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From burned slopes to streams: how wildfire affects nitrogen cycling and retention in forests and fire-prone watersheds

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Abstract Wildfire is a major driver of nitrogen (N) cycling and export from terrestrial to aquatic systems. While fire is a natural process in many watersheds, it can still degrade water quality by rapidly flushing N to streams. This can be particularly problematic in watersheds that experience high levels of N deposition or where climate change is promoting larger and more severe fires. The extent and duration of postfire N export, and the potential consequences for downstream water quality, depend on how N inputs, internal cycling, and outputs vary before, during, and after fire. Here we review the major factors controlling N cycling and retention in forests and adjacent shrublands, and how fire modifies these controls. We connect burned slopes to streams to describe how fire exports N to aquatic environments. We also consider the implications for municipal watersheds and water resources management. We close by identifying critical knowledge gaps in projecting how fire will affect watershed N cycling and retention in the future.

Keywords Wildfire · Nitrogen cycling · Nitrogen retention · Water quality · Drinking water

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Introduction

Forests and shrublands dominate many mountainous watersheds and act as natural treatment systems for drinking water. It is estimated that forests save 4.1 trillion U.S. dollars yearly in water treatment costs (Bladon et al. 2014). However, these landscapes are also fire-prone, which can periodically limit their filtration capacity and degrade water quality (Burton et al. 2016). Wildfires release many solutes, such as nitrogen (N), sodium (Na^+), chlorine (Cl^-), and sulfate (SO_4^{2-}) (Smith et al. 2011), which can create impure water and generate harmful byproducts during drinking water treatment processes (Hohner et al. 2019). In this review, we focus on N, which can fertilize and pollute streams, lakes, and reservoirs following wildfire, putting drinking water infrastructure, aquatic ecosystems, and recreational activities at risk. However, N is also a critical element for recovering upslope vegetation and therefore, global change processes that alter the way N cycles and moves through a watershed can have large consequences for ecosystems from slopes to streams.

Climate change is causing larger, more severe fires in many ecosystems (Westerling et al. 2006; Abatzoglou and Williams 2016; Hanan et al. 2021) and therefore increasing fire-induced N export to streams (Hanan et al. 2017). Many studies predict that this trend will continue through the twenty-first century (Rogers et al. 2011; Barbero et al. 2015; Parks et al. 2016; Halofsky et al. 2018). In western North America, the effects of climate change and wildfire on N export can vary substantially among watersheds that experience different climate conditions and differ in topography, vegetation, and associated fire regimes (Gresswell 1999). For example, areas that historically burned under a low frequency, high severity fire regime (i.e., wet forests west of the Cascade Mountains in Oregon and Washington or high elevation forests in the northern Rocky Mountains) may be particularly vulnerable because large amounts of N are contained in abundant aboveground biomass/fuels (Rozendaal et al. 2017). Similarly, areas that experience high levels of N deposition (i.e., many chaparral ecosystems in southern and central California) can also experience intense postfire N export (Fenn et al. 2003). Understanding and predicting how postfire N export varies among ecosystems and watersheds, and how N export influences water quality, is important for wildfire mitigation and postfire management.

Excess contaminant loading to drinking water sources, including inputs resulting from wildfires, increases treatment costs (Nunes et al. 2018) and is forcing municipalities to adapt their treatment methods to handle higher concentrations of N, sediment, and dissolved organic matter (Robinne et al. 2019). Nutrient-enriched streams and drinking water can have negative consequences for human health (i.e., by causing methemoglobinemia in infants), aquatic ecosystems (i.e., by causing algal blooms), and recreation. Usually, dissolved N (and other solutes, suspended sediments, etc.) are diluted as water moves downstream, meeting other uncontaminated rivers (Samuels et al. 2006). However, relying on dilution may not be adequate for addressing further increases in nutrient inputs that result from human-driven changes to the N cycle (e.g., increasing rates of deposition and fertilization), larger and more severe wildfires, downstream land disturbances, and other future environmental changes (Li et al. 2016).

Wildfire-caused nutrient export is a key concern for many western U.S. water managers (Sham et al. 2013). If nutrient levels exceed maximum contaminant guidelines, the water is rendered temporarily unpotable. The U.S. Clean Water Act sets the Maximum Contaminant Levels (MCLs) at 10 mg L^{-1} for NO_3^- and 1 mg L^{-1} for NO_2^- in surface drinking water (Clean Water Drinking Act, 1972). However, postfire streamwater NO_3^- concentrations have been found to well-exceed this EPA threshold (e.g., 220 mg L^{-1}) (Tecle and Neary 2015). Even when postfire concentrations reach just below the threshold (e.g., > 9 mg L^{-1}), they can still be problematic for water treatment (U.S. Geological Survey 2012). While these effects are often transient, elevated nutrient levels in source watersheds have been recorded for more than ten years after severe fires (Emelko et al. 2011; Rhoades et al. 2019). Given that the number of large forest fires and length of wildfire season has increased, coupled with the uncertainties about climate change, managing water supplies from fire-prone watersheds is an evolving challenge (Hallema et al. 2018).

