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RESEARCH REVIEW

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Do lakes feel the burn? Ecological consequences of increasing exposure of lakes to fire in the continental United States

Ian M. McCullough[1] | Kendra Spence Cheruvelil[1,2] | Jean-François Lapierre[3] | Noah R. Lottig[4] | Max A. Moritz[5,6] | Jemma Stachelek[1] | Patricia A. Soranno[1]

[1]Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan

[2]Lyman Briggs College, Michigan State University, East Lansing, Michigan

[3]Département de Sciences Biologiques, Université de Montréal, Montréal, QC, Canada

[4]Trout Lake Station, University of Wisconsin–Madison, Boulder Junction, Wisconsin

[5]Bren School of Environmental Science & Management, University of California Santa Barbara, Santa Barbara, California

[6]University of California Cooperative Extension, Agriculture and Natural Resources Division, Santa Barbara, California

Correspondence
Ian M. McCullough, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824.
Email: immccull@gmail.com

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Abstract

Wildfires are becoming larger and more frequent across much of the United States due to anthropogenic climate change. No studies, however, have assessed fire prevalence in lake watersheds at broad spatial and temporal scales, and thus it is unknown whether wildfires threaten lakes and reservoirs (hereafter, lakes) of the United States. We show that fire activity has increased in lake watersheds across the continental United States from 1984 to 2015, particularly since 2005. Lakes have experienced the greatest fire activity in the western United States, Southern Great Plains, and Florida. Despite over 30 years of increasing fire exposure, fire effects on fresh waters have not been well studied; previous research has generally focused on streams, and most of the limited lake-fire research has been conducted in boreal landscapes. We therefore propose a conceptual model of how fire may influence the physical, chemical, and biological properties of lake ecosystems by synthesizing the best available science from terrestrial, aquatic, fire, and landscape ecology. This model also highlights emerging research priorities and provides a starting point to help land and lake managers anticipate potential effects of fire on ecosystem services provided by fresh waters and their watersheds.

KEYWORDS
burn severity, climate change, LAGOS, MTBS, watershed, wildfire

1 | INTRODUCTION

Increasing wildfire activity has been well documented in the western United States, including increases in fire season length (Westerling, 2006) and area burned by large wildfires (Dennison, Brewer, Arnold, & Moritz, 2014; Stavros, Abatzoglou, Larkin, McKenzie, & Steel, 2014). These increases are strongly linked to rising air temperatures and fuel aridity associated with anthropogenic climate change (Abatzoglou & Williams, 2016; Westerling, 2016). Declines in summer precipitation are also strongly related to recent increases in wildfire extent, but are less easily attributed to anthropogenic activities (Holden et al., 2018). Extended warm, dry periods are associated not only with increased wildfire extent but also with large, high-severity fires that may substantially restructure landscapes and terrestrial ecosystems (Lauvaux, Skinner, & Taylor, 2016; Tepley & Veblen, 2015).

Fire-prone landscapes often include watersheds for rivers, streams, lakes, and reservoirs, which provide ecosystem services (e.g., drinking water and recreation opportunities) for millions of people. Although increases in wildfire activity likely threaten fresh waters and the services they provide humans, fire effects have rarely been studied at the broad spatial and temporal scales relevant to fire regimes and land management, and past research has focused on fresh waters other than lakes and reservoirs (hereafter, lakes), primarily streams (Bisson et al., 2003; Bixby et al., 2015; Gresswell, 1999; Smith, Sheridan, Lane, Nyman, & Haydon, 2011). As low-lying, downstream recipients of water and material transport from land to water, lakes integrate numerous processes that occur in their watersheds and airsheds and are strongly tied to the surrounding land (Williamson, Dodds, Kratz, & Palmer, 2008). Fires alter vegetation structure, soil properties, and runoff dynamics in lake watersheds, which may have potentially major consequences for lakes (Figure 1a–f). Unlike streams and rivers, lakes have water residence times (i.e., flushing rates) of months to several years. Therefore, effects of fire on lake ecosystem properties and services may be more persistent than in other fresh waters, warranting specific consideration of lakes.

There is currently no framework for integrating the complex effects of fire on lakes, which limits our ability to predict lake responses to fire across variable fire regimes and lake and watershed characteristics. In this review, our objectives are to (a) document exposure of lakes to fire across the continental United States from 1984 to 2015; (b) review past research on the effects of fire on the physical, chemical, and biological properties of lake ecosystems; and (c) propose a conceptual framework for the effects of fire on lakes by synthesizing research from aquatic, terrestrial, landscape, and fire ecology. Our framework hypothesizes integrated physical, chemical, and biological effects of fire on lakes using best available science and illustrates the complex set of interacting processes that collectively influences lake responses to fire. Therefore, it can be used to identify critical future research priorities and vulnerable lake ecosystem services.

2 | INCREASING FIRE ACTIVITY IN LAKE WATERSHEDS OF THE CONTINENTAL UNITED STATES

Understanding responses of lakes to fire first requires quantification of fire occurrence and extent in lake watersheds. Monitoring Trends in Burn Severity (MTBS) is the most comprehensive fire database available for the continental United States (Eidenshink et al., 2007). MTBS documents area burned, fire type (wildfires, prescribed fires, and wildland fire use), and burn severity using Landsat imagery for all fires >404 ha in the western United States (North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Texas, and westward) and >202 ha in the eastern United States. Using MTBS (May 2017 data release), we calculated area burned, number of fires by type, and burn severity from 1984 to 2015 in watersheds for all 137,465 lakes ≥4 ha in the continental United States based on lakes in LAGOS-US (https://lagoslakes.org/products/data-products/) and GIS functions in the R packages raster (Hijmans, 2016), rgeos (Bivand & Rundel, 2017), and sp (Pebesma & Bivand, 2005). Individual lake watersheds were unavailable and there is no practical method for estimating watershed area for all United States lakes, so we used 1,500 m buffers around lakes as proxies. We chose this buffer size because frequency distributions of 1,500 m buffer area and watershed area were highly similar for 51,000 lakes ≥4 ha in the northeastern and midwestern United States (Soranno et al., 2017; Figure S1a,b) and because lake area and 1,500 m buffer area were highly correlated for all 137,465 lakes in our study (Pearson's $r = 0.89$; Figure S2).

