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Fire effects on aquatic ecosystems: an assessment of the current state of the science

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Abstract: Fire is a prevalent feature of many landscapes and has numerous and complex effects on geological, hydrological, ecological, and economic systems. In some regions, the frequency and intensity of wildfire have increased in recent years and are projected to escalate with predicted climatic and landuse changes. In addition, prescribed burns continue to be used in many parts of the world to clear vegetation for development projects, encourage desired vegetation, and reduce fuel loads. Given the prevalence of fire on the landscape, authors of papers in this special series examine the complexities of fire as a disturbance shaping freshwater ecosystems and highlight the state of the science. These papers cover key aspects of fire effects that range from vegetation loss and recovery in watersheds to effects on hydrology and water quality with consequences for communities (from algae to fish), food webs, and ecosystem processes (e.g., organic matter subsidies, nutrient cycling) across a range of scales. The results presented in this special series of articles expand our knowledge of fire effects in different biomes, water bodies, and geographic regions, encompassing aquatic population, community, and ecosystem responses. In this overview, we summarize each paper and emphasize its contributions to knowledge on fire ecology and freshwater ecosystems. This overview concludes with a list of 7 research foci that are needed to further our knowledge of fire effects on aquatic ecosystems, including research on: 1) additional biomes and geographic regions; 2) additional habitats, including wetlands and lacustrine ecosystems; 3) different fire severities, sizes, and spatial configurations; and 4) additional response variables (e.g., ecosystem processes) 5) over long (>5 y) time scales 6) with more rigorous study designs and data analyses, and 7) consideration of the effects of fire management practices and policies on aquatic ecosystems.
Key words: wildfire, aquatic ecosystems, streams, rivers, wetlands, ecosystem, biota, prescribed burns

Fires are natural disturbances and agents of landscape change that have a diversity of effects across a variety of spatial scales. Perceptions of the consequences of fire are closely tied to human values (Langston 1995). For example, the use of fire distinguishes humans from other animal species, enhances food nutritional value, and promotes the expansion of valued plant and animal resources. Fire also was an integral driver of the invention and adoption of tools, other technological innovations, and, ultimately, the industrialization and urbanization of human societies, creating the modern world we know today (Pyne 2012). In contrast, humans generally view uncontrolled fire as harmful and destructive of natural vegetation, property, and life. However, from an ecological perspective, fires have structured many ecosystems with resilient successional trajectories (Pyne et al. 1996, Gresswell 1999, Bowman et al. 2009). Fire management and policy tend to be focused on protecting human property and life and on protecting or salvaging the economic value of terrestrial resources, such as timber, but fire also affects freshwater resources, habitats, and biodiversity.

Given the critical importance of water resources to human populations and natural communities globally, a thorough understanding of the effects of fire on water

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resources is increasingly important for guiding fire management practices and policy decisions. Some short-term effects of fire on freshwater ecosystems can be similar to the effects of landuse changes (e.g., agricultural and urban development and logging), but fire is a pulsed disturbance, and the duration of its effects on freshwater ecosystems depends on terrestrial ecosystem recovery. In contrast, landuse changes constitute a press disturbance with more permanent effects (Allan 2004, Wootton 2012, Verkaik et al. 2013). The purpose of this special series of articles is to illustrate the importance and complexities of fire as a prime driver of change in the physical, chemical, and biological characteristics of freshwater habitats in different geographic regions and biomes (Fig. 1). Given the projected effects of climate change on fire frequency and intensity (Knowles et al. 2006, Seager et al. 2007, Pausas and Fernández-Muñoz 2011, Westerling et al. 2011), we argue that our focus on the effects of fire on freshwater ecosystems is timely.

Most previous work on the effects of fire on freshwater ecosystems has concentrated on wildfire effects on the physical, chemical, and biological characteristics of forested, montane streams and wetlands in the western USA (Gresswell 1999, Pilliod et al. 2003, Rieman et al. 2003). Authors of articles in this special series expand on these topics by considering fire effects on a variety of organisms (ranging from algae and riparian vegetation to spiders and fish) and processes (including microclimate, hydrology, and biogeochemistry; nutrient inputs, uptake, and limitation; and subsidies between terrestrial–aquatic habitats and tributary–mainstem systems). These organismal and process studies were done across a wide array of geographic areas (North America, Europe, Australia, Asia), biomes (boreal forest, Mediterranean shrublands, tropical savanna, temperate, tropical, and semitropical wetlands and forests), and habitats (rivers, riparian zones, lakes, wetlands). Previous work has focused on the effects of fire on state variables, but a number of authors in this series

