A Possible Role for River Restoration Enhancing Biodiversity through Interaction with Wildfire

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PERSPECTIVE

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A possible role for river restoration enhancing biodiversity through interaction with wildfire

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Abstract

Background: Historically, wildfire regimes produced important landscape-scale disturbances in many regions globally. The “pyrodiversity begets biodiversity” hypothesis suggests that wildfires that generate temporally and spatially heterogeneous mosaics of wildfire severity and post-burn recovery enhance biodiversity at landscape scales. However, river management has often led to channel incision that disconnects rivers from their floodplains, desiccating floodplain habitats and depleting groundwater. In conjunction with predicted increases in frequency, intensity and extent of wildfires under climate change, this increases the likelihood of deep, uniform burns that reduce biodiversity.
Predicted synergy of river restoration and biodiversity increase: Recent focus on floodplain re-wetting and restoration of successional floodplain habitat mosaics, developed for river management and flood prevention, could reduce wildfire intensity in restored floodplains and make the burns less uniform, increasing climate-change resilience; an important synergy. According to theory, this would also enhance biodiversity. However, this possibility is yet to be tested empirically. We suggest potential research avenues.
Illustration and future directions: We illustrate the interaction between wildfire and river restoration using a restoration project in Oregon, USA. A project to reconnect the South Fork McKenzie River and its floodplain suffered a major burn (“Holiday Farm” wildfire, 2020), offering a rare opportunity to study the interaction between this type of river restoration and wildfire; specifically, the predicted increases in pyrodiversity and biodiversity. Given the importance of river and wetland ecosystems for biodiversity globally, a research priority should be to increase our understanding of potential mechanisms for a “triple win” of flood reduction, wildfire alleviation and biodiversity promotion.

KEYWORDS
disturbance ecology, fire mosaics, floodplain, pyrodiversity, riparian, river restoration, stage zero restoration, succession, wildfire

1 | INTRODUCTION

Wildfires are a major disturbance globally, affecting ecosystem processes, biodiversity and function, in addition to the services that these provide (McLauchlan et al., 2020). Although anthropogenic change in land use has decreased global burned area since 1930, climatic changes have increased average global fire season length since 1979 (Arora & Melton, 2018; Jolly et al., 2015). Therefore, in many regions globally, fire regimes (generally parameterized as "frequency, size, seasonality, intensity and type"; Krebs et al., 2010) are rapidly changing and are expected to change further with climate change and changes in land use (Stephens et al., 2013). For example, 2020 was a record year for wildfires, with >40,000 km^2 burned in the USA (National Interagency Fire Center, 2022) and >338,000 km^2 burned across Australia (Binskin et al., 2020). During the same year, a record-breaking wildfire occurred across the Pantanal in South America, which is the largest contiguous tropical river–wetland complex in the world (Garcia et al., 2021). Many freshwater ecosystems have co-evolved with fire; in others, fire has been introduced recently (Bixby et al., 2015; Robinne et al., 2021). In addition to their negative impacts for people, economies and ecosystems (Higuera et al., 2019; McWethy et al., 2019), recent wildfires are a key but understudied driver of water-quality impairment for river systems, as highlighted in a recent large-scale study of the western USA (Ball et al., 2021). Although rivers and streams make up only $0.58 \pm 0.06\%$ of the surface of the Earth (Allen & Pavelsky, 2018), freshwater ecosystems support *c*. 10% of global species and provide critical ecosystem services, such as drinking water. Floodplains extend much further and are among the most productive land globally (Strayer & Dudgeon, 2010; Tockner & Stanford, 2002). Therefore, understanding the interaction between changing wildfire regimes and freshwater ecosystems is increasingly important to ensure their future resilience.

One factor contributing to widespread increase in wildfire risk is floodplain dehydration caused by draining wetlands and training multi-threaded rivers into single channels associated with historical river management (Brown et al., 2018; Grill et al., 2019; Montgomery, 2008; Robinne et al., 2021; Walter & Merritts, 2008). The standard paradigm for river management generally includes activities directly impacting channel and flow characteristics, such as damming, levees and channelization (Poff et al., 1997). This management, in combination with indirect processes, such as groundwater extraction and alteration of watershed land use, reduces the lateral, vertical and longitudinal connectivity between rivers and their floodplains, lowers groundwater levels (Cluer & Thorne, 2014) and, ultimately, contributes to riparian drying, loss of successional floodplain habitat mosaics and increased fire risk in many basins (Pettit & Naiman, 2007a; Shafroth et al., 2002). In recent years, there has been increasing emphasis on redressing some of these problematic historical river management activities. However, most restoration projects are channel-centric, resulting in only modest floodplain reconnection. We refer to this as "conventional" restoration, which ranges from reach-scale channel reshaping to dam removal. Conventional restoration has consistently been over-reliant on physical river processes, while failing to restore pre-Anthropocene hydromorphic processes, such as groundwater connectivity and biotic nutrient exchange (Johnson et al., 2020). This limits the potential for reducing wildfire vulnerability and negative effects on biodiversity.

Globally, of rivers >1,000 km in length, only *c*. 37% have not been altered anthropogenically (e.g., by consumptive water use, development of floodplain infrastructure or damming) across their entire length (Grill et al., 2019). Although specific restoration objectives and outcomes will differ depending on a host of regional characteristics, there has long been recognition of a global requirement for river restoration to re-establish more "natural" flooding regimes (Poff et al., 1997), particularly when considering interactions between flooding and wildfire in many ecosystems (Robinne et al., 2021). A key river restoration paradigm attempting to re-establish pre-Anthropocene river system processes, in order that self-formed and self-sustaining river–wetland corridors can develop over time, is termed restoration to "Stage Zero" conditions (see Wohl et al., 2021; Box 1). This paradigm follows the stream evolution model proposed by Cluer and Thorne (2014), prompting the recovery of anastomosing planforms lost owing to channelization, slowing of stream velocities, re-establishment of hydrological reconnection across the floodplain, and recharging of groundwater aquifers (Powers et al., 2019; Scagliotti, 2019).