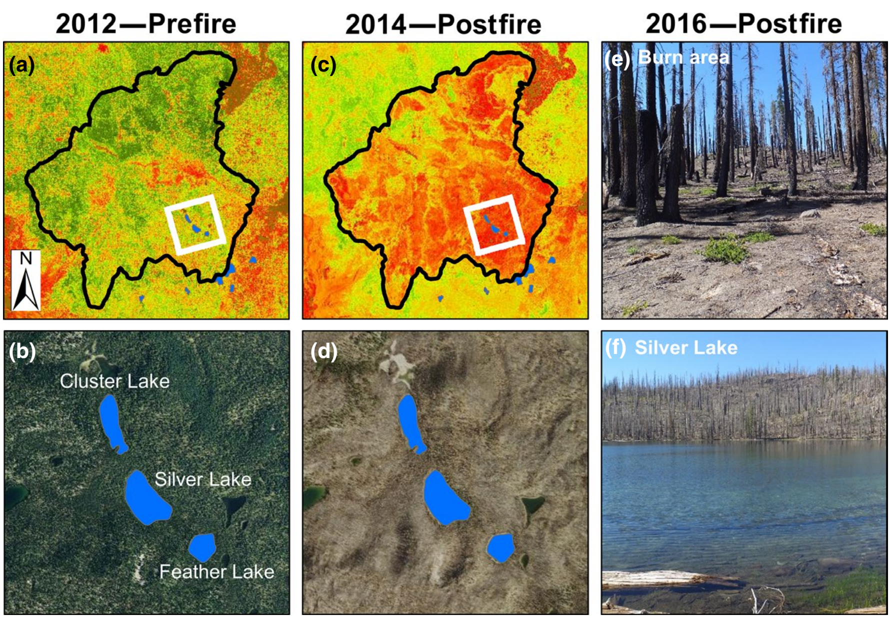

FIGURE 1 Example exposure of lakes to wildfire from the 2012 Reading Fire, Lassen Volcanic National Park, California (black outline = 10,874 ha burn extent, from Monitoring Trends in Burn Severity). (a, c) Pre- and postfire vegetation greenness (NDVI; green = high, red = low) from July 2012 and 2014, respectively. (b, d) Pre- and postfire aerial photos (NAIP) from same respective dates of area (white box) surrounding lakes (≥4 ha). (e) High-severity burns (>70% vegetation mortality) with exposed soil and potential for increases in nutrients, sediments, ions, and organic materials in runoff. (f) Silver Lake in June 2016. Image sources: (a–d) California Department of Fish and Game, (e, f) I. M. McCullough

Fire activity has increased in lake watersheds across the continental United States from 1984 to 2015, particularly since 2005 (Figure 2). Over this period, 8,702 lake watersheds experienced ≥1 fire (6.3% of lakes), including 6,106 watersheds with ≥1 wildfire (4.4% of lakes; Figure 3) and 2,623 watersheds with ≥1 prescribed fire (1.9% of lakes; Figure S3a). Increasing occurrence of wildfires in

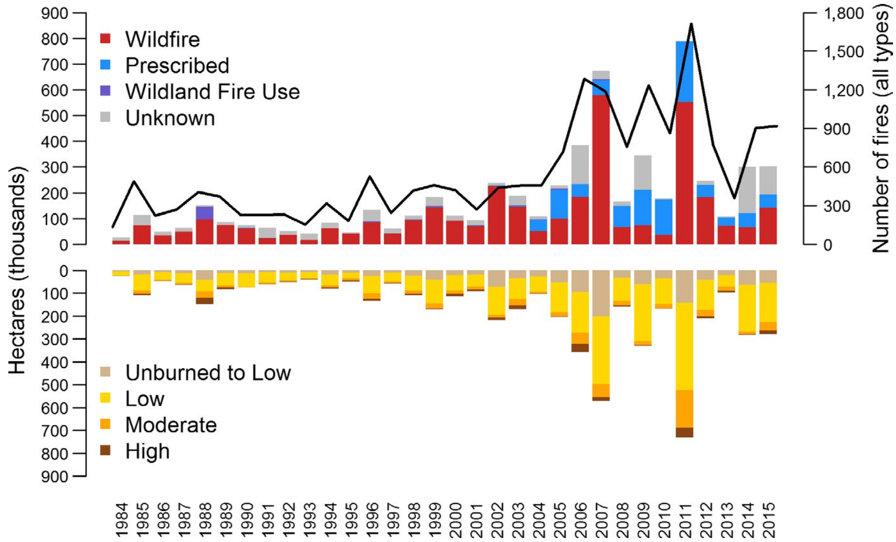

FIGURE 2 Fire by type, number of fires, and burn severity class in lake watersheds (1,500 m lake buffers) in the continental United States from 1984 to 2015. Annual area burned is lower in bottom plot because the Monitoring Trends in Burn Severity category "increased greenness," which occurs in fire polygons in upper plot, was excluded. High-severity ≥ 70% vegetation mortality, Moderate = 20%–70% vegetation mortality, Low ≤ 20% vegetation mortality

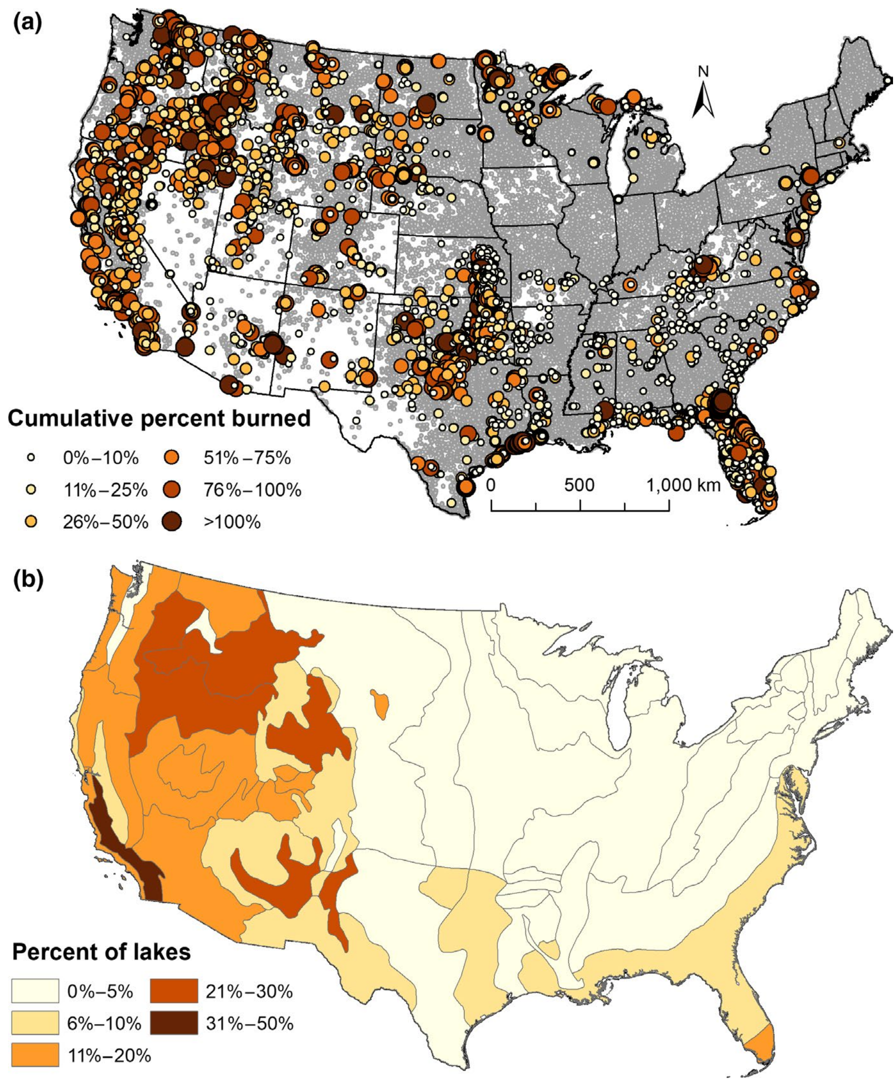

FIGURE 3 (a) Cumulative percent of lake watersheds (1,500 m lake buffers) burned (wildfire only) from 1984 to 2015 in the continental United States. Colored dots represent watersheds with at least one wildfire (n = 6,106) and gray dots represent watersheds without wildfire (n = 131,359). (b) Percent of lakes in each Bailey's province (ecoregions) with at least one watershed wildfire from 1984 to 2015

lake watersheds is consistent with documented increases in wildfires across much of the western United States (Dennison et al., 2014; Stavros et al., 2014). This reflects an increasing background rate of wildfire activity across the continental United States from 1984 to 2015 (Pearson's $\chi^2 = 66$, $df = 31$, $p < 0.001$). Wildfire constituted the majority of total area burned in most years. Prescribed fires were rare prior to 2004, but increased substantially in area thereafter. Total area burned and number of fires in lake watersheds increased markedly after 2005 and peaked in 2011. Fires were predominantly of low severity (<20% vegetation mortality) across all years, but moderate- and high-severity (20%–70% and >70% vegetation mortality, respectively) burn area both peaked in 2011 (163,708 and 43,760 ha, respectively), coinciding with peaks in total area burned and number of fires (Figure 2). Cumulative area burned from 1984 to 2015 was ≥100% (due to repeat burns) in 720 lake watersheds (8.3% of lakes with ≥1 fire). This result shows that some watersheds completely burned over a 32 year period, mostly due to wildfire (Figures S3a and S5).

