**Title**

# Variable impact of wildfire smoke on ecosystem metabolic rates in lakes

**Running Head**

Smoke affects lake metabolism

**Authors**

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## Abstract

Increasingly severe wildfires release smoke plumes that cover entire continents, depositing aerosols and reducing solar radiation fluxes to millions of freshwater ecosystems, yet little is known about their impacts on inland waters. This large scale study 1) quantified annual and seasonal trends in the spatial extent of dense smoke cover in California, USA, over the last 18 years (2006 - 2022), and 2) assessed the impacts of dense smoke cover on daily gross primary production (GPP) and ecosystem respiration (R) in 10 lakes spanning a large gradient in nutrient concentration and water clarity, during the three smokiest years in our dataset (2018, 2020, 2021). We found that the maximum spatial extent of dense smoke cover between June-October has increased to 70% of California's area since 2006, with the greatest increases in August and September. In the three smokiest years, lakes were exposed to an average of 33 days of dense smoke between July and October, resulting in substantial reductions in shortwave radiation fluxes and 3 to 4-fold increases in atmospheric fine particulate matter concentrations (PM2.5). However, responses of lake GPP to smoke cover were extremely variable among and within lakes, as well as between years. In contrast, the response of rates of ecosystem respiration to smoke was related to lake nutrient concentrations and water temperature –respiration rates decreased during smoke cover in cold, oligotrophic lakes but not in warm, eutrophic lakes. The impacts of dense, prolonged smoke cover on inland waters are likely to be highly variable within and among regions due to mediating effects of lake attributes and seasonal timing of wildfires.

## Key Words

Wildfire, smoke, lakes, ecosystem metabolism, primary productivity, respiration, nutrients, shortwave radiation

## Introduction

Increasingly frequent and severe wildfires associated with climate change release vast quantities of smoke into the atmosphere[1], generating plumes that travel thousands of kilometers[2] and expose millions of water bodies to smoke for weeks to months[3]. Aerosols within smoke plumes absorb or scatter solar radiation[4], reducing total fluxes to terrestrial and aquatic ecosystems and altering the spectral composition of light. Smoke aerosol particles also contain carbon and nutrients such as phosphorus (P) and nitrogen (N), which can fertilize receiving ecosystems[5,6]. Both reduced solar radiation and particle deposition affect physical and biological processes in aquatic ecosystems, for example by reducing water temperature[7] or altering rates of gross primary production (GPP) and ecosystem respiration (R)[8]. Changes in ecosystem metabolic rates can alter critical ecosystem processes such as carbon and nutrient cycling, rates of carbon burial and greenhouse gas emission, and food web structure[9]. Currently, little is known about how ecosystem metabolic rates may respond to wildfire smoke in lakes spanning gradients in size or productivity.

Smoke effects on ecosystem metabolic rates (i.e., GPP or R) have rarely been measured, despite the increased exposure of ecosystems to high-density smoke[3]. To date, studies of smoke impacts on ecosystems focus primarily on the effects of altered radiation fluxes to forest or cropland production[10–12], or on the effects of aerosol deposition on phytoplankton growth in oligotrophic marine systems[6,13,14]. Existing studies of smoke effects on inland waters are limited to single site case studies (e.g., Castle Lake[8,15]; Lake Tahoe[16]) or focus on relatively few response variables (e.g., water temperature[7], cyanobacterial blooms[17]). The influence of smoke cover on freshwater ecosystems at spatial scales greater than single sites is not yet understood but is of growing importance, as wildfires release smoke across whole continents[18]. A lack of regional-scale

studies limits understanding of variability in lake responses or its causes. While the influence of smoke cover on aquatic systems was first described decades ago[16], limnological research has not kept pace as wildfire smoke becomes a global rather than local phenomenon.

While the effects of smoke on ecosystem rates of primary production and respiration have rarely been explored, the roles of light, temperature, and nutrients in regulating ecosystem metabolic rates have a strong theoretical underpinning and long history of empirical study[19,20]. Predicting ecosystem responses to smoke relies on understanding how the relative importance of different drivers varies across ecosystems or through time within individual systems. For example, the same reduction in photosynthetically active radiation (PAR) due to smoke might reduce rates of primary production in a eutrophic lake where phytoplankton are light-limited but increase rates of production in a clear-water lake where phytoplankton are photo-inhibited (Figure 1a). Likewise, the effect of aerosol deposition on ecosystem metabolic rates (i.e., the fertilization effect) depends on the concentration and nutrient stoichiometry of smoke particulates[3], as well as on ambient nutrient concentrations within lakes (Figure 1c). In contrast, reduced water temperature due to smoke cover should decrease ecosystem metabolic rates across all systems, dependent on the temperature coefficient ($Q_{10}$; Figure 1b). The few existing studies of smoke effects on ecosystem metabolic rates illustrate high variability in responses in both terrestrial and aquatic systems. In a forest where smoke cover decreased total PAR fluxes, GPP was reduced at the leaf scale but increased at the canopy scale because smoke increased diffuse PAR and illuminated a greater proportion of the canopy[10]. Likewise, while GPP increased during smoke cover in surface waters within a mesotrophic lake, it declined deeper in the water column where phytoplankton were light-limited[8]. How individual ecosystems respond to smoke will

consequently depend on both how smoke affects fundamental drivers (light, temperature, nutrients) and on system-specific attributes such as water clarity and nutrient concentrations.

Here we present the first regional investigation of the effects of smoke exposure on ecosystem metabolic rates in inland waters. First, we quantified annual and seasonal trends in the spatial extent of medium and high-density smoke cover (hereafter 'med-high density') in California, USA, over 18 years (2006 - 2022) using remote sensing. We then asked the following broad questions: 1) Are responses of ecosystem metabolism to smoke uniform across different types of lakes? 2) Do smoke density, duration, or seasonal timing influence how ecosystems respond? and 3) to what extent are responses in GPP and R to smoke coupled or decoupled?

To address these questions, we quantified changes in daily shortwave radiation (SW), atmospheric fine particulate matter concentrations (PM2.5), water temperature, and ecosystem metabolism during periods of med-high density smoke cover in 9 freshwater lakes and one freshwater tidal slough in California (Figure 2a, Table 1), where wildfire extent has increased five-fold since the 1970s[21]. We measured responses to smoke in 2018, 2020, and 2021, the three worst fire seasons on record in California[22]. We estimated rates of ecosystem metabolism from hourly dissolved oxygen (DO) measurements in both pelagic (open-water) and littoral (near-shore) environments within study sites (total = 22 datasets). Study sites spanned wide ranges in nutrient availability, water clarity, and size, from ultra-oligotrophic (e.g., Lake Tahoe) to hyper-eutrophic (e.g., Clear Lake).

We hypothesized that ecosystem metabolic responses to smoke would vary primarily in relation to water clarity and organic matter and nutrient availability, with GPP and R tending to increase in the surface waters of oligotrophic systems but decrease in meso- or eutrophic-systems. We

expected to see greater changes in metabolism during dense, prolonged smoke cover compared to short, intermittent smoke events. Finally, we expected the magnitude of change in GPP and R to be coupled in oligotrophic systems, where available carbon pools are lower and respiration is primarily fueled by recent autochthonous production[23]. However, we expected GPP and R would be decoupled in more productive systems, where high organic matter (OM) and nutrient concentrations fuel respiration by heterotrophs irrespective of changes in GPP[24].