Regarding wildfire–restoration interactions, we predict that among floodplain reconnectivity-style restoration paradigms, those like Stage Zero, which restore historical braided channel forms, will better enhance biodiversity, via more extensive shifting floodplain mosaics, than floodplain reconnectivity projects working on single channels. However, restoration to "Stage Zero" conditions and its theoretical roots in the Stream Evolution Model is designed for alluvial river systems, specifically within Europe and North America (Cluer & Thorne, 2014). Analogous to restoration to "Stage Zero" conditions, but moving beyond alluvial temperate Northern Hemisphere systems, recently proposed river restoration paradigms such as "pond and plug", "process-based restoration" or "biomic river restoration" recognize the requirement for restoration of hydromorphic, biological and geochemical processes present in non-degraded river ecosystems globally (Beechie et al., 2010; Johnson et al., 2020; Rodriguez et al., 2017; Box 1; Table 1). Although recognizing that restoration objectives might differ slightly between paradigms, local river characteristics, biomes and historical management, for convenience we use the term "floodplain reconnection" hereafter to refer to restoration that reconnects rivers extensively to their floodplains. We distinguish this from "conventional" channel-centric restoration that does not involve extensive floodplain reconnection (Figure 1). This distinction is particularly key for the expected river restoration–wildfire interactions. Future research should consider the role of different restoration paradigm objectives in non-alluvial river systems in shaping flooding–wildfire interaction effects on biodiversity.

BOX 1 **Defining floodplain reconnectivity river restoration**

What is river restoration?

River restoration projects are highly diverse, from small-scale (<1 km) projects to promote habitat heterogeneity to broad floodplain reconnection involving restoration of watershed-scale processes (Wohl et al., 2005). Widespread alteration of river systems and surrounding watershed processes throughout the Anthropocene means that restoration to "reference" conditions is not always possible. Therefore, restoration can instead be seen as the recovery of beneficial abiotic and biotic processes (Dufour & Piégay, 2009). Processes restored by floodplain reconnectivity restoration paradigms, and their expected interactions with wildfire for biodiversity outcomes, are summarized in Table 1.

Defining river restoration in the context of wildfire

Rivers can affect wildfires via a number of mechanisms, which include acting as a fire break (Coffman et al., 2010), increasing soil moisture (Fairfax & Whittle, 2020) and producing variable fuel in successional floodplain mosaics (Pettit & Naiman, 2007b). In accordance with the shifting habitat mosaic hypothesis (Kleindl et al., 2015), all these mechanisms are controlled fundamentally by the levels of river–floodplain connectivity in restoring shifting floodplain mosaics and their associated biotic and abiotic processes. Therefore, despite the diversity of "river restoration" definitions, floodplain connectivity can distinguish projects that are more likely to have a positive impact on wildfire mosaic outcomes for biodiversity. Wohl et al. (2015) define river restoration as either "reconnection", restoring the latitudinal, longitudinal and vertical connectivity between a river and its surroundings (important for successional flooding–wildfire mosaics), or "reconfiguration", restoring the physical structure of a river. Importantly, however, many successful restoration projects require reconfiguration to achieve reconnection; for example, input of large woody debris reduces streamflow, initiates sediment deposition and enhances floodplain reconnection (Box 2).

An example of a floodplain reconnectivity restoration paradigm

In the Pacific Northwest (PNW) Region, from 2010, the US Forest Service began implementing the Stage Zero river restoration paradigm, aiming to reinstate self-sustaining hydromorphic, biological and geochemical processes associated with pre-Anthropocene river systems (Wohl et al., 2021). Although similar to other floodplain reconnectivity restoration paradigms (e.g., floodplain reconnection, natural flood management), Stage Zero restoration is novel in its recognition that in alluvial river systems, pre-disturbance streams were likely to comprise a river–wetland–floodplain complex with a multi-threaded planform and high lateral, longitudinal and vertical connectivity (Cluer & Thorne, 2014; Powers et al., 2019). As such, Stage Zero promotes frequent lateral connection at low to moderate flows, rather than only infrequently at the highest flows, as expected for many floodplain reconnection projects. We predict that among reconnection restoration paradigms, more extensive floodplain reconnectivity (as with Stage Zero) will interact to produce more heterogeneous habitat mosaics under wildfires.

Monitoring indicates that floodplain reconnectivity restoration generates multiple co-benefits for riverine ecosystem services, including flood risk management, improvement in water quality (e.g., via denitrification), carbon sequestration, and increased biodiversity (Edwards et al., 2020; Federman, 2022; Hinshaw & Wohl, 2021; Jennings, 2021; Kondolf, 2011). Frequent and prolonged inundation of the floodplain associated with extensive reconnection and restoration of geomorphological processes creates a complex, shifting mosaic of contrasting, successional habitats (Kleindl et al., 2015; Kondolf, 2011). With respect to fire, we hypothesize (summarized in Figure 1; Table 1) that this will: (1) change the behaviour of a wildfire, promoting generation of a fine-scale "wildfire mosaic" instead of a more uniform burn (Kleindl et al., 2015; Wilkin et al., 2016); (2) enhance post-burn recovery of biodiversity, owing to the presence and

TABLE 1 The expected interaction between key processes restored via floodplain reconnectivity restoration and wildfire mosaics for positive biodiversity outcomes

Restored process		Reference	Expected interaction with wildfire	Expected biodiversity outcome	Key complicating factors
Natural flow regime	Groundwater replenishment from increased hyporheic exchange	Cluer & Thorne (2014); Robinne et al. (2021)	Increased soil moisture decreases burn severity	Higher recovery and resilience of vegetation and soil microbiome	Complex interactions between nutrient cycling and temperature; local climate; geology; short-term tree mortality on floodplains with drier-adapted vegetation; barriers to flow (e.g., upstream damming)
	Successional floodplain habitat mosaics	Federman (2022); Hauer et al. (2016)	Patchier burn severity		
	Higher aquatic biodiversity productivity and connectivity	Bond et al. (2019); Jennings (2021)	Higher potential for post-fire population replenishment	Higher resilience of aquatic biodiversity	
High diversity of riparian vegetation	Restored successional floodplain habitat mosaic for high vegetation diversity	Cluer & Thorne (2014)	Wetted vegetation can act as a fire break; more variability in fire resilience of vegetation; bank stabilization	Higher recovery and resilience of biodiversity; lower post-fire sediment input	Invasive species; watershed-scale processes (e.g., deforestation and water-quality degradation)
Ecosystem engineer species	Restoration of biological processes associated with rivers [e.g., beaver dams or hydropsychid caddisfly larvae (*Trichoptera*) structures]	Fairfax & Whittle (2020); Johnson et al. (2020); Pollock et al. (2014)	Range of specific biological–wildfire interactions (e.g., increased wetted areas from beaver dams provide refugia for biodiversity)	Higher recovery and resilience of aquatic biodiversity	Long time-scales for biodiversity restoration; problematic invasive species; complex multi-level interactions across trophic networks, hard to understand
Depositional environment from physical reconnection of river–floodplain complex	Higher sediment (and associated nutrient) deposition owing to larger, shallower wetted area; greater heterogeneity of aquatic microhabitats	Robinne et al. (2021); Scagliotti (2019)	Higher resilience of river processes and biodiversity to post-wildfire debris flows and scour; creation of aquatic microhabitats	Higher recovery and resilience of aquatic diversity to sediment loading	Pollutants associated with sediment (e.g., from agricultural land); upstream alteration of sediment movement [e.g., damming (prevents sediment) and afforestation (enhances sediment)]

Note: Reconnection-based river restoration restores vertical, longitudinal and lateral connectivity between a river and its surrounding environment (Wohl et al., 2015).

