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Climate Sensitivity of Lentic Mountain Ecosystems

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By

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ABSTRACT

Lentic freshwater ecosystems are threatened by unprecedented global change. Often considered sentinels for change, lentic ecosystems like lakes and ponds are particularly sensitive and vulnerable to the effects of global change because they respond rapidly to changes in the environment and integrate information from their surrounding catchment within their ecosystem. These sensitive lentic ecosystems are increasingly threatened by climate-driven shifts like warming air temperatures, increasing hydroclimatic variability, and changing ice phenologies. Additionally, global-change phenomena such as increasingly extreme wildfire activity further threaten these ecosystems. In particular, mountain lentic ecosystems are experiencing some of the world's greatest rates of change in air temperature and precipitation regimes, respond strongly to climate forcing, and may be particularly sensitive to global change. In this dissertation, I investigated the climate sensitivity of lentic ecosystems in three primary ways. First, we quantified lake exposure to wildfire smoke across North America, and reviewed the known and theoretical impacts of that exposure. Then, we investigated how wildfire smoke affects lake and pond temperature and ecosystem metabolism across a watershed. Finally, we addressed the impact of hydroclimatic variability on lake zooplankton assemblage, abundance, and diversity. We found that the physical, biological, and chemical processes in lakes likely all respond to wildfire smoke exposure, and that in small, oligotrophic mountain lakes and ponds, smoke reduces water temperatures and ecosystem metabolism. These studies highlight that as wildfires increase in frequency and intensity, smoke from those fires have the potential to impact lentic ecosystem processes from local to continental scales. We also found that while much of the research on climate impacts focuses on the effects of warming, climate change-driven extremes in hydroclimate significantly determines lake zooplankton community abundance, biomass, and diversity. With increasingly extreme variability in hydroclimate, mountain lake zooplankton communities may undergo major shifts in assemblage and abundance. As we face increasing challenges driven by both climate change and human behavior, lakes and ponds can serve as key indicators of change in an ever-changing world.

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INTRODUCTION

Global change in lentic ecosystems

Lentic freshwater ecosystems are experiencing unprecedented global change. Water temperature is rising as a direct and rapid response to climate forcing (Adrian et al., 2009), total ice cover is decreasing (Sharma et al., 2020) and ice-off dates are shifting earlier (Preston et al., 2016). In addition, human activity and behavior has exacerbated the effects of climate change in several ways (Vitousek, 1994), including increasing the frequency and likelihood of extreme wildfires (Pausas & Keeley, 2021). These changes present great risks to lentic ecosystems like lakes and ponds, which respond rapidly to changes in the environment, integrate information from their surrounding catchment within the ecosystem, and are particularly sensitive to the effects of global change as a result (Adrian et al., 2009).

Thermal sensitivity

Most fundamental lentic ecosystem processes are either directly or indirectly affected by the fluxes of energy at the air-water interface (Bryson, 1964), providing a direct link between climate change and the ecosystem. These energy exchanges with the atmosphere drive thermal and mixing regimes in lentic ecosystems, mediated by within-system factors such as waterbody size and clarity, or extrinsic factors such as wind, runoff, precipitation, or shading. Mixing frequency and temperature regimes can drive key ecosystem processes, including carbon and nutrient cycling and oxygen availability, which are critical to supporting and maintaining life across the food web. Waterbody size (*i.e.*, surface area and depth) can affect stratification strength, where deeper lakes with smaller surface areas tend to have the strongest stratification strengths (Holgerson et al., 2022; Stefan et al., 1996). Additionally, water clarity can affect vertical light attenuation within the water column, which influences the depth of solar radiation and stratification strength and plays a critical role in the overall heat budget (Tanentzap et al., 2008). Extrinsic factors that reduce water clarity, such as sediment or nutrient-laden runoff, or shading that blocks sunlight from entering the waterbody, such as clouds, trees, cliffs, or wildfire smoke, can reduce the amount of energy entering the system. Because of these many interacting factors working to both increase and decrease waterbody temperature, even in the face of warming air temperature and lake surface temperature trends (Schmid et al., 2014; Woolway et al., 2020), some ecosystems are cooling rather than warming (Tanentzap et al., 2008), and there is differential warming even at the within-lake scale (Niedrist et al., 2018). Understanding mechanisms of and causes for change in lentic thermal regimes and the impacts of these changes on lentic ecosystem structure and function is critical as climate change drives thermal shifts.

Metabolic sensitivity

The impacts of thermal dynamics on lentic ecosystem structure and function directly impacts rates of ecosystem metabolism, the balance between organic matter produced (primary production) versus consumed (ecosystem respiration). Primary production and ecosystem respiration facilitate the flow of energy in a system and as a result, fundamentally structure organismal to ecosystem level processes. Rates of primary production and respiration form the basis of food webs, regulate nutrient flows, and drive carbon cycling. Ecosystem metabolic regimes balance rates of primary production and respiration and serve as an integrator of how energy is incorporated in and flows through a system (Odum, 1956). As a result, whole-ecosystem metabolism and its variability over time serves as a sensitive integrator of change (Hanson et al., 2006), and can be a good metric for quantifying lentic ecosystem responses to global change. There is also large temporal variation in metabolic rates within systems, highlighting the sensitivity of metabolic rates to ecosystem processes (Staehr & Sand-Jensen, 2007). This sensitivity to fine-scale deviations from seasonal trends makes ecosystem metabolic rates useful not only as integrators of change, but also indicators of change.

Climate and waterbody warming is overall accelerating ecosystem metabolic rates (Kraemer et al., 2017), but differences in factors such as waterbody size, geomorphology, community structure, or nutrient stoichiometry can increase or decrease the temperature dependence of ecosystem metabolism in aquatic ecosystems (Jankowski et al., 2014) or affect temporal variability in metabolic rates (Staehr et al., 2012). Because ecosystem metabolism is a metric that integrates biological, physical, and chemical ecosystem processes, understanding and quantifying the complex drivers of change of ecosystem metabolic rates will provide an ecosystem-level picture of the effects of global change on aquatic ecosystems.

Mountain lakes and ponds as sensitive and ideal study systems for global change

In mountain ecosystems, rates of air temperature increases are among the highest globally (Wang et al. 2014). In the western United States, mountain precipitation is projected to increasingly fall as rain, rather than snow, decreasing the overall winter snowpack (Hayhoe et al. 2004). In California, this is compounded by increasing drought risk due to anthropogenic warming (Diffenbaugh et al. 2015). Models under extreme conditions (no change to greenhouse gas emissions) even project persistent low snow to snow-free winters in this region within ~35-60 years (Siirila-Woodburn et al. 2021). In mountain lentic systems characterized by high interannual climate variation and steep landscape gradients, responses to climate change could be highly variable, and are often mediated by factors such as landscape features or basin morphometry (Sadro et al. 2012). In addition to lakes, there is also growing evidence that smaller lentic water bodies, such as ponds, are globally abundant, yet functionally distinct from large lakes (Oertli et al. 2002, Williams et al. 2004, De Meester et al. 2005, Downing 2010). Because of their small size, ponds may function as an early warning system for long-term effects on larger aquatic systems (Céréghino et al. 2014), making them a key component of understanding the impacts of global change on lentic ecosystems. As a result, when combined with the observed climatic changes occurring at high elevations, California's small mountain ponds and lakes are uniquely suited to test hypotheses on climate effects on ecosystem structure, function, and diversity in aquatic systems. However, their sensitivity to climate change, or the degree to which mountain lentic systems respond to climate variables, has not been well established.

Global-scale problems require collaborative interdisciplinary solutions

These global change issues span scales of space and time, disciplines, and international borders, with local to global implications. As a result, opportunities to address lentic ecosystem sensitivity to major global change issues can often be maximized through an interdisciplinary, team science approach (Weathers et al., 2016). International research networks such as the Global Lakes Ecological Observatory Network that work jointly to collect, analyze, and share data are able to utilize local to global scale data to address complex, interdisciplinary global change problems in a diverse set of ways (Hanson et al., 2016). Through collaboration and open science practices, we can answer a greater diversity of questions around the impacts of global change.

In this dissertation, I investigate the effects of global change on lentic ecosystems in three primary ways: (1) Quantifying continental-scale lake exposure to wildfire smoke and evaluating the known and theoretical impacts of that smoke exposure through a large team science approach, (2) investigating the effects of wildfire smoke on primary production and ecosystem metabolism in mountain lake ecosystems, and (3) evaluating the influence and impact of increasingly extreme hydroclimatic variability on mountain lake biodiversity.

Chapter overview

The frequency and severity of wildfires is increasing in many regions globally as wildfire seasons start earlier and last longer (Flannigan et al., 2013; Nagy et al., 2018). These wildfires produce large smoke plumes that can decrease solar radiation and deposit ash particles across ecosystems. Several key physical, chemical, and biological processes in aquatic ecosystems are controlled by factors affected by smoke. Some of the clearest examples of smoke effects on aquatic ecosystems come from ocean ecosystems, where smoke and ash transported long distances from large wildfires have caused large phytoplankton blooms (Ardyna et al., 2022; Tang et al., 2021) or altered ocean biogeochemistry (Coward et al., 2022; Li et al., 2021; Liu et al., 2024). In lakes, however, evidence of wildfire smoke causing shifts in variables like temperature, productivity, chemistry, or biodiversity is limited primarily to single-lake case studies (e.g., Lake Tahoe, Goldman et al. 1990; Castle Lake, Scordo et al. 2021, 2022). In the one regional study of smoke effects on lakes, smoke reduced ecosystem metabolic rates, but the high spatiotemporal variability of smoke has made it difficult to parse out the mechanisms driving the wide range of differences in responses at the regional scale (Smits, Scordo, Tang, Cortés, et al., 2024). While studies have examined the direct effects of wildfire on lakes in catchments that have burned (McCullough et al., 2019), the impact of wildfire smoke on lakes is not currently well established.

In chapter 1, **I led a large team science effort to investigate the impact of smoke on lakes** in three primary ways. First, we evaluated the spatial extent of smoke effects on lakes from 2019-2021 to determine how many lakes in North America have been affected by wildfire smoke, and how long these lakes are influenced by smoke. Second, we produced a conceptual model to better understand the potential impacts of smoke cover on the biological, physical, and chemical characteristics of lakes. Finally, we conducted a literature review to investigate the important mechanisms identified in the conceptual model to determine the extent of our knowledge. We established the concept of the “lake smoke-day” as a term to quantify and describe the number of days lakes are exposed to smoke. We found that between 2019-2021, 98.9% of lakes in North America experience at least 10 smoke-days annually.

In chapter 2, we studied the effects of wildfire smoke on the temperature and ecosystem metabolism of 2 lakes and 4 ponds in a high-elevation (2800-3230 m) watershed in the Sierra Nevada mountains of California, where extended drought is increasing the chance for extreme wildfire conditions (Goss et al., 2020). The only regional-scale study investigating the impacts of smoke on lake ecosystem metabolism demonstrated that wildfire smoke generally reduced rates of ecosystem metabolism, but quite unequally across systems – in part due to trophic status, and in part due to the high spatiotemporal variability in smoke density. For this chapter, we sought to control for trophic status and variability in smoke density by studying oligotrophic lakes and ponds in a single watershed, experiencing the same smoke events at the same time.

Smoke from major wildfires in 2020 and 2021 covered our study watershed for an average of 37 lake smoke-days between August and October. Using a network of high frequency measurements of water temperature and dissolved oxygen, we found that although lakes and ponds all responded to smoke, the magnitude of effects varied. Smoke reduced water temperature, with the magnitude of response controlled in part by waterbody size. Changes in rates of primary production associated with smoke were more varied, but also tended to scale with waterbody size. These results suggest that the impacts of smoke on small lakes and ponds are mediated by multiple factors, but that smaller waterbodies may be particularly vulnerable to the effects of smoke. Understanding the factors that mediate lake and pond sensitivity to smoke is a priority given current and projected wildfire regimes in a climate-modified world.

In addition to increasing lake exposure to wildfires and wildfire smoke, climate change is exposing lakes to warming and increasingly extreme hydroclimatic variability. In mountain ecosystems, climate change is driving changes in air temperature and the winter snowpack at rates that surpass most places on the planet. Mountain lake ecosystem structure and function is tightly linked with the timing and availability of water, and are likely to be greatly affected by climate-driven changes in precipitation timing and amounts. Although freshwater systems account for less than 0.01% of the world's water by volume, they support nearly 6% of all described species (Dudgeon et al., 2006). These species maintain critical ecosystem functions while responding to environmental conditions from immediate to evolutionary time scales. However, our understanding of the long-term impacts of climate variability on freshwater biodiversity, particularly on small-bodied invertebrates, is limited. Zooplankton are ideal model organisms to study the effects of climate change on aquatic communities, as they play a key role in trophic energy flow, are fundamental to ecosystem-level biogeochemical fluxes, and have short life cycles that allow them to respond quickly to environmental change. **In chapter 3, we used 37 years of lake zooplankton and environmental data in a single mountain lake to investigate the impact of hydroclimate and global change on lake zooplankton community assemblage, abundance, and diversity.** We found that winter snowfall totals significantly influence zooplankton abundance and diversity. Among taxonomic groups, snowfall totals and ice-off date had the strongest effect on cladocerans and significant but less strong effects on copepods and rotifers, highlighting the potential for community shifts based on hydroclimate due to differences in the strength of responses among taxonomic groups. With global change predicted to increase hydroclimatic variability and shift ice phenology, high elevation lake zooplankton communities may undergo significant community restructuring, with whole ecosystem-level implications for trophic energy flow and biogeochemical cycling.

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CHAPTER 1 – Wildfire smoke impacts lake ecosystems

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Abstract

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

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

Data Availability Statement:

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

1.1 | Introduction

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

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

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

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

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

A critical first step in understanding how lakes respond to smoke is characterizing the spatiotemporal dynamics of their exposure. Here we quantify the spatial and temporal extents of smoke cover in relation to burned area and lake locations for all lakes $\geq$ 10 hectares in North America (Farruggia et al., 2024). We used the National Oceanic and Atmospheric Administration Hazard Mapping System Smoke Product (NOAA HMS; Ruminski et al., 2006) from 2019-2021 and the HydroLakes and NHDPlus databases of North American lake maps (Buto & Anderson, 2020; Messager et al., 2016). Our analysis is constrained to North America because of the availability of comprehensive continental-scale smoke and lake geospatial products. For any given lake, a lake smoke-day was defined as a day on which any portion of the lake boundary intersected with an area characterized as smoke by NOAA HMS, which categorizes daily smoke density as light (low), medium, or heavy (high) based on the aerosol optical depth (AOD) from visible satellite imagery (see Ch. 1 Supplemental Methods for details). This smoke-day concept, here for the first time applied in the context of lakes, has previously been used to demonstrate smoke exposure by ecoregion, and provides a basis for this lake-specific metric (Paul et al., 2023). Smoke-days for each lake were subsequently summed on an annual basis. To visualize lake exposure to smoke at the continental scale, we divided North America into 5000 km^2 pixels and for each pixel weighted the number of smoke-days by the corresponding total lake area for that pixel (Fig. 1.1 b-d; see Ch. 1 Supplemental Methods for details). It is important to note that while the NOAA HMS product AOD measurements have been validated and correlated to measured ground-level fine particulate matter ($PM_{2.5}$) concentrations during large fires (Preisler et al., 2015), because this is an optical smoke product based on satellite imagery, smoke mapping can be affected by weather conditions, such as cloud interference. Furthermore, it does not consider the varying height of smoke in the atmosphere, which can lead to highly variable relative rates of atmospheric smoke and ash deposition and light attenuation at the same measured level of smoke density. As a result, our estimates of lake exposure to smoke may be larger than actual exposure. Nonetheless, the spatial scale of this dataset facilitates characterization of wildfire impacts on lakes at the continental scale, and the lake smoke-day metric provides an index by which we can evaluate the impacts of smoke on lakes.

Wildfires burn in spatially discrete areas, but smoke can be transported vast distances and dispersed heterogeneously. For example, smoke from fires burning in Quebec and Nova Scotia in 2023 was transported throughout the Northeast to mid-Atlantic areas of the United States and across the Atlantic Ocean to Western Europe (Copernicus AMS, 2023; NOAA NESDIS, 2023). Given the continental to intercontinental scale of smoke transport, lakes in regions that rarely or never experience wildfire directly may be exposed to smoke for substantial periods of time (Fig. 1.1, 1.2). Smoke cover in North America was temporally variable, but seasonally widespread and persistent across the three years we analyzed (Fig. 1.1, 1.3). Aggregated on an annual basis, 99.3% of the surface area of North America was covered by smoke between the years 2019 and 2021 (Supplemental Table 1.1). During that same period, less than 0.04% of the surface area of North America burned directly each year. The mean number of lakes per day in North America exposed to smoke across our three study years ranged from 1,325,069 - 1,332,077, representing a staggering 98.9 - 99.4% of the estimated total number of lakes $\geq$ 10 hectares on the continent

(Supplemental Table 1.1). The mean number of smoke-days lakes experienced annually during our study period was 38.7, 22.8, and 62.7 days (2019, 2020, and 2021, respectively). The maximum number of smoke-days ranged up to 143 days.

There are several interacting factors that may determine the extent to which lakes are exposed to smoke. The spatial extent, density, and duration of smoke cover establish a template for potential exposure. However, weather conditions affecting the smoke plume and the spatial distribution of lakes within the plume area ultimately determine how many lakes are exposed. For example, the distribution of mean number of smoke-days by latitude differed considerably across years (Fig. 1.2a) and the peak number of smoke-days did not necessarily correspond to regional variation in lake density (Fig. 1.2b). Although 2019 and 2021 had virtually identical smoke cover on an aerial basis, differences in duration of smoke cover and geographic distribution of smoke with latitude meant lake smoke-day exposure was 21% higher in 2021.

The seasonal timing of smoke cover and density that lakes were exposed to varied across study years (Fig. 1.3). Smoke affected lakes nearly year-round, starting in mid-February (week 9) and continuing through December (week 52). While the majority of lake exposure to smoke occurred between May and September, the timing of peak lake exposure to smoke ranged over a narrower period of about two months, from mid-July (week 29) to mid-September (week 38). These are typically the hottest, driest months in North America and coincide with annual peak productivity for many lakes. In 2020, most of the lake-smoke exposures did not occur until after the summer season, into October (Fig. 1.3). Many lakes experience multiple smoke-days in a single week during peak fire periods, demonstrating the pervasive nature of smoke events.

There was a similar pattern among years in the density and spatial extent of smoke and the area burned by wildfires. Between 2019 and 2021, the area of land burned annually in North America was less than 0.01% of the total area of the continent, whereas the area covered by smoke was over 75% of the total area of the continent (Supplemental Table 1.1). 2021 had the largest number of high-density lake smoke-days (Fig. 1.3), which is also the year from our study period with both the largest area burned (0.03% of total area) and the largest area covered by smoke (87.9% of total area covered by smoke). Similarly, 2020 had the lowest number of high-density smoke-days (Fig. 1.3), the smallest area burned (0.0007% of total area) and smallest area covered by smoke (75.2% of total area) (Supplemental Table 1.1).

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

2 | Mechanisms by which smoke affects lakes

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

2.1 | Transport of smoke and ash to lake ecosystems

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

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

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

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

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

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

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

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

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

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

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

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

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

2.5 | Smoke and ash composition and effects on lake chemistry

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

Fire intensity and landscape properties not only influence the chemical and mineral composition of smoke and ash, they also influence the bioavailability of the nutrients bound within. Phosphorus (P), a key limiting nutrient in many lake ecosystems, occurs in much higher concentrations in smoke and ash compared to unburned vegetation. In some cases, smoke and ash can contain 50-times the P concentration of unburned vegetation (Raison et al., 1985); Zhang et al. (2002) found P concentrations within a smoke plume to be ~10 times greater than found over the Tahoe basin. Wildfire also alters the composition of finer particulate matter such as $PM_{2.5}$ – for example, fire episodically elevated atmospheric concentrations of P by >10,000%

(Olson et al., 2023), and in a global meta-analysis, fire was primarily responsible for a 40% increase in atmospheric P deposition to lakes as compared to pre-industrial deposition rates (Brahney et al., 2015). Phosphorous deposition rates near burned areas have been measured as high as 200-700 mg m^2yr^{-1} (Ponette-González et al., 2016; Tamatamah et al., 2005), and are thought to contribute to the eutrophication of lake ecosystems in the area (Brahney et al., 2015; Tamatamah et al., 2005). Deposition rates can be higher from distant fires burning hotter and emitting smaller particles than cooler fires burning locally (Vicars et al., 2010). Though nitrogen (N) and C are more readily volatilized than P, significant concentrations of these nutrients can still be transported by smoke and ash and affect lake nutrient concentrations. Increased concentrations of N, P, potassium, calcium and water-soluble organic C in freshwaters have been attributed to wet deposition from biomass burning in surrounding catchments (Bakayoko et al., 2021; Langenberg et al., 2003; Zhang et al., 2002). Boy et al. (2008) compared the composition of atmospheric deposition in Ecuador during times of burning and no burning and found elevated deposition rates of total N by 171%, nitrate by 411%, ammonium by 52%, and total P by 195%. One observational study showed that lakes near regions of heavy biomass burning have elevated P concentrations and tend towards N limitation (Brahney et al., 2015). Overall, smoke and ash deposition has the potential to influence the relative availability of key lake nutrients (Vicars et al., 2010), which can alter the biotic structure of lake ecosystems (Elser et al., 2009). Still, deposition-driven changes in and lake responses to these nutrients (such as N or P limitation) likely vary by factors such as distance from wildfire and lake trophic status, and should be further investigated along a variety of gradients.

