

ORIGINAL ARTICLE

# Linking Fire, Food Webs, and Fish in Stream Ecosystems

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## ABSTRACT

As wildfire regimes shift, resource managers are concerned about potential threats to aquatic ecosystems and the species they support, especially fishes. However, predicting fish responses can be challenging because wildfires affect aquatic ecosystems via multiple pathways. Application of whole-ecosystem approaches, such as food web modeling, can act as heuristic tools that offer valuable insights that account for these different mechanisms. We applied a dynamic food web simulation model that mechanistically linked stream trophic dynamics to the myriad effects that wildfires can have on aquatic and riparian ecosystems at a local stream reach-scale. We simulated how wildfires of different severity may influence short- (months to years) and long-term (years to decades) periphyton, aquatic invertebrate, and fish biomass dynamics in forested headwater streams of

the western Pacific Northwest (USA). In many cases, wildfire increased modeled periphyton, invertebrate, and fish biomass over both short- and long-time periods. However, modeled responses varied extensively in their direction (that is, positive or negative), magnitude, and duration depending on fire severity, time since fire, and trophic level. The shapes of these response trajectories were especially sensitive to predicted wildfire effects on water temperature, canopy cover, riparian shading, and instream turbidity. Model simulations suggest a single fire could result in a wide range of aquatic ecosystem responses, especially in watersheds with mixed burn severity. Our analysis highlights the utility of whole-ecosystem approaches, like food web modeling, as heuristic tools for improving our understanding of the mechanisms linking fire, food webs, and fish and for identifying contexts where fires could have deleterious impacts on fishes.

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**Key words:** Wildfire; Disturbance; Aquatic-terrestrial linkages; Ecosystem modeling; Food webs; Fish.

## HIGHLIGHTS

- We applied a food web simulation model to integrate the complex ways wildfires can influence aquatic ecosystems.
- Model simulations revealed that wildfires had diverse effects on aquatic ecosystems that varied with fire severity and time.
- Sensitivity analyses identified key mechanisms driving fish responses to wildfire, including riparian canopy cover and shading, water temperature, and instream turbidity.

## INTRODUCTION

As wildfire disturbance regimes shift, the severity and spatial extent of wildfires is increasing (Halofsky and others 2020; Rogers and others 2020; Hagmann and others 2021), causing wildfires to interact with forested landscapes in new places and in new ways (Turner 2010). This has direct implications for the river networks that permeate the landscape (Allan 2004; Davis and others 2013). Recent research has shown that the total stream length affected by fire in the western USA has increased over the last 40 years at a rate of over 300 km/year (Ball and others 2021). As a result, resource managers are concerned about the potential risk wildfires pose to sensitive aquatic species such as salmonid fishes (Family: Salmonidae) (Bisson and others 2003; Luce and others 2012). However, wildfires can have complex effects on aquatic and riparian ecosystems that can vary extensively in their magnitude and direction (Minshall and others 1989; Gresswell 1999; Dwire and Kauffman 2003; Pettit and Naiman 2007), making predictions of fire effects on top predators, like fish, difficult (Bixby and others 2015; Gomez Isaza and others 2022). New approaches are needed to synthesize the multiple pathways through which fires can influence aquatic ecosystems and identify the mechanisms driving these responses. Here, we demonstrate how whole-ecosystem approaches, such as food web modeling, can provide valuable insights that improve understanding of the mechanisms driving fish responses to fire (Power 2001; Bellmore and others 2017; Geary and others 2020).

Aquatic ecosystems are tightly linked with adjacent riparian forests, especially small low-order forested streams (Vannote and others 1980; Baxter and others 2005), and forest disturbances like wildfire can have a myriad of direct and indirect effects on aquatic and riparian ecosystems (Min-

shall and others 1989; Gresswell 1999; Davis and others 2013). Foundational work by Minshall (1989, 1997, 2003) and Gresswell (1999) provided the conceptual basis of understanding for how fires influence aquatic ecosystems. Minshall and others (1989) and Gresswell (1999) detailed how fires can have a series of direct effects on physical attributes of watersheds, especially when combined with post-fire storm events that can strongly affect channel morphology, instream sediment, nutrients, temperature, and flow regimes. At the same time, loss of riparian vegetation from wildfire can disrupt riparian controls on shade, stream temperature, terrestrial resource inputs, and aquatic primary production (Minshall and others 1989; Gresswell 1999). These co-occurring changes in instream and riparian conditions can influence biological communities across multiple trophic levels from basal resources to top predators like salmonid fishes (Minshall and others 1989, 1997; Gresswell 1999). Conceptual models developed by Minshall and Gresswell also emphasized that fire effects can be highly dynamic through time. In general, post-fire changes in sediment and nutrient concentrations are predicted to be relatively short-lived (for example, 1–5 years) (Minshall and others 1997; Minshall 2003). Comparatively, other responses such as the availability of aquatic and terrestrial basal resources may persist for longer periods of time (for example, over 10–20 years) (Spencer and others 2003; Rugenski and Minshall 2014). Such conceptual models suggest that even when wildfires have what can be perceived as negative effects, these effects are often limited to the first few years post-fire, and are frequently followed by an eventual post-fire recovery highlighting the ultimate resilience of aquatic systems (Romme and others 2011; Rugenski and Minshall 2014).

In the last 20–30 years, a growing body of work has contributed much in the way of highlighting the *variability* in fish and aquatic ecosystem responses to wildfire (Verkaik and others 2013; Bixby and others 2015; Gomez Isaza and others 2022; Erdozain and others 2024). Recent empirical studies have shown that aquatic responses to fire often vary with fire severity (Jackson and others 2012; Cooper and others 2015). Typically, water quality and aquatic ecosystem responses are smaller following lower severity fires and greater following higher severity fires (Malison and Baxter 2010a, b; Jackson and others 2012; Cooper and others 2015). Empirical studies have also revealed that aquatic responses to fire can vary spatially depending on the context of where a wildfire burns (Bixby and

