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Bixby, RB, Cooper, SD, Gresswell, RD et al. (3 more authors) (2015) Fire effects on aquatic ecosystems: an assessment of the current state of science. Freshwater Science, 34 (4). 1340 - 1350. ISSN 2161-9549

https://doi.org/10.1086/684073

RH: Fire effects on aquatic ecosystems

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 with 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 land use changes. Further, 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, this special issue examines the complexities of fire as a disturbance in shaping freshwater ecosystems and highlights the state-of-the-science through 16 research papers. These papers cover key aspects of fire effects on vegetation loss and recovery in catchments to impacts 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 issue expand our knowledge of fire effects in different biomes, water bodies, and geographic regions, encompassing aquatic population, community, and ecosystem responses. Each paper has been summarized in this overview with an emphasis on each paper's contributions to knowledge on fire ecology and freshwater ecosystems. This overview concludes with a list of research needs to further our knowledge of fire impacts on aquatic ecosystems, including research: 1) on additional biomes and geographic regions; 2) on additional habitats, including wetlands and lacustrine ecosystems; 3) on different fire severities, sizes, and spatial configurations; 4) on additional response variables (e.g., ecosystem processes); 5) over longer (> 5 years) time scales; 6) with more rigorous study designs and data analyses; and 7) considering the impacts of fire management practices and policies.

Keywords: Wildfire, aquatic ecosystems, streams, rivers, wetlands, ecosystem, biota, prescribed burns

Introduction

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, destroying natural vegetation, property, and life. From an ecological perspective, however, many ecosystems have co-evolved with fire, with resilient successional trajectories (Pyne et al. 1996, Gresswell 1999, Bowman et al. 2009). Although 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, 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 fire effects on water resources is increasingly important for guiding fire management practices and policy decisions. Although some short-term effects of fire on freshwater ecosystems can be similar to the effects of land use changes (e.g., agricultural and urban development and logging), fire is a pulsed disturbance, with the duration of its effects on freshwater ecosystems depending on terrestrial ecosystem recovery. In contrast, land use changes constitute a press disturbance with more permanent effects (Allan 2004, Wootton 2012, Verkaik et al. 2013). The purpose of this special issue 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 (Figure 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 hydrology, sediment transport, geomorphology, water quality, aquatic macroinvertebrate communities, and fish populations in forested, montane streams in the western U.S. (Gresswell 1999, Rieman et al. 2003). This issue of Freshwater Science expands on these topics by considering fire effects on a diversity of organisms (ranging from algae and riparian vegetation to spiders and fish) and processes (including micro-climate, hydrology, and biogeochemistry; nutrient inputs, uptake, and limitation; and subsidies between terrestrial/aquatic habitats and tributary/main stem 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 semi-tropical wetlands and forests), and habitats (rivers, riparian zones, lakes, wetlands). Although prior work has focused on the effects of fire on state variables, many papers in this issue concentrate on effects of fire on ecosystem processes or rate variables, including nutrient uptake (Diemer et al., this issue), nutrient limitation (Klose et al., this issue), leaf decomposition (Rodriguez-Lozano et al., this issue), subsidies from river tributaries to river main stems (Harris et al., this issue) and subsidies from streams to riparian zones (Jackson et al., this issue).

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

Building on a series of research needs identified by Verkaik et al. (2013), we evaluate how the papers published in this issue address some of the knowledge gaps in the literature on fire effects on aquatic ecosystems. Specifically, 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 that are reported in this special issue can provide a foundation and springboard for future research studies, leading to the formulation of effective fire management practices and policies that sustain better 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. Although there is an extensive literature on the responses and recovery of upland vegetation to fire, information on fire effects on riparian and wetland vegetation is limited (Dwire and Kauffman 2003, Pettit and Naiman 2007). Because of differences in the microclimate, foliar moisture, structure, composition, and life histories of riparian/wetland and upland plant species, these plant communities often show very different responses to fire (Van de Water and North 2011). Although basin-wide effects of fire on sediment and nutrient inputs have been studied extensively, 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).