While periodic wildfire and subsequent N fluxes are a natural component of many forested and shrubland systems, environmental changes such as anthropogenic N deposition and climate change can exacerbate N export to streams. Here we review N cycling and fluxes in fire-prone watersheds during three key stages: before fire, during fire, and after fire (Fig. 1). Processes occurring at each of these stages can influence N cycling and retention in subsequent stages. First, we describe N cycling and fluxes in undisturbed watersheds. Then, we briefly review how fire alters ecosystem N storage and fluxes through changes to soil, vegetation, and in-stream processing. We also discuss mechanisms of postfire N export to streams, focusing primarily on forested watersheds in the western U.S., which range from semi-arid to mesic and many contain shrub/chaparral cover at lower elevations. Our goal is to review prefire N conditions and cycling, discuss how wildfires can affect N cycling and export, and explore the consequences of climate change-caused alterations to wildfire characteristics and the potential for increased N export. Increased

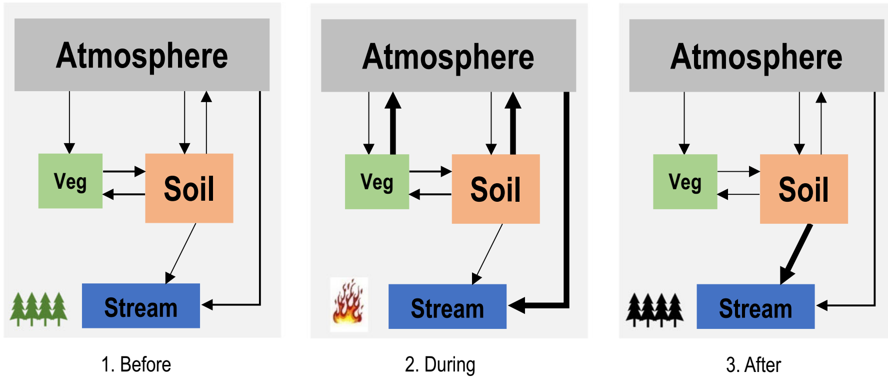

Fig. 1 Conceptual diagram of N stores and fluxes in a watershed (1) before, (2) during, and (3) after fire. (1) Before fire, N is stored in the atmosphere, vegetation, soils (including litter and rocks), and streams (which are small, often transient stores relative to the others). During this stage, there can be relatively small N fluxes to streamwater depending on the N status of the system (N-saturated or N-limited). (2) Fire transforms and moves N through combustion, oxidation, and volatilization back to the atmosphere while simultaneously depositing N with ash on burned hillslopes or in surface waters. Much N also remains in the soil. (3) After fire, N is transported with soil erosion, surface runoff, and leaching to the streams or taken up by recovering vegetation

understanding of these processes has key implications for water quality planning and management.

Before fire

Nitrogen is distributed among multiple pools within an ecosystem or watershed, including the atmosphere, vegetation (live and dead), rocks, soil, and streams (which are small, often transient stores relative to the others). N availability is dictated by local environmental drivers (i.e., aquatic and terrestrial habitat compositions and precipitation regimes) and in a recently undisturbed watershed, N pool sizes and fluxes vary with season, input/output rates, soil properties, geology, and climate. Therefore, the distribution of N can vary substantially among ecosystems and over time (Gessel et al. 1973; Cole and Rapp 1981; Johnson and Lindberg 1992; Brockley et al. 1992; Klopatek et al. 2006; Johnson and Turner 2014). For example, some forests in coastal Oregon are hypothesized to be N-saturated because of high rates of N-fixation by red alder (*Alnus rubra*) (Compton et al. 2003). Similarly, in western Wyoming, human sources, such as artificial fertilizer or septic/sewage effluent, cause N enrichment (Eddy-Miller et al. 2013). In other watersheds (e.g., many in central Idaho), aquatic N is low due to factors such as low NO_3^- concentrations in the surrounding soils, smaller populations of anadromous fish, which release N when they decompose, and wildfire suppression, which would otherwise release N to the soil and stream water (Delwiche 2010).

Ecosystems can be N-limited or N-saturated, which affects how N is internally cycled and subsequently lost (in the absence of a large disturbance) (Aber et al. 1989). An ecosystem becomes N-saturated when N inputs exceed the biotic demands (Fenn et al. 2008), which can promote leaching (Riggan et al. 1985; Aber et al. 1989; Stoddard 1994). N-saturated systems can also have elevated NO_3^- concentrations in the soil (Aber et al. 1989) and tend to lose NO_3^- with runoff (Jin-yan and Jing 2003). However, N leaching is not a perfect indicator of N saturation in many xeric and Mediterranean climates where seasonal N flushes are decoupled from the active growing season when plants would take up the exported N (Homyak et al. 2014). This decoupling can be particularly pronounced following fire when supply increases and demand decreases (Hanan et al. 2017). Therefore, to understand the relationship between prefire N status and postfire N export, we must consider N stores and pathways from the atmosphere, vegetation, rocks, and soil to streams.