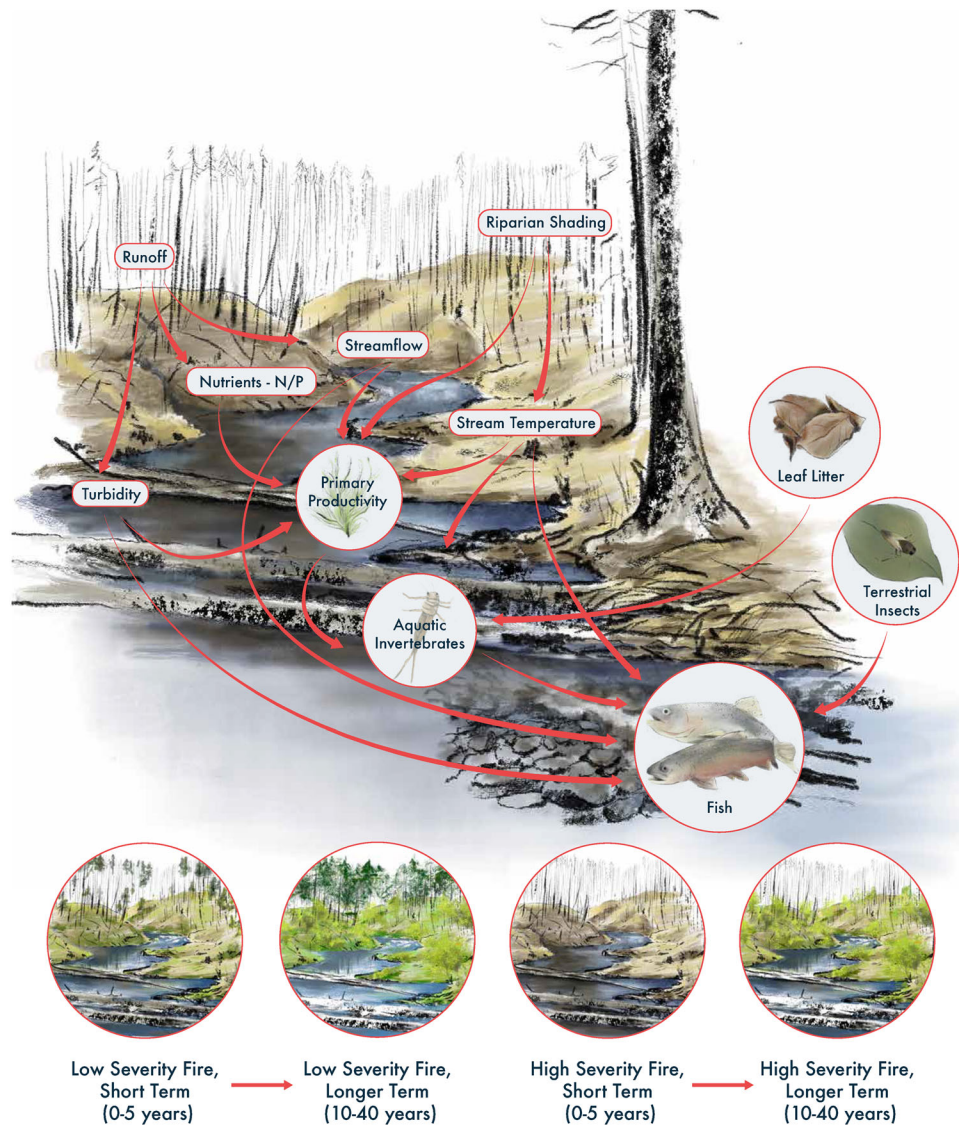
others 2015; Verkaik and others 2015). For example, in mountainous regions post-fire landslides and debris flows are a common occurrence, resulting in mobilization of large volumes of sediment into streams and rivers, leading to abrupt local and downstream declines and even extirpations of fish populations (Burton 2005; Howell 2006; Rust and others 2019; Reale and others 2021; Preston and others 2023). In contrast, in regions with topographies less prone to erosion or with less frequent high intensity precipitation events, post-fire reductions in riparian vegetation can lead to increases in nutrients and solar radiation that interact to boost aquatic productivity across multiple trophic levels (Silins and others 2014; Emelko and others 2016; Swartz and Warren 2022). These contrasting results highlight just two potential sources of heterogeneity in fire effects that can lead to dramatically different outcomes.

Although observations from recent empirical work have shed new light on the context dependency of wildfire effects, inferences from empirical studies remain limited for several reasons. First, empirical investigations essentially act as case studies that do not necessarily pertain to other locations and contexts due to inherent spatial heterogeneity both within and across watersheds. Second, empirical studies tend to be biased toward short-term responses due to the logistical challenges of longer-term investigations (Minshall and others 1997). Third, empirical studies are inherently retrospective in nature and can only evaluate past disturbance events, and thus, may have little inferential power to anticipate the effects of future fires as wildfire disturbance regimes shift and fire moves into new areas (Turner 2010; Davis and others 2013). As a result, new approaches are needed to update our conceptual frameworks and anticipate the implications of wildfires and shifting fire regimes for fish and aquatic ecosystems, especially in regions where fire effects are poorly understood (Davis and others 2013).

As fire activity increases, resource managers want to know whether wildfire poses risk for sensitive aquatic species like salmonid fishes (Bisson and others 2003; Luce and others 2012). However, it can be difficult to predict how top predators like salmonid fishes respond to fire without also understanding how the broader ecosystem responds (Bascompte 2010; Bellmore and others 2017; Naman and others 2022). As a result, application of whole-ecosystem or food web perspectives that integrate top predators with their broader ecosystem can lend important insights into the mechanisms driving fish responses to wildfire

(Bellmore and others 2017; Geary and others 2020; Naman and others 2022). Fish responses to fire likely depend on multiple interacting pathways that affect both the physical habitat conditions that support fish as well as the trophic interactions supporting fish (Figure 1). An understanding of how these physical and biological pathways change after fire, how they interact with one another, and how they vary in space and time can provide essential clues of how fish are likely to respond to fire. Moreover, the pathways linking fires and fish are likely dynamic through time as fire effects can simultaneously push and pull the system in different directions, causing fish responses to follow diverse sets of trajectories through time (Figure 2). As a result, the application of a food web perspective, which integrates the multiple direct and indirect effects on the physical habitat and trophic resources supporting fish, can more effectively articulate not just *how*, but *why* fish are likely to respond to fire (ATP; Bellmore and others 2017; Geary and others 2020; Naman and others 2022).

In our study we applied a dynamic food web simulation model, the Aquatic Trophic Productivity model (ATP; Bellmore and others 2017; Whitney and others 2019), to explore aquatic ecosystem responses in low-order forested streams to wildfire. Food web models can provide holistic insights into responses to environmental change and disturbance (McIntire and Colby 1978; Power 2001). In this regard, the ATP model has been previously applied to understand how river food webs respond to a range of human-mediated and natural disturbance processes such as stream restoration practices (Bellmore and others 2017; Whitney and others 2020), dam removal (Bellmore and others 2019), forest harvest, and climate change (Benjamin and others 2022). The objectives of our study were to: (1) link the dynamics of the ATP model with the multiple pathways that wildfires influence aquatic ecosystems (Figure 1) in headwater streams in westside forests of the Pacific Northwest, USA (PNW), a region characterized by infrequent, high severity fire regimes with little recent fire history (Reilly and others 2017) and so fire effects remain poorly understood; (2) simulate how wildfires influence the biomass dynamics of periphyton, in-stream terrestrial detritus, aquatic invertebrates, and fishes over short- (months to years) to long-time (years to decades) scales; and (3) identify the potential mechanisms driving fish biomass responses to fire. To address these objectives, we ran model simulations comparing how different fire severities influence stream ecosystem dynamics across multiple trophic levels. This version of the



