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Title: Wildfire smoke impacts lake ecosystems

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Abstract

Wildfire activity is increasing globally. The resulting smoke plumes can travel hundreds to thousands of kilometers, reflecting or scattering sunlight and depositing ash within ecosystems. Several key physical, chemical, and biological processes in lakes are controlled by factors affected by smoke. The spatial and temporal scales of lake exposure to smoke are extensive and underrecognized. We introduce the concept of the lake smoke-day, or the number of days any given lake is exposed to smoke in any given fire season, and quantify the total lake smoke-day exposure in North America from 2019 - 2021. Because smoke can be transported at continental to intercontinental scales, even regions that may not typically experience direct burning of landscapes by wildfire are at risk of smoke exposure. We found that 99.3% of North America was covered by smoke, affecting a total of 1,333,687 lakes >=10 ha. An incredible 98.9% of lakes experienced at least 10 smoke-days a year, with 89.6% of lakes receiving over 30 lake smoke-days, and lakes in some regions experiencing up to 4 months of cumulative smoke-days. Herein we review the mechanisms through which smoke and ash can affect lakes by altering the amount and spectral composition of incoming solar radiation and depositing carbon, nutrients, or toxic compounds that could alter chemical conditions and impact biota. We develop a conceptual framework that synthesizes known and theoretical impacts of smoke on lakes to guide future research. Finally, we identify emerging research priorities that can help us better understand how lakes will be affected by smoke as wildfire activity increases due to climate change and other anthropogenic activities.

Keywords: Wildfire smoke, lakes, climate change, smoke-days, smoke plumes, ash deposition, solar radiation, wildfire

1.1 | *Introduction*

Smoke from wildfires has become one of the most visible and widely reported global-change disturbances (Groff, 2021). In part, this is because the frequency and severity of wildfires are increasing in many regions of the world. Not only do wildfires now occur regularly in regions where they were once rare (*e.g.*, the Arctic), wildfire seasons start earlier and last longer (Abatzoglou et al., 2019; Flannigan et al., 2013). Large wildfires create smoke plumes that can stretch for thousands of kilometers and linger for days to weeks at landscape scales, filtering sunlight and transporting fine particulate matter. Greenhouse gas emissions from wildfires now contribute a fifth of the total annual global carbon emissions (Lu et al., 2021; Megner et al., 2008; Nakata et al., 2022; Shrestha et al., 2022; Val Martin et al., 2018; van der Werf et al., 2017). The geographic scale and cross-boundary aspect of wildfire smoke make it inescapable for millions of people, resulting in adverse health effects that disproportionately impact the most vulnerable and disadvantaged human population demographic (Black et al., 2017; Bowman & Johnston, 2005; Holm et al., 2021; Johnston et al., 2012). While many of the individual and societal impacts of smoke are often readily apparent, effects on aquatic ecosystems are far less clear.

Studies of wildfire effects on ecosystems have historically focused on the direct effects of burning within watersheds, yet effects of smoke regulate several fundamental drivers of ecosystem function. By absorbing and reflecting downwelling solar radiation, smoke alters light availability across a wide spectrum that includes ultraviolet (UV), photosynthetically active radiation (PAR), and longwave radiation – dense smoke can reduce radiative inputs by as much as 50% (475 W m^{-2}) (McKendry et al., 2019). Reduced solar irradiance alters light and thermal regimes within ecosystems, affecting organisms from physiology to behavior, such as vertical migration in lake zooplankton (Urmy et al., 2016). Ash particles deposited within ecosystems can affect several biogeochemical processes, including the availability and cycling of nutrients.

The atmospheric nature of smoke means such effects can span vast spatial scales and widely impact ecosystems.

As integrators of terrestrial and aquatic processes, lakes may be particularly vulnerable to smoke. By modifying the availability of light, distribution of heat, and cycling of nutrients, smoke is a potential driver of fundamental physical, chemical, and ecological functions in lakes. Moreover, atmospheric deposition of ash particles from smoke can be concentrated within lakes (Brahney et al., 2014). Worldwide, millions of lakes are potentially exposed to smoke each year. The implications of smoke effects extend far beyond the ecology of these ecosystems given their cultural, economic, and societal importance. Given the importance of lakes in global carbon cycling, even small changes in rates of organic matter cycling may have profound impacts on global carbon budgets.

We currently lack a sense of scope, synthetic understanding of, or conceptual framework for identifying and understanding the effects of smoke across a broad range of lentic ecosystems. Conceptual models to date have drawn primarily from case studies of single systems, or have focused on the effects of wildfires burning within watersheds rather than the effects of smoke and ash at broader spatial scales (McCullough et al., 2019; Paul et al., 2022; Scordo et al., 2022). Our analysis addresses these critical knowledge gaps directly by: 1) quantifying lake exposure to smoke through space and time across the North American continent during three years of wildfire activity (2019 - 2021); 2) reviewing the current understanding of the mechanisms by which smoke affects physical, chemical, and biological aspects of lakes; and 3) developing a conceptual framework that synthesizes known and theoretical impacts of smoke on lakes and 4) identifying research priorities for future studies.

1.2 | *Spatial and temporal exposure of North American lakes to wildfire smoke*

A critical first step in understanding how lakes respond to smoke is characterizing the spatiotemporal dynamics of their exposure. Here we quantify the spatial and temporal extents of smoke cover in relation to burned area and lake locations for all lakes >= 10 hectares in North America. We used the National Oceanic and Atmospheric Administration Office of Satellite and Product Operations Hazard Mapping System Smoke Product (NOAA HMS; Ruminski et al., 2006) from 2019-2021 and the HydroLakes and NHDPlus databases of North American lake maps (Buto & Anderson, 2020; Messager et al., 2016). Our analysis is constrained to North America because of the availability of comprehensive continental-scale smoke and lake geospatial products. For any given lake, a lake smoke-day was defined as a day on which any portion of the lake boundary intersected with an area characterized as smoke by NOAA HMS, which categorizes daily smoke density as light (low), medium, or heavy (high) based on the aerosol optical depth from visible satellite imagery (see supplemental for details). Smoke-days for each lake were subsequently summed on an annual basis. To visualize lake exposure to smoke at the continental scale, we divided North America into 5000 km^2 pixels and for each pixel weighted the number of smoke-days by the corresponding total lake area for that pixel (Fig. 1 b-d; see supplemental methods for details).

Wildfires burn in spatially discrete areas, but smoke can be transported vast distances and dispersed heterogeneously. For example, smoke from fires burning in Quebec and Nova Scotia in 2023 was transported throughout the Northeast to mid-Atlantic areas of the United States and across the Atlantic Ocean to Western Europe (Copernicus AMS, 2023; NOAA NESDIS, 2023). Given the continental to intercontinental scale of smoke transport, lakes in regions that rarely or never experience wildfire directly may be exposed to smoke for substantial periods of time (Fig. 1, 2). Smoke cover in North America was temporally variable, but seasonally widespread and persistent across the three years we analyzed (Fig. 1, 3). Aggregated on an annual basis, 99.3% of the surface area of North America was covered by smoke between the years 2019 and 2021 (Supplemental Table 1). During that same period, less than 0.04% of the surface area of North America burned directly each year. The mean number of lakes per day in North America exposed to smoke across our three study years ranged from 1,325,069 - 1,332,077, representing a staggering 98.9 - 99.4% of the estimated total number of lakes >= 10 hectares on the continent (Supplemental Table 1). The mean number of smoke-days lakes experienced annually during our study period was 38.7, 22.8, and 62.7 days (2019, 2020, and 2021, respectively). The maximum number of smoke-days ranged up to 143 days.

