

1 **Title: Wildfire smoke impacts lake ecosystems**

2 **Running title: Wildfire smoke impacts lake ecosystems**

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

89

90 **Keywords:** Wildfire smoke, lakes, climate change, lake smoke-day, smoke plumes, ash  
91 deposition, solar radiation, wildfire

92

93 **Data Availability Statement:**

94 The data that support the findings of this study are openly available in the Environmental Data  
95 Initiative at <https://doi.org/10.6073/pasta/ed65a4722119ae4b104236d0f954b5df>

## 96 **1.1 | Introduction**

97 Smoke from wildfires has become one of the most visible and widely reported global-change  
98 disturbances (Groff, 2021). In part, this is because the frequency and severity of wildfires are  
99 increasing in many regions of the world. Not only do wildfires now occur regularly in regions  
100 where they were once rare (*e.g.*, the Arctic), wildfire seasons start earlier and last longer  
101 (Abatzoglou et al., 2019; Flannigan et al., 2013). Large wildfires create smoke plumes that can  
102 stretch for thousands of kilometers and linger for days to weeks at landscape scales, filtering  
103 sunlight and transporting fine particulate matter. Greenhouse gas emissions from wildfires now  
104 contribute a fifth of the total annual global carbon (C) emissions (Lu et al., 2021; Megner et al.,  
105 2008; Nakata et al., 2022; Shrestha et al., 2022; Val Martin et al., 2018; van der Werf et al.,  
106 2017). The geographic scale and cross-boundary aspect of wildfire smoke make it inescapable  
107 for millions of people, resulting in adverse health effects (Black et al., 2017; Bowman &  
108 Johnston, 2005; Holm et al., 2021; Johnston et al., 2012). However, effects of smoke on aquatic  
109 ecosystems are far less clear.

110 Studies of wildfire effects on ecosystems have historically focused on the direct effects of  
111 burning within watersheds, yet effects of smoke regulate several fundamental drivers of  
112 ecosystem function. By absorbing and reflecting downwelling solar radiation, smoke alters light  
113 availability across a wide spectrum that includes ultraviolet (UV), photosynthetically active  
114 radiation (PAR), and longwave radiation – dense smoke can reduce radiative inputs by as much  
115 as 50% ( $475 \text{ W m}^{-2}$ ) (McKendry et al., 2019). Reduced solar irradiance alters light and thermal  
116 regimes within ecosystems, affecting organisms from physiology to behavior, such as vertical  
117 migration in lake zooplankton (Urmy et al., 2016). Smoke and ash particles deposited within  
118 ecosystems can affect several biogeochemical processes, including the availability and cycling  
119 of nutrients. The atmospheric nature of smoke means such effects can span vast spatial scales  
120 and widely impact ecosystems.

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

130 We currently lack a sense of scope, synthetic understanding of, or conceptual framework for  
131 identifying and understanding the effects of smoke across a broad range of lentic ecosystems.  
132 Aside from one example of a conceptual model of wildfire-generated pollutants that includes  
133 effects on aquatic ecosystems broadly (Paul et al., 2023), conceptual models to date have  
134 drawn primarily from case studies of single systems, or have focused on the effects of wildfires  
135 burning within watersheds rather than the effects of smoke and ash at broader spatial scales  
136 (McCullough et al., 2019; Paul et al., 2022; Scordo et al., 2022). Our analysis addresses these  
137 critical knowledge gaps directly by: 1) quantifying lake exposure to smoke through space and  
138 time across the North American continent during three years of wildfire activity (2019 - 2021); 2)  
139 reviewing the current understanding of the mechanisms by which smoke affects physical,  
140 chemical, and biological aspects of lakes; 3) developing a conceptual framework that  
141 synthesizes known and theoretical impacts of smoke on lakes; and 4) identifying research  
142 priorities for future studies.

143

144 **1.2 | *Spatial and temporal exposure of North American lakes to wildfire smoke***

145 A critical first step in understanding how lakes respond to smoke is characterizing the  
146 spatiotemporal dynamics of their exposure. Here we quantify the spatial and temporal extents of  
147 smoke cover in relation to burned area and lake locations for all lakes  $\geq 10$  hectares in North  
148 America (Farruggia et al., 2024). We used the National Oceanic and Atmospheric  
149 Administration Hazard Mapping System Smoke Product (NOAA HMS; Ruminski et al., 2006)  
150 from 2019-2021 and the HydroLakes and NHDPlus databases of North American lake maps  
151 (Buto & Anderson, 2020; Messenger et al., 2016). Our analysis is constrained to North America  
152 because of the availability of comprehensive continental-scale smoke and lake geospatial  
153 products. For any given lake, a lake smoke-day was defined as a day on which any portion of  
154 the lake boundary intersected with an area characterized as smoke by NOAA HMS, which  
155 categorizes daily smoke density as light (low), medium, or heavy (high) based on the aerosol  
156 optical depth (AOD) from visible satellite imagery (see Supporting Information for details). This  
157 smoke-day concept, here for the first time applied in the context of lakes, has previously been  
158 used to demonstrate smoke exposure by ecoregion, and provides a basis for this lake-specific  
159 metric (Paul et al., 2023). Smoke-days for each lake were subsequently summed on an annual  
160 basis. To visualize lake exposure to smoke at the continental scale, we divided North America  
161 into 5000 km<sup>2</sup> pixels and for each pixel weighted the number of smoke-days by the  
162 corresponding total lake area for that pixel (Fig. 1 b-d; see Supporting Information for details). It  
163 is important to note that while the NOAA HMS product AOD measurements have been validated  
164 and correlated to measured ground-level fine particulate matter (PM<sub>2.5</sub>) concentrations during  
165 large fires (Preisler et al., 2015), because this is an optical smoke product based on satellite  
166 imagery, smoke mapping can be affected by weather conditions, such as cloud interference.  
167 Furthermore, it does not consider the varying height of smoke in the atmosphere, which can  
168 lead to highly variable relative rates of atmospheric smoke and ash deposition and light  
169 attenuation at the same measured level of smoke density. As a result, our estimates of lake  
170 exposure to smoke may be larger than actual exposure. Nonetheless, the spatial scale of this

171 dataset facilitates characterization of wildfire impacts on lakes at the continental scale, and the  
172 lake smoke-day metric provides an index by which we can evaluate the impacts of smoke on  
173 lakes.