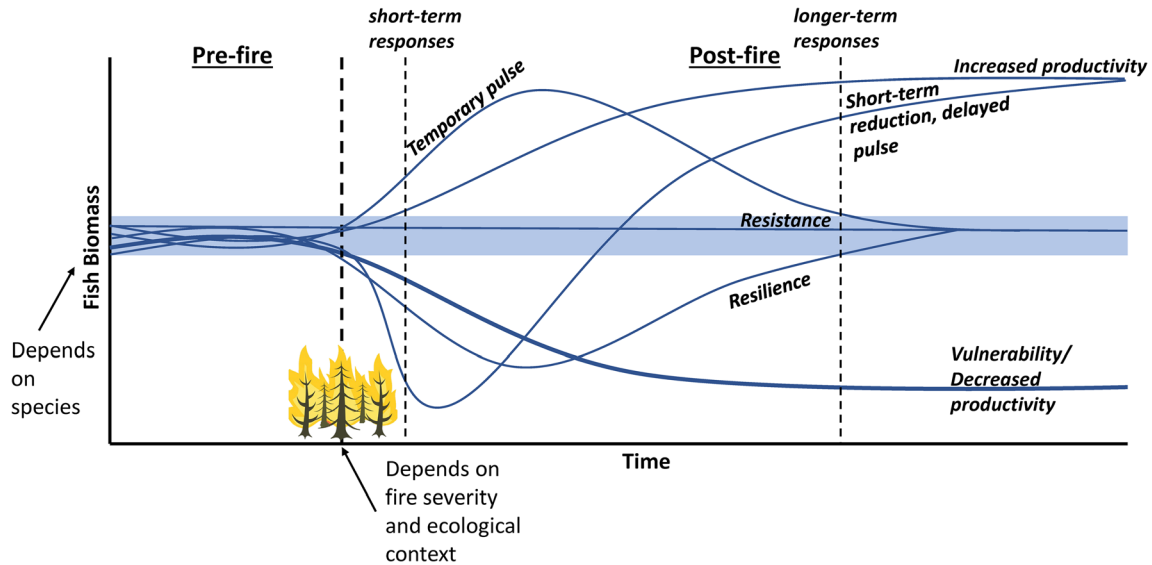
**Figure 1.** Wildfires can have complex effects on aquatic and riparian ecosystems that affect the physical habitats and the trophic interactions supporting fish. An understanding of the pathways linking fires and fish, how they interact, and how they vary over space and time can provide improved insights and predictions of the mechanisms driving fish responses to wildfire. Moreover, the relative strength of these pathways likely vary with fire severity (low vs. high severity) and the amount of time post-fire (short term vs. longer term), leading to different ecological outcomes. Illustration by Cecil Howell.

model focused on small low-order forested streams, as they compose over 80% of the stream network by length and due to their tight connections with riparian forests (Vannote and others 1980; Power and Dietrich 2002). Responses were modeled over time to capture immediate and longer-term post-fire effects as well as post-fire recovery trajectories (Minshall and others 1989; Gresswell 1999).

## METHODS

### Model Description and Parameterization

The ATP model is structured to represent the generalized trophic dynamics of lotic ecosystems and simulate the resulting biomass of different ecosystem components (Supplemental Figure S1). The ATP simulates the energetic capacity of a stream to support producer and consumer biomass by linking the food web dynamics to instream physical conditions and riparian vegetation conditions (Bellmore and others 2017). As such, model simulations



**Figure 2.** Conceptual models of post-fire trajectories of potential fish biomass over time. Fish responses to fire are likely highly variable through time depending on the severity of the fire, the ecological context of where the fire takes place, as well as the species of fish in question. Potential post-fire responses that may emerge include resistance (no response to fire), resilience (a short-term negative response followed by recovery to pre-fire levels), temporary pulse (a short-term positive response followed by recovery to pre-fire levels), increased productivity (sustained post-fire increases), vulnerability (sustained post-fire decreases), and complex (for example short-term reduction followed by an eventual pulse).

estimate the potential biomass a stream can support and how that may change over time. At the base of the model food web are biomass stocks of periphyton (for example, attached algae and heterotrophic microbes on the streambed) and terrestrial detritus (for example, leaf litter from riparian vegetation) that are consumed by aquatic invertebrates, which along with terrestrial invertebrates that enter the stream from the riparian forest, are consumed by fish. Fish and aquatic invertebrate consumption rates are modeled as a function of both: (1) density dependence, whereby consumption rates decrease as conspecific densities increase; and (2) food availability, whereby consumption rates increase as resource availability goes up following a type II functional response (see Bellmore and others 2017). In turn, consumers deplete the availability of resources when consumption exceeds the rate of resource renewal, which can result in density-dependent resource limitation. As a result, the ATP model incorporates the bottom-up (resource availability) and top-down (predation) processes that drive food web dynamics. The model runs on a daily time step and tracks the potential biomass of periphyton, terrestrial detritus, aquatic and terrestrial invertebrates, and fish through time in units of grams of ash-free dry mass per square meter ( $\text{g AFDM}/\text{m}^2$ ). The model operates at a

reach-scale and estimates of potential biomass of producer and consumers a stream reach could support. Producer (periphyton) and consumer biomass (fish and invertebrates) increases when primary production or energy assimilation exceeds energy losses to respiration, mortality and predation/grazing. For more information about model structure and the mathematical equations used, see Bellmore and others (2017) and Whitney and others (2019).

Biomass dynamics in the ATP model are mechanistically linked to the seasonal patterns of riparian forest and instream physical environmental conditions typical of many gravel-bed headwater streams in the PNW (Bellmore and others 2017; Whitney and others 2019; Benjamin and others 2022). This includes important functions in the model inputs controlling local, reach-scale riparian forest conditions (canopy cover, shading, and canopy composition) and instream conditions (flow regimes, thermal regimes, nutrient concentrations, and turbidity) (see Supplemental Figure S2a). For example, in the model riparian shading controls the amount of light available for primary production (Whitney and others 2019). Riparian canopy cover and composition controls the type and abundance of terrestrial inputs of leaf litter and invertebrates (Whitney and others 2019). Streamflow controls

the seasonal patterns of stream depth, width, velocity, and shear stress, via a one-dimensional hydraulic model which in turn influences the retention and export of organisms and organic matter (Bellmore and others 2017), as well as the amount of wetted habitat available and suitable to support biological production of all trophic levels (Benjamin and others 2022). Stream temperature influences the metabolism of all trophic levels as well as the decay rate of organic matter and periphyton (Whitney and others 2019). Nutrient concentrations (nitrogen and phosphorus) control nutrient limitation of stream periphyton (Benjamin and others 2022). Instream turbidity (a measure of suspended sediment concentrations and light penetration in water) influences light availability for periphyton production (Whitney and others 2019) as well as foraging efficiency of top predators (Benjamin and others 2022).

In this analysis, we parameterized the ATP model to represent small forested headwater streams of the PNW. Many parameters were based on the Trask watershed in NW Oregon previously used in a model analysis by Benjamin and others (2022). For parameters with partial or incomplete datasets (for example nutrient concentrations or instream turbidity), we made assumptions on seasonal patterns based on best understanding of likely conditions for the region. See Table S1 for data sources. Specifically, we parameterized the model with daily flow, temperature, nutrient, and turbidity regimes that represent seasonal dynamics commonly found in forested headwater streams in this region (Supplemental Figure S2a). We parameterized the model to represent typical riparian forest conditions along headwater streams, including: canopy cover, riparian shading, and canopy composition (deciduous versus coniferous) (see Supplemental Figure S2a). We modified the original structure of the ATP model described in Bellmore and others (2017) according to updates made in Benjamin and others (2022) to represent the structure of food webs found in forested headwater PNW streams. Aquatic invertebrates were divided into two stocks: one that primarily consumes periphyton (algivores) and one that primarily consumes terrestrial detritus (detritivores), although resource switching occurs between these invertebrate groups (Rosi-Marshall and others 2016). Fish were also divided into two stocks to represent the fish assemblage typical of PNW headwater streams, including a stock of resident salmonids (for example, resident rainbow or cutthroat trout) and a stock of benthic sculpin (*Cottus* spp.). Fish compete for invertebrate prey resources, but distinct foraging preferences are

incorporated into the model where salmonids feed on a combination of aquatic and terrestrial invertebrates, whereas sculpin feed preferentially on aquatic invertebrates (Falke and others 2020; Benjamin and others 2022).