Smoke and ash can also concentrate and transport polycyclic aromatic hydrocarbons (PAHs), hazardous air pollutants (HAPs), and toxic metals such as arsenic (As), chromium, copper, cadmium, mercury (Hg), nickel, lead, antimony, and zinc to lake systems. Concentrations vary by fire intensity as metals and organic compounds are volatilized (Bodí et al., 2014), and many metals can re-adsorb to ash in the atmosphere (Cerrato et al., 2016). Hg is volatilized at relatively low temperatures with a substantive component becoming recalcitrant (0-75%) (Ku et al., 2018), and can result in high soil Hg concentrations that can eventually be transported to aquatic ecosystems (Webster et al., 2016). Experimentally, toxic methylmercury can leach from wildfire smoke and ash once deposited to anoxic sediments (Li et al., 2022). Empirically, lake sediment Hg fluxes have been found to nearly double during periods of high fire occurrence (Pompeani et al., 2018). Other metals, such as As, are volatilized at higher temperatures and can be concentrated in particles from low- to medium-intensity fires (Wan et al., 2021). The type of vegetation or material burned can also change the concentration of particle constituents. For example, particles from burned *Eucalyptus* leaches higher concentrations of As, cadmium, cobalt, chromium, lead, and vanadium, whereas particles from burned *Pinus* leaches higher concentrations of copper, manganese, nickel, and zinc (Santos et al., 2023). High concentrations of heavy metals have been reported in ash residues from residential and structural burns (Nunes et al., 2017; Pereira et al., 2014; Plumlee et al., 2007; Wan et al., 2021), and high concentrations of toxic metals such as copper and lead can be found in $PM_{2.5}$ hundreds of kilometers from the burned area (Boaggio et al., 2022). Concentrations of PAHs can also increase in lake sediments following fire, with low molecular weight PAHs increasing on average more than four-fold (Denis et al., 2012), though in one case remained well beneath lethal concentrations reported for benthic freshwater species (Jesus et al., 2022). In addition, smoke days can have elevated concentrations of HAPs (Rice et al., 2023), some of which may have deleterious effects on aquatic biodiversity (Finizio et al., 1998). Whether heavy metal, PAH, or HAP concentrations in smoke and ash or rates of loading to lake systems occur at concentrations and rates that would affect aquatic organisms has not to our knowledge been determined.

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

There remain several key unknown effects of wildfire smoke and ash deposition on lake ecosystems. First, the literature on the limnological responses to wildfire deposition is heavily skewed towards paleolimnology for field level studies, with few pre- and post-wildfire observational studies, especially from outside of burned catchments. Second, the post-wildfire persistence of direct deposition effects, particle redistribution, or catchment flushing over time are unknown. Third, particle debris in wet deposition is highly oxidizable and therefore could be effective at reducing oxygen concentrations either through photooxidation or microbial respiration. As a result, smoke and ash deposition could decrease dissolved oxygen concentrations while increasing pH, which together can be deleterious to cold-water aquatic organisms (Brito et al., 2021; Earl & Blinn, 2003), and should be further investigated. Finally, smoke and ash have the potential to increase *in-situ* metal concentrations beyond toxicity thresholds (Burton et al., 2016) but little information exists on what other deleterious compounds may leach from wildfire smoke and ash, particularly if residential and commercial areas are burned.

2.6 | Effects of smoke and ash on ecosystem metabolic rates

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

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

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

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

2.7 | Effects of smoke and ash on lake food webs

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

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

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

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

The effects of smoke and ash on lakes are the outcome of mechanisms that operate across multiple spatial and temporal scales (Scordo et al., 2022). Because smoke density can change rapidly with distance from wildfires, the proximity of a lake to wildfire may modulate the magnitude of the teleconnection effect of smoke on lakes (Fig. 1.4a). Generally, lakes face the highest density of smoke, largest particle size, and rates of deposition nearest to wildfire (Fig. 1.4b), which can dramatically decrease the relative availability of UV and PAR. The temporal dynamics of smoke can be highly variable at very short time scales, causing large swings in radiative inputs to lakes. Resulting shifts in UV and/or PAR from reflection or scattering by smoke can cause cascading effects on lake physical, chemical, and biological variables (Fig. 1.4c). Lakes at intermediate (*i.e.*, tens to hundreds of kilometers) or large (*i.e.*, continental to intercontinental) distances from wildfires may still experience significant effects from smoke and ash deposition, but the relative importance of each and the associated shifts in UV and PAR may vary considerably. At intermediate to larger scales, smoke density and ash deposition can be patchy in space and time. Smoke transported at large scales may be more spatially homogeneous with less dense smoke and lower deposition (smaller particle sizes and lower density) over large areas (Fig. 1.4a).

Particles from smoke and ash can vary in terms of chemical characteristics, density, and particle size (Fig. 1.4b). The potential effects these particles on lakes are dependent partly on the quantity and quality of the ash (*i.e.*, density, mass, composition) and partly on background lake nutrient concentration. Ultimately, however, the quality of smoke and ash likely determines the potential for nutrient enrichment following deposition. Smoke and ash quality governs the stoichiometry and trace nutrient concentrations available to autotrophs and heterotrophs. Thus, a mass balance approach that considers both quantity and quality of smoke and ash is necessary to gauge potential impacts to nutrient concentrations in lakes.

Smoke and ash deposition can ultimately change ecosystem metabolic rates through two main pathways (Fig. 1.4c). These pathways include a fertilization effect through nutrient deposition (section 2.4) and reducing availability of PAR and UV light throughout the water column (section 2.2), with each pathway mediated by trophic status and lake size (Fig. 1.4d). If deposition causes a shift in nutrient limitation, it is likely to have a positive impact on net ecosystem production (NEP) by stimulating primary production more than respiration. Variations in lake morphometry and watershed size or hydrology are likely to mediate the metabolic response of lakes to smoke and ash deposition by regulating deposition rates, transport and transformation of particles within the water column, and residence times. Consequently, the effects of particle deposition on ecosystem function might span large time scales.

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

4 | Conclusions: knowledge gaps and research priorities

Despite evidence that smoke and ash deposition impact biological, physical, and chemical processes in lakes, large knowledge gaps impede our ability to predict and manage the responses of lakes to smoke and ash. Measuring the extent and effects of smoke and ash deposition remain challenging. We propose several potential research priorities, practical methodologies, and collaboration avenues here. While current atmospheric monitoring networks are a critical source of data on particle phase pollutants including wildfire-derived particles, they do not comprehensively sample and characterize smoke and ash particles at larger size fractions. For example, in the United States, state and federal air quality regulations primarily monitor PM_{10} and $PM_{2.5}$ size classes that exclude most ash material on a per-mass basis (Pisaric, 2002). Satellite remote sensing of AOD can help improve measurement of atmospheric particle loading (Sokolik et al., 2019), but cannot estimate particle concentrations or distinguish between particle size classes. Pairing remotely-sensed measurements of smoke plumes and airborne fire particles with satellite remote sensing of water quality offers opportunities to analyze the ecological responses of lakes to smoke with high frequency over the long-term. A more detailed characterization and quantification of the attributes of smoke and ash (*e.g.*, beyond coarse density measurements, or presence/absence) is crucial to these efforts. Key questions include: How does the composition, size, and density of particles vary with distance from wildfire? How do deposition rates on lakes vary in relation to local landscape and weather factors?

Moreover, few studies explicitly evaluate the individual and interactive effects of smoke both as a driver of variation in UV and PAR, and as external load of C and nutrients. In watersheds with direct burns, differentiating loading effects from smoke effects is equally important. Identifying the types of lakes that are most sensitive to the teleconnection effects of wildfire vs. direct watershed burning should be a priority, and our conceptual synthesis offers testable hypotheses (Fig. 1.4). Key questions include: How does lake size, lake clarity, or hydrological connectivity affect lake responses to smoke? Are the effects of wildfire smoke transient compared to direct burn effects?

In general, field and experimental studies that collect pre- and post-fire data in lakes are scarce and forced on smaller lakes (McCullough et al., 2019). Larger scale studies are necessary to disentangle the mediating effects of scale and watershed context on the responses of lakes to smoke and ash deposition (Fig. 1.4). Studies that address this should encompass key gradients

(Section 3) such as lake size or clarity, and are necessary to better understand how smoke affects a broad range of lake types. Key questions include: How does lake trophic status or size mediate responses at regional or larger scales? What is the seasonal variation in lake responses to smoke within and across lakes?

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

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

As wildfires, fueled by global change (Abatzoglou et al., 2019), increase in frequency and intensity (Flannigan et al., 2013; M. W. Jones et al., 2022), there is a need to understand their environmental impacts beyond the direct effects of biomass combustion at the watershed scale. Our analysis of lake smoke-days indicates that many regions that historically have not been considered at high risk of wildfires are already experiencing smoke events (Fig. 1.1, Fig. 1.2) and these have the potential to become increasingly pervasive and long-lasting (Fig. 1.3). Here we have reviewed how these smoke events and corresponding deposition can have far-reaching environmental consequences for lakes across spatial and temporal scales. We have also synthesized how these environmental consequences are modified by the characteristics of lakes and the characteristics of both smoke and ash themselves. Because lakes reflect processes within their surrounding catchments and the flowing waters that feed into them, they can also act as sentinels of wider landscape-level changes associated with smoke and ash deposition, such as nutrient and energy cycling (Williamson et al., 2008). Drawing upon research from diverse disciplines beyond limnology, including fire ecology, climatology, and atmospheric chemistry will be key to advancing our understanding of the environmental impacts of wildfire smoke in an increasingly flammable world.

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Figures

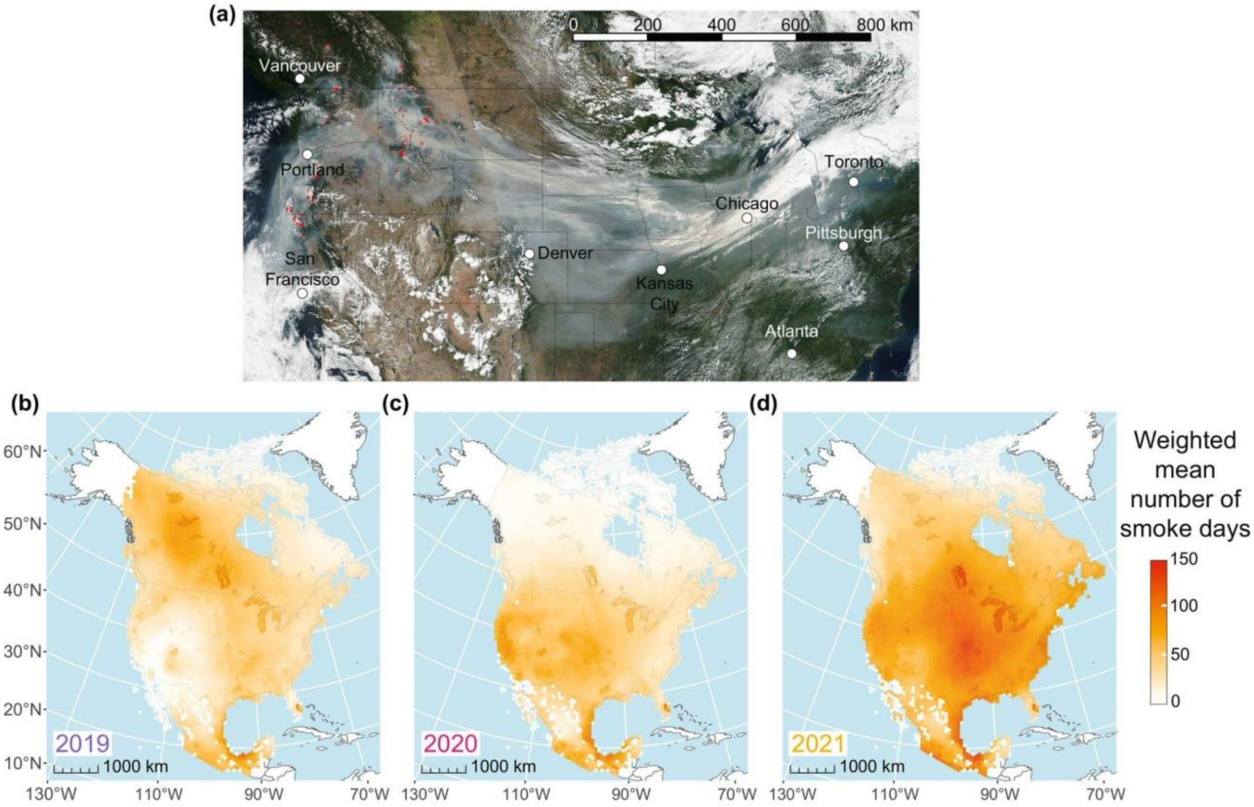

Figure 1.1: (a) Continental-scale smoke transport across North America, moving wildfire smoke from fires in the West thousands of kilometers to the East. Actively burning wildfires are outlined in red. Image: NASA - Jeff Schmaltz LANCE/EOSDIS MODIS Rapid Response Team, GSFC. Sept. 4 2017. (b-d) Map of weighted mean number of smoke-days per 5000 km^2 hexagon for (b) 2019, (c) 2020, and (d) 2021. Values are weighted by the area of each lake within each 5000 km^2 hexagon. Projected in Albers Equal Area (EPSG: 102008). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

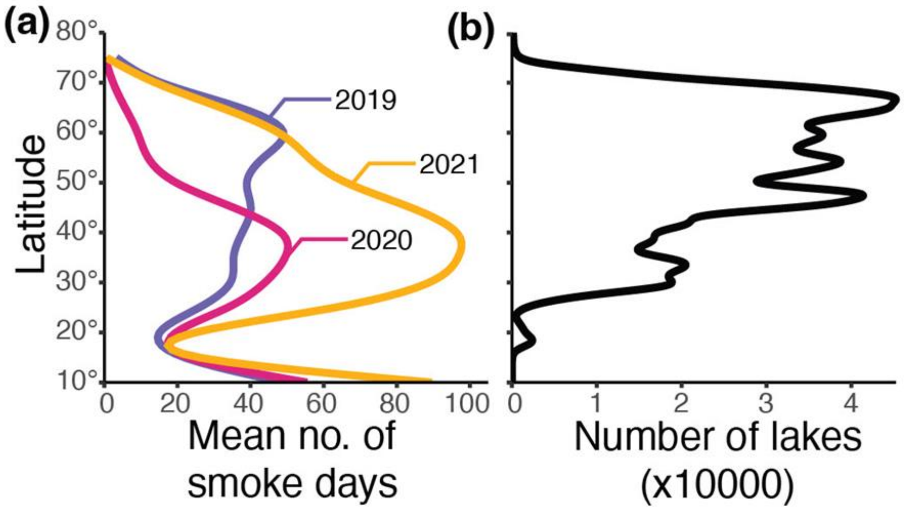

Figure 1.2: Summary of North American smoke-days **(a)** and lake count **(b)** with latitude. Latitude values are in degrees according to EPSG:4326. Lines in (a) are based on a generalized additive model with a k of 10.

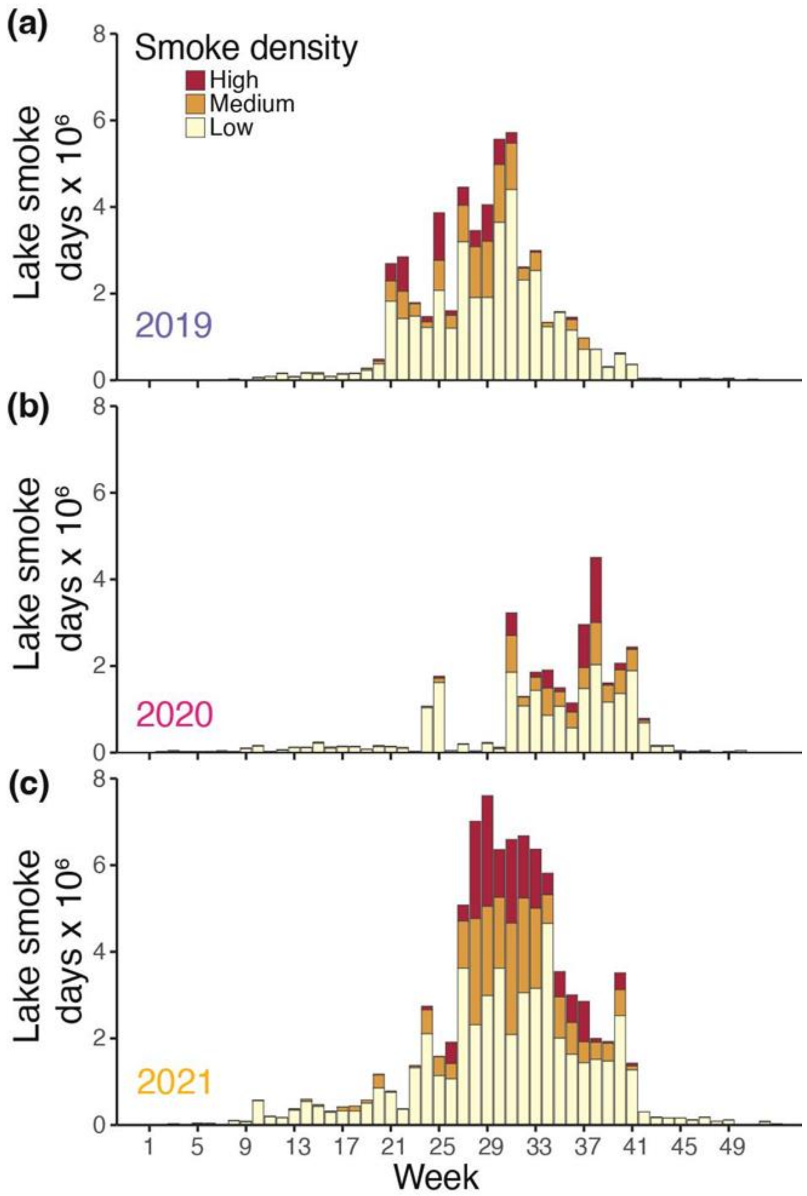

Figure 1.3: Number of cumulative lake smoke-days for each week in North America. For example, in Week 31 of 2019, the 1.3 million lakes experienced nearly 6 million cumulative smoke-days of exposure, with many of the lakes experiencing multiple days of exposure in this week. Exposure is categorized by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

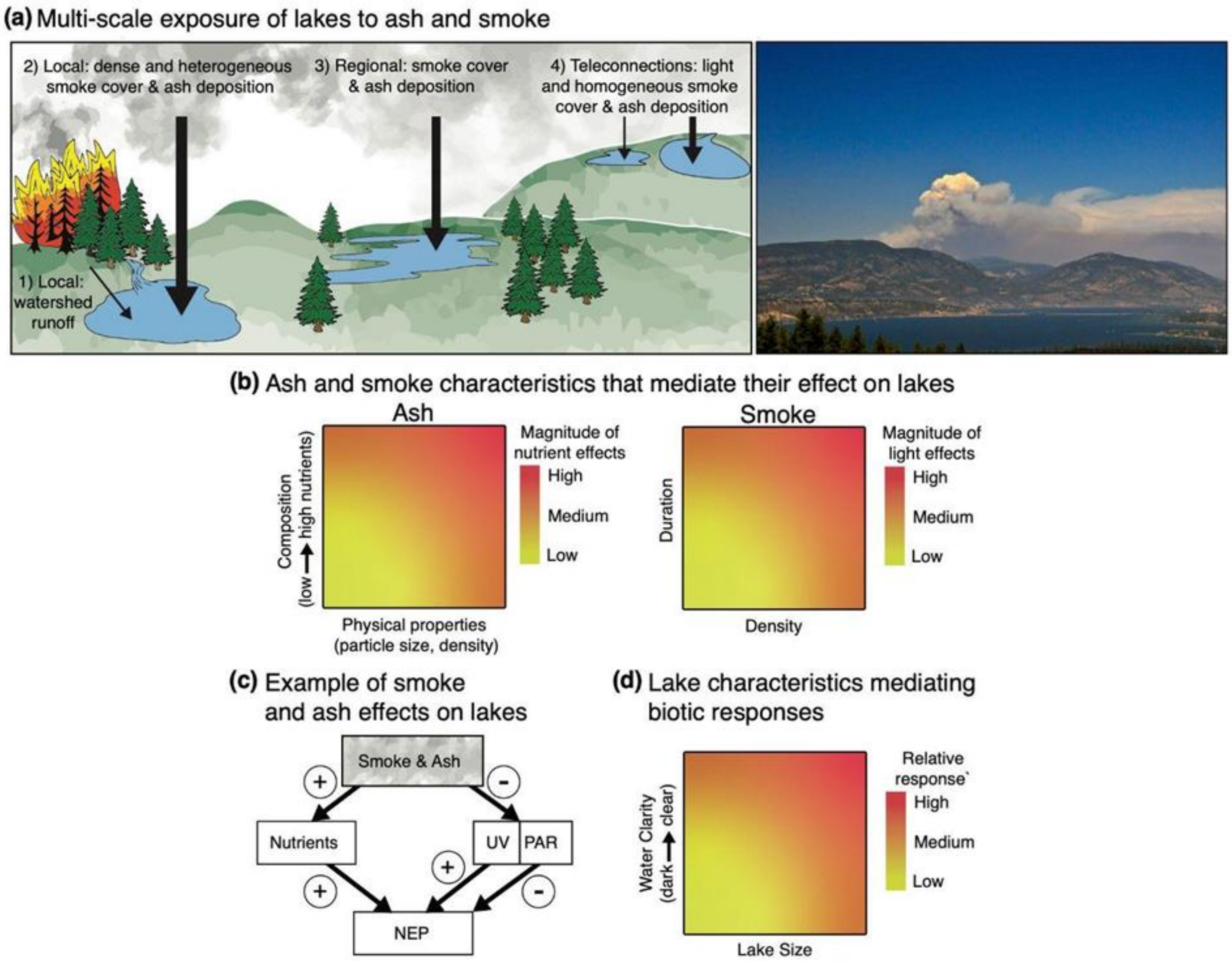

Figure 1.4: Lake responses to smoke and ash involve processes operating at multiple spatial and temporal scales, mediated by factors intrinsic to both smoke and lakes. Our current conceptual understanding is that: deposition rates are expected to decline with increasing distance from fire **(a)**; Smoke 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

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CHAPTER 2 – Wildfire smoke reduces water temperature and shifts metabolic rates in lakes and ponds across a watershed

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Abstract

Pervasive and long-lasting smoke from wildfires can alter fundamental drivers of lake ecosystem structure and function such as water temperature and ecosystem metabolism. However, due in part to the high spatiotemporal variability of wildfire smoke, understanding and quantifying the effects of smoke on lake temperature and ecosystem metabolism remains challenging. To control for the high variability in smoke, we studied six small oligotrophic lentic waterbodies in a single watershed, all experiencing the same smoke events at the same time. We examined thermal and metabolic responses to smoke in a single watershed that experienced an average of 37 days of high- and medium-density smoke in 2020 and 2021. Smoke reduced water temperature and rates of metabolism, with the magnitude of response controlled partly by waterbody size and smoke density. Smoke reduced rates of primary production from 3-49% and rates of ecosystem respiration from 12-60%, highlighting the potential for major impacts of smoke on local and global carbon cycling, particularly given current and projected wildfire regimes.

