DR. DANIEL F. GOMEZ ISAZA (Orcid ID : 0000-0003-3112-8683)

DR. REBECCA L CRAMP (Orcid ID : 0000-0001-9798-2271)

Article type : Review

Fire and rain: A systematic review of the impacts of wildfire and associated runoff on aquatic fauna

Running title: Postfire impacts on aquatic fauna

Daniel F. Gomez Isaza[1]*; Email: daniel.gomezisaza@uq.net.au, Ph: +64 22 609 3584

Rebecca L. Cramp[1]; Email: r.cramp@uq.edu.au

Craig E. Franklin[1]; Email: c.franklin@uq.edu.au

ORCID iDs

Daniel F. Gomez Isaza: 0000-0003-3112-8683

Rebecca L. Cramp: 0000-0001-9798-2271

Craig E. Franklin: 0000-0003-1315-3797

[1] The University of Queensland, St Lucia, Brisbane, Queensland, 4069, Australia

* Corresponding author

Keywords: aquatic ecosystems, bushfire, biota, climate change, climate extremes, conservation, conservation physiology, disturbances.

Abstract

Climate and land-use changes are expected to increase the future occurrence of wildfires, with potentially devastating consequences for freshwater species and ecosystems. Wildfires that burn in close proximity to freshwater systems can significantly alter the physicochemical properties of water. Following wildfires and heavy rain, freshwater species must contend with complex combinations of wildfire ash components (nutrients, polycyclic aromatic hydrocarbons, and metals), altered light and thermal regimes, and periods of low oxygen that together can lead to mass mortality events. However, the responses of aquatic fauna to wildfire disturbances are poorly understood. Here we provide a systematic review of available evidence on how aquatic animals respond to and recover from wildfire disturbance. Two databases (Web of Science and Scopus) were used to identify key literature. A total of 83 studies from across 11 countries were identified to have assessed the risk of wildfires on aquatic animals. We provide a summary of the main ecosystem-level changes associated with

wildfires and the main responses of aquatic fauna to such disturbances. We pay special focus to physiological tools and biomarkers used to assess how wildfires impact aquatic animals. We conclude by providing an overview of how physiological biomarkers can further our understanding of wildfire-related impacts on aquatic fauna, and how different physiological tools can be incorporated into management and conservation plans and serve as *early warning signs* of wildfire disturbances.

Introduction

Climate and land use changes are transforming ecological fire regimes on a global scale (Benali et al., 2017; Pausas & Ribeiro, 2013; Rogers, Balch, Goetz, Lehmann, & Turetsky, 2020). Wildfires are widely recognised as a natural and important phenomenon of various ecosystem, but the increased occurrence and intensity of wildfires are having severe, negative effects on ecosystems (Verkaik et al., 2013; Williams-Subiza & Brand, 2021). Rising temperatures, shifts in precipitation and prolonged droughts, coupled with poor forest management and changing land-uses have contributed to aggravated wildfires (Benali et al., 2017; Westerling et al., 2011). As such, wildfire seasons have been extended, and the frequency, size, and duration of wildfires have increased (Pausas & Ribeiro, 2013; Rogers et al., 2020). For example, the Australian megafires of 2019 – 2020 were unprecedented in scale and severity. The fires burnt through 97,000 km^2 of south-eastern Australia across subtropical, Mediterranean, and temperate bioregions and lasted an astonishing eight months (July 2019 – March 2020) (Collins et al., 2021). Similarly, the five most recent wildfires that ripped through California, USA, were the most severe and intense in the state's recorded history (Ball, Regier, González-Pinzón, Reale, & Van Horn, 2021 and references within). These events are mere examples of the increasing severity of wildfire events. Disturbingly, though, the threat of wildfires on the earth's biodiversity has yet to be realised. Wildfire research and management efforts have been primarily directed towards terrestrial systems (Engstrom, 2010; McLauchlan et al., 2020; Ward et al., 2020), while wildfire disturbances to aquatic environments have garnered little attention (c.f., Bisson et al., 2003; Bixby et al., 2015; Leigh et al., 2015). The limited attention on aquatic environments is likely due to a lack of synthesis on the effects of wildfires on aquatic environments and our poor understanding of wildfire impacts on aquatic animals. However, available evidence indicates that the increasing severity of wildfire events will exert strong influences on freshwater ecosystems and threaten freshwater biodiversity (Monaghan, Machado, Corado, Wrona, & Soares, 2019; Silva et al., 2020; Verkaik et al., 2013).

Wildfires can have indirect consequences on freshwater systems that completely change the physicochemical environment (Fig. 1; Bixby et al., 2015; Leigh et al., 2015; Vaz et al., 2015). Following a wildfire, heavy rains can wash burnt ash directly into freshwater systems (Cooper et al., 2015; Earl & Blinn, 2003). Wildfire ash is laden with complex combinations of nutrients, metals, sediment, and other organic and inorganic matter that profoundly alter physicochemical parameters of freshwaters (e.g., increase water pH, conductivity, turbidity, lower oxygen levels; Earl & Blinn, 2003; Silva et al., 2016). Moreover, the loss of basin vegetation following a fire increases the risk of erosion (by wind and water) and runoff, especially after heavy rains, and facilitates sediment transport into freshwaters (Bixby et al., 2015; Vaz et al., 2015). Sediment runoff is exacerbated by the hydrophobic nature of heavily burnt soils that reduce water infiltration and hydraulic conductivity (Saxe, Hogue, & Hay, 2018; Smith, Sheridan, Lane, Nyman, & Haydon, 2011). Severe wildfires also reduce riparian vegetation cover, meaning that waterbodies are exposed to increased light penetration and subsequently increases in water temperature (Beakes, Moore, Hayes, & Sogard, 2014; Koetsier, Tuckett, & White, 2007). Together, these physicochemical changes are expected to have pronounced effects on residing species, but we lack an understanding of how freshwater species cope with and recover from wildfire disturbances and associated runoff.

The impacts of wildfires and runoff on aquatic fauna have centred on understanding population and community level effects (e.g., community composition, species richness, abundance data; Howell, 2006; Lyon & O'Connor, 2008; Robson, Chester, Matthews, & Johnston, 2018). Although these data are useful in providing baseline information of wildfire impacts, they can be limited in their utility to conservation because they: 1. provide no information on the physiological status of individuals and species (e.g., locomotor performance, immune function, reproduction), 2. cannot provide information on the extent and timescale to recovery (e.g., recovery from toxic wildfire ash components, re-establishment of diet), and 3. can mask underlying effects (e.g., toxic effects, energetic status) of wildfire disturbance. For instance, following a major wildfire, salmonid fishes were found to reside at equal densities in fire-affected and reference sites of Scott Creek, California, but individuals residing in fire-affected reaches suffered significant loss of physiological condition (as indicated by mass and length estimates) and lost mass in the summer following the fire disturbance (Beakes et al., 2014). Similarly, the survival of freshwater amphipods, *Hyalella azteca*, was unaffected by wildfire ash, but investigations into oxidative enzyme biomarkers revealed significant oxidative stress (Plomp, Klemish, & Pyle, 2020). The use of physiological tools can provide key insight into the sublethal impacts of wildfires and allow for an understanding of how aquatic animals respond to and recover from wildfire disturbances, though their utility to conservation and management has yet to be realised.

Here, we performed a systematic review to assess how aquatic animals respond to and recover from wildfire disturbance. The aim of this review was three-fold: (1) to highlight the main risks of wildfires disturbances to aquatic fauna; (2) to identify how existing literature has utilised physiological tools to assess wildfires impacts on aquatic animals; and (3) to highlight the role that physiological tools can play in managing and mitigating fire-related threats to aquatic fauna.

Review protocol

Our review protocol followed PRISMA guidelines (Preferred Reporting Items for Systematic Reviews and Meta-Analyses, Fig. S1; Moher et al., 2015) and a ROSES (RepOrting standards for Systematic Evidence Syntheses; Haddaway, Macura, Whaley, & Pullin, 2018) form is included as a supplementary file (Table S1). We performed a systematic search using the Scopus and Web of Science Core Collection (WoS) online databases on 29th April 2021. Both databases were accessed through The University of Queensland's library subscription. Searches were refined by document type and subject area. The exact search strings were as follows:

Scopus = (TITLE-ABS-KEY (("fire" OR "bushfire" OR "wildfire")) AND TITLE-ABS-KEY ((("runoff" OR "rainfall" OR "flood" OR "polycyclic aromatic hydrocarbons" OR "PAHs" OR "metals" OR "ash" OR "slug" OR "inorganic" OR "sediment" OR "turbidity" OR "oxygen" OR "temp*"))) AND TITLE-ABS-KEY ((("fish" OR "amph*" OR "tadpole" OR "crust*" OR "aquat*" OR "invert*" OR "freshwater")))) AND (LIMIT-TO (DOCTYPE , "ar") OR LIMIT-TO (DOCTYPE , "cp") OR LIMIT-TO (DOCTYPE , "cr") OR LIMIT-TO (DOCTYPE , "ed")) AND (LIMIT-TO (SUBJAREA , "ENVI") OR LIMIT-TO (SUBJAREA , "AGRI") OR LIMIT-TO (SUBJAREA , "EART") OR LIMIT-TO (SUBJAREA , "BIOC") OR LIMIT-TO (SUBJAREA , "MULT") OR LIMIT-TO (SUBJAREA , "PHAR") OR LIMIT-TO (SUBJAREA , "VETE")).

Web of Science = TOPIC: (("fire" OR "bushfire" OR "wildfire")) AND TOPIC: (("runoff" OR "rainfall" OR "flood" OR "polycyclic aromatic hydrocarbons" OR "PAHs" OR "metals" OR "ash" OR "slug" OR "inorganic" OR "sediment" OR "turbidity" OR "oxygen" OR "temp*")) AND TOPIC: (("fish" OR "amph*" OR "tadpole" OR "crust*" OR "aquat*" OR "invert*" OR "freshwater")) Refined by: [excluding] DOCUMENT TYPES: (review OR book chapter) AND WEB OF SCIENCE CATEGORIES: (Environmental Sciences OR Ecology OR Geosciences Multidisciplinary OR Marine Freshwater Biology OR Water Resources OR Biodiversity Conservation OR Zoology OR Engineering Environmental OR Environmental Studies OR Fisheries OR Multidisciplinary Sciences OR Material Sciences Multidisciplinary OR Toxicology OR Evolutionary Biology OR Veterinary Sciences OR Biology OR Entomology OR Mineralogy OR Physiology OR Behavioural Science).

We identified 1240 and 773 studies meeting the search terms in Scopus and WoS, respectively. In addition, we performed backwards and forwards searches to find additional studies cited in/citing three related papers (Bixby et al., 2015; Lyon & O'Connor, 2008; Rieman & Clayton, 1997). A total of 489 duplicates were removed, leaving 1524 papers for title and abstract screening (Fig. S1, PRISMA). We used Rayyan software to screen title and abstracts (Ouzzani, Hammady, Fedorowicz, & Elmagarmid, 2016). Titles and abstracts were screened based on a predefined decision tree (Fig. S2). Approximately 93% of papers were excluded after title and abstract screening. The full text of the remaining 119 papers were then screened and excluded if: 1) no data on the responses of aquatic animals to wildfires were presented (n = 29); 2) wrong publication type (e.g., reviews, perspectives; n = 6); and 3) non-English full text (n = 1). We extracted meta-data from included papers, including the year of publication, field of research, study duration (< 1 year = short-term, 1 – 10 years = mid-term, > 10 years = long-term; Leigh et al., 2015), focal taxonomic group (macroinvertebrates, amphibians, or fish), and geographic region. We used the *bibliometrix* package (Aria & Cuccurullo, 2017) in *RStudio* (version 1.2.1335) to performed a bibliometrics analysis of included papers. Specifically, a thematic map analysis of the most frequently used keywords (in the title, abstract and keywords) appearing in included papers were used to identify main risks and common approaches used to address wildfires-related disturbances to aquatic fauna.

Results

Our review protocol yielded 83 studies describing the impacts of wildfire and runoff on aquatic taxa (see Table S2 for a full list). This field of research still in its infancy (Fig. 2a). The earliest publication included in our analysis was published in 1991, and only eight studies were published between the years 1991-2001. Research on the impacts of wildfires on aquatic animals has increased exponentially since the 2010s. Included studies were conducted across 11 countries. Most of the research (90% of studies, 74/83 studies) has been conducted across four countries (United States = 44 studies, Portugal = 12 studies, Australia = 10 studies, and Canada = 8 studies), with few studies having been conducted elsewhere (n = 15; Argentina, Brazil, Botswana, Norway, South Africa, Spain, and the UK). Research on the impacts of wildfires on aquatic animals has centred on the impacts at the community- and population-levels, as well as ecotoxicological impacts of wildfire ash on individuals (Fig. 2b). Few studies have utilised physiological tools to address the impact of wildfire or wildfire-runoff components on aquatic fauna (< 10%). Moreover, most studies have investigated the short-term (< 1 year; 58% of studies) responses of aquatic fauna to wildfires, with few studies having examined the long-term impacts (> 10 years, 13% of studies; Fig. 2c). Most studies examining the impact of wildfires and runoff on aquatic fauna have been conducted *in situ*, with fewer laboratory (including micro- and mesocosm) examinations (Fig. 2d). Laboratory experiments have included non-lethal (n = 12 studies) and lethal (n = 11 studies) endpoints. Non-lethal endpoints include the monitoring of growth/developmental rates, feeding, behavioural traits, and biochemical assays (Table S2). Laboratory studies simulate post-fire conditions by manipulating levels of aqueous extracts of ashes, using wildfire runoff, or by introducing wildfire ash into experimental tanks (Table S2). Work has primarily focused on the responses of macroinvertebrate (54% of studies) and fishes (but predominantly salmonids; 40% of studies) to wildfire (Fig. 2e). Few studies have examined the responses of amphibians to wildfire (6% of studies).