2.1 | Spatial patterns of fire activity in United States lake watersheds

We analyzed spatial patterns of fire activity in United States lake watersheds according to both US states ($n = 48$) and Bailey's provinces (i.e., ecoregions; $n = 35$; Figure S4; USFS, 1994) in the continental United States. Exposure of lakes to wildfire was generally greater in the western United States than in other locations, except for Florida (Figure 3). Area burned in lake watersheds and number of watersheds experiencing wildfire was concentrated (a) west of the Rockies, (b) in the Southern Great Plains, and (c) in Florida (Figure 3a). In the west, California, Montana, and Idaho had the greatest number of lakes with watershed wildfire (493, 348, and 296 lakes, respectively), which account for 14.2%, 10.6%, and 30.7% of lakes in these respective states (Table S1). States with the largest percentages of lakes with watershed wildfire were Idaho (296 of 964 lakes; 30.7%), Arizona (85 of 372 lakes; 22.8%), and Nevada (82 of 381 lakes; 21.5%). In the Southern Great Plains, Oklahoma, Texas, and Kansas, respectively, had 285, 570, and 74 lake watersheds with wildfire, which account for 10.8%, 5.6%, and 4.1% of lakes in these respective states; however, wildfires were mostly concentrated in eastern Oklahoma, eastern Kansas, and northern Texas. Florida had the most lake watersheds with wildfire of any state (1,013 lakes; 10.1%), but also the third highest number of lakes (10,076 lakes; Table S1). Overall, lake-rich northeastern and midwestern regions experienced relatively low exposure to wildfire, whereas the few lakes in the more fire-prone western and central regions were most exposed to fire. Florida was the exception, where lakes and wildfires were both widespread.

Spatial patterns of wildfire activity across ecoregions were similar to those observed for US states. Although western ecoregions generally had higher percentages of lakes with watershed wildfire, these ecoregions contain relatively few lakes and overall more lake watersheds experienced wildfire in lake-rich portions of the United States (Table S2; Figure 3b). The five ecoregions with ≥20% of lakes with watershed wildfire all occurred in the western United States, but the ecoregion with the most lake watersheds with wildfire (1,427 lakes; 7.1%) was the Outer Coastal Plain Mixed Forest (southeastern United States), which includes 19,881 lakes and most of Florida, where fires are particularly prevalent (Table S2). In addition, the Everglades ecoregion of south Florida experienced proportionally more wildfire in lake watersheds: 12.1% of lakes (159 lakes). In contrast, the ecoregion with the greatest percentage of lakes with watershed wildfire was the California Coastal Range Open Woodland-Shrub Coniferous Forest-Meadow, which contains just 202 lakes, 51% of which experienced wildfire (102 lakes). Unlike the analysis of US states, the ecoregion-based analysis of wildfire in lake watersheds somewhat obscured the prevalence of lake watershed fires in the Southern Great Plains: only 6.6% and 5.7% of lake watersheds experienced wildfire in the Great Plains Steppe and Shrub (59 of 761 lakes) and Prairie Parkland (Subtropical; 437 of 6,172 lakes) ecoregions, respectively. Nonetheless, the analysis of both states and ecoregions generally both demonstrated that lakes in the relatively lake-poor western United States were most exposed to fire, whereas lakes in lake-rich areas were less exposed to fire, except for Florida.

Prescribed fires were relatively common in the Southern Great Plains and southeastern United States, particularly Florida. In Florida, the number of lake watersheds with fire was split approximately equally between wildfire and prescribed fire (Table S1; Figure S3a). More lakes experienced prescribed fire than wildfire in Kansas, South Carolina, Mississippi, Louisiana, Alabama, and Arkansas. Notably, 15.1% of all lakes in Kansas experienced prescribed fire, compared to ≤6.0% of lakes in each of these other states. Most ecoregions experienced relatively few (<10%) lake watersheds with prescribed fire. Similar to wildfires, the ecoregion with the most lake watersheds with prescribed fire (1,254 lakes; 6.3%) was the Outer Coastal Plain Mixed Forest (southeastern United States). With the exception of the Everglades ecoregion (80 lakes; 6.1%), all other ecoregions with ≥5% of lakes with watershed prescribed fire were relatively lake-poor (Black Hills Coniferous Forest: 2 of 21 lake watersheds; Arizona-New Mexico Mountains Semi-Desert Open Woodland-Coniferous Forest-Alpine Meadow: 17 of 228 lake watersheds; and Ouachita Mixed Forest-Meadow: 9 of 159 lake watersheds; Table S2; Figure S3b). Overall, prescribed fire was less common than wildfire in lake watersheds across the continental United States. Unlike wildfire, large prescribed fires in lake watersheds were relatively uncommon in the western United States and were instead mostly concentrated in the southeastern United States and Southern Great Plains.

2.2 | The role of small fires

Our estimate of 8,702 lake watersheds with fire since 1984 is likely conservative given that our study only contains fires >404 ha in the western United States and >202 ha in the eastern United States. Although large fires constitute a high proportion of total area burned, small fires comprise most fire occurrences in North America (Cui & Perera, 2008). Statistical estimates of small fire occurrence increased wildfire area burned by 16% in the continental United States from 2002 to 2010 compared to area burned by large fires in MTBS (Randerson, Chen, Werf, Rogers, & Morton, 2012). Therefore, many additional small lake watersheds may have experienced recent fire and accounting for small fires can improve estimates of lake exposure to fire, particularly in lake-rich regions where small fires represent larger proportions of total area burned (e.g., boreal Asia; Randerson et al., 2012). Data on small fires, however, are currently unavailable at the continental scale.

3 | REVIEWING BEST AVAILABLE SCIENCE ABOUT FIRE EFFECTS ON LAKES

Existing knowledge on the effects of fire on lakes is incomplete because it is primarily based on a relatively small number of mostly nutrient-poor lakes in boreal latitudes of North America. Some patterns have emerged from these studies; exports of material (e.g., carbon, nutrients, contaminants) tend to increase from land to lakes, which affect lake thermal structure, productivity, and food web structure. These effects were typically rapid, proportional to fire extent and/or burn severity, and lasted for 2–3 years following fire. Below, we review in more detail previous research on the physical, chemical, and biological responses of lakes to fire, noting key interactions among responses. Detailed findings for each study and reported fire characteristics are summarized in Tables S3 and S4.

