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Post-fire soil emissions of nitric oxide (NO) and nitrous oxide (N_2O) across global ecosystems: a review

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Abstract Wildfires may increase soil emissions of trace nitrogen (N) gases like nitric oxide (NO) and nitrous oxide (N_2O) by changing soil physicochemical conditions and altering microbial processes like nitrification and denitrification. When 34 studies were synthesized, we found a significant increase in both NO and N_2O emissions up to 1 year post-fire across studies spanning ecosystems globally. However, when fluxes were separated by ecosystem type, we found that individual ecosystem types responded uniquely to fire. Forest soils tended to emit more N_2O after fire, but there was no significant effect on NO. Shrubland soils showed significant increases in both NO and N_2O emissions after fires; often with extremely large but short-lived NO pulses occurring immediately after fire. Grassland NO emissions increased after fire, but the size of this effect was small relative to shrublands. N_2O emissions from burned grasslands were highly variable with no significant effect. To better understand the variation in responses to fire across global ecosystems, more consistent measurements of variables recognized as important controls on soil fluxes of NO and N_2O (e.g., N cycling rates, soil water content, pH, and substrate availability) are needed across studies. We also suggest that fire-specific elements like burn severity, microbial community succession, and the presence of char be considered by future studies. Our synthesis suggests that fires can exacerbate ecosystem N loss long after they burn, increasing soil emissions of NO and N_2O with implications for ecosystem N loss, climate, and regional air quality as wildfires increase globally.

Keywords Nitrogen · Wildfire · Soil · Hole-in-the-pipe model · Nitrification · Denitrification

Introduction

Wildfires burn as much as 3% of the Earth's surface each year (Shi & Touge 2022) and are predicted to increase in frequency and severity (Ellis et al. 2022; Jones et al. 2020). Burning causes rapid changes in soil physical, chemical, and biotic properties with strong effects on nitrogen (N) cycling (Gustine et al. 2022; Pressler et al. 2019; Ulery et al. 2017). Fires can volatilize upwards of 65% of the N bound in vegetation to the atmosphere during combustion, as well as burn off soil organic layers which can store large amounts of ecosystem N (Boby et al. 2010; Dannenmann et al. 2018; Gustine et al. 2022). Following combustion, the remaining nitrogenous

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compounds in wildfire ash (predominantly ammonium; NH_4^+) can enrich soils with N and facilitate the succession of recovering plant communities. However, this N-rich ash may be susceptible to loss via wind erosion, run-off, and leaching; especially if no plants survive to take up the excess N (Hanan et al. 2016). While stochastic loss pathways can account for large portions of the N lost after fires (hydrologic export of N can be 14 times higher after fire; Gustine et al. 2022), high uncertainty in these estimates leaves up to half of post-fire ecosystem N loss unaccounted for (Goodridge et al. 2018). One explanation may be that significant N loss occurs through microbial and/or chemical processes that emit dinitrogen (N_2) and trace gases like nitric oxide (NO) and nitrous oxide (N_2O) to the atmosphere. Gaseous losses driven by microbial metabolism of post-fire N may perpetuate ecosystem N loss for years, representing loss pathways that are currently unaccounted for in even the most detailed post-fire N budgets to date (Goodridge et al. 2018; Hanan et al. 2016, 2017).

Beyond the implications of post-fire N losses to ecosystem recovery, productivity, and N loss dynamics, NO and N_2O play important roles in air quality and global climate. NO regulates the oxidative capacity of the atmosphere and is a precursor for tropospheric ozone formation (Crutzen 1979). Tropospheric ozone is a powerful oxidizing air pollutant which can harm plant tissues and have cascading stress effects on ecosystems as well as deleterious effects on human health (Grulke & Heath 2020; Moore et al. 2008). N_2O is a powerful greenhouse gas with ~300 times the warming potential of CO_2 (Griffis et al. 2017) and has replaced chlorofluorocarbons as the most important molecule destroying stratospheric O_3 in the twenty-first century (Ravishankara et al. 2009). Thus, quantifying post-fire fluxes of NO and N_2O is not only necessary to improve our understanding of post-fire ecosystem N loss, but also to provide information on how changing fire regimes could feed back on regional air quality and global climate. Here, we review 34 studies which measured post-fire fluxes of NO and/or N_2O from burned soils across diverse ecosystems to ask how post-fire environments influence soil emissions of NO and N_2O.

Background

Nitrification and denitrification are the most important microbial processes producing NO and N_2O in soils (Firestone & Davidson 1989). During nitrification, ammonia (NH_3; measured as NH_4^+ in soils) is oxidized by nitrifiers to nitrate (NO_3^-) under aerobic conditions. During denitrification, NO_3^- is reduced to dinitrogen gas (N_2) under suboxic conditions. In both cases, NO and N_2O are emitted as byproducts. The key factors that control these process rates and the ratio of NO:N_2O emitted have been conceptualized by the classic "hole-in-the-pipe" metaphor (hereafter, the HIP model) developed by Firestone and Davidson (1989; Fig. 1A). According to the HIP model, on an ecosystem scale, the availability of N substrates and the rate at which microbes are processing N is a good indicator of the potential for gaseous N loss (Davidson et al. 2000; Firestone & Davidson 1989). At finer scales, NO and N_2O loss can also be regulated by numerous factors that partition NO and N_2O production, the most important of which are: soil water content, availability of NH_4^+ or NO_3^-, the activity of N cycling microbial communities, and soil properties such as temperature and pH (Firestone & Davidson 1989). Since fires alter these major control variables in generally predictable ways, the HIP model could help make general predictions about the implications of wildfires for NO and N_2O emissions (Fig. 1B).

Soil water content

Soil water content controls microbial access to oxygen, which determines whether nitrification (aerobic) or denitrification (anaerobic) dominates and often predicts NO:N_2O emission ratios (Davidson et al. 2000). Fires can reduce shade from aboveground vegetation and combust soil organic matter, changing soil texture and forming hydrophobic layers in some surface soils (DeBano 2000) which can alter water infiltration and promote dry/aerobic conditions (Parsons et al. 1996; Pinto 2002; Weitz et al. 1998). Aerobic soil may initially promote nitrification which is associated with high NO flux (Firestone & Davidson 1989); however, as hydrophobic layers degrade, soils could become saturated for longer periods of time following rain due to lack of plant transpiration (Graham et al. 2016). This could increase N losses via denitrification or leaching during the wet season