In this issue, Douglas et al. examine the effects of annual intensely managed fires on the composition and structure of riparian vegetation in Australia's savannas. In an experiment conducted in whole catchments, they compared riparian vegetation characteristics in burned and unburned watersheds. Vegetation sampling was conducted one year after three years 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 low frequency, low intensity fires and others adapted to frequent high-intensity fires. This research 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, thus creating new habitats and changing existing habitats (Stanford et al. 2005). Kleindl et al. (this issue) extend 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). By applying a combination of path and graphical analysis to 22 years of data, they examined relationships among hydrology, fire, land use, geomorphic position, and floodplain habitat patch dynamics. Results suggest that three factors (fire, stream power, and geomorphic position) collectively explained much of the variation in floodplain vegetation patch composition across study reaches and years with wildfire having the strongest total effect. Long-term investigation of disturbance and recovery pathways in a floodplain allow the authors to expand the shifting habitat mosaic concept from one driven only by major hydrologic events to one incorporating the influences of other riverscape and landscape disturbances, particularly fire.

Microclimate and hydrology

Fire effects on terrestrial and wetland vegetation, and on soils, in turn, 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 represent compounded effects of two types of disturbances, including post-fire seasonal or interannual increases in runoff and erosion associated with storms or snowmelt (Gresswell et al. 2004, Gresswell et al. 2006) superimposed on less frequent changes in vegetation driven by fire.

Fire also can affect the physical characteristics of ecotones, including transitions from riparian and wetland areas to uplands. Two years following wildfire, Watts and Kobziar (this issue) compared air temperature, relative humidity (RH), and vapor pressure deficit (VPD) within patches of pond cypress and adjacent grasslands in south Florida, USA. Increasing differences in air temperature, RH, and VPD were observed with distance from the dome centers into savanna habitats but, surprisingly, microclimates were either similar or, in some cases cooler or more humid, in burned compared to unburned domes. The authors attribute this response to vigorous vegetative regrowth following fire. This study increases our understanding of interactions between cypress domes and ecotonal microclimates, thus 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. (this issue) develop the first conceptual model of smoldering fires in wetlands, focused on relationships among fire, wetland hydrology, and carbon dynamics. This model underscores the complex and integrated feedbacks between burn depths and extent of smoldering fires on local and regional hydrology, with increased burn depths and extended hydroperiods reducing initiation and frequency of fire in these habitats.

Covering approximately 17% of the land surface area in the United Kingdom, peatlands are distributed broadly across the headwater areas of most major river catchments. Brown et al. (this issue) synthesize 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 peak flows are actually greater during the largest rainfall events. Further, concentrations of dissolved organic carbon (DOC) in surface waters are higher in burned than unburned basins. 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 datasets with high temporal and spatial resolution document hydrochemical responses to fire, and subsequent floods and debris flows, that are often non-linear and rapid (Krause et al. 2015). For example, water quality data analyzed from a network of sondes in the Rio Grande watershed, New Mexico, documented dramatic decreases in dissolved oxygen and pH as debris pulses moved downstream into a large river system following a large wildfire in headwater areas (Dahm et al. 2015).

Reale et al. (this issue) show 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 2nd and 4th order streams in the Jemez Mountains and Rio Grande in New Mexico. Although there was no difference in precipitation before versus after the fire, episodic post-fire storms results in significantly elevated turbidity and specific conductance (SC) (linked to soil, sediment, rock and ash debris, and solutes entrained from burned catchment areas). There is also greater variability in dissolved oxygen concentrations, in a second-order stream, with more muted responses downstream, in a 4th order river. An additional study of four sites over four months encompassing the wildfire also shows stronger fire effects on turbidity and SC in 1st and 2nd order streams than in higher order downstream sites, implying that flow pathways, geomorphology, and biogeochemical processes moderate fire effects on water quality along the river continuum.

Because fires kill or damage vegetation and alter soil chemistry, thereby reducing uptake, nutrients, such as nitrogen and phosphorous, are often mobilized by fire, resulting in increased loading to stream and river ecosystems (Sherson et al. 2015). These post-fire nutrient pulses, which are usually associated with floods, can increase nutrient concentrations many fold. Diemer et al. (this issue) 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. show that forest fires in boreal forests alter stream chemistry for many years, affecting the retention and export of nitrogen and phosphorus in these stream networks. Streams within catchments that burned within the last 4-10 years in Central Siberia had lower DOC and higher nitrate (NO_3) concentrations, differing from nutrient responses to fire in boreal regions of North America.