174 Wildfires burn in spatially discrete areas, but smoke can be transported vast distances and  
175 dispersed heterogeneously. For example, smoke from fires burning in Quebec and Nova Scotia  
176 in 2023 was transported throughout the Northeast to mid-Atlantic areas of the United States and  
177 across the Atlantic Ocean to Western Europe (Copernicus AMS, 2023; NOAA NESDIS, 2023).  
178 Given the continental to intercontinental scale of smoke transport, lakes in regions that rarely or  
179 never experience wildfire directly may be exposed to smoke for substantial periods of time (Fig.  
180 1, 2). Smoke cover in North America was temporally variable, but seasonally widespread and  
181 persistent across the three years we analyzed (Fig. 1, 3). Aggregated on an annual basis,  
182 99.3% of the surface area of North America was covered by smoke between the years 2019  
183 and 2021 (Supporting Information Table 1). During that same period, less than 0.04% of the  
184 surface area of North America burned directly each year. The mean number of lakes per day in  
185 North America exposed to smoke across our three study years ranged from 1,325,069 -  
186 1,332,077, representing a staggering 98.9 - 99.4% of the estimated total number of lakes  $\geq 10$   
187 hectares on the continent (Supporting Information Table 1). The mean number of smoke-days  
188 lakes experienced annually during our study period was 38.7, 22.8, and 62.7 days (2019, 2020,  
189 and 2021, respectively). The maximum number of smoke-days ranged up to 143 days.

190 There are several interacting factors that may determine the extent to which lakes are exposed  
191 to smoke. The spatial extent, density, and duration of smoke cover establish a template for  
192 potential exposure. However, weather conditions affecting the smoke plume and the spatial  
193 distribution of lakes within the plume area ultimately determine how many lakes are exposed.  
194 For example, the distribution of mean number of smoke-days by latitude differed considerably  
195 across years (Fig. 2a) and the peak number of smoke-days did not necessarily correspond to

196 regional variation in lake density (Fig. 2b). Although 2019 and 2021 had virtually identical smoke  
197 cover on an aerial basis, differences in duration of smoke cover and geographic distribution of  
198 smoke with latitude meant lake smoke-day exposure was 21% higher in 2021.

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

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

217 Our analysis demonstrates three key findings: 1) the spatial extent of smoke is widespread and  
218 capable of crossing continents; 2) the number of lakes affected by smoke in any given year is  
219 variable, but can represent a large majority of all lakes; importantly, in aggregate this can



220 constitute tens of millions of lake smoke-days; and 3) the timing of lake exposure to smoke  
221 peaks from July-September, which typically coincides with peak lake productivity in North  
222 America, and can extend into October.

223

## 224 **2 | Mechanisms by which smoke affects lakes**

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

232

### 233 **2.1 | *Transport of smoke and ash to lake ecosystems***

234 Smoke and ash can be transported thousands of kilometers in the atmosphere and deposited  
235 onto lakes far from the source of wildfire. Definitions of smoke and ash vary widely across  
236 disciplines, especially as they relate to particle size classes (e.g., Bodí et al., 2014; T. P. Jones  
237 et al., 1997). Generally, smoke is composed of smaller particles and ash the larger size  
238 fractions of residual unburned material, but there is no standard size cutoff to distinguish  
239 between smoke and ash. As a result, we hereafter use the broad term “smoke and ash” or  
240 “particles” when specifically discussing particle transport or deposition from either smoke or ash,  
241 recognizing that this material exists along a continuum of sizes and that the size distribution of  
242 the material is an important defining characteristic.

243 The distances smoke and ash particles can be transported vary with particle size and density,  
244 wind speed and direction, and ejection height (Adachi et al., 2022). The latter will vary with fire

245 intensity and associated updrafts. Strong convection currents associated with intense wildfires  
246 can lead to emissions of large particulates high into the atmospheric column, allowing for  
247 regional transport (Fromm et al., 2010; Lareau & Clements, 2016).

248 Satellite imagery can provide key information on the spatial and temporal extent of smoke  
249 plumes (e.g., NOAA's HMS Smoke Product), but our understanding of the potential for wildfires  
250 to produce particles across all size classes and the distances they may travel is hampered by  
251 limitations in atmospheric monitoring networks. In the United States, for example, all  
252 government aerosol monitoring programs focus primarily on particles  $<10\mu\text{m}$  in size ( $\text{PM}_{10}$ ) or  
253  $<2.5\mu\text{m}$  ( $\text{PM}_{2.5}$ ), but particles from wildfire can also include substantially larger sizes—whole  
254 pinecones have been known to travel up to 20 km through the strong updrafts created during  
255 wildfire events (Pisaric, 2002). Most atmospheric models are designed to simulate emission and  
256 transport of smaller particles and are challenged with larger particle sizes, lower densities, and  
257 irregular shapes of fire charcoal and ash (Fanourgakis et al., 2019). As a result, while we can  
258 quantify the distance and aerial extent of wildfire smoke cover from current monitoring systems,  
259 there are still considerable gaps in our knowledge of the amount and particle size of smoke and  
260 ash deposition into lake ecosystems. Monitoring and modeling of particles of a wider size range  
261 are critical to understanding the effects of wildfire smoke on lakes.

## 262 **2.2 | *The effects of smoke on light transmission to lake ecosystems***

263 Wildfire smoke influences the magnitude and spectral composition of incident solar radiation  
264 that can reach the surface of a lake, altering it before it enters and is transmitted through the  
265 water column. The effect of smoke on radiative inputs varies based on smoke density, particle  
266 composition, and particle sizes. These attributes cause either attenuation or scattering of light  
267 (Hobbs et al., 1997). The holistic impacts on light are characterized through the AOD, an index  
268 for light extinction within the atmosphere (McCarthy et al., 2019; Suo-Anttila et al., 2005).

269 Importantly, smoke attenuates electromagnetic radiation unequally, reducing light in a selective  
270 manner that decreases the ratio between ultraviolet B radiation (UV-B) and PAR (Scordo et al.,  
271 2021, 2022; Williamson et al., 2016). Unsurprisingly, the effects of smoke on PAR are large and  
272 variable. Dense smoke, as often occurs in closer proximity to a wildfire, can reduce surface  
273 irradiance by up to 50% or more ( $475 \text{ W m}^{-2}$ ) (McKendry et al., 2019), whereas reductions from  
274 more diffuse smoke, such as smoke that has traveled over continental scales, may not be as  
275 extreme. For example, modeled data from a wildfire in western Russia suggested insolation was  
276 reduced by  $80\text{-}150 \text{ W m}^{-2}$  (8-15%) across Eastern Europe (Péré et al., 2015). Somewhat  
277 counterintuitively, low density smoke can increase diffuse radiation, thereby increasing PAR  
278 (McKendry et al., 2019; Rastogi et al., 2022). However, the extent to which such increases in  
279 diffusive light alter water column light dynamics remain untested.

