

REVIEW

Fire impacts on the biology of stream ecosystems: A synthesis of current knowledge to guide future research and integrated fire management

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Abstract

Freshwater ecosystems host disproportionately high biodiversity and provide unique ecosystem services, yet they are being degraded at an alarming rate. Fires, which are becoming increasingly frequent and intense due to global change, can affect these ecosystems in many ways, but this relationship is not fully understood. We conducted a systematic review to characterize the literature on the effects of fires on stream ecosystems and found that (1) abiotic indicators were more commonly investigated than biotic ones, (2) most previous research was conducted in North America and in the temperate evergreen forest biome, (3) following a control-impact (CI) or before-after (BA) design, (4) predominantly assessing wildfires as opposed to prescribed fires, (5) in small headwater streams, and (6) with a focus on structural and not functional biological indicators. After quantitatively analyzing previous research, we detected great variability in responses, with increases, decreases, and no changes being reported for most indicators (e.g., macroinvertebrate richness, fish density, algal biomass, and leaf decomposition). We shed light on these seemingly contradicting results by showing that the presence of extreme hydrological post-fire events, the time lag between fire and sampling, and whether the riparian forest burned or not influenced the outcome of previous research. Results suggest that although wildfires and the following hydrological events can have dramatic impacts in the short term, most biological endpoints recover within 5–10 years, and that detrimental effects are minimal in the case of prescribed fires. We also detected that no effects were more often reported by BACI studies than by CI or BA studies, raising the question of whether this research field may be biased by the inherent limitations of CI and BA designs. Finally, we make recommendations to help advance this field of research and guide future integrated fire management that includes the protection of freshwater ecosystems.

KEYWORDS

biodiversity, fish, invertebrate, leaf decomposition, prescribed burn, riparian, river, wildfire

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1 | INTRODUCTION

Freshwater ecosystems and their associated riparian habitats harbor disproportionately high biodiversity and provide irreplaceable services for nature and society, yet they are experiencing a level of degradation and biodiversity loss even higher than terrestrial ecosystems (Albert et al., 2021; Carpenter et al., 2011; Dodds et al., 2013; Dudgeon et al., 2006). Global change is predicted to cause dramatic increases in wildfire potential across the globe (Liu et al., 2010) and to shift fire regimes by changing fuels, ignitions, and fire weather (Kelly et al., 2020), potentially affecting freshwater systems. Climate change but also land use changes are altering fire regimes, with fire becoming more common in regions where it used to be rare or absent (e.g., tropical forests undergoing deforestation), larger and more severe in fire-prone ecosystems such as boreal or Mediterranean forests, or reduced/absent in fire-dependent grassland and savanna ecosystems (Kelly et al., 2020). Thus, these and other emerging changes in the fire regime pose a global challenge for understanding how to sustain biodiversity and the provision of aquatic ecosystem services in the Pyrocene.

Although the impacts of fire on freshwater ecosystems receive much less attention than terrestrial ecosystems, aquatic systems are also influenced by this catchment disturbance (Bixby et al., 2015). Wildfires commonly increase overland water flow due to reduced infiltration, evapotranspiration, and interception, which in turn increases erosion and the frequency of debris and sediment flows in streams (Paul et al., 2022). These flows can cause direct mortality of stream fauna or indirect effects by generating stream channel and riparian reorganizations that profoundly alter habitat and food availability and quality as well as food web dynamics (Jones et al., 2012; Paul et al., 2022). Post-fire sediment and ash inputs to streams can also increase the transport of pollutants such as metals and polycyclic aromatic hydrocarbons (PAHs) known for their toxic, mutagenic, and carcinogenic properties (Abraham et al., 2017; Kieta et al., 2023; Raelison et al., 2023). Nutrient mobilization after fire can contribute to downstream eutrophication and harmful algal blooms, adversely affecting drinking water quality, recreational uses, and wildlife (Morales et al., 2023; Raelison et al., 2023). Increases in light availability and water temperature resulting from burned riparian vegetation can also alter stream processes such as primary production and respiration as well as the distribution of species such as cold-water salmonids (Bixby et al., 2015; Gresswell, 1999; Paul et al., 2022). Also, fire-related changes in the input and characteristics of terrestrial organic matter such as wood or leaf litter can have structural and functional implications for stream ecosystems (Musetta-Lambert et al., 2017; Vaz et al., 2015).

Several review articles summarized the effects of fire on aquatic systems, but most focused on abiotic components—namely water quality (e.g., Abraham et al., 2017; Kieta et al., 2023; Morales et al., 2023; Raelison et al., 2023; Smith et al., 2011).

However, fires can also influence freshwater biodiversity and the many processes it regulates, with clear implications for the delivery of ecosystem services such as water purification (e.g., aquatic biota filtrates excessive nutrients and pollutants), food provision (e.g., fish, amphibians, reptiles, mollusks, crustaceans, and other aquatic invertebrates are a critical source of protein, essential fatty acids and micronutrients for many people) and recreation (e.g., angling, wildlife watching and photography, swimming or boating are reliant on good water quality which is directly related to aquatic biodiversity and processes) (Lynch et al., 2023). The reviews including biotic endpoints provided a valuable overview of the research conducted to date, but some important gaps remain which our review aims to fill. While some reviews are over 20 years old and miss the most recent research, others have a limited geographic scope and most lack a quantitative analysis of the responses reported by previous studies (e.g., Gomez Isaza et al., 2022; Gresswell, 1999; Minshall, 2003; Verkaik et al., 2013). In addition, prescribed fires and functional indicators tend to be overlooked with the focus being on wildfires and structural biotic indicators. This provides an incomplete picture of overall ecological integrity as stream ecosystem structure and function can respond differently to disturbance (Feckler & Bundschuh, 2020; Sandin & Solimini, 2009). Regarding prescribed fire, there is growing support for its use to restore fire-dependent processes, ecosystems, and species, and as a management tool to prevent large, severe wildfires (Fernandes et al., 2013; Ryan et al., 2013). However, the ecological effects of prescribed fires on stream and riparian ecosystems remain largely unknown (Bixby et al., 2015; Klimas et al., 2020; Paul et al., 2022). Finally, none of the reviews analytically assessed the factors that may influence the directionality of stream responses (e.g., the presence of debris flows post-fire) nor the robustness of the sampling design used to measure the effects of fire. Because some designs (e.g., before-after and control-impact) are much more prone to biases than others (e.g., before-after-control-impact or BACI) (Christie et al., 2020), it is important to examine how this aspect may influence our understanding. This is because, without a control, before-after fire differences can simply reflect environmental variability over time, while without before data, unburned-burned differences can simply reflect pre-existing differences between groups (Christie et al., 2020).

In this review, we build upon the previous research by quantitatively analyzing the effects of prescribed wildfires on a suite of structural and functional biological stream responses. Specifically, the objectives of this review are to: (1) contextualize and characterize the literature about the fire effects on biological endpoints compared to abiotic endpoints in terms of year of publication, geographic location, study design, type of fire (prescribed or wildfire), indicators measured and duration of the effects, (2) quantitatively summarize the responses of different biological endpoints (namely benthic invertebrates, fish, periphyton and functional indicators) to fire, (3) model the factors that influence the directionality of the

responses, and (4) detect limitations and knowledge gaps to help guide future studies and make recommendations.

2 | METHODS

2.1 | Data source and collection

We systematically searched the studies assessing the effects of fire on stream ecosystems following PRISMA guidelines (O'Dea et al., 2021) and using the Scopus online database (Scopus, 2023) on August 14, 2023. The exact search string was as follows: TITLE (wildfire OR burn OR fire) AND TITLE (water OR stream OR river OR aquatic OR riparian) AND TITLE-ABS-KEY (invertebrate OR fish

OR periphyton OR biofilm OR nutrient OR chemistry OR sediment OR breakdown OR decomposition OR amphibian OR spider OR macrophyte). This search returned 490 studies. After removing four duplicates, the titles and abstracts were screened using the Rayyan software (Ouzzani et al., 2016) and pre-defined inclusion/exclusion criteria (Figure 1). Our review focused on studies measuring the effect of fire (both wildfire and prescribed fire) on stream/river ecosystems. Thus, we excluded articles (1) from other environments (e.g., wetlands, ocean, ponds, forest soils, groundwater, runoff), (2) that did not measure the direct effect of fire (e.g., ash or fire suppressant effects), (3) that did not conduct in-situ measurements (e.g., modeling or simulations, lab or mesocosm experiments, and review articles), or (4) that measured the effect of fire in a different context (e.g., paleoecology, medicine, and firefighting). We read the full text