Our bibliometrics analysis revealed a clustering of keywords around three major themes (Fig. 3): (i) population and community level (e.g., species richness, community structure) impacts of wildfire disturbances, (ii) ecosystem level impacts of wildfires (water contamination, water quality) on freshwaters, and (iii) toxicity of wildfire runoff components.

Discussion

Impacts of wildfires on water quality

Light

Wildfires can partially or completely destroy riparian vegetation that exposes underlying aquatic habitat to increases light (Figs. 1 & 4; Cooper et al., 2015; Malison & Baxter, 2010; Rodriguez-Lozano, Rieradevall, Rau, & Prat, 2015). For instance, a major wildfire completely removed the riparian vegetation of streams in Vall d'Horta, northern Spain, that caused photosynthetically active radiation (PAR) to double (10 versus 21 $\mu mol\ m^{-2}\ s^{-1}$) at fire affected sites compared to control sites (Rodriguez-Lozano et al., 2015). Most significantly, riparian cover can take years to recover; canopy cover had not returned to reference levels by within five years after the Vall d'Horta wildfire. Increases in light availability, coupled with warmer waters (from increases in solar radiation) and elevated nutrient concentrations, in burnt freshwater habitats stimulates primary productivity, where algal growth is spurred (Cunillera-Montcusí et al., 2019; Robson et al., 2018) and community composition is altered to the benefit of a few disturbance-adapted taxa (Cooper et al., 2015; Mellon, Wipfli, & Li, 2008; Verkaik, Prat, Rieradevall, Reich, & Lake, 2014; Williams-Subiza & Brand, 2021). Juvenile fishes tend to benefit from an increased primary productivity (e.g., greater access to food, improved growth; Koetsier et al., 2007; Silins et al., 2014), but larger fish can be negatively affected (Rosenberger, Dunham, Neuswanger, & Railsback, 2015; Tonn et al., 2003).

This review found that no studies have directly examined the impact of elevated light quantity (or elevated PAR) on aquatic taxa within the context of wildfires. However, increased light levels due to the removal of riparian vegetation can have adverse effects on body morphology, disease resistance, metabolism, and mortality of aquatic animals (reviewed by Pusey & Arthington, 2003). Changes in light can also increase egg and larval mortality due to increased ultraviolet-B radiation (Alton & Franklin, 2017; Pusey & Arthington, 2003) and decrease the ability aquatic animals to discriminate between mates and increase conspicuousness to predators (Alton, Wilson, & Franklin, 2011; Cerri, 1983). Moreover, the progression of global climate change is projected to increase the amount of PAR reaching freshwater habitats due to ongoing stratospheric ozone depletion (Herman, 2010), which may exacerbate effects on aquatic animals. Given that wildfires can profoundly alter the light availability in freshwaters, research into the direct effects of elevated light (and elevated PAR) on aquatic taxa within the context of wildfires is warranted.

Water temperature

The loss of riparian vegetation can profoundly alter the thermal conditions of freshwaters (Hitt, 2003; Koontz, Steel, & Olden, 2018; Rhoades, Entwistle, & Butler, 2011). Wildfires can significantly raise water temperatures by a magnitude of 0.8 to 15°C (Gresswell, 1999; Koontz et al., 2018). The impact of fires on water temperature can be immediate, with the severity depending on the fire's intensity, convection, and the volume of water in the burned region (Rieman & Clayton, 1997). For example, Koetsier et al. (2007) recorded a 5°C increase in stream water temperatures following a forest fire that scoured much of the surrounding vegetation along the Boise River Catchment (Idaho, USA), whereas water temperature was increased by 2°C at sites that suffered mid-intensity burns. Wildfire can also affect the thermal regimes of freshwaters for extended time periods (months to years). Koontz et al. (2018) reported a consistent increase in the frequency of relatively warm days and a decrease in the frequency of cold days in streams along the Pacific Northwest region of the USA in the year after a wildfire. Similarly, seven years after a fire, there was no evidence that maximum stream temperatures were returning to pre-fire norms in Bitterroot River Basin, Montana (Mahlum, Eby, Young, Clancy, & Jakober, 2011). Long-term increases in water temperature following a fire are dependent on the degree of stream channel reorganisation, stream discharge rates, burn severity, change in canopy cover and the increase in solar radiation (Beakes et al., 2014; Cooper et al., 2015; Dunham, Rosenberger, Luce, & Rieman, 2007; Koetsier et al., 2007; Rhoades et al., 2011; Woltemade & Hawkins, 2016). Woltemade and Hawkins (2016) estimate that canopy cover removal following a large-scale forest fire would increase average temperatures by 2.2 – 5.9°C in streams of low discharges and by 1.0 – 4.4°C in moderate discharge streams. Similarly, a strong positive relationship between stream temperature and light flux in burned streams, with light flux (and therefore water temperature) being greatest in pools where vegetation had burned closest to the water's edge (Beakes et al., 2014).

The biological responses of aquatic ectotherms to changes in water temperature are relatively well understood (Huey & Kingsolver, 1989; Little, Loughland, & Seebacher, 2020; Pörtner & Peck, 2010) and includes an increase in metabolism and associated physiological rates (Little et al., 2020). Ectothermic species tolerate thermal increases up to an upper limit, defined as the critical thermal maximum, after which further increases in temperature are lethal (Pörtner & Peck, 2010). Although the localised mortality of aquatic organisms is often reported following major wildfire events (Burton, 2005; Driessen, 2019; Johnston, G., Robson, & Chester, 2014; Silva et al., 2020), this review found no evidence of direct mortality of aquatic fauna attributable to extreme water temperatures caused by wildfires. However, periods of warming during and after a fire could result in local extirpation of species if species-specific thermal limits are surpassed. Hitt (2003) described some anecdotal accounts of a localised fish kill one month following a major fire, which was attributed to warmer water temperatures. Similarly, fish densities declined drastically in reaches affected by high severity wildfire in Cottonwood Creek in the Boise National Forest in Southwest Idaho (Burton, 2005). Contrarily, Dunham et al. (2007) reported no mortality of native aquatic species (rainbow trout *Oncorhynchus mykiss* and tailed frog larvae *Ascaphus montanus*) across almost every site sampled, despite a 4 – 12°C upwards shift in stream water temperatures across 13 years following a wildfire in the Boise River Basin (USA). However, in a follow-up study, Rosenberger et al. (2015) found that although rainbow trout were found in burned reaches, fish densities were significantly lower in burned than in unburned streams. Fire-induced warming can also affect life-history traits (e.g., timing of reproduction, age and size at maturity, sex-ratios, longevity, etc.) that can affect population dynamics (Pusey & Arthington, 2003). For instance, trout living in warmer waters following wildfires displayed an earlier onset of maturity and matured at a smaller body size than fish from unwarmed streams (Rosenberger et al., 2015). This could have substantial population implications for populations of fish living in warmed streams because age and size at maturation are fundamental correlates of an individual's life-time fitness (e.g., reproductive output, survival; Kuparinen et al., 2011), which could have different consequences depending on degree of warming, the species, etc.

There is some evidence to suggest that wildfire-induced warming of freshwaters may increase the energetic costs for organisms. In an opportunistic experiment, Beakes et al. (2014) examined the immediate and short-term impacts (pre-fire, during and 1 year post fire) of wildfire on the distribution and bioenergetics of rainbow trout after a wildfire burned through a major tributary of the Scott Creek watershed in central California. After the wildfire, fish from burned and reference streams were surveyed (measured, tagged, and released) and recaptured 3-months later to estimate individual growth over the summer. Beakes et al. (2014) found that fish living in burned regions suffered a 3.8% loss in body mass over the 3-month summer period, whereas fish residing in reference pools gained mass (~9.9% mass increase) over the same time. Beakes et al. (2014) also took advantage of bioenergetics modelling (which accounts for increases in temperature during and after the fire) to explore the energetic costs of wildfires on fish. Beakes et al. (2014) estimate the post-fire energetic costs for rainbow trout to be up to 4% higher than the costs of fish living in unburned, reference streams. Consistent with these results, Rosenberger et al. (2015) reported that rainbow trout living in fire-warmed streams had significantly lower lipid contents than fish inhabiting unburned streams, which is indicative of elevated energetic demands in fish living in warmer waters affected by wildfires. To offset these higher costs, fish would need to increase prey consumption rate, utilise finite energy reserves (glycogen and/or lipid stores), or seek less energetically expensive habitats (e.g., cool, well oxygenated waters). However, stomach contents of rainbow trout revealed that fish from the burned streams consumed much smaller prey and, after standardising the mass of prey (mg) by fish mass (g), consumed less prey per fish (0.99 mg/fish mass) than fish from reference regions (2.03 mg/fish mass) (Beakes et al., 2014). This suggests that fish in fire-affected streams were unable to increase prey consumption and may be forced to migrate in search of better habitat or risk energetic deficits. Further work is required to understand how changing fire regimes interact with the many physicochemical changes (i.e., increased water ash content, turbidity, nutrients) that occur during and following a wildfire event to impact organismal performance and survival.

The removal of basin vegetation during a wildfire facilitates the runoff of ash into freshwaters (Fig. 4; Bozek & Young, 1994; Leigh et al., 2015). Post-fire ash is composed of a complex milieu of nutrients, ions (e.g., Mg^{2+}, Si^{4+}, K^{+}, Ca^{2+}), sediment, metals, polycyclic aromatic hydrocarbons (PAHs), and residual fire suppressants that can severely impact aquatic fauna (Brito, Passos, Muniz, & Oliveira, 2017; Campos, Abrantes, Keizer, Vale, & Pereira, 2016; Earl & Blinn, 2003; Hall & Lombardozzi, 2008; Harper et al., 2019; Schafer, Hearn, Kefford, Mueller, & Nugegoda, 2010; Silva et al., 2016). The exact mixture of wildfire ash can depend on the geographic region, vegetation type, soil and biomass characteristics, on burn intensity, and fire-fighting approach (Barber et al., 2003; Harper et al., 2019). Post-fire rainfall and wind events facilitate the deposition of ash into freshwaters (Cerdà & Doerr, 2008; Leigh et al., 2015; Reneau, Katzman, Kuyumjian, Lavine, & Malmon, 2007). For example, a period of heavy rainfall (153 mm over 6 days) removed 36 mm of wildfire ash following a high intensity wildfire in eastern Spain (Cerdà & Doerr, 2008). Wildfire intensity also plays a role in determining erosion events; heavily burned and de-vegetated catchments facilitate wind and rain erosion. Severely burned soils are denatured, becoming hydrophobic and aid the runoff of course sediment and vegetation erosion (Saxe et al., 2018; Smith et al., 2011). Once in freshwaters, wildfire ash can affect aquatic animals due to direct toxicity (e.g., toxicity of PAHs, metals) and indirectly by lowering water quality (e.g., increase turbidity, conductivity, oxygen depletion; Fig. 1).

Wildfire ash

To date, most of the research on wildfire ash has been ecotoxicological (i.e., toxic endpoints, threshold effects of wildfire ash on organisms) or examined behavioural responses to wildfire ash (Fig. 2b). For example, Gonino, Figueiredo, Manetta, Alves, and Benedito (2019) assessed the 24-h acute toxicity of exposure to wildfire ash (concentrations from 0 – 2500 mg/L) in native Brazilian (*Astyanax lacustris, Moenkhausia forestii* and *M. bonita*) and invasive (*Oreochromis niloticus* and *Poecilia reticulata*) fishes. Native fishes were susceptible to elevated ash concentrations whereas invasive fishes were resilient to ash concentrations up to 2500 mg/L (Gonino, Figueiredo, et al., 2019). Most research on the acute toxic effects of wildfire ash on aquatic taxa point to low-no direct toxicity (Brito et al., 2017; Campos et al., 2012; Silva et al., 2015), but effects are more pronounced following longer-term exposures or when sublethal disruptions are considered.