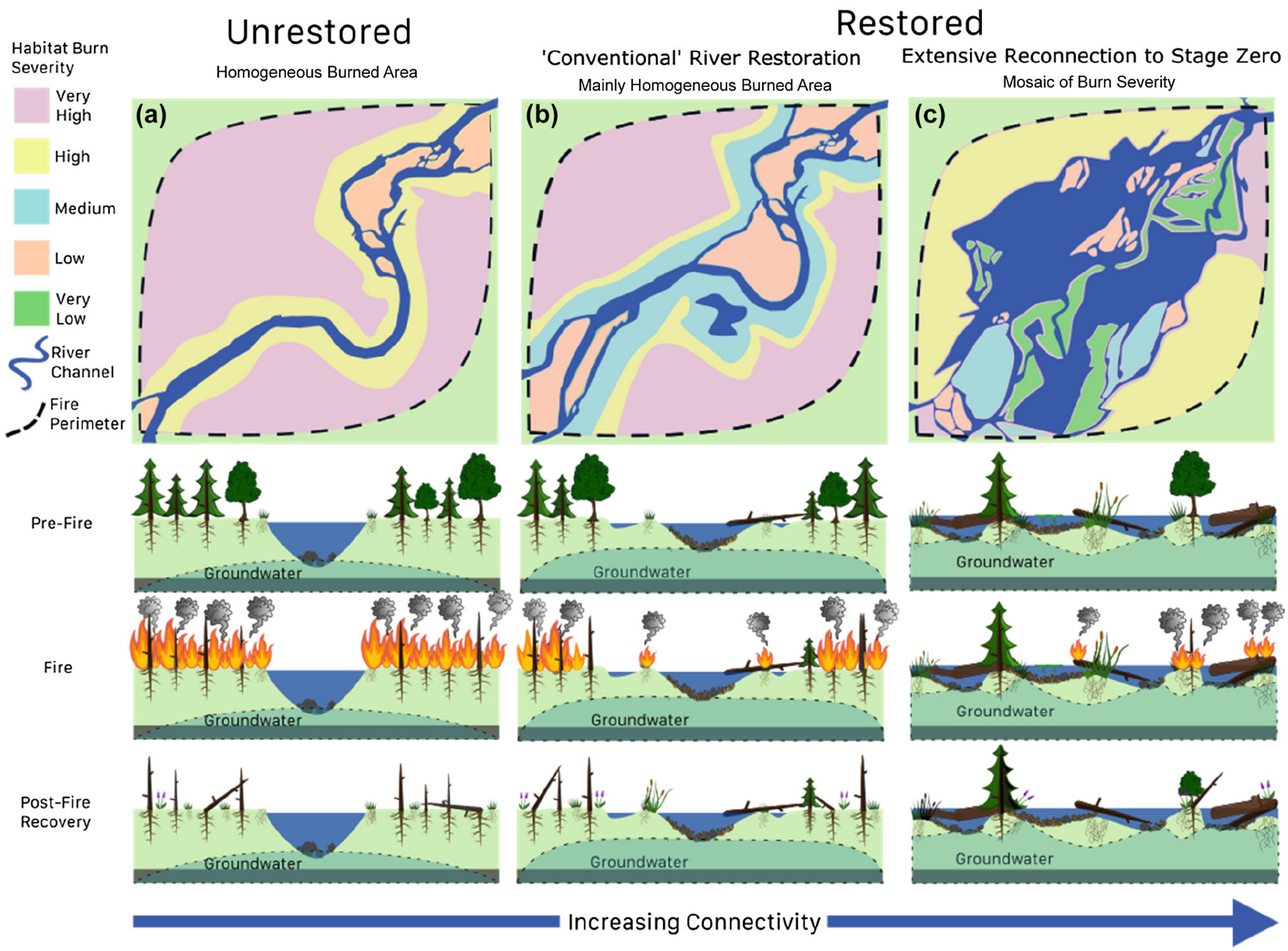

FIGURE 1 Conceptual comparison of river and floodplain habitat mosaics within unconfined river valleys that are (a) unrestored; (b) conventionally restored with partial floodplain reconnection (e.g., 1–2 year flood return interval); or (c) restored with extensive floodplain reconnectivity, including historical anastomosing channel form for this example alluvial system. Note that comparisons are between unrestored and restored river reaches and between different restoration conditions following a severe wildfire. Restored reaches are expected to display more heterogeneous post-fire burn mosaics, in which: (1) biodiversity declines less (more resistance) owing to patchier and lower overall burn severity creating fire refugia; and (2) biodiversity recovers more quickly or even increases, owing to higher and more proximate seed availability and a more conducive (cooler and wetter) regeneration microclimate (Fairfax and Whittle, 2020; Jones & Tingley, 2021; Krawchuk et al., 2020). Biodiversity enhancement is hypothesized to be greatest in river reaches with restored floodplain reconnectivity, because conventional river restoration is associated with floodplain drying and relatively homogeneous burn severity. Note that groundwater might be expected to rise after wildfires owing to reduced evapotranspiration.

persistence of wildfire refugia, which have the potential subsequently to reduce the impact of post-wildfire erosion and sediment loading on biodiversity (Dwire & Kauffman, 2003; Fairfax & Whittle, 2020; Shakesby & Doerr, 2006); and (3) enhance landscape-scale biodiversity, owing to higher heterogeneity of fine-scale, post-burn niches of more variable burn severity, both within and between burned patches (Kleindl et al., 2015; Parr & Andersen, 2006; Figure 1).

Despite the potential importance for managing risks related to floods, wildfires and biodiversity loss, the ways in which extensive floodplain reconnectivity projects interact with wildfires have not been studied empirically. Here, we discuss the theoretical basis and key mechanisms involved, use a case study (Box 2) to elucidate river restoration–wildfire interactions and co-benefits, and suggest future research priorities.