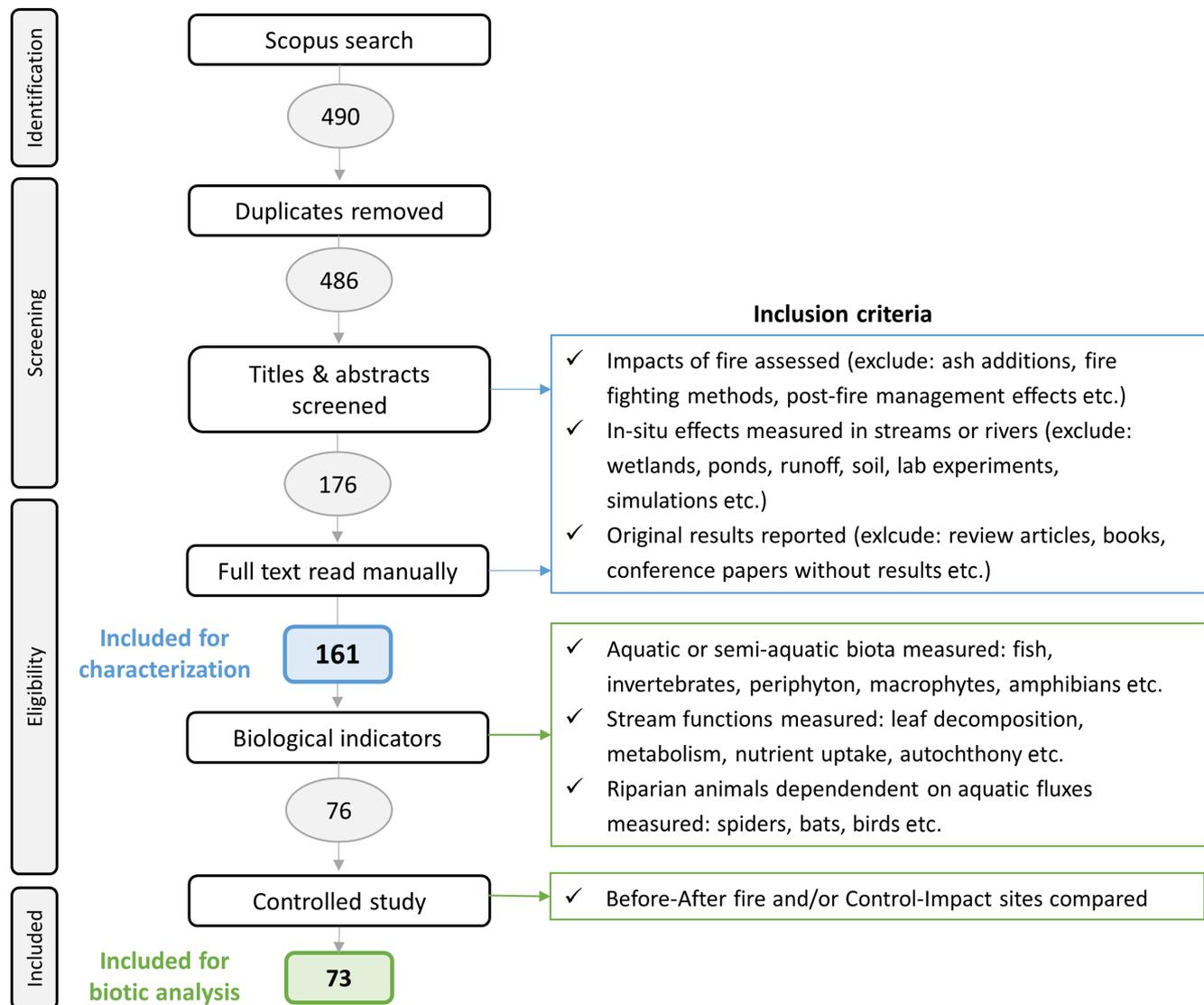


FIGURE 1 PRISMA diagram (O'Dea et al., 2021) showing the systematic search for literature on the impacts of fire on stream ecosystems as well as the pre-defined decision tree and the criteria for the inclusion/exclusion of studies. Numbers indicate the number of studies that met the criteria in each step. In blue are the studies that were used to address the first objective (i.e., to contextualize and characterize the literature on biological endpoints compared to abiotic endpoints), and in green the second and third objectives (i.e., to quantitatively summarize the responses of different biological endpoints to fire and to model the factors that influence the directionality of the responses).

of the 176 papers that this process returned to confirm that they met the aforementioned criteria, which reduced the number of selected papers to 161.

The selected papers were used to characterize the research conducted to date on the impacts of fire on stream ecosystems (first objective) by extracting the following information: (1) year of the publication, (2) country and biome where the study was conducted, (3) main land cover and land use of the catchment, (4) category (abiotic vs. biotic) and stream parameters measured (see Figure 2a), (5) stream size and slope, (6) type of fire (prescribed or wildfire) and fire regime attributes, (7) time lag between the fire and sampling, and (8) study design in terms of statistical design (after, before-after (BA), control-impact (CI), and BACI) and sampling unit (a point along the stream, a longitudinal stream reach, or watershed scale—samples taken from upstream to downstream sections of a basin). When more than one stream parameter or indicator was measured in the same study, each parameter was treated as a separate case. All these aspects were selected because they can either modulate the effect of fire on aquatic ecosystems and/or our ability to detect such effects. Therefore, their characterization is important to understand how well accounted for are in the literature and to detect potential knowledge gaps that guide future studies.

To address the second and third objectives, the selection of papers was further narrowed down by applying new selection criteria (Figure 1). Only the articles that measured at least one biotic stream parameter (85 papers that exclusively considered abiotic articles were excluded) and compared burned conditions to unburned control conditions (three articles that only described post-fire conditions were excluded) were selected. These 73 studies were further characterized by extracting the following information: (1) the response of the stream parameter to fire (significant increase, significant decrease, or non-significant differences, $\alpha=0.10$), (2) the presence/absence of an extreme hydrological event within the first year post-fire (e.g., 100-year recurrence interval floods, sediment or debris flows), and (3) whether the riparian forest was burned or remained mostly intact. When a study reported more than one response to fire for one parameter (e.g., an increase in the parameter 1 year post-fire but a decrease 10 years post-fire), each particular response was treated as a separate case.

2.2 | Data analysis

First, we calculated the percentage of observations for each stream parameter based on their response to fire (increase, decrease, or

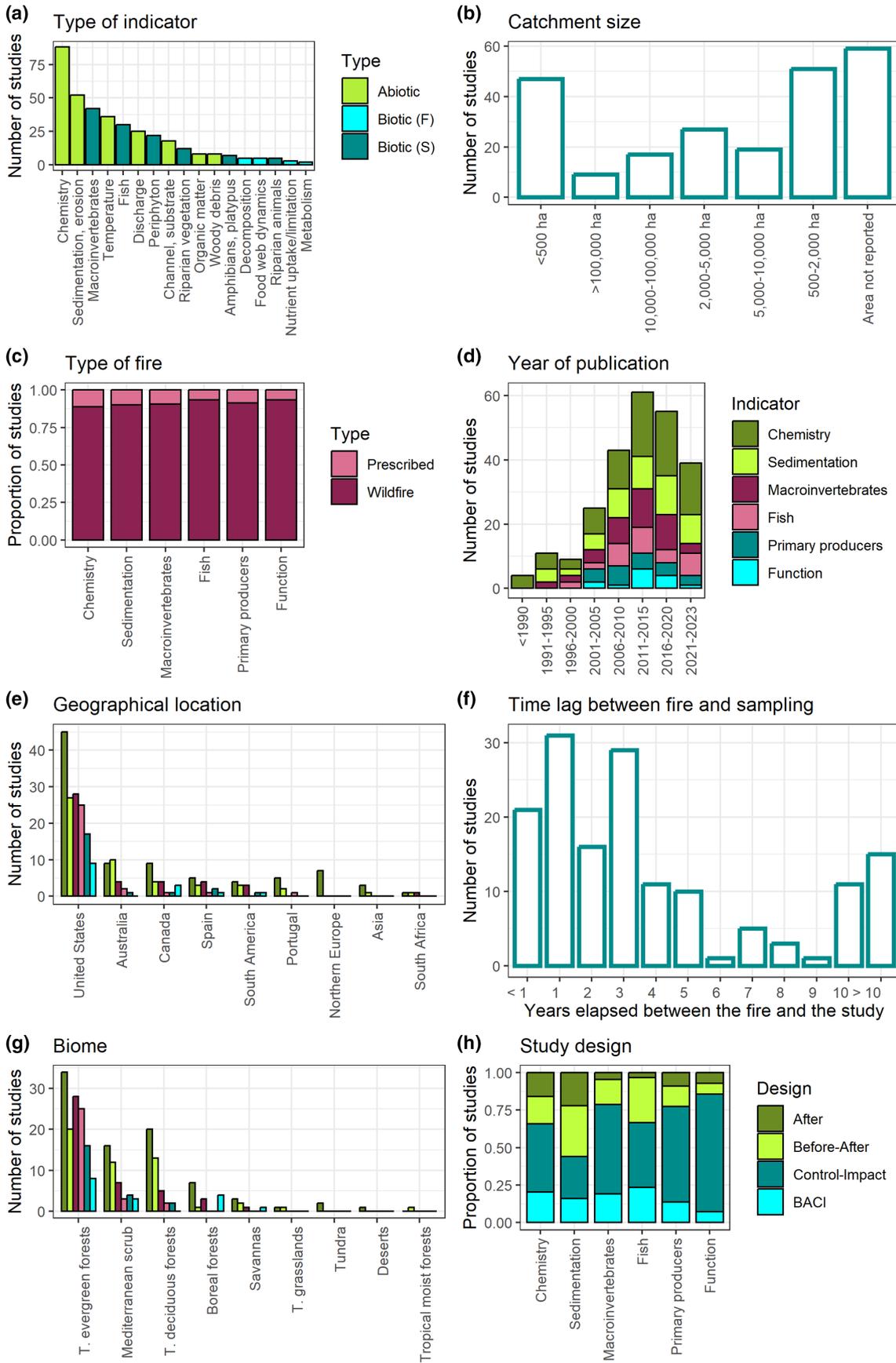
no difference) using all records from the database previously created. The results that were not supported by any statistical analysis were excluded from this summary. Then, to understand what factors could be driving the different responses of a given stream indicator to fire, we analyzed the relationship between the reported response and several binary or numerical explanatory variables: (1) presence of an extreme hydrological event within 1 year post-fire (yes/no), (2) time lag between the fire and the sampling (months in a logarithmic scale), (3) type of fire (wildfire/prescribed), and (4) status of the riparian forest (burned/unburned). This was done by building ordinal logistic regression models with a logit link function in the case of response variables with three outcomes (decrease, no change, and increase) (*clm* function of the *ordinal* package, Christensen, 2022) and logistic regressions with a logit link function based on binomially distributed data for response variables with two outcomes (e.g., differences in community composition yes/no) (*glm* function in R). The significance of the effect of each explanatory variable was assessed based on ANOVA tests and the effects were visualized using boxplots. Note that fire regime attributes were not included as explanatory variables due to the lack of reporting consistency across studies (see Section 3.1 for further details). All statistical analyses were performed in R 3.6.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Literature characterization