Atmosphere

Nitrogen enters terrestrial systems via atmospheric deposition (wet and dry), abiotic and biological fixation of dinitrogen (N_2) gas, parent material weathering, and industrial fixation (i.e., fertilizer). Different pathways may dominate in different regions depending in large part on their precipitation regimes (Cook et al. 2018). For example, wet deposition accounts for 21–64% of total N deposition in moist regions whereas in the American southwest, up to 75% of total deposition occurs as dry deposition (Li et al. 2016). Deposition can provide critical nutrients to N-limited ecosystems but too much N can have undesirable environmental effects, such as promoting non-native plant invasion, altering ecosystem function, and degrading surface waters (Aber 1992; Fenn and Poth 1998; Baron 2006; Eshleman et al. 2013; Eshleman and Sabo 2016).

Nitrogen can move from the canopy to the forest floor via throughfall deposition. Measuring throughfall deposition is useful for understanding ecosystem N status because it includes both wet and dry deposition and informs how N deposition directly influences soil biogeochemical and plant processes (Fenn et al. 2013); it is also strongly positively correlated with increased NO_3^- leaching to streams (Fenn et al. 2008). However, quantifying throughfall deposition only provides an estimate of the lower bound of tolerance for forest ecosystems because canopies retain some deposited N (Lovett and Lindberg 1993). Thus, throughfall measurements may underrepresent deposition in drier systems where precipitation is highly stochastic (Cook et al. 2018).

Vegetation

Nitrogen limitation is a major control on vegetation growth and can trade off with other factors that promote or constrain growth, such as light, water, and other nutrients. For example, in a disturbed old growth forest, regeneration is co-limited by light and N availability (Soto et al. 2017). Additionally, with elevated CO_2 concentrations in the atmosphere fertilizing plants, some researchers have found that N will be the main resource constraining growth in many ecosystem types in the future (Feng et al. 2015; Terrer et al. 2019). However, others have shown that with warmer temperatures, soil N availability might increase with increasing microbial activity, leading to greater productivity (Noyce et al. 2019). The effects of climate warming on plant-soil feedbacks is an active area of research and many uncertainties remain (Sistla et al. 2012; Pugnaire et al. 2019).

Ecosystem type and environmental conditions are critical factors regulating N cycling in fire prone watersheds. For example, aridity can modulate canopy cover and soil pH (McCulley and Jackson 2012; Delgado-Baquerizo et al. 2013) and as a result N is often limiting in very arid stands (Wang et al. 2014). To offset these types of environmental limitations, unique combinations of ecosystem characteristics can emerge. For example, some plant species can assimilate NO_3^- through their leaves (Black et al. 2002), which can substantially reduce N limitation as N deposition increases in the future (Bourgeois et al. 2019).

Soils

In addition to the ocean and atmosphere, soil is another major store of organic and inorganic N. Soil N concentrations vary with climate and biotic processes. N is distributed throughout the soil profile but most of it is found in the O and A horizons—the top two layers of the soil composed of mainly organic material and minerals. The top meter of global soil is estimated to contain 9.5×10^{13} kg N; in warm deserts, soils store about 0.2 kg m^{-3} N, while wet forest soil can contain 1.6 kg m^{-3} soil N (Post et al. 1985). Old growth forests and wetter forests tend to have greater amounts of soil N than young and/or dry forests (Gessel et al. 1973; Moghimian et al. 2020). Unmanaged old growth forests have more coarse woody debris and other downed biomass, which contribute more N to soils (Fisk et al. 2002). For example, in a variety of Washington and Oregon soils, total N in the O-horizons varies from 100 to 2000 kg ha^{-1} in response to forest age, elevation, and temperature and moisture levels (Gessel et al. 1973). Other factors influencing soil N loads include plant community composition and soil physical, chemical, and biological properties.

Soil properties also influence soil microbial community composition and N cycling processes. Most N exists in biologically unavailable forms (i.e., bound in complex organic molecules comprising vegetation, litter, and soil organic matter). Therefore, N must be transformed into usable forms—predominantly NH_4^+ and NO_3^-—through microbially-mediated redox reactions in the soil. When N is limiting, most inorganic N exists as NH_4^+ and can be immobilized by microbes, making it unavailable for plants. When N is less limiting, nitrification is carried out by highly specialized chemoautotrophic microorganism that oxidize NH_4^+ into NO_2^- and NO_3^-. Nitrification releases H^+ ions into the soil and is therefore acidifying. Nitrifiers are very sensitive to soil pH, with optimal rates occurring when pH is greater than 6.0 (Sahrawat 2008; Nguyen et al. 2017). If nitrification rates are high, soil acidification can create a negative feedback where nitrifiers are inhibited by low pH and nitrification rates decline (Jin-yan and Jing 2003). However, when NH_4^+ substrate is extremely abundant, nitrification can happen even in very acidic soils (De Boer and Kowalchuk 2001; Hanan et al. 2016a; Li et al. 2018, b). For example, at Hubbard Brook Experimental Forest, New Hampshire, high rates of N deposition increased nitrification even when pH was as low as 4.3 (Likens et al. 1970).