There are several interacting factors that may determine the extent to which lakes are exposed to smoke. The spatial extent, density, and duration of smoke cover establish a template for potential exposure. However, weather conditions affecting the smoke plume and the spatial distribution of lakes within the plume area ultimately determine how many lakes are exposed. For example, the distribution of mean number of smoke-days by latitude differed considerably across years (Fig. 2a) and the peak number of smoke-days did not necessarily correspond to regional variation in lake density (Fig. 2b). Although 2019 and 2021 had virtually identical smoke cover on an aerial basis, differences in duration of smoke cover and geographic distribution of smoke with latitude meant lake smoke-day exposure was 21% higher in 2021.

The seasonal timing of smoke cover and density that lakes were exposed to varied across study years (Fig. 3). Smoke affected lakes nearly year-round, starting in mid-February (week 9) and continuing through December (week 52). While the majority of lake exposure to smoke occurred between May and September, the timing of peak lake exposure to smoke ranged over a narrower period of about two months, from mid-July (week 29) to mid-September (week 38). These are typically the hottest, driest months in North America and coincide with annual peak productivity for many lakes. In 2020, most of the lake-smoke exposures did not occur until after the summer season, into October (Fig. 3). Many lakes experience multiple smoke-days in a single week during peak fire periods, demonstrating the pervasive nature of smoke events.

There was a similar pattern among years in the density and spatial extent of smoke and the area burned by wildfires. Between 2019 and 2021, the area of land burned annually in North America was less than 0.01% of the total area of the continent, whereas the area covered by smoke was over 75% of the total area of the continent (see Supplemental Table 1). 2021 had the largest number of high-density lake smoke-days (fig. 3), which is also the year from our study period with both the largest area burned (0.03% of total area) and the largest area covered by smoke (87.9% of total area covered by smoke). Similarly, 2020 had the lowest number of high-density smoke-days (Fig. 3), the smallest area burned (0.0007% of total area) and smallest area covered by smoke (75.2% of total area) (Supplemental Table 1).

Our analysis demonstrates three key findings: 1) the spatial extent of smoke is widespread and capable of crossing continents; 2) the number of lakes affected by smoke in any given year is variable, but can represent a large majority of all lakes; importantly, in aggregate this can constitute tens of millions of lake smoke-days; and 3) the timing of lake exposure to smoke peaks in the mid-summer for North America which coincides with peak lake productivity, and can extend into the autumn.

2 | Mechanisms by which smoke affects lakes

Here, we conduct a literature review to synthesize our understanding of the mechanisms through which smoke and ash affect the structure and function of lakes. The large spatial scales of smoke plumes make them potential teleconnections of wildfire impacts on lakes (Williamson et al., 2016). However, as the number of studies that focus exclusively on the effects of wildfire smoke is limited, we include inference drawn from studies of smoke effects in directly burned watersheds despite the challenges of conflating teleconnection effects through the atmosphere with watershed loading effects. In some cases, we draw from first principles to infer effects.

2.1 | *Transport of smoke and ash to lake ecosystems*

Smoke and ash can be transported thousands of kilometers in the atmosphere and deposited onto lakes far from the source of wildfire. The distances ash particles can be transported vary with particle size and density, wind speed and direction, and ejection height (Adachi et al., 2022). The latter will vary with fire intensity and associated updrafts. Strong convection currents associated with intense wildfires can lead to emissions of large particulates high into the atmospheric column, allowing for regional transport (Fromm et al., 2010; Lareau & Clements, 2016).

Satellite imagery can provide key information on the spatial and temporal extent of smoke plumes (*e.g.*, NOAA's HMS Smoke Product), but our understanding of the potential for wildfires to produce aerosols across all size classes and the distances they may travel is hampered by limitations in atmospheric monitoring networks. In the United States, for example, all government aerosol monitoring programs focus primarily on particles <10μm in size (PM10) or <2.5μm (PM2.5), whereas ash particles can be substantially larger–whole pinecones have been known to travel up to 20 km through the strong updrafts created during wildfire events (Pisaric, 2002). Most atmospheric models are designed to simulate emission and transport of smaller aerosols and are challenged with larger particle sizes, lower densities, and irregular shapes of fire charcoal and ash (Fanourgakis et al., 2019). As a result, while we can quantify the distance and aerial extent of wildfire smoke cover from current monitoring systems, there are still considerable gaps in our knowledge of the amount and particle size of ash deposition into lake ecosystems.

2.2 | *The effects of smoke on light transmission to lake ecosystems*

Wildfire smoke influences the magnitude and spectral composition of incident solar radiation that can reach the surface of a lake, altering it before it enters and is transmitted through the water column. The effect of smoke on radiative inputs varies based on smoke density, aerosol composition, and particle sizes. These attributes cause either attenuation or scattering of light (Hobbs et al., 1997). The holistic impacts on light are characterized through the aerosol optical depth, an index for light extinction within the atmosphere (McCarthy et al., 2019; Suo-Anttila et al., 2005). Importantly, smoke attenuates electromagnetic radiation unequally, reducing light in a selective manner that decreases the ratio between ultraviolet B radiation (UV-B) and PAR (Scordo et al., 2021, 2022; Williamson et al., 2016). Unsurprisingly, the effects of smoke on PAR are large and variable. Dense wildfire smoke, as often occurs in closer proximity to a wildfire, can reduce surface irradiance by up to 50% or more (475 W m^{-2}) (McKendry et al., 2019), whereas reductions from more diffuse smoke, such as smoke that has traveled over continental scales, may not be as extreme. For example, modeled data from a wildfire in western Russia suggested insolation was reduced by 80-150 W m^{-2} (8-15%) across Eastern Europe (Péré et al., 2015). Somewhat counterintuitively, low density smoke can increase diffuse radiation, thereby increasing PAR (McKendry et al., 2019; Rastogi et al., 2022). However, the extent to which such increases in diffusive light alter water column light dynamics remain untested.

The effects of smoke on lake heat budgets and physical dynamics remains largely undescribed. By attenuating radiative inputs to lakes, smoke reduces rates of warming during the day. However, by reflecting longwave radiation back into lakes at night, smoke might also act to reduce heat loss. Moreover, ash particles within lakes may further alter heat budgets by increasing light attenuation within the water column. For instance, in Castle Lake (California, USA) following 22 consecutive days of severe smoke cover, cooler epilimnion temperatures compared to previous years' averages contributed to a 7% decrease in heat content of the water, which remained low for the rest of the open water season (Scordo et al., 2021). Similarly, wildfire smoke decreased water temperature in all 12 rivers and streams investigated in one study in the Klamath River Basin (California, USA) (Davis et al. 2018). In Lake Tahoe (California/Nevada, USA), smoke cover resulted in a reduction in incident PAR by approximately half, leading to reduced PAR at depth, though attenuation of PAR due to ash deposition was minimally affected (Goldman et al., 1990). Changes in insolation as a result of wildfire smoke have important implications for both physical and biological properties of lakes by reducing lake temperatures and altering the amount of PAR or UV-B received (as discussed in section 2.6).