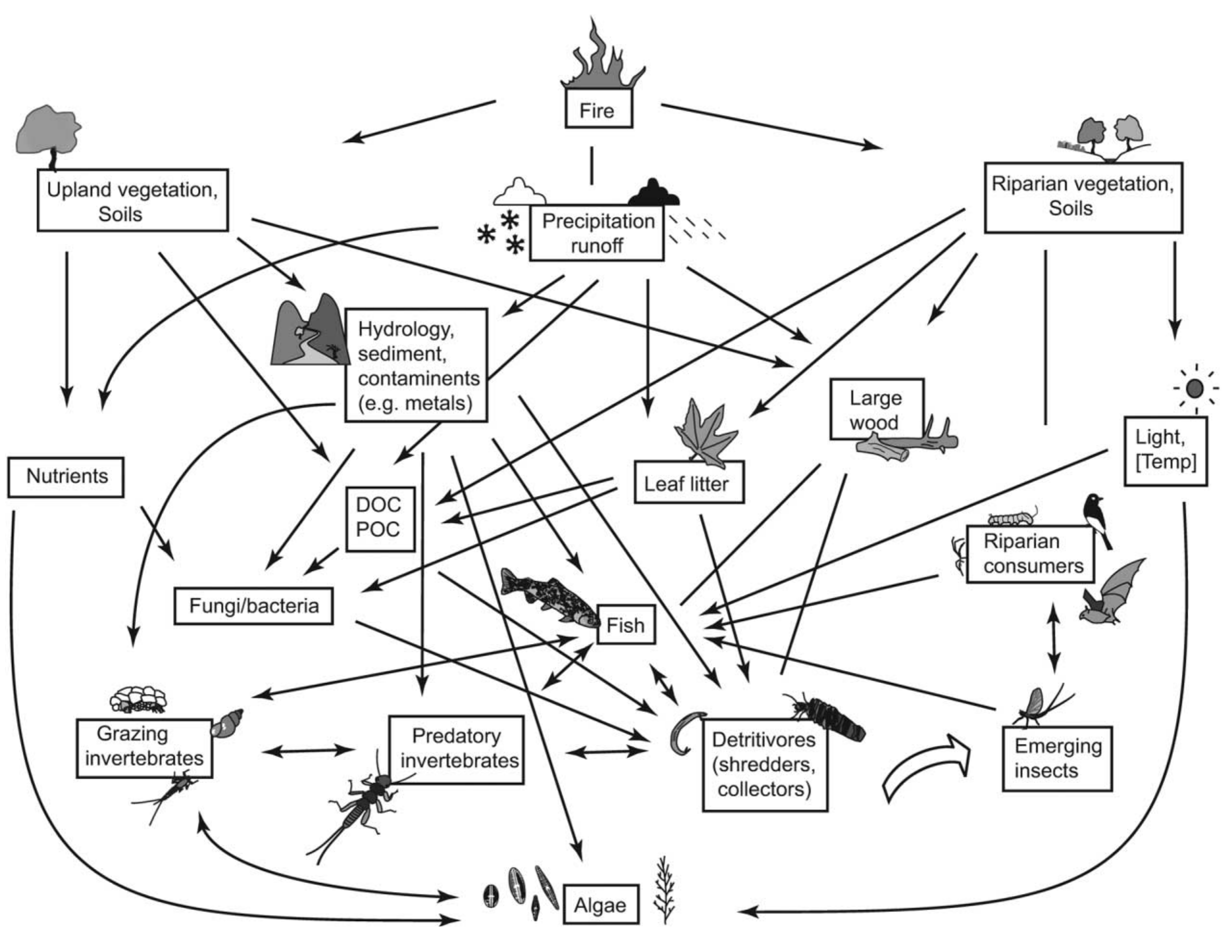

Figure 1. Path diagram showing probable cause–effect relationships leading from fire to stream communities. Lines without arrows indicate factors that are associated with each other, unidirectional arrows point from driver to response variables, and double-headed arrows indicate consumer–resource interactions where consumers depress and benefit from the consumption of their resources. Temp = temperature, DOC = dissolved organic C, POC = particulate organic C.

concentrated on effects of fire on ecosystem processes or rate variables, including nutrient uptake (Diemer et al. 2015), nutrient limitation (Klose et al. 2015), leaf decomposition (Rodríguez-Lozano et al. 2015), subsidies from river tributaries to river main stems (Harris et al. 2015), and subsidies from streams to riparian zones (Jackson and Sullivan 2015).