2 | PYRODIVERSITY AND POST-WILDFIRE HABITAT IN RIVER ECOSYSTEMS

The "pyrodiversity begets biodiversity" hypothesis (He et al., 2019; Jones & Tingley, 2021; Martin & Sapsis, 1992; Parr & Andersen, 2006) predicts that habitat mosaics, produced by an array of vegetation conditions resulting from varying attributes of fire effects in space and time, can enhance landscape-scale biodiversity. The strength of the relationship between diversity in fire and biodiversity depends strongly on fire regime attributes (i.e., frequency, severity, patch size and seasonality, among others; e.g., Agee, 1996). In turn, these are shaped by species traits, regional biophysical characteristics and biome (Jones & Tingley, 2021; Tingley et al., 2016). Accordingly, empirical evidence for the generalizability of the pyrodiversity

BOX 2 River restoration–wildfire interactions in practice: South Fork McKenzie River

In 2018 and 2019, the lower South Fork McKenzie River (SFMR), Oregon, USA (within the indigenous territories of the Kalapuya and Molalla peoples) was reconnected hydrologically to its floodplain, resulting in the re-establishment of a 0.8 km^2 river–floodplain–wetland complex, in the largest Stage Zero river restoration project implemented to date (Hinshaw & Wohl, 2021). To establish a pre-project baseline against which to measure the benefits of this restoration, a $1.2 million monitoring programme was initiated in 2017. Effectiveness monitoring encompasses systematic resurveying of biotic and abiotic variables, including inundation area, depth to groundwater, sediment composition and storage, geomorphic complexity and dynamism, flow velocity, stream temperatures, large wood dynamics, vegetative composition, macroinvertebrate production and diversity, salmon spawning use, juvenile salmon residence time, growth and survival, environmental DNA and high-resolution remotely sensed imagery.

In <36 h during September 2020, enhanced by extreme fuel aridity and dry east winds, the Holiday Farm Fire burned >600 km^2 of the forested McKenzie River basin, including the restoration site. Historical wildfire records indicate that the project site has a fire return period between *c*. 35 and *c*. 150 years, generally displaying mixed burn severity (Spies et al., 2018; USDA, 2015). The last high-severity, stand-replacing wildfire was in 1902, in the south section of the study site, which fits within the SFMR historical wildfire return interval (Reilly et al., 2021; Reilly et al., in press). However, in the last century, fire suppression in the wider McKenzie River Basin region has increased future risk of high-intensity, stand-replacing wildfires for the SFMR study site (USDA, 2016). This site provides a novel pseudo-experimental set-up, enabling comparison of pre-burn, immediately post-burn and short- to medium-term wildfire recovery between restored and unrestored stretches of the SFMR, addressing the research gap of robust wildfire–aquatic ecosystem study designs identified by Bixby et al. (2015).

To leverage and supplement the original monitoring programme, in February 2021 we initiated a multi-disciplinary project to measure and evaluate post-burn conditions. The aim was to understand the degree to which Stage Zero restoration changed the behaviour of the wildfire from a uniform, severe burn to a "fire mosaic", whether the presence and persistence of wildfire refugia result in more rapid post-burn recovery of biodiversity (Fairfax & Whittle, 2020), and whether the wildfire increased biodiversity owing to higher heterogeneity of post-burn niches, both within and between burned patches (Parr & Andersen, 2006).

This project will enable us to test the "pyrodiversity begets biodiversity" hypothesis empirically, in addition to providing a robust investigation of whether wildfire-related shifting habitat mosaics interact with heterogeneous floodplain mosaics to enhance biodiversity (Kleindl et al., 2015; Parr & Andersen, 2006). Initial observations indicate that unrestored parts of the landscape suffered a severe, uniform burn, whereas restored areas displayed more heterogeneous burn mosaics and exhibited faster recovery (Figures 2 and 3).

Further information about restoration to Stage Zero conditions can be found on the Stage Zero information hub website (http://stagezeroriverrestoration.com/index.html).

begets biodiversity hypothesis is both mixed and context dependent (Moritz et al., 2014; Pastro et al., 2011). For example, in tropical riparian systems, which are generally more fire sensitive, occasional lower-intensity fires can produce beneficial local-scale shading heterogeneity to enhance biodiversity (Kellman & Meave, 1997). However, tropical riparian systems generally experience very high vegetation mortality during high-intensity fires associated with drought, with protracted post-fire recovery (Flores et al., 2014, 2020). Furthermore, there is a paucity of examples for aquatic systems describing direct linkages between pyrodiversity and either riparian and aquatic habitat variability or species biodiversity (Bixby et al., 2015).

Anthropogenically driven climate change is increasing the frequency, intensity and duration of droughts and wildfires (Abatzoglou & Williams, 2016; Williams et al., 2019). This, in conjunction with general trends of wildfire suppression (preventing smaller burns and leaving greater fuel loads), has heightened the risk of high-intensity wildfires globally (Jones et al., 2020; Liu et al., 2010). For example, empirical evidence from Australia and the Pacific Northwest of the USA strongly implies that post-colonization "suppression-based" wildfire regimes have altered vegetation structure and increased vulnerability to high-intensity wildfire compared with pre-colonial, indigenous burning management (Fletcher et al., 2021; Hagmann et al., 2021; Halofsky et al., 2020; Haugo et al., 2019; Holz et al., 2021; Mariani et al., 2022; Trauernicht et al., 2015; Walsh et al., 2018). These high-intensity and historically unprecedented wildfire events increasingly incur negative impacts on river ecosystem biodiversity; for example, via high sediment loading, which degrades post-wildfire water quality (Robinne et al., 2021). The role of indigenous wildfire management in promoting biodiversity via the production of successional habitat mosaics and reduced high-intensity fire risk is supported by palaeoecological evidence and has the potential to be mirrored in present-day management (Adeleye et al., 2021). Consequently, "patch mosaic burning" (PMB), wherein either low-intensity fires are lit during wetter, cooler periods outside natural ignition periods or frequent, naturally ignited wildfires are