Abiotic endpoints were the most commonly investigated stream endpoints in the studies identified by our search (Figure 2a), with 85% versus 51% of the 161 studies measuring abiotic and biotic indicators, respectively. More than half of the studies measured water chemistry (54.7%), one-third of the studies reported sedimentation and erosion-related variables (32.3%), and almost one-quarter of the studies measured water temperature (22.4%). Regarding biotic variables, benthic macroinvertebrates (BMI) were the most commonly studied component of the food web (26.1% of the studies), followed by fish (18.6%) and algae or periphyton (13.7%). Other fauna including amphibians, spiders, emerging insects, bats, and the platypus were less studied (7, 5, 3, 1, and 1 studies, respectively). Riparian vegetation was considered in 7.5% of the studies, while woody debris and standing organic matter were measured by eight studies each (5.0%). Finally, functional stream indicators were less commonly studied than structural ones and included leaf decomposition,

FIGURE 2 Summary of the literature examining the effects of fire on stream ecosystems in terms of (a) abiotic and biotic (structural—S and functional—F) components of the ecosystem assessed, (b) the drainage area (in hectares) of the streams examined in each study, (c) the type of fire, (d) the number of studies measuring a given indicator published every 5 years, (e) the country and (g) biome in which the study of different indicators (see d for color-coding) was conducted, (f) the time elapsed between the fire and the study (i.e., whether short-term versus long-term effects are assessed), and (h) the proportion of studies following a given study design for each indicator. Note that in panels (a, d, e, and g) one study can be computed more than once if it measured more than one indicator; in panel (b), one study can be computed more than once if streams with different catchment size classes were examined.



food web dynamics, nutrient uptake or limitation, and stream metabolism (1.2%–3.1% of the studies).

The number of studies that matched our criteria increased from 1.2 per year during the decade of the 90s, to 3.8 in the 2000s, 6.7 in the 2010s, and 9.5 in the 2020s. The first studies tended to focus on abiotic indicators, but it was not until the 90s that we found the first studies examining the effects of wildfire on biotic endpoints (macroinvertebrates and fish) (Figure 2d). The effects of fire on periphyton and functional stream endpoints started to be studied more recently, namely from the 2000s and 2010s onwards, respectively.

Regarding the geographical location, 89% of the studies were conducted in five countries, with the United States (and especially western states) producing most of the studies (62%) followed by Australia (10%), Canada (8%), Portugal (4%), and Spain (4%). The remaining studies were conducted in northern Europe (7), Asia (6), South America (5), and South Africa (2). The distribution of the different types of indicators varied across regions (Figure 2e). None of the biological indicators were examined in the reviewed studies in northern Europe and Asia, functional indicators were missing in Portugal and Australia, macroinvertebrates in Portugal, and fish in South America.

More than half of the studies were conducted in the temperate evergreen forest biome followed by the temperate deciduous forest (18.6%), mediterranean scrub (16.1%), and savanna (2.5%). Temperate grassland, tundra, tropical moist forest, and desert biomes were examined by few studies (2, 2, 1, and 1, respectively) and only for abiotic endpoints (Figure 2g). Studies conducted on the temperate deciduous forest did not include functional endpoints, whereas the studies on boreal forest and savanna biomes did not consider fish or aquatic primary producers. Forest was the most common land cover in these studies, with 78.3% of the studies reporting this land cover in their catchments and with both protected forests (e.g., national parks, wilderness areas, and national forests) and forests managed for timber being well represented. Shrubland and grassland land covers were reported in the catchments of 20.5% and 18.0% of the studies, while agricultural and urban land uses were only reported in 13.7% and 9.9% of the studies.

Regarding fire type, the majority of the studies (93%) assessed the effects of wildfires on stream ecosystems, 6% of the studies dealt with prescribed burns, and only 1% of the studies compared both. The type of fire studied did not vary much across indicators (Figure 2c), with studies assessing the effect of prescribed fire ranging from 7% in the case of fish and functional indicators to 11% in the case of water chemistry-related indicators. In terms of the time lag between the fire and the sampling, 32% of the studies measured the short-term (1 year or less since fire) effects of fires, 35% measured the effects 2–4 years after the fire and 28% of the studies analyzed longer-term effects (5 or more than 5 years since fire), with 9% of the latter studies measuring the effects more than 10 years after the fire (Figure 2f).

Overall, fire regime was poorly documented in the reviewed articles. The proportion of the catchment burned, fire severity, and

fire intensity were the three attributes that were most commonly reported (61.5%, 50.3%, and 7.4% of the studies, respectively). Fires burning most of the catchment were the most represented ones in the literature (62% of the studies reporting this attribute examined streams with more than 75% of the catchment burned), but lower burned extents were also well represented (e.g., 30% of the studies included streams with less than 50% of the catchment burned). Regarding severity, there was considerable heterogeneity and ambiguity in the way this attribute was reported. More than half of the articles reporting severity used qualitative sentences such as “watershed X burned at medium to high severity” or “most of our study sites experienced low to moderate severity burns” while others reported the proportion of the catchment that burned at high, moderate, or low severity. Even then, some studies based the assessment on soil burn severity, others on the mortality of the vegetation and others did not specify what the severity was referring to. The quantitative intensity of the fire (kilowatts per meter) was more commonly reported for prescribed burns (16.7% of the studies) than for wildfires (1.3%). Although, overall, fire behavior (e.g., intensity, flame height, and rate of spread) and effects (severity) were better characterized in studies assessing prescribed burns than wildfires, still 75% of the prescribed fire studies did not report fire regime or did it in a qualitative way.

Regarding the study design, 43% of the studies analyzed differences between burned and unburned watersheds (CI studies), 25% of the studies compared sites before and after the fire (BA studies), and 16% of the studies only assessed trends of burned sites after the fire (AI studies). Only 17% of the studies followed a complete BACI design and could determine whether the differences between burned and control sites differed before and after the fire (i.e., whether differences were indeed attributable to the effect of fire or not). The relative proportion of each type of design varied with the stream indicator studied (Figure 2h). The share of “after” studies was greatest in sedimentation studies (22%) and lowest in fish studies (3%), whereas the proportion of BACI studies was greatest in fish studies (23%) and lowest in functional studies (7%); the proportion of CI studies in turn was greatest in functional studies (79%) and lowest in sedimentation studies (28%).