## Model Limitations and Caveats

The ATP model applied in this analysis is intended as a heuristic tool that simulates the generalized food web dynamics of forested headwater stream ecosystems of the PNW. However, there are some limitations to the model that the reader should keep in mind. First, model simulations estimate the *energetic capacity* to support consumers based on riparian and instream habitat conditions, and can be thought of as the *potential biomass* a stream can support. The ATP model tracks population biomass, not the number of individuals in a population, nor the parameters commonly found in population dynamics models (for example, reproduction and recruitment). Second, ATP model simulations are not presumed to be precise predictions, but rather hypotheses about how stream food web dynamics may change over time. Third, this application of the ATP model operates at a *local, reach-scale*, but does not capture the broader spatial patterns throughout a watershed. Nevertheless, model simulations provided by the ATP can offer unique whole-system insights that improve understanding into how a stream ecosystem may respond to a disturbance like wildfire.

## Modeling Fire Effects on Aquatic Ecosystems

To represent the complex ways that wildfires can influence aquatic ecosystems, we incorporated a series of different fire effects into the model that reflect current understanding (Table 1). We focused on local and upstream reach-scale processes that often occur simultaneously after fire from the loss of riparian vegetation and changes in watershed hydrology that can lead to increased runoff and streamflow, and increased erosion of sediments (Minshall 1989; Gresswell 1999; Bixby and others 2015). To model the effects of wildfire, we modified the baseline conditions of the model meant to represent the seasonal patterns of a forested watershed (Supplemental Figure S2a) by the fire effects described in Table 1 to different magnitudes and extents as depicted in Figure 3 to represent low, moderate, and high severity fires. Table 1 summarizes the environmental inputs to the model that were modified to represent wildfire conditions,

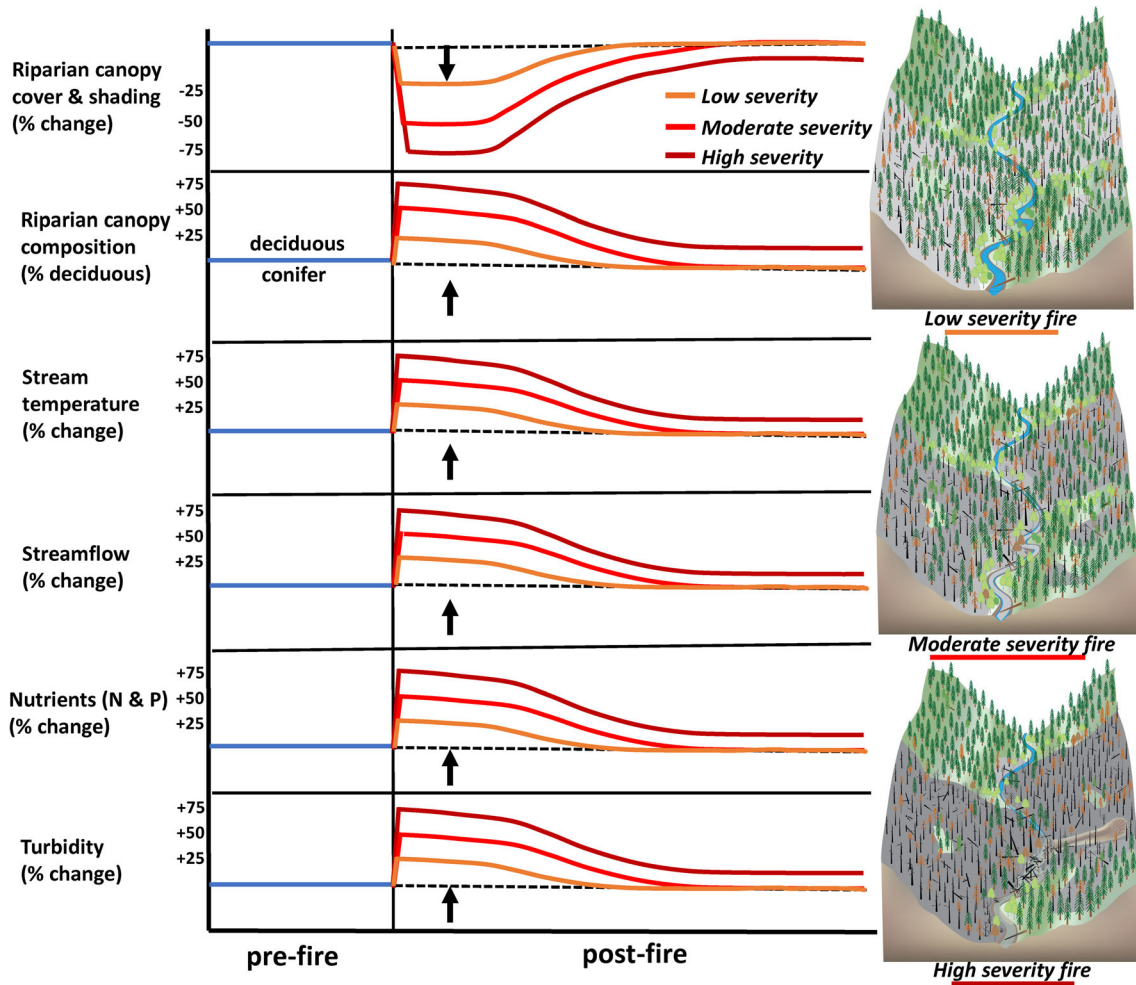
**Table 1.** Fire Effects on Aquatic Ecosystems Included in the Model

Variable	Fire effect	Key references
1) Riparian canopy cover	Fire reduces riparian canopy cover, which can decrease the quantity of leaf litter and terrestrial invertebrate inputs	Jackson and others (2012); Verkaik and other (2013); Cooper and others (2015); Musetta-Lambert and others (2017)
2) Riparian canopy composition	Fire shifts the post-fire composition of riparian vegetation, which shifts the quantity and composition of terrestrial inputs	Dwire and Kauffman (2003); Jackson and others (2012); Musetta-Lambert and others (2017)
3) Riparian shade	Fire reduces riparian shade, which can increase light influx to the stream channel and increase primary production	Amaranthus and others (1989); Koetsier and others (2007); Beakes and others (2014)
4) Stream temperature	Post-fire reductions in riparian shade can increase stream temperatures	Dunham and others (2007); Beakes and others (2014); Swartz and Warren (2022)
5) Streamflow	Post-fire loss of vegetation shifts watershed hydrology via reduced evapotranspiration, which can increase streamflow	Hallema and others (2018); Niemeyer and others (2020)
6) Nutrients-Nitrogen	Post-fire loss of vegetation increases nitrogen export and concentrations in streams	Spencer and others (2003); Bladon and others (2008); Rhoades and other (2019)
7) Nutrients-Phosphorus	Post-fire erosion of sediment increase phosphorus concentrations in streams	Silins and others (2014); Emelko and other (2016)
8) Turbidity	Post-fire erosion of sediment increases instream turbidity which a) limits solar radiation reaching the streambed and b) limits foraging efficiency of top predators	Reale and others (2015); Rust and others (2019)

how fire impacts each variable, and how each variable impacts the dynamics of the model food web. Figure 3 illustrates the assumed response trajectory (% change) for each of these environmental inputs relative to unburned conditions. To calculate fire effects, the percentages within each response trajectory (Figure 3) are multiplied by the baseline conditions of the model (see Supplemental Figure S2b). The model is structured so all fire effects run simultaneously and are linked to the rest of the model food web to ultimately affect fish. In the model, fish are sensitive to both physical and biological processes including aquatic and terrestrial invertebrate prey resources, water quality (temperature, streamflow, nutrients, and turbidity), available habitat quantity and quality, and presence of competitors. As a result, fire can have both direct and indirect effects on fish through changes in physical habitat conditions and energetic prey resources. For example, fire can increase water temperatures, which depending on how they compare to temperature thresholds of fish species can increase or decrease fish biomass via changes in their metabolism and availability of prey (Bellmore and others 2017).