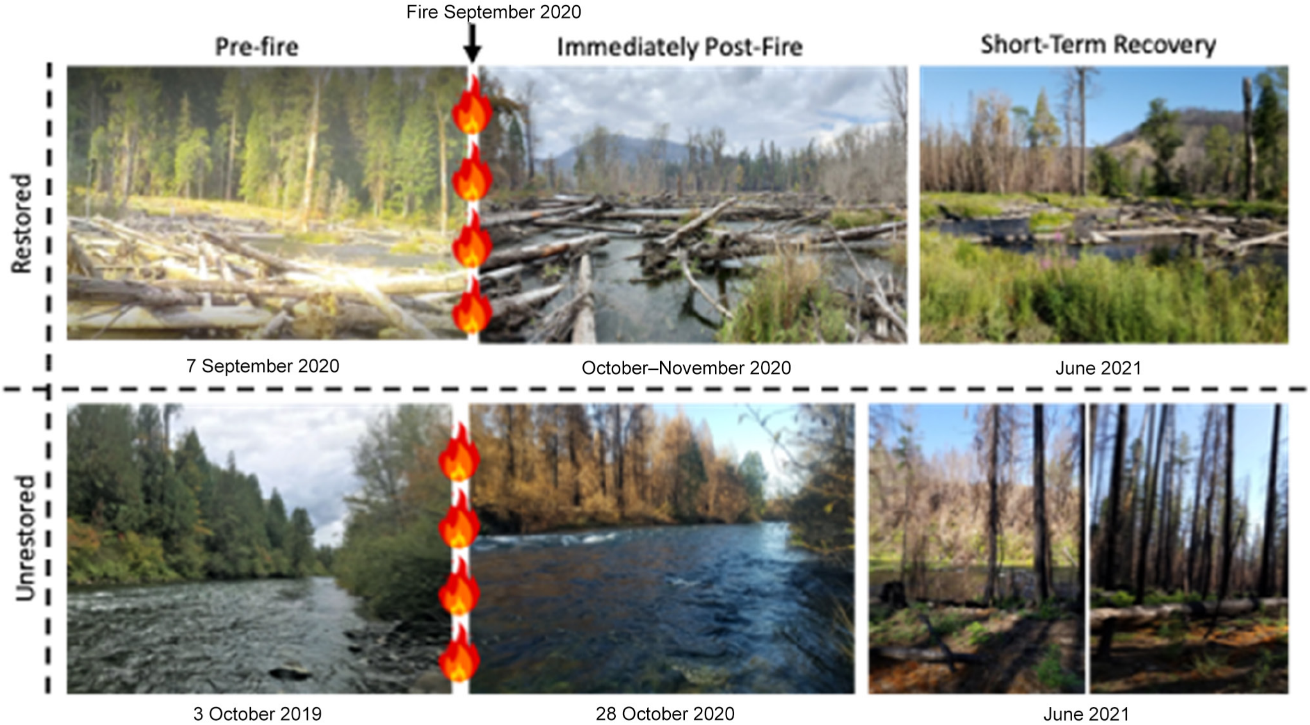

FIGURE 2 Comparison of restored and unrestored reaches of the South Fork McKenzie River, Oregon, USA, before (autumn 2019 and summer 2020), immediately after (October–November 2020) and during the initial post-burn recovery period (June 2021) for the "Holiday Farm" wildfire, which occurred in September 2020. Photograph credits: Robert Ashworth, Colin Thorne, Lisa Renan, Mickey Means-Brous, Dan Scott and Kate Meyer. Note that burn was generally more heterogeneous and habitat recovery faster in the restored reach.

permitted to burn, is being used increasingly as a management tool to reduce the risk of large, high-intensity wildfires, enhance habitat heterogeneity and restore hydrological processes (Greenwood et al., 2021; Stephens et al., 2021). For example, in the tropical savannas of Chapada dos Veadeiros National Park, Brazil, where in 2017 a drought-induced, high-intensity fire devastated riparian biodiversity, smaller prescribed burns are being used to reduce high-intensity fire risk and conserve biodiversity (Flores et al., 2020).

Acknowledging the importance of wildfire in promoting pyrodiversity and subsequent biodiversity in wildfire-prone ecosystems, recent research recognizes that in areas susceptible to both wildfires and flooding, these disturbance processes interact to reshape "visible" (current) and "invisible" (historical) successional habitat patch dynamics to varying degrees, and therefore, biodiversity (Kleindl et al., 2015). In these systems, wildfire generally becomes a more dominant shaper of floodplain habitat mosaics during drier periods, and flooding becomes more dominant during wetter periods (Bisson et al., 2003; Kleindl et al., 2015; Rood et al., 2007). For example, in the lower Colorado River (North America), reduced flooding attributable to flow regulation by upstream dams drives replacement of native willow (*Salix* spp.) and cottonwood (*Populus* spp.) by the more salt- and drought-tolerant invasive saltcedar (*Tamarix ramosissima* Lebed.), with negative impacts on migratory bird populations (Nagler et al., 2005). Even with flood-pulse events, regeneration of mature native forest stands is currently inhibited by tree mortality incurred by intermittent wildfires on drier floodplains, meaning that management to restore native habitat mosaics requires restoration of combined wildfire and flood regimes (Nagler et al., 2005).

Importantly, even when more natural flooding and fire regimes are restored, effects on aquatic systems are variable and depend on local or watershed-scale processes. For instance, in Yosemite and Kings Canyon-Sequoia National Parks, USA, a policy to allow naturally ignited fires to burn from *c.* 1970, following a century of fire suppression, reduced forest cover (and therefore, evapotranspiration) in Illilouette Basin, subsequently increasing streamflow, soil moisture and pyrodiversity. In contrast, only marginal change was observed in neighbouring Sugarloaf Basin, probably owing to regional differences in precipitation and fire regimes (Stephens et al., 2021). It follows that, in order to understand how the pyrodiversity begets biodiversity hypothesis applies to rivers with restored floodplain connectivity, the inter-relationships between flood and wildfire processes and spatial mosaics, and their specific ecosystem attributes, must be elucidated. Future research should consider how interactions between successional habitat mosaics from flooding and fire disturbances relate to the intermediate disturbance hypothesis, which posits that biodiversity will be highest at "intermediate" disturbance frequencies and intensities (Fox, 2013). This is particularly important because projected increases in wildfire severity and frequency in many global regions might alter biodiversity–disturbance outcomes.