We often overlook rocks as a source of N to ecosystems and watersheds but their contribution can be substantial (Morford et al. 2011). Rocks can contain 0.3 to 34% of total N in soils (Whitney and Zabowski 2004) and as they weather, rocks can increase ecosystem N budgets by 8–26% (Houlton et al. 2018). For example, in the Lake Tahoe Basin, California and Nevada, rocks hold 19% of the total soil N and rock content is directly proportional to the total C and N concentrations in the top 2 mm of soil (Johnson et al. 2012). N concentration in rocks can be > 1000 mg N kg^{-1} (Holloway and Dahlgren 2002) and in areas with N-rich rocks (350–950 mg N kg^{-1}), they can elevate the N content of the soil by up to 50% (Morford et al. 2011). Worldwide, N geochemistry and regional climate controls the magnitude of rock weathering and consequent N contributions to ecosystems (Houlton et al. 2018).

Outputs

When N is limiting, plants and microorganisms compete for available N through uptake and immobilization, respectively. N can also be lost through denitrification, runoff, and leaching; these outputs typically increase with decreasing N limitation. Complete denitrification is a microbial process that removes N from an ecosystem by transforming NO_3^- to gaseous N_2 and in the process, releases N_2O and NO_x (Parton et al. 2001). Rates of denitrification depend on the ecosystem N status, its vegetation composition, seasonality, soil moisture, temperature, and the availability of organic material. Because the riparian zone is a major site of denitrification, managers sometimes design vegetated riparian buffer zones to promote biological N removal, thereby reducing N fluxes to adjacent streams (Martin et al. 1999; Mayer et al. 2005).

Nitrogen can also leave an ecosystem through runoff and leaching (Cameron et al. 2013). Runoff is the process of water moving over land surfaces; at equilibrium, N leaching is a function of how much N is available (e.g., the extent to which and ecosystem is N-saturated) and how quickly plants and soil microbes take it up (Aber et al. 1991). Factors, such as wildfires, other disturbances, ecosystem management, climate change, and changes in N deposition rates can perturb equilibrium leaching rates (Dirnböck et al. 2016; Schleppi et al. 2017). In N-limited or balanced ecosystems, NO_3^- levels in runoff rarely exceeded 0.2 mg NO_3^- L^{-1} (Fenn et al. 2008; Rhoades et al. 2011). Ecosystems are considered “leaky” when runoff has more than 0.5 mg NO_3^- L^{-1} (Gundersen et al. 2006).

Nitrogen concentrations in runoff and leachate vary seasonally with temperature and moisture (Klopatek et al. 2006; Skorbiłowicz and Ofman 2014). For example, rainfall can increase rates of mineralization and nitrification (Fisk et al. 2002; Chen et al. 2017). However, during the growing season, much of this N can be taken up or immobilized by plants and soil microbes, which reduces N leaching and runoff (Kelley et al. 2017; Lin et al. 2019). In regions where elevated temperatures correspond with elevated precipitation, N is taken up rapidly for growth, which reduces fluxes to streams (Skorbiłowicz and Ofman 2014). However, in areas with wet winters, N export to streams can occur even when ecosystems are N-limited because plants are less active due to low temperatures. For example, in snow-dominated ecosystems, there is less demand N demand from plants and soil microbes when temperatures are cooler. As a result, N concentrations in surface runoff and lateral flows are higher during snowmelt (Rhoades et al. 2011), in part due to higher rates of N leaching. Leaching can also increase after autumn leaf fall (Fisk et al. 2002).

In ecosystems where spring and summer precipitation coincide with the peak growing season, elevated stream NO_3^- concentrations can indicate an N-saturated system (Fenn and Poth 1998; Fenn et al. 2008).

However, this metric breaks down in semiarid and/or Mediterranean climates, which are characteristic of many of the ecosystems in the western U.S. In these systems, the timing of precipitation is decoupled from the peak growing season, which can generate substantial N fluxes to streams (even in unpolluted systems) at the onset of winter rainy season when plant growth is slow (Homyak et al. 2014). This seasonal pulse can be exacerbated following fire due to increased levels of ash-deposited N on soil surfaces, coupled with a loss of vegetation that might otherwise be able to take up some of the available N, even if growth is slow (Hanan et al. 2017).

During fire

Fires actively change the form and distribution of biomass in ecosystems and watersheds. The extent of these changes is generally described as fire severity (Parson et al. 2010). Fire severity is a metric for quantifying fire effects on ecosystems. Because it is an indirect measurement (i.e., fire effects rather than a measure of the fire temperature itself), it is not ideal for deriving direct relationships between heating and biogeochemical processes (Smith et al. 2016). However, researchers still frequently use it to characterize fire because direct measurements of radiant energy and/or residence time are often not available.

Atmosphere

When combusted, N held in vegetation, litter, and soil can be volatilized or attached to smoke particles; remaining N can be deposited on soil surfaces with ash (Baird et al. 1999; Caon et al. 2014; Lindaas et al. 2021). Because N volatilizes at relatively low temperatures, fire always reduces total ecosystem N content (Neary et al. 1999; Kirkman 2011; Johnson and Turner 2014). However, the amount of N that is volatilized depends on fire characteristics, including temperature, fuel moisture and composition, and high-heat residence time (Binkley and Fisher 2000). Thus, severe fires, which typically burn at higher temperatures and have longer residence times, tend to volatilize more N (Knicker et al. 1996; Baird et al. 1999; Neary et al. 1999).