## Methods

### *Study sites and in-situ data collection*

We collected continuous hourly DO and water temperature data from 10 water bodies distributed across the northern two-thirds of California, USA, from June-October in 2018, 2020, and 2021 (Table 1; Figure 2). Study sites are located in several of the major mountain ranges in California, including the southern Sierra Nevada (5 sites; 'Sequoia lakes'), northern Sierra Nevada (2 sites; Lake Tahoe and Dulzura Lake; 'Tahoe lakes'), Klamath Mountains (1 site; Castle Lake), and northern Coast Range mountains (1 site; Clear Lake), as well as within the Sacramento-San Joaquin River Delta (1 site; Delta). Sites span large gradients in elevation (0 - 3200 m.a.s.l), size (0.2 - 49624 ha), water clarity ($k_d$ 0.09 - 2 $m^{-1}$), and trophic status (ultra-oligotrophic - hypereutrophic; Table 1).

Water bodies were instrumented with continuous in situ DO and temperature sensors at 1-2 locations per site (14 total). In 7 sites (Sequoia lakes, Clear Lake, and Delta), DO and temperature were measured only in pelagic (mid-lake) habitats. In two lakes (Castle, Dulzura), DO and temperature were measured in both pelagic and littoral habitats. In Lake Tahoe, DO and temperature were only measured in two littoral sites. For all lakes, DO and temperature data

were only available for a subset of the three study years (Table 1). In addition to hourly sensor data, for each lake and year we obtained water chemistry data collected from lake surface waters (0- 3 m depth) between June 1 and November 1, for the following constituents: chlorophyll-a concentration (μg $L^{-1}$), total dissolved phosphorus (TDP; μg $L^{-1}$), and total dissolved nitrogen (TDN; μg $L^{-1}$). Water chemistry data were used to classify lake trophic status but were not collected at sufficient temporal resolution to evaluate changes associated with smoke cover.

Meteorological data corresponding to time periods of in-situ sensor data collection were obtained for each lake from the nearest available weather station (SW radiation, W $m^{-2}$; wind speed, m $s^{-1}$; air temperature, °C). We also obtained mean daily atmospheric fine particulate matter concentrations (< 2.5 μm in diameter; PM2.5; μg $m^{-3}$) from the nearest PurpleAir or EPA sensor. No PM2.5 data are available for the Sequoia Lakes in 2020. In total, we compiled 22 hourly DO and water temperature datasets, 9 corresponding hourly meteorological datasets, 8 daily PM2.5 datasets, and 19 water chemistry datasets (detailed site and dataset descriptions can be found in Supplementary Methods).

*Quantifying patterns and trends in California smoke cover*

We used the smoke plume product from the NOAA/NESDIS Satellite Analysis Branch's Hazard Mapping System (HMS)[38], to quantify the spatial and temporal patterns of smoke cover in California from 2006 to 2022. This product provides a daily smoke plume density polygon over North America at a 4 km resolution by integrating near real-time polar-orbiting and geostationary satellite imagery from Geostationary Operational Environmental Satellite Program (GOES), Moderate Resolution Imaging Spectroradiometer (MODIS), and Advanced Very High Resolution Radiometer (AVHRR). This remote sensing product classified smoke plumes into

three categories: low, medium, and high density, based on the estimated smoke concentrations of 5, 16, 27 $\mu$g m$^{-3}$, respectively.

To quantify the spatial extent and duration of smoke cover in California for each year, we made an annual composite map of smoke cover by intersecting daily smoke plume polygons with each intersecting polygon recording the number of smoke days for a given year. All areas exposed to smoke for at least one day were then summarized to quantify the annual spatial extent of smoke cover. This process was repeated for each month to evaluate the seasonal and interannual patterns of smoke cover extent in California, for each smoke density. In further analyses, we focused on medium and high-density smoke cover (hereafter 'med-high density') rather than low density smoke cover because we assumed more dense smoke cover would be of greater ecological relevance (e.g., more likely to reduce SW radiation fluxes and deposit particulates into lakes).

We assessed time series of maximum med-high density smoke cover extent in the months June-October, as well as annual and seasonal means, for monotonic trends by computing Sen's slopes and applying the Mann-Kendall test using the 'wql' package in R[39].

In addition to quantifying smoke cover throughout California, we generated a daily smoke density sequence over each study lake from 2006 - 2022. First, we obtained lake shapefiles from the California Lake database maintained by California Department of Fish and Wildlife (CDFW)[40]. For study sites that were not included in the California Lake database (e.g., small ponds in Sequoia National Park), we used a 100 meter buffer around the central point in the lake as an approximation of the lake surface. We then assigned a daily smoke density value to each lake by comparing spatial relationships between smoke plume polygons and lake surfaces. If a

smoke plume intersected a lake's surface area, we assigned the corresponding smoke density to the lake based on the date. If multiple smoke densities were assigned to the same lake on the same date, only the highest smoke density was assigned.

*Characterizing lake exposure to smoke during study period*

We identified periods of smoke cover for each lake during the study years (2018, 2020, 2021) using a combination of the daily smoke density value (described in previous section), SW radiation measurements from weather stations, PM2.5 concentrations, and visual inspection of Sentinel satellite images to confirm the presence of smoke plumes.

We classified each day as 'smoke' or 'non-smoke' as follows: we modeled theoretical 'clear-sky' SW radiation ($SW_{clear.sky}$) for each day using a statistical clear sky algorithm[41]. We then subtracted the measured daily mean SW ($SW_{meas}$) from $SW_{clear.sky}$ ($SW_{diff} = SW_{clear.sky} - SW_{meas}$). We calculated the median value of $SW_{diff}$ on days with smoke density of zero across all 9 meteorological datasets (median $SW_{diff}$ = 20 W $m^{-2}$). Days were conservatively classified as smoke days if they met two conditions: 1) daily mean SW radiation was reduced by more than 20 W $m^{-2}$ and 2) smoke density was medium or high.

For each lake-year combination, we characterized the following attributes of smoke exposure: 1) the total number of smoke days between July 1-Oct 1; 2) the intermittence of smoke cover, defined as the mean, median, and maximum number of consecutive smoke days that occurred in each dataset; and 3) the cumulative reduction in SW radiation relative to clear sky values on smoke days ('cumulative SW deficit'). We calculated cumulative SW deficit by summing $SW_{diff}$ on all smoke days between July 1 and October 1, when the majority of smoke days occurred.

Attributes of smoke cover were only quantified between July 1 - October 1 because some datasets were incomplete outside this seasonal window.