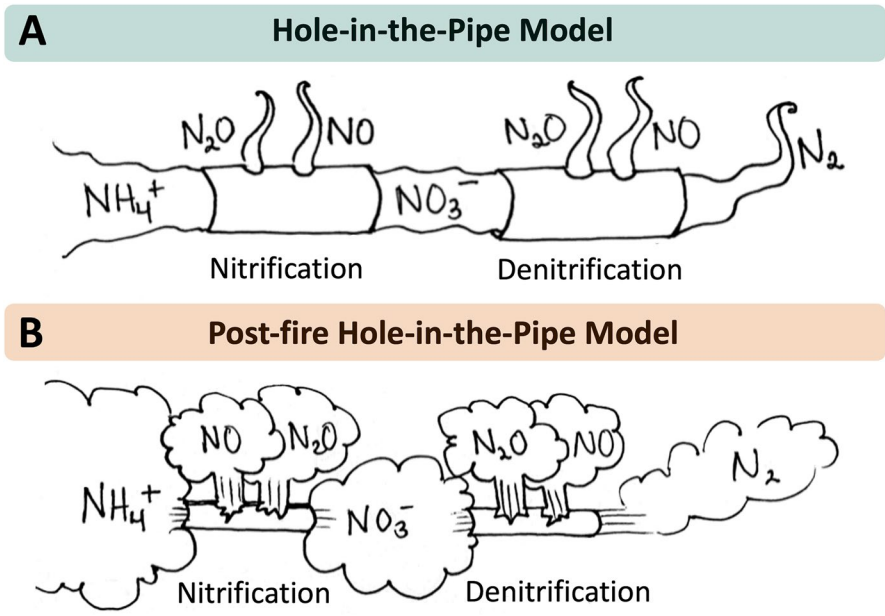

Fig. 1 **A** is a rendition of the HIP model by Firestone and Davidson (1989). Pipes represent the microbial processes of nitrification and denitrification. The "flow rate" of substrates (NH_4^+ and NO_3^-) determines the rate of NO and N_2O production while their ratios are partitioned by water content. NO is assumed to be the major product of nitrification which occurs in aerobic conditions, and N_2O is assumed to be the major product of denitrification which occurs under anaerobic conditions (Anderson & Levine 1986). **B** conceptualizes the possible effects of fire on the HIP model: substrate availability increases due to ash inputs while pipes are restricted due to lower microbial activity after fires heat-kill many microbes. NO and N_2O production is nonetheless increased as microbial communities recover and process large amounts of N substrates with less competition from plants, analogous to the pipes cracking under pressure

and might correspond to high N_2O emissions (Hubbert et al. 2012; Liu et al. 2013, 2015; Niboyet et al. 2011). Soil hydrophobic layers likely occur heterogeneously across burned landscapes as their formation depends on specific burn temperatures and organic matter types (DeBano 2000; Graham et al. 2016). Thus, even studies in similar climates with similar vegetation types have found different trends in post-fire soil moisture (Dannenmann et al. 2011, 2018; Karhu et al. 2015). Because soil moisture may vary both spatially and temporally after fires, measurements of soil moisture paired as directly as possible with flux measurements of NO and N_2O are recommended to further clarify the correlation of post-fire changes in soil moisture with N gas emissions.

Substrate availability

Because N-bearing compounds tend to have higher combustion temperatures relative to C (most organic material will combust at 460 °C, whereas roughly half of N will volatilize above 500 °C), wildfires can lower soil C:N ratios to as low as 7 in some cases (Knicker 2007) and increase available forms of soil N (Goodridge et al. 2018; Graham et al. 2016; Gustine et al. 2022), particularly NH_4^+ which is generated by combustion (Knicker 2007). High NH_4^+ in ash and thermal decomposition of soil organic matter may increase microbial access to N and accelerate nitrification rates (Ball et al. 2010; Ellingson et al. 2000). As nitrifiers metabolize NH_4^+ and generate NO_3^-, denitrifying organisms from a broad range of taxa may reduce NO_3^- to NO, N_2O, or N_2 (Firestone & Davidson 1989; Zhang et al. 2018). Denitrifying organisms also require labile forms of carbon (C), which can increase as fires heat litter layers and leave behind pyrogenic organic material from plant combustion (Dicen et al. 2020). Thus, the increase in microbially accessible forms of C and N substrates after fire could be expected to accelerate nitrification and denitrification activity, possibly leading to increased soil emissions of NO and N_2O. However,

vegetation type, burn frequency and severity, plant recovery and nutrient uptake, and site-specific conditions that determine how long N-rich ash may remain at the site (e.g., precipitation, wind, slope, etc.) likely control microbial access to substrates (Graham et al. 2016; Gustine et al. 2022; Knicker 2007; Rundel & Parsons 1984) in ways that have not been extensively documented.

Microbial communities

Wildfires can alter the abundance, structure, and function of both nitrifying and denitrifying microbial communities by heat-killing microbial cells or changing soil conditions (Liu et al. 2015; Long et al. 2014; Pressler et al. 2019). For example, the rate limiting step of nitrification—NH_3 oxidation—is controlled by two groups of organisms: ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB; Carey et al. 2016). AOA and AOB each process N with different efficiencies (Prosser et al. 2019), suggesting that shifts in dominance between these groups could drive changes in N emissions (Long et al. 2014; Mushinski et al. 2019). Specifically, AOB are thought to dominate in soils with high NH_4^+ and pH (conditions which are frequently associated with post-fire environments; Ball et al. 2010; Long et al. 2014; Smithwick et al. 2005; Ulery et al. 2017) and produce higher NO and N_2O emissions (Avrahami & Bohannan 2009; Prosser et al. 2019; Tzanakakis et al. 2022). Thus, if nitrifying communities are able to quickly recover from the heat-kill effects of fire, increased N gas emissions associated with AOB nitrification may be expected (Long et al. 2014).

In contrast to nitrification, denitrification is carried out by a broad range of taxa with NO and N_2O emissions generally corresponding to microbial diversity indices (Hayatsu et al. 2008; Mushinski et al. 2019). Microbial biomass and diversity are often severely reduced by fires (Pressler et al. 2019); nonetheless, high N_2 production has been measured in post-fire environments, suggesting that high rates of denitrification may persist despite reduction in abundance and diversity of microbial communities (Dannenmann et al. 2011, 2018). While wildfires can reduce soil microbial biomass by up to 96% and soil microbial diversity by 99% in surface soils (Pressler et al. 2019; Pulido-Chavez et al. 2023), the surviving microbial communities in deeper soils may be able to capitalize on the abundance of resources in the post-fire environment with little competition, allowing them to sustain high N cycling rates (Fig. 1B). Post-fire N cycling is likely linked to microbial recovery and successional dynamics post-fire (Enright et al. 2022; Pulido-Chavez et al. 2023), but studies explicitly linking N dynamics with post-fire microbial succession are currently rare. Overcoming the logistical/methodological challenges of simultaneously measuring both biogeochemical parameters and microbial community shifts presents an exciting opportunity for interdisciplinary collaboration.