The size of the fluvial systems under examination was the most reported aquatic attribute, either as drainage catchment area or Strahler stream order (63% and 45% of the studies, respectively). Most studies focused on small headwater streams (Figure 2b), with half of the studies that reported drainage area only examining streams draining an area smaller than 2000 ha, and headwater streams belonging to first, second, or third stream orders being examined in 87.5% of the studies reporting stream order. Larger streams and rivers were not as well represented in the reviewed studies, with only nine of them focusing on streams draining 50–1000 km² and five on rivers draining >1000 km². Regarding the range of stream sizes examined within a single study, most studies (52.0%) focused on only one size class or two (25.5%). However, several studies assessed a wide range of stream sizes (i.e., including headwaters, middle-sized streams, and larger rivers), with 10%

and 5% of the studies including streams from four and five different size classes, respectively. Stream channel slope was only reported in 35.4% of the studies, with 75.4% of these studies sampling streams with gradients below 5%, almost half of the studies including channels with gradients between 5% and 10%, 28% of the studies reporting gradients between 11% and 15%, and 17.5% of the studies examining streams with slopes >15%. Finally, the sampling unit was a point along a stream, a stream reach (mean length = 580m, median length = 100m, mode = 50m), or a watershed in 43.5%, 40.4%, and 13.7% of the studies, respectively.

3.2 | Analysis of biotic indicators

3.2.1 | Benthic stream macroinvertebrates

Approximately one-third (34%) of the studies reported a decrease in macroinvertebrate abundance due to fire, 28% of the studies an increase, and 38% of the studies did not detect any significant effect. Note also that five out of six BACI studies did not detect significant effects (Table 1). When including the studies that examined macroinvertebrates in leaf packs, the proportion of studies reporting no significant effects increased to 45%. Several characteristics of the studies seemed to influence the outcome. Time since fire was significantly related to the type of outcome ($\chi^2 = 6.8$, $p = .009$), showing that the greater the time lag between the fire and the study, the less likely it became to detect a decrease in macroinvertebrate abundance. The presence of extreme post-fire hydrological events was also significantly related to the reporting of negative effects on abundance ($\chi^2 = 8.6$, $p = .003$) (Figure 3b). Finally, although the model did not consider significant the effect of fire type, it is noteworthy that all four studies measuring the effects of prescribed fires did not detect any effects on macroinvertebrate abundance (Figure 3b).

Regarding macroinvertebrate richness, the majority (58%) of studies did not detect any fire effect, 37% of the studies reported a decrease and 5% an increase (Table 1). As it was the case with abundance, a decrease in richness was more commonly reported by studies examining shorter-term effects ($\chi^2 = 3.5$, $p = .05$) and fires that were followed by extreme hydrological events ($\chi^2 = 4.3$, $p = .03$) (Figure 3a). All 3 studies assessing the effects of prescribed fire did not detect any effect on richness. It is also noteworthy that no effects were more commonly reported by BACI studies than by other study designs.

Over two thirds (70%) of the studies reported significant differences in macroinvertebrate community composition based on NMDS ordination (Table 1). The most common change was an increase in the relative abundance of Chironomidae and/or a decrease in the proportion of Ephemeroptera-Plecoptera-Trichoptera-%EPT-families (i.e., pollution sensitive taxa), with 69% of the studies reporting such a shift in composition (Table 1). Time since fire, extreme hydrological events or fire type were not significantly related to the outcome of the studies (Figure 3c,d).

Regarding the relative abundance of functional feeding groups (FFGs), over half of the studies reported a negative effect of fire on shredder and scraper relative abundance and an increase in % collector-gatherers (Table 1). Around a third of the studies did not detect an effect of fire on the proportion of these FFGs. Only studies assessing wildfire effects examined FFGs and no time since fire nor extreme hydrological events after fire seemed to influence the outcome.

Finally, two studies found a greater emergence of adult aquatic insects in burned streams without extreme hydrological events compared to unburned streams, whereas two other studies with extreme hydrological events post-fire detected a decrease in emergence (significant in only one study) as well as shifts in the timing (Table 1).

3.2.2 | Fish

Sixty-two percent of the studied cases detected a decrease in the density of fish due to fire (two-third of these cases followed a BA design) (Table 1). Most of the remaining cases (36%) did not detect an effect of fire on fish, with only one study reporting an increase in fish density. The negative effects of fire on fish density were significantly likelier when extreme hydrological events followed the fires ($\chi^2 = 4.5$, $p = .03$) (Figure 4a). In addition, time since fire had a positive influence, with negative effects becoming less likely as time since fire increased ($\chi^2 = 4.6$, $p = .03$). The two studies that looked at prescribed fire did not detect effects on fish density.

Regarding condition indicators, fish in impacted sites, especially if reorganized due to flooding or debris flows, tended to be longer in size as shown by all six studies that reported this indicator (Table 1). However, the condition factor was either lower after fire ($n = 1$) or comparable in control and impact sites ($n = 2$) or before and after the fire ($n = 1$).

3.2.3 | Aquatic primary producers

More than half of the studied cases (61%) that measured algal biomass (using chlorophyll *a* concentration as a proxy) did not detect any differences in algal biomass (almost all of those followed a CI design), while 26% reported an increase as a result of fire and 13% a decrease (Table 1). All the studies examined the effects of wildfire and none of them the effects of prescribed fire. While time since fire and hydrological events were not significantly related to the results of these studies, whether the riparian forest was burned or intact was significantly related to the direction of the results (Figure 4b). An increase in chlorophyll *a* was more common in cases where the riparian forest got burned ($\chi^2 = 4.0$, $p = .04$).

Regarding biofilm biomass (measured and reported as ash-free dry mass), in 67% of the cases, fire did not affect it, while in 20% of the cases, an increase was reported, and in 13% a decrease (Table 1). A decrease was more often reported by short-term studies and as time since fire increased, an increase in biofilm biomass was likelier

TABLE 1 The number of cases that report increases, decreases, or no changes after fire in a suite of biological stream parameters reported by the 73 publications included in this review.

	Macroinvertebrates							Fish	
	Abundance	Richness	Community	Chironomidae vs. EPT	% shredder	% collector-gatherer	% scraper	Density	Size
Decrease	10 (34%)	7 (37%)	14 (70%) ^a	11 (%69) ^b	4 (50%)	0	4 (67%)	23 (62%)	0
Before > after	3	1	1	2	0	0	0	15	0
Control > Impact	6	5	8	7	2	0	2	6	0
BACI negative	1	1	4	2	2	0	2	2	0
Increase	8 (28%)	1 (5%)	-	-	1 (12%)	4 (57%)	0	1 (3%)	6 (100%)
Before < After	0	0	-	-	0	0	0	0	1
Control < Impact	8	1	-	-	1	2	0	0	4
BACI positive	0	0	-	-	0	2	0	1	1
No effect	11 (38%)	11 (58%)	6 (30%)	5 (31%)	3 (38%)	3 (43%)	2 (33%)	13 (35%)	0
Before = After	2	0	1	0	0	0	0	5	0
Control = Impact	4	4	1	3	2	2	1	2	0
BACI no effect	5	7	4	2	1	1	1	6	0
Total	29	19	20	16	8	7	6	37	6

^aChanges in community composition. If yes, it is shown under row “Decrease,” if not under row “no effect.”

^bIncrease in Chironomidae and/or decrease in EPT (Ephemeroptera-Plecoptera-Trichoptera). If yes, it is shown under row “Decrease,” if not under row “no effect.”

^cTwo of the studies did not run stable isotope mixing models to quantify autochthony.

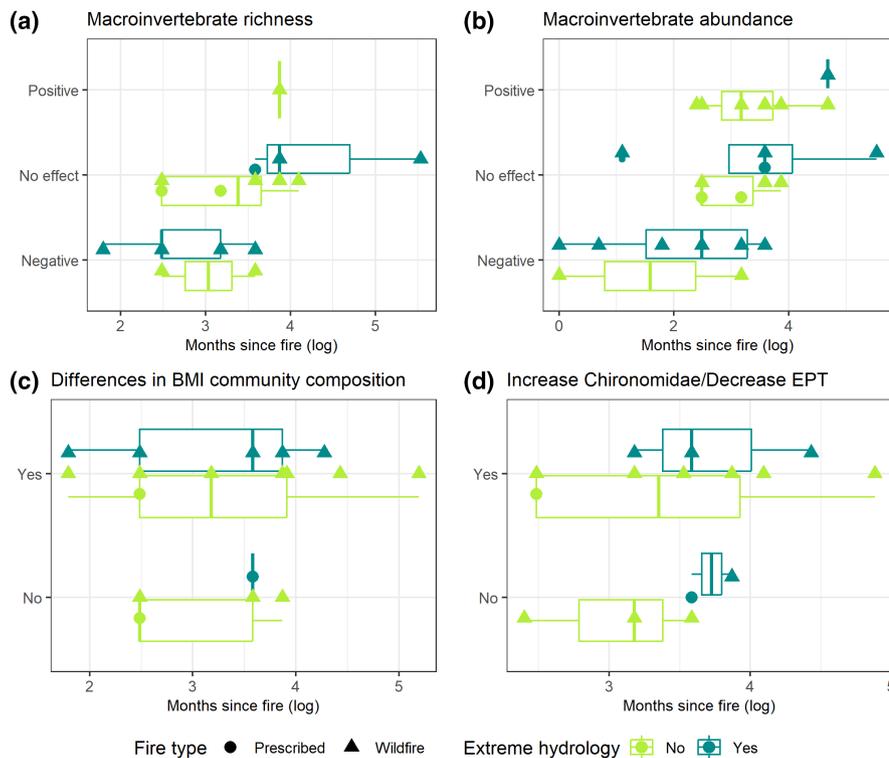


FIGURE 3 Results (y-axis) of studies measuring the effect of fire (prescribed—circles or wildfire—triangles) on benthic macroinvertebrate (BMI) (a) richness, (b) abundance, (c) community composition, and (d) increase in Chironomidae and/or decreases in EPT (Ephemeroptera-Plecoptera-Trichoptera). The x-axis represents the time lag between the fire and sampling, while colors show the presence or absence of extreme hydrological events post-fire.