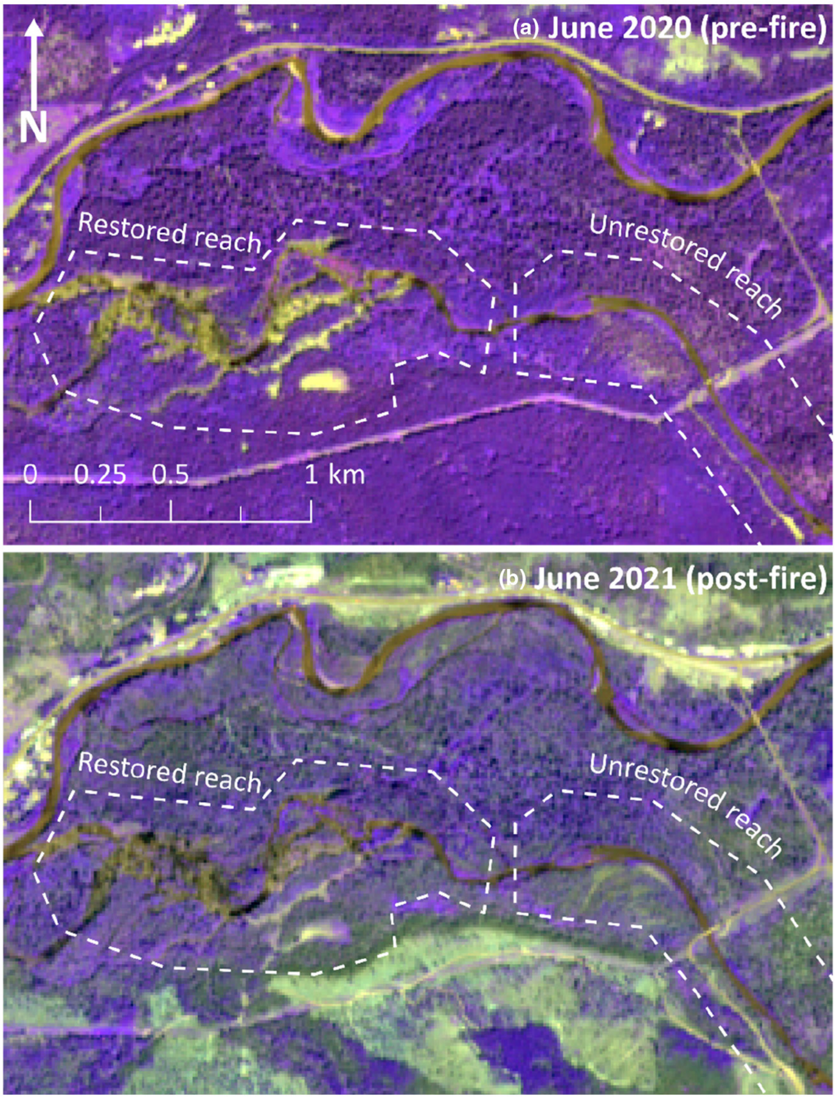

FIGURE 3 False-colour Sentinel 2 satellite images of the South Fork McKenzie restoration project site for: (a) 26 June 2020 (pre-fire; Sentinel 2A); and (b) 26 June 2021 (post-fire, Sentinel 2B). False colour bands [band 1 (red) = green; band 2 (green) = red; band 3 (blue) = near infrared] were chosen to maximize interpretability for colour-blindness. Blue/purple areas indicate vegetation; yellow/green areas highlight areas of vegetation loss that, in the post-fire imagery, are primarily attributable to the "Holiday Farm" wildfire in September 2020. Note that areas of vegetation loss are much more prevalent in the riparian zone of the unrestored reach than in the restored floodplain.

3 | RIVER RESTORATION AND WILDFIRE DYNAMICS

Although a few studies have considered the effect of wildfire management or peatland restoration on aquatic ecosystems (Bixby et al., 2015; Granath et al., 2016), to our knowledge, no study has assessed empirically the influence of river restoration involving explicit floodplain reconnection on the behaviour and effects of wildfires. Research into the collective impacts of wildfires and floods in generating habitat mosaics is also limited (Bixby et al., 2015). However, research into key mechanistic links between aquatic ecosystems and fire processes has been synthesized, notably by Bixby et al. (2015) and Robinne et al. (2021). Relevant studies generally display more positive post-wildfire biodiversity trends under more "natural" wildfire and flooding regimes, compared with those that have been altered heavily (Cordes et al., 1997; David et al., 2018; Nagler et al., 2005; Robinne et al., 2021; Rood et al., 2007). Therefore, it is expected that the re-establishment of extensive floodplain connectivity should reduce fuel connectivity, resulting in a larger range of fire effects that, in turn, promote biodiversity (exemplified in Box 2). Further studies are required to identify the environmental processes responsible for generating these predicted positive outcomes (predicted in Table 1).

Although studying wildfire–river restoration interactions has the potential to inform broad-scale ecosystem management, local variables, such as climate, species present and their functional characteristics, will alter observed biodiversity outcomes. For example, Dallaire et al. (2019) define 127 river reach categories globally, with differing combinations of factors such as hydrology, climate and biology. For example, ecosystems in the Mediterranean Basin and in many across Australia are highly wildfire prone, implying that over long time periods these river ecosystems have adapted, and therefore, ecosystem resilience to wildfires is generally higher than in other, less fire-prone regions (Leigh et al., 2015; Verkaik et al., 2013). However, river ecosystem recovery in comparable fire-prone ecosystems is highly sensitive to pre- and post-fire climatic conditions (Leigh et al., 2015). For instance, in the temperate Pacific Northwest of the USA, wetter forests west of the Cascade Range display longer historical return intervals and higher fire severities than drier forests east of the Cascades (Halofsky et al., 2018), and their postfire responses depend on wet years in the latter ecosystem (e.g., Busby et al., 2020).

Despite the well-known heterogeneity in post-wildfire biodiversity response between river systems, research on wildfire–flooding interactions is biased towards montane streams in western North America (Bixby et al., 2015). Furthermore, most floodplain reconnectivity restoration projects (e.g., Stage Zero) have occurred in North America in depositional and historically fire-prone river systems, with a focus on reinstating lateral, vertical and longitudinal connectivity between river–floodplain–wetland complexes (Bond et al., 2019; Fisher, 2018; Guida et al., 2015; Hinshaw & Wohl, 2021; Scagliotti, 2019). More research is therefore required to understand differences between flooding–wildfire interactions and related river restoration–wildfire interactions in biomes beyond North America, in order to inform locally relevant ecosystem management.

Recent widespread alteration in wildfire regimes will also alter flooding–wildfire interactions, and consequently, the effects of river restoration on wildfires (Robinne et al., 2021). In addition to direct effects of wildfire on river ecosystems, watershed-scale processes (e.g., debris flows and altered potential evapotranspiration) will be impacted by altered fire regimes, producing further impacts on river systems. More frequent and high-intensity wildfires have the potential to impact river restoration outcomes negatively. For example, in the Colorado Rocky Mountains, USA, restoration involving beaver activities and application of mulch to stabilize burned hillslopes was used to reduce post-wildfire river sediment load from debris flows. However, a high-intensity, stand-replacing wildfire (possibly indicative of recent climatic alteration of regional fire regimes), combined with severe precipitation events, prevented mulch treatments from stabilizing hillslopes via vegetation regrowth (Rathburn et al., 2018).