Model simulations were run in Stella Architect version 3.1 (<https://www.iseesystems.com/>) for 50

years total 10 years pre-fire and 40 years post-fire. The latter was intended to represent the amount of time forest stands are thought to return to closed canopy conditions for westside forests in the PNW region (Warren and others 2016; Spies and others 2018). Simulations are not meant to represent responses at specific locations, but instead reflect the generalized patterns expected in forested headwater streams in this region. This was intended to ensure the model would be broadly applicable to a range of conditions and locations rather than representing a specific watershed. We ran the model as a continuous time series to simulate unburned forest conditions typical of second-growth forest stands in our region, as well as the initial post-fire responses (1–5 years), and longer-term (10–40 years) post-fire recovery. We did not take into account climate change or other shifts in baseline conditions in these initial modeling scenarios so we could focus on fire effects. We assumed post-fire environmental conditions that influence the stream food web would return to their pre-fire state within this timeframe, similar to conceptual models made by Minshall and others (1989) and Gresswell (1999). We also focused on a single fire event, rather than evaluating the effects of multiple fires in a fire regime.



**Figure 3.** Conceptual models of potential post-fire changes in riparian and instream conditions that may emerge relative to an unburned forested watershed. This conceptual framework suggests that fire effects are 1) likely dynamic through time, and 2) that the magnitude and extent of those fire effects varies with fire severity. Fire severity categories followed the levels of initial magnitude of change described in Reilly and others (2017). Low severity fire consisted of a 25% initial change that recovered after ~ 15 years, moderate severity fire consisted of a 50% initial change that recovered after ~ 25 years, and high severity fire consisted of a 75% initial change that did not recover completely within the timeframe of this analysis (40 years post-fire). These fire severity categories were applied to the following model inputs: riparian canopy cover, riparian shade, riparian canopy composition, stream temperature, streamflow, nutrients (nitrogen and phosphorus), and turbidity. Arrows describe direction of post-fire response. For the purposes of this exercise, we have assumed that each model input that changes with fire follows similar temporal trajectories. However, we acknowledge that each may follow their own unique temporal trajectory and that fires may have other effects on riparian and instream conditions that we do not include in this initial version of the model. Watershed drawings by Kathryn Ronnenberg.

### Fire Severity Scenarios

To explore how variation in fire severity may influence aquatic ecosystems and fish both immediately after fire and through time, we ran model simulations where we varied model inputs (riparian canopy cover, riparian shading, riparian canopy composition, stream temperature, streamflow, turbidity, and nutrient concentrations) to different magnitudes and extents to represent different fire severities relative to unburned forest conditions

(Figure 3). To do this we adjusted all model inputs representing fire effects according to the different fire severity classes in the PNW as described by Reilly and others (2017) (Figure 3). Reilly and others (2017) use a common methodology aiming at the pairing of satellite-based burn ratio values with burn severity assessed on the ground to generate burn severity maps displaying low-moderate-high severity classes (Miller and Thode 2007; Miller and Quayle 2015; Lyndersen and others 2016; Harvey and others 2019). Accordingly, for the



purposes of this exercise, a low severity fire consisted of a maximum of 25% initial change in model inputs that recovered relatively quickly ( $\sim 15$  years), a moderate severity fire consisted of a 50% initial change that took longer to recover ( $\sim 25$  years), and a high severity fire consisted of a minimum of 75% initial change that did not recover completely (that is, within 10% of pre-fire conditions) within the time frame of analysis of 40 years. In model simulations, fire effects were dynamic through time with the magnitude and duration of effects varying with fire severity (Figure 3). Although model simulations depict fire effects as relatively simple trajectories that gradually recover over time to illustrate the utility of the model, we recognize that post-fire effects often follow more complex dynamics which could be explored in future simulations (Minshall and others 1989).

To assess the aquatic ecosystem responses to fire, we plotted model simulation results as the percent change in potential biomass for each component of the food web and how they varied relative to unburned conditions across each level of fire severity (low, moderate, and high). To show how the ecosystem responded to fire, we constructed food web diagrams that estimated how the amount of potential energy flow from one food web member to another changed with different fire severities (low vs. high) relative to unburned conditions and time since fire (short-term  $\sim 5$  years post-fire vs. long-term  $\sim 20$  years post-fire).

## Sensitivity Analyses

We conducted sensitivity analyses to further explore variation in model simulations and responses to fire in two different ways. First, to understand the potential mechanisms driving fish responses to wildfire in the model, we conducted a one-way sensitivity analysis to see which individual fire effects may have the greatest influence on fish responses. To do this, we ran model simulations in Stella with fire effects turned on one at a time and evaluated changes in potential biomass responses at each fire severity level (low, moderate, and high). This was repeated for both fish stocks (salmonids and sculpin) with each of the following variables: riparian canopy cover, riparian shade, riparian canopy composition, stream temperature, stream-flow, nitrogen, phosphorus, and turbidity. Variables with persistent negative effects on fish biomass were considered to be potential drivers of vulnerability according to the temporal trajectories in Figure 2. This analysis focused on understanding

the relative importance of environmental factors associated with fire that may affect fish, but did not consider the intrinsic attributes of fish species that may lead to species-specific responses.

Second, fish in PNW forested headwater streams likely experience a range of potential responses to wildfire due to the combination of spatial heterogeneity in watershed conditions and heterogeneity in fire severity across landscapes (Jackson and others 2015). Thus, aquatic ecosystems likely integrate a range of post-fire conditions that ultimately affect fish. To represent this heterogeneity, we conducted a global sensitivity analysis in Stella whereby we drew random combinations of fire effects at different severities (low, moderate, high) with a Latin hypercube sampling design for multiple runs ( $n = 100$ ) to ensure even draws across the entire distribution of potential fire effect combinations (Ford 2010; Bellmore and others 2017). This resulted in 100 different potential fish biomass response trajectories to wildfire. This exercise was intended to provide a measure of the potential variability in fish responses to fire across headwater streams that experience different levels of fire impact, but this analysis does not account for all sources of spatial variability across the landscape so is not meant to capture all possible responses.