This special series was developed in conjunction with a special symposium held at the Joint Aquatic Sciences Meeting in Portland, Oregon, in May 2014. The articles collectively emphasize the pervasive influence of fire on the structure and function of aquatic ecosystems throughout the world and underscore the importance of considering effects of fire on freshwater systems when furthering our knowledge of drivers of ecosystem change and when guiding or developing effective natural resource management practices and policies.

We built on a list of research needs identified by Verkaik et al. (2013) to evaluate how the papers in the present special series address some of the knowledge gaps in the literature on fire effects on aquatic ecosystems. We focus on key aspects of fire effects on riparian and wetland vegetation, microclimate and hydrology, water quality, organic matter subsidies, and stream biota. We conclude with a list of the most critical research needs. The research advances reported in this special series can provide a foundation and springboard for future research leading to the formulation of effective fire management practices and policies that better sustain freshwater resources, habitats, and biodiversity.

RIPARIAN AND WETLAND VEGETATION

When terrestrial vegetation is consumed by fire, nutrients are mobilized, runoff and erosion increases, and soils may be altered. Habitat changes occur that favor some species and impede others. The literature on the responses and recovery of many upland vegetation types to both wildfire and prescribed fire is extensive. Because of differences in the microclimate, foliar moisture, structure, composition, and life histories of riparian/wetland and upland plant species, these plant communities can respond very differently to fire (Dwire and Kauffman 2003, Van de Water and North 2011). Although the role of fire has been studied in some wetland vegetation types, such as those occurring in the Everglades (Richardson 2010), existing knowledge on fire effects is limited for many wetland plant communities. Recent studies have provided data on riparian vegetation responses to fire (Pettit and Naiman 2007, Halofsky and Hibbs 2009, Jackson et al. 2012, Verkaik et al. 2013), as well the influence of riparian conditions on fire behavior (Halofsky and Hibbs 2008), but information is lacking for many riparian plant species and communities. Watershed-wide effects of fire on sediment and nutrient inputs have been studied extensively, but the specific effects of riparian or wetland burning on freshwater ecosystems, including organic matter loading, biogeochemical cycles, light and temperature levels, and, ultimately, the aquatic biota, have rarely been delineated (Cooper et al. 2015).

Douglas et al. (2015) examined the effects of intensely managed fires on the composition and structure of riparian vegetation in Australia's savannas. They compared riparian vegetation characteristics in burned and unburned watersheds in an experiment conducted in whole watersheds. Vegetation was sampled 1 y after 3 y of sequential annual burning. The application of prescribed burning significantly reduced woody species richness, total species abundance, total basal area, the abundance of small trees, canopy cover, and the richness and cover of vines, but increased grass cover. Results of this study identified riparian plant species that appeared to be adapted to different fire frequencies and showed that riparian areas are considerably more sensitive to fire than the surrounding savanna.

The floodplain shifting habitat mosaic concept proposes that habitat patch dynamics are driven by flood pulses that alter the geomorphology of channels, banks, and floodplains, thereby creating new habitats and changing existing habitats (Stanford et al. 2005). Kleindl et al. (2015) extended the shifting habitat mosaic concept to examine the effects of multiple, different disturbances, including floods and fire, on the composition of vegetation along the riparian corridor of the Flathead River (British Columbia and Montana). They applied a combination of path and graphical analysis to a 22-y data set to examine relationships among hydrology, fire, land use, geomorphic position, and floodplain habitat patch dynamics. Three factors (fire, stream power, and geomorphic position) collectively explained much of the variation in floodplain vegetation patch composition across study reaches. Wildfire had the strongest total effect. Long-term investigation of disturbance and recovery pathways in a floodplain allowed the authors to expand the shifting habitat mosaic concept from one in which landscape dynamics are driven only by major hydrologic events to one that incorporates the influences of other riverscape and landscape disturbances, particularly fire.

MICROCLIMATE AND HYDROLOGY

Fire effects on terrestrial and wetland vegetation and on soils influence aquatic ecosystems by altering microclimatic regimes, increasing runoff and river discharge, and enhancing erosion and sediment inputs, transport, and deposition (Gresswell 1999, Benda et al. 2003, Coombs and Melack 2013). As a consequence, fire effects on aquatic ecosystems are the compounded effects of 2 scales of disturbances: seasonal or interannual increases in runoff and erosion associated with storms or snowmelt superimposed on longer-term consequences of fire disturbance.