Longer term investigations reveal that aquatic taxa can be sensitive to wildfire ash (Garcia & Carignan, 2005; Ré et al., 2020; Riggs et al., 2017). In a 7-day bioassay, freshwater clam *Corbicula fluminea* were resilient to short-term exposures (1 – 3 days) of wildfire ash extracts (aqueous extract of ashes, AEA) but mortality climbed to above 45% after 7-days of exposure (Silva et al., 2016). Similarly, in a field-based experiment, Earl and Blinn (2003) deposited 1,140 L of ash slurry from a medium intensity wildfire into Meadow Creek (Gila National Forest, New Mexico) over a 1.25 h period. Macroinvertebrate densities were measured (before, 24-h after, 1 month after and 1 year after) in ashed and reference reaches of Meadow creek before and after (24 h, 1-2 month, 1 year) ash was introduced. Macroinvertebrate density did not differ between reference and ashed-reaches 24 h after ash was deposited, but was lower 2-months after in the ashed reaches. One year after ashing, macroinvertebrate density remained lower in ashed than in reference reaches (Earl & Blinn, 2003). Some lifestage or lifehistory traits may also be more sensitive to the impacts of wildfire ash. For instance, investigation into the effects of ash exposure on embryonic life stages of fish showed that zebrafish (*Danio rerio*) experienced developmental delays at ash concentrations of 75 g/L, but adult survival was unaffected (Oliveira-Filho et al., 2018). Similarly, the fecundity (number of egg masses per snail and eggs per snail) of the freshwater snail *Biomphalaria glabrata* was reduced following as little 2-weeks of exposure to 50 g/L to wildfire ash extracts (Oliveira-Filho et al., 2018). Stage-specific impacts of ash exposure have also been assessed in amphibians (McDonald, Grayson, Lin, & Vonesh, 2018; Muñoz, Felicísimo, & Santos, 2019); survivorship of Cope's grey treefrog (*Hyla chrysoscelis*) tadpole was unaffected following 3-weeks of ash exposure, but exposed tadpoles suffered from slowed growth and development compared to unexposed individuals (McDonald et al., 2018). Moreover, adult frogs tend to avoid laying eggs in fire-affected habitats, and egg masses that are laid contain significantly fewer eggs compared to untreated controls despite an equal number and quality of adults among treatments (McDonald et al., 2018; Muñoz et al., 2019). These results indicate that long-term assessments are necessary to gain insight into the lasting impacts of wildfire ash on aquatic fauna.

Wildfire ash can significantly alter various behaviours of fish (Gonino, Branco, Benedito, Ferreira, & Santos, 2019). Gonino, Branco, et al. (2019) exposed Iberian barbel (*Luciobarbus bocagei*) to control (no ash), low (1.0 g/L), or high (2.0 g/L) concentrations of wildfire ash for 24 h and then assessed key behavioural traits (activity, boldness, shoal cohesion). Exposure to wildfire ash was found to significantly disrupt all measured behaviours; most significantly, fish exposed to high ash loads showed drastic reduction in activity levels, spending 56% of their time resting compared control (unexposed) fish, which spent just 31% of their time resting. Wildfire ash also decreased fish boldness and shoal cohesion, though only at the highest ash concentration. The mechanism/s underlying these behavioural alterations are unknown but may be linked to the clogging of the gills (Authman, Zaki, Khallaf, & Abbas, 2015; Kostić et al., 2017), increased metabolic costs (Rowe, Hopkins, Zehnder, & Congdon, 2001), ash toxicity (Brito et al., 2017; Harper et al., 2019;

Silva et al., 2015), or caused by some unmeasured factors (e.g., inorganic trace elements; Gonino, Branco, et al., 2019; Silva et al., 2016). These behavioural alterations are likely to have fitness consequences as reduced exploratory behaviours would prevent fish from escaping poor water conditions and decreased shoaling behaviours may increase the risk of detecting and evading predators (Goldenberg, Borcherding, & Heynen, 2014; Ward, Herbert-Read, Sumpter, & Krause, 2011). Contrarily, some behavioural changes may be adaptive, namely boldness, preventing fish from adopting risky behaviours and increase their survivorship in adverse environments (Biro & Dingemanse, 2009).

The multifactorial nature of wildfire ash makes it is difficult to establish which wildfire ash components contribute to direct toxicity. In a comparative study, Harper et al. (2019) assessed the chemical composition and toxicity of ash generated from wildfires in six contrasting vegetation types distributed globally (UK grassland, Spanish pine forest, Spanish heathland, USA chaparral, Australian eucalypt forest and Canadian spruce forest). Significant differences in chemical composition were found across locations and vegetation types had pronounced effects on the acute toxicity to *Daphnia magna*. Ash from the Australian eucalypt, USA chaparral, and Canadian spruce all caused detectable toxic effects (immobilisation percentage at 24 h) to *D. magna* whereas the UK and Spanish ash did not cause any discernible effects (Harper et al., 2019). Based on principle components analysis, Harper et al. (2019) concluded that the main characteristics underlying toxicity of the Australian, USA, and Canadian ashes to be the high pH, nitrate (NO_3^-), and high conductivity levels, whereas soluble concentrations of metals and PAHs are unlikely to be linked to acute toxicity. These data indicate that physicochemical composition of the ash/runoff/river water impacted by wildfire must be done as this depends not only on the type of burned vegetation but also on the extent and severity of the wildfire. Therefore, wildfire effects become themselves difficult to predict. The effects of wildfire on aquatic fauna are not generalisable and need to be evaluated on a case-by-case basis.

Turbidity

Sediment levels have also been documented to spike following wildfire and periods of heavy rainfall. Sediment (total suspended sediment TSS, mg/L) and turbidity (NTU) levels rose to 30 mg/L and 3000 NTU, respectively, following periods of high precipitation compared to 4 mg/L and 14 NTU at control sites (Rust, ell, Todd, & Hogue, 2019). The runoff of sediment following a wildfire often coincide with large-scale fish kill events (Bozek & Young, 1994;

Lyon & O'Connor, 2008; Rust et al., 2019; Silva et al., 2020). Shortly following a wildfire, Rust et al. (2019) documented an acute and dramatic fish kill event in the Upper Rio Grande, Colorado, USA, during rainfall that followed a severe wildfire, which caused turbidity and sediment levels to spike. Similarly, Lyon and O'Connor (2008) surveyed sections of the Ovens and Buckland river catchments in south-eastern Australia before, directly after, and 12, 24 and 36 months following high rainfall had deposited fire-related sediment into river reaches. The immediate impacts of sediment runoff were severe; fish abundances fell by between 95–100%, primarily due to low aquatic oxygen levels, which plunged to below 0.5 mg/L. Fish abundances were still reduced at impacted sites at 12 months post-sediment runoff, but signs of recovery were documented at 24 months. Similar mortality events occurred following Australia's catastrophic 2019-20 megafires and the heavy rainfall that followed, during which thousands of fish were found dead across various rivers and tributaries of the Murray-Darling Basin (Silva et al., 2020). Post-fire sediments have also shown to negatively impact aquatic fauna in laboratory and *in-situ* bioassays. Sediment dwelling invertebrates (*Chironomus riparius, Atyaephyra desmarestii,* and *Echinogammarus meridionalis*) suffered from a reduction in feeding activity when exposed to sediment impacted by wildfire runoff, which is hypothesised to reduce the available energy budget for detoxification, growth, and reproduction that could potentially trigger trophic and functional disruption at the ecosystem level (Ré et al., 2021).

Nutrients

Water concentrations of nutrients (total and dissolved nitrogen and phosphate) can increase several fold following wildfires and heavy rains (Cooper et al., 2015; Corbin, 2012; Lyon & O'Connor, 2008; Rust et al., 2019). Most predominantly, nitrate (NO_3^-) concentrations can be increased by up to 500 – 600% following fires and heavy rains (Cooper et al., 2015). Nutrient concentrations can also increase in stream water as a result of atmospheric fallout (e.g., smoke) from fires outside the catchment (Earl & Blinn, 2003; Spencer, Gabel, & Hauer, 2003). The most well documented impact of elevated nutrient concentrations on freshwater systems is the stimulation of algal growth and altered food web interactions (Cooper et al., 2015; Malison & Baxter, 2010; Rodriguez-Lozano et al., 2015; Spencer et al., 2003). For instance, isotopic analyses (mainly nitrogen, $\delta^{15}N$; carbon, $\delta^{13}C$; and hydrogen, δD stable isotope signatures) of fish and macroinvertebrates from fire-affected sites showed a consistent shift towards algal-derived dietary resources compared to organisms from reference sites (Cooper et al., 2015; Moreno, Fjeld, & Lydersen, 2016; Silins et al., 2014; Spencer et al., 2003). Similarly, Carvalho et al. (2019) reported a significant reduction in the activity of microbial decomposers and invertebrate shredders suggesting that wildfires can have major impacts on detrital food webs in streams. The implications of this shift in dietary sources are unclear but changed dietary resources could favour some species and life-stages over others, which could alter population dynamics of disturbed systems (Silins et al., 2014). Shifts in dietary composition can also alter fitness related traits of aquatic animals (e.g., capacity for sustained exercise, growth, investment into reproduction/reproductive traits; Felip, Blasco, Ibarz, Martin-Perez, & Fernández-Barràs, 2013; Goldstein, D'Alessandro, & Sponaugle, 2017; Olsson et al., 2008), though further work is required to understand how prolonged dietary shifts impact the physiology and fitness of animals residing in fire-affected freshwater habitats. Nutrient concentrations typically remain elevated for a few months following a heavy downpour (Earl & Blinn, 2003; Oliveira-Filho et al., 2018), but nutrient concentrations can remain elevated for years (5+ years) post wildfire (Silins et al., 2014; Spencer et al., 2003). High levels of nutrients (coupled with elevated light and water temperature levels) can leave strong legacy effects on freshwater systems. For instance, Koetsier et al. (2007) found that 10 years post-fire, the diets of rainbow trout were still altered. Stomach contents analyses revealed that fish residing in streams with a burn history (10 years post burn) consumed a greater proportion of aquatic invertebrates and inorganic matter than fish inhabiting reference, unburned streams, which consumed predominantly organic material (Koetsier et al., 2007).

This review found that few other impacts of elevated nutrient and sediment levels have been assessed within the context of wildfires. Despite this, it is well documented in the wider literature that elevated nutrient and sediment concentrations can have toxic effects on aquatic animals (Earl & Whiteman, 2010; Gomez Isaza, Cramp, & Franklin, 2020a; Na, Shimei, Erchao, Jiayan, & Liqiao, 2009). For instance, elevated concentrations of nitrate can impair the aerobic performance of aquatic animals (fish, crustaceans), with severe performance (Gomez Isaza, Cramp, & Franklin, 2018, 2020b) and fitness consequences (Soucek & Dickinson, 2016). Elevated levels of phosphate can also be toxic, albeit at extreme concentrations (96 h $LC50 = 3900$ mg/L; Na et al., 2009), but can have beneficial growth impacts at sublethal concentrations (Earl & Whiteman, 2010). Similarly, high levels of suspended sediment can detrimentally impact aquatic animals by initiating a stress response (increased corticosteroids, glucose, and haematocrit and reduced leukocrit levels), reducing feeding and growth, causing physical damage to the gills (erosion of mucus lining, abrasion of tissue, sediment binds directly to gill epithelium, increased lamellar thickness, reduced interlamellar area) that clog the gills, impairing oxygen uptake, and ultimately resulting in mortality (Kemp, Sear, Collins, Naden, & Jones, 2011; Rosewarne, Svendsen, Mortimer, & Dunn, 2014; Sutherland & Meyer, 2007). Exposure to elevated levels of nutrients and sediment can also make aquatic animals more susceptible to other concurrent threats, such as hypoxia and heat (Gomez Isaza, Cramp, & Franklin, 2020c, 2021; Gorokhova et al., 2010; Rodgers et al., 2021), and future research requires a holistic investigation into how concurrent threats impact aquatic fauna.

Polycyclic Aromatic Hydrocarbons and Metals

Concentrations of polycyclic aromatic hydrocarbons (PAHs) and metals (mainly Mg^{2+}, Fe, Cu^{+}) can increase several fold following wildfires and heavy rains (Campos et al., 2012; Harper et al., 2019; Silva et al., 2016). Many PAHs and metallic substances found in wildfire ash are recognised as priority contaminants by various legislative bodies (e.g., United States Environmental Protection Agency, Australian and New Zealand Environment and Conservation Council (1992), the European Union, article #2455/2001/EC, and the World Health Organisation) due to their toxic, mutagenic, and carcinogenic properties as well as their environmental persistence and tendency for bioaccumulation along the food chain (Ali, Khan, & Ilahi, 2019; ANZECC, 1992; Sun, Zhang, Ma, Chen, & Ju, 2017; WHO, 2003). Yet, despite these environmental concerns, current research suggests that ash-loaded runoff and aqueous extracts of wildfire ash pose limited acute toxic effects on aquatic animals (microcrustaceans: *D. dubia* and *Ceriodaphnia dubia;* freshwater snails *B. glabrata,* and zebrafish *D. rerio*) (Brito et al., 2017; Campos et al., 2012; Silva et al., 2015). Few long-term toxicity datasets exist for wildfire-derived extracts of PAHs and metals (but see Campos *et al.*, 2012).

Although acute exposure to extracts of wildfire runoff do not appear to cause mortality to aquatic taxa, PAHs and metallic constituents can accumulate in tissues and have been associated with oxidative and neuronal stress (Nunes et al., 2017; Plomp et al., 2020; Pradhan et al., 2020). Metals (mainly mercury accumulation has been investigated) and PAHs can accumulate at high concentrations in specific organs (mostly, the guts, gills, and liver) of aquatic animals (Bandowe et al., 2014; Garcia & Carignan, 2005; Plomp et al., 2020). Mean tissue concentrations of copper (Cu) were four-times greater in the freshwater amphipod, *Hyalella azteca*, exposed to aqueous extract of ash compared to controls (Plomp et al., 2020).