## RESULTS

### Fire Severity Scenarios

Model simulations resulted in substantial variability in the direction, magnitude, and duration of aquatic ecosystem responses to the different wildfire severity scenarios in forested headwater streams of the PNW (Figure 4, Table 2). As expected, losses of riparian vegetation associated with wildfire decreased the in-stream biomass of coniferous and deciduous detritus relative to the background no-fire scenario (Figure 4a, b), with greater reductions at higher fire severity levels (Figure 4a, b). Wildfire reduced the instream biomass of conifer detritus more than deciduous across all fire severities due to assumed post-fire shifts in riparian composition toward early-successional deciduous species (conifer: 60–97% initial reduction, deciduous: 30–73% initial reduction) (Figure 4a, b). Both conifer and deciduous detritus biomass recovered to pre-fire levels after 15 years with low severity fire, 25 years after moderate severity fire, and did not recover completely after 40 years with high severity fire (Figure 4a, b), following assumed patterns of riparian canopy regrowth (Figure 3a). Post-fire losses of riparian vegetation led to reduc-

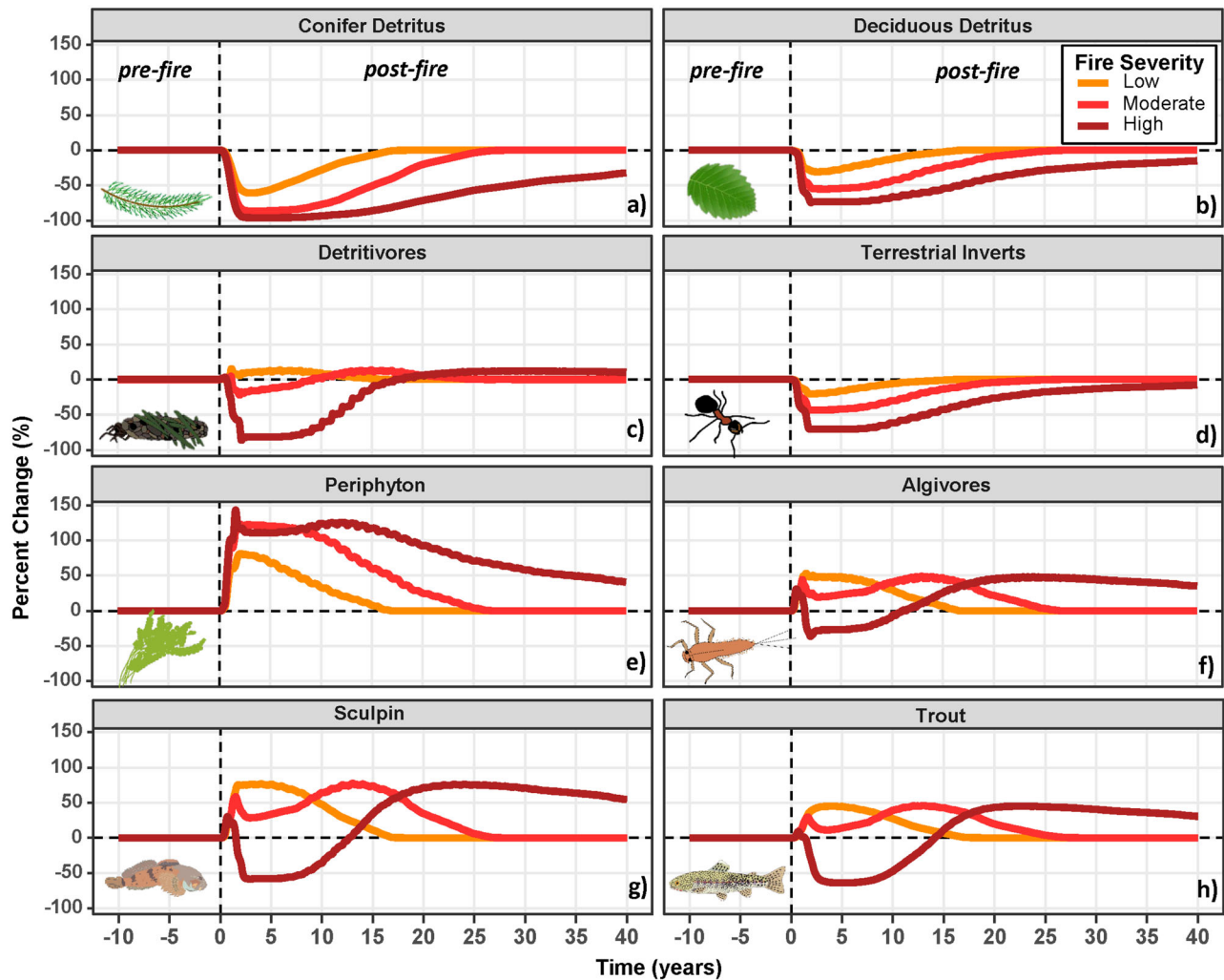


Figure 4. Model simulations reveal complex aquatic ecosystem responses to fire in westside headwater streams of the Pacific Northwest that varied extensively through time, with fire severity, and across trophic levels. Modeled aquatic responses included: **a** conifer detritus, **b** deciduous detritus, **c** aquatic invertebrate detritivores, **d** terrestrial invertebrates, **e** periphyton, **f** aquatic invertebrate algivores, **g** sculpin, and **h** trout. Model simulations represent the energetic capacity of a stream to support biomass based on the physical instream and riparian habitat conditions as well as the transfer of energy among trophic levels within an ecosystem. Modeled responses are shown as the percent change in potential biomass for each fire severity relative to unburned forested conditions. An interactive version of the model is available here: (<https://exchange.iseesystems.com/public/david-roon/wildfire-effects-on-aquatic-ecosystems-model>).

tions in terrestrial invertebrate biomass that mirrored the reductions in terrestrial detritus, where low severity fire resulted in the smallest reductions that persisted for the shortest period of time (20% initial reduction persisting for 15 years) relative to moderate (43% initial reduction persisting for 25 years) and high severity fire (70% initial reduction for 40 years) (Figure 4d). In contrast, post-fire increases in solar radiation and nutrients led to increases in stream periphyton biomass and the magnitude and extent of periphyton responses increased with fire severity (low severity: 81% initial increase persisting for 15 years; moderate

severity: 123% initial increase persisting for 25 years; high severity: 150% initial increase persisting for 40 years) (Figure 4e).