Fire also can affect the physical characteristics of ecotones, including transitions from riparian and wetland areas to uplands. Watts and Kobziar (2015) compared air temperature, relative humidity (RH), and vapor pressure deficit (VPD) in patches of pond cypress (cypress domes) and adjacent grasslands in southern Florida, USA, 2 y after wildfire. Increasing differences in air temperature, RH, and VPD were observed with distance from the dome centers into savanna habitats, but microclimates were either similar or, in some cases cooler or more humid, in burned than in unburned domes. Watts and Kobziar (2015) attributed this response to vigorous vegetative regrowth following fire. Their study increases our understanding of interactions between cypress domes and ecotonal microclimates, thereby increasing the ability of resource managers to maintain these unique plant communities under predicted scenarios of greater variability in climate and fire regimes.

Given that the ecological effects of smoldering fires are largely unknown, Watts et al. (2015) developed the first conceptual model of smoldering fires in wetlands in Florida. They focused on relationships among fire, wetland hydrology, and C dynamics. Their model underscores the complex and integrated feedbacks between burn depths and extent of smoldering fires on local and regional hydrology and predicts that increased burn depths and extended hydroperiods reduce initiation and frequency of fire in these habitats.

Peatlands cover ~17% of the land surface area in the UK and are distributed broadly across the headwater areas of most major river watersheds. Brown et al. (2015) synthesized current knowledge about how rivers in peatlands respond to both wildfires and prescribed burns. The hydrologic response of peatland streams to fire is complex. Peak flows are lower during many precipitation events but greater during the largest rainfall events in burned than in unburned watersheds. Furthermore, concentrations of dissolved organic C (DOC) in surface waters are higher in burned than unburned watersheds. The authors present a conceptual model that illustrates linkages and feedbacks among the hydrological, chemical, and biological properties and processes of watersheds following fire. This model provides a framework for identifying knowledge gaps and for forecasting changes in peatland streams related to the removal of vegetation by wildfire or prescribed burning.

WATER QUALITY

Fire effects on water quality are of particular concern to water resource managers because of potential effects on water supply systems and aquatic communities. Advances in technology and instrumentation (e.g., sondes) allow the collection of continuous water-quality data to monitor changes related to complex disturbances, such as wildfires. Chemical data sets with high temporal and spatial resolution document hydrochemical responses to fire and subsequent floods and debris flows that are often nonlinear and rapid (Krause et al. 2015). For example, water-quality data analyzed from a network of sondes in the Rio Grande watershed, New Mexico (USA), showed dramatic decreases in dissolved O_2 and pH as debris pulses moved downstream into a large river system after a large wildfire in headwater areas (Dahm et al. 2015).

Reale et al. (2015) demonstrated the value of collecting high-resolution, continuous data from networks of water-quality sensors and streamflow gages to assess initial and long-term effects of wildfire on the water quality of 2^{nd}- and 4^{th}-order streams in the Jemez Mountains and in the Rio Grande, New Mexico. Precipitation did not differ before and after the fire, but episodic postfire storms resulted in significantly elevated turbidity and specific conductance (SC) (linked to soil, sediment, rock and ash debris, and solutes entrained from burned watershed areas). Dissolved O_2 concentrations were variable in a 2^{nd}-order stream and more muted downstream in a 4^{th}-order river. An additional study of 4 sites over 4 mo encompassing the wildfire also showed stronger fire effects on turbidity and SC in 1^{st}- and 2^{nd}-order streams than in higher-order downstream sites. These results suggest that flow pathways, geomorphology, and biogeochemical processes moderate fire effects on water quality along the river continuum.

Fires kill or damage vegetation and alter soil chemistry, thereby reducing uptake. Therefore, nutrients, such as N and P, are often mobilized by fire, which results in increased loading to stream and river ecosystems (Sherson et al. 2015). These postfire nutrient pulses, which usually are associated with floods, can increase nutrient concentrations many fold. Diemer et al. (2015) extend our knowledge of long-term fire effects on nutrient dynamics in streams to the boreal forests of Central Siberia. Boreal forest streams and their ecosystems are highly susceptible to the effects of climate change, including the intensity, frequency, duration, and extent of forest fires. Diemer et al. (2015) showed that fires in boreal forests alter stream chemistry for many years and affect the retention and export of N and P in these stream networks. Streams in watersheds that had burned within the 4 to 10 y before the study in Central Siberia had lower DOC and higher NO_3^- concentrations, differing from nutrient responses to fire in boreal regions of North America.