However, investigation is needed to understand how PAHs and metal accumulation impacts the function of affected tissues, and whether tissue accumulation impair whole-animal functioning and performance. Moreover, metals and PAHs can induce oxidative stress by the accumulation of reactive oxygen species (ROS; Javed, Ahmad, Usmani, & Ahmad, 2017; Jayawardena, Angunawela, Wickramasinghe, Ratnasooriya, & Udagama, 2017; Santana et al., 2018) and several oxidative biomarkers (catalase, CAT; glutathione-Stransferases, GSTs; glutathione reductase, GRed; and total and selenium-dependent glutathione peroxidase, tGPx and Se-GPx) have been used to reveal such effects. In mosquito fish (*Gambusia holbrooki*), exposure to wildfire ash runoff decreased gill GRed and liver Se-GPx activity levels, and increased gill GSTs activity (Nunes et al., 2017). These observed changes are indicative of an overproduction of ROS leading to an increase in pro-oxidative conditions. Similarly, exposure of the stream invertebrate *Allogamus ligonifer* to post-wildfire runoff and stream water from a burnt catchment inhibited the activity of cholinesterases (ChEs; Pradhan et al., 2020), which can disrupt neuro-muscular functions that play an essential role in cholinergic neurotransmission (Gagnaire, Geffard, Xuereb, Margoum, & Garric, 2008; Pradhan, Silva, Silva, Pascoal, & Cassio, 2016). As such, oxidative and neuronal stress biomarkers may be used as early-warning signs of wildfire ash toxicity in aquatic species.

Fire suppressants

Fire suppressants are commonly used to control the spread of wildfire or reduce their intensity (Giménez, Pastor, Zárate, Planas, & Arnaldos, 2004). Fire suppressants are applied either on the ground or by aerial means and are intended for terrestrial application. However, fire suppressants can enter aquatic environments during accidental drops or enter through surface runoff. Fire suppressants can cause significant mortality of aquatic fauna; for example, a mass fish kill followed the misapplication of fire suppressants in the Fall River (Oregon, USA; Calfee & Little, 2003).

Fire suppressants are composed of primarily water (~85%), inorganic salts (~10%; fertilisers, e.g., diammonium phosphates and ammonium polyphosphate salts) and other additives (colour, thickeners, corrosion inhibitors, and bactericides; Giménez et al., 2004). The primary risk associated with the use of fire-suppressant chemicals to freshwater organisms is through their adverse effects on water quality (Angeler, Martin, & Moreno, 2005; Boulton, Moss, & Smithyman, 2003; Calfee & Little, 2003). Many fire suppressants are rich in ammonium salts that, when dissociated to ammonia, can be toxic to aquatic animals. Indeed, various acute toxicity tests report significant mortality of aquatic fauna (*Daphnia sp.,* rainbow trout *Oncorhynchus mykiss,* and fathead minnow *Pimephales promelas*) following the application of fire suppressants (Angeler et al., 2005; Buhl & Hamilton, 1998, 2000; Calfee & Little, 2003; Dietrich, Myers, Strickand, Van Gaest, & Arkoosh, 2013; Dietrich et al., 2014; Gaikowski, Hamilton, Buhl, McDonald, & Summers, 1996). For example, the commercial fire-suppressant, Fire-TrolR 934 (composed of ammonium polyphosphate), has been extensively used worldwide as a fire control agent despite its toxic effects to aquatic fauna. In a laboratory toxicity test, *D. curvirostris* were exposed to sediment treatments treated with Fire-TrolR 934 at concentrations of 0, 1, 3, or 5 L m^{-2} (Angeler et al., 2005). *D. curvirostris* suffered reduced emergence success with increasing application rate, leading to a complete failure with application levels of 3 L m^{-2}. Treatments above 3 L m^{-2} also reduced the hatching success of *D. curvirostris*. Toxicity was attributed direct toxicity of ammonium salt plus the deterioration of water quality following application of fire suppressant. At an application rate of 1 L m^{-2}, water pH was increased by 0.5 of a pH unit (control = 8.25, Treatment = 8.86), and by 1.0 pH unit (increased to 9.25) at an application of 5 L m^{-2}. Similarly, water conductivity was increased at elevated concentrations of the fire suppressant and dissolved oxygen was significantly reduced (2.11 mg L^{-1} in control to 0.71 mg L^{-1} in the 3 L m^{-2} application treatment). Fire suppressant toxicity tests have also been conducted across various life-stages of salmonids. Interestingly, eyed eggs were most tolerant of elevated fire-suppressant exposure compared to swim-up fry and 60 to 90 d post-hatch salmonids due to the protective egg casing that limits ammonia uptake (Buhl & Hamilton, 1998, 2000; Gaikowski et al., 1996). Behavioural responses to fire suppressants have also been quantified in the laboratory. Using a counter-current avoidance assay, rainbow trout showed almost complete avoidance of the fire-suppressant Fire-Trol GST-R even at the lowest concentration used (0.65 mg/L; Wells, Little, & Calfee, 2004). A single study has examined the impact of fire suppressants on free-ranging animals. A field experiment in Kangaroo Island, Australia, showed that the application of fire-suppressants altered the water chemistry of affected streams; phosphorus concentrations were elevated, dissolved oxygen levels were reduced (~65 – 60% saturation), and water turbidity almost doubled (7 – 8 NUT at impacted sites compared to 4 – 4.5 NTU at reference sites) at sites where the fire suppressants had been applied (Boulton et al., 2003). However, aerially applied fire-suppressant had no apparent effects on macroinvertebrate assemblage composition or taxon richness two weeks after the chemical application or 3-months later after flushing rains. No information exists on the physiological condition of aquatic animals exposed to fire suppressants under laboratory or field settings. Overall, toxicity tests show that fire suppressants need to be diluted 100 – 1000 times to avoid acute toxic effects (Angeler et al., 2005; Calfee & Little, 2003; Gaikowski et al., 1996) and therefore it is essential that delivery near freshwaters are avoided.

How can physiological tools help elucidate and mitigate fire-related impacts?

The effects of wildfire on aquatic animals are far-reaching (Fig. 1). Wildfire and associated runoff can completely transform the physicochemical environment of freshwaters, with profound implications for aquatic animals, ranging from localised declines to mass mortality events of aquatic animals. Above we detailed the current state-of-knowledge of how aquatic animals respond to wildfires and associated runoff. However, research efforts have been biased towards assessing population and community levels responses (Fig. 2b), and little information is currently available on how wildfires impact the physiology and performance of aquatic animals. In the face of growing wildfire risk, physiology is perfectly placed to provide mechanistic insight into the impact of wildfires on aquatic animals (Cooke et al., 2013; Madliger, Franklin, Love, & Cooke, 2020; Madliger, Love, Hultine, & Cooke, 2018; Seebacher & Franklin, 2012). Physiological tools can provide information on the physiological status of aquatic animals, determine the timescale of recovery, and provide robust science advice needed to support management and conservation efforts against wildfire risks, including determining regulatory guidelines

Assessment of physiological status

Measuring species' responses to wildfire and runoff requires rapid and reliable assessments to enact management and conservation actions. Quantifying responses to complex ecological processes, like wildfires, and incorporating them into management frameworks presents practical challenges, because it is difficult to develop, implement, and maintain appropriate monitoring efforts (Cooke & O'Connor, 2010; Cooke et al., 2013). Therefore, environmental and biological data must provide informative indices that can be easily, but frequently monitored to be effectively incorporated into decision making (Madliger et al., 2018). Physiological tools can provide a suite of informative indices required to monitor the status of individuals, populations and their response to wildfire risks. Various physiological tools have been developed and revised as decision-support tools to provide insight into the physiological status of animals (Madliger et al., 2020; Madliger et al., 2018). Physiological tools are particularly useful for the management of wildfire and runoff in freshwaters, because they can reveal fitness impacting changes (e.g., changes in energy expenditure, immune function, reproductive status) that are not immediately obvious from individual (e.g., behaviour), population, or community level responses (Cooke et al., 2014). For example, stress hormones have been related to reproductive success in smallmouth bass (*Micropterus dolomieu*) (Alegra, Gutowsky, Zolderdo, & Cooke, 2017), differences in cardiovascular physiology have been linked to thermal tolerance among sockeye salmon populations (Eliason et al., 2011), and the ability of tadpoles to cope with desiccation is associated with basal immune responses (Gervasi & Foufopoulos, 2008). Physiological indicators can also reveal the impacts of wildfire and runoff across levels of biological organisation (i.e., whole animal down to gene level responses; Table 1), providing an in-depth assessment into the physiological status of aquatic animals post wildfires, which can be used as indicators for different management interventions/actions (Cooke et al., 2013; Madliger et al., 2018).

Physiological indicators reveal cause-and-effect relationships that advance our understanding of the changes caused by wildfires and, therefore, improve our management and conservation efforts (Cooke et al., 2014; Seebacher & Franklin, 2012). This review found that basic morphometric measurements of mass and length are the most commonly used tools to assess physiological-/condition-status of aquatic animals in response to wildfire risk (see Table S2). Enzyme activity, isotopic analyses, and body condition (e.g., hepatosomatic index) are other physiological tools used to assess the responses of aquatic animals to wildfire risks (Table S2). However, the number of studies using physiological tools to assess the responses of aquatic animals to wildfire risk are currently in the minority (Fig. 2b). Mass and length estimates are common tools, likely because these measures can be obtained with relative ease and with minimal training, making them easy to implement (Wuenschel, McElroy, Oliveira, & McBride, 2018). However, mass and length estimates can easily be complemented with more detailed assessments of physiological status (Table 1). Many of physiological tools have been validated across various taxa and can be perform across various species, life stages, and even in the field (see Madliger et al., 2020; Madliger et al., 2018). Pros and cons can be drawn for various biomarkers, and their utility for management and conservation can depend on the timescale of interest, cost, and the invasiveness of the procedure. Blood samples, for instance, are relatively easy and cheap to obtain and provide a wealth of information on an animal's physiological condition (e.g., blood-chemistry, hormones, glucose, lactate levels, haemoglobin) – but are limited because they generally reflect a snapshot of the animal's condition at the time that it was collected (e.g., Andrewartha, Munns, & Edwards, 2016; Cooke et al., 2008; and reviewed in Stoot et al., 2014). Contrarily, tissue samples (e.g., for measurement of oxidative biomarkers, 'omics' approaches, etc.) are invasive (often resulting in death of the animal) and difficult to obtain but provide a profile of the changing conditions experienced by the animal over the course of years – decades (Aerts et al., 2015; Izral, Brua, Culp, & Yates, 2021). The use of both short- and long-term biomarkers is pertinent to assessing wildfires impacts, as wildfire effects can be short- and long-lasting and differ across temporal scales (e.g., longevity of thermal regimes, runoff, persistence of nutrient, PAHs levels) (Leigh et al., 2015). The cause-and-effect understanding gained from physiological biomarkers can be incorporated into numerical models that explore organismal-level performance to wildfire and runoff scenarios and support management decisions (Moyano et al., 2020; Teal, Marras, Peck, & Domenici, 2018).

Determine regulatory guidelines and early warning signs

Physiological measures can help identify environmental thresholds and early warning signs that constrain organismal performance. These thresholds can, in a cause-and-effect manner, be linked to long-term changes in vital rate (e.g., growth, survival, reproduction) of wild populations and thereby provide robust science advice needed to support management and conservation efforts (Cooke et al., 2013). In terms of wildfire risk, we know that aquatic animals can be exposed to cocktails of stressors (Leigh et al., 2015; Rodgers, 2021). Yet not all levels of each stressor are threatening, nor is it always feasible to manage wildfire runoff components to very low levels. However, knowledge of physiological responses and endpoints can be used to delineate regulatory guidelines and inform environmental 'trigger points' that mobilise management actions. These trigger points can be altered based on the responses of sensitive species (e.g., native versus introduced species), life stages (i.e., stages that are most threatened by wildfire and runoff components), or during critical periods (e.g., spawning, migration; Cooke et al., 2012; Gonino, Figueiredo, et al., 2019; Rodgers et al., 2019). For instance, we know that ash extracts of wildfire ash exceeding 50 g L^{-1} lower the fecundity of freshwater snails (*B. glabrata*), but do not affect the development of zebrafish larvae (Oliveira-Filho et al., 2018). Based on these data, trigger points may be set so that ash extracts do not exceed 50 g L^{-1} to conserve the more sensitive species. Similarly, elevations in water temperature from wildfires might only be threatening if thermal regimes exceed species' specific and life stage specific thermal limits, but we must understand the physiological capabilities of species to set temperature guidelines (Cooke et al., 2012). The many interacting stressors associated with wildfire and runoff can complicate the setting of guidelines and environmental trigger points for conservation and management because wildfire stressors likely interact in ways that are non-linear (Côté, Darling, & Brown, 2016; Rodgers & Gomez Isaza, 2021). However, we can systematically assess how the various wildfire threats interact to impact physiological traits and establish adequate trigger points based on these interactions.

Determine timescale of recovery

Physiological tools are particularly useful for the assessment of recovery from wildfire and runoff because physiological responses are typically rapid when compared with changes in organismal abundance or community structure (Cooke et al., 2014). Physiological biomarkers therefore offer 'real-time' assessments of wildfire impacts on aquatic animals, allowing us to track recovery dynamics and effectiveness of remediation strategies (Adams & Ham, 2011; Hook, Gallagher, & Batley, 2014; Johansen & Esbaugh, 2017; McKenzie et al., 2017). For instance, measures of whole animal performance (e.g., swimming performance, muscle strength, aerobic scope measurements) that incorporate the workings of many physiological systems have been used to assess responses to and recovery from environmental stressors *in situ* (Cooke et al., 2012; McKenzie et al., 2007; Raby et al., 2015). McKenzie et al. (2007) found that complex physiological traits of exercise performance and metabolic rate served as successful biomarkers of sub-lethal toxic effects of exposure to complex mixtures of pollutants in rivers and provide a mechanistic explanation of presence or absence of fishes in polluted river reaches. Nutritional and condition indices were also successful in assessing the recovery of fish populations exposed to point-source discharge of various contaminant, before and after remedial action (Adams & Ham, 2011). Understanding the mechanistic processes involved between stressors, the responses of biota, and the recovery dynamics of aquatic systems to wildfire and runoff will be pivotal to reduce the uncertainty behind environmental management and regulatory decisions and improve our ability to predict the consequences of restoration and remedial actions for freshwater ecosystems.