Soil properties

Soil pH, temperature, and the presence of pyrolyzed organic matter (PyOM) are also known to influence fluxes of NO and N_2O (Davidson et al. 2000; Firestone & Davidson 1989; Hanley et al. 2013; Pilegaard 2013; Tang et al. 2022; Ulery et al. 2017; Zhang et al. 2021). Residual calcium oxide (CaO) left behind in the ash layer can form calcium carbonate ($CaCO_3$) in the presence of water, elevating soil pH in some instances to as high as 10–12 (Goforth et al. 2005; Ulery et al. 2017). Changes in pH can alter microbial metabolic functions, nutrient availability, and may favor AOB over AOA nitrifier communities (Prosser et al. 2019) with potential effects on N emissions. Wildfires also reduce shade and can increase soil temperatures, possibly accelerating microbial metabolisms and increasing emissions (Anderson & Poth 1989; Kim & Tanaka 2003). Burning can leave behind charcoal and forms of PyOM which may resemble biochar (a form of black carbon created under conditions of high-heat low-oxygen; Santín et al. 2017). While charcoal has been found in some cases to increase nitrification rates and AOB abundances and could thereby increase NO and N_2O emissions (possibly due to its capacity to sorb polyphenols and terpenes that otherwise inhibit nitrification; Ball et al. 2010), biochar can lower N_2O emissions by almost 40% (Kaur et al. 2022). It remains unclear whether biochar promotes more efficient reduction of N_2O to N_2 by denitrifiers as some have proposed (Hanley et al. 2013; Kaur et al. 2022) or if there are other mechanisms at work because N_2 emissions are rarely measured simultaneously with N_2O (Case et al. 2015; Tang et al. 2022; Zhang et al. 2021). The two studies that measured N_2 from soils found conflicting

effects of fire despite similar climate and vegetation (Dannenmann et al. 2011, 2018). Lastly, fires can alter the availability of iron and favor the reduction of iron oxides (Baalousha et al. 2022; De Marco et al. 2005) which could alter rates of chemodenitrification (abiotic production of NO and N_2O; Heil et al. 2016). Chemodenitrification is almost completely unexplored in post-fire soil environments. While post-fire changes in soil physical and chemical structure may increase nitrification rates, the influence of these factors on denitrification and chemodenitrification is difficult to predict.

Building on the HIP model, we would expect nitrification and NO emissions to increase after fires due to increased NH_4^+ availability, lower soil moisture, shifts toward AOB nitrification, and higher pH and soil temperature (Ball et al. 2010; Firestone & Davidson 1989; Long et al. 2014). However, the impacts of fire on denitrification and N_2O emissions may be more uncertain due to interactions with fire-specific factors that are not explicitly represented in the HIP model. While the HIP model may predict that denitrifiers may produce N gases at rates proportional to substrate availability so long as C and N substrates and oxygen requirements are met, this may not be the case after fires. For example, fires can kill microbes and dramatically alter soil microbial communities (Pulido-Chavez et al. 2023), suggesting denitrification rates could rely on microbial community structure, diversity, and post-fire recovery trajectories. Other additional factors that may govern N emissions post-fire could include burn severity, reduced iron phases known to govern abiotic N gas emissions, and the presence of biochar-like PyOM compounds which may reduce N_2O emissions. In this sense, burn severity may act as a master distal (environmental) factor governing the proximal (cellular level) factors that regulate emissions in the HIP model.

For both NO and N_2O, the factors which exert the strongest control on post-fire emissions could vary by ecosystem type, dominant vegetation, plant biomass, soil type, fire history, and climate. To better capture the overall effect of fire on soil emissions of NO and N_2O, we review studies evaluating N trace gas emissions after wildfires across major ecosystem types and find that wildfires generally increase soil emissions of NO and N_2O with possible long-term effects on ecosystem N loss dynamics, regional air quality, and global climate. We used metanalytical techniques to estimate the overall effect sizes of fire on NO and N_2O fluxes across ecosystems but did not perform a meta-regression due to the lack of consistency in explanatory variables measured between studies.

Methods

Data collection

As a result of the small number of studies that have measured N emissions in post-fire environments across varying ecosystems, we were unable to conduct a formal meta-analysis or meta-regression. Nevertheless, we used a meta-analytical approach to summarize the main effects of wildfire on NO and N_2O emissions across ecosystem types. The following keywords were searched in Web of Science, Google Scholar, and the University of California Library database: "NO", "nitric oxide", "N_2O", "nitrous oxide", "N", "fire", "wildfire", "burn", "greenhouse gas", "emissions", and "soil" up until December 1, 2022. Studies were included if at least one of the sites studied had burned (either by prescribed fires, slash-and-burn management practices, pyrocosm experiments, or wildfires) and at least one of the following had been measured: soil NO emissions or soil N_2O emissions. Only experimental papers with reported mean, standard deviation or standard error, and sample size were included. No reviews or modeling outputs were included in data analysis. Data was extracted from the papers included ($n = 34$) by manually extracting mean NO and N_2O fluxes from tables and graphs (if no numeric values were reported, means were extracted using plot digitizer free online software: https://plotdigitizer.com/app). Most studies measured NO and N_2O under field conditions after wildfire; however, we also included instances where controlled or experimental burn set-ups were used to avoid discarding data which closely approximates the effect of a wildfire. When fluxes were measured over multiple time points after fire, fluxes were binned as < 1 year post-fire and > 1 year post-fire. For the final analysis, we included only fluxes measured up to one-year post-fire, and comment individually on studies that record fluxes after 1 year or were performed in ecosystems that did not fit into the broad categories of "forest", "shrubland", or "grassland" where relevant. When there were multiple means

reported for different timepoints and an overall average was not available, we chose the timepoint with the highest fluxes; when multiple burn severities were reported, we chose the highest severity; when one study reported fluxes from multiple ecosystem types, or sites with different soil types, we used all that were relevant and extracted data as separate flux values (see extracted values in supplementary file Table S1).

Statistical approach

To estimate the effect size of burning on NO and N_2O emissions, the standardized mean differences (SMD; Eq. 1) and respective variances (Eq. 2) for each study were calculated using Hedge's g via the escalc function in the metafor package in R (Hedges 1981, 1982; Viechtbauer 2010; R Core Team 2022):

$$\mathrm{SMD} = \frac{mean1 - mean2}{\sqrt{\frac{(n1-1)SD_1^2+(n2-1)SD_2^2}{n1+n2-2}}} \quad (1)$$

The sample error variance of the standardized mean difference was calculated with:

$$\mathrm{SE}^2_{\mathrm{SMD}} = \frac{n1+n2}{n1*n2} + \frac{SMD^2}{2(n1+n2)} \quad (2)$$

Where mean1 and mean2 represented the burned and unburned groups with respective sample sizes n1 and n2 and respective standard deviations SD1 and SD2.

To synthesize the effect sizes between studies and estimate an overall mean effect, we chose a random effects model approach, which can account for the variation between studies when estimating the overall effect using the rma.mv function in the metafor package (Crystal-Ornelas 2020; Viechtbauer 2010; R Core Team 2022).