Organic matter subsidies

By damaging or killing upland vegetation, fires modify the inputs of dissolved and particulate (e.g., as ash and charcoal) organic matter into streams (Earl and Blinn 2003). Where riparian or wetland vegetation is destroyed or damaged by fire, the canopy opens, 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, there can be a pulse of leaf and woody debris from damaged vegetation after riparian fires. Allochthonous inputs often decrease subsequently to the loss of riparian vegetation but organic inputs eventually rebound as riparian vegetation recovers (Britton 1990). Further, post-fire hydrological conditions can greatly affect the biomass of organic matter on stream bottoms with floods often mobilizing and transporting organic matter to downstream areas. Riparian trees damaged by fire may not fall into or across streams until years after the fire, usually associated with wind throw or flood events (Robinson et al. 2005, Bendix and Cowell 2010).

After four post-fire years, Harris et al. (this issue) compare watersheds that were burned then affected by subsequent debris flows to watersheds that had not burned or had been burned without subsequent debris flows. They document a major increase in sediment export during spring runoff in the burned, but not unburned, catchments. Furthermore, stream DOC concentrations are 75% greater in drainages with fires and debris flows than in unburned watersheds, but concentrations of chlorophyll a and the chlorophyll a:organic matter ratio are higher in unburned watersheds. Macroinvertebrate export from tributary streams to the main stem is dominated by r-strategist taxa (Chironomidae, Baetidae, and Simuliidae) in streams that were burned, and the export of invertebrate biomass is greater from streams in burned basins with debris flows than from streams draining unburned basins (Harris et al., this issue).

Vaz et al. (this issue) review changes in large wood inputs, distributions, characteristics, and related effects on invertebrate communities, based primarily on their research in Portuguese streams. In a separate study described in the same paper, they also examine the effects of wildfire on large wood subsidies to a lake in northern Minnesota. Their results extend our knowledge of the effects of wildfire on large wood inputs to streams and lakes, suggesting that fire may simplify the structure of wood in streams while resulting in increased habitat complexity in lakes.

Although Rodriguez-Lozano et al. (this issue) reported that stream macroinvertebrate functional feeding groups recover quickly, within one or two years, after wildfire, they find that leaf litter inputs were reduced and leaf litter breakdown rates were higher in a stream draining a burned basin than in a stream in an unburned basin 8 years post-fire. The 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 burned stream where leaf litter inputs are 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) and results in both Vaz et al. and Rodriguez-Lozano et al. suggest that fire effects on detrital dynamics can be long-lived (exceeding 5 years) (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 post-fire floods, which scour stream substrates and remove most organisms (Gresswell 1999, Minshall 2003). Further, effects on aquatic communities can be modified by pre- or post-fire drought (Rugenski and Minshall 2014). The responses of different types of organisms to fire and floods or droughts and related to life cycles, dispersal abilities, and the availability and distribution of refugia, with short-lived, fast-colonizing species often dominating after fires and floods or droughts (Minshall 2003, Grace 2006, Malison and Baxter 2010a).

Working in southern California, Klose et al. (this issue) studied the impacts of wildfire and post-fire flooding on algal abundance, community composition, and nutrient limitation (using nutrient diffusing substrata) in stream reaches in unburned and burned catchments. They also consider reaches where riparian vegetation did and did not burn. Results suggest that algal responses (e.g., density, biovolume, chlorophyll a, and species composition) to fire and nutrient enrichment are primarily driven 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 post-fire. 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 cooler headwater systems. In contrast, Whitney et al. (this issue) quantify changes in riverine habitat, benthic algal chlorophyll a concentration, and both warm- and cold-water invertebrate and fish communities following consecutive fires that covered >100 km^2 in southwestern New Mexico, USA. Cumulative fire effects, fire size, and post-wildfire rainfall are strongly associated with siltation of river beds, decreases in chlorophyll a concentration, and decreases in the biomass of most insect taxa and 6 out of 7 native fish species. Among native fish species, the headwater chub Gila nigra (100%) and spikedace Meda fulgida are lost from streams in burned basins for up to two years post-fire. Fish kills are thought to have resulted from hypoxia, and elevated concentrations of ammonium, trace metals, and ferrocyanides, generated by wildfires. Non-native warm-water fish, crayfish, and tadpoles are less affected by fire, suggesting that fires threaten native taxa more strongly than invasive taxa.