280 Though studies on the effects of smoke on lake heat budgets and physical dynamics remain  
281 limited, findings to date suggest smoke reduces lake heat content. By attenuating radiative  
282 inputs to lakes, smoke reduces rates of warming during the day. However, by reflecting  
283 longwave radiation back into lakes at night, smoke might also act to reduce heat loss. Moreover,  
284 smoke and ash particles within lakes may further alter heat budgets by increasing light  
285 attenuation within the water column. For instance, in Castle Lake (California, USA) following 22  
286 consecutive days of severe smoke cover, cooler epilimnion temperatures compared to previous  
287 years' averages contributed to a 7% decrease in heat content of the water, which remained low  
288 for the rest of the open water season (Scordo et al., 2021). Similarly, wildfire smoke decreased  
289 water temperature in all 12 rivers and streams investigated in one study in the Klamath River  
290 Basin (California, USA) (Davis et al. 2018). In Lake Tahoe (California/Nevada, USA), smoke  
291 cover resulted in a reduction in incident PAR by approximately half, leading to reduced PAR at  
292 depth, though attenuation of PAR due to ash deposition was minimally affected (Goldman et al.,  
293 1990). Changes in insolation as a result of wildfire smoke have important implications for both

294 physical and biological properties of lakes by reducing lake temperatures and altering the  
295 amount of PAR or UV-B received (as discussed in section 2.6).

### 296 **2.3 | Atmospheric deposition rates and delivery of smoke and ash to lake ecosystems**

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

309 In the context of lakes, the catchment area to lake area ratio and catchment hydrology,  
310 topography, and land cover will influence whether smoke and ash particles are remobilized to  
311 lake basins. The precipitation regime and timing of the fire may dictate when this occurs. Similar  
312 to the heterogeneity in deposition in terrestrial ecosystems, deposition measured around Lake  
313 Tahoe (California/Nevada, USA) during a period of wildfire smoke was highly heterogeneous in  
314 both space and time (Chandra et al., 2022). Though we are unaware of any studies explicitly  
315 examining the role of catchment properties on particle mobilization to lake ecosystems, Brahney  
316 et al. (2014) found that particulate deposition was more readily mobilized to lake ecosystems in  
317 steep, poorly vegetated catchments where up to 30% of the catchment-deposited material made

318 its way to the lake basin. Precipitation and subsequent runoff can redistribute smoke and ash  
319 particles to lake ecosystems, which may occur many months post-deposition, particularly if  
320 deposition occurs on or beneath snow (McCullough et al., 2023). Further studies on smoke and  
321 ash deposition rates and redistribution are needed to understand the time scales for in-lake  
322 smoke and ash delivery and the associated physical, chemical, and biological responses.

#### 323 **2.4 | *Physical settling and transformation of smoke and ash particles in lakes***

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

334 Transformation of particles within the lake through processes such as aggregation, breakup,  
335 remineralization, and zooplankton grazing can modify suspended particulate matter  
336 sequestration rates by several orders of magnitude (Burd & Jackson, 2009). In lakes,  
337 phytoplankton produce transparent exopolymer particles, which promote particle aggregation in  
338 water (Passow, 2002). Direct observations showed rapid (days to weeks) particle sequestration  
339 in Lake Tahoe (California/Nevada, USA) following ash deposition events in the small size  
340 classes (<10  $\mu\text{m}$ ) within regions of high phytoplankton concentrations (Chandra et al., 2022),  
341 which point towards the importance of transformation processes such as particle aggregation

342 and zooplankton grazing on controlling particulate residence times in lake ecosystems (e.g.,  
343 Burd & Jackson, 2009; Jackson & Lochmann, 1992; Jokulsdottir & Archer, 2016). Hydrodynamic  
344 processes such as advective and turbulent particle fluxes and double diffusive instabilities, or  
345 particle-particle interactions such as hindered settling all also have the potential to significantly  
346 modify the residence times of particles (Richardson & Zaki, 1954; Scheu et al., 2015).  
347 Characterizing the influence of these processes is essential to understanding the fate and long-  
348 term impacts of fine suspended particulate matter deposited in lakes by wildfires. While there is  
349 limited literature characterizing this process for smoke and ash particles, a growing body of  
350 evidence points towards the significance of the aggregation process mediating suspended  
351 particulate matter concentrations in lakes (Logan et al. 1995; Hodder and Gilbert 2007; de  
352 Vicente et al. 2009; de Lucas Pardo et al. 2015).

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

## 364 **2.5 | Smoke and ash composition and effects on lake chemistry**

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

379 Fire intensity and landscape properties not only influence the chemical and mineral composition  
380 of smoke and ash, they also influence the bioavailability of the nutrients bound within.  
381 Phosphorus (P), a key limiting nutrient in many lake ecosystems, occurs in much higher  
382 concentrations in smoke and ash compared to unburned vegetation. In some cases, smoke and  
383 ash can contain 50-times the P concentration of unburned vegetation (Raison et al., 1985);  
384 Zhang et al. (2002) found P concentrations within a smoke plume to be ~10 times greater than  
385 found over the Tahoe basin. Wildfire also alters the composition of finer particulate matter such  
386 as PM<sub>2.5</sub> – for example, fire episodically elevated atmospheric concentrations of P by >10,000%  
387 (Olson et al., 2023), and in a global meta-analysis, fire was primarily responsible for a 40%  
388 increase in atmospheric P deposition to lakes as compared to pre-industrial deposition rates  
389 (Brahney et al., 2015). Phosphorous deposition rates near burned areas have been measured

390 as high as 200-700 mg m<sup>2</sup>yr<sup>-1</sup> (Ponette-González et al., 2016; Tamatamah et al., 2005), and  
391 are thought to contribute to the eutrophication of lake ecosystems in the area (Brahney et al.,  
392 2015; Tamatamah et al., 2005). Deposition rates can be higher from distant fires burning hotter  
393 and emitting smaller particles than cooler fires burning locally (Vicars et al., 2010). Though  
394 nitrogen (N) and C are more readily volatilized than P, significant concentrations of these  
395 nutrients can still be transported by smoke and ash and affect lake nutrient concentrations.  
396 Increased concentrations of N, P, potassium, calcium and water-soluble organic C in  
397 freshwaters have been attributed to wet deposition from biomass burning in surrounding  
398 catchments (Bakayoko et al., 2021; Langenberg et al., 2003; Zhang et al., 2002). Boy et al.  
399 (2008) compared the composition of atmospheric deposition in Ecuador during times of burning  
400 and no burning and found elevated deposition rates of total N by 171%, nitrate by 411%,  
401 ammonium by 52%, and total P by 195%. One observational study showed that lakes near  
402 regions of heavy biomass burning have elevated P concentrations and tend towards N limitation  
403 (Brahney et al., 2015). Overall, smoke and ash deposition has the potential to influence the  
404 relative availability of key lake nutrients (Vicars et al., 2010), which can alter the biotic structure  
405 of lake ecosystems (Elser et al., 2009). Still, deposition-driven changes in and lake responses to  
406 these nutrients (such as N or P limitation) likely vary by factors such as distance from wildfire  
407 and lake trophic status, and should be further investigated along a variety of gradients.