ORGANIC MATTER SUBSIDIES

Fires modify the inputs of dissolved and particulate (e.g., ash and charcoal) organic matter into streams by damaging or killing upland vegetation (Earl and Blinn 2003). Where riparian or wetland vegetation is destroyed or damaged by fire, the canopy opens, thereby decreasing allochthonous inputs and increasing light and temperature levels, which promote autochthonous production, with repercussions for aquatic communities and food webs (Beakes et al. 2014, Cooper et al. 2015). In some cases, a pulse of leafy and woody debris from damaged vegetation can occur after riparian fires. Allochthonous inputs often decrease subsequent to the loss of riparian vegetation, but organic inputs eventually rebound as riparian vegetation recovers (Britton 1990). Furthermore, postfire hydrological conditions can greatly affect the biomass of organic matter on stream bottoms when floods mobilize and transport organic matter to downstream areas. Riparian trees damaged by fire may not fall into or across streams until years after the fire, usually in association with wind throw or floods (Robinson et al. 2005, Bendix and Cowell 2010).

Harris et al. (2015) compared watersheds that were burned and then affected by subsequent debris flows to watersheds that had not burned or had been burned without debris flows 4 y after a major fire. They document a large increase in sediment export during spring runoff in the burned, but not in the unburned, watersheds. Stream DOC concentrations were 75% greater in watersheds with fires and debris flows than in unburned watersheds, but concentrations of chlorophyll *a* and the chlorophyll *a* : organic matter ratio were higher in unburned watersheds. Macroinvertebrate export from tributary streams to the main stem was dominated by *r*-strategist taxa (Chironomidae, Baetidae, and Simuliidae) in streams draining burned watersheds, and export of invertebrate biomass was greater from streams in burned watersheds with debris flows than from streams in unburned watersheds (Harris et al. 2015).

Vaz et al. (2015) reviewed changes in large wood inputs, distributions, structural complexity, and invertebrate associations after fires. Their review was based primarily on their research in Portuguese streams, but they also examined the effects of wildfire on large wood subsidies to a lake in northern Minnesota, USA. Their results extend our knowledge of the effects of wildfire on large wood inputs to streams and lakes and suggest that fire may simplify the structure of wood in streams but increase habitat complexity in lakes.

Rodríguez-Lozano et al. (2015) reported that stream macroinvertebrate functional feeding groups recovered within 1 or 2 y after wildfire but that leaf-litter inputs decreased and leaf-litter breakdown rates increased in a stream draining a watershed that had burned 8 y before the study relative to a stream in an unburned watershed. Their results suggest that microbially mediated leaf decomposition rates are enhanced by increased temperatures engendered by the opening of the riparian canopy by fire and that total (microbial + shredder) leaf breakdown rates were increased by shredder aggregation in coarse-mesh leaf bags in the stream in the burned watershed where leaf litter inputs were low. These results contribute to a very limited literature on fire effects on detrital dynamics and leaf breakdown rates (Koetsier et al. 2010, Jackson et al. 2012). Results reported by Vaz et al. (2015) and Rodríguez-Lozano et al. (2015) suggest that fire effects on detrital dynamics can be long-lived (>5 y) (also see Robinson et al. 2005).

STREAM BIOTA

Although immediate effects of fire on the stream biota may be muted, stream biological communities usually change radically with postfire floods, which scour stream substrates and remove most organisms (Gresswell 1999, Minshall 2003). Furthermore, effects on aquatic communities can be modified by pre- or postfire drought (Rugenski and Minshall 2014). The responses of different types of organisms to fire and floods or droughts are related to their life cycles, dispersal abilities, and the availability and distribution of refugia. Short-lived, fast-colonizing species often dominate after fires and floods or droughts (Minshall 2003, Grace 2006, Malison and Baxter 2010a).

Klose et al. (2015) studied the effects of wildfire and postfire flooding in southern California on algal abundance, community composition, and nutrient limitation (assessed with nutrient-diffusing substrata) in stream reaches in unburned and burned catchments. They also considered reaches where riparian vegetation did or did not burn. Results suggest that algal responses (e.g., density, biovolume, chlorophyll *a*, and species composition) to fire and nutrient enrichment are driven primarily by fire effects on riparian canopy cover and associated light and temperature levels, flood disturbance intensities, and nutrient concentrations. Decreased riparian cover mediated faster algal recovery postfire. The results provide insights into processes that create and maintain habitat heterogeneity in riparian and stream habitats.