Verkaik et al. (this issue) consider how stream macroinvertebrate community responses to fire are mediated by interactions with preceding droughts or subsequent flood events. This global-scale, multi-site analysis includes data from central Idaho, USA, northeastern Spain, and Victoria, Australia. Macroinvertebrate community responses to wildfire after 9-11 months were similar across all three regions (i.e., lower taxonomic richness, higher total macroinvertebrate abundance and high percentages of Chironomidae, Simuliidae and Baetidae), but the magnitude of the response differs between among regions. The greatest differences in stream macroinvertebrate communities between burned and unburned basins are found in Australia, where fire is accompanied by ongoing drought and persistent low flows. In contrast, stream 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.

These effects of wildfire and hydrological disturbances on stream invertebrates also can affect subsidies of emerging stream insects to riparian zones, altering the availability of food resources for riparian predators (Malison and Baxter 2010b). Jackson et al. (this issue) 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. More specifically, they assessed the effects of wildfire on stream geomorphology; the density and community composition of aquatic benthic macroinvertebrates; and the densities, tissue mercury 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 are were not statistically significant, modelling suggests that variability in benthic invertebrate density, catchment-scale fire frequency, and precipitation are important predictors of tetragnathid spider density and trophic position. Perhaps most importantly, precipitation is 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). Although wildfires and subsequent floods have been observed to kill or remove fish in isolated, small, headwater streams, fish populations appear to recover quickly, provided there are no barriers to fish immigration (Gresswell 1999). Sedell et al. (this issue) use a qualitative, heuristic model to map the predicted distribution of post-fire debris slides in the Colorado Rocky Mountains. They compare these maps to the distribution of Colorado River cutthroat trout populations. The results indicate that interconnected trout populations would be resilient to wildfire-induced debris flows. Surprisingly they also show that trout populations in headwater streams and lakes likely act as refuge populations for the recolonization of lower stream reaches that are at much higher risk from debris flows.

Rosenberger et al. (this issue) documented that rainbow trout are present throughout streams in burned basins after a decade following fires and debris flows, but that individuals in older age classes are least abundant in streams in burned basins with debris flows and most abundant in streams in unburned basins. Rainbow trout from burned watersheds also are characterized by fast growth, low lipid content, and early maturity compared to those in unburned watersheds. Gresswell (2004) reported that stream temperatures were higher in burned basins with debris flows than in unburned basins and burned basins without debris flows. Rosenberger et al. (this issue) developed models whose output suggests suggested that moderate warming, associated with wildfire and channel disturbance history, associated with faster individual trout growth, exacerbating competition for limited food resulting in decreases in trout densities.

Future Research Recommendations

The papers included in this issue expand our knowledge of the effects of fire on aquatic ecosystems to different geographic regions, biomes, habitats, and response variables, including both rate and state variables. The research presented here emphasizes the importance of fire 'type' [wildfire versus 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 post-fire 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. Impacts depend on the characteristics (e.g., extent, intensity, severity, timing, frequency) of fires and the previous or subsequent hydrological events (e.g., drought and floods). Impacts also depend on features of catchments (e.g., slopes, soils, and vegetation) and receiving waters (e.g., lentic or lotic, discharge, geomorphology, and biota). Future research on fire effects on aquatic systems requires increased focus on a wider array of combinations of fire, hydrology, catchment geomorphology, and aquatic conditions, and models integrating fire effects and natural resource management. As a consequence, we propose that future research be expanded to:

1. Additional geographic areas and biomes. Although fire is regularly used to manage savannas and to clear rainforests or wetlands for agricultural activities, 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 additional 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., this issue) 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 focuses on streams, with few data 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, the inclusion of other

aquatic habitats support generalizations (or conversely unique characteristics) that describe fire effects on a large variety of aquatic ecosystems.