Results: overall effect of fire on soil NO and N_2O flux

Of the 34 studies available, 17 measured post-fire NO fluxes (Fig. S1) and 25 measured N_2O (Fig. S2). While there was high variation between studies, we found a significant increase in both NO and N_2O across studies conducted in various ecosystems around the world (Fig. 2). Nevertheless, we note that many studies individually reported no significant effect of fire or even negative effects, indicating suppression of NO and/or N_2O after fires is also possible. Responses to fire varied widely between the ecosystems represented by this dataset, which includes boreal and tropical forests, arid and tropical shrublands, and both humid and arid grassland ecosystems. Therefore, to more clearly understand soil N cycling responses to fire globally, it is important to consider these effects within the context of ecosystems of similar vegetation types and climate regimes.

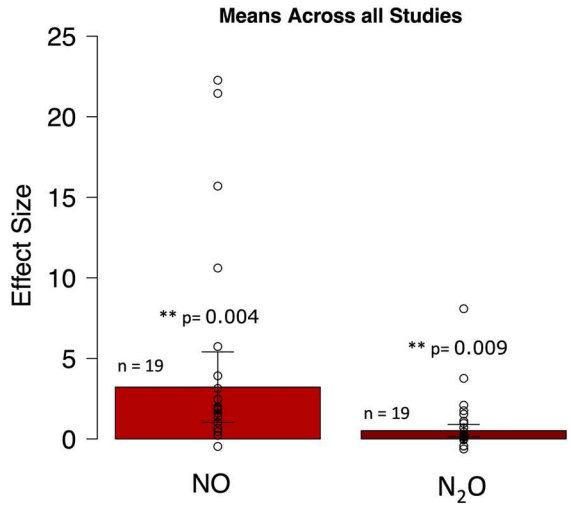

Fig. 2 Grand means for soil NO and N_2O emissions across all studies reporting fluxes ≤ 1 year post-fire. Only one study measured NO fluxes past 1 year post-fire, so fluxes were binned at ≤ 1 year post-fire. There was no significant overall effect of fire for N_2O emissions past 1 year post-fire (grand mean effect size = − 0.16, SE = 0.27, p = 0.54) nor was there any significant effect when all post-fire timepoints were considered (grand mean effect size = 0.24, n = 33, SE = 0.17, p = 0.16). Individual study effect sizes were estimated using Hedge's g (open circles) and overall mean effects were estimated using a random effects model reported as mean (bar height) with 95% CI (error bars). N_2O emissions: grand mean effect size = 0.51, n = 19, SE = 0.19, p = 0.009; NO emissions: grand mean effect size = 3.21, n = 19, SE = 1.12, p = 0.004

Forests

Forested ecosystems can burn in a variety of ways depending on fire type (i.e. crown fire, understory fire, stand replacing fire) and fuel loads (Agee 1998; Keeley 2009). The severity of a forest fire can determine the extent of ash and char deposition, soil

organic matter combustion, and the depth of soil heating (Keeley 2009). Thus, forests may present a wide range of fire effects on soils and, consequently, N cycling may vary substantially based on fire severity.

Studies that measured NO and N_2O in forested ecosystems up to 1 year post-fire showed a significant positive effect of fire on N_2O emissions, but not NO emissions (Fig. 3A). This lack of significance for NO emissions may be due to studies in forested ecosystems being disproportionally focused on N_2O emissions, with 16 studies measuring N_2O (9 were conducted in tropical forests and 7 were conducted in temperate and boreal forests) and only 3 studies measuring NO (tropical forests only). Although the majority of N_2O measurements in temperate forests focused on chronosequences and longer times post-fire, there