($\chi^2=3.6$, $p=.06$; Figure 4c). Instead, an increase was more likely in the absence of extreme hydrological events post-fire ($\chi^2=3.1$, $p=.08$). One of the studies measured the effect of prescribed fire as opposed to wildfire and detected a decrease in biofilm biomass within 2 months post-fire but recovery within a year. Finally, all three

studies that reported the autotrophic index did not detect a significant effect of fire (BACI=2, CI=1).

The only study that examined the effect of fire on macrophyte biomass reported a decrease immediately after fire as a result of fire-linked flood events (Table 1). However, shortly after, macrophyte

Aquatic primary producers			Functional		Other animals				
Chlorophyll <i>a</i>	Ash-free dry mass	Macrophyte biomass	Leaf decomposition	Autochthony	Amphibians	Emergent insects	Spiders	Platypus	Bats
3 (13%)	2 (13%)	1 (100%)	2 (40%)	0	4 (40%)	1 (25%)	1 (25%)	0	0
1	0	1	1	0	2	0	0	0	0
2	1	0	1	0	2	1	1	0	0
0	1	0	0	0	0	0	0	0	0
6 (26%)	3 (20%)	0	2 (40%)	4 (80%) ^c	0	2 (50%)	2 (50%)	0	1 (100%)
0	0	0	2	0	0	0	0	0	0
4	2	0	0	4	0	2	2	0	1
2	1	0	0	0	0	0	0	0	0
14 (61%)	10 (67%)	0	1 (20%)	1 (20%)	6 (60%)	1 (25%)	1 (25%)	1 (100%)	0
1	1	0	1	0	2	0	0	1	0
13	8	0	0	1	3	1	1	0	0
0	1	0	0	0	1	0	0	0	0
23	15	1	5	5	10	4	4	1	1

biomass rebounded probably due to the fertilization of nutrient-rich ash and sediments. Two years later, macrophyte biomass decreased again following high flows, showing that the effect of fire on macrophytes was mediated by stream hydrology.

3.2.4 | Ecosystem functioning

Out of the five studies that measured leaf decomposition after wildfires, two reported lower decomposition, two greater decomposition, and one no changes due to fire (Table 1). Regarding food web dynamics, out of the five studies that measured this endpoint using stable isotopes, four reported an increase in the consumption of autochthonous food resources related to fire, whereas one did not detect any effect (Table 1). Two of the studies looked at autochthony in riparian spiders and three in benthic stream macroinvertebrates.

One of the two studies reporting stream metabolism measured greater primary production in burned than unburned sites and no differences in respiration (the riparian forest was burned and there were no extreme hydrological events after the fire). The second study measured greater sediment respiration in burned streams. Regarding nutrient limitation, two studies reported lower nitrogen limitation in streams with burned catchment and riparian forest. However, one of these studies also looked at burned streams with intact riparian forests and did not detect nitrogen limitation, suggesting that primary production is limited by other factors in these cases. One study assessed terrestrial and aquatic nitrogen biogeochemistry and detected an increased transfer and incorporation into aquatic primary producers after wildfires but not after prescribed fires.

3.2.5 | Riparian fauna

In four studies, fire did not seem to affect amphibian larvae (tailed frog tadpoles in two studies, American bullfrog tadpoles in one study) density, but one study observed a decline in coastal giant salamander density in two of the three severely burned watersheds. Another study reported decreases in newt eggs after fire but no differences in adults, whereas another study reported lower numbers of two species of riparian salamanders (the two most aquatic species) in burned sites compared to control sites but no differences in a third species (the most terrestrial one) (Table 1).

Two studies observed greater spider abundance in burned sites compared to unburned sites, a third study did not detect significant differences in spider density between burned and unburned sites, and a fourth study reported a significant decrease (Table 1). One study reported greater bat echolocation in severely burned compared to unburned riparian forests. One study did not detect differences in platypus numbers after fire nor after fire followed by sediment pulses.

4 | DISCUSSION

Our review reveals a high variability in the response of stream and riparian biota and ecosystem functions to fire. However, our analysis demonstrates that part of this variability can be explained by the presence of extreme hydrological events post-fire, the time lag between the fire and sampling, the burn status of the riparian forest, the type of fire, and the robustness of the study design. Below we

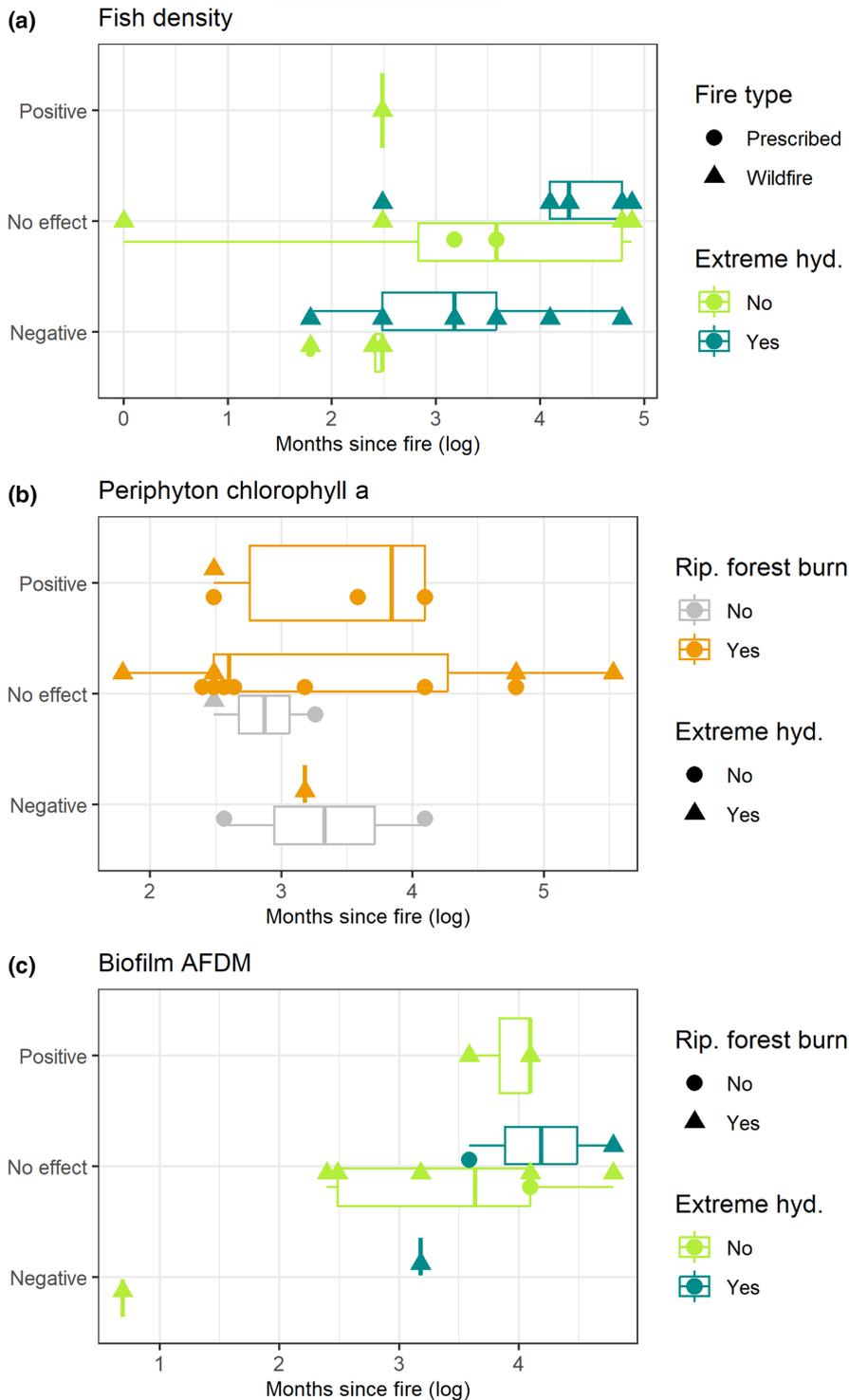


FIGURE 4 Results (y-axis) of studies measuring the effect of fire on (a) fish density, (b) algal biomass measured using chlorophyll *a* as a proxy, and (c) biofilm biomass measured as ash-free dry mass. The x-axis represents the time lag between the fire and sampling. Colors in (a) and (c) and shapes in (b) show the presence or absence of extreme hydrological events post-fire. The colors in (b) and the shapes in (c) represent whether the riparian forest was burned or not. Shapes in (a) depict the origin of the fire (prescribed or wildfire).

explore and discuss these effects and make recommendations to ensure that the knowledge needed for a sound integrated fire management that protects aquatic ecosystems is generated.