Introduction

Persistent wildfire smoke can block light and deposit nutrients for weeks at a time, altering key drivers of aquatic ecosystem function even in systems located far from burned areas (Farruggia et al., 2024). In marine ecosystems, impacts are clear – smoke and ash transported from large wildfires have caused large phytoplankton blooms in the Arctic and Southern Oceans (Ardyna et al., 2022; Tang et al., 2021), and substantially altered biogeochemical concentrations at multiple locations in the Pacific Ocean (Coward et al., 2022; Li et al., 2021; Liu et al., 2024). In lentic ecosystems, exposure to smoke is extensive – between 2019 and 2021, 89% of lakes in North America experienced over 30 days of smoke per year (Farruggia et al., 2024). However, the presence, density, and composition of wildfire smoke itself is highly variable in both space and time, which so far has limited our understanding of smoke effects on lentic ecosystems to single-lake case studies (e.g., Lake Tahoe, (Goldman et al., 1990); Castle Lake, (Scordo et al., 2021, 2022)) or has been complicated by high variability in individual lake responses to smoke at the regional scale (Smits, Scordo, Tang, Cortés, et al., 2024). Though we know regional variability can be high, much of our understanding of smoke impacts on lentic ecosystems beyond individual case studies is limited.

Wildfire smoke can reduce incoming solar radiation (McKendry et al., 2019) which in turn can reduce water temperature (David et al., 2018) and shift fundamental ecosystem processes including physical mixing regimes (Woolway & Merchant, 2019), phytoplankton growth rates (Staehr & Sand-Jensen, 2006), and ecosystem metabolism (Brown et al., 2004). However, the magnitude and direction of these shifts likely vary by factors such as lake trophic status, biota, or physical structure (Adrian et al., 2009). Direct evidence of wildfire smoke causing decreases in lake water temperature is limited to a few single-lake case studies (Scordo et al., 2022; Urmy et al., 2016), though it has been demonstrated in river and stream ecosystems (David et al., 2018) and has strong theoretical underpinnings for lakes more broadly (Farruggia et al., 2024; Scordo et al., 2022; Smits, Scordo, Tang, Cortés, et al., 2024). Given the major role temperature plays in fundamental lake processes, quantifying the magnitude and direction of smoke effects on lake temperature while controlling for key determinants such as trophic status and smoke characteristics is crucial for understanding the extent to which smoke disrupts lake thermal dynamics.

Smoke transported to lakes outside of burned areas has also been found to shift lake ecosystem metabolic rates (Scordo et al., 2021, 2022; Smits, Scordo, Tang, Cortés, et al., 2024), though evidence for this is limited mostly to single-lake case studies. Whole-ecosystem metabolism can serve as a sensitive and integrative indicator of change (Hanson et al., 2006), as it incorporates both autotrophic and heterotrophic responses. Rates of ecosystem metabolism (Gross Primary Productivity, GPP; Net Ecosystem Productivity, NEP; and Respiration, R) are governed by complex and sometimes interacting processes, including processes driven by water temperature, light, and nutrients – all of which can be altered by smoke, where the magnitude of change likely depends on smoke density and duration, and waterbody characteristics such as trophic state, and water clarity (Farruggia et al., 2024). The direction of change – whether smoke increases or decreases metabolic rates – also varies across systems (Scordo et al., 2022; Smits, Scordo, Tang, Cortés, et al., 2024). This high variability in smoke over space and time has made determining the magnitude and direction of ecosystem metabolic responses to smoke cover challenging.

Because of the high spatiotemporal variability of smoke, our ability to identify and quantify how and how much smoke changes lentic ecosystem structure and function has been limited. Using high frequency water temperature, dissolved oxygen, and meteorological data from before and during smoke events, we address this critical knowledge gap by investigating the magnitude and direction of the effects of wildfire smoke on temperature and rates of ecosystem metabolism of four ponds and two lakes in a single watershed, all experiencing the same smoke events. In doing so, we control for landscape-scale variability in smoke and trophic status and investigate ecosystem responses to smoke along a gradient of waterbody size. Our analysis specifically addresses the following broad question: How does smoke density and waterbody size mediate lake thermal and metabolic responses to smoke? Here, we investigate the magnitude and direction of change for lentic waterbody temperature and rates of ecosystem metabolism across two different smoke events. We expect reductions in waterbody temperature will scale with smoke density, where higher density smoke will block more incoming solar radiation, which in turn will reduce waterbody temperature (Scordo et al., 2022), though the magnitude of effect likely varies by waterbody size, as lentic waterbody thermal dynamics are influenced by surface area and depth (Holgerson et al., 2022; Magee & Wu, 2017). Higher smoke density and greater reductions in light and temperature will also likely reduce metabolic rates (Smits, Scordo, Tang, Cortés, et al., 2024), but the magnitude of the effect may vary based on whether the system is primarily pelagic or primarily littoral (Scordo et al., 2022).

Methods

Overview and site description:

In order to determine thermal and metabolic responses to smoke, we measured high frequency water temperature and dissolved oxygen (DO) data from six waterbodies from within in the same watershed (Tokopah Basin; watershed area 1908 ha; sites range from 2800-3229 m.a.s.l) located in the Sequoia-Kings Canyon National Park in the southern Sierra Nevada Mountains of California (“Sierra”) (Fig. 2.1A). Our study period spans July 2 – October 2 from 2020-2022, during which two major wildfires (2020; 2021) occurred near our study watershed (Fig. 2.1B), encompassing major smoke events that significantly reduced shortwave radiation (W m^{-2}) (Fig. 2.1C). Our sites represent a range in waterbody size (surface area, depth) that encompass the median depth of the majority of lentic waterbodies in the Sierra (Melack, 2020). All sites are oligotrophic, with seasonal ice-cover during the winter and high snowmelt volume that often exceeds total lake volume (Sadro et al., 2018). The largest/deepest site (Emerald Lake; surface area 2.7 ha; maximum depth 10 m), is a long-term study site and is representative of the thousands of lakes across the Sierra (Tonnessen, 1991). The smallest/shallowest site (TOK30; surface area 0.1 ha; maximum depth 1.5 m) and our other 3 pond sites are representative of Sierra ponds, which have a mean depth of 1.2 m and are the most abundant aquatic ecosystem in the Sierra by number (Melack, 2020).

To quantify site exposure to smoke, we utilized an existing remote sensing dataset applied to our study area which categorizes each day of our study period as a “smoke day” or not at a 4 km resolution (Smits, Scordo, Tang, Farruggia, et al., 2024). A day was considered “smoke day” if smoke density was medium or high and shortwave radiation was reduced by more than 20 W m^{-2} from clear sky conditions (Meyers et al., 2019). The high, medium, and low smoke density categories are from the National Oceanographic and Atmospheric Administration Hazard Mapping System smoke product (see Fig. 2.1C), which are based on estimated concentrations of 27, 16, and 5 μgm^{-3}. We used smoke day data from two points within the watershed and applied the categories by proximity (Emerald, EMLPond1, TOK11 share smoke day data; Topaz, TopazPond, TOK30 share smoke day data).

Instrumentation:

We instrumented each site at the deepest point of each waterbody with one vertical array measuring dissolved oxygen (DO) (PME miniDOT) in the upper mixed layer, and water temperature (Onset HOBO Water Temperature Pro v2 or PME miniDOT) at two or more depths in the water column. We collected continuous water temperature and DO from each site at 60-

minute resolution (Emerald, Topaz) or 15-minute resolution summarized to hourly averages (EMLPond1, TOK11, TopazPond, TOK30). We utilized meteorological measurements from two stations – one ~50 m from the shore of Emerald Lake, and one ~150 m from the shore of Topaz Lake. Each meteorological station measured air temperature (°C), wind speed (m/s), and short and long wave radiation (Wm^{-2}) at 10 second intervals summarized to hourly averages. The station nearest Emerald Lake also recorded precipitation (mm), summarized to daily totals.

Waterbody heat gain:

We calculated hourly whole waterbody heat content (Joules m^{-2}) using the LakeAnalyzer package in R (Read et al., 2011), which utilizes a time series of temperature profiles and the waterbody bathymetry to estimate the heat content of the entire waterbody. For sites where bathymetry was not available (EMLPond1, TOK11, TopazPond, TOK30), we approximated bathymetry using surface area and maximum depth, by assuming a simplified inverted cone shape. We calculated total daily heat gain (Joules m^{-2}) from hourly heat content by calculating the difference between daily maximum and daily minimum (considering only morning hours) heat content for each day.

We compared the median heat gain on smoke days vs. non-smoke days at each site using a Mann-Whitney U test, a non-parametric method for comparing two groups, with a significance threshold of $p<0.05$.

Multivariate autoregressive state space time series modeling:

We used multivariate autoregressive state-space (MARSS) modeling to quantify the relationship between water temperature and smoke, and compare multiple possible metrics for smoke cover (shortwave radiation, smoke density, and PM 2.5) (E. Holmes E. et al., 2012). As water temperature is often temporally autocorrelative from day to day, and as both water temperature and smoke can vary widely through time, we chose to use MARSS modeling because it accounts for temporal correlation and process error when estimating the effect of covariates, and can incorporate environmental covariate time series data to directly quantify the effects of smoke on water temperature. We used the MARSS package in R (E. E. Holmes et al., 2024) to fit the multivariate model. The model we used is as follows:

(1) $\mathrm{x}_t = x_{t-1} + \mathrm{C}_t \mathrm{c}_t + \mathrm{w}_t$ where $\mathrm{w}_t \sim \mathrm{MVN}(0, \mathrm{Q})$

(2) $\mathrm{y}_t = \mathrm{Z}\mathrm{x}_t + \mathrm{v}_t$ where $\mathrm{v}_t \sim \mathrm{MVN}(0, \mathrm{R})$

We aggregated water temperature and the covariates (C) used in the time series model to daily averages. The covariates in this model were shortwave radiation, smoke density, and $\mathrm{PM}_{2.5}$. These covariates all represent quantitative measurements of smoke at different scales. Shortwave radiation data was acquired from the two meteorological stations within our watershed (Fig. 2.1A), smoke density was derived from the NOAA HMS Smoke Product, and $\mathrm{PM}_{2.5}$ was acquired from a single sensor located approximately 30 km from and 2750 m elevation lower than our study area. We tested three kinds of process error (Q): diagonal and equal (all sites have the same error), diagonal and unequal (each site has its own variance), and splitting sites into two groups by spatial proximity, where sites in proximity share process variance (Emerald Lake, EMLPond1, TOK11 shared process variance; Topaz Lake, Topaz Pond, TOK30 shared process variance). We set observation error (R) to be equal at all sites, and modeled each site as a separate state process (Z) (Supplemental Table S2.1).

We tested several model covariate (C) structures. We first estimated a single effect without covariates, representing our null model (Models 1-3; Supplemental Table S2.1). We then modeled covariates with a shared effect among all sites (Models 4-6, 10-12, 16-18; Supplemental Table S2.1). Finally, we modeled covariates with separate effects estimated for each site (Models 7-9, 13-15, 19-21; Supplemental Table S2.1).

We computed parametric confidence intervals for the parameters fitted in the MARSS models using the function *MARSSparamCIs* from the R package MARSS.

Estimating ecosystem metabolism:

We estimated free-water aquatic ecosystem metabolism by modeling daily rates of gross primary production (GPP; mg DO L^{-1} d^{-1}), ecosystem respiration (R), and net ecosystem production (NEP) using the LakeMetabolizer package in R (Winslow et al., 2016). We used hourly DO (mg/L), water temperature (°C), PAR (μmol m^{-2} s^{-1}), wind speed (m s^{-1}), waterbody surface area (m^2), depth of the surface mixed layer (Z_{mix}), the attenuation coefficient for PAR (k_d) to model daily ecosystem metabolism rates using a Kalman filter. Estimating metabolism using a Kalman filter provides better accuracy for time series with high variability because it accounts for both process and observation error (Batt & Carpenter, 2012). We excluded unrealistic metabolism estimates (i.e., negative GPP or positive R).

We compared the median GPP, R, and NEP on smoke days versus non-smoke days at each site using a Mann-Whitney U test, a non-parametric method for comparing two groups, with a significance threshold of $p<0.05$.

Results

Smoke reduced shortwave radiation, particularly under medium- and high-density smoke (Fig. 2.1C; Supplemental Fig. S2.2). There were more medium- and high-density smoke days in

2021 than in 2020 (Fig. 2.2). With this decline in shortwave, water temperature also decreased at every site during the smoke periods in both 2020 and 2021 (Fig. 2.2, Supplemental Fig. S2.3-S2.5). Smoke reduced daily heat gain, but the magnitude of response varied nonlinearly by waterbody size (within years across sites) and by smoke event (within sites across years). Across sites, smoke reduced daily heat gain in both 2020 and 2021. In 2020, only the two mid-sized sites, EMLPond1 (3.1 m maximum depth) and TOK11 (2.3 m maximum depth), showed a significant reduction in median daily heat gain (Fig. 2.3), with a 15.6% and 22.9% reduction, respectively (Supplemental Table S2.5). However, in 2021 all 6 sites showed significant reduction in median daily heat gain, ranging from a reduction of 13% - 28%, highlighting the difference in responses to these two smoke events. Within sites, daily heat gain was reduced to a larger magnitude and to greater significance in 2021 than in 2020, despite the greater frequency of high-density smoke days in 2020 (39 smoke days in 2020 versus 35 smoke days in 2021). For example, in Emerald, Topaz, TopazPond, and TOK30 in 2020, median daily heat gain did not differ significantly between smoke days and non-smoke days. However, in 2021, there is a clear and significant difference between median daily heat gain on smoke days and non-smoke days for each of these sites (Fig. 2.3). Though there are more smoke days in 2020, the change in shortwave radiation between a clear sky day and measured shortwave during the smoke event had higher maximums in 2021 than 2020 (Fig. 2.1C), highlighting the importance of fine-scale variability in smoke density.

Although these periods of temperature decreases and reductions in daily heat gain coincided with regular seasonal cooling (Fig. 2.2), the MARSS models demonstrated that smoke decreased water temperature even during seasonal cooling. Across all years, shortwave radiation most improved model fit to the water temperature data ($\Delta AIC_c > 25$ relative to no-covariate model), followed by Smoke Density ($\Delta AIC_c > 13$ relative to no-covariate model) then $PM_{2.5}$ ($\Delta AIC_c > 5$ relative to no-covariate model) (Fig. 2.3). We found no support for process error other than diagonal and equal, and no evidence for modeling site-specific effects of covariates. Measurements of shortwave radiation were lower during periods of medium to high density smoke cover (Fig. 2.1C; Fig. 2.2).

When evaluating the site-level effects of shortwave on water temperature, there was a slight but nonsignificant difference between sites, where mid-sized ponds experienced the greatest reduction in temperature with reductions in shortwave (Table S3).

Smoke effects on ecosystem metabolism:

Seasonal mean GPP for each site in a non-smoke summer (2022) ranged from 0.31 to 1.28 mg O_2 m^{-2} day^{-1} (Fig. 2.4, Table S6), while seasonal mean R ranged from 0.35 to 1.74 mg O_2 m^{-2} day^{-1} (Fig. 2.5, Table S6). NEP was consistently negative across all sites (Supplemental Fig. S2.6). In sites that are primarily littoral (EMLPond1, TOK11, TOPAZPOND, TOK30), metabolic rates were higher than in pelagic sites - seasonal mean GPP was 0.88 ± 0.43 mg O_2 m^{-2} day^{-1}, seasonal mean R is 1.06 ± 0.57 mg O_2 m^{-2} day^{-1}. In sites that are primarily pelagic (Emerald, Topaz), seasonal mean GPP was 0.47 ± 0.29 mg O_2 m^{-2} day^{-1}, and seasonal mean R was 0.54 ± 0.35 mg O_2 m^{-2} day^{-1} (Table S7).

Smoke significantly reduced both GPP and R at nearly all sites in both smoke years, 2020 and 2021 (Fig. 2.4; Fig. 2.5). Metabolic responses to smoke varied nonlinearly by waterbody size (within years across sites) and by smoke event (within sites across years).

In 2020, most sites experienced a significant reduction in GPP during smoke days, with reductions in mean GPP as high as 37% (0.29 mg O_2 m^{-2} day^{-1}) and as low as 5.5% (0.06 mg O_2

m^{-2} day^{-1}) (Table S8). The exception is the smallest site, TOK30, where GPP increased slightly during smoke days (0.05 mg O_2 m^{-2} day^{-1}, a 3.2% increase in median GPP). TopazPond experienced a small but nonsignificant decrease in rates of GPP between smoke days and non-smoke days. The two mid-sized sites, EMLPond1 (3.1 m maximum depth) and TOK11 (2.3 m maximum depth), experienced the greatest magnitude of change in GPP during smoke days in 2020, with a 37% and 35% (0.29 and 0.23 mg O_2 m^{-2} day^{-1}) reduction in median GPP during smoke days, respectively.

In 2021, nearly all sites experienced significant reductions in GPP, and at a greater magnitude than in 2020: sites experienced as high as a 49% (EMLPond1; a 0.40 mg O_2 m^{-2} day^{-1}) and as low as 15% (TopazPond; a 0.16 mg O_2 m^{-2} day^{-1}) reduction in median GPP during smoke days. Emerald Lake experienced a small but nonsignificant reduction in median GPP during smoke days (0.07 mg O_2 m^{-2} day^{-1}, a 18% reduction). The mid-sized sites again were among the sites experiencing the greatest reductions in GPP, with EMLPond1 seeing the greatest reduction in median GPP (0.40 mg O_2 m^{-2} day^{-1}, a 49% reduction), followed by Topaz (0.16 mg O_2 m^{-2} day^{-1}, a 41% reduction) and TOK11 (0.28 mg O_2 m^{-2} day^{-1}, a 35% reduction).

Rates of R also decreased during smoke days in both 2020 and 2021, with EMLPond1 (the mid-sized site) experiencing the greatest reductions in R during smoke days across sites, and greater magnitudes of change within sites in 2021 than 2020. In 2020, most sites experienced a significant reduction in R during smoke days, with reductions in median daily R on smoke days as high as 39% (EMLPond1; 0.38 mg O_2 m^{-2} day^{-1}) and as low as 15% (Topaz; 0.10 mg O_2 m^{-2} day^{-1}). The exception was the smallest site, TOK30 (1.3 m maximum depth), where daily R increased significantly on smoke days in 2020 (2.01 mg O_2 m^{-2} day^{-1}, an 86% increase). EMLPond1, the mid-sized site, experienced the greatest reduction in R by far, but unlike with rates of GPP, the largest and smallest sites had the next greatest reductions – median R during smoke days reduced by 0.04 mg O_2 m^{-2} day^{-1} (30%) in the largest site (Emerald), and 0.29 mg O_2 m^{-2} day^{-1} (19%) in one of the smallest sites (TopazPond).

In 2021, all but one site experienced significant reductions in R during smoke days, and at a greater magnitude than in 2020: there were reductions in median daily R on smoke days as high as 60% (EMLPond1; 0.61 mg O_2 m^{-2} day^{-1}) and as low as 18% (TopazPond; 0.22 mg O_2 m^{-2} day^{-1}). TOK30, the smallest site, experienced a small but nonsignificant decrease in R (0.20 mg O_2 m^{-2} day^{-1}, a 12% decrease). EMLPond1, the mid-sized site, experienced the greatest reduction in R by far, followed by the largest sites – median R during smoke days reduced by 0.07 mg O_2 m^{-2} day^{-1} (38.3%) in the largest site (Emerald), and 0.26 mg O_2 m^{-2} day^{-1} (38.03%) the next largest site (Topaz). All sites had a negative median NEP on both smoke days and non-smoke days (Supplemental Fig. S2.6; Supplemental Table S2.6).

Discussion

Over 89% of North America's large lakes are exposed to extended periods of smoke each year (Farruggia et al., 2024). Major smoke events in California in 2020 and 2021 covered the entire Tokopah watershed with high- and medium-density smoke for an average of 37 days during our study period and drove significant reductions in water temperature and metabolic rates in lentic waterbodies across the watershed. Smoke reduced incoming shortwave radiation, causing near-immediate decreases in water temperatures across all waterbodies in the watershed. This also resulted in significant decreases in daily heat gain in a third of the waterbodies in 2020 and all waterbodies in 2021, with reductions in daily median heat gain ranging from 3.76% - 28.78%. Smoke also reduced rates of median daily GPP and R in most sites – median reductions in GPP on smoke days ranged from 0.02 to 0.40 mg O_2 m^{-2} day^{-1}, and reductions in R on smoke days ranged from 0.04 to 0.61 mg O_2 m^{-2} day^{-1}. However, the magnitude of those reductions varied across sites within the same smoke event, and also varied within sites across different smoke events, underscoring the importance of both waterbody size and variability in smoke density in determining the magnitude of waterbody responses to smoke. Our findings highlight the clear impact of smoke on small oligotrophic lentic waterbodies, both regionally and globally, and emphasize that the high variability of smoke density can, in part, account for variability in the magnitude and direction of lentic waterbody responses to smoke.