2.3 | *Atmospheric deposition rates and delivery of ash to lake ecosystems*

Deposition rates of ash to lakes have rarely been quantified, but can be highly heterogeneous in terrestrial ecosystems both spatially and temporally. Spatially, ash deposits in forests post-fire can range from 14-193 g m^{-2} (Bodí et al., 2014). Temporally, terrestrial redistribution and movement of ash can last from hours to weeks or longer, depending on particle properties, terrain characteristics and meteorological conditions. Much of the ash might be redistributed or removed from a burned site within days or weeks after fire (Cerdà & Doerr, 2008; Pereira et al., 2014). For example, following an experimental shrubland fire, there was an almost complete removal of the ash layer after one day when wind speeds reached 90 km/h (Mataix Solera, 2000). In contrast, there are examples of ash persisting for weeks. Pereira et al. (2014) measured temporal dynamics of ash layer thickness over 45 days across a burned grassland and found increases in ash thickness in some areas over time that were attributed to ash redistribution by wind.

In the context of lakes, the catchment area to lake area ratio and catchment hydrology, topography, and land cover will influence whether ash is remobilized to lake basins. The precipitation regime and timing of the fire may dictate when this occurs. Similar to the heterogeneity in ash deposition in terrestrial ecosystems, ash deposition measured around Lake Tahoe (California/Nevada, USA) during a period of wildfire smoke was highly heterogeneous in both space and time (Chandra et al., 2022). Though we are unaware of any studies explicitly examining the role of catchment properties on ash mobilization to lake ecosystems, Brahney et al. (2014) found that particulate deposition was more readily mobilized to lake ecosystems in steep, poorly vegetated catchments where up to 30% of the catchment-deposited material made its way to the lake basin. Precipitation and subsequent runoff can redistribute ash to lake ecosystems, which may occur many months post-ash deposition, particularly if ash is deposited on or beneath snow (McCullough et al., 2023). Further studies on ash deposition rates and redistribution are needed to understand the time scales for in-lake ash delivery and the associated physical, chemical, and biological responses.

2.4 | *Physical settling and transformation of ash particles in lakes*

The fate of ash particles in lakes is determined by complex interacting physical and biological factors that can result in transport, diffusion, and transformation of particles through the water column. When deposited onto the surface of a lake, gravitational settling transports ash particles to depth at a vertical settling rate which is a function of particle size, density, geometry, and the viscosity of the water (*e.g.*, Johnson et al., 1996). Because settling rates are proportional to particle size, the finest particles have the potential to remain in suspension for months to years and have the longest-lasting impacts on water clarity, even if they constitute a relatively small proportion of total particulate mass. These physical properties of ash drive particle stability in the environment and influence potential for mobilization to, and transformation in, lakes from within the watershed (Rodela et al., 2022).

Transformation of particles within the lake through processes such as aggregation, breakup, remineralization, and zooplankton grazing can modify suspended particulate matter sequestration rates by several orders of magnitude (Burd & Jackson, 2009). In lakes, phytoplankton produce transparent exopolymer particles, which promote particle aggregation in water (Passow, 2002). Direct observations showed rapid (days to weeks) ash particle sequestration in Lake Tahoe (California/Nevada, USA) following ash deposition events in the small size classes (<10 mm) within regions of high phytoplankton concentrations (Chandra et al., 2022), which point towards the importance of transformation processes such as particle aggregation and zooplankton grazing on controlling ash particulate residence times in lake ecosystems (*e.g.,* Burd & Jackson, 2009; Jackson & Lochmann, 1992; Jokulsdottir & Archer, 2016). Hydrodynamic processes such as advective and turbulent particle fluxes and double diffusive instabilities, or particle-particle interactions such as hindered settling all also have the potential to significantly modify the residence times of particles (Richardson & Zaki, 1954; Scheu et al., 2015). Characterizing the influence of these processes is essential to understanding the fate and long-term impacts of fine suspended particulate matter deposited in lakes by wildfires. While there is limited literature characterizing this process for smoke and ash particles, a growing body of evidence points towards the significance of the aggregation process mediating suspended particulate matter concentrations in lakes (Logan et al. 1995; Hodder and Gilbert 2007; de Vicente et al. 2009; de Lucas Pardo et al. 2015).

In addition to vertical settling, ash particles can be dispersed horizontally across lakes via physical transport processes driven by the surface area, fetch, and thermal stratification of the lake (*e.g.,* Imboden & Wüest, 1995). When a lake is stratified, a strong density gradient may inhibit vertical settling (Boehrer et al., 2017). However, wind driven shear can cause hypolimnetic upwelling events (Monismith, 1986) or, in larger lakes, cause internal waves (Mortimer, 1974). Both mechanisms have the potential to disperse particles across lakes and lake zones. The inherent variability in wind patterns controlling smoke will also affect deposition of particles on the surface as well as the inflows of allochthonous particulate matter. Due to the heterogeneity of atmospheric particle deposition and within-lake transport processes, higher resolution measurements of horizontal transport are required to understand the spatial distribution of particles in lakes.

2.5 | *Smoke and ash composition and effects on lake chemistry*

Wildfire smoke disperses ecologically relevant nutrients, toxic metals, and organic compounds, which can be deposited into lakes as ash (Earl & Blinn, 2003; Olson et al., 2023). The composition ash and the delivery of nutrients, metals, and compounds to lakes will vary by fire intensity and landscape properties (*e.g.*, type of vegetation burned, land-use, topography, and the presence of human structures) (Plumlee et al., 2007; Santín et al., 2015; Wan et al., 2021). Fire temperature in part determines ash composition and color, which can be useful for understanding the likely contributions of ash to aquatic ecosystems before it reaches the water itself. Low-temperature fires (<250°C) have brown and red ash that is organic-rich due to incomplete combustion (Bodí et al., 2014; Pereira et al., 2014). Medium temperature fires (>450°C) have black to dark gray ash that is rich in carbonates, and high temperature fires (> 580°C) result in dark gray to white ash mainly composed of oxides (Bodí et al., 2014; Pereira et al., 2014). As wildfire temperatures increase, ash carbon content decreases as both organic carbon and eventually carbonates are lost, and mobilization potential through the watershed increases (Rodela et al., 2022).

Fire intensity and landscape properties not only influence the chemical and mineral composition of ash, they also influence the bioavailability of the nutrients bound within. Phosphorus (P), a key limiting nutrient in many lake ecosystems, occurs in much higher concentrations in ash compared to unburned vegetation. In some cases, ash can contain 50-times the P concentration of unburned vegetation (Raison et al., 1985) and fire has episodically elevated atmospheric concentrations of P by >10,000% (Olson et al., 2023). In a global meta-analysis, fire was primarily responsible for a 40% increase in atmospheric P deposition to lakes as compared to pre-industrial deposition rates (Brahney et al., 2015). Phosphorous deposition rates near burned areas have been measured as high as 200-700 mg $m^2 yr^{-1}$ (Ponette-González et al., 2016; Tamatamah et al., 2005), and are thought to contribute to the eutrophication of lake ecosystems in the area (Brahney et al., 2015; Tamatamah et al., 2005). Though nitrogen (N) and carbon are more readily volatilized than P, significant concentrations of these nutrients can still be transported by ash and affect lake nutrient concentrations. Increased concentrations of N, P, potassium, calcium and water-soluble organic carbon in freshwaters have been attributed to wet deposition from biomass burning in surrounding catchments (Bakayoko et al., 2021; Langenberg et al., 2003; Zhang et al., 2002). Boy et al. (2008) compared the composition of atmospheric deposition in Ecuador during times of burning and no burning and found elevated deposition rates of total N by 171%, nitrate by 411%, ammonium by 52%, and total P by 195%. One observational study showed that lakes near regions of heavy biomass burning have elevated P concentrations and tend towards N limitation (Brahney et al., 2015). Overall, ash deposition has the potential to influence the relative availability of key lake nutrients, which can alter the biotic structure of lake ecosystems (Elser et al., 2009). Still, deposition-driven changes in and lake responses to these nutrients (such as N or P limitation) likely vary by factors such as distance from wildfire and lake trophic status, and should be further investigated along a variety of gradients.