3.1 | Physical responses of lakes to fire

3.1.1 | Light environment

Several studies have demonstrated effects of fire on light environments in lakes. The extinction coefficient of photosynthetically active radiation (PAR) increased approximately by 17%–75% in boreal Québec lakes up to 3 years postfire and was correlated with the watershed area burned/lake area ratio, primarily due to increased concentrations of dissolved organic carbon (DOC; Carignan, D'Arcy, & Lamontagne, 2000). Similarly, Allen, Prepas, Gabos, Strachan, and Chen (2003) found that declines in postfire visible light attenuation in the Swan Hills, Alberta were correlated with water residence time. France (1997) and McEachern, Prepas, Gibson, and Dinsmore (2000) reported significantly reduced lake water clarity (Secchi depth) in the Experimental Lakes Area (ELA), Ontario and Caribou Mountains, Alberta, respectively, primarily due to DOC. Lathrop (1994), however, found relatively small reductions in lake water clarity (Secchi depth; 0.4–0.9 m) in Yellowstone Lake, Wyoming across four sample stations up to 3 years postfire that were within the historical range of variability up to 10 years prefire. Finally, Schindler et al. (1996) found that PAR increased 0.16–0.20 m per year in two ELA lakes 15 years postfire. However, because these observations coincided with air temperature increases and precipitation decreases, they cannot be attributed directly to fire.

3.1.2 | Thermal environment

Comparatively fewer studies have examined effects of fire on lake temperatures, stratification, and ice cover duration. Although Schindler et al. (1996) found declines in the ice-free season of approximately 15 days and annual increases in water temperatures of 0.06–0.09°C per year over a 15 year period following fire, these changes coincided with air temperature increases and precipitation decreases. Loss of shoreline vegetation from wind damage, fire, or logging deepened lake thermoclines by 1–1.5 m up to 15 years postdisturbance across 23 lakes with burned shorelines in the ELA of Ontario. This change could theoretically reduce thermal habitat for cold-water fishes (France, 1997), but habitat was assessed in only two ELA lakes (Schindler et al., 1996). As such, although lake water temperature increases and declines in ice cover and cold-water fish habitat may be expected following fire due to riparian vegetation loss, direct observations are currently limited.

3.2 | Chemical responses of lakes to fire

3.2.1 | DOC

Many of the studies referenced above also documented increases in carbon concentrations following fires, measured as changes in DOC or water color. Observed postfire changes, however, varied widely across studies due to variability in fire extent, burn severity, and lake productivity. Carignan et al. (2000) found that median DOC increased up to 20% at 3 years postfire following moderate- to high-severity fire. McEachern et al. (2000) reported that mean color and DOC were 2.3- and 1.5-fold greater, respectively, up to 2 years following high-severity fire. Similarly, Scrimgeour, Tonn, Paszkowski, and Goater (2001) found that mean color approximately doubled in lakes with watershed fires in the Caribou Mountains, Alberta up to 2 years postfire. Fire extent and burn severity were not quantified, but these watersheds had not burned for at least 40 years, suggesting that fuel accumulation led to a substantial amount of high-severity fire. Allen et al. (2003) found that mean lake DOC and color were 1.4- and 2.3-fold greater up to 2 years postfire, respectively, for 20%–90% watersheds burned (mean = 62%). These lakes, however, were more productive and had longer water residence times than those studied by Carignan et al. (2000) and McEachern et al. (2000); postfire DOC increases were confounded by autochthonous (in-lake) DOC production, which coincided with increases in nutrient concentrations and primary productivity (described below). Overall, the few available studies suggest that fires can increase DOC concentrations, particularly in unproductive lakes, by increasing allochthonous DOC inputs, but that large and/or severe fires can consume organic materials in lake watersheds and mitigate or reduce allochthonous DOC influxes in the short term. Postfire DOC concentrations in productive lakes, particularly those with longer residence time, however, may also be influenced by autochthonous DOC production and coincident increases in nutrient concentrations and primary productivity following fire.

3.2.2 | Nutrients

These same previous studies also reported increases in lake nutrient concentrations following fire, which like changes in DOC, also varied according to fire extent, burn severity, and lake productivity. Carignan et al. (2000) observed that two- to sixfold increases in total nitrogen (TN) and total phosphorus (TP) concentrations in lakes with watershed fires persisted up to 3 years postfire, and that these increases were proportional to the watershed area burned/lake area ratio. McEachern et al. (2000) found twofold increases in mean TP and soluble reactive orthophosphate (SRP) and 1.2-fold or greater mean increases in various N forms up to 2 years postfire. TP concentrations were strongly correlated with percent watershed burned and time since fire. Scrimgeour et al. (2001) found mean SRP was approximately fivefold greater in lakes with watershed fires up to 2 years postfire. Kelly, Schindler, St. Louis, Donald, and Vladicka (2006) reported fourfold increases in TP and two- to ninefold increases in various N forms in an Alberta lake (72% watershed burned) compared to prefire data from 1 to 3 decades prior. In contrast, McColl and Grigal (1977) and Lewis, Lindberg, Schmutz, and Bertram (2014) found no increases in TP or N forms up to 3 years postfire in Minnesota lakes (65% and 70% watershed burned) and up to 7 years postfire in Alaska lakes (mostly moderate-severity fire, percent watershed burned unknown), respectively. McColl and Grigal (1977) attributed the lack of nutrient increases due to vegetation uptake, whereas prefire nutrient concentrations in Lewis et al. (2014) were large enough to prevent detection of increases due to fire. In summary, fires can generally be expected to increase nutrient concentrations in lakes, but increases may not be detectable at low levels of disturbance (i.e., low percent watershed burned and/or low-severity burns) or in productive lakes with large prefire nutrient pools.

3.2.3 | Ions and pH

Some studies also documented changes in ion concentrations and pH in lakes following fire. Carignan et al. (2000) found two- to sixfold increases in median K, Cl, Ca, Mg, and SO_4 concentrations up to 3 years postfire. In the cases of K and Cl, increases were proportional to watershed area burned, whereas SO_4 was weakly correlated with the watershed burn area/lake area ratio. Similar relationships were not found for Ca and Mg, likely due to confounding variation in geology across lake watersheds and lesser, delayed mobility of divalent cations (Carignan et al., 2000). Conversely, Allen et al. (2003) reported no increases in K, Cl, Ca, Mg, and Na concentrations up to 2 years postfire, which they attributed to dilution of increased surface water exports from burned watersheds following fire (due to vegetation loss), as well as larger surface water/groundwater input ratios (groundwater was a source of Ca and Mg). Additionally, McEachern et al. (2000) detected no differences in mean Ca, Mg, Na, K, Cl concentrations in lakes with watershed fires up to 2 years postfire, whereas McColl and Grigal (1977) found no changes in Ca, Mg, and K concentrations up to 3 years postfire. Acidic soils in boreal landscapes absorb cations, reducing inputs to lakes (McColl & Grigal, 1977). Lathrop (1994) documented median decreases in Ca of 1.1–2.4 mg/L, but results were inconsistent across sample stations and lakes for Na, K, and Cl in two Wyoming lakes up to 3 years postfire. Results were also inconsistent across studies for pH. Lathrop (1994) reported pH declines at two of four sample stations in Yellowstone Lake, Wyoming up to 3 years postfire. Although McEachern et al. (2000) found mean pH significantly increased by 0.7 up to 2 years postfire, Allen et al. (2003) reported mean pH declines of 0.3 in lakes with watershed fires, which were insignificant. Allen et al. (2003) noted, however, that lake pH was negatively correlated with the watershed burned area/lake area ratio, so larger fires may have increased pH, citing previous work in boreal watersheds showing increased SO_4 in lakes with watershed fires (e.g., Carignan et al., 2000, McEachern et al., 2000). Overall, previous research has found mixed results for effects of fire on lake ion concentrations and pH and that effects can vary based on fire extent, watershed soils, geology, and hydrology.