*Estimating aquatic ecosystem metabolic rates*

We modeled daily rates of gross primary production (GPP; mg DO $L^{-1}$ $d^{-1}$), ecosystem respiration (R), and net ecosystem production (NEP = GPP - R) in the surface mixed layer of our study sites using hourly DO (mg $L^{-1}$), water temperature (° C), PAR (μmol $m^{-2}$ $s^{-1}$), and wind speed (m $s^{-1}$) measurements using the Lake Metabolizer R package[42]. For pelagic sites in lakes that stratified seasonally or periodically (Emerald Lake, Topaz Lake, Castle Lake, Clear Lake) we estimated metabolic rates in the surface mixed layer. We calculated mixed layer depth ($Z_{mix}$) using depth-distributed water temperature measurements from fixed depth sensors or vertical profiles using LakeAnalyzer in R[43]. For littoral sites within stratified lakes (Castle Lake, Dulzura Lake, Lake Tahoe), and in small, shallow water bodies that did not stratify (TOK 11 Pond, EML Pond 1, Topaz Pond), $Z_{mix}$ was set to lake depth at the location of the DO sensor. In the tidally-influenced Delta, $Z_{mix}$ was set to the mean depth of the channel within the range of the tidal excursion (see Supplementary Methods for details on data used in metabolism models).

To estimate oxygen fluxes across the air-water interface, we used a wind-based gas exchange model that accounted for lake surface area[44]. We set gas exchange to zero during periods when the DO sensor was below the diel thermocline. We estimated average PAR within the surface mixed layer by converting shortwave radiation measurements from weather stations to surface PAR and then using the attenuation coefficient for PAR ($k_d$; $m^{-1}$ Table 1) and $Z_{mix}$ to estimate mean water column PAR as in Staehr et al[45]. Days with unrealistic metabolism estimates (negative GPP, positive R) were excluded from results.

*Quantifying effects of smoke cover on ecosystem metabolic rates*

We quantified ecosystem metabolic responses to smoke cover (e.g., compared GPP, R, and NEP between smoke and non-smoke days) by fitting generalized additive mixed models (GAMMs) to the data using the 'mgcv' R package[46]. To facilitate comparisons across sites spanning from hyper-eutrophic (Clear Lake) to ultra-oligotrophic (Lake Tahoe), we first standardized metabolism time series by mean and variance (z-score). We modeled daily metabolic estimates as a function of smoke cover (categorical: smoke or non-smoke) and day of year (doy; smooth term). We included an interaction between the smooth function of doy and smoke (e.g., estimated separate seasonal smooths for non-smoke and smoke days) in order to visualize the effect of smoke cover on seasonal patterns in metabolism. We included a random effect of site in all models to account for the non-independence of repeated measurements in each lake. GAMM models were fitted using default thin plate regression splines for the smooth terms.

## Results

*Increased spatial extent and duration of medium-high density smoke in California since 2006*

Over the last 18 years (2006 - 2022), the months July, August, and September had the greatest maximum spatial extent of med-high density smoke cover in California (maximum coverage > 40%; Figure 2b), followed by June (30%) and October (18%). Two of the main study years (2020, 2021) were outliers in the seasonal timing of smoke cover: the maximum extent of med-high density smoke exceeded 70% of California in September and October in both years (Figure 2b red points in boxplot; Supplementary Figure 1).

From 2006 to 2022, the maximum extent of med-high density smoke increased significantly in every month between June and October. Maximum smoke extent increased the fastest in August (23,360 $km^2$ $year^{-1}$ or 5.5% of California's area $year^{-1}$, Kendall's S = 68, p = 0.005, n=18) and September (20,392 $km^2$ or 4.8% $year^{-1}$, S=80, p=0.001), followed by July (16,704 $km^2$ or 3.9% $year^{-1}$, S = 67, p = 0.006). Averaged across the predominant smoke season (June - October), the maximum extent of med-high density smoke cover has increased by ~300,000 $km^2$, or 70% of California's area, over the last 18 years (S = 83, p = 0.0007; dashed line in Figure 2c). Our study years (2018, 2020, 2021) had the greatest spatial extent of med-high density smoke since 2006 (Figure 2c).

The duration of med-high density smoke cover at the 10 study sites was highly variable among years but increased dramatically during the study years (Figure 2d). From 2006 - 2022, sites experienced an average of 15 med-high density smoke days per year (range 0 - 69 days). There were regional differences in smoke duration between the study years (2018 - 2021; Figure 2a), likely related to proximity to wildfires and prevailing wind patterns. For example, in 2021 smoke affected the northern Sierra Nevada mountains, Klamath mountains and Sacramento Delta more than the southern Sierra Nevada mountains.

*Variable lake exposure to smoke (2018, 2020, 2021)*

Across all site-year combinations where independent meteorological data were available (n = 1043 days), daily mean SW radiation fluxes on smoke days were significantly less than those on non-smoke days (205 versus 254 W $m^{-2}$; t = -11.613, $p < 2.2 \times 10^{-16}$, df = 888.97; Figure 3a), a reduction of 20% relative to clear-sky estimates ($SW_{diff}$ = mean reduction 57 W $m^{-2}$; n = 394).

Atmospheric PM2.5 concentrations were elevated on smoke days compared with non-smoke days (92 versus 17 μg $m^{-3}$; $t = 11.411$, $p < 2.2 \times 10^{-16}$, df = 306.31; Figure 3b).

Exposure to smoke varied in duration, intermittence, and intensity across the 9 meteorological datasets (Table 2). During the three study years (2018, 2020, 2021) study sites experienced an average of 33 smoke days between July 1 and Oct 1 (range 23 - 45 days; Table 2). The timing of smoke events varied among sites and years, but in general August and September had more smoke days than July (mean of 14 days versus 3 days), matching the results from the 18-year smoke time series (Figure 2b). The mean length of smoke events (consecutive smoke days) ranged from 3 - 8 days, but there was large variation in the maximum length of smoke events across the datasets (4 - 21 days; Table 2). The cumulative deficit in SW fluxes due to smoke (e.g., smoke intensity; $10^6$ J $m^{-2}$) varied three-fold among lake-years, with the greatest SW reductions at Emerald Lake (2020, 2021) and Lake Tahoe (2021) and the least at Castle Lake in 2018 (Table 2; Figure 3c-d).

*Responses of ecosystem metabolism to smoke*

Rates of ecosystem metabolism were highly variable among the 10 sites and were temporally and spatially variable within lakes (Supplementary Table 1, Supplementary Figures 2, 3). Volumetric rates of GPP in pelagic habitats ranged from 0.11 ± 0.09 mg DO $L^{-1}$ $d^{-1}$ in oligotrophic Emerald Lake to 1.43 ± 1.26 mg DO $L^{-1}$ $d^{-1}$ in hyper-eutrophic Clear Lake. Littoral habitats and shallow ponds tended to have higher volumetric rates of GPP than pelagic sites or deeper lakes, ranging from 0.59 ± 0.16 mg DO $L^{-1}$ $d^{-1}$ in TOK 11 Pond to 1.62 ± 0.30 mg DO $L^{-1}$ $d^{-1}$ in Dulzura Lake. In Castle and Dulzura, where we estimated metabolism in both pelagic and littoral habitats, mean rates of GPP in littoral areas were >3 times the corresponding rates in mid-lake surface water

(Supplementary Table 1). Sites with warmer water temperatures and higher chlorophyll-a (chla), total dissolved N (TDN), and total dissolved P (TDP) concentrations had higher rates of GPP (see Supplementary Table 2 for water chemistry summary; Supplementary Table 3 for correlation matrix). Respiration rates were strongly correlated with GPP overall (Pearson's r = 0.94, n = 1772 metabolism days), though the strength of this correlation varied considerably among datasets (0.34 - 0.96; Table S1). Similar to GPP, R was highest in warm lakes with higher chlorophyll-a (chla) and nutrient concentrations (e.g., Delta and Clear Lake). Mean NEP was negative in 18 out of 22 datasets; only 3 littoral sites (Castle Lake, Dulzura Lake, and Lake Tahoe) and one pelagic site (Castle Lake) had positive mean NEP.