4.1 | Impacts of fire on stream ecosystems

Our results show great variability in the response of some benthic macroinvertebrate indicators to fire. For example, responses in density vary between an 82% decline (Whitney et al., 2015) and a 75%

increase (Verkaik et al., 2015) after fire, and responses in taxon richness between reductions of 70% (Rinne, 1996) and increases of 30% (Silins et al., 2014). We did not detect a clear direction in the response of macroinvertebrate abundance to fire, as increases, decreases and no significant changes were reported by a similar number of studies (28%, 34%, and 38%, respectively). However, regarding taxon richness, decreases post-fire were reported by more studies than increases (37% vs. 5%), but non-significant differences were the most common result (58% of the studies). Our analysis sheds some light on these seemingly conflicting results by quantitatively identifying

factors that influence the directionality of the response of BMIs to fire. The time elapsed between the fire and the sampling is one such factor, as decreases in density and richness were more common in studies looking at recent fires (short-term effects, <5 years) than in studies assessing longer-term effects (>10 years). This corroborates the idea that most invertebrates recover within 5–10 years post-disturbance (Minshall, 2003; Paul et al., 2022). For example, Vieira et al. (2004) reported a reduction in macroinvertebrate richness and abundance to near zero after the first 100-year flood following the 1996 Dome wildfire, but numbers returned to pre-fire levels within 1 year. However, there are cases in which taxon richness remains lower in burned than unburned watersheds beyond 10 years post-fire (Musetta-Lambert et al., 2020; Rosenberger et al., 2011).

Another influential factor we detected was the severity of the hydrological events after the fire, with decreases in macroinvertebrate abundance or richness being more commonly reported for fires followed by flooding or debris or sediment flows. Wildfires increase overland flow due to reduced infiltration, evapotranspiration, and interception, which in turn increases erosion and the frequency of debris and sediment flows in streams (Paul et al., 2022), especially where slopes are steep and post-fire precipitations intense (Nyman et al., 2015). Turbidity values higher than 1200 or 3000 NTU were measured following high-severity fires (Rust et al., 2019; Thompson et al., 2019), with such high sediment concentrations being lethal to many BMIs due to abrasion, burial, clogging, and/or oxygen and pH dips (Jones et al., 2012). Post-fire sediment and ash inputs to streams have also been shown to increase the transport of contaminants such as metals and PAHs known for their toxic, mutagenic, and carcinogenic properties (Abraham et al., 2017; Kieta et al., 2023; Raelison et al., 2023). Additionally, sediment and debris flows can indirectly affect BMIs by causing stream channel and riparian reorganizations that profoundly alter habitat (e.g., siltation of gravel beds), food availability and quality (e.g., scouring of biofilms) as well as food web dynamics (e.g., elimination of predators) (Jones et al., 2012; Paul et al., 2022). Thus, it is not surprising that post-fire sediment or debris flows influence the directionality of the effect on BMIs, with our results showing that negative effects and longer recovery times are more common in fires followed by such disturbances. This means that factors influencing the likelihood of these events (slope, rainfall patterns, fire severity, etc.) as well as the traits that make BMIs more or less resilient to the effects listed above will influence the effect of fires on BMIs.

The lack of clear patterns in the directionality of the effects on macroinvertebrate community structure contrast with the much clearer effects on community composition. Our analysis shows that more than two-thirds of the studies detected a significant change in composition post-fire and that such changes were not related to time since fire. In fact, differences in composition have been reported even 15 years post-fire (Musetta-Lambert et al., 2020). These compositional changes can be explained by the fact that the response of BMIs to fires is mediated by life history traits (Jager et al., 2021). For example, species with traits granting resistance (e.g., small size, attachment to streambed, and hydrodynamic shape) and resilience (e.g., multivoltinism, strong dispersal, and generalist feeder)

to hydrologic disturbance should have a competitive advantage under postfire floods. This may explain why over two thirds of the studies we reviewed detected a significant increase in the relative abundance of chironomids and simuliids (which are generalist feeders with strong larval dispersal and multivoltine reproduction) and/or a decrease in %EPT (which are sensitive to disturbance-related changes in water quality). Post-fire recolonization tends to be led by the former, whereas the latter take longer to recover (Mellon et al., 2008; Vieira et al., 2004), and differences can be as substantial as a 20-fold difference in the Diptera:EPT ratio between burned and unburned streams (Silins et al., 2014).

Such compositional differences can have functional implications as well as cascading trophic effects. Our review shows that changes in the abundance of functional feeding groups due to fire are common, with over half of the studies reporting an increase in collector-gatherer (generalist feeders) and a decrease in shredder and scraper (specialist feeders) invertebrates. The decrease in shredders could be related to the reduction in leaf litter input associated with burned riparian forests as well as to the increased downstream flushing of coarse particulate organic matter (Cooper et al., 2015; Rodríguez-Lozano et al., 2015). In turn, reductions in shredders could influence the very important stream function of leaf decomposition, which is mostly mediated by microbes and shredders. However, our review showed that the effect of fire on this endpoint is very variable, with the few studies that measured it reporting increases ($n=2$), decreases ($n=2$), and no effects ($n=1$). The directionality did not seem to be related to factors such as time since fire, as reductions in leaf decomposition in burned sites were reported as long as 15 years post-fire in boreal streams (Musetta-Lambert et al., 2020). Although more studies are needed to clarify trends, this variability could simply reflect the many abiotic and biotic factors that influence this process (Abelho, 2001) and that are known to vary with fire (Morales et al., 2023; Paul et al., 2022; Raelison et al., 2023). For instance, the reduction in shredders could be compensated by increased microbial decomposition resulting from higher water temperature and nutrient concentrations after fire.

The changes in the macroinvertebrate community (prey) described above could also have cascading trophic effects on aquatic and riparian predators such as fish, birds, and spiders. Beakes et al. (2014) observed that trout in the burned sites were consuming smaller and less prey than fish in reference sites, which along with increased water temperatures resulted in bioenergetically stressful conditions and decreases in fish biomass. Indeed, all six studies in this review that reported fish length observed an increase in burned sites, which are likely related to warmer water temperatures that lead to faster growth, which in turn can exacerbate competition for limited food resources and lead to lower lipid content (Rosenberger et al., 2015) or lower fish condition (Warren et al., 2022). Regarding riparian predators, two out of four studies reported an increase in the emergence of insects in sites that burned several years ago, which could partly explain the greater density of spiders observed in burned sites in two out of four studies, as well as the greater bat echolocation reported by one study (Harris et al., 2018; Malison & Baxter, 2010; Mellon et al., 2008). In recently burned streams, in

turn, a reduction in the density of emerging insects resulted in lower riparian spider densities (Preston et al., 2023).

Fish density tends to decrease after fire as shown by 62% of the cases we reviewed. In addition to the above-described indirect biological effects of fire on fish, direct mortality has been also widely documented. For example, monsoon rains after The West Fork Complex fire in Colorado caused acute and dramatic fish kills (Rust et al., 2019), steelhead trout were extirpated from burned basins in California (Cooper et al., 2015), and so did brook trout, rainbow trout, and Gila trout after fires in Arizona and New Mexico (Rinne & Neary, 1996). Direct mortality has been associated with lethal water temperatures as well as chemical toxicity from smoke, ash, or the use of fire retardants (Gresswell, 1999). Additionally, less acute indirect effects caused by warmer temperatures, habitat alteration due to channel restructuring, and chemical contamination can reduce fish densities by forcing emigration or disrupting feeding and reproduction. As it was the case with BMIs, decreases in fish density were more commonly reported when an extreme hydrological event followed the fires, probably due to the debris and sediment flows that exacerbate all the direct and indirect effects described above. But even if highly disruptive in the short term, debris flows can be important to maintain habitat complexity and suitable spawning and rearing areas for fish in the long term (Burton, 2005; Smith et al., 2021). Thus, negative effects on fish were also more common among shorter-term studies, suggesting that fish densities tend to recover within 5–10 years (Gresswell, 1999; Paul et al., 2022). However, the recovery time will depend on multiple factors such as the regeneration of riparian vegetation and associated temperature regimes (Dunham et al., 2007; Rosenberger et al., 2015), but also on human factors such as barriers to fish migration (dams, culverts, etc.) and invasive species (Neville et al., 2009).