The N that is not volatilized is left as white and black or grey ash, which increases N availability (Bodí et al. 2014). Complete combustion of organic material forms white ash. Black or grey ash is the organic ash mixture that comes from only partially combusted organic materials (i.e. the ash weighs 30–90% of the original material's weight) (Ranalli 2004). Because NH_4^+ has higher volatilization temperature than NO_3^-, it is typically more concentrated in ash following fire. Although ash can provide a N source for recovering ecosystems, it can also be easily mobilized by wind or precipitation events (Balfour et al. 2014; Neris et al. 2021).

Vegetation

Severe fires affect more components of an ecosystem than low severity surface fires. Fire severity and the path a fire travels is controlled by environmental factors, such as high fuel moisture levels, slope, wind, fuel surface to volume ratios, and fuel packing ratios (Butler et al. 2007; Banerjee et al. 2020). Low severity ground fires typically only consume vegetation and other organic matter found on the surface. High severity fires crown fires (i.e., fires that burn the canopy) can affect more parts of an ecosystem, such as both the under- and overstory vegetation and ladder fuels (i.e., fuels that bring a fire from the surface to the canopy). As a result, high severity crown fires typically have more intense and longer-lasting effects on watershed N dynamics than low severity fires.

Soil

Fire has immediate effects on soil physical and chemical properties, which can affect postfire N cycling. Depending on the temperature of the fire and soil type, fire can reduce soil sulfur, phosphorus, N, and amino acid concentrations. It can also kill bacteria and fungi, and char organic matter (Neary et al. 2005). Because N tends to volatilize, if a high severity fire burns hot and long enough, it can affect soil N compounds below the top two horizons, and likely disrupt microbial communities deep in the soil profile (Sharma et al. 2017). In addition to mortality effects, fire can create a water-repellent soil layer by combusting waxy or resinous hydrophobic compounds that distill downwards in the soil and inhibit water infiltration for several years postfire (Pierson et al. 2003; Bodí et al. 2014). Fire can also immediately increase soil pH by destroying organic acids and depositing base-forming cations with ash (Giovannini et al. 1990). Many of these changes can persist for years after a fire occurs (Hanan et al. 2016a).

Postfire

After fire, various pathways exist for N movement through a watershed. These pathways depend on prefire ecosystem conditions, fire temperature and duration, and the rate of postfire recovery (N uptake and immobilization). The challenge is connecting changes in upland N storage to N delivery to streams. Many of the mechanisms that govern N cycling and export in an undisturbed ecosystem also persist once an ecosystem is disturbed (i.e., postfire). However, the magnitude and timing of N cycling and export usually change after a fire (i.e., rates of leaching and denitrification can respond to changes in soil biogeochemical cycling and vegetation demand) (Hanan et al. 2016a).

Vegetation

Ecosystem composition and fire characteristics influence postfire vegetation recovery rates in upland areas. Hardwoods and seed bank shrub species, such as *Ceanothus* spp., regrow rapidly and can dominate early successional communities, particularly if early colonizers are associated with N-fixing bacteria (Hanson and Stuart 2005; Shatford et al. 2007). Burn severity is also an important control on vegetation recovery. For example, four years after the Hayman Fire in Colorado, ponderosa pine (*Pinus ponderosa*) seedlings were observed in 52% of the plots that burned at low severity and 37% of the plots that burned at moderate severity (Rhoades et al. 2011). However, in areas burned at high severity, it takes longer for seedlings to reestablish and regrow, likely because seed banks have been destroyed (Radek 1997; Rhoades et al. 2011).

Regrowth of riparian zones is a critical factor in buffering against long-term N export to streams (Stephens et al. 2004). Because riparian zones are unique in their biophysical characteristics and moisture regimes, they are often very productive areas, burn at a lower severity than surrounding areas, and can even act as a natural fire break (Kobziar and McBride 2006; Hunsaker and Long 2014). Riparian zones act as physical buffers against nutrient and debris inputs to the stream and take up much of the N that is delivered downslope from burned areas, which prevent N from entering streams (Stephan et al. 2015; Pinay et al. 2018; Hill 2019). Riparian zones are also a hotspot for denitrification because of their high soil moisture (Burgin et al. 2010). Therefore, even if riparian vegetation is consumed in fire and N plant uptake is reduced, denitrification can still persist and some of the N solutes arriving from upslope ecosystems may still be removed before they enter the stream (Pettit and Naiman 2007). Thus, the preservation and/or rapid regrowth of vegetation is key for preventing large fluxes of N to streams (Robichaud et al. 2021).

Time since fire is also a major control on streamwater chemistry. Systems with rapid vegetation recovery (i.e., during the first growing season) usually have less elevated streamwater N concentrations compared to systems with slower and more prolonged regrowth (Rodríguez-Cardona et al. 2020). N concentrations in streamwater diminish over time as vegetation and microbial communities reestablish and the soil loses its hydrophobic properties (Oliver et al. 2012; Santos et al. 2019). While high severity fire may leave more available N on soil surfaces, it also destroys plant biomass and reduces photosynthetic potential, which can in turn prolong streamwater N export (Jiang et al. 2015). The extent of vegetation removal and rate of recovery also change the light exposure and stream temperature (in-stream effects will be discussed in Sect. 6), which also has further implications for downstream water quality (Betts and Jones 2009; Cooper et al. 2015).