Conclusion

The growing global risk of wildfires is set to expose aquatic ecosystems and species to a dynamic set of environmental changes. This review synthesised the state-of-knowledge of the impacts of wildfire and associated runoff on aquatic species. Wildfire impacts on aquatic systems are complex, and our understanding of the major impacts of wildfires have focused on the community and ecosystem level effects on aquatic life. There is a paucity of knowledge on how wildfire threats impact aquatic species, how long these effects last, how the various wildfire impacts interact, and how we can develop guidelines to detect early signs of wildfire risk. By taking a physiological approach, we will gain a deep, cause-and-effect understanding of how aquatic animals respond to wildfire threats, which will allow us to better predict how future wildfire and runoff events are likely to influence aquatic animals. With the increasing global risk of wildfires, there is an urgent need for fundamental data on how wildfires shape the persistence of aquatic species, which will enable management and conservation efforts to better protect species against wildfire and runoff.

Funding

This research received support from the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub (Project 8.3.7)

Conflict of interest

The authors declare no competing interests.

Data availability statement

The data that supports the findings of this study are available in the supplementary material of this article.

References

Adams, S. M., & Ham, K. D. (2011). Application of biochemical and physiological indicators for assessing recovery of fish populations in a disturbed stream. *Environmental Management, 47*, 1047–1063.

Aerts, J., Metz, J. R., Ampe, B., Decostere, A., Flik, G., & De Saeger, S. (2015). Scales tell a story on the stress history of fish. *PloS One, 10*, e0123411.

Alegra, D. A., Gutowsky, L. F. G., Zolderdo, A. J., & Cooke, S. J. (2017). Parental care in a stressful world: Experimentally elevated cortisol and brood size manipulation influence nest success probability and nest-tending behavior in a wild teleost fish. *Physiological and Biochemical Zoology, 90*, 85–95.

Ali, H., Khan, E., & Ilahi, I. (2019). Environmental Chemistry and Ecotoxicology of Hazardous Heavy Metals: Environmental Persistence, Toxicity, and Bioaccumulation. *Journal of Chemistry, 2019*, 6730305.

Alton, L. A., & Franklin, C. E. (2017). Drivers of amphibian declines: effects of ultraviolet radiation and interactions with other environmental factors. *Climate Change Responses, 4*, 6.

Alton, L. A., Wilson, R. S., & Franklin, C. E. (2011). A small increase in UV-B increases the susceptibility of tadpoles to predation. *Proceedings of the Royal Society B: Biological Sciences, 278*, 2575–2583.

Andrewartha, S. J., Munns, S. L., & Edwards, A. (2016). Calibration of the HemoCue point-of-care analyser for determining haemoglobin concentration in a lizard and a fish *Conservation Physiology, 4*, cow006.

Angeler, D. G., Martin, S., & Moreno, J. M. (2005). Daphnia emergence: a sensitive indicator of fire-retardant stress in temporary wetlands. *Environment International, 31*(4), 615-620.

ANZECC. (1992). *Australian Water Quality Guidelines for Fresh and Marine Waters*. Canberra, Australia: Australian and New Zealand Environment and Conservation Council.

Aria, M., & Cuccurullo, C. (2017). bibliometrix: An R-tool for comprehensive science mapping analysis. *Journal of Informetrics, 11*, 959-975.

Authman, M. M., Zaki, M. S., Khallaf, E. A., & Abbas, H. H. (2015). Use of fish as bio-indicator of the effects of heavy metals pollution. *Journal of Aquaculture Research and Development, 6*, 1-13.

Ball, G., Regier, P., González-Pinzón, R., Reale, J., & Van Horn, D. (2021). Wildfires increasingly impact western US fluvial networks. *Nature Communications, 12*, 2484.

Bandowe, B. A. M., Bigalke, M., Boamah, L., Nyarko, E., Saalia, F. K., & Wilcke, W. (2014). Polycyclic aromatic compounds (PAHs and oxygenated PAHs) and tracemetals infish species from Ghana (West Africa): Bioaccumulationand health risk assessment. *Environment International, 65*, 135-146.

Barber, T. R., Lutes, C. C., Doorn, M. R. J., Fuchsman, P. C., Timmenga, H. J., & Crouch, R. L. (2003). Aquatic ecological risks due to cyanide releases from biomass burning. *Chemosphere, 50*(3), 343-348.

Beakes, M. P., Moore, J. W., Hayes, S. A., & Sogard, S. M. (2014). Wildfire and the effects of shifting stream temperature on salmonids. *Ecosphere, 5*, 1-14.

Benali, A., Mota, B., Carvalhais, N., Oom, D., Miller, L. M., Campagnolo, M. L., & Pereira, J. M. C. (2017). Bimodal fire regimes unveil a global-scale anthropogenic fingerprint. *Global Ecology and Biogeography, 26*, 799-811.

Biro, P. A., & Dingemanse, N. J. (2009). Sampling bias resulting fromanimal personality. *Trends in Ecology & Evolution, 24*, 66-67.

Bisson, P. A., Rieman, B. E., Luce, C., Hessburg, P. F., Lee, D. C., Kershner, J. L., . . . Gresswell, R. E. (2003). Fire and aquatic ecosystems of the western USA: current knowledge and key questions. *Forest Ecology and Management, 178*, 213-229.

Bixby, R. J., Cooper, S. D., Gresswell, R. E., Brown, L. E., Dahm, C. N., & Dwire, K. A. (2015). Fire effects on aquatic ecosystems: an assessment of the current state of the science. *Freshwater Science, 34*(4), 1340-1350.

Boulton, A. J., Moss, G. L., & Smithyman, D. (2003). Short-term effects of aerially-applied fire-suppressant foams on water chemistry and macroinvertebrates in streams after natural wild-fire on Kangaroo Island, South Australia. *Hydrobiologia, 498*(1), 177-189.

Bozek, M. A., & Young, M. K. (1994). Fish mortality resulting from delayed-effects of fire in the greater Yellowstone ecosystem. *Great Basin Naturalist, 54*(1), 91-95.

Brito, D. Q., Passos, C. J. S., Muniz, D. H. F., & Oliveira, E. C. (2017). Aquatic ecotoxicity of ashes from Brazilian savanna wildfires. *Environmental Science and Pollution Research, 24*(24), 19671-19682.

Buhl, K. J., & Hamilton, S. J. (1998). Acute toxicity of fire-retardant and foam suppressant chemicals to early life stages of Chinook salmon (*Oncorhynchus tshawytscha*). *Environmental Toxicology and Chemistry, 17*, 1589-1599.

Buhl, K. J., & Hamilton, S. J. (2000). Acute toxicity of fire-control chemicals, nitrogenous chemicals, and surfactants to rainbow trout. *Transactions of the American Fisheries Society, 129*, 408-418.

Burton, T. A. (2005). Fish and stream habitat risks from uncharacteristic wildfire: Observations from 17 years of fire-related disturbances on the Boise National Forest, Idaho. *Forest Ecology and Management, 211*(1), 140-149.

Calfee, R. D., & Little, E. E. (2003). Effects of a fire-retardant chemical to fathead minnows in experimental streams. *Environmental Science and Pollution Research, 10*(5), 296-300.

Campos, I., Abrantes, N., Keizer, J. J., Vale, C., & Pereira, P. (2016). Major and trace elements in soils and ashes of eucalypt and pine forest plantations in Portugal following a wildfire. *Science of the Total Environment, 572*, 1363-1376.

Campos, I., Abrantes, N., Vidal, T., Bastos, A. C., Gonçalves, F., & Keizer, J. J. (2012). Assessment of the toxicity of ash-loaded runoff from a recently burnt eucalypt plantation. *European Journal of Forest Research, 131*(6), 1889-1903.

Carvalho, F., Pradhan, A., Abrantes, N., Campos, I., Keizer, J. J., Cassio, F., & Pascoal, C. (2019). Wildfire impacts on freshwater detrital food webs depend on runoff load, exposure time and burnt forest type. *Science of the Total Environment, 692*, 691-700.

Cerdà, A., & Doerr, S. H. (2008). The effect of ash and needle cover on surface runoff and erosion in the immediate post-fire period. *Catena, 74*, 256-263.

Cerri, R. D. (1983). The effect of light intensity on predator and prey behaviour in cyprinid fish: Factors that influence prey risk. *Animal Behaviour, 31*, 736-742.

Collins, L., Bradstock, R. A., Clarke, H., Clarke, M. F., Nolan, R. H., & Penman, T. D. (2021). The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters, 16*, 044029.

Cooke, S. J., Blumstein, D. T., Bucholz, R., Caro, T., Fernández-Juricic, E., Franklin, C. E., . . . Wikelski, M. (2014). Physiology, Behavior, and Conservation. *Physiological and Biochemical Zoology, 87*, 1-14.

Cooke, S. J., Hinch, S. C., Donaldson, M. R., Clark, T. D., Eliason, E. J., Crossin, G. T., . . . Farrell, A. P. (2012). Conservation physiology in practice: how physiological knowledge has improved our ability to sustainably manage Pacific salmon during up-river migration. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*, 1757–1769.

Cooke, S. J., & O'Connor, C. M. (2010). Making conservation physiology relevant to policy makers and conservation practitioners. *Conservation Letters, 3*, 159-166.

Cooke, S. J., Sack, L., Franklin, C. E., Farrell, A. P., Beardall, J., Wikelski, M., & Chown, S. L. (2013). What is conservation physiology? Perspectives on an increasingly integrated and essential science. *Conservation Physiology, 1*, cot001.

Cooke, S. J., Suski, C. D., Danylchuk, S. E., Danylchuk, A. J., Donaldson, M. R., Pullen, C., . . . Goldberg, T. L. (2008). Effects of different capture techniques on the physiological condition of bonefish *Albula vulpes* evaluated using field diagnostic tools. *Journal of Fish Biology, 73*, 1351-1375.

Cooper, S. D., Page, H. M., Wiseman, S. W., Klose, K., Bennett, D., Even, T., . . . Dudley, T. L. (2015). Physicochemical and biological responses of streams to wildfire severity in riparian zones. *Freshwater Biology, 60*(12), 2600-2619.

Corbin, T. A. (2012). Short-term effects of a wildfire on the water quality and macroinvertebrate community of a saline stream. *International Journal of Wildland Fire, 21*(5), 537-544.

Côté, I. M., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences, 283*, 20152592.

Cunillera-Montcusí, D., Gascón, S., Tornero, I., Sala, J., Ávila, N., Quintana, X. D., & Boix, D. (2019). Direct and indirect impacts of wildfire on faunal communities of Mediterranean temporary ponds. *Freshwater Biology, 64*, 323-334.

Dietrich, J. P., Myers, M. S., Strickand, S. A., Van Gaest, A. L., & Arkoosh, M. R. (2013). Toxicity of forest fire retardant chemicals to stream-type chinook salmon undergoing parr–smolt transformation. *Environmental Toxicology and Chemistry, 32*, 236-247.

Dietrich, J. P., Van Gaest, A. L., Strickl, , S. A., Hutchinson, G. P., Krupkin, A. B., & Arkoosh, M. R. (2014). Toxicity of PHOS-CHEK LC-95A and 259F fire retardants to ocean- and stream-type Chinook salmon and their potential to recover before seawater entry. *Science of the Total Environment, 490*, 610-621.

Driessen, M. M. (2019). Fire resilience of a rare, freshwater crustacean in a fire-prone ecosystem and the implications for fire management. *Austral Ecology, 44*(6), 1030-1039.

Dunham, J. B., Rosenberger, A. E., Luce, C. H., & Rieman, B. E. (2007). Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. *Ecosystems, 10*(2), 335-346.

Earl, J. E., & Whiteman, H. H. (2010). Evaluation of phosphate toxicity in Cope's gray treefrog (*Hyla chrysoscelis*) tadpoles. *Journal of Herpetology, 44*, 201-208.

Earl, S. R., & Blinn, D. W. (2003). Effects of wildfire ash on water chemistry and biota in South-Western USA streams. *Freshwater Biology, 48*(6), 1015-1030.

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jerries, K. M., . . . Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science, 332*, 109-112.

Engstrom, R. T. (2010). First-Order Fire Effects on Animals: Review and Recommendations. *Fire Ecology, 6*, 115–130.

Felip, O., Blasco, J., Ibarz, A., Martin-Perez, M., & Fernández-Barràs, J. (2013). Beneficial effects of sustained activity on the use of dietary protein and carbohydrate traced with stable isotopes ^{15}N and ^{13}C in gilthead sea bream (*Sparus aurata*). *Journal of Comparative Physiology B, 183*, 223–234.

Gagnaire, B., Geffard, O., Xuereb, B., Margoum, C., & Garric, J. (2008). Cholinesterase activities as potential biomarkers: characterization in two freshwater snails, *Potamopyrgus antipodarum* (Mollusca, Hydrobiidae, Smith 1889) and *Valvata piscinalis* (Mollusca, Valvatidae, Müller 1774). *Chemosphere, 71*, 553-560.

