increases in exchangeable cations through ash deposition promoting nitrification (DeLuca and Sala, 2006). The effects of mineralization rates on inorganic N concentrations are clearer: a meta-analysis demonstrated that ammonium concentrations increase immediately (days to months) after a fire, while nitrate concentrations peak 6–12 months after a fire (Wan et al., 2001). But over long timescales of repeated burning, inorganic N declines (Pellegrini et al., 2018, 2020).

Extracellular enzymes involved in decomposition produced by microbes offer another avenue to evaluate fire effects on soil carbon and nutrient cycling but have received little attention in past syntheses. After a single fire, activity of decomposing enzymes can increase (Boerner et al., 2006; Rietl and Jackson, 2012). This result suggests fire may elevate nutrient turnover, which could then help explain the increase in inorganic nutrients observed following prescribed burning (Wan et al., 2001). Contrastingly, fire can reduce the activity of enzymes in decomposing litter layers (Köster et al., 2016), as well as soil pools (Pourreza et al., 2014). Shifts in enzyme activity may result from lower substrate availability due to reduced inputs, lower microbial biomass resulting from heat-induced mortality, turnover in species composition, or other unexplored mechanisms.



5. The press response: repeated burning

5.1 Elemental concentrations in soils: Divergence of pulse-press

The pulse effect of fire on soil C and N concentrations can be minimal and vary across ecosystems, climates, and fire intensities. In contrast, repeated

burning over decades can have more consistent effects on soil C and N, suggesting that the pulse effect of a single fire does not correspond with the press effect of repeated burning (i.e., the two are decoupled). For example, we updated our previous global meta-analysis (Pellegrini et al., 2018) of 48 sites (citations included below and in the references in Pellegrini et al., 2018) with data from four additional sites (Burns, 1952; Godwin et al., 2017; Guénon et al., 2013). The sites included in the analysis have (i) experienced altered fire frequencies (either due to natural variability or intentional manipulation) for 9 or more years, and (ii) the burned plots in all the sites have experienced more than one fire event. Re-analysis including the new sites confirmed the previous findings of a strong depletion effect of repeated burning on total soil C and N in savanna-grasslands and broadleaf forests (on average, frequently burned plots had -22% ($P < 0.001$) and -23% ($P < 0.001$) less C and N than fire-protected plots, respectively), but enrichment in needleleaf forests (on average, frequently burned plots had $+24\%$ ($P = 0.001$) and $+15\%$ ($P = 0.03$) more C and N than fire protected plots, respectively).

Moreover, the effect of frequent burning increased through time in savanna-grasslands and broadleaf forests, with the largest losses of soil C and N occurring in sites that experienced the longest alteration of fire frequencies. Consequently, the response of mineral soil C and N to a single fire event can be decoupled from the response to decades of repeated burning (Fig. 3). The different responses according to ecosystem type illustrate that the direction of the decoupling can depend on plant community composition, which may be due to a variety of processes that we do not explore here.

Further analyses demonstrated that tropical and temperate ecosystems responded in similar ways. In analyses of soil C and N, there were no significant differences in the response ratios between tropical (we aggregated sub-tropical and tropical regions) and temperate regions that were savanna-grassland and broadleaf forest ecosystems (region effect for C: $Q_M = 0.3$, $P > 0.50$, for N: $Q_M = 1.1$, $P = 0.30$). In the cases of P and Ca, all ecosystems converged on similar responses (region effect for P: $Q_M = 0.03$, $P > 0.50$, for Ca: $Q_M = 0.37$, $P > 0.50$). Most tropical sites are tropical savannas. However, many of the tropical savannas have enough rainfall and extensive wet season to allow closed-canopy forests to form in the absence of fire (Pellegrini et al., 2014). Consequently, the fire experiments in these wet savannas provide a useful baseline for how drier tropical forests may respond to fire.