408 Smoke and ash can also concentrate and transport polycyclic aromatic hydrocarbons (PAHs),  
409 hazardous air pollutants (HAPs), and toxic metals such as arsenic (As), chromium, copper,  
410 cadmium, mercury (Hg), nickel, lead, antimony, and zinc to lake systems. Concentrations vary  
411 by fire intensity as metals and organic compounds are volatilized (Bodí et al., 2014), and many  
412 metals can re-adsorb to ash in the atmosphere (Cerrato et al., 2016). Hg is volatilized at  
413 relatively low temperatures with a substantive component becoming recalcitrant (0-75%) (Ku et  
414 al., 2018), and can result in high soil Hg concentrations that can eventually be transported to



415 aquatic ecosystems (Webster et al., 2016). Experimentally, toxic methylmercury can leach from  
416 wildfire smoke and ash once deposited to anoxic sediments (Li et al., 2022). Empirically, lake  
417 sediment Hg fluxes have been found to nearly double during periods of high fire occurrence  
418 (Pompeani et al., 2018). Other metals, such as As, are volatilized at higher temperatures and  
419 can be concentrated in particles from low- to medium-intensity fires (Wan et al., 2021). The type  
420 of vegetation or material burned can also change the concentration of particle constituents. For  
421 example, particles from burned *Eucalyptus* leaches higher concentrations of As, cadmium,  
422 cobalt, chromium, lead, and vanadium, whereas particles from burned *Pinus* leaches higher  
423 concentrations of copper, manganese, nickel, and zinc (Santos et al., 2023). High  
424 concentrations of heavy metals have been reported in ash residues from residential and  
425 structural burns (Nunes et al., 2017; Pereira et al., 2014; Plumlee et al., 2007; Wan et al., 2021),  
426 and high concentrations of toxic metals such as copper and lead can be found in PM<sub>2.5</sub>  
427 hundreds of kilometers from the burned area (Boaggio et al., 2022). Concentrations of PAHs  
428 can also increase in lake sediments following fire, with low molecular weight PAHs increasing  
429 on average more than four-fold (Denis et al., 2012), though in one case remained well beneath  
430 lethal concentrations reported for benthic freshwater species (Jesus et al., 2022). In addition,  
431 smoke days can have elevated concentrations of HAPs (Rice et al., 2023), some of which may  
432 have deleterious effects on aquatic biodiversity (Finizio et al., 1998). Whether heavy metal,  
433 PAH, or HAP concentrations in smoke and ash or rates of loading to lake systems occur at  
434 concentrations and rates that would affect aquatic organisms has not to our knowledge been  
435 determined.

436 Given its variable composition, smoke and ash can have variable effects on lake ecosystem  
437 function. Some studies have found only small or transient chemical effects from fire-derived  
438 deposition. Earl and Blinn (2003) found most lake chemical variables were only influenced by  
439 smoke and ash for 24 hours. Furthermore, Scordo et al. (2021) found no changes in N and P

440 limitation for algal growth at Castle Lake (California, USA) after the lake was covered by wildfire  
441 smoke for 55 consecutive days. In some cases, transient or limited observational effects may  
442 occur because smoke and ash deposition rates may not be sufficient to induce a strong  
443 ecological response. In other cases, responses may be limited because nutrients are rapidly  
444 taken up by primary producers. A bioassay experiment in Lake Tahoe (California/Nevada, USA)  
445 using wildfire particles with a high N:P ratio led to increased growth of picoplankton and  
446 cyanobacteria (Mackey et al., 2013). Picoplankton growth may not increase chlorophyll-a or  
447 biomass substantively; thus, the ecosystem response may be hard to detect using conventional  
448 methods (Mackey et al., 2013). Paleolimnological studies have shown a range of responses  
449 from minimal shifts in sedimentary P and production proxies to a near doubling of sedimentary P  
450 and substantive increases in production (e.g., Charette & Prepas, 2003; Paterson et al., 2002;  
451 Prairie, 1999). There is little information on the fate of smoke and ash once deposited into lake  
452 ecosystems (but see section 2.4). Whether smoke and ash deposition is rapidly oxidized or  
453 sedimented will influence the short- and long-term effects in lakes.

454 There remain several key unknown effects of wildfire smoke and ash deposition on lake  
455 ecosystems. First, the literature on the limnological responses to wildfire deposition is heavily  
456 skewed towards paleolimnology for field level studies, with few pre- and post-wildfire  
457 observational studies, especially from outside of burned catchments. Second, the post-wildfire  
458 persistence of direct deposition effects, particle redistribution, or catchment flushing over time  
459 are unknown. Third, particle debris in wet deposition is highly oxidizable and therefore could be  
460 effective at reducing oxygen concentrations either through photooxidation or microbial  
461 respiration. As a result, smoke and ash deposition could decrease dissolved oxygen  
462 concentrations while increasing pH, which together can be deleterious to cold-water aquatic  
463 organisms (Brito et al., 2021; Earl & Blinn, 2003), and should be further investigated. Finally,  
464 smoke and ash have the potential to increase *in-situ* metal concentrations beyond toxicity

465 thresholds (Burton et al., 2016) but little information exists on what other deleterious compounds  
466 may leach from wildfire smoke and ash, particularly if residential and commercial areas are  
467 burned.

## 468 **2.6 | *Effects of smoke and ash on ecosystem metabolic rates***

469 Wildfire smoke can impact the metabolic rates of lakes through several mechanisms linked to  
470 changes in physical and chemical conditions. The extent to which reductions in PAR and UV  
471 and their relative ratio may either stimulate (Tang et al., 2021) or inhibit (Staeher & Sand-Jensen,  
472 2007) pelagic primary productivity depends on the extent to which the autotrophic community is  
473 light or nutrient limited or experiences photoinhibition for some portion of the day, all of which  
474 may vary with time or depth in lakes. Consequently, responses of primary productivity to smoke  
475 will likely depend on smoke density and particle size distributions as well as the timing of  
476 exposure. Low to medium smoke density may increase primary production and light-use  
477 efficiency through selective filtering of UV, increased diffuse scattering of PAR, and an overall  
478 alleviation of photoinhibition (Hemes et al., 2020; McKendry et al., 2019). In contrast, higher  
479 density smoke may reduce primary production by attenuating PAR to a large degree (Davies &  
480 Unam, 1999; Scordo et al., 2021).

481 Likewise, the extent to which nutrient additions through smoke and ash deposition stimulate  
482 photosynthesis and respiration depends on nutrient and DOM concentrations within the  
483 receiving system and relative ratios between autotrophic and microbial heterotrophic biomass,  
484 which can vary seasonally both across and within lakes. Moreover, processes driving metabolic  
485 responses might be temporally decoupled. For example, one study examined 15 years of fire-  
486 related atmospheric particle nutrient concentrations and found cyanobacteria increased in  
487 smoke covered lakes 2-7 days after smoke exposure (Olson et al., 2023), suggesting deposited  
488 nutrients may have an impact once light regimes are no longer influenced by smoke. Such

489 spatiotemporal variability complicates decoupling effects from altered light regimes versus  
490 nutrient additions from smoke and ash, making it difficult to predict how individual lakes will  
491 respond outside of specific spatial and temporal contexts. However, individual case studies and  
492 one regional analysis provide a template for understanding the mechanisms involved.