Aquatic invertebrates displayed more complex responses to wildfire than basal resources and terrestrial invertebrates, and responses varied between functional groups (Figure 4c, f). Detritivores, which relied primarily on terrestrial detritus, increased in biomass by 13% in response to low severity fire, but decreased by 22% with moderate severity fire and by 87% with high severity fire (Figure 4c). Initial post-fire decreases in detritivore biomass associated with moderate and high sever-

**Table 2.** Summary of Model Simulation Results and Corroborating Literature

Modeled response variable	Fire severity	Direction	Magnitude (peak change)	Duration (years)	Corroborating literature
Periphyton	Low	+	+ 75%	15	Rugenski and Minshall (2014); Silins and others (2014); Cooper and others (2015); Emelko and others (2016); Swartz and Warren (2022)
	Moderate	+	+ 125%	25	
	High	+	+ 130%	40 +	
Terrestrial detritus-conifer	Low	-	- 60%	15	Jackson and others (2012); Mussetta-Lambert and other (2017)
	Moderate	-	- 80%	25	
	High	-	- 95%	40 +	
Terrestrial detritus-deciduous	Low	-	- 25%	15	Koetsier and others (2007); Jackson and others (2012); Mussetta-Lambert and other (2017)
	Moderate	-	- 50%	25	
	High	-	- 70%	40 +	
Terrestrial invertebrates	Low	-	- 20%	15	Koetsier and others (2007); Rosenberger and others (2011); Jackson and others (2012); Mussetta-Lambert and others (2019)
	Moderate	-	- 40%	25	
	High	-	- 60%	40 +	
Aquatic invertebrates-algivores	Low	+	+ 50%	15	Minshall and others (1997); Mihuc and Minshall (2005); Cooper and others (2015)
	Moderate	+	+ 50%	25	
	High	+	+ 50%	40 +	
Aquatic invertebrates-detritivores	Low	Mixed (- / +)	- 25% / + 50%	15	Mihuc and Minshall (2005); Cooper and others (2015); Rodriguez-Lozano and others (2015)
	Moderate	Mixed (- / +)	- 25% / + 15%	25	
	High	Mixed (- / +)	- 75% / + 15%	40 +	
Fish-sculpin	Low	+	+ 75%	18	Swartz and Warren (2022)
	Moderate	+	+ 75%	28	
	High	+	+ 75%	40 +	
Fish-resident trout	Low	Mixed (- / +)	- 60% / + 75%	18	Burton (2005); Howell (2006); Koetsier and others (2007); Silins and others (2014); Rosenberger and others (2015); Emelko and others (2016); Swartz and Warren (2022)
	Moderate	+	+ 50%	28	
	High	Mixed (- / +)	- 60% / + 50%	40 +	

ity fire were followed by delayed increases in detritivore biomass associated with riparian vegetation recovery and a shift to a higher proportion of deciduous vegetation cover (Figure 4c). Algivores, which relied primarily on periphyton, initially increased in biomass by 50% with low severity fire, 45% with moderate severity fire, and 30% with high severity (Figure 4f). Following these short-term increases, algivores exhibited distinct response trajectories to each fire severity scenario. For low severity fire, initial increases in algivore biomass were followed by subsequent declines, whereas algivore biomass stayed high and peaked 13 years following moderate severity fire. For high severity fire, algivore biomass declined below background for 10 years, before recovering and peaking 25 years after fire and remained elevated 40 years post-fire (Figure 4f).

Modeled fish biomass followed similar trajectories over time to aquatic invertebrates, but the relative magnitude of those responses varied between fish species (Figure 4 g, h). In general, sculpin tended to exhibit stronger responses to fire than trout, likely because sculpin fed preferentially on aquatic invertebrates (algivores and detritivores), whereas trout fed on a combination of aquatic and terrestrial invertebrates—allowing for prey switching when one of these prey sources declined. In the low severity fire scenario, both sculpin and trout biomass peaked initially after fire by 77% for sculpin and by 45% for trout and recovered to pre-fire conditions after 15 years (Figure 4 g, h). Comparatively, initial increases in fish biomass to fire were followed by subsequent declines and recoveries that peaked at different points with the more severe fire scenarios. With

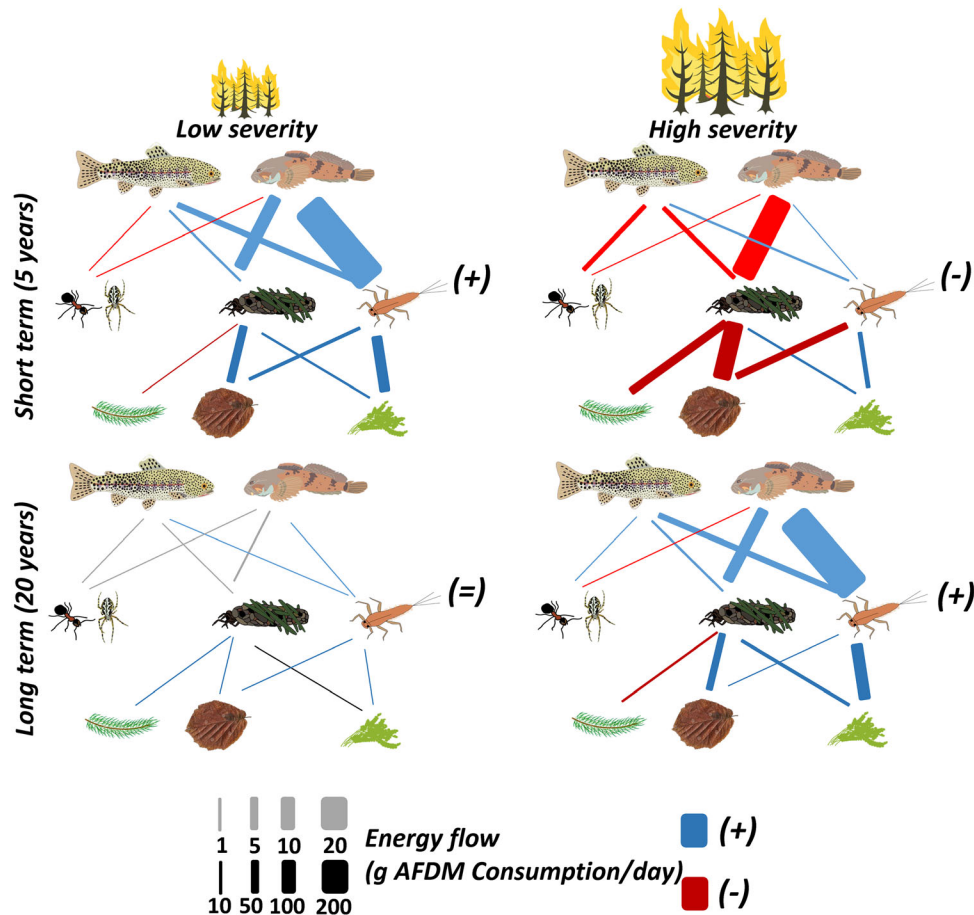
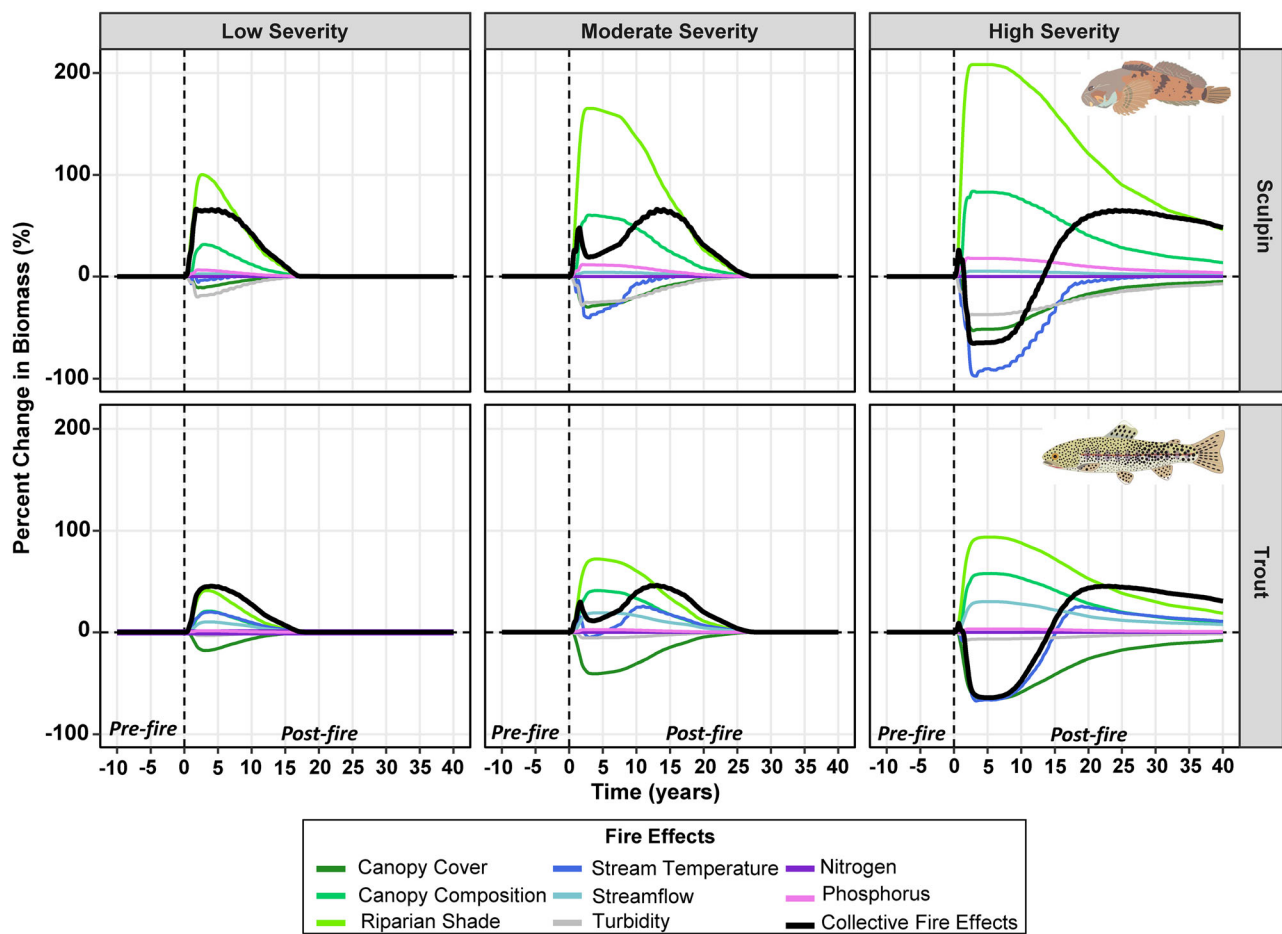