3.3 | Biological responses of lakes to fire

3.3.1 | Primary and secondary productivity

Research has found mixed effects of fire on lake primary and secondary productivity. Several studies reported increased primary productivity (measured as chlorophyll-*a* [chl-*a*] concentration) due to postfire nutrient influxes. Scrimgeour et al. (2001) and Kelly et al. (2006) found that chl-*a* was 1.5- to 3.5-fold greater up to 2–3 years postfire. Planas, Desrosiers, Groulx, Paquet, and Carignan (2000) showed that benthic primary productivity increased substantially more than pelagic primary productivity (150% and 25% increases, respectively) up to 3 years postfire with postfire chl-*a* proportional to the watershed area burned/lake area ratio. Although these lakes were primarily P-limited preceding fire, the disproportionate increase in benthic algal biomass was attributed primarily to increased exports of NO_3 following fire. Nutrient increases were correlated with shifts in pelagic algal biomass in favor of photoautotrophic diatoms following fire (Planas et al., 2000). In contrast, McEachern et al. (2000) and Allen et al. (2003) found no significant increases in chl-*a*, likely because of light limitation (DOC) offset nutrient increases. Lewis et al. (2014) found no increases in chl-*a* because relatively small nutrient influxes from fire were biologically irrelevant in eutrophic lakes.

At higher trophic levels, Lewis et al. (2014) reported four- to sixfold increases in shredders and twofold increases in predatory macroinvertebrates up to 2 years postfire, but no changes in filterers, gatherers, scrapers, or predatory waterbirds. Scrimgeour et al. (2001) found that increases in primary productivity coincided with 1.5-fold increases in macroinvertebrate biomass up to 2 years postfire. Patoine, Pinel-Alloul, Prepas, and Carignan (2000) found total zooplankton biomass increased 50% up to 2 years postfire, especially rotifers and crustaceans. Overall, fires can have complex effects on lake primary and secondary productivity. Although fires generally increase nutrient concentrations in lakes and can influence phytoplankton community structure, light limitation can negate potential increases in primary productivity. Studies of bottom-up cascading effects of increased primary productivity on secondary productivity generally suggest that zooplankton also increase and certain macroinvertebrate taxa become favored following fire.

3.3.2 | Mercury bioaccumulation

Finally, a few studies reported increased mercury concentrations in lakes following fire and examined bioaccumulation across a range of trophic levels. Allen, Prepas, Gabos, Strachan, and Zhang (2005) found no changes in methyl mercury (MeHg) in four of five macroinvertebrate taxa and brook stickleback (*Culaea inconstans*), a small fish, up to 2 years postfire. Kelly et al. (2006) found that postfire, nutrient-induced increases in primary productivity in an Alberta lake increased fish growth rates, but also restructured the food web, causing a fivefold MeHg increase in rainbow trout (*Oncorhynchus mykiss*) and a 45% increase in lake trout (*Salvelinus namaycush*) up to 3 years postfire. As lake primary productivity increased due to postfire nutrient influxes, the trophic position of fish increased due to diet shifts, leading to biomagnification (Kelly et al., 2006). Although Garcia and Carignan (2000), found no change in MeHg in northern pike (*Esox lucius*) up to 3 years postfire, MeHg in northern pike was positively correlated with zooplankton MeHg and concentrations of nutrients and DOC, but negatively correlated with pH, suggesting the potential for biomagnification with greater MeHg, nutrient, and DOC inputs. In contrast, Allen et al. (2005) found that increasing primary productivity from nutrient influxes reduced MeHg in macroinvertebrates by diluting MeHg in phytoplankton, but macroinvertebrate MeHg was negatively correlated with pH. In summary, past research indicates that fires have the potential to increase mercury inputs to lakes and lead to biomagnification across trophic levels, but other factors such as water chemistry and lake productivity can mediate effects of mercury on lake biota.

3.4 | Applying stream-fire research to lakes

Our review of the available literature reveals that existing lake-fire research is limited to just 14 studies of a single to a few lakes (≤10, with one exception) and fire events (12), mostly in boreal landscapes (Tables S3 and S4). Although these studies provide useful foundational knowledge, anticipating potential effects of fire on lakes across diverse landscapes and fire regimes requires building upon past lake-fire research by integrating knowledge from other ecological subdisciplines.

Previous stream-fire studies documenting both short- and long-term physical, chemical, and biological responses to fire can be used to infer potential responses of lakes that have not been documented in lake-fire studies and for geographies not studied previously. For example, N and P concentrations in Montana streams increased 5–60 times over background levels during fire events due to leaching of ash and diffusion of smoke gases, but returned to background levels within weeks (Spencer, Gabel, & Hauer, 2003). Although fish-kills were observed the day after fire, possibly due to elevated water temperatures, smoke gases, or altered water chemistry, stable isotopes showed N enrichment in macroinvertebrates and fish resulting from increased autochthonous primary productivity up to 5 years postfire (Spencer et al., 2003). In a study of Colorado streams, water temperatures and concentrations of nutrients, sediments, and metals remained above background levels up to 5 years postfire, particularly in watersheds with >45% high-severity fire (>70% vegetation loss; Rhoades, Entwistle, & Butler, 2011). Streams in burned watersheds averaged 4.5°C greater summer water temperatures compared to streams in unburned watersheds (Rhoades et al., 2011). Although snowmelt and precipitation mediate inputs of nutrients, sediments, and ions to streams from burned portions of watersheds (Mast, Murphy, Clow, Penn, & Sexstone, 2016; Oliver, Bogan, Herbst, & Dahlgren, 2012), streams can transport these or other fire-related materials to waterbodies in unburned watersheds (Oliver, Reuter, Heyvaert, & Dahlgren, 2012). In summary, streams represent a proximal freshwater response to fire; similar responses may occur in lakes, or propagate downstream to lakes. However, it remains unclear how much of the fire signal transfers from streams to lakes and how sensitive lakes are to stream inputs, which likely depends on lake volume and residence time, and as discussed in Section 3, also on prefire chemical conditions. Therefore, there is an urgent need for more lake-fire studies, particularly in fire-prone regions outside of the boreal region.

4 | AN INTEGRATIVE FRAMEWORK FOR LAKE RESPONSES TO FIRE

4.1 | A conceptual model

In the previous section, we discussed how stream studies may translate to lake responses to fires. Here, we extend this exercise and borrow from the aquatic, terrestrial, landscape, and fire ecology literatures to develop an integrative conceptual framework of potential fire effects on lakes (Figure 4; Table S3). We base the framework on various interacting meteorological, catchment, and limnological processes that potentially influence physical, chemical, and biological properties of lake ecosystems. The mechanisms and outcomes depicted and described in our framework represent hypothesized relationships based on best available science and can be used to guide future research.