493 Although a comparatively small number of studies have measured the impact of wildfire smoke  
494 on rates of production, the patterns observed suggest changes consistent with expectations  
495 based on light and nutrient availability. The response of primary production to smoke from  
496 wildfires shows a strong depth dependence in clear water lakes. For example, surface  
497 productivity in ultra-oligotrophic Lake Tahoe (California/Nevada, USA) is typically low, with a  
498 productivity maximum developing deeper than 60m. Heavy smoke from a wildfire outside the  
499 catchment caused productivity at depth to decline to near zero, and productivity within the  
500 surface layer to triple from 10-31 mg C m<sup>-3</sup>d<sup>-1</sup>. The net effect was a record-level increase in  
501 integrated water column productivity (Goldman et al., 1990). The authors theorized that the  
502 reduction in photoinhibition alone was insufficient to cause a 3-fold increase in production and  
503 hypothesized that smoke and ash deposition contributed N, P, and/or micronutrients that  
504 stimulated production. In Castle Lake (California, USA), fires burning outside the catchment  
505 resulted in smoke cover that lasted for 55 days (Scordo et al., 2021, 2022). During this period,  
506 both incident and underwater UV-B, PAR, and heat were reduced concomitant with a 109%  
507 increase in epipelagic production. Similar to Lake Tahoe, productivity in Castle Lake shifted  
508 upwards in the water column in the pelagic zone. In contrast, littoral-benthic productivity did not  
509 change in Castle Lake, possibly reflecting adaptation to high-intensity UV-B light in these  
510 habitats (Scordo et al., 2022). In a regional study of smoke effects on 10 lakes spanning  
511 gradients in trophic state, water clarity, and size, lake responses were variable (Smits et al.,  
512 2024). While rates of GPP were reduced overall on smoky days, the magnitude and direction of  
513 response varied greatly among individual lakes, suggesting changes in productivity were

514 mediated by factors such as the seasonal timing of exposure and nutrient stoichiometry within  
515 lakes at the time of exposure.

516 The effect of smoke on rates of ecosystem respiration are rarely reported. One of the few  
517 studies to explicitly evaluate impacts of smoke on respiration found little effect in a mesotrophic  
518 lake (Scordo et al., 2021), in contrast to the comparatively large increases in respiration that can  
519 be found in lakes within burned watersheds (Marchand et al., 2009). Given the coupling of  
520 production and respiration, it is likely that changes in respiration associated with smoke alone  
521 will mirror those of production. However, smoke and ash deposition may affect respiration  
522 independently of production by stimulating microbial metabolism through the addition of  
523 nutrients and/or C. Phosphorus is often in high demand among microbial communities, and ash  
524 with high concentrations of biogenically available P may stimulate increases in microbial  
525 metabolic activity (Pace & Prairie, 2005). Likewise, lakes where microbial communities are  
526 substrate-limited by C are likely to see increased metabolic activity associated with pyrogenic C  
527 leachate into dissolved organic C (Py-DOC). Py-DOC is highly labile and water soluble (Myers-  
528 Pigg et al., 2015), making it highly available to microbes, which can drive increases in  
529 respiration. The extent to which C and N from ash cause an increase or decrease in respiration  
530 will be dependent on the degree of coupling between autotrophic and heterotrophic  
531 metabolisms and the extent to which microbial growth efficiency increases or decreases. Smits  
532 et al. (2024) found the response of respiration to smoke cover in their 10 study lakes to vary as  
533 a function of temperature and lake trophic state – respiration rates decreased during smoke  
534 cover in cold, oligotrophic lakes but not in warm, eutrophic lakes. The effect of smoke and ash  
535 deposition on lake metabolism more broadly is still poorly understood and may theoretically  
536 increase or decrease production to respiration ratios depending on the characteristics of the  
537 smoke, ash composition, and initial conditions of the lake. At regional scales, lake responses  
538 may be highly variable and difficult to predict without context-specific understanding of lakes

539 (Smits et al. 2024). This highlights that future studies need to examine impacts on metabolism in  
540 the context of the timing of lake exposure with respect to seasonal nutrient and  
541 phytoplankton/bacterioplankton community dynamics.

## 542 **2.7 | Effects of smoke and ash on lake food webs**

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

557 Smoke and ash concentrations in lakes may have toxicological influences on the survival of  
558 aquatic and amphibian species, which can be highly susceptible to wildfire-derived heavy  
559 metals and PAHs, though effects vary among species and sources of particles (Brito et al.,  
560 2017; Campos et al., 2012; Harper et al., 2019; Santos et al., 2023; Silva et al., 2015). For  
561 instance, ecotoxicity assays indicate that ash is toxic to *Ceriodaphnia spp.* at low concentrations  
562 but has no detectable effect on gastropods or fish (Brito et al., 2017). Smoke and ash can also

563 contain large concentrations of inorganic Hg, which can be converted into methylmercury, a  
564 highly toxic and bioavailable form that accumulates in fish (Kelly et al., 2006). The source of the  
565 smoke and ash can differentially impact pH, metal, and ion concentrations with differing  
566 toxicities to specific organisms. Harper et al. (2019) found that *Daphnia magna* was sensitive to  
567 particles derived from some plants such as spruce (*Picea*) or eucalypt (*Eucalyptae*), whereas  
568 other plants, such as ash (*Fraxinus*) had no observable toxicity. However, the authors note that  
569 this may be related to mechanical challenges filter feeders face with high particle loads rather  
570 than toxicity. Observational and experimental studies of macroinvertebrate communities have  
571 shown a range of responses to smoke and ash from almost no response to statistically  
572 significant reductions in density and shifts in community composition for one year following the  
573 introduction of ash (Earl & Blinn, 2003). However, it is unknown whether these shifts in  
574 macroinvertebrate communities were the result of toxicity, as non-toxic but ash-driven  
575 deleterious conditions, such as reduced dissolved oxygen and increasing pH conditions can  
576 also negatively affect cold-water aquatic organisms (Brito et al., 2021; Earl & Blinn, 2003).  
577 Whether the effects on secondary production are due to particle loads, metals, ions, pH, or  
578 reductions in oxygen remain poorly understood. The indirect effect of smoke and ash on lake  
579 food webs may mirror that of primary production if biomass is controlled from the bottom-up by  
580 nutrients or may decrease through toxicity. Research is needed to identify the relative  
581 contribution of indirect and direct effects of smoke and ash to secondary lake productivity, as  
582 well as the time scales over which smoke effects occur.