Soil

Fire releases N from vegetation, litter, and surface soils and deposits it on soil surfaces with ash (Turner et al. 2007). Fire also makes N more available in soil by releasing it from organo-clay minerals and promoting rapid mineralization from increased substrate inputs and reduced competition with plants (Giovannini et al. 1990; Turner et al. 2007; Dijkstra et al. 2017). Many studies have observed increases in soil NH_4^+ and NO_3^- concentrations immediately after fire (in both N-saturated and N-limited watersheds) (Christensen 1973; Hobbs and Schimel 1984; Kutiel and Naveh 1987; Turner et al. 2007; Delwiche 2010; Stephan et al. 2015; Fernelius et al. 2017; Goodridge et al. 2018). For example, after a wildfire in Rocky

Mountain mixed conifer forests, soil NH_4^+ concentrations were 44.2 ± 29.1 mg kg^{-1}, relative to 6.8 ± 5.6 mg kg^{-1} in unburned sites; NH_4^+ and NO_3^- concentrations remained elevated for 3 years postfire (Stephan et al. 2015). However, pulses in N availability do not always occur immediately after fire in N-limited systems (Boerner 1982). For example, after a slash burning and prescribed fire in a ponderosa pine forest, soil NO_3^- concentrations did not increase; however, one year after the fire, nitrification rates increased and NO_3^- concentrations became 20 times greater than in unburned areas. Within five years, both NH_4^+ and NO_3^- returned to prefire conditions (Covington et al. 1991; Covington and Sackett 1992).

Elevated postfire nitrification can be problematic for water quality because NO_3^- is highly mobile in soils. Fires typically accelerate nitrification by increasing NH_4^+ availability and soil pH and decreasing vegetation uptake (due to plant mortality) (Rhoades et al. 2011; Hanan et al. 2016a). For example, in a ponderosa pine forest in Northern Arizona, annual net nitrification was found to be 1.98 to 3.51 g N m^{-2} yr^{-1} in burned areas compared to 0.15 to 1.87 g N m^{-2} yr^{-1} in unburned areas (Kurth et al. 2014). While elevated nitrification can last for multiple years following high severity fires (Hanan et al. 2016b), soils typically return to prefire conditions more rapidly after low severity fires (sometimes on the order of months) (Certini 2005). However, elevated postfire nitrification has been observed to last for up to a decade after a strand-replacing fire (Kurth et al. 2014).

Soil microbial biomass can also influence postfire N cycling and export to streams but fire effects on microbial biomass can be highly variable because microbial biomass responds to both direct heating and biogeochemical changes in the soil environment over the course of recovery (DeBano et al. 1998; Choromanska and DeLuca 2002; Smith et al. 2008). The extent to which heat energy penetrates the soil profile and destroys soil microbial biomass is a function of prefire soil water content (drier soils transmit more heat energy) (Massman 2015). For example, severe fire has been found to almost completely sterilize the surface soil layer (0–5 cm) and reduce microbial biomass by 50% in the lower horizon (5–10 cm). Four years after the fire, microbial biomass in the surface layer and lower horizons were 70% and 45% of prefire biomass content, respectively (Prieto-Fernández et al. 1998).

The rate that microbial biomass recovers and immobilizes or mineralizes available N depends on both prefire N status and postfire litter and carbon inputs. Microbial biomass can rebound quickly when postfire litter and carbon inputs are sufficient (Stirling et al. 2019). Some studies have found that microbial biomass begins returning to prefire conditions one year after fire and that the magnitude of recovery depends on both burn severity and postfire resource availability (i.e., C and N) (Dumontet et al. 1996; Smith et al. 2008). Alternatively, ash inputs can lead to a short-term spike in microbial biomass because it supplies C and other nutrients; however, that can be followed by sharp decline after the first postfire growing season when those resources become depleted (Hanan et al. 2016a). Rapid recolonization of soil microbes in N-limited systems may in turn promote N immobilization and therefore decelerate N cycling and loses to streams (Hanan et al. 2016b; Stirling et al. 2019). However, in systems that are less N-limited, biomass recovery may instead enhance decomposition and N mineralization, which may promote nitrification and leaching (Vourlitis and Hentz 2016).

Water repellent soil conditions or hydrophobic layers generated during fire can continue to reduce hydraulic conductivity and infiltration capacity for years after fire. Hydrophobic layers increase runoff and erosion (Robichaud et al. 2010) while simultaneously reducing N leaching because less water is transported through the soil profile (Imeson et al. 1992; Robichaud 2000; Certini 2005; Balfour et al. 2014; Fernelius et al. 2017). However, water repellency can also delay the reestablishment of vegetation after the fire, which might otherwise take up mobilized N (Fernelius et al. 2017). Thus, if hydrophobic layers enable NO_3^- to accumulate in soil microsites that are hydrologically disconnected from plant roots, leaching may occur once hydrophobic layers breakdown. Hydrophobic layers have been observed for 5 months (McNabb et al. 1989), 15 months (Rodríguez-Alleres et al. 2012), 2 years (Huffman et al. 2001), and 6 years (Dyrness 1976) following fire. The persistence, depth, and size of a hydrophobic layer depends on fire severity (high severity fires have more persistent, larger, and deeper hydrophobic layers), topography (steeper slopes have large repellent layers), and soil properties (Rodríguez-Alleres et al. 2012; Li et al. 2021).