4.2 | Lake temperatures, stratification, and ice cover

By modifying the physical structure of the landscape, fires can alter the physical structure of lakes. In particular, reduced vegetation cover and altered vegetation structure can increase wind and solar radiation exposure of a lake when fires occur near lakes (Figure 4a,b). Radiation

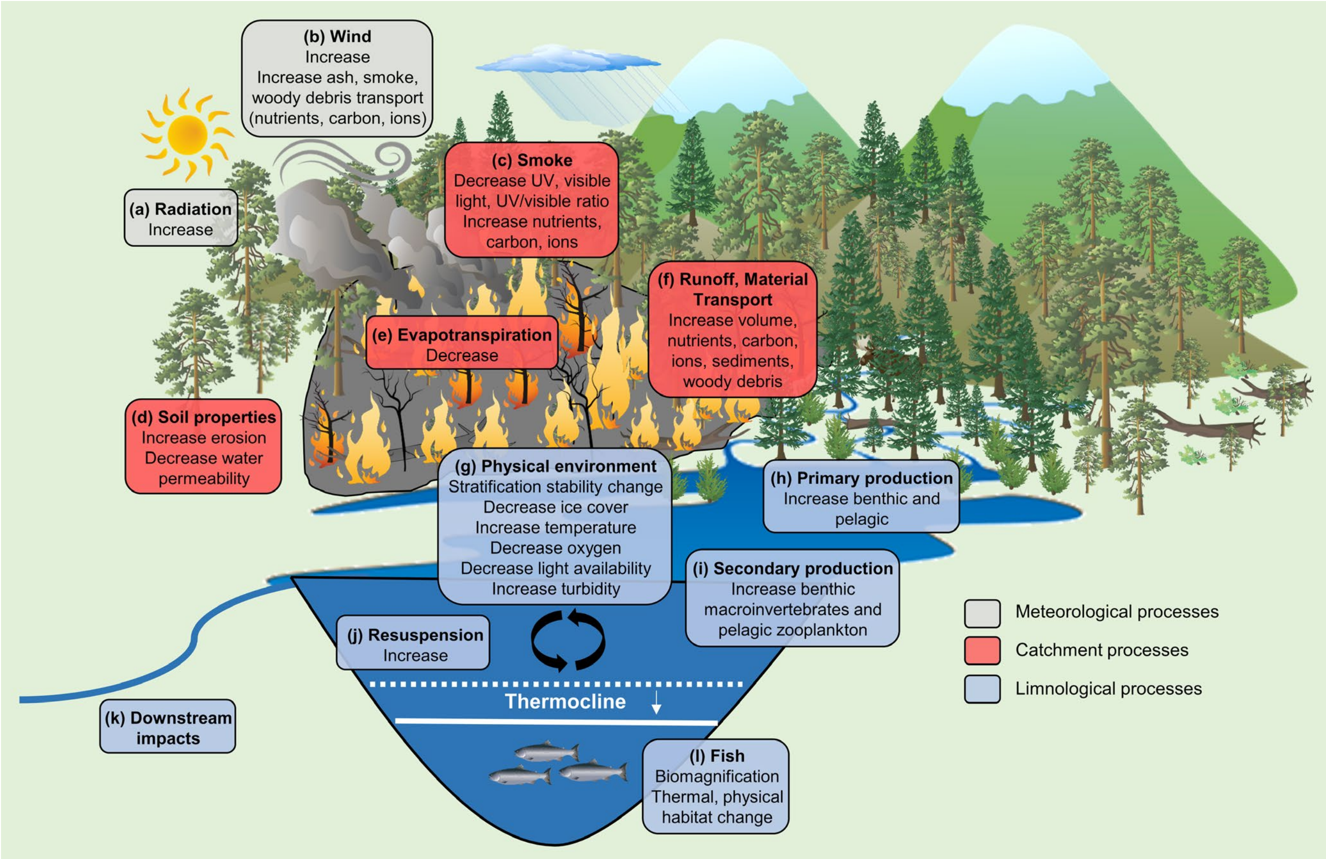

FIGURE 4 Conceptual model of hypothesized physical, chemical, and biological responses of lakes to fire based on best available science. Meteorological, catchment, and limnological processes interact and form feedbacks with weather, lake, landscape, and fire characteristics. Direction of change is specified for all processes except for stratification stability, which may increase or decrease due to wind exposure or increase due to radiation exposure, and fish habitat, which may decrease or increase depending on species' tolerances. Letters within boxes refer to descriptions in the main text. Vector images were courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)

can increase water temperature, length of the ice-free season, and thermocline depth, potentially increasing stratification stability (Figure 4g; Schindler et al., 1996). Increased solar radiation includes both visible and UV radiation; however, smoke during fires reduces total radiation and the UV/visible ratio (Figure 4c; Williamson et al., 2016). Wind exposure can also deepen thermoclines due to wind turbulence, increasing stratification stability, particularly in larger lakes with a long fetch (France, 1997). In smaller lakes, however, fetch has a smaller effect on thermocline depth; cooling of surface waters due to increased wind exposure can reduce stratification stability (if lakes are deep enough to be stratified). In such lakes the direct and indirect effect of vegetation structure on the heating of shorelines and the protection from wind are expected to be more important. Based on these known effects, we hypothesize that lake physical structure will be most sensitive to fires in small and shallow lakes with relatively complex perimeters and large proportions of lake shorelines burned.

4.3 | Nutrients and sediments

Fire-driven changes in the landscape further affect the loading of material to lakes, which may also affect lake thermal regimes as well as other chemical and biological properties. Erosion and runoff from burned areas can increase sediment loads to lakes and tributaries, reducing light penetration (Figure 4d,f,g; Earl & Binn, 2003; Oliver, Reuter, et al., 2012; Rhoades et al., 2011). Runoff can also increase due to reduced evapotranspiration, soil absorption of water, and canopy interception of precipitation in burned areas after vegetation loss (Figure 4d–f; Bart, 2016; Ice, Neary, & Adams, 2004; Wright, 1976). Vegetation loss and altered soil properties after fire also influence runoff chemistry. Soil erosion, soil exposure, and reduced plant uptake can increase N and P concentrations in runoff, particularly near lakes and tributaries if vegetation buffers have burned (Figure 4d,f; Allen et al., 2003; Carignan et al., 2000; Kelly et al., 2006; McEachern et al., 2000; Scrimgeour et al., 2001). Increased water column turbulence due to wind and reduced shoreline vegetation may result in P resuspension from lake sediments, particularly in shallow lakes (Figure 4g,j; Søndergaard, Jensen, & Jeppesen, 2003). Increased wind also can increase transport of ash and smoke, sources of bioavailable nutrients to lakes and tributaries, potentially from fires outside the focal lake watershed (Figure 4b,c; Earl & Binn, 2003; Spencer et al., 2003). Overall, existing evidence suggests an increase in the loading of solutes and particles to lakes and a potential for increased internal cycling of nutrients, which should all lead to decreased water transparency following fire. We hypothesize that lakes with short water residence times and relatively high sediment surface in contact with the epilimnion may have a stronger, immediate response to fires than large lakes because the incoming water with altered chemistry represents a greater fraction of the lake water, but also has greater probability of being flushed out of the system before durable effects on the trophic structure can be established.

4.4 | Organic materials

Fires have the potential to influence organic matter dynamics along two separate pathways. First, falling or wind-transported ash represents a potential source of particulate organic carbon (POC) via wind directly into lakes and tributaries that can come from fires both within and outside the focal lake watershed (Figure 4b,f; Earl & Binn, 2003). Runoff from burned areas can increase DOC and POC in lakes (Allen et al., 2003; McEachern et al., 2000; Scrimgeour et al., 2001). Conversely, reduction of allochthonous sources of POC and DOC due to removal of vegetation and soil organic layers can result in decreases in organic matter inputs to lakes from the watershed or hydrologically linked upstream systems immediately following fire (Carignan et al., 2000). Increases in lake DOC reduce water clarity and increase water color (Allen et al., 2003; McEachern et al., 2000; Søndergaard et al., 2003). The overall evidence suggests increased loadings of organic material with potential decreases in transparency and primary productivity, but organic inputs may stimulate autochthonous production. However, the strength, and even direction of the effects of fire on terrestrial loading of organic materials appear to vary across regions, particularly in those with contrasting levels of soil organic carbon. We hypothesize that regions with older soils containing higher amounts of organic carbon will tend to export more DOC following fire, whereas lakes in postglacial or alpine landscapes with lesser amounts of organic carbon may experience a decrease in DOC following fire if the little soil organic carbon leached from soils is not rapidly replaced.