The potential divergence between pulse and press responses of soil C and N are hypothesized to occur because changes in soil C and N are regulated

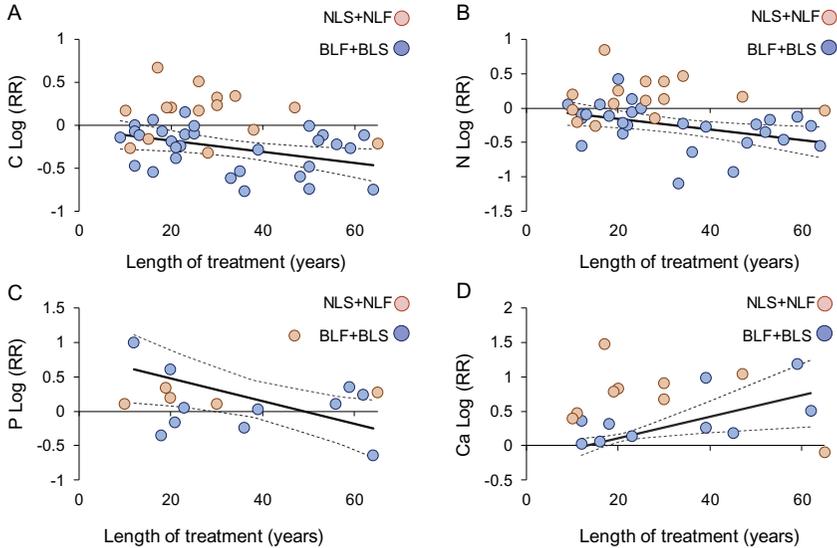


Fig. 3 Meta-regression between the length of fire treatment for sites that experienced at least 10 years of altered fire frequencies and the log response ratio of soil carbon (C, panel A), nitrogen (N, panel B), phosphorus (P, panel C), and calcium (Ca, panel D). The x-axis 'length of fire treatment' represents the number of years that fire frequencies differed between the high vs. low fire frequency treatments (in some cases due to natural variability in fire regime but in others due to intentional manipulation). Values shown are split into sites classified as either broadleaf forests and broadleaf savannas (BLF + BLS) or needleleaf forests and needleleaf savannas (NLF + NLS). Lines indicate significant meta-regressions, which were present only for BLF + BLS, C: $P=0.019$; N: $P=0.015$; P: $P=0.021$; Ca: $P=0.010$ for significant slopes. The responses of soil carbon and nutrients were not correlated with length of fire manipulation treatment in the NLF + NLS sites ($P > 0.05$).

by the long turnover time of soil organic matter and the rate at which plant biomass inputs (e.g., litterfall or root production and turnover) into soil changes with fire. Through successive burns, plant biomass inputs into soils declines due to repeated combustion of leaf litter, tree mortality, and losses of root biomass (Pellegrini et al., 2015, 2020; Raison et al., 1993; Reich et al., 2001). Consequently, repeated burning is predicted to change soils over decades as lower biomass inputs have an increasingly noticeable effect, which is consistent with the observations that repeated burning reduces soil C and N over decadal timescales (observed in Pellegrini et al. (2018) and updated with additional data in Fig. 3). Consequently, fire-driven losses of plant biomass inputs can change mineral soil C and N storage over decadal timescales as repeated burning depletes plant biomass storage and inputs into soils.

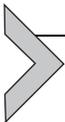
In contrast to C and N, the responses of Ca and P to single and repeated fires are similar (Fig. 3). For P, our previous meta-analysis found that across all sites the initial enrichment of P in soils persisted even after 30 years of repeated burning, but then became insignificant as frequent burning continues (Pellegrini et al., 2018). Our updated analysis illustrates that the enrichment and then decline of soil P emerges only in savanna-grasslands and broadleaf forests (study length, $P=0.02$, Fig. 3). Consequently, the initial redistribution of P into soils is sustained over multiple decades, but over time the enrichment decreases, which is likely due to various loss processes, such as erosion and leaching (Bêche et al., 2005; DeBano and Conrad, 1978). Soil P in needleleaf forests responded differently because it remains unchanged through time regardless of the number of fires. However, more data are needed to verify the lack of temporal change in needleleaf ecosystems because one of the longest studies used a relatively weak P extraction method (Mehlich 3) that likely does not capture changes in the more recalcitrant soil P fractions (Cross and Schlesinger, 1995); if that study is removed from the meta-analysis, soil P in needleleaf ecosystems declined.

Calcium enrichment with more frequent burning is more stable through time (Fig. 3) but with two nuances: (i) the enrichment is significantly greater in needleleaf ecosystems than in savanna-grasslands and broadleaved forests, and (ii) the enrichment in savanna-grasslands and broadleaf forests increases with the length of time plots experienced higher fire frequencies. The more consistent enrichment of Ca than P with fire is intuitive given its higher volatilization temperature.