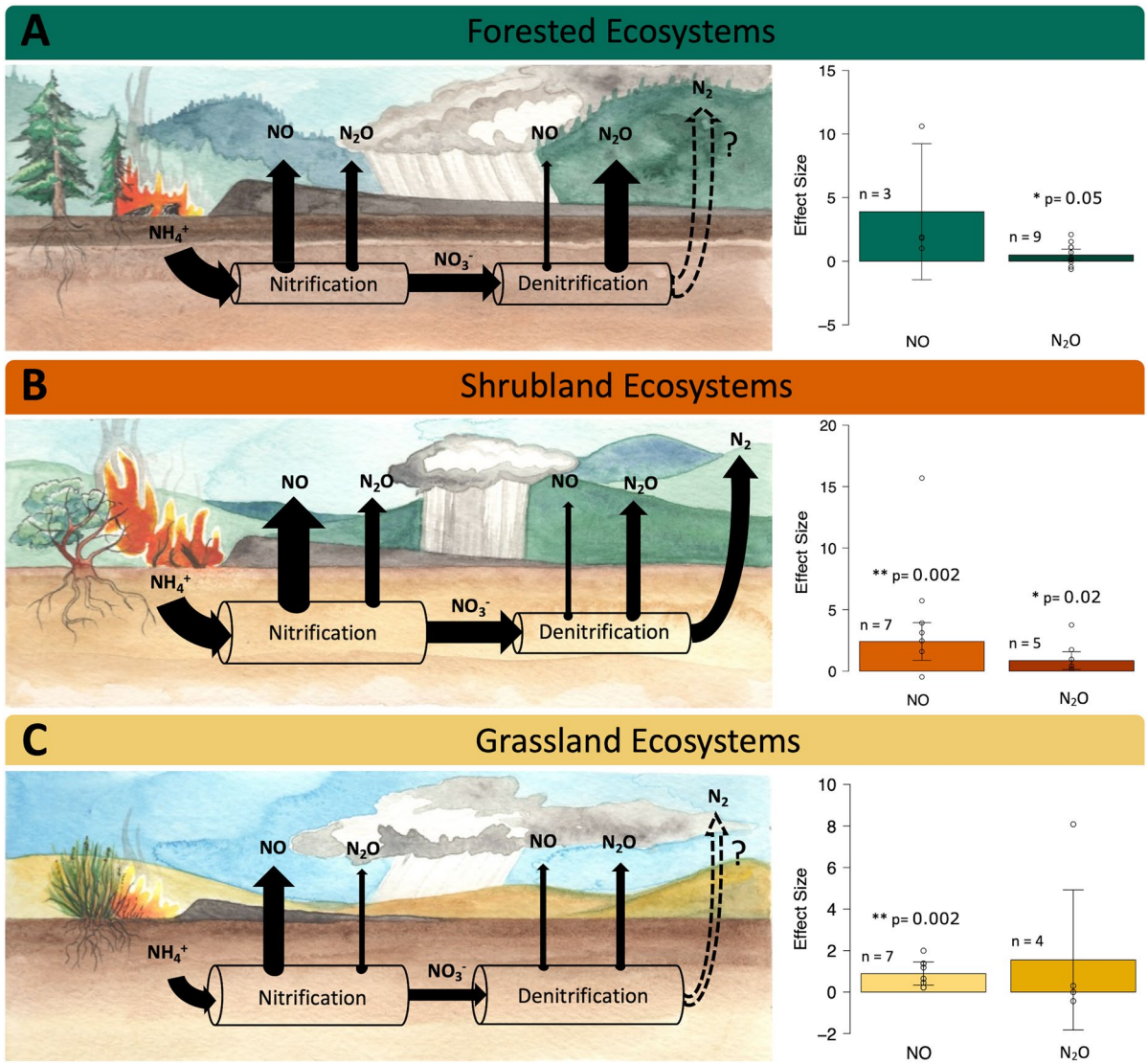

Fig. 3 Pooled effect sizes for each ecosystem type ≤ 1 year post-fire. Individual study effect sizes were estimated using Hedge's g (open circles) and overall mean effects were estimated using a random effects model reported as mean (bar height) with 95% CI (error bars). Diagrams **A**, **B**, and **C** show conceptual summaries of how processes responsible for changes in NO and N_2O emissions might differ across ecosystem types, with arrow width indicating possible changes in fluxes associated with each of the main process in the HIP model. Dashed lines indicate speculations where no data is currently available

were no significant effects of fire on NO or N_2O after 1 year for either temperate or tropical forests. Despite the average increase in N_2O across all forested ecosystems, response to fire differed between tropical and temperate/boreal forests, with boreal forests tending to decrease N_2O emissions and tropical forests increasing NO and N_2O emissions. Thus, to better understand the context-dependency of N cycling processes, we group studies by broad climatic similarities to further examine such trends and explore possible mechanisms driving NO and N_2O emissions post-fire.

Tropical forests

Nitric oxide

Weitz et al. (1998) and Neff et al. (1995) both noted statistically significant short-lived bursts of NO from Costa Rican tropical secondary forests up to 3 months post-fire which they attributed to increased nitrification rates. Verchot et al. (1999) also observed NO fluxes up to 6 times higher than unburned fluxes within 6 months after fire in a Brazilian primary forest but observed no corresponding increase in nitrification potential or net mineralization to explain this. While these studies agree that fires increase NO emissions in tropical forests at least in the short-term (up to 6 months), they point out the need to collect more post-fire NO data with accompanying measurements of explanatory variables in tropical forests.

Nitrous oxide

Studies in tropical forested ecosystems included sites in Indonesia, Central and South America, and Australia. Despite this diversity, six out of nine studies in tropical forests reported significantly increased N_2O emissions after fires. Of these six, half associated increased nitrification rates with increased N_2O emissions (Ishizuka et al. 2002; Melillo et al. 2001; Weitz et al. 1998) while the other half did not measure any explanatory variables (Arai et al. 2014; Luizao et al. 1989; Takakai et al. 2006). Verchot et al. (1999) found no change in nitrification or net mineralization rates following fire and Zhao et al. (2015) found no difference in N_2O emissions between burned and unburned plots, despite measuring an increase in NH_4^+. This could point to a delayed response of denitrification to fire as the main process producing N_2O, but Liu et al. (2013), the only study that reported a significant decrease in N_2O following a fire in a wet sclerophyll Australian forest, found that fire did not significantly change denitrification gene abundances and that the abundance of denitrifier genes did not correlate to N_2O fluxes after 2 years. Instead, changes in factors such as pH, water content, N substrate availability, and microbial biomass better explained the decrease in N_2O emissions. These results highlight the importance of measuring explanatory variables at fine scales to help explain variation in post-fire NO and N_2O fluxes.

Boreal and temperate forests

None of the studies included in our analysis measured NO in boreal or temperate forests and only one quantified nitrification rates (with inconclusive relationships to fire; Ullah et al. 2009), pointing out a research gap we encourage future studies to investigate.

Nitrous oxide

Out of seven studies, only two reported increased N_2O emissions following fire (Gathany & Burke 2011; Ullah et al. 2009). Ullah et al. (2009) observed high N_2O emissions 2 years after fire in a Canadian mixed boreal forest but did not find a significant overall effect of fire on N_2O emissions because of high variability (and could not relate any environmental variables to fluxes). Gathany & Burke (2011), the only study in a temperate Rocky Mountain Ponderosa forest, measured significant increases in N_2O emissions at both 1 and 3 years post-fire. Of the explanatory variables they considered (burn severity, temperature, water content, aspect, time since fire), they identified fire severity as the most important factor accounting for variability in N_2O emissions, with lower burn severity corresponding to higher N_2O fluxes.

The remaining five studies in boreal forests measured post-fire decreases in N_2O emissions, largely focusing on soil temperature as the main explanatory variable of interest. While soil temperatures tended to increase after fire (Kim & Tanaka 2003; Köster et al. 2017; Ribeiro-Kumara et al. 2020a, b; Takakai et al. 2008), and several studies found a positive correlation between N_2O and soil temperature (Kim & Tanaka 2003; Ribeiro-Kumara et al. 2020b),

this was not enough to offset the general decrease in N_2O emissions following fire (Kim & Tanaka 2003; Köster et al. 2017; Morishita et al. 2015; Ribeiro-Kumara et al. 2020b; Takakai et al. 2008). Similarly, no significant correlations between N_2O and water content were found (Köster et al. 2017; Morishita et al. 2015; Ribeiro-Kumara et al. 2020b). However, Morishita et al. (2015) found N_2O emissions varied based on fire severity in an Alaskan boreal forest, and were higher at moderate-severity than at high-severity sites. They also noted that variability of N_2O emissions increased after fire and suggested there may be N_2O hotspots generated by fires. Köster et al. (2017) measured decreased N_2O emissions in a burned Canadian subarctic boreal forest and found that while time since fire had little effect, and correlations with soil moisture and temperature were inconclusive, N_2O fluxes decreased with bulk soil %C and %N. Because high combustion temperatures could reduce bulk soil %C and %N along a temperature gradient, this could also reflect a relationship with burn severity (Knicker 2007).

Because fires generally increase available forms of C and N along with soil temperatures (Dicen et al. 2020; Smithwick et al. 2005) and sometimes increase soil moisture due to lack of plant transpiration (Takakai et al. 2008), the HIP model would predict increased N_2O emissions. However, because the majority of studies in forests reported decreases in N_2O following fires, this may point to the importance of considering fire-specific factors in addition to the core explanatory variables of the HIP model, particularly burn severity (Gathany & Burke 2011; Kim & Tanaka 2003; Morishita et al. 2015). Burn severity may determine the extent of microbial community turnover (Pressler et al. 2019; Taş et al. 2014) and control the presence of biochar-like PyOM compounds which may restrict N_2O emissions (Köster et al. 2017 notes there is substantial char left over after boreal forest fires; Hanley et al. 2013; Tang et al. 2022). Furthermore, high severity fires in boreal forests often remove mosses and lichens that tend to account for a large portion of N_2O fluxes in unburned forests (Köster et al. 2017; Lenhart et al. 2015). Hermesdorf et al. (2022) observed a similar decrease in N_2O production after fire in Arctic heath despite increased N substrate availability. Overall, N_2O emissions in boreal forests appear to be curtailed by fire, particularly at high burn severities, but because few studies incorporate fine-scale burn severities or PyOM characterization, and only one study in boreal forests quantified microbial communities (detecting no change in N_2O; Taş et al. 2014) the mechanisms behind this remain unclear.