Rates of GPP (z-scored) were significantly lower on smoke days than on non-smoke days (GAMMs: parametric effect = -0.22 ± 0.05 (SE), $p = 1.97 \times 10^{-5}$, n= 1772; Figure 4a). Though GPP declined seasonally, smoke cover further reduced rates relative to the seasonal decline (Figure 4d). Median GPP was lower during smoke days in most of the datasets (negative ΔGPP; Figure 4g), decreasing by up to 70% in Clear Lake (OA) in 2020. However, median GPP was higher in certain sites and years, increasing by up to 50% in the littoral zone of Lake Tahoe in 2021 (Extended Data Figure 3; Supplementary Table 1). Respiration rates were lower on smoke days (effect = -0.24 ± 0.05, $p = 5.64 \times 10^{-7}$, n = 1772, Figure 4b), and smoke cover accelerated seasonal declines in R (Figure 4e). Median rates of R were up to 52% lower during smoke days (EML Pond 1 in 2021). Only mesotrophic or eutrophic sites showed higher median rates of R during smoke days (positive ΔR; Figure 4h), increasing by up to 44 % in Clear Lake (OA) in 2021. Unlike GPP and R, NEP was not significantly different between smoke and non-smoke days across all the datasets (effect = 0.03 ± 0.05, p = 0.60; Figure 4c, f). NEP tended to be

more positive on smoke days in oligotrophic sites and more negative in mesotrophic or eutrophic sites (Figure 4i).

Because GPP and R were coupled in most sites, responses of GPP and R to smoke (ΔGPP, ΔR) were also positively correlated (Figure 5a; effect = 0.52 ± 0.16, $R^2$ = 0.30, p = 0.005, n = 22). However, no lake attribute or smoke variables explained GPP responses to smoke; ΔGPP was not related to log-TDP (Figure 5b; p = 0.43), log-TDN (p = 0.37), log-chla (p = 0.69), mean summer water temperature (p = 0.36), or other site or smoke variables (Supplementary Table 3). In contrast, ΔR was positively correlated with site variables such as mean summer water temperature (effect = 0.09 ± 0.02 , $R^2$=0.38; p = 0.0012), log-TDP (Figure 5c; effect 0.19 ± 0.04, $R^2$ = 0.41, p = 0.00073), log-TDN (effect 0.45 ± 0.13, $R^2$ = 0.33, p = 0.003), and log-chla (effect 0.22 ± 0.05, $R^2$ = 0.39, p = 0.001); respiration rates were lower on smoke days in cold, low-nutrient lakes. R was also reduced in sites that experienced more prolonged smoke cover (number of smoke days; effect = -0.04 ± 0.015, $R^2$ = 0.27, p = 0.007) and greater smoke intensity (higher SW deficit, $10^6$ J $m^{-2}$; effect = -0.0005 ± 0.0001, $R^2$ = 0.40, p = 0.0008). However, because the oligotrophic lakes in the Tahoe basin and Sequoia National Park were also exposed to more prolonged and high-density smoke than the mesotrophic and eutrophic sites (Table 2; Figure 3c-d), we were not able to robustly distinguish the effects of smoke exposure attributes and lake variables on metabolic responses. Though littoral and pelagic habitats within the same water bodies responded differently to smoke cover, across sites there were no consistent differences in metabolic responses between the two habitat types.

## Discussion

*Overview*

Our study of the impact of wildfire smoke on inland waters found highly variable responses in both GPP and R. On average, GPP and R were significantly lower on smoke days, but the magnitude and direction of responses varied considerably among and within sites, and between years. Median differences in GPP between non-smoke and smoke days ranged from +0.5 to - 0.9 mg DO $L^{-1}$ $d^{-1}$. Responses in R also varied but were more clearly linked to site characteristics such as nutrient concentrations and water temperature. The average spatial extent of med-high density smoke between June-October has increased to over 50% of California's area since 2006, and smoke is associated with significant reductions in SW radiation and 3 to 4-fold increases in atmospheric PM2.5, suggesting widespread impacts to California's thousands of lakes, ponds, and tidal freshwaters[25]. These findings establish that metabolic responses of inland waters to smoke, both in the western U.S. and globally, will be highly dependent on spatial and seasonal context of smoke coverage as well as physical and chemical attributes of individual ecosystems.

*Multiple mechanisms drive lake metabolic responses to wildfire smoke*

We identify several mechanisms responsible for the variation in responses of ecosystem metabolic rates to wildfire smoke. All sites were exposed to multiple weeks of high-density smoke cover and reduced SW radiation fluxes (Table 2), yet GPP responses often differed in magnitude and direction, even within the same site, underscoring the need to better understand how changes in light affect aquatic primary producers in different habitats. In many of our datasets, GPP did not change substantially during smoky periods, suggesting that primary producers were neither strongly light-limited nor strongly photo-inhibited (Figure 1a). Lack of strong light-limitation in our datasets is not surprising given that we only estimated GPP in

surface waters—Scordo et al. [8] found that smoke cover increased GPP in surface waters but inhibited GPP in deeper waters and prevented the seasonal formation of a deep chlorophyll maximum[8]. In oligotrophic water bodies with deep chlorophyll maxima, smoke cover may substantially reduce whole-lake GPP. However, we were surprised by the variable responses in littoral habitats, where we expected minimal responses due to structural and physiological adaptations by benthic algae to high-light (PAR and UV) conditions[26]. Sensitivity of aquatic primary producers to photo-inhibition has been shown to be highly taxon-specific[27], thus better characterization of algal community composition may be required to understand smoke responses in shallow or near-shore aquatic habitats.

Nutrient fertilization from smoke aerosol deposition can stimulate aquatic primary production, especially in oligotrophic systems (Figure 1c)[6]. Phosphorus, a critical and often limiting nutrient in freshwater ecosystems, is present in significantly higher concentrations in ash compared to the unburned vegetation from which it originates[28]. However, there are few studies examining the fate of smoke particles in lakes and results are often ambiguous. Alpine lakes in proximity to biomass burning exhibited increased P concentrations and subsequently N-limitation[29]. In ultra-oligotrophic Lake Tahoe, the addition of ash from smoke increased primary productivity relative to a control treatment, yet no significant differences were found in time series of nitrate, ammonium, or phosphate concentrations, leading the researchers to conclude that trace metals in ash, rather than N or P, increased production[16]. Scordo et al.[8] found that smoke increased particulate N and C in a mesotrophic lake, but smoke did not change the type and level of macronutrient limitation in bioassays. We did not measure nutrient concentrations at temporal resolution sufficient to test hypotheses related to nutrient fertilization, but in lakes where GPP

was higher during smoke cover, it is plausible that nutrient fertilization may have stimulated primary production.