Drivers of lentic thermal responses to smoke

Medium- and high-density smoke reduced shortwave radiation (Fig. 2.1C), and therefore the amount of heat entering each waterbody, driving significant reductions in water temperature (Fig. 2.2; GAM results) and daily heat gain (Fig. 2.3) across our study watershed. Though the water temperature and daily heat gain of all sites were affected by smoke, the magnitude of response varied nonlinearly by waterbody size, with mid-size sites (~2-3 m maximum depth) experiencing the greatest reductions in daily heat gain between non-smoke and smoke conditions (Supplemental Fig. S2.8). The magnitude of response also varied within the same site – nearly all sites experienced greater reductions in daily heat gain during smoke days in 2021 than in 2020, emphasizing the role of variation in smoke density in determining thermal responses to smoke. In studies of smoke effects on lentic systems more broadly, there is evidence for waterbody size driving the direction of thermal responses to smoke, particularly in small systems. In small (0.2 km^2 surface area; maximum depth 35 m), meso-oligotrophic Castle Lake (California, USA), smoke decreased incident solar radiation and water temperature (Scordo et al., 2021). Conversely, in large (496 km^2 surface area; maximum depth 501 m), oligotrophic Lake Tahoe

(California and Nevada, USA) smoke reduced incident ultraviolet light but had little effect on water temperature (Urmy et al., 2016). Because water temperature, stratification, and mixing regimes in lentic systems are heavily influenced by the volume of water being heated or cooled (*i.e.*, surface area and depth) (Holgerson et al., 2022; Magee & Wu, 2017), depth and physical mixing dynamics may play a significant role in determining lentic waterbody thermal responses to smoke. Surface and epilimnetic water temperatures are tightly coupled to air temperature (Piccolroaz et al., 2013) and respond quickly to climate forcing (Adrian et al., 2009) but deep-water temperature trends often vary less than surface temperatures (Winslow et al., 2017), which could explain why smaller systems experience a greater magnitude of thermal response to smoke than larger systems. However, in our case, this relationship between depth and thermal sensitivity did not scale linearly with size - our shallowest sites (< 2 m) experienced a lesser thermal reduction due to smoke than our mid-sized sites. In these tiny systems, where the ratio of water to benthic substrate is low, mediation of heat by benthic sediments could contribute significantly to whole-ecosystem thermal dynamics, making watershed-scale climatic forcing less influential.

Drivers of lentic metabolic responses to smoke

At the watershed scale, ecosystem metabolic responses to smoke were nearly uniform in terms of the direction of the response across sites, but varied widely in terms of the magnitude of the response. Additionally, we also saw differences in the magnitude of response within sites for both GPP and R (Fig. 2.4; Fig. 2.5), where the same sites responded differently to smoke across years, in most cases with a greater magnitude of response in 2021 than 2020 (Supplemental Fig. S2.8). This high variation in waterbody metabolic responses to smoke has been seen in other lake ecosystems, though the magnitude and direction of responses differ from what we found. For example, we found a reduction in GPP under smoke, but in Castle Lake (California, USA), smoke resulted in an increase in epi-pelagic GPP, but had no effect on epi-pelagic R or littoral GPP or R (Scordo et al., 2022). Epi-pelagic GPP in Castle Lake was 5-14% higher during smoke years, whereas our sites experienced reductions in rates of GPP from 3-49% and reductions in rates of R from 12-60%, highlighting the high responsiveness of our watershed to smoke cover in comparison to other ecosystems. Lake Tahoe (California and Nevada, USA) also experienced record-level increases in primary productivity in the upper mixed layer during smoke, likely due to a combination of both light reduction in a photo-inhibited system and the addition of nutrients from ash deposition (Goldman et al., 1990). In a regional study of the impact of smoke on lake ecosystem metabolism in California, rates of R generally decreased in the regional study similarly to what we found in our watershed (Smits, Scordo, Tang, Cortés, et al., 2024). However, rates of GPP both increased and decreased during smoke in this regional study, likely as a result of differences in lake attributes and variability in smoke density and duration (Smits, Scordo, Tang, Cortés, et al., 2024), whereas in our watershed, all sites but one experienced a decrease in GPP during smoke. Because our sites all experienced the same smoke events simultaneously and shared the same trophic status, the consistency in the direction of the metabolic responses to smoke we found underscores the influence of these factors in determining the magnitude and direction of the response, particularly for GPP.

There may also be differences in metabolic responses to smoke based on whether a system is primarily littoral or primarily pelagic. In the case of our study, our shallower sites were ponds with primarily littoral habitat, and our deepest two sites were lakes with large pelagic zones. The nonlinear relationship between magnitude of response and waterbody size could be explained in part by these gradients (Supplemental Fig. S2.8). There are clear benthic-pelagic gradients in lake metabolism, where rates of GPP and R tend to be greater in benthic-littoral zones than in pelagic zones (Van De Bogert et al., 2007). Under the influence of smoke, these gradients could result in distinct differences in lake responses to smoke, even at the within-lake scale (e.g., Scordo et al. 2022). However, when comparing pelagic and littoral responses to smoke within mesotrophic Castle Lake, California, Scordo et al. (2022) found an increase in GPP in the pelagic zone under smoke with no response in the littoral – whereas we found overall decreases in GPP during smoke with greater responses in the littoral than the pelagic sites. There are multiple possible reasons for this: first, in our smallest waterbodies, benthic contributions to ecosystem metabolism may overtake water column metabolism, particularly in the late summer when ponds are warm and the ratio of water to benthic substrate is low. This may also explain why our shallowest sites (<2 m maximum depth) experienced less change than our mid-sized sites – in these tiny systems, the large benthic contribution to metabolism may overshadow watershed-scale processes. Second, the temperature of a lake littoral system may be cooler than that of an entirely littoral pond. Warmer overall temperatures could drive rates of ecosystem metabolism, causing ponds to cycle carbon at faster rates than lake littoral zones, resulting in differing responses to external forcing. Third, our sites are oligotrophic, whereas Castle Lake is mesotrophic. Differences in nutrient and light limitation could drive opposing responses to reductions in light and deposition of nutrients.

Though we utilized high-frequency sensor data for much of this study, we did not have high-frequency chemistry data. From our manually collected water chemistry samples, we were unable to determine if water chemistry was altered as a result of smoke. We were unable to sample water chemistry during the smoke events, due to the actively burning fires. Additionally, the timing of smoke in the late summer/early fall complicates the interpretability of chemical effects (Supplemental Fig. S2.7), as most of the precipitation after these fires was snow rather than rain, so there was no watershed flushing of deposited ash. Spring snowmelt volumes are large, so there was no noticeable carryover of deposition to the next year. These complex interactions between intrinsic waterbody characteristics such as waterbody size or trophic status and extrinsic drivers of ecosystem metabolism affected by highly variable smoke has made it difficult to identify clear mechanistic relationships between smoke and metabolic rates across multiple systems.

Conclusions

We demonstrated that wildfire smoke affects the thermal and metabolic dynamics of small oligotrophic waterbodies, and that while lentic waterbodies all responded fairly uniformly to smoke across a watershed, the scale of response varies in part due to waterbody size and smoke density. The large declines we measured in temperature, GPP, and R during periods of smoke could cause shifts in thermal and mixing regimes, or could impact the food web by reducing rates of cycling, highlighting the need to better understand whole-ecosystem implications of smoke impacts on small lentic ecosystems. Major basic questions in this field remain: How does deposition from smoke events affect water chemistry, and how does deposition affect rates of ecosystem metabolism? What role does trophic status play in mediating the magnitude and direction of thermal and metabolic responses to smoke in aquatic ecosystems? What are the implications of reduced rates of GPP and R on food webs? How does the seasonal timing of wildfire smoke and ash deposition impact seasonal nutrient limitations? What effect does smoke have on local and global carbon cycling in aquatic ecosystems? What physical, chemical, and biological processes drive smoke responses in shallow (< 2m maximum depth) ecosystems?

While we found that waterbody size in part drove differences in the magnitude of lake thermal and metabolic responses to smoke, the underlying mechanisms that determine this relationship, particularly on the small and shallow end of the spectrum, are still unclear. Though exposure to smoke for small lakes and ponds (<10 hectares) has not yet been quantified, small waterbodies overwhelmingly make up the majority of lentic systems. This is true both regionally, where, for example, small waterbodies are the most abundant ecosystem in the Sierra (Melack, 2020), and globally, where over 95% of lentic waterbodies are <10 hectares (Downing, 2010; Verpoorter et al., 2014). These small systems are hotspots for diversity and carbon cycling and subsidize terrestrial food webs. With millions of small waterbodies potentially exposed to smoke each year, this study highlights the potential for large-scale impacts of smoke on local and global carbon cycling, particularly given current and projected wildfire regimes in a climate-modified world.

Figures

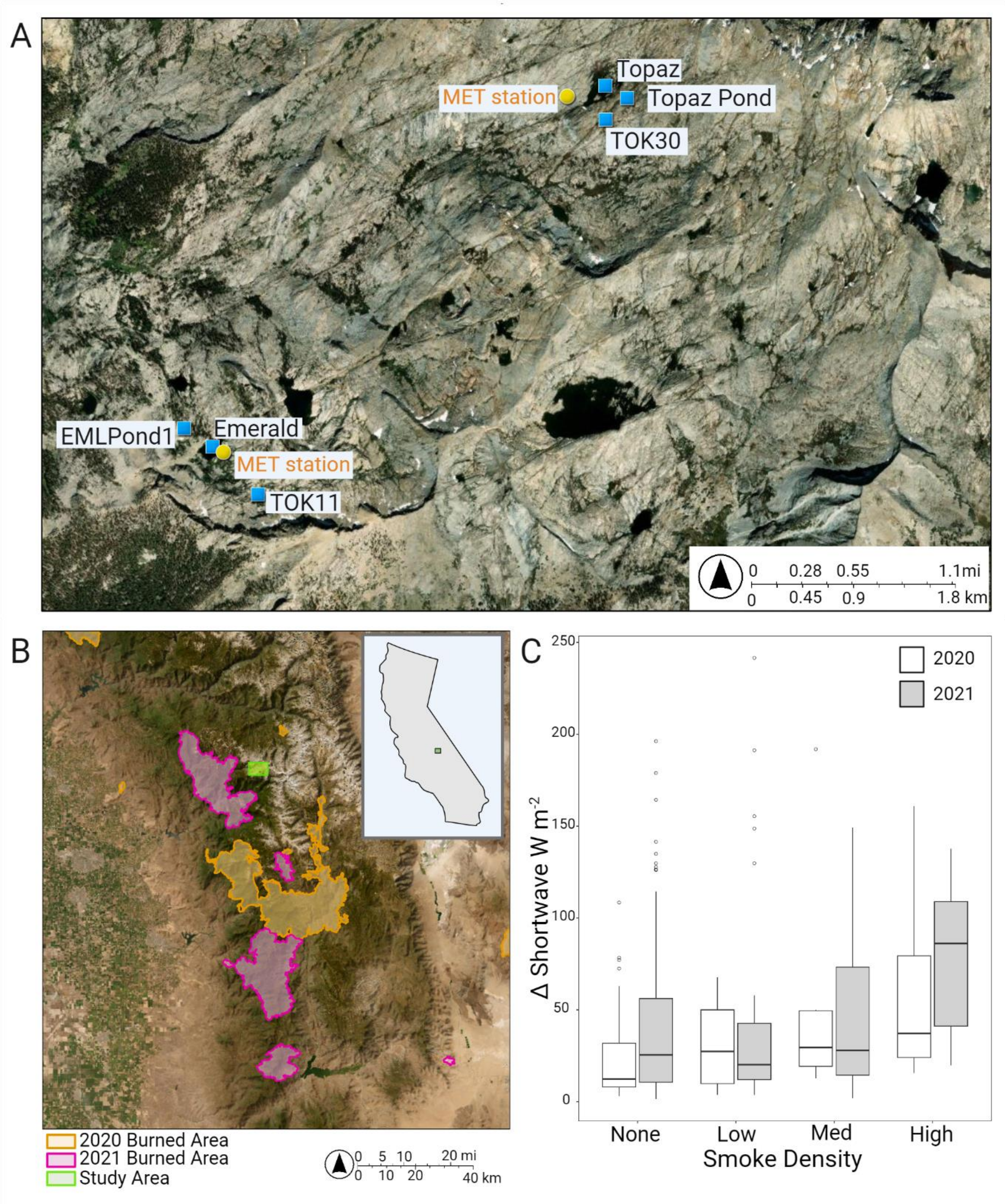

Figure 2.1: (A) Location of study sites (blue squares) and meteorological stations (yellow circles) within the Tokopah watershed (2800-3229 m.a.s.l). (B) Location of study watershed (green box) in the Southern Sierra Nevada Mountains of California, with burned areas from large fires in 2020 (gold) and 2021 (pink) marked, which covered our study watershed in smoke. (C) In years with large smoke events (2020; 2021), the difference between clear sky shortwave and measured shortwave (y-axis), grouped by smoke density category (x-axis).

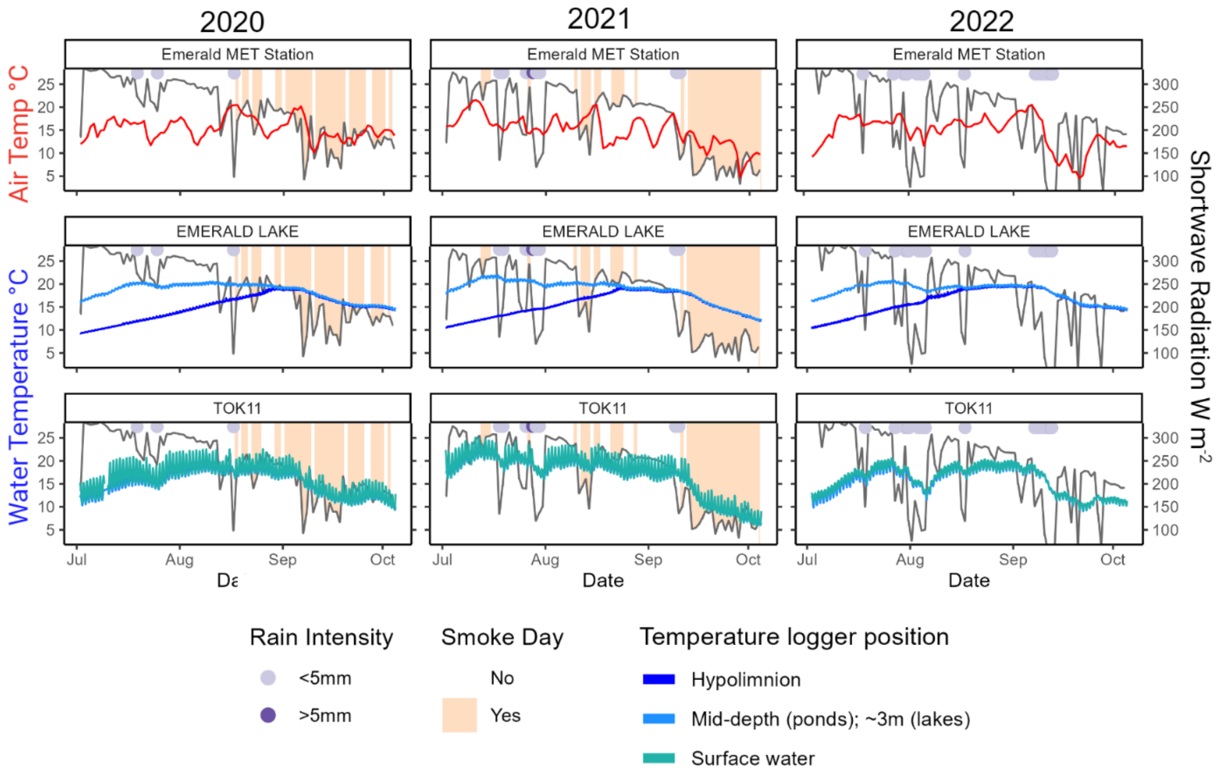

Figure 2.2: Air (red lines) and water (blue lines) temperature time series for each study year in select sites – a representative lake (Emerald; maximum depth 10 m), and a representative pond (TOK11; maximum depth 2.3 m). Shortwave radiation is plotted in the background of each plot (black line), along with smoke day category (orange background denotes a smoke day, defined as a day with smoke density category of medium or high and a reduction in shortwave of more than 20 W m^{-2} from clear sky conditions). Rain events are marked at the top of each plot - light purple if daily precipitation total was < 5 mm and dark purple if daily precipitation total was > 5 mm. In dry hydroclimatic years (2020-2022 were dry), the smallest rain events to cause increases in stream discharge in this watershed during summer were storms producing > 5 mm of runoff, hence the distinction here. The meteorological station (Emerald MET station) is located adjacent to the two plotted sites (Emerald, TOK11).

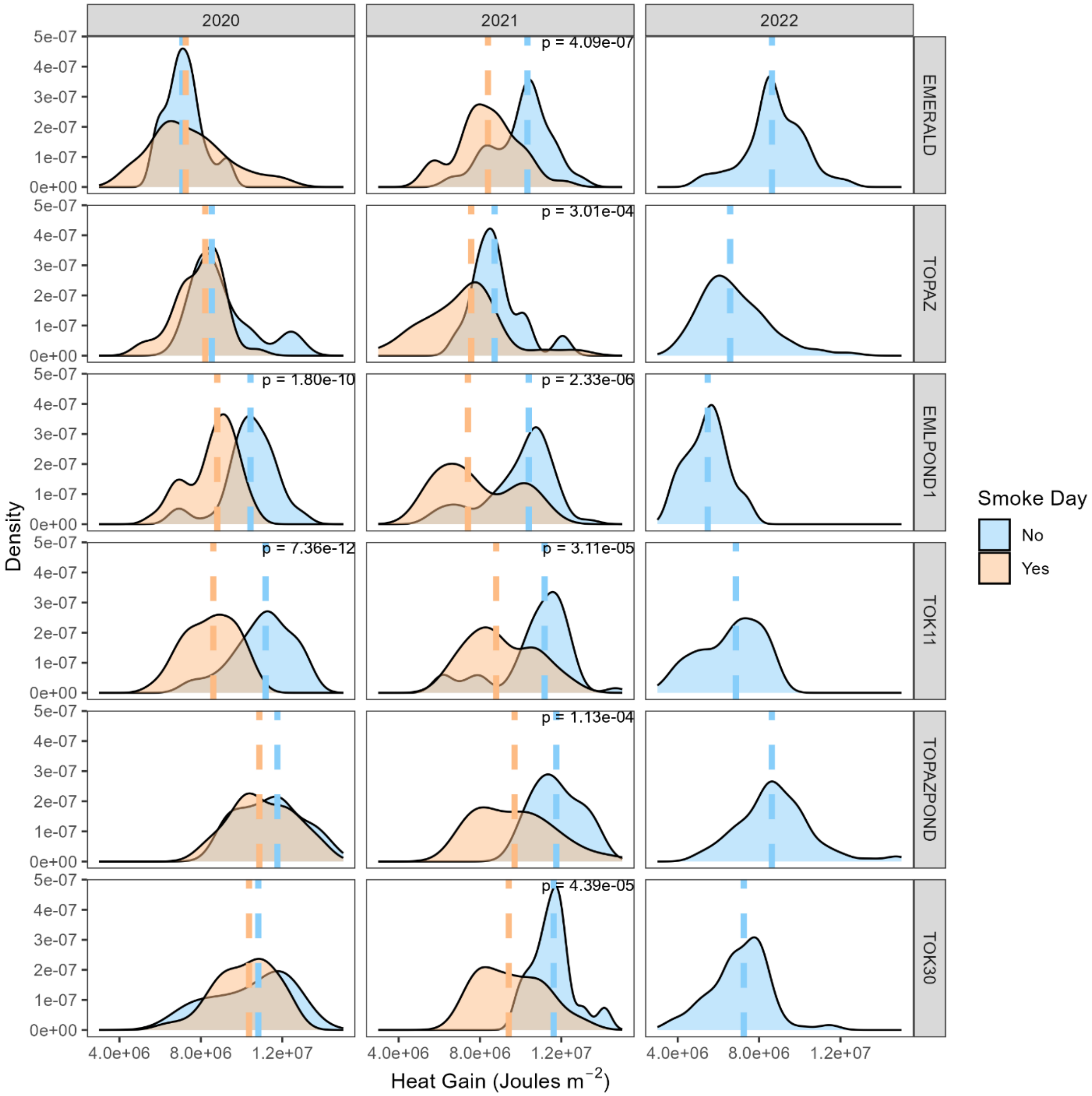

Figure 2.3: Density plots of daily heat gain by site for each year, colored by whether it was a smoke day (orange) or not a smoke day (blue). Median daily heat gain for each type of day is denoted by the dashed vertical lines. We compared the median heat gain on smoke days vs. non-smoke days at each site using a Mann-Whitney U test, with a significance threshold of $p<0.05$. The p-value is displayed in the upper right corner of each plot if $p<0.05$. Rows are ordered by waterbody size, from large to small.