N export to streams

Watershed and fire characteristics interact to control the extent and duration of water quality impacts (Elliot 2013). For example, strong hydrologic connectivity and gradients from steep slopes can tightly couple burned hillslopes to streams (Bladon et al. 2008; Serpa et al. 2020). The most persistent and pronounced effects on water quality occur when fires are severe, there are strong winds during fire, there is heavy precipitation following the fire, fire occurs on steep slopes, and in places where the soil has low cation-exchange capacity (Ranalli 2004; Oliver et al. 2012). These conditions result in the most persistent and pronounced effects because they make N more available and mobile. Finally, prefire N status can influence postfire N export. For example, in systems that are already N-saturated, postfire N export to streams may be substantially higher (Johnson et al. 2008).

Snowmelt, the timing of precipitation, and high flow periods postfire are major factors influencing spikes in streamwater N. Large runoff events from high intensity rainstorms can flush N from soils, exporting 14 times more N than undisturbed areas (Earl and Blinn 2003; Murphy et al. 2015; Neris et al. 2021). Therefore, a few dry years after a severe fire can reduce the negative effects on water quality (Bladon et al. 2008; Engle et al. 2008; Oliver et al. 2012). Similarly, snowmelt delivers significant amounts of inorganic N from burned areas to streams. Many studies have observed similar postfire N export patterns: an increase in NO_3^- concentrations in runoff during rainfall events and in the months following wildfire, reaching peak concentrations during snowmelt one to two years postfire, and then declining to prefire concentrations in subsequent years (Tiedemann et al. 1978; Feller and Kimmins 1984; MacKay and Robinson 1987; Gluns and Toews 1989; Brass et al. 1996; Williams and Melack 1997; Gerla and Galloway 1998; Ranalli 2004; Bladon et al. 2008; Bayley et al. 2011; Minshall et al. 2011).

Erosion and ash transport are additional postfire nutrient export mechanisms. Erosion is a function of fire severity, topographic characteristics, and climate (Robichaud et al. 2010). Eroded soils carry adsorbed nutrients, which can be transported downslope and deposited in waterbodies (Certini 2005); NO_3^- is often the main form of N adsorbed to and carried with soils (Pacheco et al. 2015). Nutrients lost via postfire erosion have been estimated to be 1% of the A horizon's C and N content through the displacement of 15 to 18 Mg soil ha^{-1} (Baird et al. 1999). Others have found N mass loss can range from 3.3 to 110 kg ha^{-1} (Pierson et al., 2019). Ash also tends to mobilize postfire through wind and precipitation, and can be directly deposited on soil surfaces and waterbodies (Spencer and Hauer 1991; Rhoades et al. 2011; Neris et al. 2021). When ash is deposited on a waterbody during and after fire, it can cause an immediate spike in N concentrations (Earl and Blinn 2003; Burton et al. 2016).

Fire effects on in-stream processes

Generally, with low severity fires, N levels in adjacent streams are not as persistently elevated as they are following high severity fires. For example, prescribed burns typically only cause a brief pulse of NO_3^- to streams within the first year (Stephens et al. 2004; Delwiche 2010). Much of the N that is mobilized following low severity fires is rapidly taken up and immobilized by surviving vegetation and soil microbes (Rhoades et al. 2011). Following high severity fires, NO_3^- concentrations in streams can be an order of magnitude higher (Stephan et al. 2012), or 50 times greater (Hauer and Spencer 1998), than in unburned watersheds. For example, in temperate conifer forests, N concentrations in streamwater at burned sites were 337 ± 337 µg L^{-1} while unburned sites were 41 ± 60 µg L^{-1} (Stephan et al. 2012).

Fires can also increase stream temperatures by reducing canopy and riparian cover, which allows more light to reach the stream. Streams can be warmer for a decade or longer after a severe wildfire (Rhoades et al. 2019), which can in turn alter in-stream processes. For example, five years after the Hayman Fire, summertime streamwater temperatures in burned catchments were on average 4 °C warmer than unburned catchments (Rhoades et al. 2011). When coupled with increases in nutrient concentrations, warmer streams can increase productivity, alter aquatic food webs and increase algal biomass (Silins et al. 2014; Cooper et al. 2015). When fire consumes riparian vegetation, algal biomass can be 5–10 times (Klose et al. 2015) or up to 71 times greater (Silins et al. 2014) than in unburned basins. However, when riparian vegetation is not consumed, algal biomass has been found to be much lower (i.e., 10–30% of that in an unburned catchment) (Klose et al. 2015). Similarly, after a high severity fire in Idaho conifer forests, in-stream moss N concentrations increased by about 40% (Stephan et al. 2012). Such increases in gross primary productivity can actually protect against water degradation by reducing downstream NO_3^- delivery (Stephan et al. 2015).