Changes in light (e.g., UV radiation) and nutrients alter ecosystem respiration rates in oligotrophic waters more so than productive waters[30]. R decreased during smoke cover in all the oligotrophic study lakes, even when GPP increased (Figure 4g, h). Reductions in UV radiation during smoke cover should have greater effects on R in oligotrophic systems for two reasons. First, UV irradiance is higher in clear-water oligotrophic waters and imposes substantial energetic costs on aquatic organisms to repair cellular damage[31], thus UV reduction during smoke cover should decrease ecosystem respiration rates by decreasing energetic costs. Second, reducing UV improves the quality (e.g., nutrient stoichiometry) of organic matter fixed by autotrophs[32], increasing bacterial growth efficiency and decreasing ecosystem respiration rates in oligotrophic systems[33,34], where bacterioplankton account for the majority of respiration[35]. Moreover, though our study did not quantify changes in nutrient concentrations associated with ash deposition, even mild fertilization in oligotrophic surface waters can increase C:N and C:P ratios in autotrophic biomass, increasing bacterial growth efficiency and reducing R. Impacts of prolonged smoke cover on carbon cycling and emissions from inland waters may depend equally on the responses of primary producers and heterotrophs.

The seasonal timing of wildfire smoke cover is another important factor that mediates lake ecosystem responses, particularly for GPP. The effects of PAR and UV reduction from smoke should vary seasonally– smoke cover in early summer, when solar radiation inputs are at their annual maximum, could stimulate GPP if phytoplankton are photo-inhibited, whereas smoke cover in autumn, when PAR is declining, may further reduce GPP (Figure 1a). The effects of nutrient fertilization from smoke should also vary seasonally in water bodies with strong

seasonal changes in nutrient limitation. For example, phytoplankton may be less nutrient-limited in autumn when mixing and thermocline deepening replenish nutrient concentrations in surface waters[36]. Two of our study years (2020, 2021) had late-season smoke cover, with dense smoke persisting through October (Figure 2b), which may have contributed to the overall reductions in GPP with smoke cover that we observed. In contrast, sites where GPP increased during smoke cover (Castle Lake pelagic in 2018, Lake Tahoe nearshore sites in 2021) had earlier exposure to smoke, with a greater number of smoke days in July (Table 2). Though our study took place during years with relatively late-season smoke cover, this pattern is not necessarily representative of smoke exposure in California or elsewhere. Smoke covered at least 50% of California during June in 7 out of 17 years (Supplementary Figure 1). The record-breaking 2023 Canadian wildfires began in May and early June, when solar radiation fluxes were highest, and covered extensive, lake-rich regions in smoke for weeks[37]. The high degree of variation in seasonal timing of smoke cover implies that lake responses could change from year-to-year depending on the timing of wildfire ignitions.

Predicting the impacts of worsening wildfire smoke on inland waters at regional to continental scales requires understanding how lake and watershed attributes mediate lake responses. In North America over a million lakes were exposed to smoke for over 30 days per year (2019-2021)[3], encompassing biomes from arctic to subtropical, and subsequently an enormous range in water temperature, clarity, and nutrient concentrations. Our study sites ranged from ultra-oligotrophic to hypereutrophic, and we observed correspondingly variable responses of lake GPP and R to smoke cover. R in particular responded differently in warm, eutrophic lakes than in cold, oligotrophic lakes (Figure 4h, 5c), whereas GPP responses were less clearly related to lake trophic status. The small, oligotrophic mountain lakes in Sequoia National Park, which are

representative of a majority of California's lakes[25], experienced the greatest relative declines in R during smoke cover and often increased NEP (Supplementary Table 1, Extended Data Figure 3), suggesting that smoke may have regionally significant impacts on aquatic carbon cycling. In other lake regions where eutrophication or high organic matter concentrations are prevalent, smoke cover may lead to reduced NEP and greater $CO_2$ fluxes from lakes if GPP decreases but respiration rates remain high.

Our results highlight the need for targeted research of smoke impacts on freshwaters, as a key set of basic questions remain unresolved: 1) How do lake attributes such as water clarity, trophic status, or lake size and depth mediate metabolic responses to smoke? 2) Do the mechanistic relationships that determine responses of GPP and R to smoke cover vary among different communities of autotrophs and heterotrophs? 3) How do attributes of smoke exposure mediate lake responses? and 4) Does prolonged, dense smoke affect aquatic carbon cycling at regional or global scales? We were unable to clearly distinguish the roles of smoke exposure attributes and lake attributes in mediating metabolic responses to smoke, due to covariation in these factors and the limited number of datasets in our study. Understanding lake responses to smoke will require extensive data collection across different hydroclimatic conditions, environmental gradients (geomorphology, vegetation, land use), and gradients in smoke exposure. Additional experimental, empirical, and modeling studies are also needed to understand the predominant mechanisms underlying whole-ecosystem metabolic responses to smoke. Even small impacts on ecosystem metabolic rates may have important implications for global carbon cycling given the large number of lakes affected by smoke globally[3]. Quantifying impacts of smoke on aquatic carbon cycling at regional to continental scales will require collaborative research within and across regions. Global-scale, opportunistic data collection by lake sensor networks such as the

Global Lake Ecological Observatory Network (GLEON; https://gleon.org/) could be used to test hypotheses and broaden our understanding of this increasing global phenomenon, as wildfires and smoke cover increase in frequency, intensity, and spatial extent.

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**Author Contributions**

APS, FS and SS designed the study. APS, MJF, AC, FS, SC, MT, JC, GS, SAV, and SW provided datasets. APS, MT, FS, AC, JC, and SS performed data analyses and made the figures. APS lead manuscript writing. All authors contributed text and edited the manuscript.