Most information on wildfire effects on stream and river ecosystems is derived from studies of single wildfire events in cool headwater systems. In contrast, Whitney et al. (2015) quantified changes in riverine habitat, benthic algal chlorophyll *a* concentration, and both warm- and coldwater invertebrate and fish communities after consecutive fires that covered >100 km^2 in southwestern New Mexico, USA. Cumulative fire effects, fire size, and post-wildfire rainfall were strongly associated with the siltation of river beds, decreases in chlorophyll *a* concentration, and decreases in the biomass of most insect taxa and 6 of 7 native fish species. Among native fish species, the Headwater Chub *Gila nigra* (100% loss) and Spikedace *Meda fulgida* were lost from streams in burned watersheds for up to 2 y postfire. Fish kills are thought to have resulted from hypoxia, and elevated concentrations of NH_4^+, trace metals, and ferrocyanides generated by wildfires. Nonnative warmwater fish, crayfish, and amphibian larvae were less affected by fire, results suggesting that fires threaten native taxa more strongly than invasive taxa.

Verkaik et al. (2015) considered how stream macroinvertebrate community responses to fire are mediated by interactions with preceding droughts or subsequent flood events. This global-scale, multisite analysis included data from central Idaho, USA, northeastern Spain, and Victoria, Australia. Macroinvertebrate community responses to wildfire after 9–11 mo (lower taxonomic richness, higher total macroinvertebrate abundance, and high percentages of Chironomidae, Simuliidae, and Baetidae) were similar across all 3 regions, but the magnitude of the response differed among regions. The greatest differences between burned and unburned watersheds in macroinvertebrate communities were found in Australia, where fire was accompanied by ongoing drought and persistent low flows. In contrast, macroinvertebrate recovery was faster in the cold–temperate climate of Idaho and the Mediterranean climate of northeastern Spain, where postfire floods may have acted to re-establish or reset biotic colonization processes. These interactions between hydrological and fire events are likely to become more pronounced with climate change.

The effects of wildfire and hydrological disturbances on stream invertebrates also can affect subsidies of emerging stream insects to riparian zones, thereby altering the availability of food resources for riparian predators (Malison and Baxter 2010b). Jackson and Sullivan (2015) investigated the effects of fire on linked aquatic and terrestrial habitats in the Mediterranean climate of California, which is characterized by high interannual variability in precipitation and frequent high-severity wildfires. They assessed the effects of wildfire on stream geomorphology; the density and community composition of aquatic benthic macroinvertebrates; and the densities, tissue Hg concentrations, trophic position, and food sources of riparian spiders (family Tetragnathidae) in Yosemite National Park. Although differences in spider responses between paired burned and unburned study sections were not statistically significant, modeling suggested that variability in benthic invertebrate density, watershed-scale fire frequency, and precipitation are important predictors of tetragnathid spider density and trophic position. Perhaps most important, precipitation was related to multiple spider responses, a relationship suggesting that climate variability could have greater effects on the aquatic–terrestrial ecological linkages than the influence of fire alone.

Effects of fire on physical and chemical conditions and on biological communities can affect populations of apex predators in streams, such as fish (Rieman et al. 2003, Sestrich et al. 2011, Beakes et al. 2014). Wildfires and subsequent floods can kill or remove fish in isolated, small, headwater streams, but fish populations appear to recover quickly, provided no barriers to fish immigration are present (Gresswell 1999). Sedell et al. (2015) used a qualitative, heuristic model to map the predicted distributions of postfire debris slides in the Colorado Rocky Mountains. They compared these maps to the distribution of Colorado River Cutthroat Trout (*Oncorhynchus clarkii pleuriticus)* populations. The results indicated that interconnected trout populations would be resilient to wildfire-induced debris flows. They also showed that trout populations in headwater streams and lakes probably act as refuge populations for the recolonization of lower stream reaches that are at much higher risk from debris flows.

Rosenberger et al. (2015) documented that Rainbow Trout (*Oncorhynchus mykiss)* were present throughout streams in burned watersheds a decade after fires and debris flows, but that individuals in older age classes were least abundant in streams in burned watersheds with debris flows and most abundant in streams in unburned watersheds. Rainbow Trout from burned watersheds also were characterized by fast growth, low lipid content, and early maturity compared to those in unburned watersheds. Dunham et al. (2007) reported that stream temperatures were higher in burned watersheds with debris flows than in unburned watersheds and burned watersheds without debris flows. Rosenberger et al. (2015) developed models whose output suggested that moderate warming associated with wildfire and channel disturbance history associated with faster individual trout growth exacerbate competition for food resulting in decreases in trout densities.