Smoke and ash can also concentrate and transport polycyclic aromatic hydrocarbons (PAHs) and toxic metals such as arsenic, chromium, copper, cadmium, mercury, nickel, lead, antimony, and zinc to lake systems. Concentrations vary by fire intensity as metals and organic compounds are volatilized (Bodí et al., 2014), and many metals can re-adsorb to ash in the atmosphere (Cerrato et al., 2016). Mercury is volatilized at relatively low temperatures with a substantive component becoming recalcitrant (0-75%) (Ku et al., 2018), and can result in high soil mercury concentrations that can eventually be transported to aquatic ecosystems (Webster et al., 2016). Experimentally, toxic methylmercury can leach from wildfire ash once deposited to anoxic sediments (Li et al., 2022). Empirically, lake sediment mercury fluxes have been found to nearly double during periods of high fire occurrence (Pompeani et al., 2018). Other metals, such as arsenic, are volatilized at higher temperatures and can be concentrated in ash from low- to medium-intensity fires (Wan et al., 2021). The type of vegetation or material burned can also change the concentration of ash constituents. For example, ash from *Eucalyptus* leaches higher concentrations of arsenic, cadmium, cobalt, chromium, lead, and vanadium, whereas ash from *Pinus* leaches higher concentrations of copper, manganese, nickel, and zinc (Santos et al., 2023). High concentrations of heavy metals have been reported in ash residues from residential and structural burns (Nunes et al., 2017; Pereira et al., 2014; Plumlee et al., 2007; Wan et al., 2021). Concentrations of PAHs can also increase in lake sediments following fire, with low molecular weight PAHs increasing on average more than four-fold (Denis et al., 2012), though in one case remained well beneath lethal concentrations reported for benthic freshwater species (Jesus et al., 2022). Whether heavy metal or PAH concentrations in smoke or rates of ash loading to lake systems occur at concentrations and rates that would affect aquatic organisms has not to our knowledge been determined.

Given its variable composition, ash can have variable effects on lake ecosystem function. Some studies have found only small or transient chemical effects from ash deposition. Earl and Blinn (2003) found most lake chemical variables were only influenced by the ash addition for 24 hours. Furthermore, Scordo et al. (2021) found no changes in N and P limitation for algal growth at Castle Lake (California, USA) after the lake was covered by wildfire smoke for 55 consecutive days. In some cases, transient or limited observational effects may occur because ash deposition rates may not be sufficient to induce a strong ecological response. In other cases, responses may be limited because nutrients are rapidly taken up by primary producers. A bioassay experiment in Lake Tahoe (California/Nevada, USA) using wildfire ash with a high N:P ratio led to increased growth of picoplankton and cyanobacteria (Mackey et al., 2013). Picoplankton growth may not increase chlorophyll-a or biomass substantively; thus, the ecosystem response may be hard to detect using conventional methods (Mackey et al., 2013). Paleolimnological studies have shown a range of responses from minimal shifts in sedimentary P and production proxies to a near doubling of sedimentary P and substantive increases in production (*e.g.,* Charette & Prepas, 2003; Paterson et al., 2002; Prairie, 1999). There is little information on the fate of ash once deposited into lake ecosystems (but see section 2.4). Whether ash is rapidly oxidized or sedimented will influence the short- and long-term effects of the ash load in lakes.

There remain several key unknown effects of wildfire smoke and ash deposition on lake ecosystems. First, the literature on the limnological responses to wildfire ash deposition is heavily skewed towards paleolimnology for field level studies, with few pre- and post-wildfire observational studies, especially from outside of burned catchments. Second, the post-wildfire persistence of direct deposition effects, ash redistribution, or catchment flushing over time are unknown. Third, particulate debris in wet deposition is highly oxidizable and therefore could be effective at reducing oxygen concentrations either through photooxidation or microbial respiration. As a result, deposition of ash from smoke could decrease dissolved oxygen concentrations while increasing pH, which together can be deleterious to cold-water aquatic organisms (Brito et al., 2021; Earl & Blinn, 2003), and should be further investigated. Finally, whether ash has the potential to increase metal concentrations beyond toxicity thresholds under field conditions is also unclear and little to no information exists on what other deleterious compounds may leach from wildfire ash, particularly if residential and commercial areas are burned.

2.6 | *Effects of smoke and ash on ecosystem metabolic rates*

Wildfire smoke can impact the metabolic rates of lakes through several mechanisms linked to changes in physical and chemical conditions. The extent to which reductions in PAR and UV and their relative ratio may either stimulate (Tang et al., 2021) or inhibit (Staehr & Sand-Jensen, 2007) pelagic primary productivity depends on the extent to which the autotrophic community is light limited or photo inhibited, which itself may vary with depth in seasonally stratified lakes. Consequently, smoke density will be an important determinant. Low to medium smoke density may increase primary production and light-use efficiency through selective filtering of UV, increased diffuse scattering of PAR, and an overall alleviation of photoinhibition (Hemes et al., 2020; McKendry et al., 2019). In contrast, higher density smoke may reduce primary production by attenuating PAR to a large degree (Davies & Unam, 1999; Scordo et al., 2021).

Likewise, the extent to which nutrient additions through ash deposition stimulate photosynthesis and respiration depends on nutrient and DOM concentrations within the receiving system and relative ratios between autotrophic and microbial heterotrophic biomass, which can vary seasonally both across and within lakes. Moreover, processes driving metabolic responses might be temporally decoupled. For example, one study examined 15 years of fire-related atmospheric particulate nutrient concentrations and found cyanobacteria increased in smoke covered lakes 2-7 days after smoke exposure (Olson et al., 2023), suggesting deposited nutrients may have an impact once light regimes are no longer influenced by smoke. Such spatiotemporal variability complicates decoupling effects from altered light regimes versus nutrient additions from ash, making it difficult to predict how individual lakes will respond outside of specific spatial and temporal contexts. However, individual case studies provide a template for understanding the mechanisms involved.

Although a comparatively small number of studies have measured the impact of wildfire smoke on rates of production, the patterns observed suggest changes consistent with expectations based on light and nutrient availability. The response of primary production to smoke from wildfires shows a strong depth dependence in clear water lakes. For example, surface productivity in ultra-oligotrophic Lake Tahoe (California/Nevada, USA) is typically low, with a productivity maximum developing deeper than 60m. Heavy smoke from a wildfire outside the catchment caused productivity at depth to decline to near zero, and productivity within the surface layer to triple from 10-31 mg C $m^{-3}d^{-1}$. The net effect was a record-level increase in integrated water column productivity (Goldman et al., 1990). The authors theorized that the reduction in photoinhibition alone was insufficient to cause a 3-fold increase in production and hypothesized that ash deposition contributed N, P, and/or micronutrients that stimulated production. In Castle Lake (California, USA), fires burning outside the catchment resulted in smoke cover that lasted for 55 days (Scordo et al., 2021, 2022). During this period, both incident and underwater UV-B, PAR, and heat were reduced concomitant with a 109% increase in epipelagic production. Similar to Lake Tahoe, productivity in Castle Lake shifted upwards in the water column in the pelagic zone. In contrast, littoral-benthic productivity did not change in Castle Lake, possibly reflecting adaptation to high-intensity UV-B light in these habitats (Scordo et al., 2022).