**Tables**

**Table 1**. Study site locations and attributes.

| Site Name | CA Region | Latitude (°) | Longitude (°) | Elevation (m.a.s.l) | Surface Area (ha) | Max Depth (m) | Chl-a (µg $L^{-1}$) | Light Attenuation ($k_d$, $m^{-1}$) | Study Periods |
|---|---|---|---|---|---|---|---|---|---|
| Delta | Sacramento -San Joaquin River Delta | 38.48 | -121.585 | 0 | 1,160 | 10 | 4.8 (3.4) | 1.58 | 8/1/2020 - 11/1/2020 |
| Clear Lake | N. Coast Range | 39.064 | -122.842 | 431 | 15,100 | 8 | 17.5 (9.4) LA[1] 59.5 (38.1) OA[2] | 0.8 | 7/1/2020- 11/1/2020 |
| Dulzura Lake (Tahoe)[3] | N. Sierra Nevada | 39.298 | -120.383 | 2,097 | 14.8 | 9.5 | 1.6 (1.1) | 0.53 | 7/1/2021 - 10/1/2021 |
| Castle Lake | Klamath | 41.227 | -122.383 | 1,646 | 20.1 | 30 | 0.79 (0.25) | 0.25 | 7/1/2018 - 10/1/2018 |
| TOK 11 Pond (Sequoia) | S. Sierra Nevada | 36.594 | -118.671 | 2,970 | 0.2 | 2.3 | 0.65 (0.60) | 0.22 | 7/1/2020 - 11/1/2020; 7/1/2021- 11/1/2021 |
| EML Pond 1 (Sequoia) | S. Sierra Nevada | 36.599 | -118.679 | 2,802 | 0.2 | 3.1 | 0.88 (0.49) | 0.22 | 7/1/2020 - 11/1/2020; 7/1/2021- 11/1/2021 |
| Topaz Pond (Sequoia) | S. Sierra Nevada | 36.625 | -118.635 | 3,229 | 0.2 | 1.9 | 0.86 (1.04) | 0.22 | 7/1/2020 - 11/1/2020; 7/1/2021- 11/1/2021 |
| Topaz Lake (Sequoia) | S. Sierra Nevada | 36.626 | -118.637 | 3,219 | 3.8 | 5 | 1.44 (0.37) | 0.22 | 7/1/2020 - 11/1/2020; 7/1/2021- 11/1/2021 |
| Emerald Lake (Sequoia) | S. Sierra Nevada | 36.598 | -118.676 | 2,800 | 2.8 | 10 | 0.74 (0.42) | 0.24 | 7/1/2020 - 11/1/2020; 7/1/2021- 11/1/2021 |
| Lake Tahoe (Tahoe) | N. Sierra Nevada | 39.103 | -120.035 | 1,897 | 49,624 | 501 | 0.31 (0.13) | 0.09 | 7/1/2020- 11/1/2020; 7/1/2021 - 11/1/2021 |

[1] LA = Lower Arm
[2] OA = Oaks Arm
[3] Names of groups of lakes corresponding to names shown in Figure 2 are included in parentheses

**Table 2**. Attributes of smoke exposure for selected study sites[4].

| Site | Year | # Smoke Days | | | | # Consecutive Smoke Days | | Mean PM2.5 (ug $m^{-3}$) | Mean $SW_{diff}$ (W $m^{-2}$) | Cum. SW Deficit ($10^6$ J $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Tot | Jul | Aug | Sept | Mean | Max | | | |
| Lake Tahoe | 2021 | 45 | 9 | 23 | 13 | 3 | 10 | 67 | 67 | 260.57 |
| Emerald Lake | 2021 | 38 | 4 | 13 | 20 | 4 | 20 | 79 | 79 | 259.62 |
| Emerald Lake | 2020 | 39 | 0 | 10 | 28 | 8 | 21 | NA | 59 | 199.59 |
| Dulzura Lake | 2021 | 36 | 9 | 20 | 7 | 3 | 9 | 55 | 55 | 169.73 |
| Clear Lake | 2020 | 30 | 0 | 12 | 17 | 3 | 7 | 60 | 60 | 154.38 |
| Delta | 2020 | 34 | 1 | 13 | 19 | 4 | 12 | 50 | 50 | 145.53 |
| Lake Tahoe | 2020 | 28 | 1 | 12 | 15 | 3 | 9 | 59 | 59 | 143.30 |
| Clear Lake | 2021 | 23 | 1 | 16 | 6 | 3 | 5 | 50 | 50 | 99.35 |
| Castle Lake | 2018 | 26 | 6 | 12 | 8 | 3 | 4 | 43 | 44 | 97.87 |

## Figures

[4] Smoke attributes were calculated for the period between June 1 – October 1 because some datasets were incomplete outside this range. Mean PM2.5 and $SW_{diff}$ refer to means on smoke days only. Sites in close proximity (e.g., small lakes and ponds in Sequoia National Park) are not shown because they lacked unique metereological datasets.

**Figure 1**. Smoke can affect aquatic ecosystem metabolism by multiple mechanisms. A) Smoke events (black horizontal arrow) reduce light (PAR) within the water column. Whether a smoke event increases or decreases GPP (colored regions) depends on the pre-smoke PAR level and on the magnitude of PAR reduction (e.g., smoke density). In this example, a smoke event reduces GPP because primary producers shift from light-saturated to light-limited conditions. B) Smoke events (black arrow) can reduce water temperature by scattering or absorbing incoming solar radiation, which should decrease metabolic rates (both GPP and R). C) The degree to which nutrient fertilization from smoke particle deposition stimulates GPP depends on ambient nutrient availability within a water body.

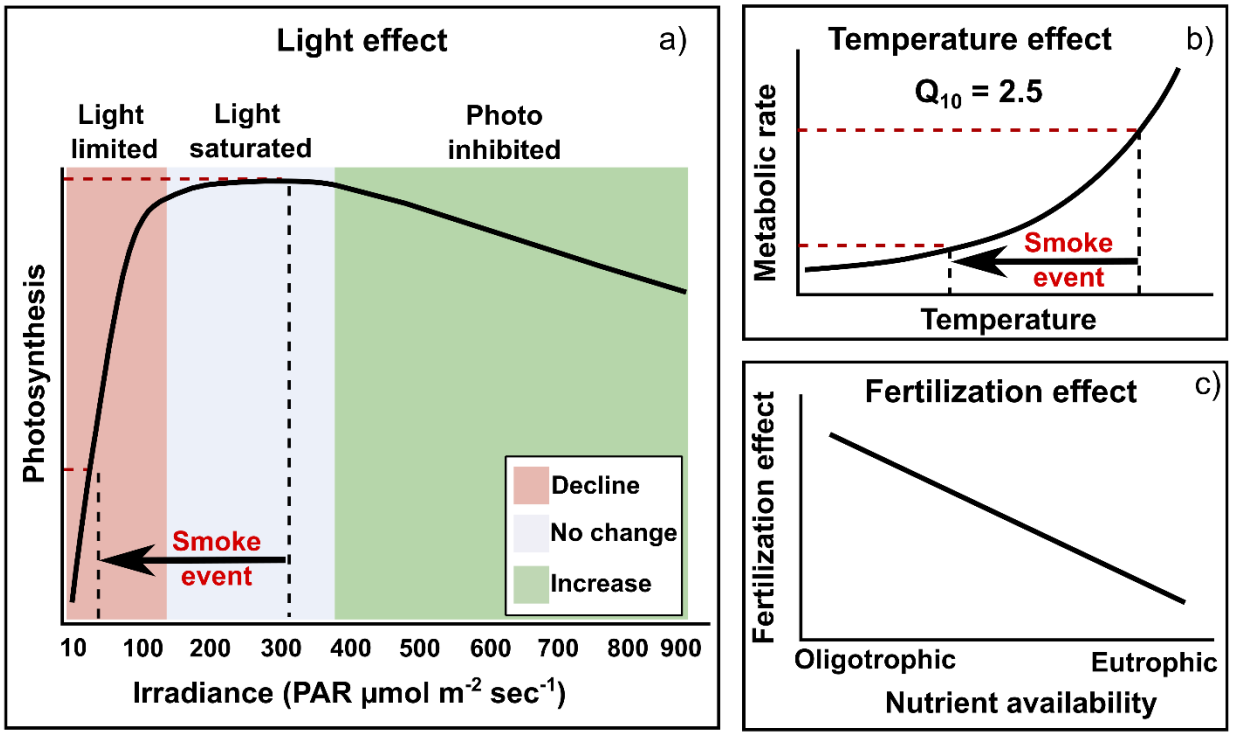


**Figure 2**. Spatial and temporal patterns in smoke cover in California (CA) and at study sites between 2006 - 2022. A) Maps show sites (colored dots) and the annual number of days with

med-high density smoke cover from 2018 – 2021 (red color gradient). Sites that are close together (ex. 5 lakes and ponds in Sequoia NP, multiple locations within the same lake) are represented by a single point. B) Seasonality of maximum spatial extent of med-high density smoke (percentage of CA; 2006-2022). September and October of 2020 and 2021 were outliers with high smoke cover extent. C) Average percentage of CA covered by med-high density smoke during June-October. Study years are shown in red, the dashed line shows the significant linear trend through time. D) Time series of total annual days with med-high density smoke cover at study sites from 2006-2022.