Although periphyton is expected to be one of the most responsive biotic indicators, the majority of the studies did not detect the effect of fire on its biomass. Algal biomass (estimated using chlorophyll *a*) as well as biofilm biomass (which includes algae, fungi, bacteria, and organic matter) did not differ between burned and unburned sites in 59% and 67% of the cases we studied, respectively, while increases were reported by 27% and 20% of the cases and decrease by 14% and 13%. These results could stem from the fact that several abiotic conditions altered by fires may antagonistically influence primary production: while scouring events, increased turbidity, and sediment deposition may reduce algal and biofilm biomass, increased nutrient and light levels resulting from fire tend to boost production (Jones et al., 2012; Kiffney et al., 2003). In fact, our analysis detected that extreme scouring events such as debris flows favor negative responses in biofilm biomass to fires (i.e., negative influences such as scouring outweigh positive ones). In turn, fires that burned the riparian forest were more likely to result in increased algal biomass (i.e., positive influences such as light outweigh negative ones). Studies comparing fires that burned the riparian forest to those that left it intact reported greater and lower algal biomass than in reference sites, respectively (Cooper et al., 2015; Klose et al., 2015), showing that when riparian forests are not burned, primary production is limited

by light as opposed to by nutrients (Klose et al., 2015). Although on average algal responses tend to recover within 5–10 years after fire (Paul et al., 2022), this recovery will depend upon how rapidly vegetation recovers. For example, Rhea et al. (2021) observed elevated nitrate concentrations (23 times), algal biomass (2.5 times), and primary production (20 times) in burned compared to unburned streams even 5–15 years after fire due to a slow vegetation recovery. The only study examining post-fire changes in macrophyte biomass reported that increases and reductions in biomass were strongly related to post-fire flood events (Thompson et al., 2019).

Although most studies measuring algal biomass did not detect an effect of fire, most studies measuring the incorporation of algal resources into food webs reported a greater autochthony in burned than unburned systems (Cooper et al., 2015; Jackson & Sullivan, 2018; Silins et al., 2014). Therefore, food web structure (i.e., time integrated measure of algae assimilation) seems to be a more reliable indicator than algal biomass (i.e., snapshot in time) to detect the effects of disturbances (Erdozain et al., 2019). This is probably because new algal growth is readily ingested by consumers due to its low biomass but high nutritional quality in small streams (Rosemond et al., 1993) and because responses are very variable in time (Klose et al., 2015). Because of this higher nutritional quality of algae compared to terrestrial food sources, the greater autochthony of the food web can result in a more efficient energy transfer to upper trophic levels (Brett et al., 2017; Guo et al., 2016). On the other hand, excessive algal productivity can lead to adverse effects such as fish kills related to hypoxia or toxic cyanobacteria blooms that threaten humans and other animals (Chorus & Welker, 2021). However, it is worth noting that two of the studies reporting an increase in autochthonous food consumption that we reviewed did not run stable isotope mixing models to quantify the contribution of each food source to consumers, and thus, the results should be interpreted with caution.

4.2 | Knowledge gaps and future directions

4.2.1 | Study design

Most of the studies we reviewed followed a control-impact design followed by before-after studies, and only 17% of the studies implemented a BACI design. This is understandable considering the fortuitous nature of wildfires and the difficulty of having before fire data unless burned watersheds were being routinely monitored or studied for other reasons. However, the BA and CI designs (as well as the only after studies that we excluded from the analysis) are much more prone to biases than the BACI design because, without a control, before-after differences can simply reflect environmental variability over time, while without before data, control-impact differences can simply reflect pre-existing differences between groups (Christie et al., 2020). This is especially true for studies with very low sample sizes such as one unburned vs. one burned stream (e.g., Mast et al., 2016; Roby & Azuma, 1995; Rodríguez-Lozano

et al., 2015) or one single stream sampled before and after the fire (e.g., Peart et al., 2012; Ryan & Dwire, 2012; Sherson et al., 2015). In fact, some of the BACI studies we reviewed would have reached different conclusions if only BA or CI results were compared. For example, Rugenski and Minshall (2014) detected a significant increase in macroinvertebrate density after the fire, but this increase was observed in both burned and unburned streams, so without control, the authors would have attributed this change to fire. Similarly, they observed greater chlorophyll *a* in burned than control streams, but these differences were observed both before and after the fire.

Therefore, it is not surprising that in our analysis no effects were more often reported by BACI studies than by CI or BA studies. For instance, significant effects of fire on macroinvertebrate abundance and richness were reported by 73% and 60% of BA or CI studies, respectively, but by only 17% and 12% of BACI studies. These results raise the question of how many of the BA or CI studies that interpret the variability to be caused by fire are not in fact biased by natural variability in time or space. Thus, we strongly advocate for BACI designs to disentangle the effects of fire from confounding factors. In the case of wildfires, their unpredictable nature highlights the need for baseline monitoring programs that allow the detection of change in ecological communities through time (Magurran et al., 2010). The planned nature of prescribed fires, on the other hand, makes them much more suitable for BACI designs, and thus, some resources should be allocated for capturing the pre-fire natural variability in control and impact sites to maximize the robustness of the conclusions.

4.2.2 | Prescribed fires

Fire is a common disturbance that has shaped the diversity of life on Earth for millions of years (He et al., 2019) and although humans have used it to modify ecosystems for thousands of years (Bowman et al., 2011), decades of fire suppression have changed natural fire regimes, led to accumulation of fuel loads and increased the risk of high severity wildfires (Ryan et al., 2013). In spite of the slow implementation (partly due to social resistance), there is growing support for the use of prescribed fire to restore fire-dependent processes, ecosystems, and species, as well as a management tool to prevent large, severe wildfires by reducing fuels (Fernandes et al., 2013; Ryan et al., 2013). However, the ecological effects of prescribed fires on stream and riparian ecosystems remain largely unknown as fewer studies assess the responses to prescribed burns compared to wildfires (Bixby et al., 2015; Klimas et al., 2020; Paul et al., 2022). This was confirmed by our review, with only 7% of the studies we analyzed dealing with prescribed fire effects.

The few studies that measured the effects of prescribed fire on biotic indicators did not detect significant effects on macroinvertebrate abundance or richness, nor on fish density (Arkle & Pilliod, 2010; Bêche et al., 2005; Britton, 1991; Caldwell et al., 2013). However, macroinvertebrate community composition shifted in two studies and biofilm biomass decreased after the prescribed burn in one study, but recovery occurred within 1 year (Bêche et al., 2005;

Caldwell et al., 2013). Thus, it seems that prescribed fires in forested watersheds have minimal detrimental effects on biological stream endpoints, especially compared to those of wildfires, matching the findings on abiotic stream indicators (Beyene et al., 2023; Klimas et al., 2020). Considering the low number of studies measuring biological stream endpoints and the growing interest in prescribed fire as a surrogate for wildfires, additional research from different biomes confirming these results is needed.

4.2.3 | Underrepresented regions, biomes, and land uses

As it is the case with abiotic indicators, most of the studies on biotic indicators we reviewed were concentrated in North America (73%, 87%, 85%, and 86% of the studies for macroinvertebrates, fish, periphyton and function, respectively), and the temperate evergreen forest biome (64%, 83%, 73%, and 50% of the studies, respectively). But because fire regimes, fire-proneness and -adaptation, precipitation patterns, and stream/riparian ecosystem characteristics vary widely across continents and biomes, the need for a better understanding of the interplay of all these factors in underrepresented regions and biomes is clear (Bixby et al., 2015; Morales et al., 2023). This is especially true for those biomes and regions where fire is a prevalent natural or anthropogenic disturbance driving key ecological dynamics (e.g., savannas, boreal forests, and grasslands), as well as for those where fire has historically been rare but is becoming increasingly common (e.g., tropical moist forest and tundra) (e.g., Barlow et al., 2020; Hu et al., 2015). Our review also shows that wilderness forest areas and managed forests dominate the literature, while pastures, agricultural, and urban areas are underrepresented. Considering that fire and stream characteristics greatly vary across these, more studies on land covers and uses other than forests are needed.

4.2.4 | Ecosystem function

Similarly, most studies assessing the effect of fire on biological components of stream ecosystems have focused on structure rather than functionality, with this being especially true for studies with a BACI design and for prescribed fires. This provides an incomplete picture of overall ecological integrity as structure and function can respond differently to disturbance (Feckler & Bundschuh, 2020; Sandin & Solimini, 2009) and there can be changes in function (e.g., leaf decomposition) without changes in structure (e.g., benthic macroinvertebrate community composition) (Mckie & Malmqvist, 2009; Riipinen et al., 2009). Because functional indicators integrate environmental conditions over time and across multiple trophic levels and biological organizations, and because they are closely related to the provision of ecosystem services (Gessner & Chauvet, 2002; Young et al., 2008), we, as others (Bixby et al., 2015; Morales et al., 2023) strongly recommend incorporating functional indicators in future studies assessing the effect of fire on stream ecosystems.