The effect of smoke on rates of ecosystem respiration are rarely reported. The only study to explicitly evaluate impacts of smoke on respiration found little effect in a mesotrophic lake (Scordo et al., 2021), in contrast to the comparatively large increases in respiration that can be found in lakes within burned watersheds (Marchand et al., 2009). Given the coupling of production and respiration, it is likely that changes in respiration associated with smoke alone will mirror those of production. However, ash deposition may affect respiration independently of production by stimulating microbial metabolism through the addition of nutrients and/or carbon. Phosphorus is often in high demand among microbial communities, and ash with high concentrations of biogenically available P may stimulate increases in microbial metabolic activity (Pace & Prairie, 2005). Likewise, lakes where microbial communities are substrate-limited by carbon are likely to see increased metabolic activity associated with pyrogenic carbon leachate into dissolved organic carbon (Py-DOC). Py-DOC is highly labile and water soluble (Myers-Pigg et al., 2015), making it highly available to microbes, which can drive increases in respiration. The extent to which carbon and nitrogen from ash cause an increase or decrease in respiration will be dependent on the degree of coupling between autotrophic and heterotrophic metabolisms and the extent to which microbial growth efficiency increases or decreases. The effect of ash deposition on lake metabolism more broadly is still poorly understood and may theoretically increase or decrease production to respiration ratios depending on the characteristics of the smoke, ash composition, and initial conditions of the lake. Additional observational and experimental studies are needed to define these relationships.

2.7 | *Effects of smoke and ash on lake food webs*

While there is some evidence that smoke can increase or decrease lake primary production through effects on light and nutrient deposition, less is known about how these changes alter the growth and abundance of organisms at higher trophic levels. In one case, smoke caused a large increase in epilimnetic primary productivity, but did not translate into any changes in zooplankton composition or biomass (Scordo et al., 2021). Fire within a lake's watershed has been shown to increase the abundance of zooplankton and macroinvertebrates as post-burn nutrient runoff fuels algal production (Garcia & Carignan, 2000; Pinel-Alloul et al., 1998; Pretty, 2020), though in some cases, dissolved organic carbon and sediment increases due to post-burn runoff can reduce water clarity enough to override the effects of post-fire nutrient increases on primary production (*e.g.*, France et al., 2000). However, it is unknown whether decreasing water clarity or ash deposition in lakes without post-burn runoff (*i.e.*, lakes outside of burned watersheds experiencing smoke) will have a similar effect. The lack of zooplankton, macroinvertebrate, and fish data from other studies of smoke effects on primary productivity prohibits any general conclusions about how smoke and ash deposition influence secondary production in lakes via this bottom-up mechanism.

Ash concentrations in lakes may have toxicological influences on the survival of aquatic and amphibian species, which can be highly susceptible to ash-derived heavy metals and PAHs, though effects vary among species and sources of ash (Brito et al., 2017; Campos et al., 2012; Harper et al., 2019; Santos et al., 2023; Silva et al., 2015). For instance, ecotoxicity assays indicate that ash is toxic to *Ceriodaphnia spp.* at low concentrations but has no detectable effect on gastropods or fish (Brito et al., 2017). Ash can also contain large concentrations of inorganic mercury, which can be converted into methylmercury, a highly toxic and bioavailable form that accumulates in fish (Kelly et al., 2006). The source of the ash can differentially impact pH, metal, and ion concentrations with differing toxicities to specific organisms. Harper et al. (2019) found that *Daphnia magna* was sensitive to ash derived from some plants such as spruce (*Picea*) or eucalypt (*Eucalypteae*), whereas other plants, such as ash (*Fraxinus*) had no observable toxicity. However, the authors note that this may be related to mechanical challenges filter feeders face with high particulate loads rather than toxicity. Observational and experimental studies of macroinvertebrate communities have shown a range of responses to ash from almost no response to statistically significant reductions in density and shifts in community composition for one year following the introduction of ash (Earl & Blinn, 2003). However, it is unknown whether these shifts in macroinvertebrate communities were the result of toxicity, as non-toxic but ash-driven deleterious conditions, such as reduced dissolved oxygen and increasing pH conditions can also negatively affect cold-water aquatic organisms (Brito et al., 2021; Earl & Blinn, 2003). Whether the effects on secondary production are due to particulate loads, metals, ions, pH, or reductions in oxygen remain poorly understood. The indirect effect of smoke and ash on lake food webs may mirror that of primary production if biomass is controlled from the bottom-up by nutrients or may decrease through toxicity. Research is needed to identify the relative contribution of indirect and direct effects of smoke and ash to secondary lake productivity, as well as the time scales over which smoke effects occur.

As smoke can alter light conditions and decrease lake temperature, smoke may also influence consumer behavior as light and temperature serve as important cues. Changes in behavior can shift, for example, distributions of animal biomass, predator-prey interactions, and water column biogeochemistry. Smoke-induced reduction of UV:PAR ratios can alter the diel vertical migration of zooplankton and affect habitat use by fish (Scordo et al., 2021, 2022; Williamson et al., 2016). In highly transparent lakes, UV light is an important dynamic cue for vertical migration behavior, whereby zooplankton occupy deeper depths during the day to avoid damaging UV radiation (Williamson et al., 2011). When smoke reduces incident UV, zooplankton may alter their migration behavior by shifting their daytime vertical distribution closer to the surface. For example, zooplankton exhibited a 4m upward shift over a 2-day period in Lake Tahoe (California/Nevada, USA) when smoke reduced incident UV radiation by 8% (Urmy et al., 2016). In contrast, zooplankton in Castle Lake (California, USA) did not change their vertical migration patterns in response to the 65% reduction in UV during a smoke period. During the smoke period, the dominant fishes (brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*)) migrated out of their usual near-shore habitat to the pelagic zone (Scordo et al., 2021). Consequently, there may have been no changes in the vertical migration patterns of zooplankton because of the opposing effects of reduced UV and increased predator presence in the epilimnion. Due to the limited available studies, it is difficult to generalize how smoke and ash deposition affect consumer behavior or production.

3 | The effect of smoke on lakes: a conceptual framework

The effects of smoke and ash on lakes are the outcome of mechanisms that operate across multiple spatial and temporal scales (Scordo et al., 2022). Because smoke density can change rapidly with distance from wildfires, the proximity of a lake to wildfire may modulate the magnitude of the teleconnection effect of smoke on lakes (Fig. 4a). Generally, lakes face the highest density of smoke, largest ash particle size, and rates of ash deposition nearest to wildfire (Fig. 4b), which can dramatically decrease the relative availability of UV and PAR. The temporal dynamics of smoke can be highly variable at very short time scales, causing large swings in radiative inputs to lakes. Resulting shifts in UV and/or PAR from reflection or scattering by smoke can cause cascading effects on lake physical, chemical, and biological variables (Fig. 4c). Lakes at intermediate (*i.e.*, tens to hundreds of kilometers) or large (*i.e.*, continental to intercontinental) distances from wildfires may still experience significant effects from smoke and ash deposition, but the relative importance of each and the associated shifts in UV and PAR may vary considerably. At intermediate to larger scales, smoke density and ash deposition can be patchy in space and time. Smoke transported at large scales may be more spatially homogeneous with less dense smoke and lower ash deposition (smaller particle sizes and lower density) over large areas (Fig. 4a).