Streams vary in how efficiently they uptake and cycle NO_3^- and NH_4^+, which is a control on downstream N delivery (Ribot et al. 2017). Recent fire history can alter physical and biological processes that regulate in-stream nutrient uptake and retention (Diemer et al. 2015). Increased levels of NO_3^- in streamwater from fire change the ratios of streamwater dissolved organic matter (DOM), dissolved organic N (DON), and dissolved organic C (DOC) to NO_3^-. Because NO_3^- uptake depends on streamwater biogeochemistry, changes in the relative concentrations of DOM, DOC, and other nutrients can reduce in-stream NO_3^- uptake efficiency and subsequently increase N delivery (Rodríguez-Cardona et al. 2020). Shorter fire return intervals (time in between fires) can delay full recovery of nutrient stoichiometry, which may alter N retention and export (Diemer et al. 2015).

Conclusions

Climate change is affecting wildfire regimes by changing regional climate and weather patterns, drying fuels, and lengthening the fire season (Westerling et al. 2006; Dennison et al. 2014; Abatzoglou and Williams 2016; Hanan et al. 2021). Severely burned areas are a major concern because of high potential for flash floods or surface erosion (Moody et al. 2008; Miller et al. 2012; Neris et al. 2021), either of which could deliver significant quantities of N to streams. As temperatures continue to rise, the greatest increase in area burned in the U.S. will likely occur in the highly productive, historically cold and temperate, wet forests of the Pacific Northwest (Littell et al. 2018). In these forests, wildfire is likely to increase in response to two major drivers: (1) warmer temperatures, which decrease fuel moisture, and (2) or less precipitation falling as snow, which decreases moisture availability in warmer months (Westerling et al. 2006; Cansler and McKenzie 2014; Littell et al. 2016). The potential consequences of these changes are not entirely known, particularly in areas that experience stand-replacing fire regimes (Halofsky et al. 2018). However, because such forests have naturally high biomass, nutrients, and fuel loads, increases in the occurrence of large, severe fires is likely to promote N export that could devastate drinking water supplies (Lewis et al. 2014).

A major challenge in planning for these events is anticipating where the fire may occur—nearby or far away from municipal drinking water intake facilities—because that will change the magnitude and timing of N fluxes arriving at a facility (Neris et al. 2021). A severe fire occurring adjacent to a higher order stream or upslope from drinking water intake facilities would have a much more significant impact on water quality compared to a fire near a first order stream or further away from intake facilities because the nutrients would have less time to dilute. However, large rivers can still be affected by upstream disturbances when fires are severe (Emmerton et al. 2020). Decision-making support tools linking watershed disturbance to downstream pollutant delivery are being developed, which may be leveraged to assist with this planning (Nunes et al. 2018); however, they are currently limited.

To evaluate the risks of N export from wildland fires, and to help watershed and resource managers prioritize areas for fuel and fire management, we need to further develop and validate predictive tools. Tools exist for predicting nutrient and sediment export, upland erosion, and runoff associated with surface and subsurface flow and deep seepage (Dun et al. 2009; Srivastava et al. 2013; Elliot et al. 2015; Lew et al. 2019). However, there are currently no methods for water utility managers to quantify the amount of N that may be delivered following a wildfire to a water intake or reservoir some distance downstream from the fire. The Water Erosion Prediction Project (WEPP) model is under development to include the Soil and Water Assessment Tool (SWAT) water quality algorithms; WEPPcloud-WATAR (Wildfire Ash Transport And Risk) is also being developed to incorporate an ash transport model and ash loading maps (https://wepp.cloud/weppcloud/; https://swat.tamu.edu) (Neitsch et al. 2011; Neris et al. 2020, 2021). Given the importance of ash in a postfire landscape, this is a critical development in modeling nutrient transport from burned slopes to streams. Understanding and predicting postfire N export is critical because excess N in waterbodies can have consequences for human and ecosystem health. Enhanced stream N export can promote eutrophic water bodies and harmful algal blooms (HABs) (Conley et al. 2009). HABs can have major socioeconomic and ecological costs because they are harmful for fish, humans, and other organisms that live in the water, use it recreationally, or consume it (Carmichael and Boyer 2016). For humans, consuming water with too much N can cause blue babies syndrome or have other toxic effects on the body (Knobeloch et al. 2000). Additionally, HABs can lead to the creation of disinfection biproducts during water treatment processes, which can make water unsafe to drink (Foreman et al. 2021). Consequently, algal blooms are a significant public health concern. Several areas of research should be further explored to improve our understanding of wildfire, N cycling, and water quality. These research questions include:

1. How quickly, in what form, and in what concentration will N arrive at a water intake or storage reservoir following a major upland runoff and/or erosion event postfire?
2. What is the best method to predict N movement from fire-disturbed landscapes to municipal water storage reservoirs and water intakes?
3. Under what circumstances will increased N deposition delay or accelerate watershed recovery to prefire N retention?
4. How will climate change-enhanced disturbances and precipitation regimes effect N export from watersheds in the future?

In summary, fire is a powerful force for transforming N cycling in many ecosystems and severe fires have longest lasting and most pronounced effect on N cycling and surface water quality. For municipal watersheds, fire has the capacity to interrupt operations and change drinking water treatment procedures, which may be worsened by climate change. Connecting burned slopes to streams and understanding the mechanisms behind postfire surface water degradation are necessary for managers to protect water resources.

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Declarations

Conflict of interest The authors know of no conflict of interest.

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