4.2.5 | Fire regime

We believe that the sampling recommendations made by Raelison et al. (2023) for water quality studies also apply for biological studies. Specifically, fire regime characteristics such as burn severity of both the upland and riparian forests and distance to the stream, as well as vegetation types should be better reported. For instance, the effects of high-intensity wildfires that burn dense forests are probably different from those of low-intensity fires in scarcely vegetated forests, which could further explain the variability in responses to fire we detected. Unfortunately, many of the studies we reviewed did not report these factors or reported them inconsistently, limiting our ability to disentangle the influence of factors such as fire severity or type of burned vegetation in the results of this review. Therefore, we strongly recommend unifying the way fire severity is reported as well as developing a metric that allows to quantify the influence of a fire on a given stream point by adding the severity of each spatial unit (e.g., 5 × 5 m cell) in the catchment weighted by time since fire and flow distance to the stream.

Other fire regime attributes may also influence water quality in the context of wildfires. Frequent fires may alter species composition, disrupt habitat structure, and influence nutrient cycling, thereby affecting biological study outcomes (He et al., 2019). Therefore, although maintaining long-term studies is challenging, we strongly encourage researchers to analyze fire frequency (particularly with prescribed burning, as the time between fires can be controlled). Fire seasonality influences the timing of disturbances in relation to plant phenology and animal behavior, potentially affecting species survival and reproduction (Miller et al., 2019). The spatial distribution of burned areas affects habitat connectivity and the mosaic of different successional stages, potentially causing impacts on the water ecosystems. Additionally, the effect of the first flush should be captured, the precipitation patterns post-fire should be described and post-fire management practices (e.g., salvage logging) should be clearly reported. All this information is key to ensure that scientific studies are useful to managers and provide findings that guide an integrated fire management that protects the delivery of aquatic ecosystem services.

4.2.6 | Downstream effects

Our review shows that the effects of fire on stream ecosystems have mostly been studied in small headwater streams. This is understandable considering that headwater streams constitute >80% of stream networks (Leopold et al., 1964) and that most of the water and material exchange with the terrestrial landscape happens in these small streams (Gomi et al., 2002). However, the intrinsically hierarchical nature and longitudinal hydrological connectivity of river networks make them fundamentally cumulative, that is, as more water converges longitudinally, materials dissolved or suspended in water accumulate (Fritz et al., 2018). Therefore, it is important to examine the large-scale landscape implications of the fire effects observed in headwaters. Five percent

of the studies that reported catchment size included streams with a wide range of sizes (e.g., <100 ha to >10,000 ha), enabling the study of how effects propagate downstream. For example, Minshall et al. (2001) reported a lower effect of fire on macroinvertebrates in larger downstream systems compared to small streams due to larger water volumes buffering changes in water temperature, but they also pointed out that post-fire recovery was faster in the smaller streams. Considering that the downstream propagation of effects depends on the ecosystem component studied and on the type of disturbance (Erdozain, Kidd, Emilson, Capell, Kreutzweiser, et al., 2021a, Erdozain, Kidd, Emilson, Capell, Luu, et al., 2021b), further studies examining whether fire-effects accumulate or dilute in larger downstream systems are necessary.

4.3 | Management implications

Our results support the idea that stream biota is highly adapted to disturbance, with post-fire recovery of most endpoints reviewed happening within 10 years. This is especially true for prescribed fires, as the few studies that measured their effect on biotic indicators did not detect significant consequences on macroinvertebrate abundance nor richness, nor on fish density (Arkle & Pilliod, 2010; Bêche et al., 2005; Britton, 1991; Caldwell et al., 2013). Macroinvertebrate community composition shifted in two studies and biofilm biomass decreased after the prescribed burn in one study, but recovery occurred within 1 year (Bêche et al., 2005; Caldwell et al., 2013). Thus, it seems that prescribed fires have minimal detrimental effects on biological stream endpoints, especially compared to those of wildfires, matching the findings on abiotic stream indicators (Beyene et al., 2023; Klimas et al., 2020). These findings support the use of fire as a management tool to prevent large-scale wildfires or to restore fire-dependent processes and species with minimal and short-lived negative consequences for the delivery of aquatic ecosystem services such as water purification, food provision, and recreation.

The role that riparian vegetation has on mediating the effect of fire on stream ecosystems has regulatory and management implications. Because riparian forests provide multiple key ecosystem services and support disproportionately high biodiversity (Graziano et al., 2022; Riis et al., 2020), their protection from catchment disturbances such as forest harvesting is common (Schilling, 2009). This has led to the widespread adoption of fixed-width riparian buffers (Richardson et al., 2012) which may fail to capture the dynamic and heterogeneous nature of these ecosystems (Kuglerová et al., 2014). Thus, there is a growing call for managing these systems in a way that emulates natural disturbance patterns (Sibley et al., 2012). Riparian forests can act as barriers to wildfire spread, but depending on the width and fuel moisture, fire intrusion into the riparian forest is not uncommon (Dwire & Boone Kauffman, 2003; Pettit & Naiman, 2007). Thus, suppressing fire from these ecosystems which have evolved with this disturbance can pose a threat to biodiversity (He et al., 2019; Jackson et al., 2015; Kelly et al., 2020). For example, Musetta-Lambert et al. (2017) observed more taxonomically rich riparian vegetation and stream macroinvertebrate communities in

sites that burned 12 years before the study compared to unburned sites. Therefore, prescribed fires in riparian areas can increase biodiversity compared to unburned fixed-width buffers and yield riparian forests that more closely resemble natural post-burned states (Arkle & Pilliod, 2010; Kardynal et al., 2009). In turn, when functions such as water quality are the priority, management efforts should go into promoting fire-resistant riparian species such as alder that speed up recovery for streams in fire-prone landscapes (Coble et al., 2023).

But considering the low number of studies measuring biological stream endpoints and the growing interest in prescribed fire as a surrogate for wildfires, additional research from different biomes confirming these results is needed. For example, it would be important to know how the timing of the fire influences the effects on stream ecosystems, as water quality endpoints have been shown to respond differently to early vs. late dry season burning (Townsend & Douglas, 2000). Based on the literature, we expect early dry season burning that maximizes the time for vegetation to recover prior to the first heavy rains to minimize the negative effects on aquatic biota. Similarly, pre-fire planning that considers aquatic systems and post-fire management actions that help reduce erosion and boost vegetation recovery need to be better understood and implemented. Given the variability and uncertainty associated with fire impacts, adaptive management practices that are flexible and responsive to new evidence stemming from long-term monitoring efforts are key.

5 | CONCLUSIONS

We conducted a systematic review to characterize and summarize the literature on the effects of fire on biological stream endpoints compared to abiotic endpoints. Most of the studies were conducted in North America and in the temperate evergreen forest biome, followed a control-impact or before-after design (as opposed to BACI), assessed more wildfires than prescribed fires, and focused on structural biotic endpoints and on small headwater streams. A second selection of publications measuring the response of biological stream endpoints to fire showed great variability. Decreases, increases and no changes were reported by studies measuring macroinvertebrate abundance and richness, fish density, amphibian density, algal biomass, or leaf decomposition. We shed some light on these seemingly contradicting results by showing that the presence of extreme hydrological events post-fire such as debris flows, the time lag between the fire and sampling, and the burn status of the riparian forest influenced the outcome of the studies. Results suggest that although wildfires and the following hydrological events can have dramatic impacts in the short term, most biological endpoints recovered within 5–10 years. The few studies that measured the effects of prescribed fire on biotic indicators showed that effects were considerably less detrimental compared to wildfires. We also detected that no effects were more often reported by BACI studies than by CI or BA studies, raising the question of whether the research on the effects of fire on stream ecosystems may be biased by the

inherent limitations of CI and BA designs. Therefore, we believe that future studies assessing the effect of fire on streams should try to (1) incorporate functional indicators, (2) focus on underrepresented regions and biomes, (3) examine prescribed fires, (4) try to implement BACI designs to disentangle the effects of fire from natural variability, (5) assess the implications of different riparian forest management and prescribed burn strategies, (6) understand how the effects in small streams are propagated into larger downstream rivers (accumulation vs. dissipation of effects), and (7) clearly and consistently report factors such as fire severity, type of vegetation burned or precipitation patterns post-fire.

AUTHOR CONTRIBUTIONS

Maitane Erdozain: Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Adrián Cardil:** Investigation; methodology; validation; writing – review and editing. **Sergio de Miguel:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in "CORA Repository de Dades de Recerca" at <https://doi.org/10.34810/data1388>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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