583 As smoke can alter light conditions and decrease lake temperature, smoke may also influence  
584 consumer behavior as light and temperature serve as important cues. Changes in behavior can  
585 shift, for example, distributions of animal biomass, predator-prey interactions, and water column  
586 biogeochemistry. Smoke-induced reduction of UV:PAR ratios can alter the diel vertical migration  
587 of zooplankton and affect habitat use by fish (Scordo et al., 2021, 2022; Williamson et al., 2016).

588 In highly transparent lakes, UV light is an important dynamic cue for vertical migration behavior,  
589 whereby zooplankton occupy deeper depths during the day to avoid damaging UV radiation  
590 (Williamson et al., 2011). When smoke reduces incident UV, zooplankton may alter their  
591 migration behavior by shifting their daytime vertical distribution closer to the surface. For  
592 example, zooplankton exhibited a 4m upward shift over a 2-day period in Lake Tahoe  
593 (California/Nevada, USA) when smoke reduced incident UV radiation by 8% (Urmy et al., 2016).  
594 In contrast, zooplankton in Castle Lake (California, USA) did not change their vertical migration  
595 patterns in response to the 65% reduction in UV during a smoke period. During the smoke  
596 period, the dominant fishes (brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus*  
597 *mykiss*)) migrated out of their usual near-shore habitat to the pelagic zone (Scordo et al., 2021).  
598 Consequently, there may have been no changes in the vertical migration patterns of  
599 zooplankton because of the opposing effects of reduced UV and increased predator presence in  
600 the epilimnion. Due to the limited available studies, it is difficult to generalize how smoke and  
601 ash deposition affect consumer behavior or production.

### 602 **3 | The effect of smoke on lakes: a conceptual framework**

603 The effects of smoke and ash on lakes are the outcome of mechanisms that operate across  
604 multiple spatial and temporal scales (Scordo et al., 2022). Because smoke density can change  
605 rapidly with distance from wildfires, the proximity of a lake to wildfire may modulate the  
606 magnitude of the teleconnection effect of smoke on lakes (Fig. 4a). Generally, lakes face the  
607 highest density of smoke, largest particle size, and rates of deposition nearest to wildfire (Fig.  
608 4b), which can dramatically decrease the relative availability of UV and PAR. The temporal  
609 dynamics of smoke can be highly variable at very short time scales, causing large swings in  
610 radiative inputs to lakes. Resulting shifts in UV and/or PAR from reflection or scattering by  
611 smoke can cause cascading effects on lake physical, chemical, and biological variables (Fig.  
612 4c). Lakes at intermediate (*i.e.*, tens to hundreds of kilometers) or large (*i.e.*, continental to



613 intercontinental) distances from wildfires may still experience significant effects from smoke and  
614 ash deposition, but the relative importance of each and the associated shifts in UV and PAR  
615 may vary considerably. At intermediate to larger scales, smoke density and ash deposition can  
616 be patchy in space and time. Smoke transported at large scales may be more spatially  
617 homogeneous with less dense smoke and lower deposition (smaller particle sizes and lower  
618 density) over large areas (Fig. 4a).

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

627 Smoke and ash deposition can ultimately change ecosystem metabolic rates through two main  
628 pathways (Fig. 4c). These pathways include a fertilization effect through nutrient deposition  
629 (section 2.4) and reducing availability of PAR and UV light throughout the water column (section  
630 2.2), with each pathway mediated by trophic status and lake size (Fig. 4d). If deposition causes  
631 a shift in nutrient limitation, it is likely to have a positive impact on net ecosystem production  
632 (NEP) by stimulating primary production more than respiration. Variations in lake morphometry  
633 and watershed size or hydrology are likely to mediate the metabolic response of lakes to smoke  
634 and ash deposition by regulating deposition rates, transport and transformation of particles  
635 within the water column, and residence times. Consequently, the effects of particle deposition  
636 on ecosystem function might span large time scales.

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

655

#### 656 **4 | Conclusions: knowledge gaps and research priorities**

657 Despite evidence that smoke and ash deposition impact biological, physical, and chemical  
658 processes in lakes, large knowledge gaps impede our ability to predict and manage the  
659 responses of lakes to smoke and ash. Measuring the extent and effects of smoke and ash  
660 deposition remain challenging. We propose several potential research priorities, practical  
661 methodologies, and collaboration avenues here. While current atmospheric monitoring networks

662 are a critical source of data on particle phase pollutants including wildfire-derived particles, they  
663 do not comprehensively sample and characterize smoke and ash particles at larger size  
664 fractions. For example, in the United States, state and federal air quality regulations primarily  
665 monitor PM<sub>10</sub> and PM<sub>2.5</sub> size classes that exclude most ash material on a per-mass basis  
666 (Pisaric, 2002). Satellite remote sensing of AOD can help improve measurement of atmospheric  
667 particle loading (Sokolik et al., 2019), but cannot estimate particle concentrations or distinguish  
668 between particle size classes. Pairing remotely-sensed measurements of smoke plumes and  
669 airborne fire particles with satellite remote sensing of water quality offers opportunities to  
670 analyze the ecological responses of lakes to smoke with high frequency over the long-term. A  
671 more detailed characterization and quantification of the attributes of smoke and ash (e.g.,  
672 beyond coarse density measurements, or presence/absence) is crucial to these efforts. Key  
673 questions include: How does the composition, size, and density of particles vary with distance  
674 from wildfire? How do deposition rates on lakes vary in relation to local landscape and weather  
675 factors?

676

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

685

686 In general, field and experimental studies that collect pre- and post-fire data in lakes are scarce  
687 and forced on smaller lakes (McCullough et al., 2019). Larger scale studies are necessary to

688 disentangle the mediating effects of scale and watershed context on the responses of lakes to  
689 smoke and ash deposition (Fig. 4). Studies that address this should encompass key gradients  
690 (Section 3) such as lake size or clarity, and are necessary to better understand how smoke  
691 affects a broad range of lake types. Key questions include: How does lake trophic status or size  
692 mediate responses at regional or larger scales? What is the seasonal variation in lake  
693 responses to smoke within and across lakes?

694

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

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

710 As wildfires, fueled by global change (Abatzoglou et al., 2019), increase in frequency and  
711 intensity (Flannigan et al., 2013; M. W. Jones et al., 2022), there is a need to understand their  
712 environmental impacts beyond the direct effects of biomass combustion at the watershed scale.

713 Our analysis of lake smoke-days indicates that many regions that historically have not been  
714 considered at high risk of wildfires are already experiencing smoke events (Fig. 1, Fig. 2) and  
715 these have the potential to become increasingly pervasive and long-lasting (Fig. 3). Here we  
716 have reviewed how these smoke events and corresponding deposition can have far-reaching  
717 environmental consequences for lakes across spatial and temporal scales. We have also  
718 synthesized how these environmental consequences are modified by the characteristics of  
719 lakes and the characteristics of both smoke and ash themselves. Because lakes reflect  
720 processes within their surrounding catchments and the flowing waters that feed into them, they  
721 can also act as sentinels of wider landscape-level changes associated with smoke and ash  
722 deposition, such as nutrient and energy cycling (Williamson et al., 2008). Drawing upon  
723 research from diverse disciplines beyond limnology, including fire ecology, climatology, and  
724 atmospheric chemistry will be key to advancing our understanding of the environmental impacts  
725 of wildfire smoke in an increasingly flammable world.