4.5 | Ions and pH

Along with nutrients, sediments, and organic material, which tend to increase in response to increased runoff following fire, ions including Si, K, Mg, Mn, Ca, Hg, Na, Cl, and SO_4 may increase in lakes and tributaries following fires due to soil exposure and erosion and reduced uptake by plants, but will likely depend on watershed soil chemistry and geology (Figure 4d,f; Allen et al., 2003; Carignan et al., 2000; Lathrop, 1994; McColl & Grigal, 1977; McEachern et al., 2000). Ions may also be transported to lakes and tributaries through smoke and ash, potentially from outside the focal lake watershed (Figure 4b,c; Earl & Binn, 2003). These various chemical changes can mediate changes in pH (Allen et al., 2003; Carignan et al., 2000; Lathrop, 1994; McEachern et al., 2000). For example, acidic soils in boreal landscapes are often a source of SO_4, which can increase acidity in lakes following fire (Allen et al., 2003; McEachern et al., 2000). There are well-known regional patterns in soil properties and geology as well as in human-driven atmospheric deposition and erosion of ions that affect lake pH, alkalinity, and conductivity (Dugan et al., 2017; Read et al., 2015). Therefore, while the consensus is that most ions should increase following fire, we hypothesize that the relative effect of fires on lake chemistry will strongly vary from well-buffered lakes in the Central Plains to northern, acidic lakes with high DOC content and low alkalinity, and that this effect will be modulated by other human activities that affect these ions (e.g., SO_4 deposition, erosion) concurrent with fires.

4.6 | Ecosystem-wide implications of fire and the importance of ecological context

Fires can have immediate and long-lasting effects on the physical and chemical properties of lakes, and these responses can have direct consequences for biota. Pelagic and benthic primary productivity can increase in response to fire due to increased nutrient inputs (Figure 4f,h; Allen et al., 2003; Kelly et al., 2006; Planas et al., 2000; Scrimgeour et al., 2001), which can lead to increases in abundance of zooplankton (Garcia & Carignan, 2000; Patoine et al., 2000) and/or benthic macroinvertebrates (Figure 4i; Lewis et al., 2014). Reduced UV exposure due to smoke can redistribute zooplankton to shallower depths (Figure 4c; Urmy et al., 2016). Increases in primary productivity, however, are mediated by light availability, which may increase or decrease depending on DOC or sediment concentrations in runoff and vegetation loss near lakes and/or tributaries (Figure 4a,g; McEachern et al., 2000; Rhoades et al., 2011), and water temperatures and thermal structure, which also depend on vegetation loss, as well as wind exposure (Figure 4b; France, 1997; Schindler et al., 1996). Vegetation loss, however, can also lead to increases in coarse woody debris in lakes (either direct-fall into lakes or tributaries, or wind-transported), providing important habitat features for fish species (Figure 4b,f,l; Bisson et al., 2003; Rieman, Hessburg, Luce, & Dare, 2010). Increasing water temperatures reduce dissolved oxygen, altering habitat availability for fish (Figure 4g,l; France, 1997; Schindler et al., 1996). Particularly for large fish at high trophic levels, Hg biomagnification may occur following fires (Figure 4l; Kelly et al., 2006), but previous studies have not shown consistent biomagnification at lower trophic levels and other fish (Allen et al., 2005; Garcia & Carignan, 2000). The biological response of lakes to fire is perhaps the most complex and the least consistent among studies, as organisms respond to confronting factors that may simultaneously, for example, stimulate or inhibit primary productivity. Moreover, fires can affect trophic networks more durably than the purely physical or chemical lake properties because these effects are propagated across food webs, with some organisms (e.g., fishes) living much longer than the immediate fire response. We argue that this is where the main knowledge gap lies as current evidence does not allow us to suggest reliable hypotheses on the net impact of fires on lake biota, let alone on how this impact could differ across regions.

Although our framework represents the major processes by which fires can affect lake ecosystem properties, we expect that lake responses to fire are potentially mediated by weather and lake, landscape, and fire characteristics (Figure 4). In other words, ecological context is important and must be considered when applying results from one study to predict potential lake responses to fire elsewhere. For example, air temperature, precipitation, and water residence time influence runoff timing and volume. Although precipitation increases nutrient and metal concentrations in lakes, droughts occurring after fire may counteract this (Schindler et al., 1996). Lake surface area may mediate ash deposition in lakes and lake morphometry may mediate lake thermal responses and internal nutrient cycling. Watershed topography, particularly in mountainous terrain, influences weather patterns, ash transport, and runoff dynamics. Soil properties may mediate nutrient concentrations in runoff (McColl & Grigal, 1977). Watershed stream, wetland and lake abundance, and hydrologic connectivity may influence inflows of nutrients and metals to lakes (Fergus et al., 2017). Water residence time may increase the persistence of fire effects on lake ecosystems; outflows may reduce persistence, but also transfer effects of fire to downstream ecosystems (Figure 4k). Finally, fire extent, severity, patch-size distribution, history, and proximity of lakes to fire may also mediate lake responses to fire. The studies we reviewed reported varying levels of detail on fire extent and burn severity, making it difficult to infer their potential effects consistently across studies (Table S4). Broadly, we expect large patches of high-severity fire near lakes and tributaries to have greater effects on lakes than small patches of low-severity fire far from lakes and tributaries (Figure 4; Pettit & Naiman, 2007). The inherent complexity associated with lake responses to fire suggests that responses among lakes likely vary and depend on different variables in different ecological contexts.

5 | BLAZING A PATH FORWARD: EMERGING RESEARCH PRIORITIES AND MANAGEMENT IMPLICATIONS

Existing evidence suggests that lake nutrients, primary and secondary productivity, ions, sediments, and organic matter should increase in response to fires, whereas water clarity and thermal habitat for cold-water fishes are expected to decrease. Moreover, it seems that compared to stream responses, lake responses may be weaker in terms of peak response, but that the responses may be sustained over longer periods of time. These expectations are based on the best available knowledge and have numerous implications for ecosystem services provided by lakes. Past studies on the effects of fires on lakes, however, have been limited in terms of total number and geographic and ecological contexts. In particular, most studies so far have been conducted on ≤10 of lakes in the boreal regions of North America (Table S3), far from where fire activity is increasing the most in the continental United States. It thus remains unclear whether these results translate well to other regions with different climate, geology, topography, land use/cover, and hydrology, among other properties. Projected increases in the frequency and severity of warm and dry periods, heightened risk of large wildfires (Cook, Ault, & Smerdon, 2015; Littell, Peterson, Riley, Liu, & Luce, 2016), and increasing occurrence of wildfire in lake watersheds across parts of the continental United States demonstrate the urgent need to expand the geographic extent of lake-fire research. Our conceptual framework identifies hypothesized physical, chemical, and biological responses of lakes to fire to be examined in future research (Figure 4). Broad-scale studies of hundreds to thousands of lakes across many regions and ecological settings, particularly in fire-prone landscapes, are therefore required for evaluating the generalizability of our framework. Next we identify four key research priorities:

1. *Reservoir-fire research is needed*. Research on reservoirs is critical because they are an important source of drinking water and recreation in many fire-prone regions, particularly those with few natural lakes and limited water supplies (e.g., western and southeastern United States). A prominent example is the Hetch Hetchy reservoir in the Sierra Nevada, California, which supplies water to the densely populated San Francisco Bay Area. In late summer 2013, the Rim Fire burned approximately 104,038 ha (determined from MTBS data), resulting in a state of emergency declaration and uncertain water supplies for millions of people. Although the fire ultimately did not damage the water supply, the incident is a jarring reminder of human vulnerability to fire in fire-prone landscapes (Polenghi-Gross, Sabol, Ritchie, & Norton, 2014).