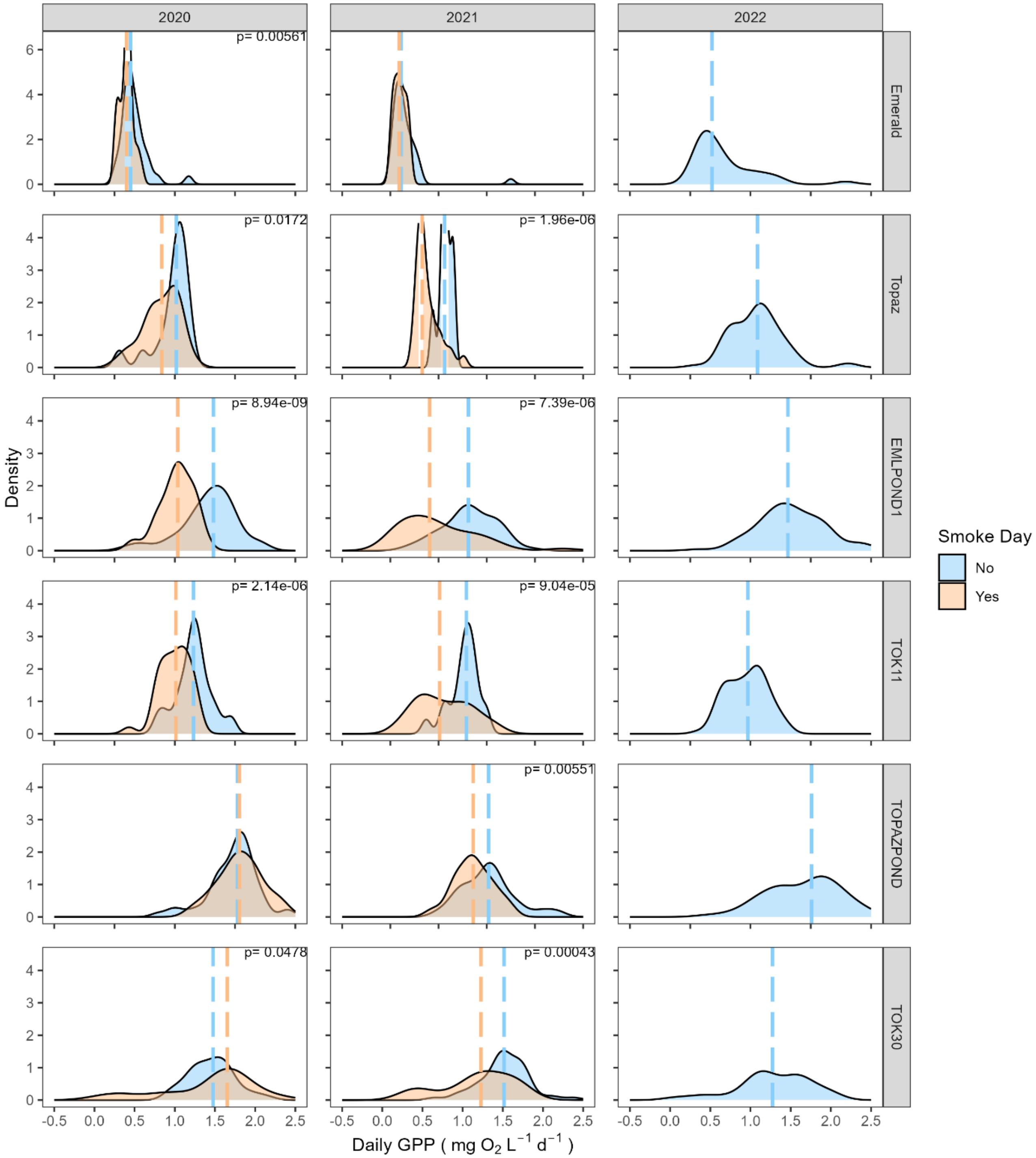

Figure 2.4: Density plots of daily gross primary productivity (GPP) by site for each year, colored by whether it was a smoke day (orange) or not a smoke day (blue). Median daily GPP for each type of day is denoted by the dashed vertical lines. We compared the median GPP on smoke days vs. non-smoke days at each site using a Mann-Whitney U test, with a significance threshold of $p<0.05$. The p-value is displayed in the upper right corner of each plot if $p<0.05$. Rows are ordered by waterbody size, from large to small.

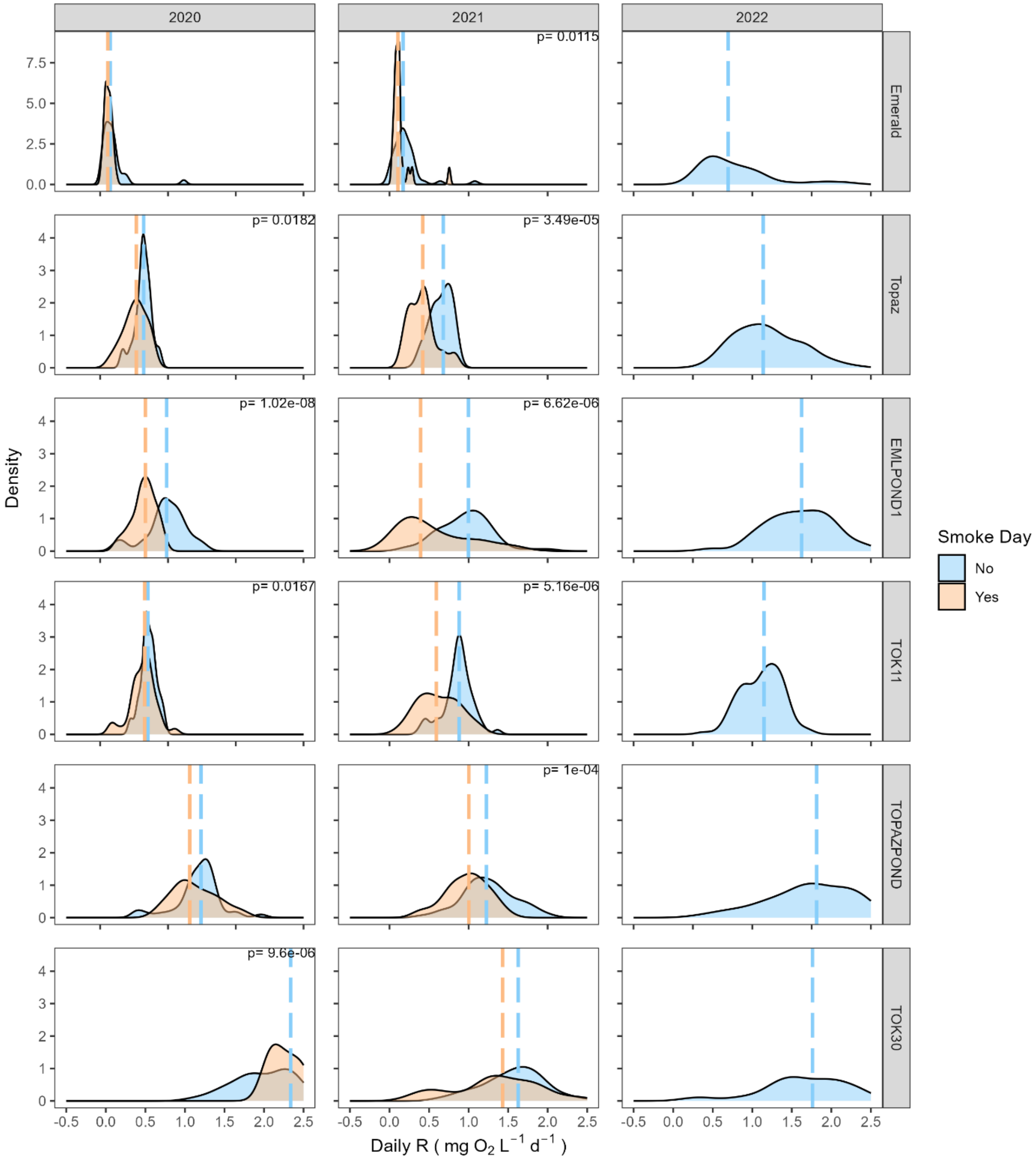

Fig. 2.5: Density plots of daily ecosystem respiration (R) by site for each year, colored by whether it was a smoke day (orange) or not a smoke day (blue). Median daily R for each type of day is denoted by the dashed vertical lines. We compared the median R on smoke days vs. non-smoke days at each site using a Mann-Whitney U test, with a significance threshold of $p<0.05$. The p-value is displayed in the upper right corner of each plot if $p<0.05$. Rows are ordered by waterbody size, from large to small.

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CHAPTER 3 – Winter hydroclimate drives mountain lake zooplankton ecology

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Abstract

Climate change is driving increasingly extreme interannual hydroclimatic variability, which can affect critical physical and biological components of lake ecosystems. Mountain lakes regularly experience high interannual hydroclimatic variability, and winter snowpack and ice cover are tightly linked to physical and chemical lake features such as thermal regimes, flushing rates, and nutrient concentrations. However, our understanding of the long-term impacts of variability on freshwater biodiversity, particularly on small-bodied invertebrates, is limited. Zooplankton are ideal model organisms to study the effects of climate change on aquatic communities, as they play a key role in trophic energy flow, are fundamental to ecosystem-level biogeochemical fluxes, and have short life cycles that allow them to respond quickly to environmental change. We sought to understand the extent to which hydroclimatic variability influences the diversity, abundance, and biomass of mountain lake zooplankton in a single lake over a 37-year time period (1984-2021). Mountain lake zooplankton follow a regular seasonal pattern, with significantly higher abundance and diversity during the ice-free season, and distinct differences in community composition between ice and ice-free periods We found that winter snowfall totals and ice-off date significantly influence zooplankton abundance and diversity. Among taxonomic groups, snowfall totals and ice-off date had the strongest effect on cladocerans and less strong but still significant effects on copepods and rotifers, highlighting the potential for community shifts based on hydroclimate due to differences in the strength of responses among taxonomic groups. With global change predicted to increase hydroclimatic variability and shift ice

phenology, high elevation lake zooplankton communities may undergo significant community restructuring, with whole ecosystem-level implications for trophic energy flow and biogeochemical cycling.

Introduction

Rising global air temperatures due to climate change is causing increasing variation in and intensification of the hydrologic cycle, including changes in the timing and amount of precipitation (Huntington, 2006; Stevenson et al., 2022). This hydroclimatic variability can drive complex and sometimes disparate physical and biological responses in lake ecosystems (Winder & Schindler, 2004), including shifts in the phenology of lake stratification (Woolway et al., 2021), changes in seasonal succession and community structure of zooplankton (Beaver et al., 2019), or cross-seasonal trophic cascades (Hébert et al., 2021). Lakes are an ideal study system in which to test for the effects of increasing hydroclimatic variability (Woolway et al., 2020). They respond rapidly to changes in the environment and are often considered sentinels for change (Adrian et al. 2009, Williamson et al. 2009). Despite the sensitivity of lakes to change and the potential for increasingly extreme hydroclimatic variability to significantly alter lake trophic pathways and community structure, studies utilizing long-term community time series to link freshwater biodiversity to changes in climate have focused primarily on fishes (*e.g.*, (Comte et al., 2021; Kuczynski et al., 2023), or focused solely on warming trends rather than variability (*e.g.*, (Carter & Schindler, 2012; Diovisalvi et al., 2018).

Mountain lake ecosystems experience very high seasonal and interannual variability in hydroclimate (Sadro et al., 2019), and key hydroclimate variables such as snowpack size and ice cover phenology drive fundamental lake ecosystem structure and function, including discharge and flushing rates, thermal stratification, water temperature, nutrient concentrations, and primary production (Oleksy et al., 2020; Preston et al., 2016; Sadro et al., 2018; Smits et al., 2020, 2021). While the strong deterministic effects of hydroclimatic variability on mountain lake physical processes and primary production have been well established, our understanding of its effects on key trophic levels such as zooplankton community structure is still limited (but see Powers et al., 2022). Zooplankton communities in mountain lakes are well suited to test the role of hydroclimate variability, because traditional top-down trophic controls on zooplankton diversity and abundance are often weaker in oligotrophic lakes (Elser & Goldman, 1991; Mehner et al., 2008; Rogers et al., 2020), and in colder, high-elevation lakes (Symons & Shurin, 2016). As a result, mountain lake zooplankton may be more susceptible to shifts in community structure driven by environmental change.

Zooplankton play an important role in trophic energy flow (Strecker & Arnott, 2008) and provide fundamental linkages to ecosystem-level biogeochemical fluxes (Yvon-Durocher & Allen, 2012), so any shifts in community structure have the potential to have ecosystem-level consequences. In mountain lake ecosystems, winter hydroclimate drives summer water temperatures and nutrient concentrations, where years with larger snowpacks result in lower mean summer temperatures and lower nutrient concentrations (Sadro et al., 2018; Smits et al., 2020); Fig. 3.1). These differences in temperature and nutrients could affect the strength and influence of trophic controls, shift distributions of biomass, and alter size spectrums within phytoplankton and zooplankton communities, with implications for food web structure and ecosystem function (Hébert et al., 2017; Petchey et al., 2008; Yvon-Durocher et al., 2011). On seasonal scales, higher seasonal temperatures can result in greater predator biomass and top-down control and lower producer biomass (Shurin et al., 2012), stronger pelagic trophic cascades (Symons & Shurin, 2016), and reduced sensitivity to nutrient enrichments (Kratina et al., 2012).

Because zooplankton hold key roles in trophic interactions, even these short-term responses to climate variables could result in changes across the food web.

Long-term climate warming can also change zooplankton communities - in one lake in Alaska, the effects of warming over four decades far outweighed biotic interactions in determining community composition (Carter et al., 2017), and earlier ice-off dates and warmer summer air temperatures significantly influenced cladoceran densities (Carter & Schindler, 2012). Climate cooling can also significantly increase species richness in lake zooplankton (Stemberger et al., 1996). There is also evidence of coupling between meteorological forcing and zooplankton biomass, where, for example, large-scale meteorological phenomena like the North Atlantic Oscillation drives warmer spring water temperatures, which then drives higher daphnid biomass (Straile, 2000). The driving influence of temperature and climate variables on zooplankton communities, biomass, and abundance across scales suggest the potential for large seasonal to interannual differences in mountain lake zooplankton community structure due to the deterministic role hydroclimatic variables play in lake thermal regimes.

There are also strong links between mountain lake ice-cover phenology and primary production - summer algal biomass is often dependent on length of the ice-free season, where algal biomass increases with length of ice-free period (Preston 2016, Oleksy 2020). This strong seasonality makes mountain lakes particularly susceptible to the effects of extreme hydroclimatic variability, as physical processes are controlled by stark seasonal differences such as ice cover, and organismal life-history often depends on phenological cues related to seasonal temperature (Winslow et al., 2017). Differences in the timing and availability of phytoplankton as a food source can result in both community and species-level shifts in zooplankton due to diversity of life history traits, which may be particularly amplified by the short ice-free season and the importance of timing growth and reproduction with optimal food and thermal conditions (Gliwicz et al., 2001; Pérez-Martínez et al., 2013). At the community level, following a common bottom-up model on seasonal zooplankton biomass dynamics in oligotrophic lakes (Sommer et al., 2012), mountain lake zooplankton grazers tend to increase in biomass and abundance during lower snowpack summers, driven in part by higher phytoplankton biomass (e.g., chlorophyll-a; (Powers et al., 2022), though they are not always perfectly coupled (Loria et al., 2020) (Fig. 3.1). At the population level, life history traits can dictate differences in responses to environmental and bottom-up pressures. For example, longer-lived copepods can utilize fat storage as an overwintering strategy and to support spring egg production (Hébert et al., 2021; Schneider et al., 2017), whereas short-lived and fast-reproducing cladocerans and rotifers do not, highlighting that zooplankton communities have the potential to undergo a wide range of shifts in diversity and/or relative abundance as a result of differences in life history and optimization strategies for dealing with their environment. Despite the potential for zooplankton communities to respond quickly to their environment in a diversity of ways and the ecosystem-level impacts of shifts in zooplankton community structure, the influence of hydroclimate on mountain lake zooplankton abundance, biomass, and diversity, particularly over long time-scales, remains poorly understood.

Here, we investigate 37 years of zooplankton community structure and abundance/biomass in Emerald Lake, an oligotrophic mountain lake in the Sierra Nevada mountains of California, USA. We identify the role and influence of variability in hydroclimate, and specifically address the following questions: (Q1) What is the seasonal and interannual variation in zooplankton diversity, abundance, and biomass? And (Q2) To what extent does hydroclimate influence zooplankton diversity, abundance, and biomass during the ice-free season?

Q1-Seasonal variation hypothesis: We hypothesize that the seasonal pattern in zooplankton diversity, abundance, and biomass to be highest during the ice-free growing season, when primary productivity is highest. We expect zooplankton abundance and biomass to follow a standard model for ice-covered oligotrophic lakes with fish. This model predicts zooplankton biomass to peak in the ice-free season following the spring phytoplankton peak, with strong physical controls (ice cover) during the winter, and stronger trophic controls during the summer (bottom-up food availability and quality, and top-down fish predation pressure) (Sommer et al., 2012). The model is corroborated by several in-situ examples from mountain lake ecosystems, which link chlorophyll-a (a proxy for phytoplankton) to increasing zooplankton biomass, and also abundance (Loria et al., 2020; Oleksy et al., 2020). Seasonal ice phenology in other mountain lake ecosystems also contributes to differences in zooplankton diversity, abundance and biomass (Loria et al., 2020; Powers et al., 2022), and diversity tends to increase with increasing productivity (Simões et al., 2013). We expect to see the same effect in Emerald Lake.

Q1-Interannual variation hypothesis: We hypothesize that there will be high interannual variability in zooplankton abundance, biomass and diversity. Additionally, *Q2-Hydroclimate variability hypothesis*: we hypothesize that variability in hydroclimate will significantly drive this interannual variability. In years with larger snowpacks, later ice-off dates and lower nutrient concentrations, we expect lower zooplankton abundance and biomass during the ice-free season due to food limitation, and higher diversity due to greater competition for limited food resources. In Emerald Lake, it has already been demonstrated that larger snowpacks and later ice-off dates result in lower nutrient concentrations, lower mean temperatures, and lower phytoplankton biomass (Sadro et al., 2018; Smits et al., 2020). Given the influence of hydroclimate on physical lake properties that drive bottom-up trophic controls, we hypothesize that hydroclimate will act as a “master” variable which significantly structures the zooplankton community, as it does in other major areas of the lake structure and function.

Methods

Study site

Emerald Lake is a small (0.027 km^2, maximum depth 10 m), high-elevation (2800 m.a.s.l) oligotrophic lake in Sequoia Kings Canyon National Park in the Sierra Nevada Mountains of California, USA. This lake has been the subject of long-term limnological research and monitoring since 1983, and is representative of the thousands of small, oligotrophic, high elevation glacial cirque lakes in the Sierra Nevada (Melack & Stoddard, 1991). Its hydrology is primarily snowmelt driven, and receives ~86% of its precipitation as snow (Sadro et al., 2018), but there is high interannual variability in snowpack size and ice-off dates. Snowpack size largely regulates ice-off dates and summer lake temperatures (Smits et al., 2020, 2021). Non-native brook trout (*Salvelinus fontinalis*) were last stocked in Emerald Lake in 1959 (ARB report), and have since maintained a self-sustaining population of about 1000 individuals (as last surveyed in 1987) (Melack et al., 1989). There are no other fish present in this historically fishless lake. The food web is relatively simple, with producers (phytoplankton), consumers (zooplankton), and predators (trout). Biogeochemical sampling has occurred throughout the study period, though has varied in frequency through time. Collection, processing, and analysis details are well-documented in (Sadro et al., 2018).

Zooplankton sampling

Zooplankton have been collected regularly from 1984 to 2021 via vertical tows using a 64-micron zooplankton net from near the deepest point of the lake (9 m) to the surface. The net diameter has varied through time, ranging from 0.13-0.30 m diameter. Samples were collected in duplicate and preserved in the field in 10% sucrose buffered formalin or in 70% ethanol. Sample frequency and timing varied through time, but most years have at least one sample during ice cover, and one sample during the ice-free season. Samples taken during the ice-covered season were retrieved using a net 0.13 m diameter, lowered to 9 m through a hole drilled in the ice with a hand ice auger at the deepest point in the lake.

Zooplankton enumeration and identification

From 1984-1994 – Zooplankton from each sample was concentrated into a known volume of de-ionized water and subsampled with a Stempel pipette. Rotifers and microcrustaceans were subsampled separately, due to the typically high abundance of rotifers. At least 100 individuals were identified and counted per subsample, and at least three subsamples were counted per sample, using a compound microscope at 25x (Engle & Melack, 1995; Melack et al., 1989). Only whole individuals were counted, molts and partial specimens were excluded. Zooplankton were identified to genus (rotifers) or species (microcrustaceans). From 2003-2009, rotifers and microcrustaceans were subsampled together rather than separately, and at least 500 individuals were identified with at least two subsamples counted. Otherwise, sample identification from this time period followed methods for 1984-1994.

From 1994-2021 – Zooplankton were similarly concentrated and subsampled, using a protocol designed by Girard and Reid (Girard, 1990) and adapted for Sierra zooplankton communities as described in (Symons & Shurin, 2016). Samples were counted using a compound microscope at 25x – 40x. All other methods were the same as the 1984-1995 period. Samples from years 1995-2001 were removed from the dataset due to poor sample preservation.

All sample enumerations were converted to density (individuals/m^3) based on sample volume, net diameter, and tow length, assuming 100% net capture efficiency.

We calculated zooplankton biomass for each species using the average length for each species (or closely related species when species-level data was not available) and published length-weight regressions (Supplemental Table 3.1).