The relative spatial and temporal scales (grain and extent) of river restoration projects and wildfires will also affect their predicted interactions. This is important to consider for ecosystem management. Much previous literature recognizes the importance of the timing and frequency of disturbance events, such as wildfires, in predicting aquatic and riparian biodiversity recovery, especially in accordance with other seasonal characteristics, such as climate (Jackson & Sullivan, 2015; Mester et al., 2015). Floodplain reconnectivity restoration projects often operate at the reach scale (e.g., most existing Stage Zero projects) and involve the restoration of pre-Anthropocene biotic and abiotic processes (Cluer & Thorne, 2014; Table 1), all of which operate on a range of spatial and temporal scales. Studies have demonstrated that reach-scale floodplain reconnectivity restoration can have positive impacts on biodiversity and nutrient cycling (Hinshaw & Wohl, 2021; Jennings, 2021), with predicted higher resilience to wildfire by increasing local heterogeneity of burn severity, as demonstrated by the case study in Box 2. However, to maximize the resilience of river systems to future wildfires, more research into restoration–wildfire interactions at different spatial and temporal scales must be undertaken to understand variable biodiversity outcomes.

Reconnection-type restoration projects occurring beyond the reach scale impact biodiversity differentially and will therefore impact post-wildfire biodiversity recovery differentially. For example, small-scale river restoration on the Cosumnes River floodplain (40 ha) provides local benefits to fish species, compared with the broader-scale Yolo Bypass (24,000 ha), where floodplain inundation can be used as a predictor for fish productivity for the whole river system (Opperman et al., 2010). Additionally, reach-scale restoration cannot address wider issues, such as excess nutrient input or sediment starvation from damming upstream (Poff et al., 1997; Roley et al., 2012; Wohl et al., 2015). Therefore, broader process alteration and restoration at the river watershed scale should be considered for restoration–wildfire interactions. For example, in Illilouette Creek Basin, California, modelling demonstrated that historical fire suppression increased tree growth and watershed evapotranspiration, and subsequently, decreased streamflow, meaning that at the watershed scale, restoration of natural river flow regimes requires wildfire regime restoration (Boisramé et al., 2019).

4 | MECHANISMS GENERATING POSITIVE BIODIVERSITY OUTCOMES FROM RIVER RESTORATION–WILDFIRE INTERACTIONS

4.1 | Proposed short-term mechanisms

Although the interaction of wildfires and river restoration is not considered directly within previous literature, research into more general river ecosystem–wildfire interactions can provide insights into likely mechanisms behind faster recovery and more heterogeneous burn severity, as indicated by preliminary visual observations in our SFMR study site in Box 2. We propose that owing to the historical role of wildfires in generally promoting native biodiversity in river corridors well connected to their floodplains (Bixby et al., 2015; Nagler et al., 2005), short-term mechanisms for post-wildfire biodiversity enhancement outcomes under floodplain reconnectivity river restoration might relate to the impact of keystone species and reducing the impact of problematic invasive species. Investigating how beaver damming activities by this keystone species and the ensuing creation of wetland habitat (an increasingly key component of North American and European river restoration schemes; Johnson et al., 2020; Wohl et al., 2015) respond to wildfire events provides an empirical example of research into wildfire–flooding interactions within a restoration context. A study using remote sensing-based vegetation indices from multiple North American fires (with varying pre-wildfire drought conditions and burn severity) concluded that beaver activity increased wildfire resistance of vegetation via increased wildfire refugia in comparison to rivers without beaver damming (Fairfax & Whittle, 2020). Likewise, beaver structures reduced high post-wildfire sediment loading on rivers in the Colorado Rocky Mountains, USA (Rathburn et al., 2018). Importantly, although useful information can be gained from remotely sensed data alone, as in much previous literature (e.g., Fairfax & Whittle, 2020; Flores et al., 2014), future research should focus on combining remotely sensed data analyses with both aquatic and terrestrial field data to allow a detailed mechanistic understanding of wildfire effects on riverine, riparian, wetland and floodplain ecosystems. [Note that beavers are present in the restored SFMR study site (Box 2), which could be linked to its relatively rapid recovery of biodiversity (Figures 2 and 3). Further work is planned for summer 2022 to investigate this.]

The relationship between invasive species and disturbances such as flooding and wildfire is complex and variable, with widely contrasting patterns reported in the literature. Under wildfire-driven increased water temperature and debris flows, post-wildfire mortality was higher, and recovery was found to be lower for invasive fish species than for some native fish species in western North America (Sestrich et al., 2011). However, some problematic invasive species have been found both to impact riverine ecosystem structure negatively and to have high resilience to wildfire, thus further increasing ecosystem vulnerability in degraded ecosystems subject to high-severity fires (Aguiar et al., 2021; Flores et al., 2021; Nagler et al., 2005; Whitney et al., 2015). For example, invasive fish species displayed smaller population declines than native species, and only invasive tadpoles or crayfish were present after consecutive wildfires in Gila River, New Mexico (Whitney et al., 2015). Likewise, the invasive riparian grass species *Arundo donax* displayed higher productivity and growth than native species after the October 2003 wildfire along the Santa Clara River, California (Coffman et al., 2010), further increasing wildfire spread, severity and vulnerability of riparian woodlands to ensuing wildfire events (Coffman et al., 2010). Although more research is required, floodplain reconnectivity river restoration could aid in restoring ecosystem habitat quality and connectivity for native species (Pearle et al., 2018), therefore altering invasive species–wildfire feedbacks in some contexts.

4.2 | Proposed longer-term mechanisms

Longer-term mechanisms for biodiversity enhancement associated with the interaction between river restoration and wildfires might include habitat connectivity, the interaction of wildfire with flooding processes and in-stream woody debris characteristics. High-severity fires can result in local extirpation of aquatic species, such as fish, via the heating of water during the fire, subsequent debris flows and the toxicity of fire-fighting chemicals (Bixby et al., 2015; David et al., 2018). In degraded or fragmented habitats, post-wildfire recolonization of locally extirpated fish populations from the regional species pool is restricted (Dunham et al., 2003). Floodplain reconnectivity river restoration, especially involving removal of longitudinal barriers to fish passage, will be likely to improve successful recolonization, owing to higher habitat connectivity and production of wildfire refugia for local populations. For example, in New Mexico, USA, native fish species took ≤2 years to recolonize burned reaches (Whitney et al., 2015) and modelling that compared post-burn debris flows in the Rocky Mountains, USA with Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) suggested that better habitat connectivity accelerated regional-scale post-wildfire recovery, particularly in river reaches more vulnerable to debris flows (Sedell et al., 2015). Reach-scale Stage Zero river restoration has been shown to enhance aquatic habitat connectivity and quality (Bond et al., 2019; Jennings, 2021), and larger floodplain reconnection projects have restored aquatic biodiversity connectivity further (Opperman et al., 2010; Wohl et al., 2015). Therefore, resilience of aquatic organisms to high-severity wildfire events could increase from the reach scale to the watershed scale depending on the extent of restoration.