Particulates from smoke can vary in terms of chemical characteristics, density, and particle size (Fig. 4b). The potential effects these particles on lakes are dependent partly on the quantity and quality of the ash (*i.e.*, density, mass, composition) and partly on background lake nutrient concentration. Ultimately, however, the quality of ash likely determines the potential for nutrient enrichment following deposition. Ash quality governs the stoichiometry and trace nutrient concentrations available to autotrophs and heterotrophs. Thus, a mass balance approach that considers both quantity and quality of ash is necessary to gauge potential impacts to nutrient concentrations in lakes.

Smoke and ash deposition can ultimately change ecosystem metabolic rates through two main pathways (Fig. 4c). These pathways include a fertilization effect through nutrient deposition (section 2.4) and reducing availability of PAR and UV light throughout the water column (section 2.2), with each pathway mediated by trophic status and lake size (Fig. 4d). If deposition of ash causes a shift in nutrient limitation, it is likely to have a positive impact on net ecosystem production (NEP) by stimulating primary production more than respiration. Variations in lake morphometry and watershed size or hydrology are likely to mediate the metabolic response of lakes to smoke and ash deposition by regulating deposition rates, transport and transformation of particles within the water column, and residence times. Consequently, the effects of particle deposition on ecosystem function might span large time scales.

In contrast, the effects of reduced solar radiation on lake metabolic rates are likely to be far more rapid and temporally variable in response to smoke dynamics. Whereas high smoke density and longer duration smoke cover will greatly reduce the amount of incident PAR and UV reaching the lake's surface (Williamson et al., 2016), highly variable or less dense smoke cover may have little net effect on primary producers. Moreover, the effect of reductions in radiative inputs on rates of production and respiration will depend in part on the extent to which autotrophs are light-limited within a given lake. Thus the same reductions in PAR and UV from smoke (Williamson et al., 2016) likely have variable effects on GPP across lakes or even across lake habitats (Scordo et al., 2021, 2022). From a theoretical standpoint, lakes adapted to high light might experience either little change or an increase in GPP depending on relative changes in solar inputs. Light limited systems might more consistently see decreases in GPP with reduced solar inputs. Changes in respiration should depend on trophic status. High productivity ecosystems or ecosystems with large terrestrial subsidies likely see little change in respiration. In contrast, clear water and oligotrophic lakes may see large responses that vary depending on the degree of metabolic efficiency and the degree of coupling between autotrophs and heterotrophs. Lake responses may vary in relation to seasonal changes in water temperature, solar irradiance, and nutrient stoichiometry, or short-term variability in watershed loading.

4 | Conclusions: knowledge gaps and research priorities

Despite evidence that smoke and ash deposition impact biological, physical, and chemical processes in lakes, large knowledge gaps impede our ability to predict and manage the responses of lakes to smoke and ash. Measuring the extent and effects of smoke and ash deposition remain challenging. Current atmospheric monitoring networks do not comprehensively sample and characterize fire aerosols. For example, in the United States, state and federal air quality regulations primarily monitor PM10 and PM2.5 size classes that exclude most ash material on a per-mass basis (Pisaric, 2002). Satellite remote sensing of aerosol optical depth can help improve measurement of atmospheric aerosol loading (Sokolik et al., 2019), but cannot estimate particle concentrations or distinguish between particle size classes. Pairing remotely-sensed measurements of smoke plumes and fire aerosols with satellite remote sensing of water quality offers opportunities to analyze the ecological responses of lakes to smoke with high frequency over the long-term. A more detailed characterization and quantification of the attributes of smoke and ash (*e.g.*, beyond coarse density measurements, or presence/absence) is crucial to these efforts. Key questions include: How does the composition, size, and density of ash vary with distance from wildfire? How do deposition rates on lakes vary in relation to local landscape and weather factors?

Moreover, few studies explicitly evaluate the individual and interactive effects of smoke both as a driver of variation in UV and PAR, and as external load of carbon and nutrients. In watersheds with direct burns, differentiating loading effects from smoke effects is equally important. Identifying the types of lakes that are most sensitive to the teleconnection effects of wildfire vs. direct watershed burning should be a priority, and our conceptual synthesis offers testable hypotheses (Fig. 4). Key questions include: How does lake size, lake clarity, or hydrological connectivity affect lake responses to smoke? Are the effects of wildfire smoke transient compared to direct burn effects?

In general, field and experimental studies that collect pre- and post-fire data in lakes are scarce and forced on smaller lakes (McCullough et al., 2019). Larger scale studies are necessary to disentangle the mediating effects of scale and watershed context on the responses of lakes to smoke and ash deposition (Fig. 4). Studies that address this should encompass key gradients (Section 3) such as lake size or clarity, and are necessary to better understand how smoke affects a broad range of lake types. Key questions include: How does lake trophic status or size mediate responses at regional or larger scales? What is the seasonal variation in lake responses to smoke within and across lakes?

Given the broad spatial extent of lake exposure to smoke, existing monitoring programs and networks, such as the Global Lake Ecological Observatory Network (https://gleon.org/), will be vital sources of data and coordinated analyses. New studies will also need to delineate smoke-exposed versus control (*i.e.*, upwind) groups carefully, and ideally track ecosystem recovery after smoke exposure, including through repeat exposure events. Key questions include: What level of smoke exposure will alter primary and secondary producer community structures? Do mechanisms driving short versus long term impacts of smoke on lakes differ?

Finally, we lack knowledge of the past prevalence and ecological impacts of smoke and ash deposition, which is essential to inform future models and management. Advances in paleolimnology, such as using monosaccharide anhydrides as indicators of biomass burning (*e.g.,* Kehrwald et al., 2020), can better characterize historical smoke exposure and ash deposition. Relating proxies of smoke and ash to those associated with lake productivity could improve our understanding of the ecological effects of smoke on lakes, though productivity may be difficult to estimate where sediments integrate over several years and fail to preserve key planktonic or benthic taxa.

As wildfires, fueled by global change (Abatzoglou et al., 2019), increase in frequency and intensity (Flannigan et al., 2013; Jones et al., 2022), there is a need to understand their environmental impacts beyond the direct effects of biomass combustion at the watershed scale. Our analysis of lake smoke-days indicates that many regions that historically have not been considered at high risk of wildfires are already experiencing smoke events (Fig. 1, Fig. 2) and these have the potential to become increasingly pervasive and long-lasting (Fig. 3). Here we have reviewed how these smoke events and corresponding ash deposition can have far-reaching environmental consequences for lakes across spatial and temporal scales. We have also synthesized how these environmental consequences are modified by the characteristics of lakes and the characteristics of both smoke and ash themselves. Because lakes reflect processes within their surrounding catchments and the flowing waters that feed into them, they can also act as sentinels of wider landscape-level changes associated with smoke and ash deposition, such as nutrient and energy cycling (Williamson et al., 2008). Drawing upon research from diverse disciplines beyond limnology, including fire ecology, climatology, and atmospheric chemistry will be key to advancing our understanding of the environmental impacts of wildfire smoke in an increasingly flammable world.