Gaikowski, M. P., Hamilton, S. J., Buhl, K. J., McDonald, S. F., & Summers, C. H. (1996). Acute toxicity of three fire-retardants and two fire-suppressant foam formulations to the early life stages of rainbow trout (*Oncorhynchus mykiss*). *Environmental Toxicology and Chemistry, 15*, 1365-1374.

Garcia, E., & Carignan, R. (2005). Mercury concentrations in fish from forest harvesting and fire-impacted Canadian Boreal lakes compared using stable isotopes of nitrogen. *Environmental Toxicology and Chemistry, 24*(3), 685-693.

Gervasi, S. S., & Foufopoulos, J. (2008). Costs of plasticity: responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian. *Functional Ecology, 22*, 100-108.

Giménez, A., Pastor, E., Zárate, L., Planas, E., & Arnaldos, J. (2004). Long-term forest fire retardants: a review of quality, effectiveness, application and environmental considerations. *International Journal of Wildfire Science, 13*, 1-15.

Goldenberg, S. U., Borcherding, J., & Heynen, M. (2014). Balancing the response to predation—the effects of shoal size, predation risk and habituation on behaviour of juvenile perch. *Behavioral Ecology and Sociobiology, 68*, 989-998.

Goldstein, E. D., D'Alessandro, E. K., & Sponaugle, S. (2017). Fitness consequences of habitat variability, trophic position, and energy allocation across the depth distribution of a coral-reef fish. *Coral Reefs, 36*, 957–968.

Gomez Isaza, D. F., Cramp, R. L., & Franklin, C. E. (2018). Negative impacts of elevated nitrate on physiological performance are not exacerbated by low pH. *Aquatic Toxicology, 200*, 217-225.

Gomez Isaza, D. F., Cramp, R. L., & Franklin, C. E. (2020a). Living in polluted waters: A meta-analysis of the effects of nitrate and interactions with other environmental stressors on freshwater taxa. *Environmental Pollution, 261*, 114091.

Gomez Isaza, D. F., Cramp, R. L., & Franklin, C. E. (2020b). Simultaneous exposure to nitrate and low pH reduces the blood oxygen-carrying capacity and functional performance of a freshwater fish. *Conservation Physiology, 8*, coz092.

Gomez Isaza, D. F., Cramp, R. L., & Franklin, C. E. (2020c). Thermal acclimation offsets the negative effects of nitrate on aerobic scope and performance. *Journal of Experimental Biology, 223*, jeb224444.

Gomez Isaza, D. F., Cramp, R. L., & Franklin, C. E. (2021). Exposure to nitrate increases susceptibility to hypoxia in fish. *Physiological and Biochemical Zoology, 94*, 124-142.

Gonino, G., Branco, P., Benedito, E., Ferreira, M. T., & Santos, J. M. (2019). Short-term effects of wildfire ash exposure on behaviour and hepatosomatic condition of a potamodromous cyprinid fish, the Iberian barbel Luciobarbus bocagei (Steindachner, 1864). *Science of the Total Environment, 665*, 226-234.

Gonino, G. M. R., Figueiredo, B. R. S., Manetta, G. I., Alves, G. H. Z., & Benedito, E. (2019). Fire increases the productivity of sugarcane, but it also generates ashes that negatively affect native fish species in aquatic systems. *Science of the Total Environment, 664*, 215-221.

Gorokhova, E., Löf, M., Pálmar Halldórsson, H., Tjärnlund, U., Lindströmm, M., Elfwing, T., & Sundelin, B. (2010). Single and combined effects of hypoxia and contaminated sediments on the amphipod *Monoporeia affinis* in laboratory toxicity bioassays based on multiple biomarkers. *Aquatic Toxicology, 99*, 263-274.

Gresswell, R. E. (1999). Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society, 128*, 193-221.

Haddaway, N. R., Macura, B., Whaley, P., & Pullin, A. S. (2018). ROSES RepOrting standards for Systematic Evidence Syntheses: pro forma, flow-diagram and descriptive summary of the plan and conduct of environmental systematic reviews and systematic maps. *Environmental Evidence, 7*, 7.

Hall, S. J., & Lombardozzi, D. (2008). Short-term Effects of Wildfire on Montane Stream Ecosystems in the Southern Rocky Mountains: One and Two Years Post-burn. *Western North American Naturalist, 68*(4), 453-462.

Harper, A. R., Santin, C., Doerr, S. H., Froyd, C. A., Albini, D., Otero, X. L., . . . Pérez-Fernández, B. (2019). Chemical composition of wildfire ash produced in contrasting ecosystems and its toxicity to Daphnia magna. *International Journal of Wildland Fire, 28*(10), 726-737.

Herman, J. R. (2010). Global increase in UV irradiance during the past 30 years (1979-2008) estimated from satellite data. *Journal of Geophysical Research, 115*, D04203.

Hitt, N. P. (2003). Immediate effects of wildfire on stream temperature. *Journal of Freshwater Ecology, 18*(1), 171-173.

Hook, S. E., Gallagher, E. P., & Batley, G. E. (2014). The role of biomarkers in the assessment of aquatic ecosystem health. *Integrated Environmental Assessment and Management, 10*, 327-341.

Howell, P. J. (2006). Effects of wildfire and subsequent hydrologic events on fish distribution and abundance in tributaries of north fork John Day River. *North American Journal of Fisheries Management, 26*(4), 983-994.

Huey, R. B., & Kingsolver, J. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology & Evolution, 4*, 131-135.

Izral, N. M., Brua, R. B., Culp, J. M., & Yates, A. G. (2021). Crayfish tissue metabolomes effectively distinguish impacts of wastewater and agriculture in aquatic ecosystems. *Science of the Total Environment, 760*, 143322.

Javed, M., Ahmad, M. I., Usmani, N., & Ahmad, M. (2017). Multiple biomarker responses (serum biochemistry, oxidative stress, genotoxicity and histopathology) in *Channa punctatus* exposed to heavy metal loaded waste water. *Scientific reports, 7*, 1675.

Jayawardena, U. A., Angunawela, P., Wickramasinghe, D. D., Ratnasooriya, W. D., & Udagama, P. V. (2017). Heavy metal–induced toxicity in the Indian green frog: Biochemical and histopathological alterations. *Environmental Toxicology and Chemistry, 36*, 2855-2867.

Johansen, J. L., & Esbaugh, A. J. (2017). Sustained impairment of respiratory function and swim performance following acute oil exposure in a coastal marine fish. *Aquatic Toxicology, 187*, 82-89.

Johnston, K., G., M. T., Robson, B. J., & Chester, E. T. (2014). Impacts of extreme events on southeastern Australian freshwater crayfish. *Freshwater Crayfish, 20*, 61–71.

Kemp, P., Sear, D., Collins, A., Naden, P., & Jones, I. (2011). The impacts of fine sediment on riverine fish. *Hydrological Processes, 25*, 1800-1821.

Koetsier, P., Tuckett, Q., & White, J. (2007). Present effects of past wildfires on the diets of stream fish. *Western North American Naturalist, 67*(3), 429-438.

Koontz, E. D., Steel, E. A., & Olden, J. D. (2018). Stream thermal responses to wildfire in the Pacific Northwest. *Freshwater Science, 37*, 731-746.

Kostić, J., Kolarević, S., Kračun-Kolarević, M., Aborgiba, M., Gačić, Z., Paunović, M., . . . Vuković-Gačić, B. (2017). The impact of multiple stressors on the biomarkers response in gills and liver of freshwater breams during different seasons. *Science of the Total Environment, 601*, 1670-1681.

Kuparinen, A., Cano, J. M., Loehr, J., Herczeg, G., Gonda, A., & Merilä, J. (2011). Fish age at maturation is influenced by temperature independently of growth. *Oecologia, 167*, 435–443.

Leigh, C., Bush, A., Harrison, E., Ho, S., Luke, L., Rolls, R. J., & Ledger, M. E. (2015). Ecological effects of extreme climatic events on riverine ecosystems: insights from Australia. *Freshwater Biology, 60*, 2620–2638.

Little, A. G., Loughland, I., & Seebacher, F. (2020). What do warming waters mean for fish physiology and fisheries? *Journal of Fish Biology, 97*, 328-340.

Lyon, J. P., & O'Connor, J. P. (2008). Smoke on the water: Can riverine fish populations recover following a catastrophic fire-related sediment slug? *Austral Ecology, 33*(6), 794-806.

Madliger, C. L., Franklin, C. E., Love, O. P., & Cooke, S. J. (2020). *Conservation Physiology: Applications for Wildlife Conservation and Management*. UK: Oxford University Press.

Madliger, C. L., Love, O. P., Hultine, K. R., & Cooke, S. J. (2018). The conservation physiology toolbox: status and opportunities. *Conservation Physiology, 6*, coy029.

Mahlum, S. K., Eby, L. A., Young, M. K., Clancy, C. G., & Jakober, M. (2011). Effects of wildfire on stream temperatures in the Bitterroot River Basin, Montana. *International Journal of Wildfire Science, 20*, 240-247.

Malison, R. W., & Baxter, C. V. (2010). Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. *Journal of the North American Benthological Society, 29*, 1324-1338.

McDonald, L. A., Grayson, K. L., Lin, H. A., & Vonesh, J. R. (2018). Stage-specific effects of fire: Effects of prescribed burning on adult abundance, oviposition habitat selection, and larval performance of Cope's Gray Treefrog (*Hyla chrysoscelis*). *Fire Ecology and Management, 430*, 394-402.

McKenzie, D. J., Blasco, F. R., Belão, T. C., Killen, S. S., Martins, N. D., Taylor, E. W., & Rantin, F. T. (2017). Physiological determinants of individual variation in sensitivity to an organophosphate pesticide in Nile tilapia *Oreochromis niloticus*. *Aquatic Toxicology, 189*, 108-114.

McKenzie, D. J., Garofalo, E., Winter, M. J., Ceradini, S., Verweij, F., Day, N., . . . Taylor, E. W. (2007). Complex physiological traits as biomarkers of the sub-lethal toxicological effects of pollutant exposure in fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences, 362*, 2043–2059.

McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., . . . Balch, J. K. (2020). Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology, 108*, 2047-2069.

Mellon, C. D., Wipfli, M. S., & Li, J. L. (2008). Effects of forest fire on headwater stream macro-invertebrate communities in eastern Washington, U.S.A. *Freshwater Biology, 53*, 2331–2343

Moher, D., Shamseer, L., Clarke, M., Chersi, D., Liberati, A., Petticrew, M., . . . PRISMA-P Group. (2015). Preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P) 2015 statement. *Systematic Reviews, 4*, 1.

Monaghan, K. A., Machado, A. L., Corado, M., Wrona, F. J., & Soares, A. M. (2019). Seasonal time-series reveal the impact and rapid recovery in richness, abundance and community structure of benthic macroinvertebrates following catchment wildfire. *Science of the Total Environment, 651*, 3117-3126.

Moreno, C. E., Fjeld, E., & Lydersen, E. (2016). The effects of wildfire on mercury and stable isotopes (δ15N, δ13C) in water and biota of small boreal, acidic lakes in southern Norway. *Environmental Monitoring and Assessment, 188*(3), 1-23.

Moyano, M., Illing, B., Polte, P., Kotterba, P., Zoblotski, Y., Gröhsler, T., . . . Peck, M. A. (2020). Linking individual physiological indicators to the productivity of fish populations: A case study of Atlantic herring. *Ecological Indicators, 113*, 106146.

Muñoz, A., Felicísimo, A. M., & Santos, X. (2019). Assessing the resistance of a breeding amphibian community to a large wildfire. *Acta Oecologica, 99*, 103439.

Na, Y., Shimei, C., Erchao, L., Jiayan, C., & Liqiao, C. (2009). Tolerance of *Physocypria kraepelini* (Crustacean, Ostracoda) to water-borne ammonia, phosphate and pH value. *Environmental Sciences, 21*, 1575-1580.

Nunes, B., Silva, V., Campos, I., Pereira, J. L., Pereira, P., Keizer, J. J., . . . Abrantes, N. (2017). Off-site impacts of wildfires on aquatic systems - Biomarker responses of the mosquitofish *Gambusia holbrooki*. *Science of the Total Environment, 581*, 305-313.

Oliveira-Filho, E. C., Brito, D. Q., Dias, Z. M. B., Guarieiro, M. S., Carvalho, E. L., Fascineli, M. L., . . . Grisolia, C. K. (2018). Effects of ashes from a Brazilian savanna wildfire on water, soil and biota: An ecotoxicological approach. *Science of the Total Environment, 618*, 101-111.

Olsson, K., Nyström, P., Stenroth, P., Nilsson, E., Svensson, M., & Granéli, W. (2008). The influence of food quality and availability on trophic position, carbon signature, and growth rate of an omnivorous crayfish. *Canadian Journal of Fisheries and Aquatic Sciences, 65*, 2293–2304.

Ouzzani, M., Hammady, H., Fedorowicz, Z., & Elmagarmid, A. (2016). Rayyan—a web and mobile app for systematic reviews. *Systematic Reviews, 5*, 210.

Pausas, J. G., & Ribeiro, E. (2013). The global fire–productivity relationship. *Global Ecology and Biogeography, 22*, 728-736.

Plomp, R. D., Klemish, J. L., & Pyle, G. G. (2020). The Single and Combined Effects of Wildfire Runoff and Sediment-Bound Copper on the Freshwater Amphipod *Hyalella azteca*. *Environmental Toxicology and Chemistry, 39*(10), 1988-1997.