Shrublands

Studies in shrubland ecosystems included three ecoregions: the chaparral ecosystems of Southern California (Anderson et al. 1988; Anderson & Poth 1989; Levine et al. 1988), the Mediterranean Macchia shrublands of Italy and Spain (Dannenmann et al. 2011, 2018; Fierro & Castaldi 2011), and Brazilian Cerrado (Anderson & Poth 1998; Pinto 2002; Poth et al. 1995). California Chaparral and Mediterranean Macchia have similar climates with hot, dry summers and cool, wet winters with annual rainfall of ~ 620–700 mm. Whereas Cerrado is considered here to be a tropical shrubland with rainfall ~ 1100–1600 mm. These shrublands all have in common well drained, aerated soils and tend to have close vegetation cover that is semi-continuous with understory grasses and herbaceous plants. Shrublands are typically more fire prone that other land cover types and experience frequent crown fires that tend to burn at high severities, leaving little intact vegetation behind (Baeza et al. 2005; Barro & Conard 1991; Oliveira et al. 2014). Shrublands in wetter climates such as the Cerrado ecosystems of South America can, however, burn at a range of severities based on fuel moisture at the time of burning (Mistry 1998). Fire severities can also depend on fine fuel loads and the maturity of the stand (Oliveira et al. 2014). When all studies in shrublands were pooled, there was a significant positive effect of fire for both NO and N_2O up to 1 year post-fire (Fig. 3B).

Dry shrublands

Many dry shrubland ecosystems undergo seasonal N fluxes driven by precipitation (Krichels et al. 2022a, b), with a buildup of N over the dry season when plants are largely dormant, followed by a pulse of N loss with the onset of rain (Austin et al. 2004). Large pulses of trace N gas emissions of NO and N_2O have been observed upon re-wetting unburned dryland soils (Homyak et al. 2016; Krichels et al.

2022a, b; Leitner et al. 2017), so it may be expected that fire will exacerbate these effects by increasing the soil available N pool and accelerating microbial activity upon wet-up (Goodridge et al. 2018; Hanan et al. 2016, 2017). California Chaparral and Mediterranean Macchia ecosystems showed a strong N cycling response to fire, with many studies reporting significant increases in NO emissions and strong positive N_2O response.

California chaparral

Nitric oxide Levine et al. (1988) found a 300% increase in NO emissions when burnt soils were wetted, and sister studies by Anderson et al. (1988) and Anderson & Poth (1989) observed similar patterns, measuring elevated in-situ soil NO emissions with the addition of water for up to 6 months following fire. Anderson & Poth (1989) estimated that NO emissions represented 75% of the total N lost from burned topsoil over a 6-month period, while in unburned plots, NO was responsible for only 33% of N loss in the same 6-month window. They also note that post-fire NO emissions in chaparral were comparable to fertilized agricultural fields and tropical forests.

Nitrous oxide While Anderson & Poth (1989) did not measure any N_2O above the instrument detection limit, Levine et al. (1988) measured a significant increase in N_2O emissions after wetting burned soils. Anderson et al. (1988) measured post-fire N_2O fluxes that did not change with acetylene addition, indicating nitrification as the more probable source of N_2O in chaparral soils; however, no unburned comparison group was measured in this study. These authors all speculate that nitrification is the primary mechanism behind both NO and N_2O emissions in post-fire chaparral soils, basing this conclusion on (1) the ratio of NO:N_2O closely matching that expected from nitrification (roughly > 1; Anderson & Levine 1986), (2) the abundance of the substrate for nitrification: NH_4^+, and (3) lack of response of N_2O emissions to inhibition of N_2O reductase via acetylene addition, indicating low contribution of denitrification. These results indicate that fire could be an important driver of gaseous N loss from chaparral soils and identify chaparral as a target ecosystem for future post-fire N cycling research.

Mediterranean Macchia

Nitric oxide The only study to measure NO in post-fire Macchia soils (Dannenmann et al. 2018) saw consistently elevated emissions over 1 year likely due to nitrification, which they calculated to represent almost 3% of the total N lost in direct combustion.

Nitrous oxide Fierro and Castaldi (2011) found significant increases in post-fire field N_2O emissions following a low-severity burn in an Italian Mediterranean shrubland with N_2O "hotspots" possibly relating to elevated nitrification activity. At another Macchia site of similar latitude, Karhu et al. (2015; excluded from analysis) found that N_2O emissions from burned soils incubated in the lab were highly variable and increased by factors that ranged between 3 and 30. The authors directly correlated this with the activity of denitrifiers using a ^{15}N labeling approach. At a site nearby, the same research group measured elevated N_2O and N_2 fluxes under field conditions over 1 year after fire (Dannenmann et al. 2018). The major N_2 production pathway is typically denitrification in terrestrial soils, so this could point a highly efficient denitrification pipeline aided by biochar-like PyOM compounds which are known to increase N_2:N_2O ratios (Hanley et al. 2013; Van Zwieten et al. 2014). In contrast, Dannenmann et al. (2011) found no change in soil emissions of N_2O in laboratory-incubated soils collected from a burned Mediterranean Macchia shrubland in southern Italy, and observed a two-fold reduction in the production of N_2 (the end product of denitrification) in burned soils. However, these soils were incubated at gravimetric water contents below 50%, which was found by Dannenmann et al. (2018) to yield no change in N_2O emissions regardless of burning. While all of these studies agree that nitrification is likely accelerated after fires to increase N gas emissions, there is also strong evidence from Karhu et al. (2015) and Dannenman et al. (2011, 2018) that despite dry soil conditions, denitrification may play a role in modifying N trace gas emissions in response to fire in Mediterranean shrublands. Nevertheless, Dannenman et al. (2018) estimates the contribution of N_2O emissions to ecosystem N loss to be relatively small.

Tropical shrublands (Brazilian Cerrado)

Nitric oxide

All three studies reported similarly high NO fluxes after wetting soils within 30 days after fire that quickly returned to pre-fire levels. Although no significant increases in nitrification or net mineralization rates after fire were found, these studies assign nitrification as the main driver of NO fluxes, citing lack of N_2O production and conditions conducive to nitrification such as well-aerated soils, increased NH_4^+, and pH as justification.