Climate data

To characterize hydroclimate variation, we utilized daily air temperature and precipitation from a data product of daily high spatial resolution (4-km) gridded surface meteorological (gridMET) data from 1983-2024 (Abatzoglou, 2013). To get snowfall totals from gridMET's precipitation dataset, we converted daily gridMET precipitation to snow based on a temperature-based regression model (Dingman, 2015), as in Smits et al., 2021. This model converts precipitation to snowfall based on air temperature, where if air temperature is <0 °C, snowfall is equivalent to precipitation, and if between 0-6 °C, snowfall = precipitation – 0.1678*air temperature. Though Emerald Lake has an on-site meteorological station, there were several gaps in the data that were too large to address through standard methods of gap-filling. The gridMET data and Emerald meteorological data are highly correlated (air temperature Pearson's correlation = 0.97) and the Emerald Basin snow water equivalent (SWE) measurements and calculated gridMET snowfall totals are also strongly correlated (Pearson's correlation = 0.88). As a result, for consistency and to reduce sources of error or variation into our modeling, we used only gridMET air temperature and snowfall data in this study, rather than using gridMET to gap-fill Emerald Lake meteorological data.

In years 1991-2013, ice-off dates were determined using in-situ sensor measurements of water temperature, light, and dissolved oxygen, as in (Smits et al., 2021). For all other years, we predicted ice-off date from 1984-2024 for years missing this data. Because gridMET winter snowfall total and Emerald Basin SWE are strongly correlated, we used snowfall totals (mm) as a proxy for SWE in any year missing this data. We then used a linear regression model to predict ice-off date based on SWE (ice-off date ~ SWE) to fill in any years missing ice-off date with a predicted ice-off date (See Ch. 3 Supplemental Methods for details and code).

Community analyses

To test for patterns and variation in zooplankton community composition, we utilized non-metric multidimensional scaling (NMDS) with a Bray-Curtis dissimilarity index using the package ‘vegan’ in R (Oksanen et al., 2022). NMDS is ideal for ecological community data as it does not require normality or assume linearity, and is robust to outliers (McCune & Grace, 2002). Presented models were run in two dimensions (k=2) under 1000 iterations. To identify whether community composition differed based on season and hydroclimate, we added ellipses around categorical groups (season – ice vs. no ice, and hydroclimate – wet, average, dry snowfall categories) at 95% confidence intervals. To test whether Shannon’s Diversity, abundance, and biomass differed based on season and hydroclimate, we used a basic one-way analysis of variance (ANOVA) to test for differences in means by season and by hydroclimate. We calculated Shannon’s Diversity Index using the function ‘diversity’ from the package ‘vegan’ in R.

Generalized additive models

We used generalized additive models (GAM) using the package 'mgcv' in R to quantify the extent to which hydroclimate influences zooplankton abundance and biomass during the ice-free season (Wood, 2023). We also used a GAM to visualize the seasonal pattern in zooplankton abundance and biomass (including both ice-free and ice-covered seasons). GAMs model nonlinear effects of predictor variables on the response variable, and provide significance testing of these relationships. Our GAMs utilized a gamma distribution with a log link function, which is appropriate for modeling positive continuous data such as zooplankton densities.

We tested the following predictors for our models: month, year, annual snowfall total, ice-off day of year (DOY), and summer mean air temperature (Table 3.1). We expected month to reveal any seasonal trends, and year to reveal any trends over the whole time series. Annual snowfall totals and ice-off DOY are highly related at Emerald Lake (Smits et al., 2020), and as a result, we expected these two predictors to share a similar effect in the model. However, we tested both snowfall totals and ice-off DOY as predictors because they may affect slightly different ecological mechanisms that matter to zooplankton, where ice-off DOY directly affects the length of the growing season and timing and amount of food availability, and snowfall total directly affects flushing rates and nutrient concentrations (Fig. 3.1).

We included summer mean air temperature as a predictor to test whether summer air temperatures (predictor) influenced summer zooplankton abundance or biomass (response). In studies that focus on the effects of warming on zooplankton biomass and abundance, summer air temperature is often a very important variable in explaining model variance (e.g., (Cremona et al., 2020). We were interested to see how much this variable explained zooplankton abundances in our model.

After determining the best model structures for total zooplankton abundance (response ~ month + year + Ice off DOY; response ~ month + year + total snowfall), we applied the same model structures to the following taxon-specific response variables: cladoceran abundance, rotifer abundance, and copepod abundance. This was to test if different taxa respond differently or similarly to hydroclimate.

Results

Hydroclimate drives variation in key environmental variables

There was high variability in total annual snowfall, mean annual temperature, and day of ice-off throughout the 37-year time series (Fig. 3.2; Supplemental Table 2). Much of the lake water chemistry was related to winter snowfall totals, with ice-free season averages of particulate Carbon (PC) (range in ice-free season averages: 10.2 - 332.7 μg/L), particulate Nitrogen (PN) (range 1.1 - 40.7 μg/L), Nitrate/nitrite (range 0.1 - 6.9 μmol/L), and dissolved organic carbon (DOC) (range 35.9 - 92.3 μmol/L) exhibiting a negative linear relationship with increasing snowfall totals. During the ice-covered season, water chemistry variables were generally not related to snowfall totals, aside from nitrate/nitrite, which had a positive linear relationship with increasing snowfall totals. Ice off date (Supplemental Figure S3.1) had a similar relationship to lake water chemistry, likely because of the strong relationship between total snowfall and ice-off date (Smits et al., 2021). There were no significant relationships between seasonal average water chemistry variables and seasonal total abundance (Supplemental Figure S3.3).

Seasonal variation in zooplankton community structure, abundance, and biomass

The zooplankton community followed a regular seasonal pattern, with higher abundance (Fig. 3.3; Fig. 3.4), biomass, (Fig. 3.3) and diversity (Fig. 3.5) during the ice-free season. In a simple GAM relating abundance and biomass to month (Fig. 3.3), month was highly significant ($p < 0.01$; see Table 3.1). The smooth term for month also predicted higher abundance and biomass during the ice-free season and lower abundance and biomass during the ice-covered season (Fig. 3.3).

The community during the ice-covered season was dominated primarily by *Bosmina longirostris* and *Keratella sp.* (Fig. 3.4). During the ice-free season, the community increased in diversity, abundance, and biomass, with *B. longirostris* and *Keratella* continuing to persist alongside a rise in abundance led primarily by copepods, *Daphnia sp.*, and *Polyarthra sp.* (Fig. 3.4A-C). Ordination illustrated two distinct patterns in zooplankton community composition between the ice-covered and ice-free season (Fig. 3.5B), where the community in the ice-covered season was a subset of the ice-free season community. Communities during ice cover were more tightly clustered, indicating that community composition during this season is less variable and more homogenous. There was a significant difference in total abundance, as well as the abundance of cladocerans, copepods, and rotifers separately in the ice vs. no ice seasons (Fig. 3.4D; ANOVA $p<0.05$). There was also a significant difference in Shannon's diversity overall and within cladocerans and rotifers in the ice vs. no ice seasons (Fig. 3.5C; ANOVA $p<0.05$).

Interannual variation in zooplankton community structure, abundance, and biomass

Zooplankton mean annual biomass ranged widely across the 37-year time series, with a 731-fold difference between the minimum and maximum values (range 807.6 - 590,839.5 μg/m^3; mean

65620.5 µg/m^3), driven primarily by cladoceran biomass (range 792.5 - 388,007.2 µg/m^3; mean 57635.1 µg/m^3), followed by copepod biomass (range 8.5 - 287,991.5 µg/m^3; mean 27670.0 µg/m^3) (Fig. 3.6A). Annual mean abundance also ranged widely with a 177-fold difference between the minimum and maximum values (range: 2,247 - 399,256 individuals/m^3; mean 97,626.5 individuals/m^3) and was heavily driven by rotifers (Fig. 3.6B). Annual mean diversity (Shannon's diversity index) was more similar through time (range: 0.24 - 1.91; mean 0.89), with few periods of lower and higher than average diversity (Fig. 3.6C).

Relationships between hydroclimate and zooplankton diversity, abundance and biomass

In both the ice and ice-free seasons, winter snowfall influenced community structure, with higher community variability in years with high snowfall totals, particularly during the ice-free season (Fig. 3.7D). Additionally, there was a more constrained community that is a subset of the average and dry in dry years with low snowfall totals (Fig. 3.7D). This difference in community structure could have been driven in part by differences in taxon-specific responses to total snowfall. Mean ice-free season copepod abundance was positively related to total snowfall, whereas cladoceran and rotifer abundance were not significantly affected by total snowfall (Fig. 3.7A). Mean ice-free season cladoceran diversity was positively related total snowfall, whereas rotifer and copepod diversity were not significantly affected by total snowfall (Fig. 3.7B). Mean ice-covered season rotifer biomass was negatively related to total snowfall, whereas copepod and cladoceran biomass were not significantly affected by total snowfall (Fig. 3.7C).

Hydroclimatic influences on zooplankton abundance

Hydroclimate significantly influenced ice-free season zooplankton abundance (Fig. 3.8A). Using generalized additive modeling (GAM), we found that total snowfall, month, and year together significantly explained 32.5% of the deviance in total zooplankton abundance, and ice-off DOY, month, and year together significantly explained 36.0% of the deviance in total zooplankton abundance (Table 3.1; Fig. 3.8A). All predictors contributed significantly to the model ($p<0.05$), except for month in the total snowfall model. The significance of month in the ice-off DOY model indicated a strong seasonal effect, reflected in the regular seasonal pattern in diversity and abundance we observed. The significance of year in both the total snowfall and ice-off DOY models indicated a trend over time, in this case a strongly non-linear U-shaped trend with the lowest predicted abundances in the early 1990s (EDF snowfall = 4.4; EDF ice-off DOY = 4.3; Fig. 3.8A). Zooplankton abundance had a strongly significant negative relationship with total snowfall and ice-off DOY, indicating that winter snowfall totals and ice-off DOY are key factors influencing zooplankton communities.

We found that summer mean air temperature did not significantly influence ice-free season total zooplankton abundance (Fig. 3.9A). However, total snowfall (Fig. 3.8A) and ice-off DOY (Fig. 3.8B) were highly significant.

We found ice-off DOY, month, and year were all highly significant in explaining the abundance of all taxonomic groups (copepods, cladocerans, rotifers) (Fig. 3.10). Cladocerans exhibited a particularly strong response, with 52.0% of deviance in abundance explained by this model. Copepods and rotifers also had significant responses, with 45.5% and 33.0% of deviance explained respectively, with month, year, and ice-off DOY all significant.

In contrast, hydroclimate did not significantly influence ice-free season zooplankton biomass (Fig. 3.8B). Using GAMs, we found that total snowfall, month, and year together explained

44.4% of the deviance in total zooplankton biomass, and ice-off DOY, month, and year together explained 42.5% of the deviance in total zooplankton abundance biomass (Supplemental Table 3.3; Fig. 3.8B). However, the only predictors that contributed significantly to the model ($p<0.05$) were month and year, where the hydroclimate predictors (total snowfall and ice-of DOY) were not significant, indicating that rather than hydroclimate, seasonality and long-term trends influence zooplankton biomass. Furthermore, we found that summer mean air temperature significantly influenced ice-free season total biomass (Fig. 3.9B; $p < 0.05$; 13.6% deviance explained).

Discussion

Across a 37-year time series, we found that mountain lake zooplankton communities are strongly structured by winter snowpack and ice-off timing, with distinct responses among taxonomic groups. Zooplankton communities followed a regular seasonal pattern, with higher abundance, biomass, and diversity during the ice-free season. Though this strong seasonal pattern persisted throughout the time series, zooplankton diversity and abundance varied significantly among years based on ice-off date and winter snowfall. Importantly, cladocerans, copepods, and rotifers experienced different strengths of influence by hydroclimate. As hydroclimatic variability becomes increasingly extreme, each of these groups could increase or decrease in abundance at a greater or lesser magnitude than the other zooplankton groups, which could fundamentally restructure the zooplankton community. Our findings highlight the clear link between biodiversity and hydroclimate in a sensitive ecosystem experiencing rapid global change. Given the fundamental role that zooplankton play in ecosystem biogeochemical cycling and trophic structures, understanding how hydroclimatic variation can shift their contributions to whole-ecosystem structure and function is imperative for understanding the impacts of and managing for global change.

Hydroclimate controls on seasonal mountain lake zooplankton community structure

Past studies on Emerald Lake have demonstrated the clear and driving influence of winter hydroclimate on lake ice phenology, summer mean water temperatures, hydrology, and nutrient concentrations (Sadro et al., 2018, 2019; Smits et al., 2020, 2021). Here, we additionally found that the zooplankton community of Emerald Lake is also strongly structured by hydroclimate (Fig. 4; Fig. 5).

Seasonally, Emerald Lake zooplankton had lowest abundance, biomass, and diversity during ice-covered seasons, and highest abundance, biomass, and diversity during the ice-free season. This seasonal succession of low-abundance winters and high-abundance summers follows a commonly referenced model from the plankton ecology group for oligotrophic lakes with fish (Sommer et al., 1986, 2012). This model attributes the seasonal zooplankton summer biomass peak to a decrease in food limitation and decrease in physical controls (ice-cover). Additionally, examples of in-situ seasonal (ice-covered vs. ice-free) differences between plankton biomass in lakes that freeze globally are consistent with what we found in Emerald Lake, with phytoplankton and zooplankton biomass peaking during the ice-free season (Hampton et al., 2017). Like the plankton ecology group model, this global study also links zooplankton to bottom-up dynamics in phytoplankton biovolume through the winter, where most lakes have lower phytoplankton and zooplankton densities during the ice-covered season (Hampton et al., 2017). In Emerald Lake, there is significantly higher total abundance and biomass in the ice-free season than the ice-covered season.

Though we did not have the sampling resolution to determine differences in the timing of zooplankton abundance peaks, high variability in snowpack could cause multiple seasonal peaks and/or variability in the timing of the seasonal peak in phytoplankton and zooplankton due to high variability in snowpack, resulting in zooplankton community shifts. Ice-off date in Emerald Lake was as late as July 28 in years with large snowpack, and as early as May 10 in years with small snowpack – a 79-day difference. Such large differences in ice-off timing can cause taxa within zooplankton communities to respond differently, based on factors such as their life history traits, competition, or predation. For example, in Green Lake 4, an oligotrophic mountain lake in the Rocky Mountains, CO, ice-off date varied by 49 days, with earlier ice off dates supporting higher *Daphnia* biomass and *Hesperodiaptomus* copepod fecundity than later ice-off dates, likely due to warmer water temperatures and a longer growing season (Loria et al., 2020). In this case, *Daphnia* biomass was lowest immediately following ice-off, likely because *Daphnia* tend to maximize early fecundity, and increased throughout the growing season, so longer, warmer ice-free seasons supported greater *Daphnia* biomass overall (Loria et al., 2020). Ice-off date also had a strong influence on lake zooplankton community structure in lakes in the Arctic (Beaver et al., 2019). In Lake Washington, 40 years of data revealed that *Keratella* abundance shifted with changes in spring phytoplankton peaks, whereas *Daphnia* and *Leptodiaptomus* did not (Winder & Schindler, 2004) – highlighting the within-community differences in changes in seasonality. Because of the variability in the timing and frequency of sample collection across years, questions about the variability in within-season phenology in Emerald Lake still remain. As climate changes drive shorter ice duration and changes in ice phenology in lakes (Sharma et al., 2021), it is critical to understand how within-community assemblages will respond to changes in ice duration and phenology.

Hydroclimate controls on interannual mountain lake zooplankton community structure

Interannually, Emerald Lake zooplankton are strongly influenced by factors controlled by winter snowfall totals, a metric of hydroclimate that drives much of the physical and chemical variation in Emerald Lake. Variation in annual snowfall controls variation in the phenology of ice-off, flushing rates, and nutrient concentrations (Sadro et al., 2018; Smits et al., 2021), and here we demonstrate that it also controls interannual variation in zooplankton community structure (Fig. 3.10). We found a negative linear relationship between zooplankton abundance and ice-off DOY and snowfall totals, but a slight positive relationship with snowfall totals and zooplankton Shannon's diversity (Fig. 3.7B). This strong influence of interannual variability and its impact on summer lake ecosystems and communities has been found across many mountain lake ecosystems – for example, in mountain lakes in the Pacific Northwest, USA, smaller snowpacks and earlier ice-off dates resulted in higher concentrations of nutrients, warmer temperatures, and greater cladoceran abundance (Powers et al., 2022). A review of North American mountain lakes found that climatic variables (precipitation and temperature) best explained beta diversity at the individual lake scale, highlighting the influence of hydroclimate on diversity as well as abundance (Loewen et al., 2019). While Emerald Lake and many mountain lakes in the Western United States face projections of a low-to-no snow future (Siirila-Woodburn et al., 2021), the steep landscape and environmental gradients inherent to mountain lakes ecosystems mean that while mountain lakes may all respond rapidly to environmental changes, the direction and magnitude of response may vary on an individual lake scale (Moser et al., 2019; Soranno et al., 1999). As a result, understanding how communities in a diversity of mountain lake ecosystems will respond to extreme hydroclimatic variability is imperative for anticipating and managing for future changes in zooplankton abundance and diversity.

Hydroclimate mediates physical and trophic controls on zooplankton

Climate variability drives interannual differences in lake water chemistry, with possible implications for bottom-up drivers of zooplankton abundance and/or biomass based on food availability. PC and PN are crucial phytoplankton-derived nutrients for zooplankton. Furthermore, inorganic N is a key nutrient for phytoplankton. In Emerald Lake, lower winter snowfall results in earlier ice-off dates, lower flushing rates during snowmelt, and less dilution of incoming nutrients during snowmelt. This in turn leads to warmer, higher nutrient water in the summer, facilitating higher phytoplankton biomass (Sadro et al., 2018). This was reflected in the water chemistry from our study period. Average PC, PN, and inorganic N during the ice-free period were highest in years with lower snowfall and earlier ice-off dates, indicating higher phytoplankton growth in years with lower snowfall. Additionally, climate variability and long-term warming trends are increasing PC and PN in Emerald Lake across years with low SWE, indicative of increasing phytoplankton biomass with climate warming (Sadro et al., 2018).

We found significant relationships between hydroclimate and zooplankton abundance (Fig. 3.8A), where lower total snowfall and earlier ice-off dates resulted in higher predicted abundances. Because low snowfall winters in Emerald Lake translates to higher summer phytoplankton biomass (Sadro et al., 2018), it is likely that zooplankton abundance is controlled, at least in part, by bottom-up factors that are ultimately driven by physical controls like winter hydroclimate. This is corroborated by what is found in other mountain lake ecosystems, where climate-driven changes in the physical lake environment, such as warmer water temperatures, mediate bottom-up controls on zooplankton communities. Phytoplankton biomass itself is tightly linked to maximum snowpack and the length of the ice-free season in other mountain lakes (Oleksy et al., 2020), demonstrating a direct link between hydroclimate and bottom-up trophic dynamics. Similar to what we observed in our study, zooplankton densities increased seasonally during periods of greater phytoplankton availability in mountain lakes in the Pacific Northwest (Powers et al., 2022), and in a survey of lake plankton globally (Hampton et al., 2017).

Though hydroclimate drives physical lake characteristics that can then determine bottom-up trophic controls, physical controls such as lake temperature may affect zooplankton communities directly, outside of these climate-driven bottom-up controls. This is evident in lakes where, for example, phytoplankton dynamics are not coupled with zooplankton dynamics. Zooplankton biomass in Green Lakes 4, a mountain lake in Colorado, USA, was not directly correlated with chlorophyll-a concentrations, but was associated with earlier ice-off (Loria et al., 2020). In Lake Baikal, a high-latitude oligotrophic lake, cladocerans increased strongly in response to lake temperature but not algal biomass over 60 years, despite major increases in chlorophyll a-over time (Hampton et al., 2008). There are also direct physiological implications of warming lake temperatures for zooplankton, unrelated to trophic controls – for example, warming can reduce individual body size in zooplankton, as it can increase the cost of development (Moore et al., 1996; Yvon-Durocher et al., 2011). Though snowpack size and phytoplankton biomass are strongly related in Emerald Lake (Sadro et al., 2018), we did not always find strong relationships between snowpack size and zooplankton abundance or biomass (Fig. 3.7; Fig. 3.8B), suggesting that the Emerald Lake zooplankton community is likely influenced by but not solely controlled by bottom-up trophic interactions.

Though top-down trophic controls on zooplankton diversity and abundance are often weaker in oligotrophic lakes (Elser & Goldman, 1991; Mehner et al., 2008; Rogers et al., 2020), the fish in Emerald Lake likely exert some controls on the zooplankton community. The introduction of non-native trout to Emerald Lake in the early 1900s likely caused a large shift in zooplankton community assemblage, particularly away from large-bodied crustaceans (Knapp et al., 2001; Symons & Shurin, 2016). In experimental manipulations of warming, higher temperatures resulted in greater predator biomass and top-down control (Shurin et al. 2012), and earlier snowmelt and climate warming in mountain lakes increases fish energetic requirements to maintain the same body weight (Christianson & Johnson, 2020). As a result, though we lack fish monitoring data from this lake, it is likely that fish feeding rates in Emerald Lake increase during summers with smaller snowpacks and earlier ice-off dates, assuming constant fish abundance (Fig. 3.1).

Quantifying the importance of extrinsic factors like hydroclimate in determining physical and trophic controls and ultimately freshwater zooplankton community structure remains a key question in improving our understanding of climate effects on biodiversity (Vadadi-Fülöp et al., 2012). Our 37-year time series provides insight into the importance of the interaction between hydroclimate and trophic controls in determining zooplankton community assemblage and abundance/biomass.