Pörtner, H. O., & Peck, M. A. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology, 77*, 1745-1779.

Pradhan, A., Carvalho, F., Abrantes, N., Campos, I., Keizer, J. J., Cassio, F., & Pascoal, C. (2020). Biochemical and functional responses of stream invertebrate shredders to post-wildfire contamination. *Environmental Pollution, 267*.

Pradhan, A., Silva, C. O., Silva, C., Pascoal, C., & Cassio, F. (2016). Enzymatic biomarkers can portray nanoCuO-induced oxidative and neuronal stress in freshwater shredders. *Aquatic Toxicology, 180*, 227-235.

Pusey, B. J., & Arthington, A. H. (2003). Importance of the riparian zone to the conservation and management of freshwater fish: a review *Marine and Freshwater Research, 54*, 1-16.

Raby, G. D., Clark, T. D., Farrell, A. P., Patterson, D. A., Bett, N. N., Wilson, S. M., . . . Cooke, S. J. (2015). Facing the river gauntlet: Understanding the effects of fisheries capture and water temperature on the physiology of coho salmon. *PloS One, 10*, e0124023.

Ré, A., Campos, I., Keizer, J. J., Goncalves, F. J. M., Pereira, J. L., & Abrantes, N. (2021). Effects of post-fire contamination in sediment-dwelling species of riverine systems. *Science of the Total Environment, 771*.

Ré, A., Campos, I., Puga, J., Keizer, J. J., Gonçalves, F., Pereira, J. L., & Abrantes, N. (2020). Feeding inhibition following in-situ and laboratory exposure as an indicator of ecotoxic impacts of wildfires in affected waterbodies. *Aquatic Toxicology, 227*, 105587.

Reneau, S. L., Katzman, D., Kuyumjian, G. A., Lavine, A., & Malmon, D. V. (2007). Sediment delivery after a wildfire. *Geology, 35*(51-154).

Rhoades, C. C., Entwistle, D., & Butler, D. (2011). The influence of wildfire extent and severity on streamwater chemistry, sediment and temperature following the Hayman Fire, Colorado. *International Journal of Wildfire Science, 20*, 430-442.

Rieman, B. E., & Clayton, J. (1997). Wildfire and Native Fish: Issues of Forest Health and Conservation of Sensitive Species. *Fisheries, 22*, 6-15.

Riggs, C. E., Kolka, R. K., Nater, E. A., Witt, E. L., Wickman, T. R., Woodruff, L. G., & Butcher, J. T. (2017). Yellow Perch (Perca flavescens) Mercury Unaffected by Wildland Fires in Northern Minnesota. *Journal of Environmental Quality, 46*(3), 623-631.

Robson, B. J., Chester, E. T., Matthews, T. G., & Johnston, K. (2018). Post-wildfire recovery of invertebrate diversity in drought-affected headwater streams. *Aquatic Sciences, 80*(2).

Rodgers, E. M. (2021). Adding climate change to the mix: responses of aquatic ectotherms to the combined effects of eutrophication and warming. *Biology Letters, 17*, 20210442.

Rodgers, E. M., & Gomez Isaza, D. F. (2021). Harnessing the potential of cross-protection stressor interactions for conservation: a review *Conservation Physiology, 9*, coab037.

Rodgers, E. M., Opinion, A. G. R., Gomez Isaza, D. F., Rašković, B., Poleksić, V., & De Boeck, G. (2021). Double whammy: Nitrate pollution heightens susceptibility to both hypoxia and heat in a freshwater salmonid. *Science of the Total Environment, 765*, 142777.

Rodgers, E. M., Poletto, J. B., Gomez Isaza, D. F., Van Eenennaam, J. P., Connon, R. E., Todgham, A. E., . . . Fangue, N. A. (2019). Integrating physiological data with the conservation and management of fishes: a meta-analytical review using the threatened green sturgeon (*Acipenser medirostris*). *Conservation Physiology, 7*, coz035.

Rodriguez-Lozano, P., Rieradevall, M., Rau, M. A., & Prat, N. (2015). Long-term consequences of a wildfire for leaf-litter breakdown in a Mediterranean stream. *Freshwater Science, 34*(4), 1482-1493.

Rogers, B. M., Balch, J. K., Goetz, S. J., Lehmann, C. E. R., & Turetsky, M. (2020). Focus on changing fire regimes: interactions with climate, ecosystems, and society. *Environmental Research Letters, 15*, 030201.

Rosenberger, A. E., Dunham, J. B., Neuswanger, J. R., & Railsback, S. F. (2015). Legacy effects of wildfire on stream thermal regimes and rainbow trout ecology: an integrated analysis of observation and individual-based models. *Freshwater Science, 34*(4), 1571-1584.

Rosewarne, P. J., Svendsen, J. C., Mortimer, R. J. G., & Dunn, A. M. (2014). Muddied waters: suspended sediment impacts on gill structure and aerobic scope in an endangered native and an invasive freshwater crayfish. *Hydrobiologia, 722*, 61–74.

Rowe, C. L., Hopkins, W. A., Zehnder, C., & Congdon, J. D. (2001). Metabolic costs incurred by crayfish (Procambarus acutus) in a trace element-polluted habitat: further evidence of similar responses among diverse taxonomic groups. *Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology, 129*, 275-283.

Rust, A. J., ell, J., Todd, A. S., & Hogue, T. S. (2019). Wildfire impacts on water quality, macroinvertebrate, and trout populations in the Upper Rio Grande. *Forest Ecology and Management, 453*.

Santana, M. S., Sandrini-Neto, L., Neto, F. F., Oliveira Ribeiro, C. A., Di Domenico, M., & Prodocimo, M. M. (2018). Biomarker responses in fish exposed to polycyclic aromatic hydrocarbons (PAHs): Systematic review and meta-analysis. *Environmental Pollution, 242*, 449-461.

Saxe, S., Hogue, T. S., & Hay, L. (2018). Characterization and evaluation of controls on postfire streamflow response across western US watersheds. *Hydrology and Earth System Science, 22*, 1221-1237.

Schafer, R. B., Hearn, L., Kefford, B. J., Mueller, J. F., & Nugegoda, D. (2010). Using silicone passive samplers to detect polycyclic aromatic hydrocarbons from wildfires in streams and potential acute effects for invertebrate communities. *Water Research, 44*(15), 4590-4600.

Seebacher, F., & Franklin, C. E. (2012). Determining environmental causes of biological effects: the need for a mechanistic physiological dimension in conservation biology. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*, 1607-1614.

Silins, U., Bladon, K. D., Kelly, E. N., Esch, E., Spence, J. R., Stone, M., . . . Tichkowsky, I. (2014). Five-year legacy of wildfire and salvage logging impacts on nutrient runoff and aquatic plant, invertebrate, and fish productivity. *Ecohydrology, 7*(6), 1508-1523.

Silva, L. G., Doyle, K. E., Duffy, D., Humphries, P., Horta, A., & Baumgartner, L. J. (2020). Mortality events resulting from Australia's catastrophic fires threaten aquatic biota. *Global Change Biology, 26*(10), 5345-5350.

Silva, V., Abrantes, N., Costa, R., Keizer, J. J., Goncalves, F., & Pereira, J. L. (2016). Effects of ash-loaded post-fire runoff on the freshwater clam *Corbicula fluminea*. *Ecological Engineering, 90*, 180-189.

Silva, V., Pereira, J. L., Campos, I., Keizer, J. J., Goncalves, F., & Abrantes, N. (2015). Toxicity assessment of aqueous extracts of ash from forest fires. *Catena, 135*, 401-408.

Smith, H. G., Sheridan, G. J., Lane, P. N. J., Nyman, P., & Haydon, S. (2011). Wildfire effects on water quality in forest catchments: a review with implications for water supply. *Journal of Hydrology, 396*, 170-192.

Soucek, D. J., & Dickinson, A. (2016). Influence of chloride on the chronic toxicity of sodium nitrate to *Ceriodaphnia dubia* and *Hyalella azteca*. *Ecotoxicology, 25*, 1406–1416.

Spencer, C. N., Gabel, K. O., & Hauer, F. R. (2003). Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management, 178*(1), 141-153.

Stoot, L. J., Cairns, N. A., Cull, F., Taylor, J. J., Jeffrey, J. D., Morin, F., . . . Cooke, S. J. (2014). Use of portable blood physiology point-of-care devices for basic and applied research on vertebrates: a review *Conservation Physiology, 2*, cou011.

Sun, C., Zhang, J., Ma, Q., Chen, Y., & Ju, H. (2017). Polycyclic aromatic hydrocarbons (PAHs) in water and sediment from a river basin: sediment-water partitioning, source identification and environmental health risk assessment. *Environ Geochem Health, 39*, 63-74.

Sutherland, A. B., & Meyer, J. L. (2007). Effects of increased suspended sediment on growth rate and gill condition of two southern Appalachian minnows. *Environmental Biology of Fishes, 80*, 389–403.

Teal, L. R., Marras, S., Peck, M. A., & Domenici, P. (2018). Physiology-based modelling approaches to characterize fish habitat suitability: Their usefulness and limitations. *Estuarine, Coastal and Shelf Science, 201*, 56-63.

Tonn, W. M., Paszkowski, C. A., Scrimgeour, G. J., Aku, P. K. M., Lange, M., Prepas, E. E., & Westcott, K. (2003). Effects of forest harvesting and fire on fish assemblages in Boreal Plains lakes: A reference condition approach. *Transactions of the American Fisheries Society, 132*(3), 514-523.

Trego, M. L., Brown, C. A., Dubansky, B., Hess, C. D., Galvez, F., & Whitehead, A. (2021). Transcriptome profiling in conservation physiology and ecotoxicology: mechanistic instights into organism-environment interactions to both test and generate hypotheses. In C. L. Madliger, C. E. Franklin, O. P. Love, & S. J. Cooke (Eds.), *Conservation* *physiology: Applications for wildlife conservation and management*: Oxford University Press.

Vaz, P. G., Merten, E. C., Warren, D. R., Durscher, K., Tapp, M., Robinson, C. T., . . . Pinto, P. (2015). Fire meets inland water via burned wood: And then what? *Freshwater Science, 34*, 1468-1481.

Verkaik, I., Prat, N., Rieradevall, M., Reich, P., & Lake, P. S. (2014). Effects of bushfire on macroinvertebrate communities in south-east Australian streams affected by a megadrought. *Marine and Freshwater Research, 65*, 359-369.

Verkaik, I., Rieradevall, M., Cooper, S. D., Melack, J. M., Dudley, T. L., & Prat, N. (2013). Fire as a disturbance in mediterranean-climate streams. *Hydrobiologia, 719*, 353-382.

Ward, A. J. W., Herbert-Read, J. E., Sumpter, D. J. T., & Krause, J. (2011). Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Acadamy of Science USA, 108*, 2312-2315.

Ward, M., Tulloch, A. I. T., Radford, J. Q., Williams, B. A., Reside, A. E., Macdonals, S. L., . . . Watsin, J. E. M. (2020). Impact of 2019–2020 mega-fires on Australian fauna habitat. *Nature Ecology & Evolution, 4*, 1321–1326

Wells, J. B., Little, E. E., & Calfee, R. D. (2004). Behavioral response of young rainbow trout (*Oncorhynchus mykiss*) to forest fire-retardant chemicals in the laboratory. *Environmental Toxicology and Chemistry, 23*(3), 621-625.

Westerling, A. L., Bryant, B. P., Preisler, H. K., Holmes, T. P., Hidalgo, H. G., Das, T., & Shrestha, S. R. (2011). Climate change and growth scenarios for California wildfire. *Climate Change, 109*, 445-463.

WHO. (2003). *Polynuclear aromatic hydrocarbons in Drinking-water*. Geneva, Switzerland: World Health Organization.

Williams-Subiza, E., & Brand, C. (2021). Functional response of benthic macroinvertebrates to fire disturbance in patagonian streams. *Hydrobiologia, 848*, 1575-1591.

Woltemade, C. J., & Hawkins, T. W. (2016). Stream temperature impacts because of changes in air temperature, land cover and stream discharge: Navarro River Watershed, California, USA. *River Research and Applications, 32*, 2020-2031.

Wuenschel, M. J., McElroy, W. D., Oliveira, K., & McBride, R. S. (2018). Measuring fish condition: an evaluation of new and old metrics for three species with contrasting life histories. *Canadian Journal of Fisheries and Aquatic Sciences, 2018*, 0076.

Figure legends

Figure 1. Concept map of the impacts of fire on aquatic animals. Fire and runoff can have immediate impacts (top panel) on aquatic animals. Fire and runoff events can also have short-, mid- and long-term impacts on aquatic animals (bottom panel). Connections are drawn between relevant concepts, though for simplicity not all connections were made.

Figure 2. Literature summary of the effects of wildfire on aquatic animals. (a) Number of studies published per year and cumulative number of studies. We summarised data in terms of (b) field of research, (c) duration of study, (d) number of *in situ* versus laboratory studies, and (e) taxonomic group examined.

Figure 3. Thematic map of the most frequently used keywords appearing in selected papers. Map was generated using the *bibliometrix* package (Aria and Cuccurullo, 2017) in RStudio.