Nitrous oxide

While all three studies measured post-fire N_2O emissions, only Poth et al. (1995) measured N_2O fluxes above the detection limit. Poth et al. (1995) found a significant but ephemeral increase in N_2O lasting only up to 30 days. N_2O emissions corresponded to higher pH and soil N status but did not respond to nitrifier inhibitors, making it difficult to infer a mechanism. The authors speculate that chemodenitrification could play a role because the soils were too water limited to sustain high denitrification rates.

Overall, shrubland ecosystems showed significant but short-lived post-fire increases in trace N gas emissions driven by elevated nitrification rates. However, no studies measured NO or N_2O past 1 year post-fire. Danennmann et al. (2018) provided one of the few post-fire N budgets that included N gas emissions and concluded that gaseous post-fire N loses over 1 year could account for up to 5% of the N lost via direct combustion. This suggests these gaseous N loss pathways may affect ecosystem N retention in the long-term if emissions remain elevated. Further clarification of the microbial community processes and mechanisms driving these fluxes may help better predict fire responses across global shrublands.

Grasslands

Grasslands tend to burn relatively quickly at low temperatures with low heat transfer to soils; leaving root systems intact and potentially disturbing microbial communities very little (Daubenmire & Cragg 1968). Because grasslands have relatively little aboveground biomass to combust, fires may leave behind small ash layers with less microbially available N, potentially resulting in smaller changes in emissions of trace N gases. However, because microbial mortality may be low, grassland soil microbes may positioned to efficiently metabolize of the influx of post-fire N granted there are no other limiting resources such as soil moisture. Dry grasslands may have more potential for high nitrification rates and NO emissions, while humid grasslands could be larger sources of N_2O flux if soils become saturated after fire. Studies in grasslands spanned North and South America, Africa, and Australia. When all grassland ecosystems were pooled, there was a significant positive effect on NO but not N_2O (Fig. 3C).

Dry grasslands

Dry grasslands were grouped as receiving < 1000 mm rainfall annually (generally ~ 700 mm) and sites were concentrated in Kruger National Park, South Africa (Levine et al. 1996; Parsons et al. 1996; Serça et al. 1998), and California, USA (Levine et al. 1988; Niboyet et al. 2011).

Nitric oxide

All four studies in dry grasslands reported increases in NO emissions after fires in combination with wetting (Levine et al. 1988, 1996; Parsons et al. 1996; Serça et al. 1998). Few of these studies measured microbial process rates directly, but all concluded that nitrification activity is the most likely explanation for elevated NO emissions after fires. The most common lines of evidence were: (1) increased NH_4^+ availability and increased rates of NO_3^- production (Levine et al. 1988, 1996; Parsons and Scholes 1996), (2) NO:N_2O ratios in the range usually associated with nitrification (> 1; Levine et al. 1988), and (3) elevated in-situ nitrification rates (Parsons et al. 1996). NO measurements in dry grasslands have not been measured beyond 2 months post-fire and the long-term effects of fire on NO emissions in dry grasslands are currently unknown.

Nitrous oxide

The two studies that measured detectable post-fire N_2O fluxes were conducted in California grasslands.

One study in a Southern California grassland found a significant increase in N_2O emissions after fire with wetting, concluding this may be due to increased nitrification because of high NO:N_2O ratios (> 2.7; Levine et al. 1988). However, the second study in a Northern California grassland found no change in N_2O emissions in the first year after fire, but in years 2 and 3 observed large increases in N_2O emissions up to 500% pre-burn levels, attributing this to denitrification (Niboyet et al. 2011). The authors speculate that this may have occurred because immediately following fire there might be lower soil moisture caused by removal of litter and plant cover, inhibiting denitrification until soil moisture returned to pre-burn levels. With higher soil moisture, denitrifier populations could recover and begin to process available C and N from the ash and decaying roots of plants killed by fire, producing the observed N_2O emissions.

Humid grasslands

Humid grasslands were considered to have > 1000 mm annual rainfall (generally ~ 1200 mm) and sites were dispersed across diverse regions of Africa (Andersson et al. 2003; Castaldi et al. 2010; Serça et al. 1998), South America (Johansson et al. 1988; Pinto et al. 2002), and Australia (Livesley et al. 2011).

Nitric oxide

All four studies that measured NO in humid grasslands reported significant increases in NO emissions after fires (Castaldi et al. 2010; Johansson et al. 1988; Pinto 2002; Serça et al. 1998). Pinto et al. (2002) observed modest increases in NO for up to 30 days following fire with a short-lived peak following rain, but no correlation with nitrification rate or N status. Castaldi et al. (2010) observed a similar increase in NO emissions, also with no significant change in nitrification rates. Johansson et al. (1988) and Serça et al. (1998) both found significant increases in NO and speculate that nitrification is responsible for the increase, but because neither study directly measured nitrification, it is difficult to infer a mechanism for the changes in NO emissions after fires in humid grasslands.

Nitrous oxide

None of the three studies that measured N_2O in humid grasslands reported significant changes in N_2O after fire (Andersson et al. 2003; Castaldi et al. 2010; Livesley et al. 2011). Pinto et al. (2002) found that in a Brazilian savanna, fire did not change in situ fluxes of N_2O at any point for up to two years following fire. In two studies in African savannas, in situ N_2O emissions in recently burned soils showed no change even after wetting (Andersson et al. 2003; Castaldi et al. 2010). This may be due to well-drained soils with low pH (~ 3.7–6) and small changes in N status after fire (Andersson et al. 2003; Castaldi et al. 2010). However, Castaldi et al. (2010) did observe elevated N_2O in lab experiments when burned soils were wet up to 70% water holding capacity relative to controls, suggesting there may be potential for fires to increase N_2O fluxes after a heavy rain event, although this level of soil saturation was never observed under field conditions by the authors. Livesley et al. (2011) corroborates these findings in a savanna in Australia and further suggests that because N_2O fluxes and nitrification rates are low year-round and are not influenced by fire, the global importance of savannas as sources of trace N gases to the atmosphere may be overestimated (Castaldi et al. 2006).

The majority of fire effects on NO and N_2O fluxes in grasslands were short-lived or relatively small. While the positive effect of fire on NO emissions was significant, the mean effect size was relatively small compared to mean effect sizes for post-fire NO emissions in shrublands (and forests, although the overall effect was not significant). Because fires in grasslands burn quickly and leave behind small amounts of ash, the stimulation of nitrification by excess NH_4^+ may be ephemeral. There may also be more competition from fast-growing grasses and forbes which may quickly take up the small post-fire N flush (30 days or less according to Pinto et al. 2002), possibly before recovering microbial communities in deeper soil layers can access it (Daubenmire & Cragg 1968).