We propose that the relative coupling or decoupling of various elements can be linked to the timescale of the mechanism regulating their input into soils. In the cases of Ca and P, the primary factor driving changes is the redistribution of ash, which occurs over days to months to a few years. However, the enrichment can change after multiple decades of increased burning potentially because of sustained leaching and erosion, suggesting that competing pathways reduce the enrichment but only on long timescales (e.g., >30 years). For C and N, the primary mechanism determining the effect of fire on soil pools is the reduction of biomass inputs into soils. Lower inputs reduce soil C and N slowly because the turnover of organic matter in soils occurs on decadal to centennial timescales in many systems (Jackson et al., 2017); consequently the lack of an observable pulse effect is likely because of insufficient time and losses to detect significant effects.

5.2 Microbial community enzymes: convergence of pulse–press

Only a few studies document the effects of changes in fire frequency on microbial community composition and activity (Bastias et al., 2006; Buscardo et al., 2015; Campbell et al., 2008; Oliver et al., 2015). These studies suggest that frequent burning generally shifts both microbial composition and activity (Ajwa et al., 1999; Buscardo et al., 2015). For example, repeatedly burned plots can have lower beta glucosidase activity relative to unburned controls (Ajwa et al., 1999; Boerner et al., 2005), suggesting slower organic matter turnover. Similarly, in an oak–hickory forest, repeated annual and periodic burning reduced the activity of acid phosphatase, alpha and beta glucosidase, sulfatase, and urease, relative to unburned plots, reductions that were all correlated with lower microbial biomass (Eivazi and Bayan, 1996). Consequently, preliminary evidence points to enzymes responding to persistent changes in fire frequency, but the causes of these changes are unclear. Mechanisms leading to shifts in enzymes could include losses of microbial biomass, shifts in C and nutrient availability, and/or changes in microbial composition. From the studies that do exist, the pulse and press response of microbes appear to be similar, where biomass and activity changes after single and multiple fires. Perhaps one reason for the convergence is the high sensitivity of microbes to mortality from heat during fire and the potential for relatively rapid compositional turnover.



6. Hierarchical responses of plants to fire-driven changes in nutrients

Fire-driven changes in soil nutrients have the potential to interact with changes in plant composition and their physiological traits. For example, fire-driven N losses may stimulate the colonization of fast growing N-fixing plants that produce a lot of nutrient rich litter, which can decompose into soils and replenish the N lost via fire; resultantly, the response of plants to low N conditions ‘compensates’ for the N losses at the level of the ecosystem. On the other hand, if the colonizing plants have traits such as high N resorption and lignin content and long-lived leaves, they can reduce the inputs of N from plant biomass into soils; resultantly, the of the plant ‘escalates’ N limitation at the landscape scale (Fig. 4).

Multiple studies have demonstrated that fire history can determine the composition of species with different, typically more conservative, traits (e.g., low specific leaf area, low concentrations of N, and high N resorption

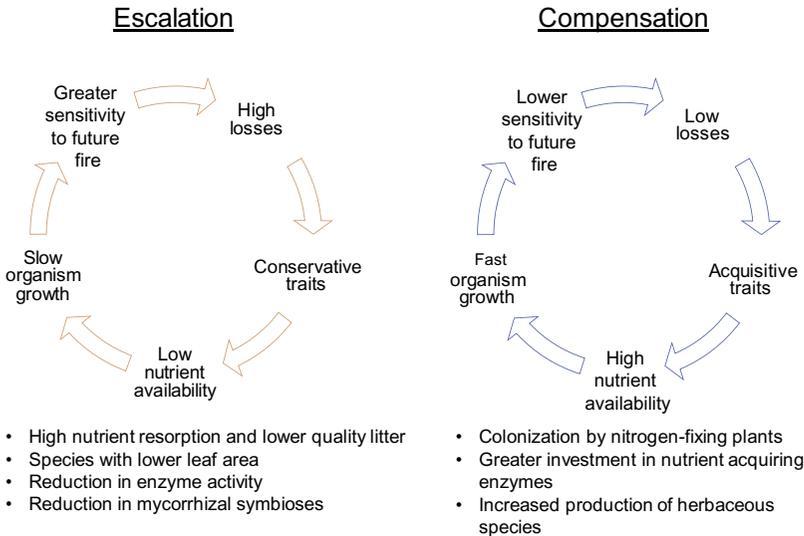


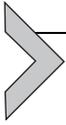
Fig. 4 Conceptual schematic of possible feedbacks between changes in soil nutrients, plant and microbial responses, and the impact of the responses on turnover in nutrients. Evidence for the examples are cited in the text.