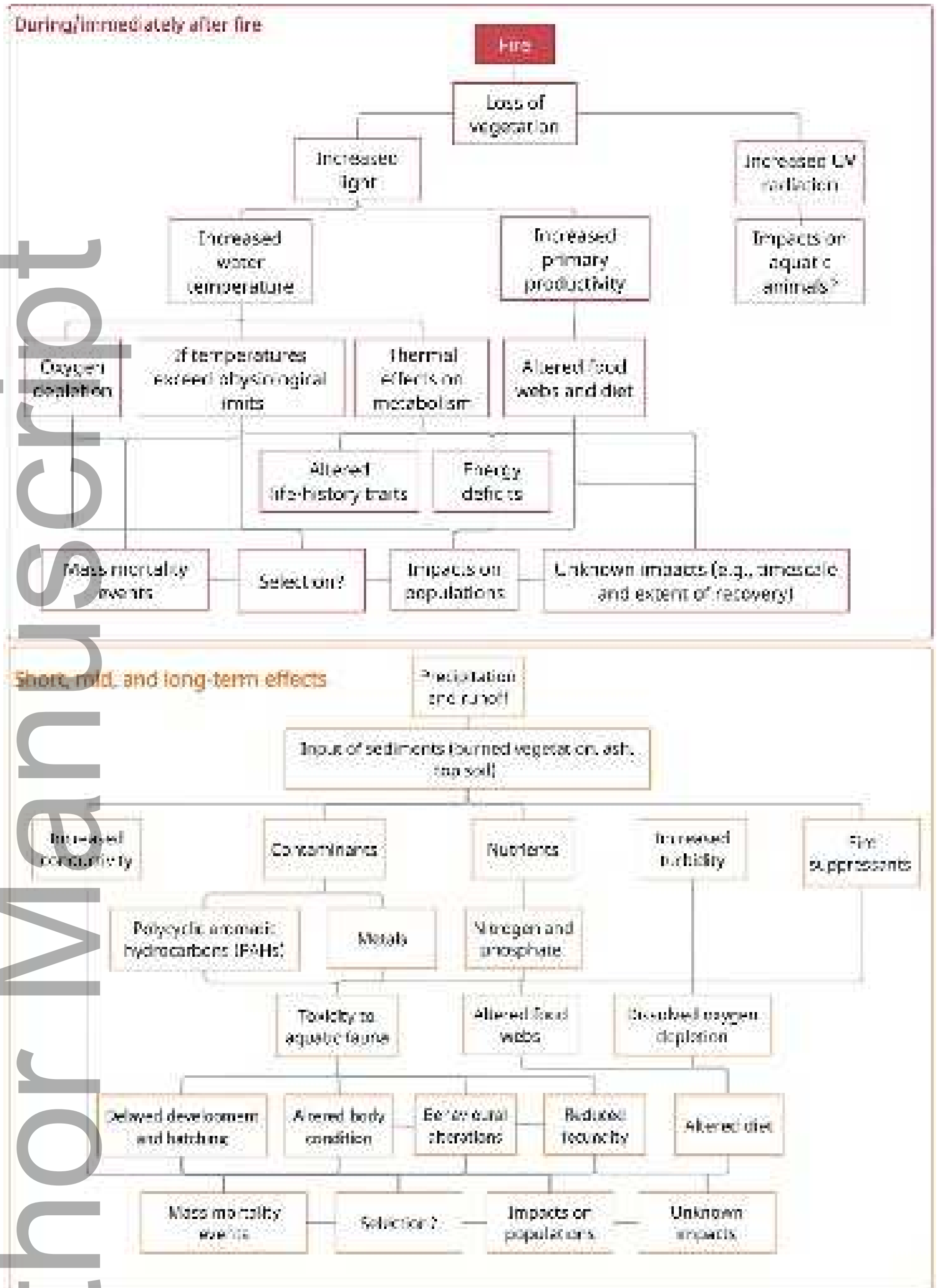
Figure 4. Unburnt (a) and burnt (b) streams within the Los Alerces National Park (Patagonia, Argentina). Image credit: Emilio A. Williams-Subiza.

1265 **Table 1.** Main wildfire impacts on aquatic animals and examples of physiological tools that may aid conservation efforts.

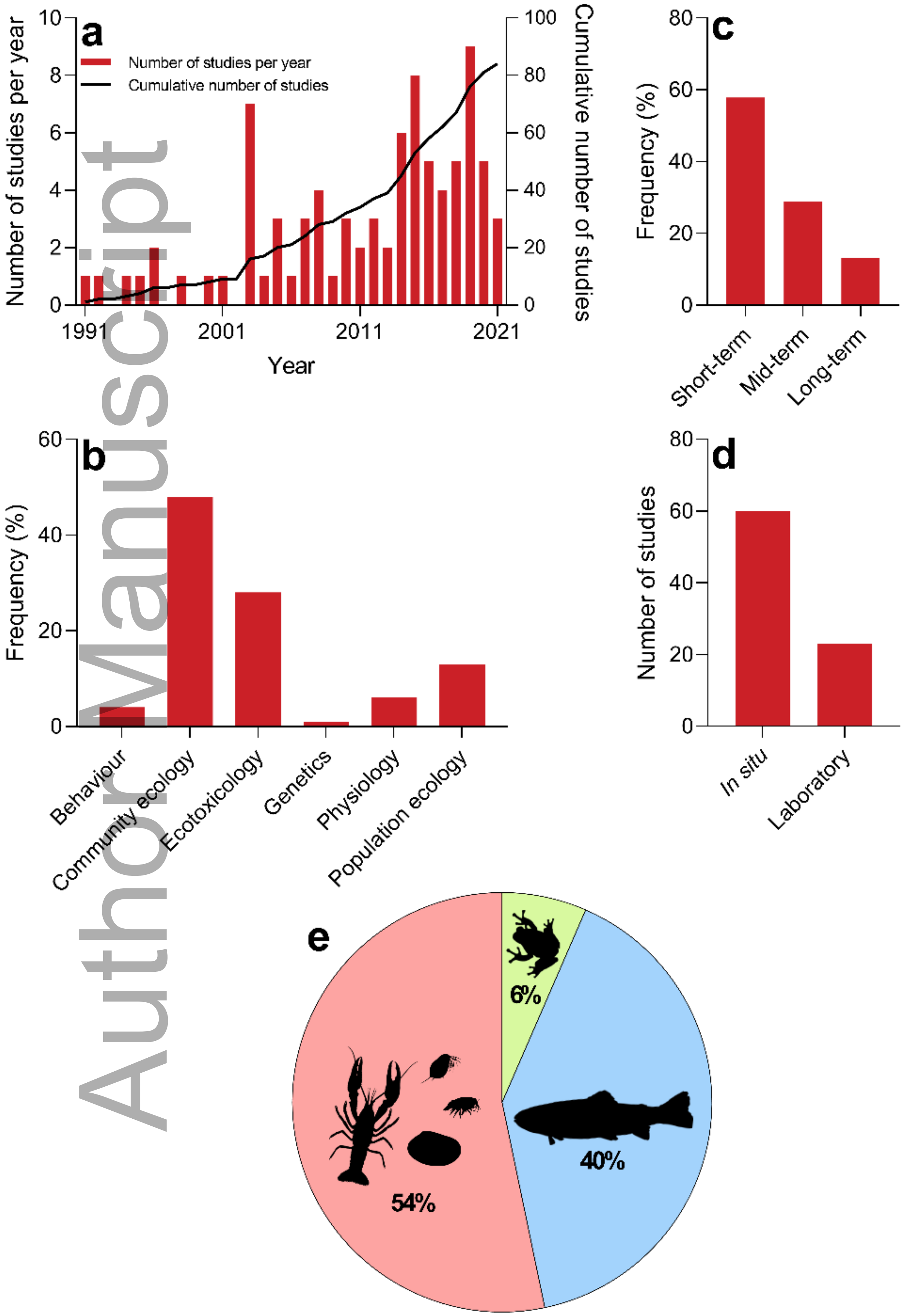
Threats/challenges post wildfire	Physiological tool	Contribution to conservation
Increased light/UV	• Physiological status (e.g., metabolic physiology, exercise physiology, behaviour, immune function) • Vital rates (growth, reproduction, survival)	• Determine extent of UV damage/impairment on physiological status • Determine impacts of light and UV on vital rates- pivotal for population persistence
Increased temperature	• Thermal tolerance (CT_{MAX}) • Thermal performance curves (e.g., locomotor performance) • Cardiovascular physiology (e.g., aerobic scope, heart rate, blood chemistry) • Life-history traits (e.g., time to maturity, size at maturity, fecundity • Biologging	• Delineate thermal limits across life-stages/populations/species for regulatory guidelines • Examine how various wildfire ash components and indirect effects (e.g., low oxygen levels) alter thermal limits • Impact of altered thermal regimes on bioenergetic costs and life-history traits (timing of maturity, size at reproduction, etc.) • Impact of altered thermal regimes on physiological status and performances • Examination of thermal plasticity (reversible, developmental, and transgenerational) • Biologging to allow long-term monitoring of species performance and physiological status under field conditions

Post-fire ash runoff (nutrients, PAHs, metals etc.)	• Pollutant accumulation in various tissues • Histopathology damage • Body condition indices (e.g., liver, spleen) • Physiological status • Stable isotopes (dietary changes) • Transcriptome profiling • Dynamic energy budget (DEB) models	• Determining regulatory guidelines for chemicals and chemical combinations • Identify detoxification cost through body condition estimates • Identify causal mechanism/s behind population decline • Determining extent and timescale to recovery from wildfire ash exposure • Stable isotope can reveal changes in diet/trophic structure and the timescale to recovery of altered systems • Gene transcription can link stressor-specific molecular initiating events and emergent physiological responses that alter fitness • Illuminate molecular mechanisms that propagate stressor exposure to states of distress (Trego et al., 2021) • DEB models link physiology with impacts on fitness and population resilience

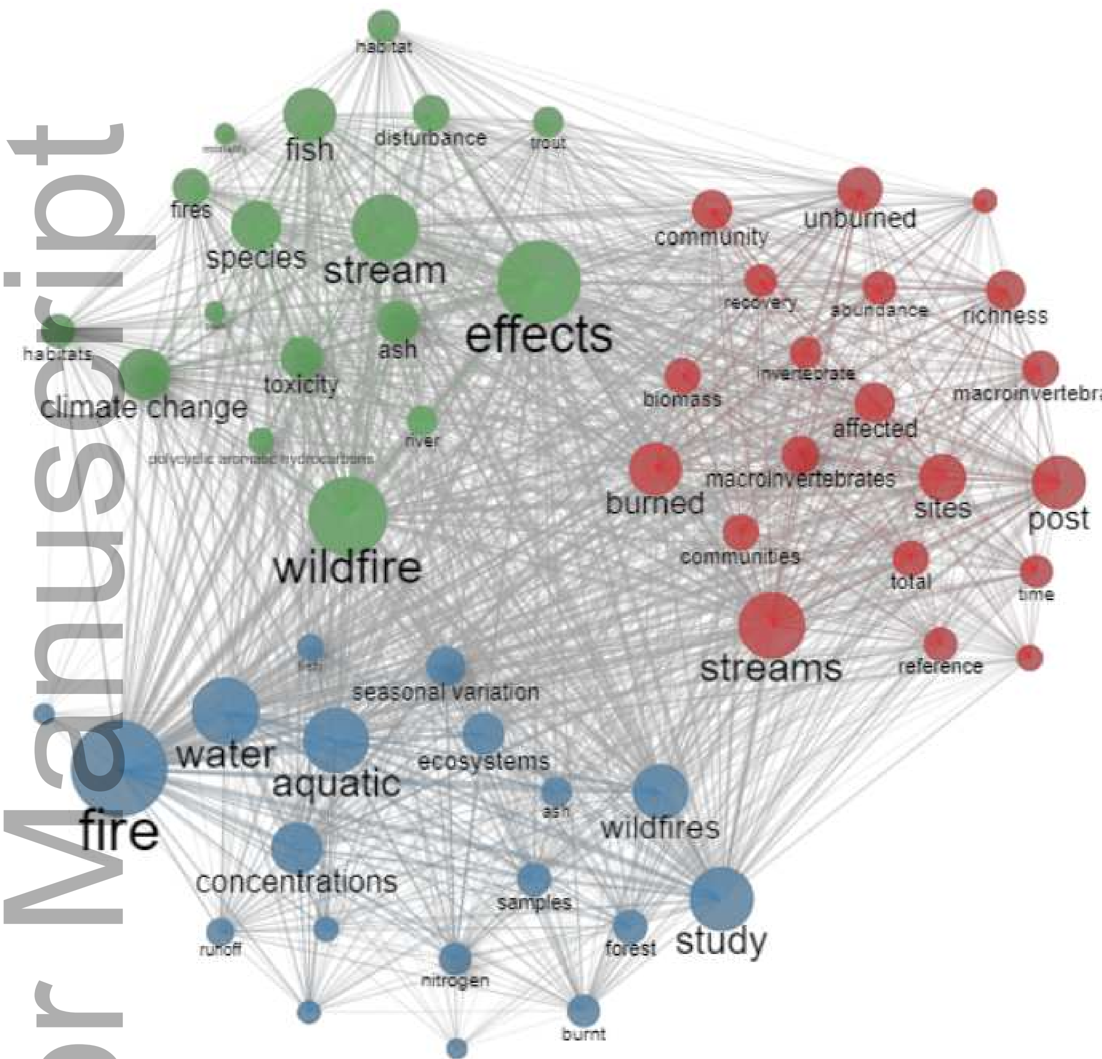
1266



gcb_16088_f1.tif



gcb_16088_f2.tif



gcb_16088_f3.tif

gcb_16088_f4.tif