Peatlands

While there were not enough studies on peatlands to include in our analysis, peatlands are nonetheless unique and globally important ecosystems which are

increasingly impacted by fire (Turetsky et al. 2014). Drained peatlands are particularly susceptible to fire and accelerated decomposition rates, which may mineralize organic N and stimulate nitrification and denitrification (Hatano et al. 2016; Jauhiainen et al. 2012; Takakai et al. 2006). Three studies tracking land use changes across tropical peatlands (all similar sites in Central Kalimantan Province, Indonesia) measured N_2O in drained forests and drained and burned forests (Arai et al. 2014; Jauhiainen et al. 2012; Takakai et al. 2006). Takakai et al. (2006) found no significant difference between burned and unburned peatland forests in the first year after fire, but a significant decrease in N_2O production from burned sites in the second year. Jauhiainen et al. (2012) similarly found that burned forests produced 10 times less N_2O than unburned 2 years after fire. At 8 years post-burn, Arai et al. (2014) measured some seasonal increases in N_2O flux in burned forests compared to unburned, but no overall significance was reported. The only study to measure N_2O emissions in a temperate peatland (Canadian Taiga plains) found a significant reduction in N_2O consumption compared to unburned sites when two wildfire affected peatland sites were combined (Schulze et al. 2023). Direct emissions of N_2O from combustion of the organic peat material during fires may be a significant source of N_2O (Hatano et al. 2016), but the long-term effects of burning on peatland soil N_2O emissions are less clear with the few available studies indicating decreased emissions in tropical peatlands and decreased consumption of N_2O in boreal zones. Draining of tropical peatlands also complicates emissions as this disturbance nearly always co-occurs with fire (Turetsky et al. 2014). We encourage more research on post-fire N gas emissions in peatlands and point out that there are currently no studies measuring post-fire soil emissions of NO from peatland soils.

Areas for future research focus

In general, the limited number of studies evaluating N emissions post-fire and uneven distribution across major ecosystem types makes it challenging to make predictions or explore controls on post-fire NO and N_2O emissions using meta-analytical approaches. Few studies made comprehensive measurements of explanatory variables, with most studies measuring between one and three variables concurrently with NO and N_2O measurements. Out of the most consistently measured variables, substrate availability, soil moisture, and nitrification rates were the most frequently correlated with NO and N_2O emissions (as predicted by the HIP model). More consistent measurement of these explanatory variables by future studies will make analysis using meta-regression techniques possible and help clarify the drivers behind post-fire N gas emissions. In some cases, however, observations did not meet expectations based on HIP model logic, raising questions about the importance of factors specific to post-fire environments. This review emphasizes the importance of measuring explanatory variables which have long been identified as important controls on NO and N_2O emissions by the HIP model as well as considering conditions unique to the post-fire environment such as burn severity, PyOM content, and changes in microbial community processes.

Burn severity & PyOM

Of the studies that incorporated some metric of burn severity, it was commonly correlated with NO and N_2O fluxes. Burn severity is likely to act as a master variable controlling how much ash and char are deposited (and thus how much excess NH_4^+), how quickly plants can recover to take up excess N, the depth of heat penetration into the soil and thus the extent of microbial community turnover, and the extent of changes in pH and soil moisture (DeBano 2000; Goforth et al. 2005; Keeley 2009; Pressler et al. 2019). Overall, relatively few studies reported burn severity despite important consequences on results. We therefore encourage future studies to report burn severity at the finest scale possible, as there may be potential to broadly infer changes in N cycling and trace N gas emissions based on routine burn severity assessments performed by agencies such as the Burned Area Emergency Response (BAER) reports generated by the US Forest Service.

Pyrogenic compounds that resemble biochar can have strong inhibitory effects on N_2O production in soils (Hanley et al. 2013; Kaur et al. 2022); however these compounds were not quantified by any of the studies included in this review. To better understand the high variation in post-fire N_2O emissions, it may

be important to consider the PyOM content of burned soils.

Microbial community successional dynamics

NO and N_2O emissions are largely driven by microbial metabolism of N substrates; however, very few studies exist that consider the post-fire recovery of microbial communities and link this to changes in N cycling dynamics. Understanding post-fire successional changes in the bacterial and archaeal ammonia oxidizing microbial communities that contribute to nitrification after a fire may help explain temporal variation in the observed fluxes. Reduction in microbial biomass and diversity as well as turnover dynamics as microbes recover after fires could correspond to changes in denitrification rates. Emerging work on pyrophilous microbes raises questions about what functions they are capable of, and if they are adapted to capitalize on the post-fire N flush, potentially driving N cycling (Enright et al. 2022; Whitman et al. 2019). Pairing microbial community analysis with N cycling measurements may provide further insight into the underlying processes driving changes in post-fire trace N gas emissions.

Isotopic tools & process dynamics

It is possible to distinguish specific processes responsible for emitting N_2O using isotopomers of the N_2O molecule (Lewicka-Szczebak et al. 2020; Yu et al. 2020); however, this method is currently underused in post-fire studies. The natural abundances of isotope ratios of N_2O such as $\delta^{15}N_2O_{bulk}$, $\delta N_2{}^{18}O_{bulk}$, and site preference, or $\delta^{15}N_2O_{SP}$ (reflects the placement of ^{15}N in the central (α) and peripheral (β) positions in the N_2O molecule; site preference $SP = \delta^{15}N\alpha - \delta^{15}N\beta$), can be used to distinguish N_2O produced from nitrification or denitrification (Stuchiner & von Fischer 2022; Sutka et al. 2006). Even finer distinctions between nitrifier nitrification, nitrifier denitrification, bacterial denitrification, and fungal denitrification or chemodenitrification are possible by plotting $\delta^{15}N_2O_{bulk}$, $\delta N_2{}^{18}O_{bulk}$, and site preference in three dimensional isotopic space (Wankel et al. 2017; Yu et al. 2020). To gain more insight into why ecosystems respond to fire differently and which processes contribute to this, we propose that these well-established isotopic tools be applied to the study of post-fire N_2O emissions.

Conclusions

Fires altered soil emissions of NO and N_2O across a wide set of ecosystems from nearly every continent. NO emissions were more strongly affected by fire than N_2O, with the most common explanation being increased nitrification rates fueled by high NH_4^+ availability. N_2O emission responses to fire varied widely across ecosystem types, but generally N_2O emissions increased in variability after fire and some studies noted that extremely high values were sometimes measured in post-fire soils, suggesting that fires may create conditions that favor N_2O hot spots. Arid shrublands were the most likely to show elevated NO and N_2O emissions after fire, while grasslands exhibited ephemeral pulses of soil NO with no significant effect on N_2O emissions. N_2O emissions in tropical forests increased, but boreal and temperate forests tended to decrease N_2O production after fires, which may hint at some important confounding factors to consider that fall outside of the HIP model such as burn severity and the presence of large amounts of char. Together, these studies suggest that fires can increase soil emissions of NO and N_2O with potential long-term consequences for ecosystem N loss and climate feedbacks as wildfires increase globally.

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Data availability All data generated or analyzed in this study are included in this article or listed in the Supplementary Information.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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