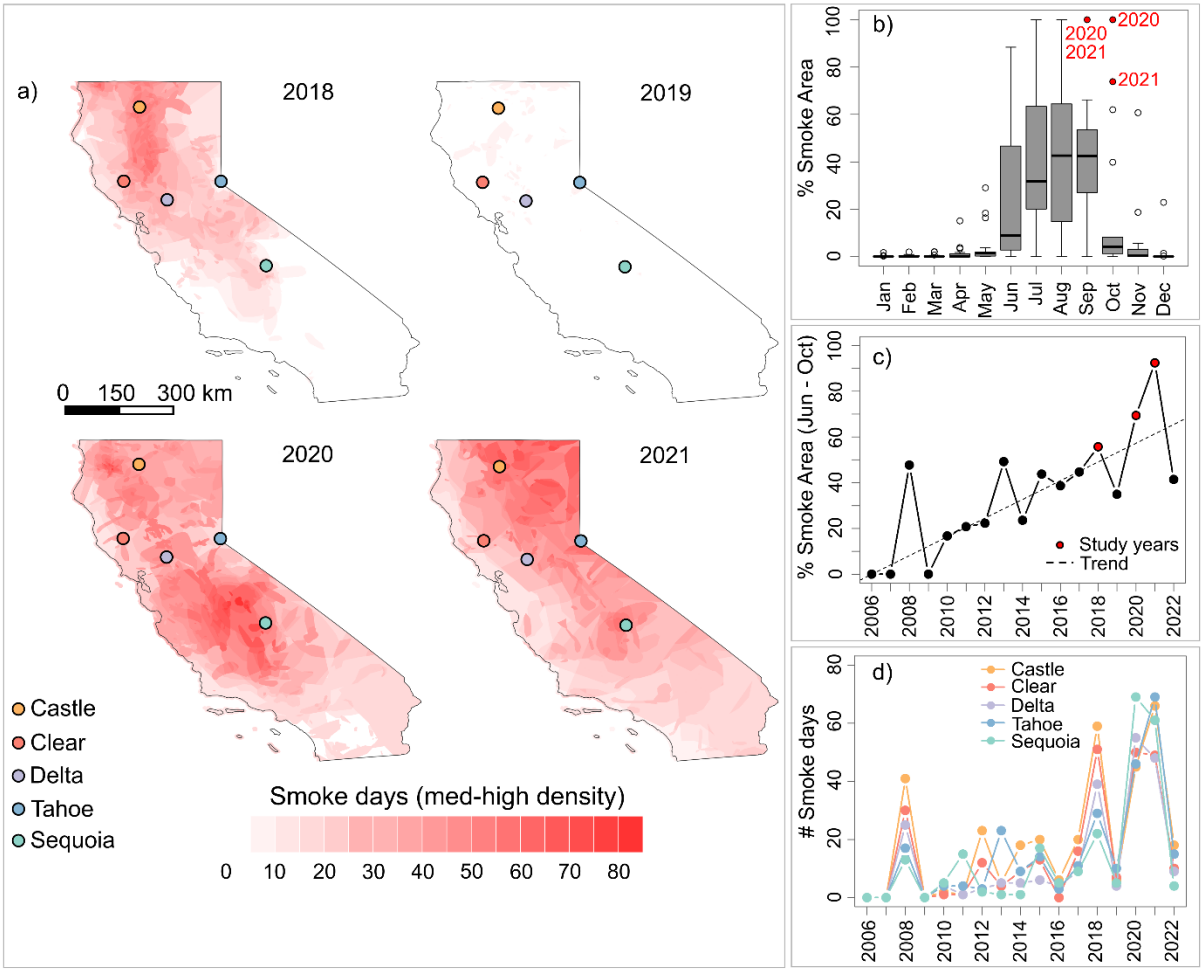

**Figure 3**. Changes in SW radiation and PM2.5 concentration during smoke cover. Density plots of A) daily average SW radiation and B) daily average PM2.5 concentration on non-smoke (n = 694; blue) and smoke (n = 349; gray) days. Dashed horizontal lines show median values across 9 unique meteorological datasets. C - D) The cumulative deficit of SW radiation due to smoke cover from July 1 (doy 183) to Nov 1 (doy 306) in 2020 and 2021 at our study sites. Horizontal sections of the lines represent non-smoke days, vertical sections represent smoke events. E-F) View of Lake Tahoe on 8/12/2020 at 14:00 PST (daily mean SW in Lake Tahoe = 340 W $m^{-2}$, PM2.5 = 2.3 µg $m^{-3}$), and a week later on 8/19/2020 14:00 PST, with view obscured by thick smoke (SW = 214 W $m^{-2}$; PM2.5 = 114 µg $m^{-3}$). Images were downloaded from http://ecam.cmucreatelab.org/embeds/tahoe2 (Heavenly). Notes: For clarity, some datasets that are geographically proximate have been omitted from panels C-D. Castle Lake's cumulative SW deficit is not shown because only data from 2018 were available. Data were not collected from the Delta in 2021.