efficiency) (Cavender-Bares and Reich, 2012; Dantas et al., 2013b; Pellegrini, 2016; Wigley et al., 2016). In Brazilian tropical savannas, for example, tree species specializing in savannas that burn frequently and have low soil N tend to have low foliar N and leaf area, and thicker, longer-lived leaves than species in forests that tend to not burn and have higher N (Dantas et al., 2013a; Hoffmann et al., 2005). Similarly, in temperate oak savannas, where frequent burning reduces soil N stocks and mineralization (Reich et al., 2001), trees from frequently burned plots withdrew a greater proportion of nutrients from leaves before senescence, producing lower quality litter that decomposed more slowly relative to individuals in fire protected plots (Hernández and Hobbie, 2008; Norris and Reich, 2009). In subtropical ecosystems such as eucalypt forests, frequent burning can reduce the relative concentrations of nutrients in foliar biomass (Butler et al., 2017). Consequently, evidence suggests that species with traits that further escalate nutrient limitation tend to increase in abundance with more frequent fire.

In addition to changes in the tissue traits of plants, fire-driven shifts in the abundance of plant species with different symbioses are thought to be important in regulating long-term effects of fire on soils (Hart et al., 2005a,b). For example, colonization by N-fixing plants may recover N lost in fire (Newland and DeLuca, 2000), and some studies have proposed that the

persistence of N fixers in the landscape is a critical factor buffering against N losses from soils (Johnson and Curtis, 2001). Subsequently, if the abundance of plants capable of N fixation increases with frequent burning, fixers may provide a critical pathway for replacing N losses (Yelenik et al., 2012). In temperate ecosystems that contain both herbaceous legumes and woody actinorhizal plants, species capable of fixing N tend to rapidly colonize burned landscapes (Newland and DeLuca, 2000; Peterson et al., 2007; Yelenik et al., 2012). Recent work has questioned the degree to which N fixers can balance N losses even when they increase in abundance following fire (Tierney et al., 2019). Moreover, the colonization of N-fixing plants in frequently burned areas is not necessarily generalizable across biomes: the relative abundance of woody plant N fixers does not appear to be influenced by fire in tropical savannas and forests but rather depends on water availability (Pellegrini et al., 2015, 2016).

Changes in the abundance of plants that form mycorrhizal symbioses may also impact the formation and turnover of soil organic matter (Taylor et al., 2016) because mycorrhizal symbionts can be strongly sensitive to fires (Cairney and Bastias, 2007). Single fires tend to have strong negative effects on fungal activity on root tips (Dove and Hart, 2017), potentially reducing the nutrient uptake capacity of plants. Studies from areas burned repeatedly over the course of multiple decades find similar negative effects of fire on fungi (Bastias et al., 2006). In ectomycorrhizal communities, such as those dominated by pines, oaks and eucalypts, frequent burning can reduce fungal species richness on root tips (Buscardo et al., 2010) and lower the abundance of colonized root tips (Tuininga and Dighton, 2004). However, there does not seem to be as clear of an effect of fire on arbuscular mycorrhizal (AM) communities, potentially because of the resilience of grasses to fire in many frequently burned ecosystems. For example, in a North American temperate grassland, 10 years of repeated burning did not reduce AM fungal colonization (Eom et al., 1999). In contrast, in African tropical savanna, ~40 years of repeated burning reduced AM colonization (Hartnett et al., 2004), suggesting a lower capacity for plants to acquire inorganic nutrients. The broad patterns of how fire changes the composition of plant species with different symbiosis strategies remains elusive, limiting inference into the role of changes in the composition of species with different symbiosis strategies in determining belowground responses to fire. However, preliminary data suggest fire can regulate the potential formation of mycorrhizal symbioses, either by directly killing the symbiont or changing the composition of plants with different symbiotic strategies.