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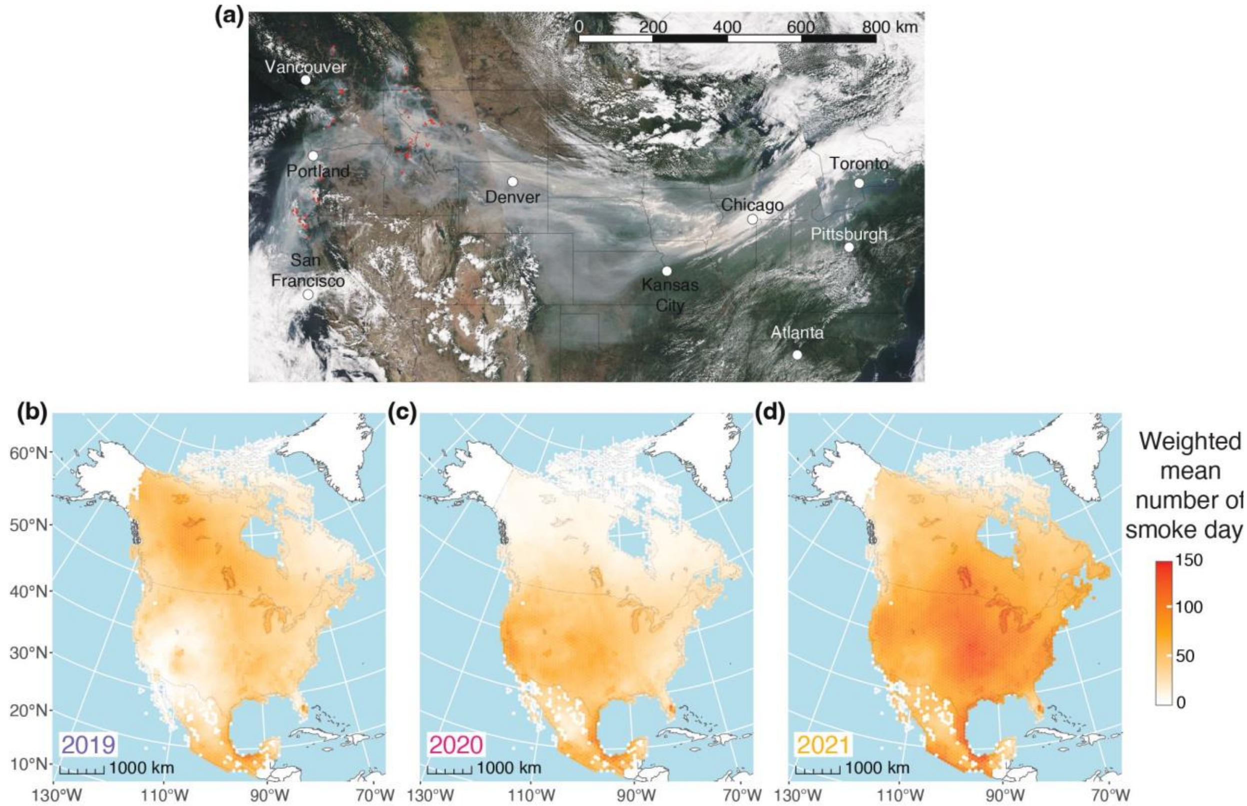

Figure 1. *(a) Continental-scale smoke transport across North America, moving wildfire smoke from fires in the West thousands of kilometers to the East. Actively burning wildfires are outlined in red. Image: NASA - Jeff Schmaltz LANCE/EOSDIS MODIS Rapid Response Team, GSFC. Sept. 4 2017. (b-d) Map of weighted mean number of smoke-days per 5000 km*^{2} *hexagon for (b) 2019, (c) 2020, and (d) 2021. Values are weighted by the area of each lake within each 5000 km*^{2} *hexagon. Projected in Albers Equal Area (EPSG: 102008).*

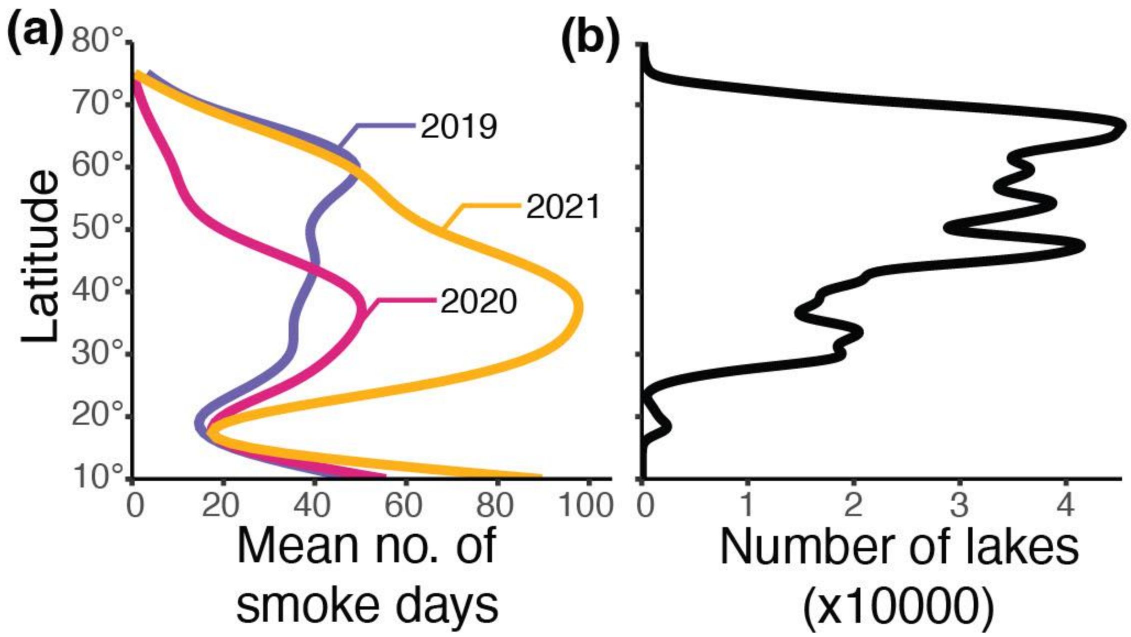

Figure 2. *Summary of North American smoke-days* ***(a)*** *and lake count* ***(b)*** *with latitude. Latitude values are in degrees according to EPSG:4326. Lines in (a) are based on a generalized additive model with a k of 10.*