More natural flooding regimes associated with extensive restoration of floodplain reconnectivity generally result in deposition of large wood, organics and fine sediments onto river floodplains. A study comparing burned and unburned sites containing wood deposited in semi-arid, riparian habitats in South Africa concluded that heterogeneity of habitat mosaics was enhanced owing to the differential impacts that wood had on localized tree mortality, nutrient cycling and vegetation succession (Pettit & Naiman, 2007b). This increase in habitat mosaic heterogeneity by woody debris interacting with wildfire might therefore result from floodplain reconnectivity restoration. Finally, wildfires alter in-stream wood characteristics both by increasing wood recruitment (e.g., via windthrow and disease susceptibility) and by burning of in-stream woody debris (Vaz et al., 2013). Research in Portuguese streams indicates that high-intensity fires can decrease channel complexity, and therefore, adversely affect important channel functions, such as provision of microhabitat features and substrate provided by in-stream wood (Vaz et al., 2021). Of >3,000 pieces of wood placed in the restored reach of the study site presented in Box 2, only *c*. 1% were burned during the Holiday Farm wildfire (K. Meyer, personal communication, March 2022). This suggests that floodplain reconnectivity river restoration might protect in-stream wood from loss of existing functional complexity during a wildfire by increasing the area wetted at base flow (Jennings, 2021). If floodplain reconnectivity river restoration increases the variability of riparian burn severity via extensive floodplain re-wetting in comparison to unrestored reaches, the functional complexity of woody debris recruited after wildfire events (e.g., through windfall and decay) might also be more varied in restored reaches, providing long-term biodiversity benefits.

Trophic cascade effects, such as a longer-term reduction in leaf litter inputs post-wildfire (Bixby et al., 2015), are also likely to differ between reconnected river corridors and unrestored river corridors. However, the current literature on the interplay between aquatic ecosystems, wildfires and trophic cascades indicates context-specific and complex processes that require more research to be understood for a management context (Jager et al., 2021; Minshall, 2003; Verkaik et al., 2015). For instance, aquatic–riparian ecosystems are influenced by the timing of climatic variables, such as precipitation, in concurrence with wildfire events (Jackson & Sullivan, 2015), or reduction of riparian shading, which promotes algal growth, producing shorter-term flood–wildfire productivity pulse events (Malison & Baxter, 2010).

5 | CONCLUSION AND FUTURE DIRECTIONS

In conclusion, although current high-severity wildfire events are broadly problematic for people and biodiversity, historically, lower-intensity wildfires in wildfire-prone landscapes operated to promote river ecosystem biodiversity through patch mosaic burning in rivers with extensive floodplain connectivity. River restoration–wildfire interactions might therefore have important implications for effective biodiversity conservation and resource management when rivers undergo floodplain reconnectivity restoration. Preliminary observations from the SFMR case study (Box 2) align with previous literature in that, in wildfire-prone landscapes, the interactions of more natural wildfire and flooding regimes are important for increasing the resilience and resistance of ecosystems to disturbances so that net gains in biodiversity can be achieved (Bixby et al., 2015; Nagler et al., 2005; Robinne et al., 2021). This is particularly relevant given that even broadly unaltered flood and wildfire regimes are often in a state of flux owing to climatic changes (Bisson et al., 2003; Flores et al., 2021).

Our work not only demonstrates how floodplain reconnectivity river restoration might offer key benefits for interacting wildfire–biodiversity management, but also expands the theoretical basis for this river restoration paradigm. We expect that pyrodiversity does beget biodiversity in riverine ecosystems through the mechanism of shifting habitat mosaics, but only when more natural pyrodiversity (given the historical ecosystem context) interacts in step with other natural disturbance regimes and when the ecosystems in question can recover from these disturbances. We therefore suggest that in river ecosystems, the pyrodiversity begets biodiversity hypothesis might be too simplistic. Recovery of biodiversity can operate either via ecosystem resilience to wildfire events in step with wildfire return intervals, through mechanisms such as viable seed banks protected from wildfires by sufficient soil moisture (Aguiar et al., 2021), or via ecosystem resistance to fire itself, through mechanisms such as wetland refugia produced by beaver dams (Fairfax & Whittle, 2020). Theoretically, both resilience and resistance of river ecosystems to wildfires might therefore be enhanced by floodplain reconnectivity river restoration, particularly when the anastomosing channel form is restored to maximize floodplain mosaics (e.g., Stage Zero restoration). Future studies should test the generalizability of these patterns by researching the impact of the following factors: (1) how wildfire–flooding interactions differ between "conventional" channel-centred river restoration and floodplain reconnectivity restoration paradigms (Figure 1); (2) different pyrodiversity components, such as wildfire severity, intensity, frequency and extent (Tingley et al., 2016); (3) how wildfire–flooding interactions in rivers with extensive channel–floodplain connectivity shape biodiversity outcomes across biomes (e.g., tropical savannas, temperate grasslands), particularly for systems that did not co-evolve with wildfire disturbances; (4) whether there is a difference between the wildfire–river restoration relationship under different wildfire management regimes; (5) how the scale of river restoration projects and wider watershed restoration (e.g., afforestation, environmental flows) affect wildfire–river restoration interactions; (6) moving beyond only taxonomic diversity indices (Tingley et al., 2016) to consider how functional, phylogenetic or interaction diversity is impacted by river ecosystem–wildfire interactions; and (7) how restored river ecosystems respond to other disturbance regimes that interact with wildfires to produce landscape-scale shifting habitat mosaics (e.g., ice or pine beetle invasions; Kleindl et al., 2015; Rood et al., 2007) in comparison to unrestored rivers.

AUTHOR CONTRIBUTIONS

All authors contributed to the paper conceptualization, background information and editing of the manuscript. B.P. wrote the manuscript based on an outline by R.F. B.P. and S.J.D. made the figures.

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DATA AVAILABILITY STATEMENT

The Sentinel 2 imagery that supports the findings in this study is openly available at the Copernicus Open Access Hub using the following link: https://scihub.copernicus.eu/

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BIOSKETCH

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The research group representing all the authors is a collaboration between US and UK researchers contributing expertise on wildfires, river restoration, river dynamics, remote sensing and biodiversity. Many members also have practical experience of restoration projects, such as the South Fork McKenzie River Stage Zero project.

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