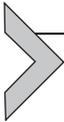
7. Relevance to tropical ecosystems

Connecting short- and long-term effects of disturbances on tropical ecosystems has been a focus of research for several decades (Brando et al., 2014; Moreira, 2000; Ryan and Williams, 2011; Uhl and Jordan, 1984). Extensive research has evaluated the effect of fire on tropical rainforests given their large extent and exposure to increased fire frequencies (Andela et al., 2017; Morton et al., 2006; Van der Werf et al., 2009). However, much research on the effects of repeated burning on tropical rainforests focuses on the response of vegetation, primarily trees, which tend to decline rapidly with more frequent and intense fires (Balch et al., 2013; Brando et al., 2014; Uhl and Jordan, 1984). In contrast to vegetation responses, very few studies have evaluated the effects of repeated burning on tropical rainforest soils and nutrient cycling. Notable exceptions have found that historical fire frequency can be important in regulating ecosystem recovery because of fire-driven N losses (Zarin et al., 2005) and potentially also through the suppression of decomposition (Metcalf et al., 2018). In contrast to the limited work on repeated burning effects on tropical rainforest soils, dozens of studies have investigated the effect of single fires on soil C and nutrients (Döckersmith et al., 1999; Kauffman et al., 2009; Ryan et al., 2011; Uhl and Jordan, 1984), which have found that slash-and-burn fires can result in a transient enrichment of soil nutrients, but intense fires can deplete soil nutrients in the top few centimetres. Our pulse–press framework leads to the hypothesis that the long-term effects of repeated burning on soils likely results in losses of C and N if the fire–return interval is short enough to prohibit the balancing of nutrient losses by atmospheric deposition and/or N fixation inputs, which can provide the necessary N for regrowth of secondary tropical rainforests (Batterman et al., 2013; Brookshire et al., 2019). Consequently, a large research gap exists between the multitude of studies on single fire effects with the reality that rainforests are being increasingly exposed to repeated burning.

In contrast to the limited work on the effect of repeated burning on tropical rainforest soils and nutrient cycling, there has been extensive work in tropical savannas and seasonal forests (Guinto et al., 2001; Holdo et al., 2012; Nardoto and Bustamante, 2003; Pellegrini et al., 2014; Turner et al., 2008; Verma and Jayakumar, 2018). Generally, fire exclusion increases the storage and turnover of soil C and nutrient stocks, whereas increased fire frequencies decreases C and nitrogen storage and turnover (Pellegrini et al.,

2018). Changes in soils arise due to combustion losses of C and nutrients from grass and tree biomass, despite savannas being a highly fire adapted system. Analyses of plant functional traits (e.g., leaf physiology) find that species adapted to repeatedly burned environments tend to have conservative nutrient use traits that may encourage lower soil nutrient availability (Dantas et al., 2013a; Hoffmann et al., 2005; Pellegrini, 2016). Aside from studies on soils and plants, little is known about how microbial communities respond to fire in tropical savanna ecosystems, limiting the understanding of mechanisms contributing to changes in biogeochemical cycling.

Even less is known about the responses of different forest and savanna types (such as seasonally flooded and peatland ecosystems). Fire effects in these ecosystem types are largely driven by weather variability resulting in dry enough conditions for fire to ignite and spread (van der Werf et al., 2010). For example, studies of peat combustion in boreal forests found moisture to be the critical factor regulating combustion (Rein et al., 2008). Seasonally inundated ecosystems also may respond differently than well-drained tropical ecosystems because of their thick organic horizons, which can be combustible as evidenced from tropical and boreal peatland ecosystems (Turetsky et al., 2015; Usup et al., 2004). Consequently, a single fire can hypothetically have large immediate effects on soils in seasonally flooded and peatland ecosystems, potentially causing the press and pulse effects to be similar.



8. Conclusions

Fire effects on ecosystems can be conceptualized through a pulse vs. press framework by considering the timescales of the processes changed by fire. Carbon and nitrogen, which are lost primarily aboveground to the atmosphere in a fire, turn over slowly in soil and change because of the long-term losses of plant biomass inputs with frequent burning. In contrast, elements enriched in ash because of their resistance to volatilization, such as calcium and phosphorus, are regulated by the intermittent pulses into the soil following a fire, resulting in a convergence of pulse and press responses. Soil microbes are sensitive to heating effects in a single fire, which tend to become magnified with repeated burning (i.e., generally larger losses of biomass and decomposition and changes in species composition), connecting pulse and press responses. Plant-soil interactions are likely critical for regulating the long-term effects of repeated burning given that species with nutrient-poor tissues with low decomposability and a greater reliance

on mycorrhizal symbioses tend to increase in abundance with frequent burning. These traits can decrease the turnover of carbon and nitrogen, creating a fire–nutrient feedback that may be a key characteristic of ecosystems that burn. However, repeated burning experiments are largely lacking in some of the ecosystems most rapidly experiencing changes in fire regimes such as tropical rainforests. In tropical rainforests, where plants are not as well adapted to fire and thus are more prone to mortality in a fire, repeated burning may have even more dramatic effects on soils and plant–soil interactions because of the rapid declines in biomass inputs and change in species composition.

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Data for the single fire studies are in the supplemental tables

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