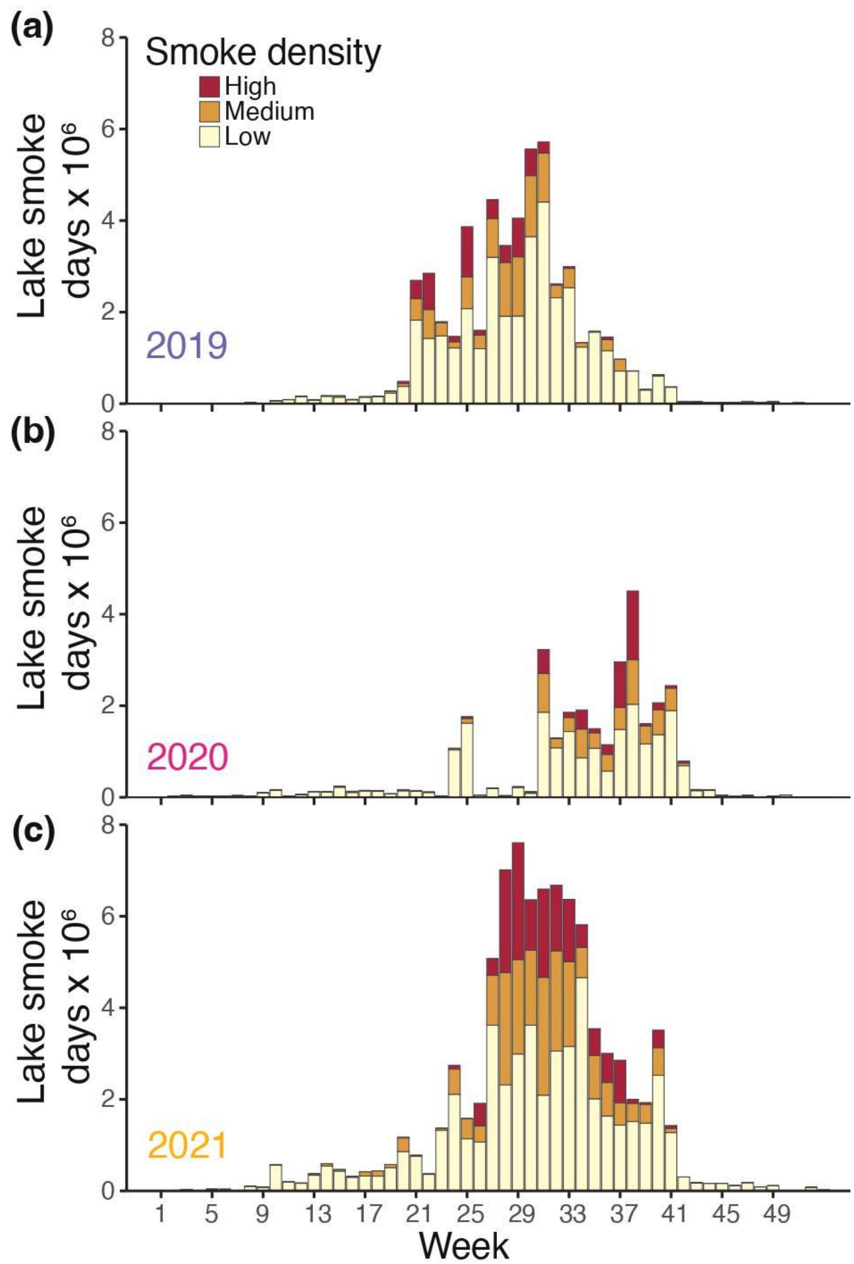

Figure 3. *Number of cumulative lake smoke-days for each week in North America. For example, in Week 31 of 2019, the 1.3 million lakes experienced nearly 6 million cumulative smoke-days of exposure, with many of the lakes experiencing multiple days of exposure in this week. Exposure is categorized by smoke density (NOAA HMS).*

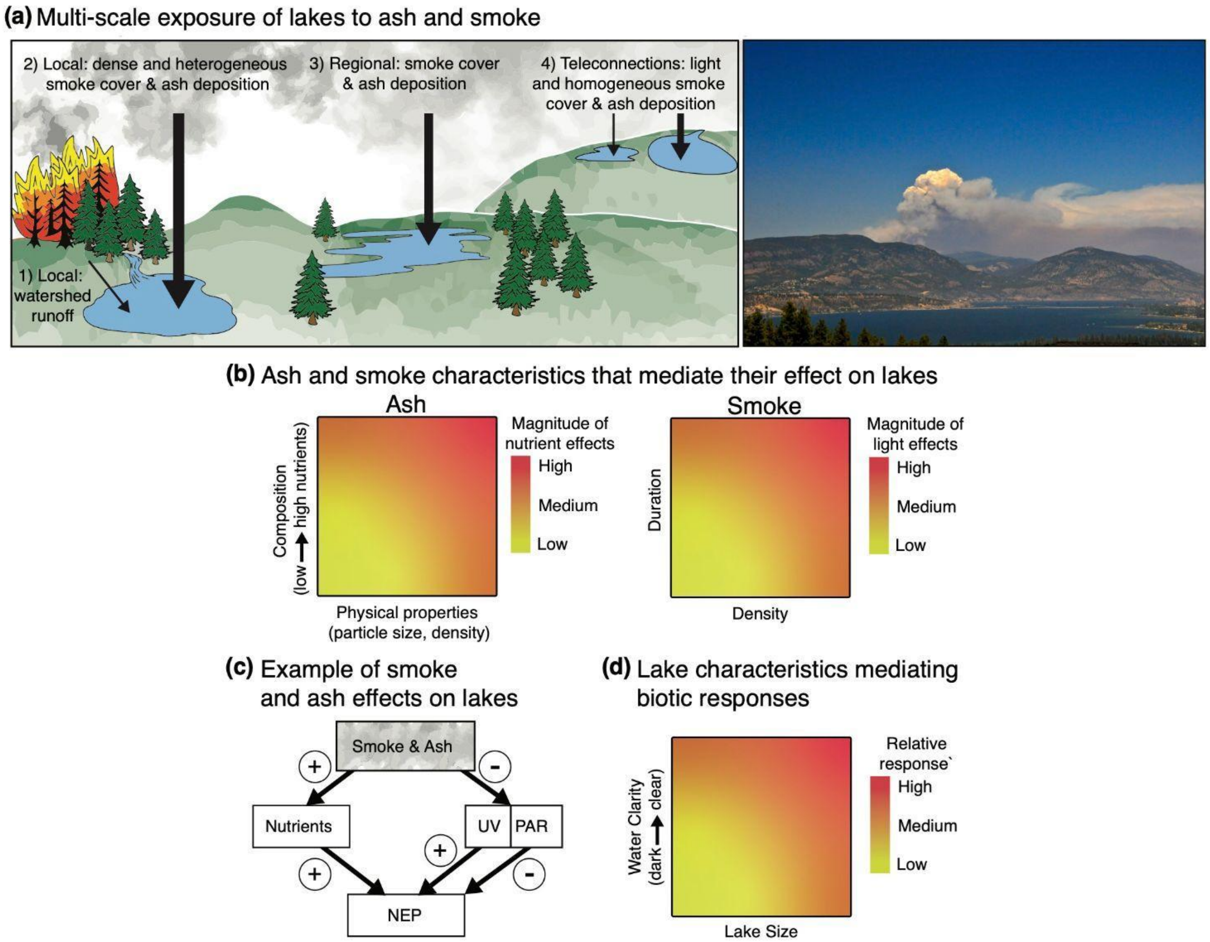

Figure 4. *Lake responses to smoke and ash involve processes operating at multiple spatial and temporal scales, mediated by factors intrinsic to both smoke and lakes. Our current conceptual understanding is that: deposition rates are expected to decline with increasing distance from fire* ***(a)****; Smoke and ash are expected to alter light and nutrient availability in lakes in relation to particle size and chemical composition, and density of smoke* ***(b)****; and the degree to which rates of primary production (GPP) are altered by smoke and deposition* ***(c)****, will in part be determined by intrinsic factors of lakes, such as water clarity and lake size* ***(d)****. Photo: Forest Fire over Okanagan Lake, British Columbia, Canada, July 2009. Jack Borno, Creative Commons: https://web.archive.org/web/20161020140539/http://www.panoramio.com/photo/59629498*

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