Compared to natural lakes, reservoirs experience more variable water levels and tend to have complex perimeters and larger watersheds (Doubek & Carey, 2017). Therefore, reservoirs may respond differently than natural lakes to fires, particularly when high water demands coincide with warm, dry weather conducive to wildfire. However, there currently exists no information about which of the hundreds of thousands of lakes in the continental United States are natural lakes or reservoirs. Thus, it is necessary both to develop broad-scale, consistent classification of both natural lakes and reservoirs, and then to study possible differences in their responses to fire. This will be especially important for reservoir managers seeking to maintain ecosystem service provision in fire-prone landscapes.

2. *Research is needed to examine lake ecosystem recovery following fire and what variables influence recovery*. As described above, ecological context, which includes weather, lake, landscape, and fire characteristics, may mediate lake responses to fire and may influence postfire recoveries, but existing evidence is currently limited. Future broad-scale research will help identify variables that make some lakes more sensitive or resilient to fires than others. This information can assist lake managers estimate the magnitude of potential ecosystem service loss following watershed fires. For example, vegetation regrowth postfire may decrease nutrient concentrations in runoff (McColl & Grigal, 1977) and increase evapotranspiration, decreasing runoff volume (Bart, 2016). Therefore, postfire successional dynamics, which are often mediated by both climate and burn severity (Savage, Mast, & Feddema, 2013; Turner, Romme, & Gardner, 1999),

may influence lake recoveries following fire. Additionally, paleolimnological analysis of lake sediment cores collected across many lakes distributed across different ecological settings can test hypotheses about the controlling factors of lake responses to fire (e.g., Paterson, Cumming, Smol, Blais, & France, 1998).

Ultimately, local- and regional-scale studies must be placed within the broader continental context that enables extrapolating results from fine to broad scales. In situ lake measurements are increasingly available in regional- to continental-scale water quality databases (e.g., LAGOS; Soranno et al., 2017, GLNC; Williams & Labou, 2017, and United States National Lakes Assessment) and integrated ecosystem change detection networks (e.g., National Ecological Observatory Network; NEON). Broad-scale fire databases such as MTBS provide a growing source of consistently mapped fire data. As such, studying lake responses to fire across a range of spatial scales, which largely has not occurred, is becoming considerably more practical than even a few years ago.

3. *Lake watershed fires need to be studied in the appropriate historical and global change contexts*. Although future exposure of lakes to fire is unclear overall due to uncertainties and feedbacks among projections for climate, land use, and fuel properties (Gergel, Nijssen, Abatzoglou, Lettenmaier, & Stumbaugh, 2017; Whitman et al., 2015), many watersheds will likely experience fire activity that increasingly diverges from historical fire regimes. Recent increases in fire activity in lake watersheds, whether attributable to changes in climate, land use management, other human activities, or a combination, suggest that some watersheds may already be experiencing more fire than historically. On the flip side, watersheds that experienced less fire activity in recent decades due to fire exclusion practices may be more likely to experience large future fires at higher severities than watersheds that recently experienced extensive burns (i.e., "fire deficits"; Parks et al., 2015). It is therefore important for future lake-fire research to consider recent and future lake watershed fires in both historical and global change contexts.

Historical fire regime classifications for the United States are available at the national scale (i.e., LANDFIRE; Rollins, 2009), and more precise landscape-scale fire regime reconstructions are often available from a variety of sources including tree rings, lake sediments, forest stand structure, or combinations (Higuera, Whitlock, & Gage, 2011; Swetnam, Falk, Hessl, & Farris, 2011; Tepley & Veblen, 2015). Such historical information, particularly when supported by multiple lines of evidence, is useful for contextualizing postfire responses and recoveries of both lakes and watersheds. Looking toward the future, however, it is important to note that many forested landscapes no longer have the same vegetation pattern and structure that supported historical fire regimes (i.e., tree density and age structure, patch-size distribution, species composition; Hessburg et al., 2015). Lengthening fire seasons under a changing climate (Westerling, 2006) and expanding human activities into fire-prone landscapes (e.g., power lines, campfires), particularly in the wildland–urban interface (Balch et al., 2017) also contribute to landscape-scale shifts in fire regimes. As such, historical fire regimes are a useful guide for characterizing potential disturbances in lake watersheds, but likely do not fully reflect current or future disturbance regimes under global change. Potential fire regimes and vegetation patterns should therefore be considered in a modern, climate change adaptation context (Schoennagel et al., 2017).

4. *There is need for collaboration across land–water boundaries in both research and management*. The above research agenda will be best addressed through strategic collaborative study of lakes across a wide range of fire-prone settings and regions among terrestrial, aquatic, fire, and landscape ecologists. In addition, future research should include long-term studies of lakes in fire-prone areas that have good prefire data, suggesting that perhaps new long-term sites should be situated in fire-prone areas identified in our study. Establishment of such programs will also enable deeper investigations of lake responses to local-scale variables and processes (e.g., links between land management history and fire behavior). Lakes can also act as natural fuel breaks and therefore influence fire behavior and extent, but continental-scale analyses of area burned in lake watersheds inherently overlook this process. Finally, although we focused on lakes due to the lack of past research and their potentially heightened sensitivity compared to other fresh waters, future research should also examine integrated responses of the entire freshwater landscape to fires. Monitoring connected networks of lakes, streams, and wetlands offers emerging opportunities to strengthen our understanding of fire-based terrestrial–aquatic ecosystem linkages at landscape scales.

As research progresses, large wildfires will continue to grip public attention owing to their destructive capabilities and endangerment of human societies (Radeloff et al., 2018; Schoennagel et al., 2017). Coexisting with frequent, large wildfires is a reality of the 21st century (Moritz et al., 2014). Yet, potentially overlooked amidst dramatic media headlines is the importance of sustaining critical ecosystem services provided by fresh waters and their watersheds (e.g., drinking water quality, erosion control, recreation). Although our conceptual framework can help lake managers anticipate effects of fire on lake ecosystem services, important decisions affecting fuel treatments and land use that ultimately influence fire behavior and lake ecosystem services are generally made by other managers. Decisions of land managers directly influence water quantity and quality of downstream waterbodies, demonstrating that land, fire, and water should not just be studied, but also managed jointly, particularly in dry, fire-prone landscapes under a changing climate (Grant, Tague, & Allen, 2013). For example, prescribed fire or fuel treatments in watersheds that supply drinking water or other important ecosystem services may reduce their vulnerability to large wildfires, particularly in the western United States dry forests where wildfires are common and water supplies are limited. It is increasingly clear that maintaining important ecosystem services provided by fresh waters will depend on strategic collaboration among diverse natural resource managers to address the terrestrial and aquatic processes influenced by changing patterns of fire.

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AUTHOR CONTRIBUTION

IMM performed data analysis and led manuscript writing. JFL and PAS assisted with literature review. All authors contributed to the conceptual model development and wrote portions of the manuscript.

ORCID

Ian M. McCullough https://orcid.org/0000-0002-6832-674X
Kendra Spence Cheruvelil https://orcid.org/0000-0003-1880-2880
Jean-François Lapierre https://orcid.org/0000-0001-5862-7955
Noah R. Lottig https://orcid.org/0000-0003-1599-8144
Max A. Moritz https://orcid.org/0000-0002-8995-8893
Jemma Stachelek https://orcid.org/0000-0002-5924-2464
Patricia A. Soranno https://orcid.org/0000-0003-1668-9271

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