3. Fires with different characteristics. To date most research has concentrated on the effects of severe or large fires on stream ecosystems; however, many fires across a landscape are small and seemingly inconsequential, but these are underrepresented in research programs. Apparently, prehistorical and historical fire practices concentrated on 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 is often focused on the most severely and extensively burned areas, and more subtle fire effects on aquatic systems are often ignored. Finally, there have been no landscape or regional quantitative assessments 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 investigated. Most studies have concentrated on documenting changes in the abundance and biomass of aquatic organisms, with little attention 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). Although this issue has provided some data on fire effects on stream ecosystem processes, such as nutrient uptake and limitation

and leaf inputs and decomposition rates, 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. Also, this issue's studies and related literature dealing with fire effects on cross-habitat subsidies could enhance our knowledge of drivers of community change in both aquatic and riparian habitats.

5. Longer time frames. Although there is a substantial literature on short-term (< 5 years) stream responses to fire (Gresswell 1999, Verkaik et al. 2013), the longer term effects of fire on aquatic ecosystems are largely unknown. Although some stream variables recover quickly after fire, Rodriguez-Lozano et al. (this issue) and Kleindl et al. (this issue) report longer term fire effects on vegetation and detritus (see also Robinson et al. 2005 for detritus, Rugenski and Minshall 2014 for algae). Although limited results indicate some fire effects can be long-lived, 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 (see Jackson et al, this issue), increasing the strength of our inferences by incorporating both pre-fire and post-fire 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) or in a manner that addresses issues related to spatial pattern (Ganio et al. 2005, Gresswell et al. 2006). Studies that compare changes through time within and among watersheds are rare, but such studies could greatly increase the scope of our conclusions. Because fire effects on aquatic ecosystems are mediated through linkages from vegetation and soils to hydrological,

geomorphological, and chemical responses to, ultimately, biotic and ecosystem process responses (e.g., Brown et al., this issue), causal pathway analysis (structural equation modeling) may strengthen inferences regarding the mechanistic routes leading from fire to stream responses (Figure 1, Grace 2006).

7. Numerous management practices have been employed 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 current interest are aquatic responses to: the use of fire retardant to contain fire spread, the construction and maintenance of in-stream structures (e.g., debris dams) to intercept post-fire sediment and debris, applications that stabilize hillslopes (e.g., hydromulch, reseeding), and pre-fire and postfire vegetation removal (e.g., via prescribed burns, mechanical removal, salvage logging) (Karr et al. 2004, Reeves et al. 2006). Most studies have shown muted and short-lived stream ecological responses to prescribed burns (Britton 1991a, Britton 1991b, Bêche et al. 2005, Arkle and Pilliod 2010). Yet, some responses have been more substantial (e.g., see Douglas et al. and Brown et al., this issue) and there has been little investigation 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 fire-fighting 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). Finally, 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), emphasizing the importance of evaluating effects of roads, building construction, and land use 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, associated with effects of global climate and land use changes. Both wildfires and prescribed fires affect terrestrial and aquatic ecosystems in numerous and complex ways. This special issue 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 is through research into unexplored habitats, biomes, and response variables. Novel approaches, including continuous monitoring, modelling, and probabilistic sampling designs, aid our abilities to generalize and predict outcomes from fire. Many of the studies in this issue 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. Finally, we recommend key research needs including the 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 the consideration of aquatic ecosystems when making fire management and policy decisions.

Acknowledgements

We thank Sheila Wiseman for drafting the figure. R. Bixby and C. Dahm acknowledge funding through the New Mexico Experimental Program to Stimulate Competitive Research (NM EPSCoR) (National Science Foundation). S. Cooper was supported by funds from the National Science Foundation's Rapid Response and Long-Term Ecological Research programs. L. Brown's contribution was supported via the EMBER (Effects of Moorland Burning on the Ecohydrology of River basins) project funded by the UK's Natural Environment Research Council (NE/G00224X/1). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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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 driving to response variables, and double-headed arrows indicate consumer-resource interactions where consumers both depress, and benefit from the consumption of, their resources.