FUTURE RESEARCH RECOMMENDATIONS

The articles in this series expand our knowledge of the effects of fire on aquatic ecosystems to different geographic regions, biomes, habitats, and both rate and state variables. The research presented here emphasizes the importance of fire 'type' (wildfire vs prescribed fire), different prescribed burn approaches (e.g., large forest burns, strips to mitigate fire spread, patches to create mosaics), fire effects on riparian and wetland vegetation, and pre- and postfire hydrological events on riparian–stream subsidies, stream and wetland communities, and ecosystem processes. All of these topics have implications for the effective management of aquatic resources. Fire effects on aquatic ecosystems are inherently complex. They depend on the characteristics (e.g., extent, intensity, severity, timing, frequency) of fires and previous or subsequent hydrological events (e.g., drought and floods) and on features of watersheds (e.g., slopes, soils, and vegetation) and receiving waters (e.g., lentic or lotic, discharge, geomorphology, and biota). Future research on the effects of fire on aquatic systems requires increased focus on a wider array of combinations of fire, hydrology, watershed geomorphology, and aquatic conditions, and models integrating fire effects and natural resource management. As a consequence, we propose that future investigations be expanded to address 7 research foci:

1. Additional geographic areas and biomes. Fire is regularly used to manage savannas and to clear rainforests or wetlands for agricultural activities, but very little information exists on the effects of fire on aquatic ecosystems in the tropics (e.g., tropical South America, Africa, Asia, Australia (Malmer 2004, Townsend and Douglas 2004, Cochrane 2010). Furthermore, the incidence of fire has increased in many regions and biomes where fire effects have been little studied (e.g., Arctic and boreal areas, temperate rainforests, grasslands, and semi-arid savannas) (Jacobs et al. 2007, Betts and Jones 2009, Larson et al. 2013, Veach et al. 2014). With the enhanced availability of data from different biomes and regions, it should be possible to undertake more detailed meta-analyses of fire effects (e.g., Verkaik et al. 2015) to look for generalities in the responses of the aquatic biota and ecosystem processes in different types of ecosystems to fire (Brown et al. 2013).
2. Other aquatic habitats. Most literature on fire effects on aquatic systems is focused on streams, with few data available on fire effects on lakes, ponds, and wetlands (Prepas et al. 2009, Kotze 2013, Lewis et al. 2014). Like the addition of different biomes mentioned above, inclusion of other aquatic habitats support generalizations (or unique characteristics) that describe fire effects on a large variety of aquatic ecosystems.
3. Fires with different characteristics. To date most research has been concentrated on the effects of severe or large fires on stream ecosystems. Many fires across a landscape are small and seemingly inconsequential, but these fires are underrepresented in research programs. Most prehistorical and historical fire practices appear to have involved frequent, small, and low-intensity fires, but current fire regimes have been greatly altered by human population expansion, increased ignition sources, and, in some areas, fuel management and fire-suppression practices (Stephens et al. 2007). Increased research on the effects of fires differing in severity, extent, and frequency could guide the formulation of fire management practices that better sustain water-associated resources. Even within a given fire perimeter, research often is focused on the most severely and extensively burned areas, and more subtle fire effects on aquatic systems are often ignored. Last, no landscape or regional quantitative assessments have been done of fire effects on aquatic ecosystems over a complete fire season or across years, including no analyses of cumulative fire effects on the regional distributions and abundances of the aquatic biota. Such assessments will require a combination of extensive and intensive sampling across the landscape using a probabilistic sampling design.
4. Additional response variables. Most investigators have concentrated on documenting changes in the abundance and biomass of aquatic organisms, with little attention given to more subtle or indirect biological responses to fire. For example, indirect, sublethal effects of fire on fish distributions, food availability, growth, reproductive potential, and population structure have received little attention (Gresswell 2004, Beakes et al. 2014). In addition, investigations of the indirect effects of fire on food webs, including subsidies, parasites, pathogens, and predators, could expand our knowledge of the ramifying effects of catastrophic disturbance on biological interactions and community structure (Hossack et al. 2013b, c, Cooper et al. 2015, Jackson and Sullivan 2015). Authors of articles in this series have provided some data on fire effects on stream ecosystem processes, such as nutrient uptake and limitation and leaf inputs and decomposition rates, but research on these and related topics (e.g., nutrient spiraling, microbial activity, primary and secondary production, stream metabolism) are promising avenues for research on the effects of fire on aquatic ecosystems.
5. Longer time frames. A substantial amount of literature is available on short-term (<5 y) stream responses to fire (Gresswell 1999, Verkaik et al. 2013), but the longer term effects of fire on aquatic ecosystems are largely unknown. Although some stream variables recover quickly after fire, a limited number of studies report long-term effects of fire on riparian vegetation, organic subsidies, and aquatic communities (Robinson et al. 2005, Hossack et al. 2013a, Rugenski and Minshall 2014, Kleindl et al. 2015, Rodríguez-Lozano et al. 2015). Limited results indicate some fire effects can be long-lived, but much longer time series of data are needed to evaluate the legacy effects of fire. Furthermore, long-term monitoring of a number of systems in a given area will increase the probability that at least one will burn by wildfire (Jackson and Sullivan 2015), increasing the strength of our inferences by incorporating both pre- and postfire data (Verkaik et al. 2013).
6. More rigorous study designs and analyses. Effects of fire on aquatic ecosystems may depend on the spatial pattern of burning. Statistical inferences could be strengthened by greater attention to site selection, which is often opportunistic or based on logistical considerations. In most cases, sites are