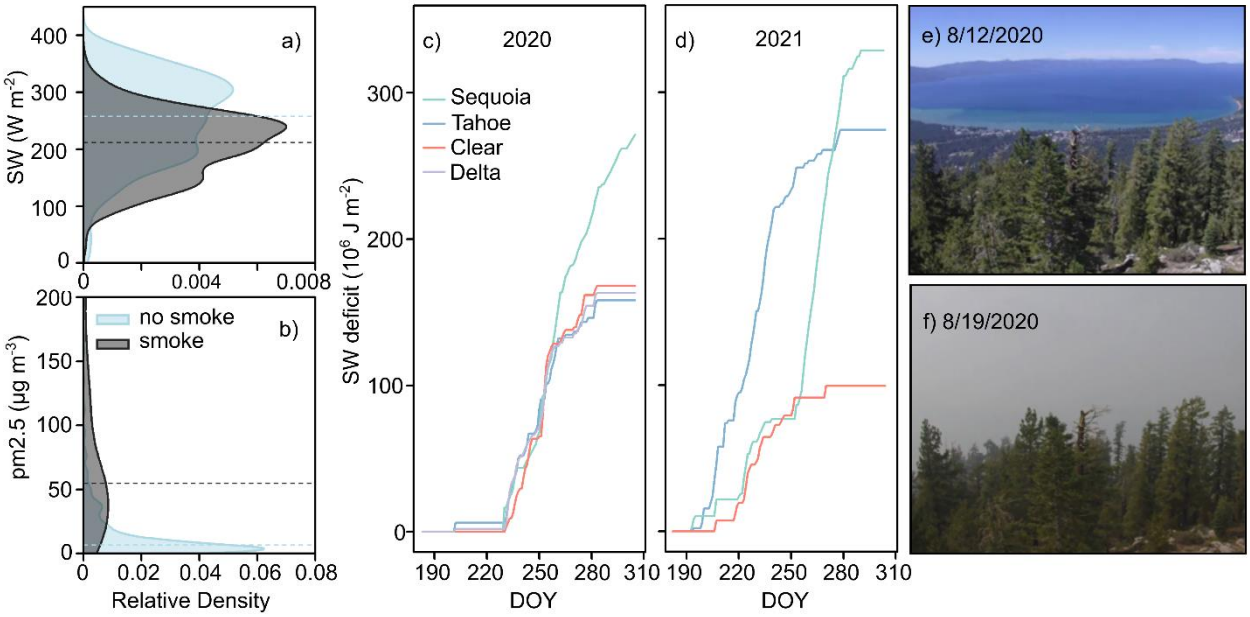


**Figure 4**. Responses of aquatic ecosystem metabolism to smoke cover. Density plots of A) daily z-scored GPP, B) R, and C) NEP on non-smoke (blue) and smoke (gray) days (n=1772). Dashed horizontal lines show the median values across 22 metabolism datasets. GAMM model smooth terms fit to day-of-year (DOY) showing how smoke cover alters seasonal trends in D) GPP, E) R, and F) NEP. Shaded areas show one standard error from the predicted line. Metabolism estimates were z-scored to facilitate comparison across datasets. G-I) The difference between median GPP, R, or NEP on smoke days versus non-smoke days (ΔGPP, R, NEP) for each dataset (n=22), ordered from most positive to most negative along the x-axis. Circles represent pelagic sites; diamonds represent littoral sites. Points and segments are colored by lake trophic status (oligotrophic=blue, mesotrophic=green, eutrophic=yellow).

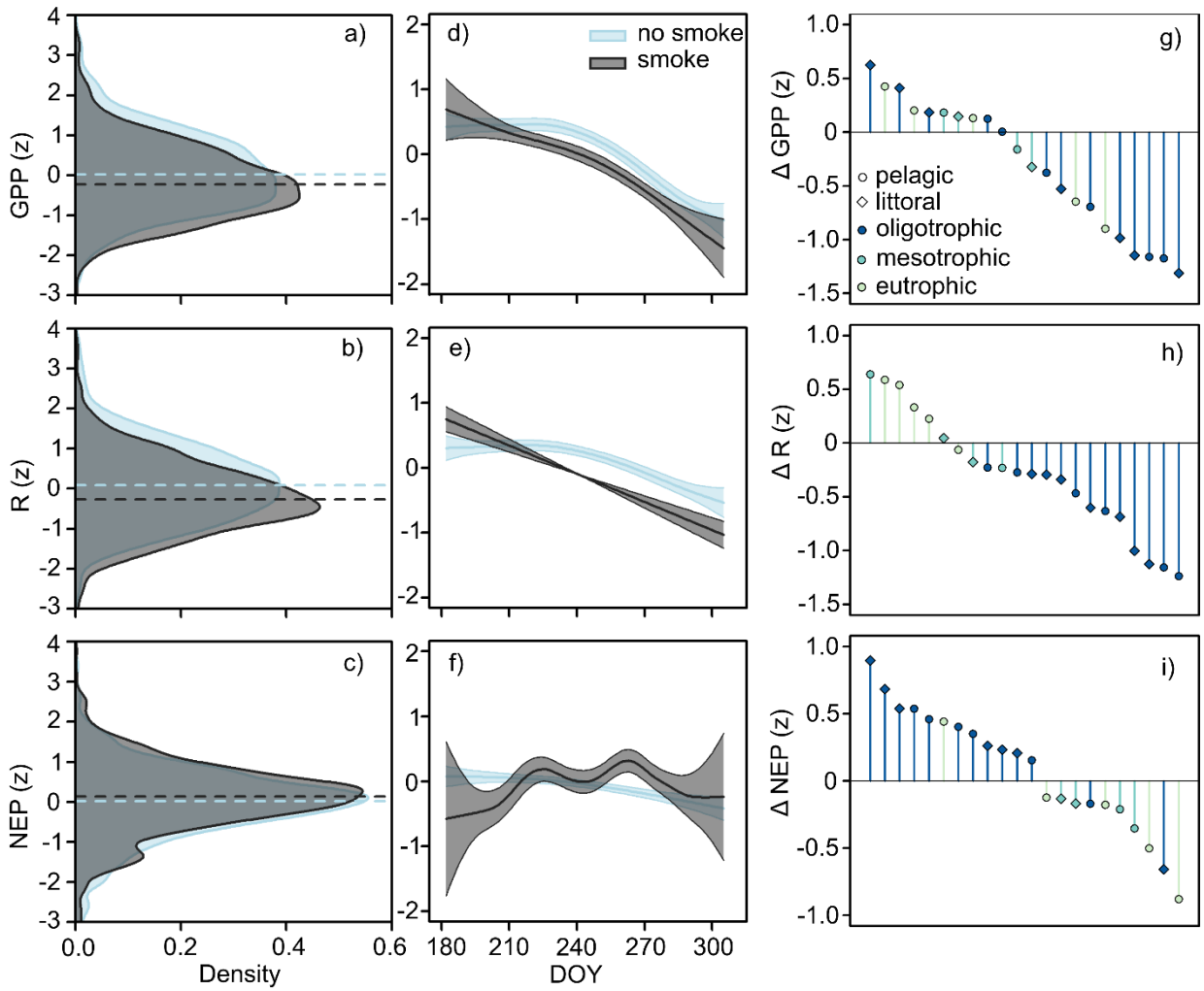
a)
b)
c)
d)
e)
f)
g)
h)
i)
GPP (z)
R (z)
NEP (z)
Density
DOY
no smoke
smoke
Δ GPP (z)
Δ R (z)
Δ NEP (z)
pelagic
littoral
oligotrophic
mesotrophic
eutrophic

**Figure 5**. Coupling between responses of GPP and R to smoke and associations with nutrient concentrations. A) For each dataset (n = 22) the median response of respiration to smoke (ΔR; z-scored; y-axis) is plotted against the median response of primary production (ΔGPP; z-scored; x-axis). Dashed horizontal and vertical lines show zero response, the gray diagonal line shows the 1:1 relationship. Circles represent pelagic sites; diamonds represent littoral sites. Points are colored by lake trophic status as in Figure 4. B) ΔGPP (z-score) plotted against mean total dissolved P (log TP; $\mu L^{-1}$). C) ΔR (z-score) plotted against log TP. The solid black line shows a significant linear relationship ($R^2$= 0.41, $p < 0.001$).