Community and trophic implications of increasing hydroclimatic variability

Winter hydroclimate drives overall zooplankton abundance, but we found differences within the community in the strength of response based on taxonomic groups (Fig. 3.10). Though our generalized additive models indicated ice-free abundances in all taxonomic groups (copepods, cladocerans, rotifers) were significantly impacted by winter hydroclimate (Table 3.1; total snowfall and ice-off DOY $p < 0.01$), cladocerans exhibited a particularly strong response, with the models explaining 52.0% (ice-off DOY) and 54.5% (total snowfall) of deviance. In comparison, for copepods, ice-off DOY explained 45.5% of deviance and total snowfall explained 49.8% of deviance. For rotifers, ice-off DOY explained 27.0% of deviance and total snowfall explained 29.2% of deviance. This disparity between taxa highlights that groups within the zooplankton community may respond differently to hydroclimatic forcing, potentially resulting in novel community assemblages, particularly as hydroclimate extremes become increasingly common.

Differences in life history strategies could help explain these why there may be these differences in community responses and outcomes during the ice-free season, and why hydroclimate extremes may amplify these differences. For example, one mountain lake study showed that *Daphnia pulicaria* and *Hesperodiaptomus shoshone* utilized contrasting reproductive strategies to deal with an environment that is ice-covered most of the year (Loria et al., 2020). *Daphnia,* which have a clonal reproductive strategy, responded much more quickly to ice-off than *Hesperodiaptomus* zooplankton, experiencing high fecundity and high population growth immediately following ice-off. *Hesperodiaptomus*, on the other hand, reproduce sexually and have several larval stages and favor long-term survival over initial dominance, and as a result, were less coupled to ice-off timing than *Daphnia*. For species like *D. pulicaria* that are tightly coupled to ice-off timing, increasing hydroclimatic extremes will likely greatly impact their abundances. In contrast, species like *H. shoshone* that are less strongly coupled to ice-off timing may be impacted less by extreme hydroclimate conditions, causing disparate responses within the community to hydroclimate. This mismatch among zooplankton groups has been document in other systems as well - in Lake Baikal, cladocerans did not respond to increases in chlorophyll-a, whereas copepods decreased in abundance, highlighting the distinct differences in how these taxa interact with phytoplankton and lake physical controls (Hampton et al., 2008). These kinds of differences in the magnitude and direction of responses to environmental conditions among taxa or species could ultimately change overall community assemblage and composition. With global change predicted to increase variability and overall shorten ice duration, oligotrophic mountain lake zooplankton communities may undergo significant community restructuring, particularly if cladocerans respond more directly to hydroclimate than copepods or rotifers, as we found in Emerald Lake. Based on the strength of relationships between predictors in our GAM models, extremely high snowpacks, for example, could result in reductions in cladoceran abundances that are a much greater magnitude than reductions in copepod or rotifer abundances, creating novel community assemblages in the face of global change.

Though investigations on climate change and biodiversity have largely focused on the effects on unidirectional warming trends, increasingly extreme hydroclimatic variability and its role in structuring major physical, chemical, and biological factors is a key component of global change, particularly in mountain lake ecosystems. We addressed this knowledge gap by quantifying the influence of hydroclimate on mountain lake zooplankton diversity, abundance, and biomass over a 37-year time series. Even so, we faced limitations related to doing long-term research at a remote mountain lake, including changing research objectives over time and the logistical challenges in sampling frequently. There was uneven sampling frequency and timing throughout the study period - while each study year included at least one sample each from the ice-covered and the ice-free season, these samples were not always taken at consistent times during the season, limiting our ability to investigate within-season community shifts or the timing and occurrence of peaks in abundance/biomass. Planning for similarity in frequency and timing of sampling zooplankton in long-term datasets would improve explanatory power. It is critical to continue working to improve future data collection and utilize historic long-term data in order to address major global change questions - given the fundamental role that zooplankton play in ecosystem biogeochemical cycling and trophic structures, understanding how global change can shift zooplankton contributions to ecosystems will provide key insight into the future resilience of mountain lake ecosystems.

Questions addressing within-season zooplankton phenology and cross-season linkages, particularly for communities experiencing increasingly extreme snowpacks and ice phenologies, still remain, including: What is the role of the environmental conditions just before ice-on in determining under-ice and cross-seasonal zooplankton communities? What is the relationship between ice-off timing and the timing of peak zooplankton biomass? And, does the timing of ice-on impact overwintering communities, and ice-off communities? Our study highlights that in evaluating global change impacts on biodiversity in mountain ecosystems, climate-driven increases in hydroclimatic variability should be a major focus – not just unidirectional warming trends. There is a need to continue working to link long-term changes in freshwater biodiversity among a diverse set of taxa to climate change, in order to anticipate whole-ecosystem impacts of biodiversity change under future climate scenarios. Furthermore, our study stresses the importance and value of long-term datasets and their role in understanding and anticipating global change.

Figures

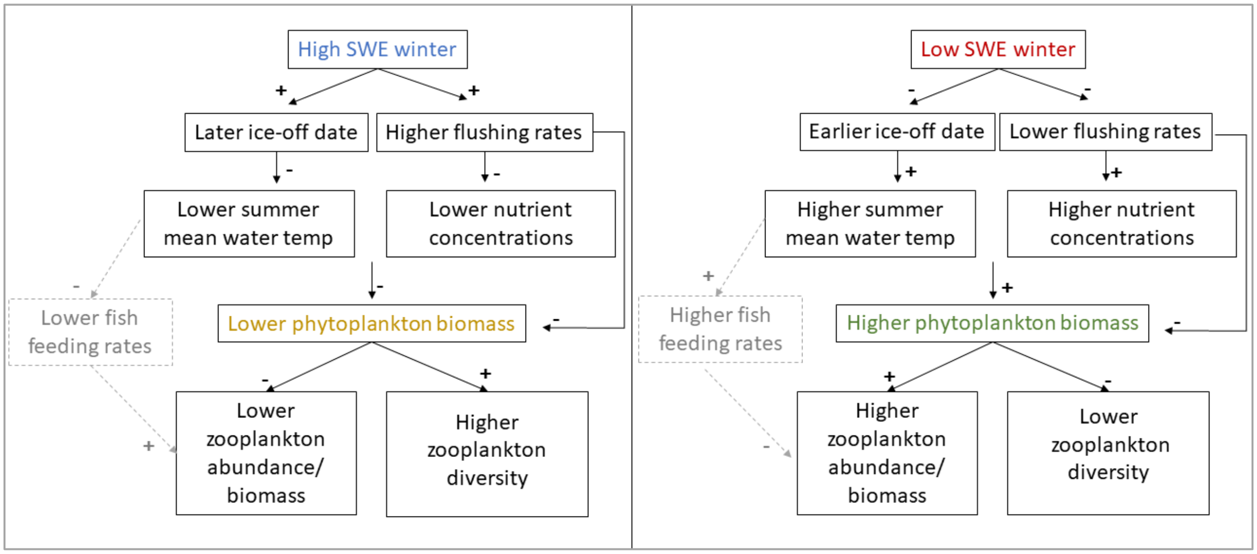

Figure 3.1: Conceptual diagram for lake temperature, nutrients, productivity, and hypothesized zooplankton outcomes based on winter hydroclimate (snow water equivalent, SWE). Winters with high SWE result in later ice-off dates and higher flushing rates due to larger snowmelt volume. These factors contribute to lower water temperatures, nutrient concentrations, and ultimately lower phytoplankton biomass. We hypothesize that these physical controls on bottom-up factors will drive lower zooplankton abundance/biomass and higher diversity in high SWE years. Winters with low SWE have earlier ice-off dates and lower flushing rates, which result in warmer summer mean water temperatures, higher nutrient concentrations, and ultimately higher phytoplankton biomass. We hypothesize that the abundance of phytoplankton during low SWE years will drive higher zooplankton abundance/biomass and lower diversity.

Model	Response	Predictors	EDF	p value	R^2	Deviance Explained
abundance ~ month	total abundance	s(Month)	1.000	0.236	0.002	0.014
abundance ~ year	total abundance	s(Year)	3.926	0.000	0.233	0.234
abundance ~ total snowfall	total abundance	s(total_snowfall)	2.896	0.035	0.071	0.104
abundance ~ IceoffDOY	total abundance	s(Iceoff.DOY.predicted)	2.934	0.000	0.067	0.155
abundance ~ summer mean temp	total abundance	s(summer_mean_temp)	2.107	0.375	0.015	0.039
abundance ~ month + year	total abundance	s(Month)	1.001	0.899	0.227	0.234
	total abundance	s(Year)	3.894	0.000	0.227	0.234
abundance ~ month + total snowfall	total abundance	s(Month)	1.003	0.069	0.053	0.097
	total abundance	s(total_snowfall)	2.104	0.019	0.053	0.097
abundance~ year + total snowfall	total abundance	s(Year)	4.414	0.000	0.274	0.311
	total abundance	s(total_snowfall)	1.003	0.000	0.274	0.311
abundance ~ month + IceoffDOY	total abundance	s(Month)	1.000	0.005	0.025	0.184
	total abundance	s(Iceoff.DOY.predicted)	2.481	0.000	0.025	0.184
abundance ~ year + IceoffDOY	total abundance	s(Year)	4.380	0.000	0.267	0.333
	total abundance	s(Iceoff.DOY.predicted)	1.001	0.000	0.267	0.333
abundance ~ total snowfall + IceoffDOY	total abundance	s(total_snowfall)	2.536	0.001	-0.011	0.183
	total abundance	s(Iceoff.DOY.predicted)	1.006	0.000	-0.011	0.183
abundance ~ month + year + total snowfall	total abundance	s(Month)	1.000	0.081	0.300	0.325
	total abundance	s(Year)	4.413	0.000	0.300	0.325
	total abundance	s(total_snowfall)	1.001	0.000	0.300	0.325
abundance ~ month + year + IceoffDOY	total abundance	s(Month)	1.000	0.008	0.300	0.360
	total abundance	s(Year)	4.323	0.000	0.300	0.360

	total abundance	s(Iceoff.DOY.predicted)	1.001	0.000	0.300	0.360
rotifer abundance ~ month + year + IceoffDOY	rotifer abundance	s(Month)	1.000	0.010	0.270	0.330
	rotifer abundance	s(Year)	4.212	0.000	0.270	0.330
	rotifer abundance	s(Iceoff.DOY.predicted)	1.002	0.000	0.270	0.330
copepod abundance ~ month + year + IceoffDOY	copepod abundance	s(Month)	4.739	0.000	0.269	0.455
	copepod abundance	s(Year)	2.740	0.018	0.269	0.455
	copepod abundance	s(Iceoff.DOY.predicted)	1.003	0.000	0.269	0.455
cladoceran abundance ~ month + year + IceoffDOY	cladoceran abundance	s(Month)	3.646	0.000	0.465	0.520
	cladoceran abundance	s(Year)	4.390	0.000	0.465	0.520
	cladoceran abundance	s(Iceoff.DOY.predicted)	1.001	0.002	0.465	0.520
rotifer abundance ~ month + year + total snowfall	rotifer abundance	s(Month)	1.000	0.110	0.272	0.292
	rotifer abundance	s(Year)	4.311	0.000	0.272	0.292
	rotifer abundance	s(total_snowfall)	1.001	0.000	0.272	0.292
copepod abundance ~ month + year + total snowfall	copepod abundance	s(Month)	5.029	0.000	0.294	0.498
	copepod abundance	s(Year)	2.988	0.000	0.294	0.498
	copepod abundance	s(total_snowfall)	2.907	0.002	0.294	0.498
cladoceran abundance ~ month + year + total snowfall	cladoceran abundance	s(Month)	3.505	0.000	0.474	0.545
	cladoceran abundance	s(Year)	3.825	0.000	0.474	0.545
	cladoceran abundance	s(total_snowfall)	2.324	0.000	0.474	0.545

Table 3.1: Generalized Additive Model structure and model output. Included is the model structure, response variable, each predictor variable, the effective degrees of freedom (EDF), p-value, R^2 value, and the deviance explained (as a decimal fraction). If the p-value was <0.0001, it is displayed here as 0.000. If the p-value was significant ($p < 0.05$), it is bolded. Other than the first model (abundance ~ month), which was run on both the ice-free season only and the full dataset (ice-covered and ice-free season), all models were run only using data from the ice-free season.

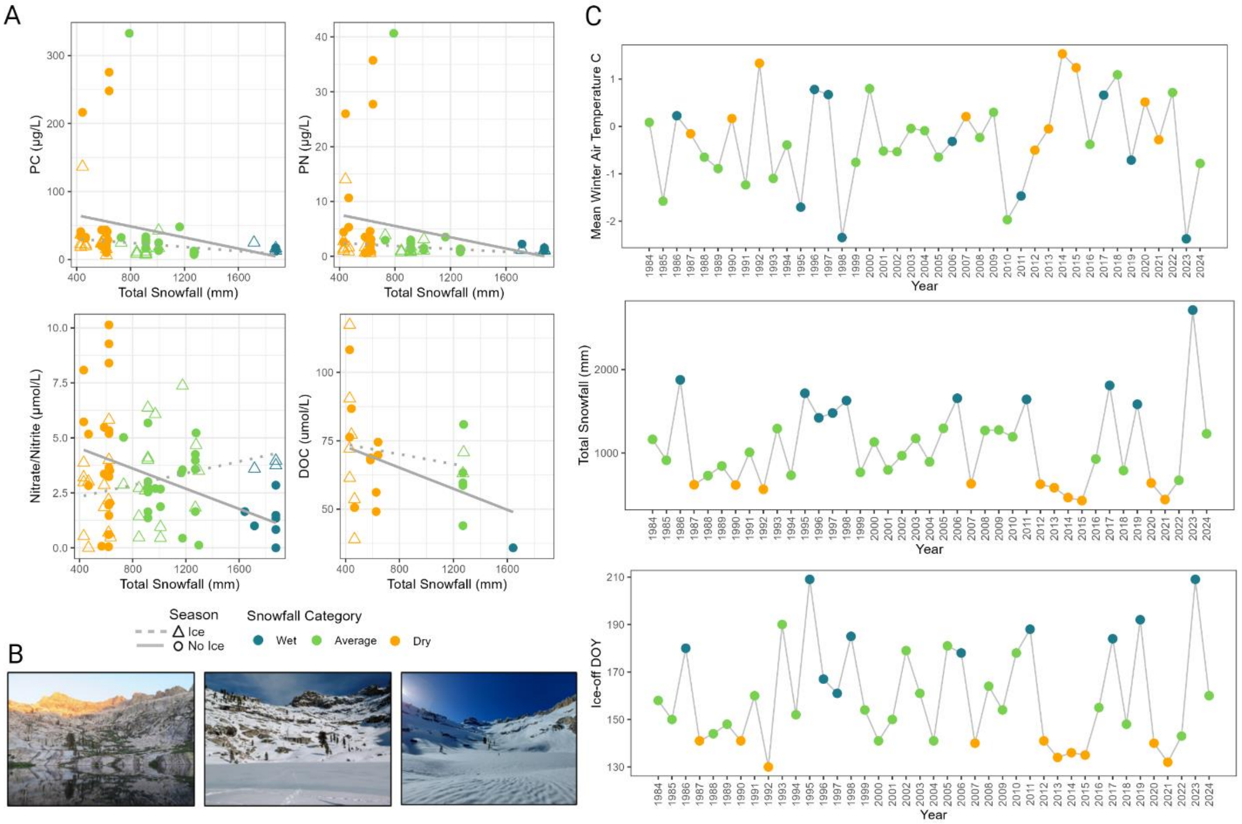

Figure 3.2: A) Average seasonal water chemistry, with the ice-covered season averages as open triangles and the dashed line, and no-ice season as circles and the solid line. Colors represent snowfall category, where “average” was the 25th-75th quantile for snowfall across the 37-year time series, “wet” was anything above that range, and “dry” was anything below that range (Sadro et al., 2019). B) Emerald Lake during the no-ice season, a low total snowfall winter, and a high total snowfall winter. C) Mean winter air temperature, total snowfall (mm) and ice-off day of year (DOY), colored by snowfall category.

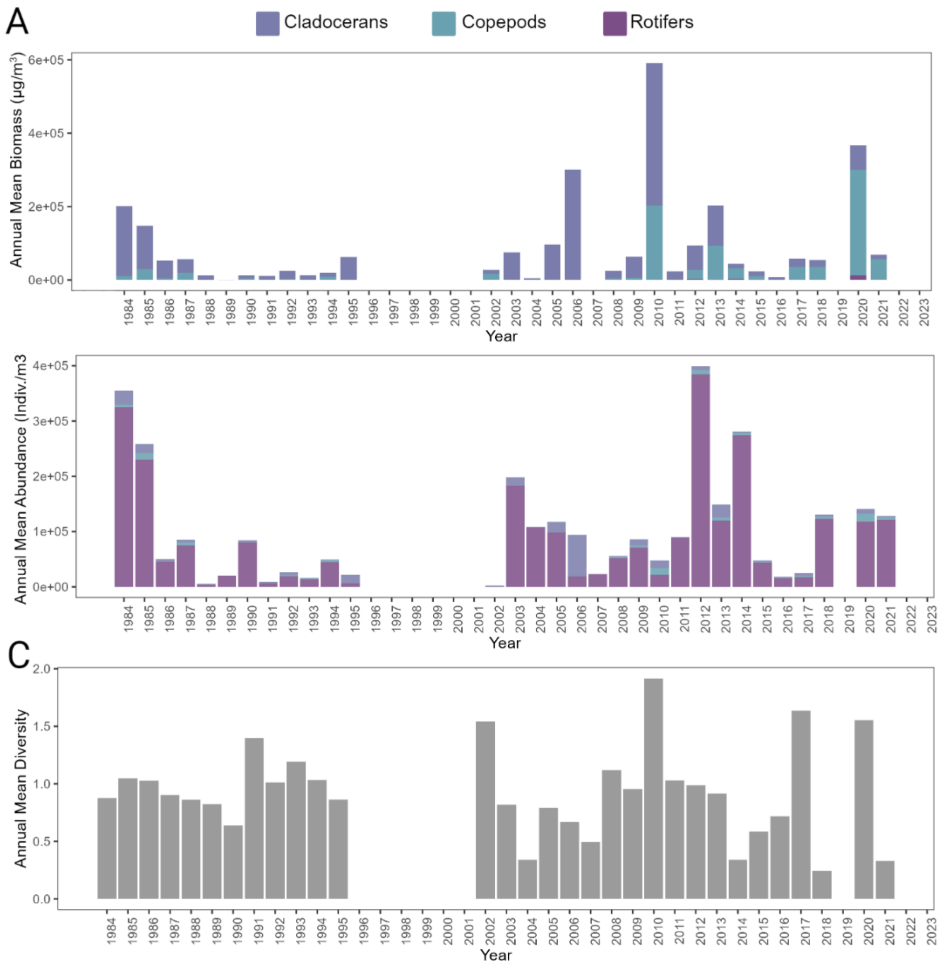

Figure 3.3: A) Mean annual zooplankton biomass over time, with cladocerans in blue, copepods in teal, and rotifers in purple. B) Mean annual zooplankton abundance through time, with the same color scheme as in (A). C) Annual mean Shannon's Diversity Index through time. Years 1996-2001, 2019, 2022-2023 were omitted from this study, rather than zeroes.

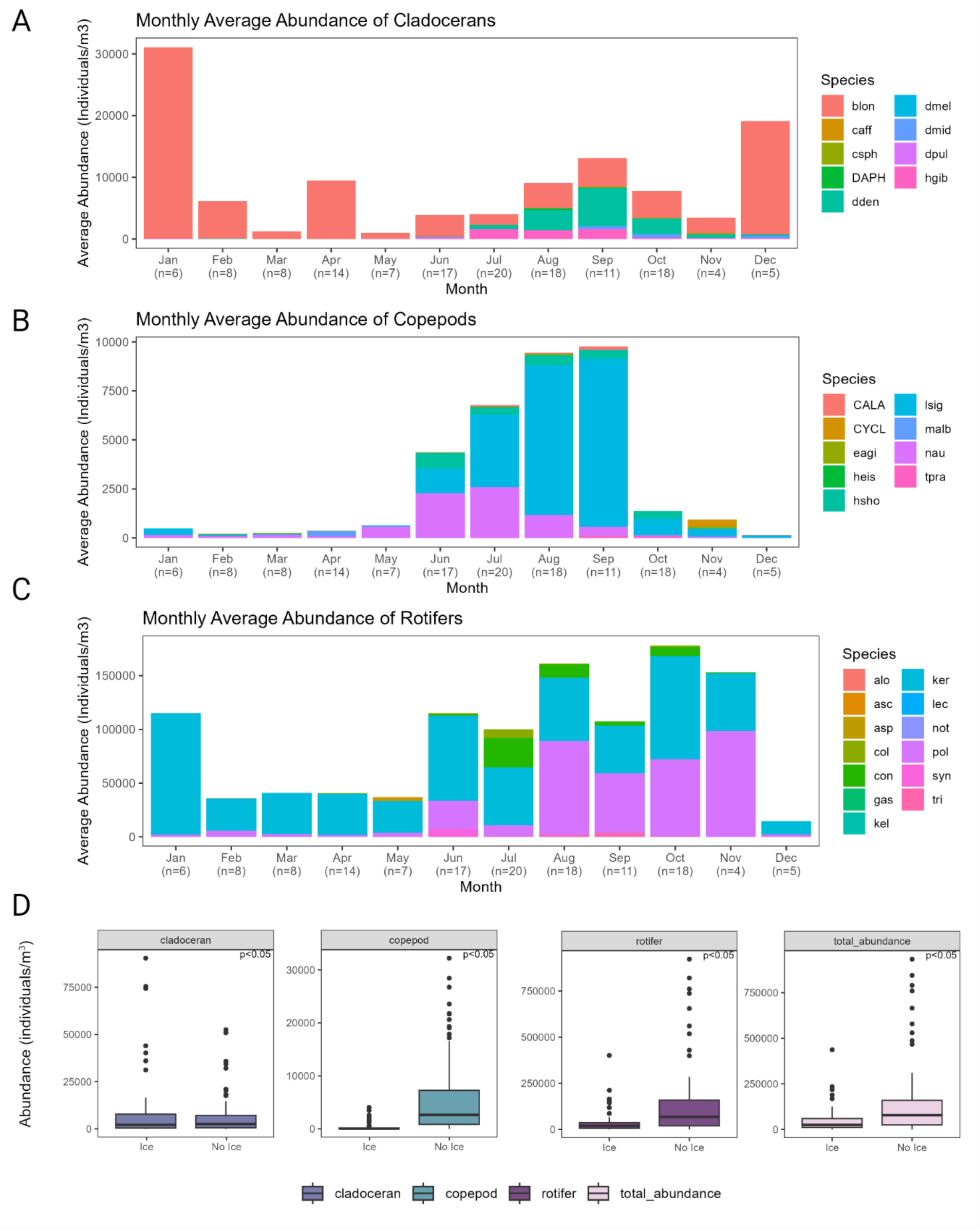

Figure 3.4: Monthly average zooplankton abundance for (A) cladocerans, (B) copepods, and (C) rotifers, colored by species. The number of samples for each month are displayed below the month label. D) Boxplots by season (Ice and No Ice) of zooplankton abundance by taxonomic group – cladocerans (blue), copepods (teal), rotifers (purple), and all taxa together (pink). If seasonal (Ice vs. No Ice) abundances were significantly different based on a one-way ANOVA, significance is indicated in the top right corner of each boxplot. Species codes in the graph represent the following species: alo (*Alona* sp.), asc (*Ascomorpha* sp.), asp (*Asplancha* sp.), blon

(*Bosmina longirostris*), caff (*Ceriodaphnia affinis*), CALA (Calanoid), col (*Collotheca* sp.), con (*Conichilus* sp.), csph (*Chydorus sphaericus*), CYCL (Cyclopoid), DAPH (*Daphnia* sp.), dden (*Daphnia dentifera*), dmel (*Daphnia melanica*), dmid (*Daphnia middendorfiana*), dpul (*Daphnia pulex*), eagi (*Eucyclops agilis*), gas (*Gastropus* sp.), heis (*Hesperodiaptomus eiseni*), hgib (*Holopedium gibberum*), hsho (*Hesperodiaptomus shoshone*), kel (*Kellicottia* sp.), ker (*Keratella* sp.), lec (*Lecane* sp.), lsig (*Leptodiaptomus signicauda*), malb (*Macrocyclops albidus*), nau (Nauplii), not (*Notholca* sp.), pol (*Polyarthra* sp.), syn (*Synchaeta* sp.), tpra (*Tropocyclops prasnius*), and tri (*Trichocerca* sp.).