not selected probabilistically (Hankin and Reeves 1988, Gresswell et al. 2004), do not address issues related to spatial pattern, and do not account for possible spatial autocorrelation (Ganio et al. 2005, Gresswell et al. 2006). Studies in which changes through time are compared within and among watersheds are rare, but such studies could greatly increase the scope of our conclusions. Fire effects on aquatic ecosystems are mediated through linkages from vegetation and soils to hydrological, geomorphological, and chemical responses to biotic and ecosystem process responses (e.g., Brown et al. 2015); causal pathway analysis (structural equation modeling) may strengthen inferences regarding the mechanistic routes leading from fire to stream responses (Grace 2006; Fig. 1).

7. Fire management practices. Numerous management practices have been used before, during, and after fires, but studies of the effects of these practices on freshwater ecosystems are limited despite the important ecosystem services and high biodiversity provided by these critical habitats. Of particular interest are aquatic responses to the use of fire retardant to contain fire spread, construction and maintenance of in-stream structures (e.g., debris dams) to intercept postfire sediment and debris, applications that stabilize hillslopes (e.g., hydromulch, reseeding), and pre- and postfire vegetation removal (e.g., via prescribed burns, mechanical removal, salvage logging) (Karr et al. 2004, Reeves et al. 2006). Most investigators have found muted and short-lived stream ecological responses to prescribed burns (Britton 1991a, b, Bêche et al. 2005, Arkle and Pilliod 2010). However, some responses have been more substantial (Brown et al. 2015, Douglas et al. 2015), and little investigation has been done of the effects of different prescribed fire severities, extent, and spatial configurations on aquatic ecosystems. The management of fire and fuel loads in riparian areas presents especially difficult challenges (Beschta et al. 2004, Stone et al. 2010, McDaniel 2015), particularly where dominated by flammable exotic taxa (e.g., *Acacia* [acacia], *Arundo* [giant reed], *Tamarix* [salt cedar]) (Lambert et al. 2010, Le Maitre et al. 2011, Drus et al. 2013). During firefighting activities, nutrients from fire retardants can increase stream nutrient concentrations (Tobin et al. 2015), have apparently caused fish kills (NMFS 2008), and, when coupled with drought, have had synergistic, negative effects on organisms in mesocosm experiments (Martin et al. 2014). Last, wildfires in many countries are started by humans, and the incidence of wildfire increases with the encroachment of human activities into wildland areas (Syphard et al. 2007, McMorrow et al. 2009). This pattern emphasizes the importance of evaluating pre- and postfire effects of roads, building construction, and landuse regulations (e.g., zoning) on stream community structure and ecosystem processes at the wildland–developed land interface.

CONCLUSIONS

In many regions, fires are becoming more severe and frequent in association with effects of global climate and landuse changes. Both wildfires and prescribed fires affect terrestrial and aquatic ecosystems in numerous and complex ways. This special series expands our knowledge of fire as a primary driver of hydrological, geochemical, and biological changes in riparian, wetland, and aquatic habitats. In some cases, this expansion occurred via research into unexplored habitats, biomes, and response variables. Novel approaches, including continuous monitoring, modeling, and probabilistic sampling designs, aid our abilities to generalize and predict outcomes from fire. Many of the studies in this series also highlight the multifaceted nature of aquatic ecosystem responses to fire; i.e., the interaction of fire with climatic variables (temperature, precipitation), which drive diverse interactions among hydrological, geomorphological, hydrochemical, biological, and ecosystem processes. Last, we recommend key research needs including expansion to additional geographic regions, biomes, habitats, and response variables; larger spatial and temporal scales; and fires with different characteristics. We also emphasize the critical need for research on the effects of fire management practices and policies on aquatic ecosystems and for consideration of aquatic ecosystems when making fire management and policy decisions.

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