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730

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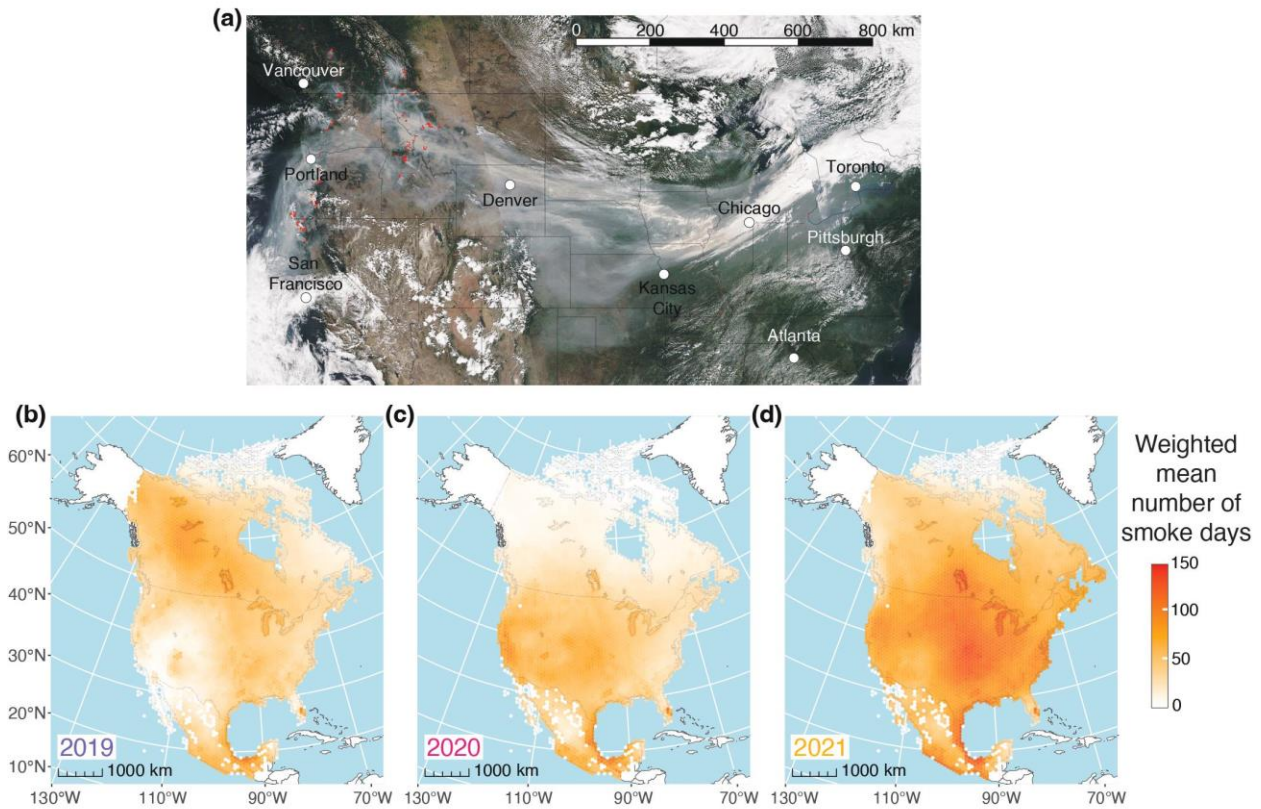
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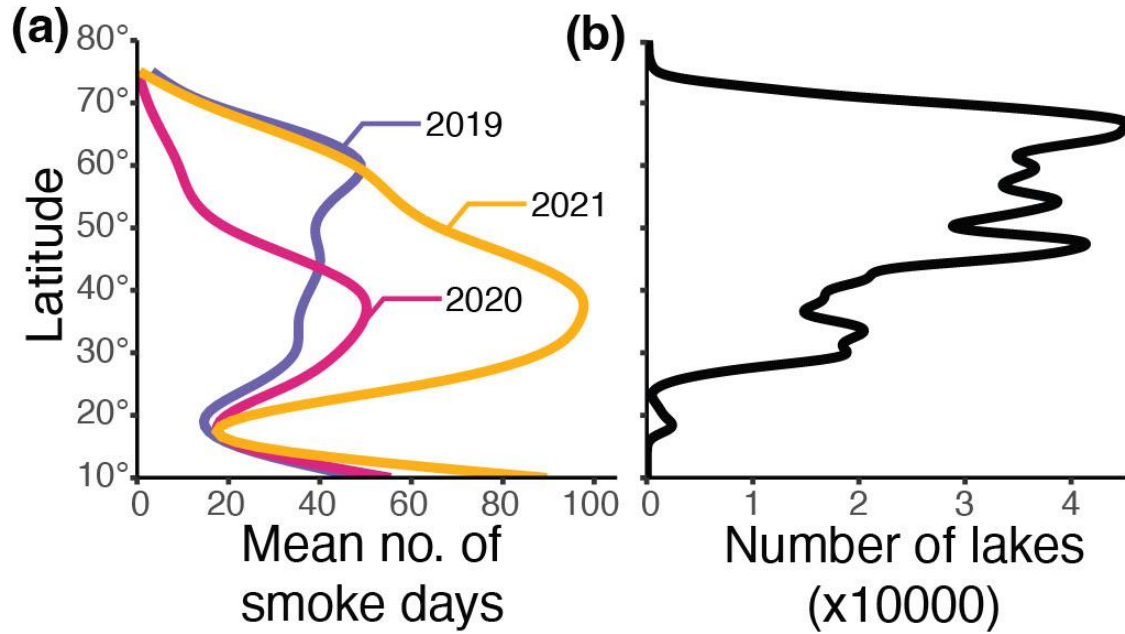
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1193 **Figure 1.** (a) Continental-scale smoke transport across North America, moving wildfire smoke  
 1194 from fires in the West thousands of kilometers to the East. Actively burning wildfires are outlined  
 1195 in red. Image: NASA - Jeff Schmaltz LANCE/EOSDIS MODIS Rapid Response Team, GSFC.  
 1196 Sept. 4 2017. (b-d) Map of weighted mean number of smoke-days per 5000 km<sup>2</sup> hexagon for (b)  
 1197 2019, (c) 2020, and (d) 2021. Values are weighted by the area of each lake within each 5000  
 1198 km<sup>2</sup> hexagon. Projected in Albers Equal Area (EPSG: 102008). Map lines delineate study areas  
 1199 and do not necessarily depict accepted national boundaries.