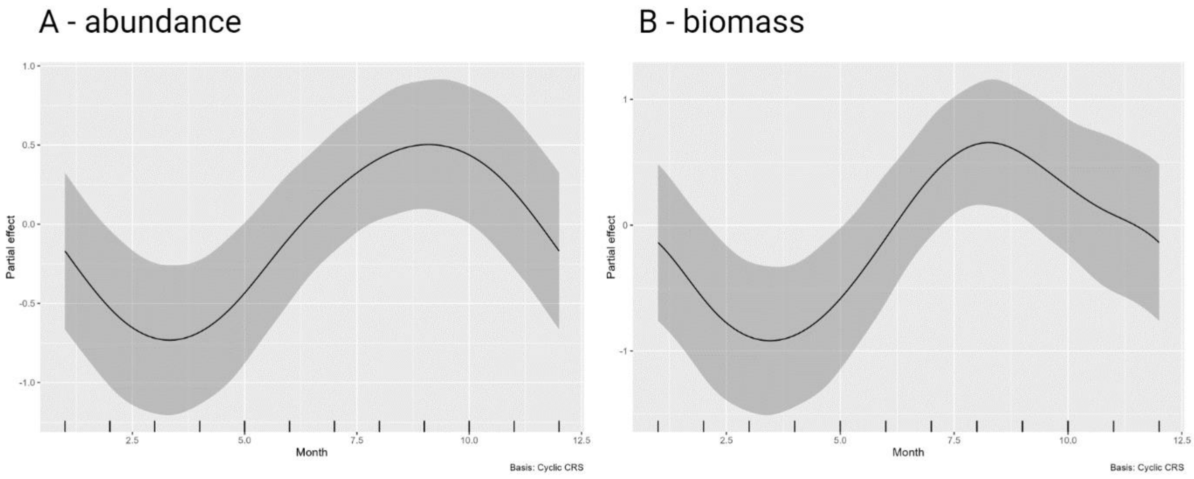

Fig. 3.5: Generalized Additive Model of total zooplankton A) abundance and B) biomass by month (x ~ s(month)). This model utilizes total zooplankton abundance/biomass across the entire year.

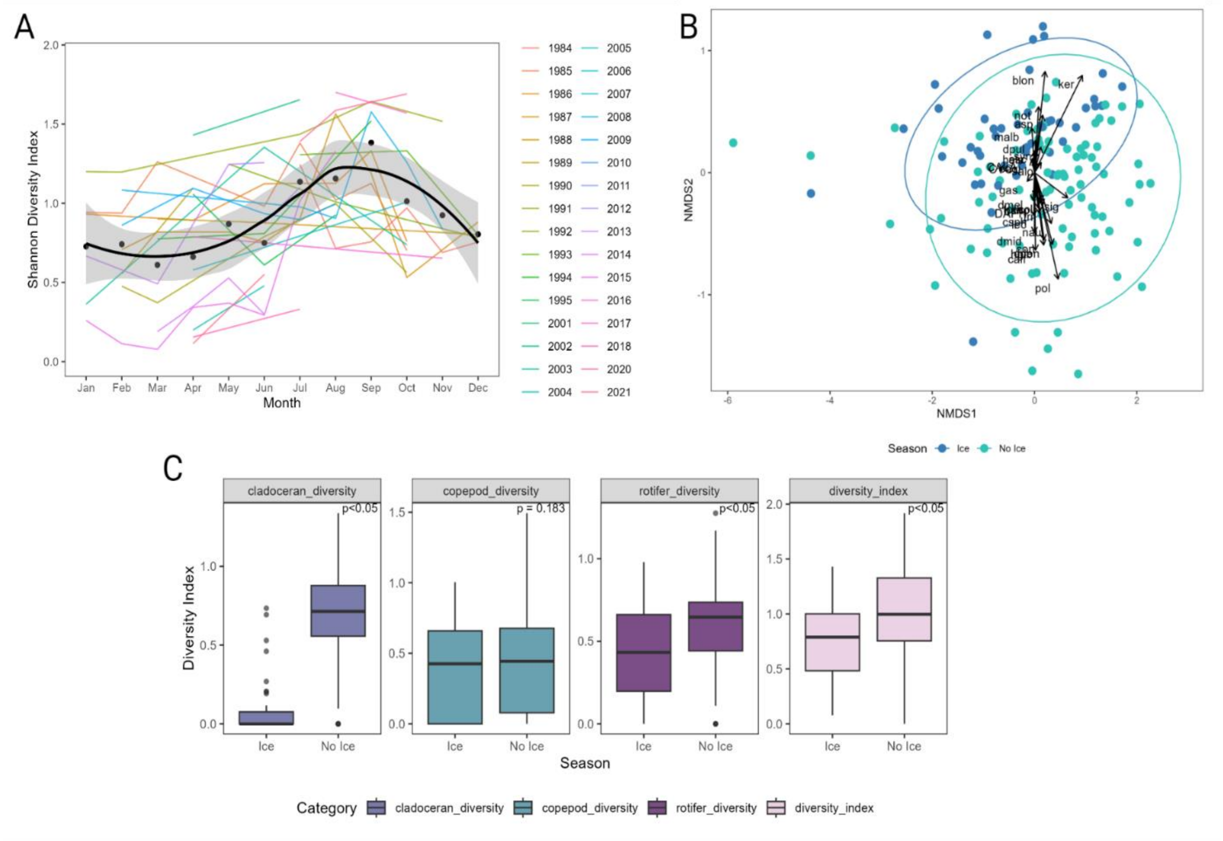

Figure 3.6: A) Shannon's Diversity Index from 1984-2021 (colored lines), with a smooth term summarizing monthly mean Shannon's Diversity Index (black and gray line). B) NMDS with 95% confidence ellipses by season (Ice vs. No Ice). Species vectors are plotted on top. C) Boxplots by season (Ice and No Ice) of zooplankton Shannon's diversity by taxonomic group – cladocerans (blue), copepods (teal), rotifers (purple), and all taxa together (pink). If seasonal (Ice vs. No Ice) diversity was significantly different based on a one-way ANOVA, significance is indicated in the top right corner of each boxplot.

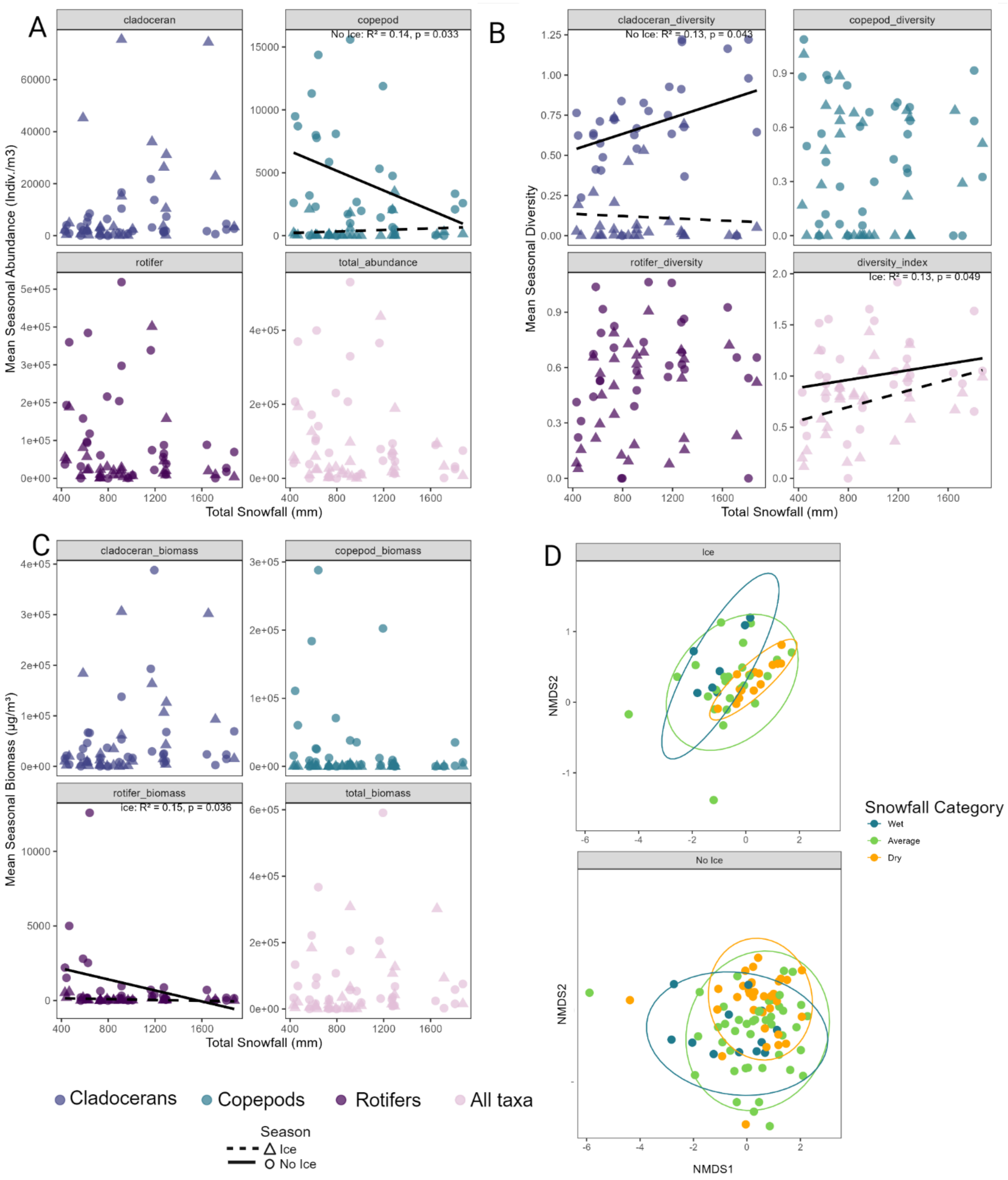

Figure 3.7: Scatterplots of zooplankton mean seasonal (ice-covered triangles vs. ice-free circles) A) abundance, B) Shannon's Diversity Index, and C) biomass, by total annual snowfall. A, B, and C have plots for every taxonomic group – cladocerans (blue), copepods (teal), rotifers (purple), and all taxa together (pink). If significant, the R^2 and p-value is displayed in the top right corner of each plot and the lines are plotted. Lines are solid for the ice-free season, and

dashed for the ice-covered season. D) NMDS, first plotted for the ice-covered season, then the ice-free season (below). 95% confidence ellipses were drawn for each snowfall category.

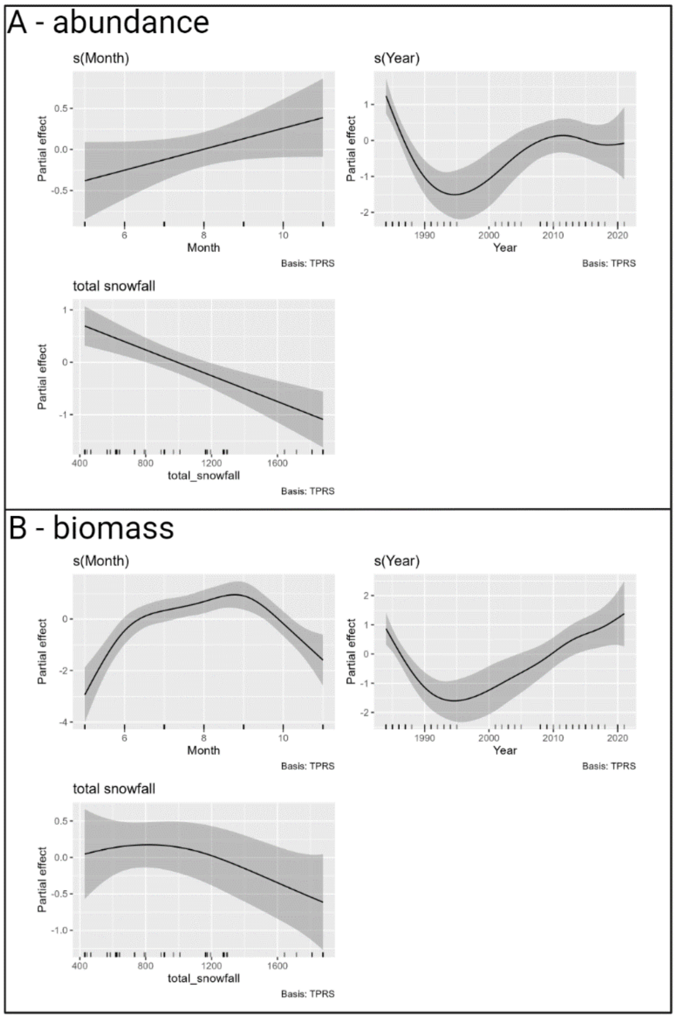

Figure 3.8: Generalized Additive Model results showing A) zooplankton abundance and B) zooplankton biomass with month, year, and total snowfall as predictors. Year and total snowfall were significant predictors for abundance, and month and year were significant predictors for biomass.

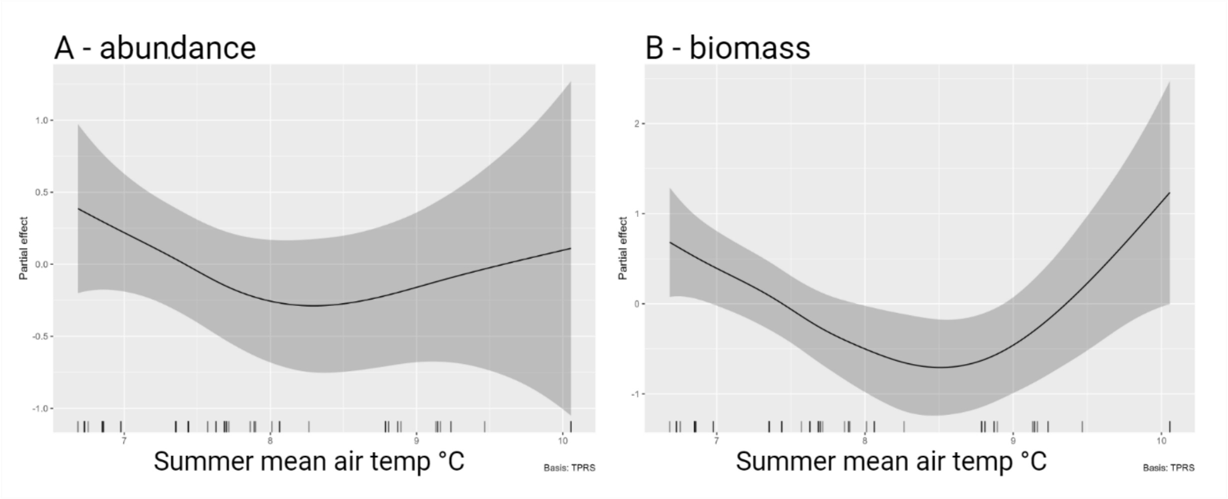

Figure 3.9: Generalized Additive Model results, with the basic model to test impact of summer mean air temperature on A) zooplankton abundance (total zooplankton abundance ~ summer mean air temperature), where total zooplankton abundance includes only the ice-free season. Summer mean air temperature was not a significant predictor for total zooplankton abundance during the ice-free season. We also tested the impact of summer mean air temperature on B) zooplankton biomass (total zooplankton biomass ~ summer mean air temperature), where total zooplankton biomass includes only the ice-free season. Summer mean air temperature was a significant predictor for biomass ($p < 0.05$; 13.6% deviance explained).

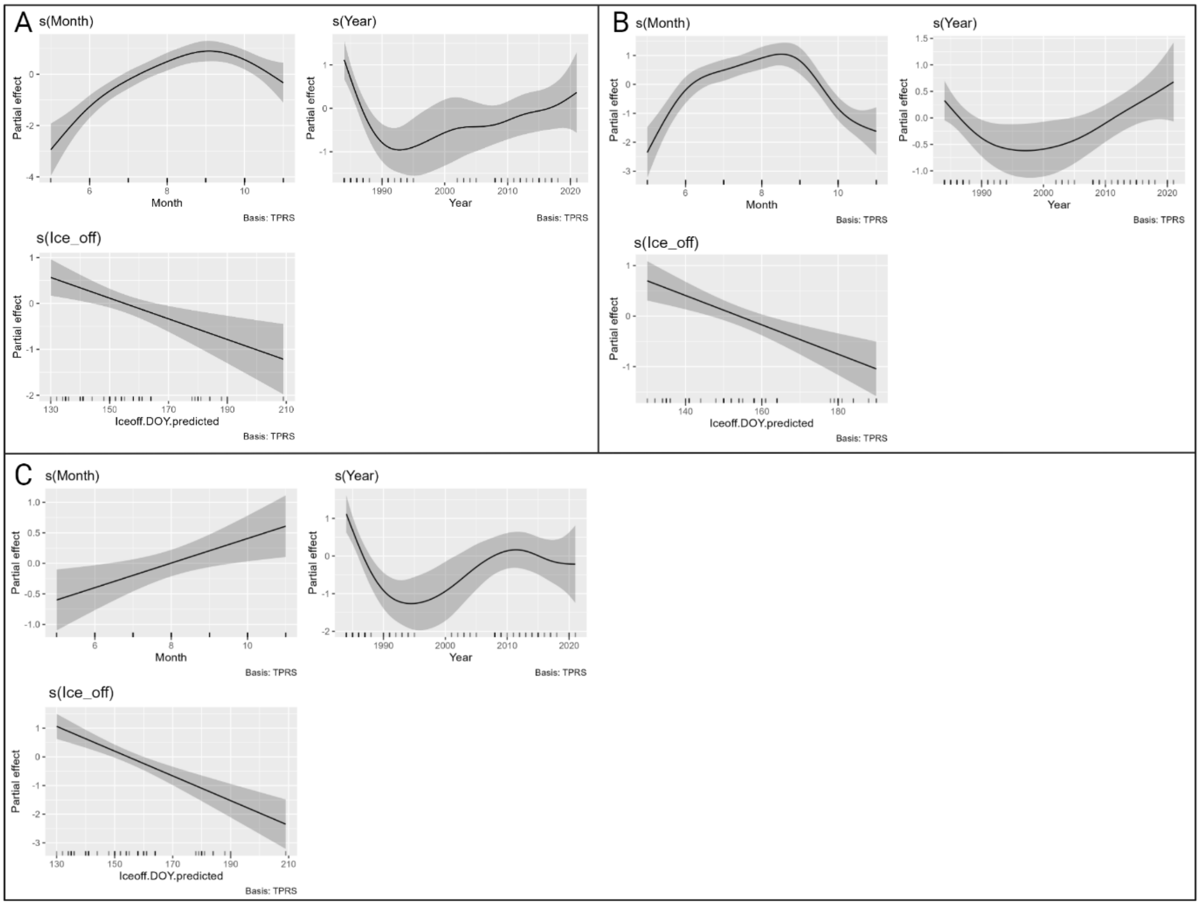

Figure 3.10: Generalized Additive Model results, with the best model (x ~ month + year + ice off DOY) results for ice-off DOY plotted, where x is total abundance for each taxonomic group: A) copepods, B) cladocerans, C) rotifers. The GAM for total_snowfall is not presented here, but is nearly identical to the plotted model output for ice-off DOY.

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