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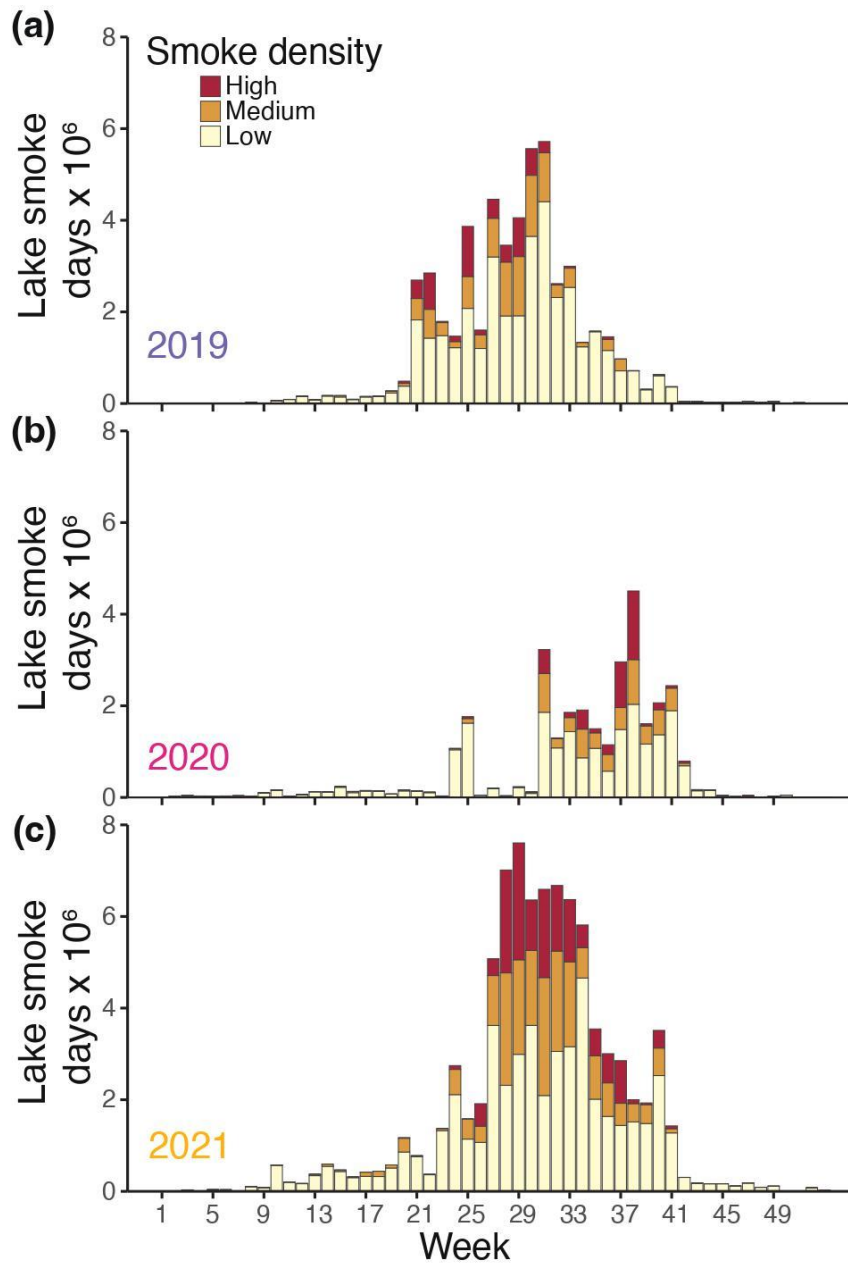
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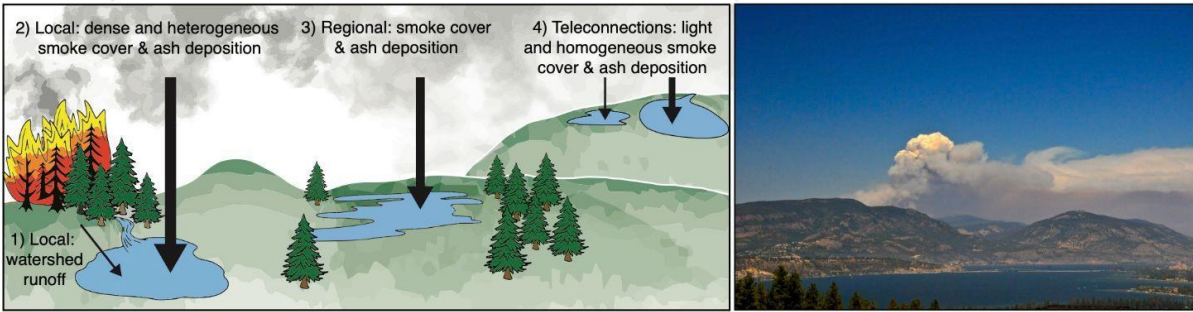
**Figure 2.** Summary of North American smoke-days (a) and lake count (b) with latitude. Latitude values are in degrees according to EPSG:4326. Lines in (a) are based on a generalized additive model with a  $k$  of 10.



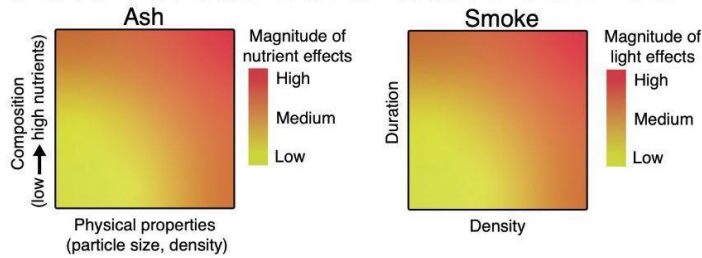
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1211 **Figure 3.** Number of cumulative lake smoke-days for each week in North America. For  
 1212 example, in Week 31 of 2019, the 1.3 million lakes experienced nearly 6 million cumulative  
 1213 smoke-days of exposure, with many of the lakes experiencing multiple days of exposure in this  
 1214 week. Exposure is categorized by smoke density (NOAA HMS).

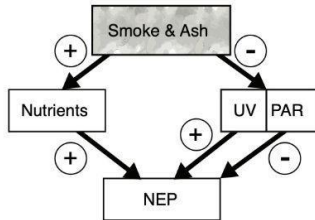
**(a) Multi-scale exposure of lakes to ash and smoke**



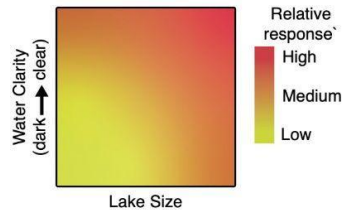
**(b) Ash and smoke characteristics that mediate their effect on lakes**



**(c) Example of smoke and ash effects on lakes**



**(d) Lake characteristics mediating biotic responses**



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**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 gross 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>