Figure 5. Food web diagrams illustrating how modeled energy flow pathways in aquatic ecosystems in westside headwater streams varied with fire severity relative to no-fire reference conditions 5 years and 20 years after fire. Width of the bars indicate the change in potential energy flow relative to unburned forests in units of g AFDM of consumption per day. Red bars indicate decreases in energy flow, blue bars indicate increases in energy flow, and gray bars indicate no change in energy flow.

moderate severity fire, sculpin and trout biomass peaked  $\sim 13$  years post-fire and then returned to pre-fire conditions after 25 years (Figure 4 g, h). In contrast, with high severity fire, fish biomass initially decreased relative to pre-fire conditions by up to 50% for a period of  $\sim 12$  years, but then recovered with fish biomass peaking  $\sim 25$  years post-fire (Figure 4 g, h).

When arranged as food web diagrams, our results indicated that wildfires shifted the pathways of energy flow through aquatic ecosystems in headwater streams relative to unburned forests, but the magnitude and direction of fire effects varied with fire severity and time after fire (Figure 5). At shorter time intervals ( $\sim 5$  years post-fire), low

severity fire increased modeled energy flow in aquatic ecosystems in westside headwater streams. Post-fire shifts in energy flow were primarily driven by increases in stream periphyton, which increased energy flow to aquatic invertebrates (algivores by  $7 \times$  and detritivores by  $2 \times$  relative to unburned forests), which then increased the energy flow to fish ( $2 \times$  for sculpin and  $1.5 \times$  for trout relative to unburned forests) (Figure 5). In contrast, high severity fire at short-term intervals decreased energy flow primarily through reductions in terrestrial resources. Post-fire reductions in terrestrial detritus decreased energy flow to aquatic invertebrates (detritivores by  $2 \times$  and algivores by  $1.5 \times$  relative to unburned forests) (Figure 5).



**Figure 6.** Sensitivity analyses can identify the potential mechanisms driving fish responses to wildfire. To illustrate this concept, here we ran a one-way sensitivity analysis where we modeled fish biomass responses (in units of percent change in potential biomass relative to unburned conditions) to individual fire effects run separately as well as all fire effects considered in the model run together (collective fire effects in black line). We ran sensitivity analyses for sculpin and trout biomass across low, moderate, and high severity fire. Individual fire effects considered in the sensitivity analysis included: riparian canopy cover (controls terrestrial inputs of leaf litter and invertebrates), riparian canopy composition (controls the quality of terrestrial resources), riparian shade (controls the amount of light that can reach the stream channel for primary production), stream temperature conditions, streamflow, turbidity, nitrogen, and phosphorus. Collective fire effects are the model outputs when all fire effects are run in at the same time.

Reductions in detritivores and terrestrial invertebrates decreased energy flow to fish ( $2 \times$  for sculpin and  $2.5 \times$  for trout relative to unburned forests) (Figure 5). However, over longer time intervals ( $\sim 20$  years post-fire), these patterns in energy flow reversed. Energy flow with low severity fire returned to baseline conditions of unburned forests after 20 years, whereas delayed increases in energy flow emerged with high severity fire. Delayed increases in energy flow associated with high severity fire were driven by increases in stream periphyton, which increased energy flow to aquatic invertebrates ( $1.5 \times$  for algivores and detritivores by 85% relative to unburned forests) and to fish (125% for sculpin and 75% for trout relative to unburned forests) (Figure 5).

### Sensitivity Analyses

Sensitivity analyses identified the individual drivers potentially influencing fish responses to wildfire, which varied in their direction, magnitude, and between fish species (Figure 6). Some variables consistently increased fish biomass such as reductions in riparian shade, which increased light availability for primary production, shifts in riparian canopy composition toward deciduous species which contributed higher quality terrestrial resources to streams, increases in streamflow which increased habitat availability, and increases in nutrient concentrations (Figure 6). Sensitivity analyses also identified potential drivers of fish vulnerability to fire that consistently decreased fish biomass such as post-fire increases in turbidity, which limited primary production and fish foraging efficiency, and loss of terrestrial resource inputs of leaf litter and terrestrial invertebrates (Figure 6). However, sensitivity analyses also identified other drivers that had more variable effects on fish biomass that depended on fire severity such as stream temperature. For example, stream temperature increased trout biomass under low severity fire, had mixed effects under moderate severity fire, and at high severity fire resulted in initial decreases in fish biomass followed by increases once stream temperature increases subsided (Figure 6). In contrast, changes in stream temperature exhibited consistent decreases in sculpin biomass. The relative strength of individual drivers varied between fish species. For example, trout appeared more sensitive to the loss of terrestrial resource inputs, whereas sculpin were more sensitive to increases in primary production and turbidity (Figure 6).

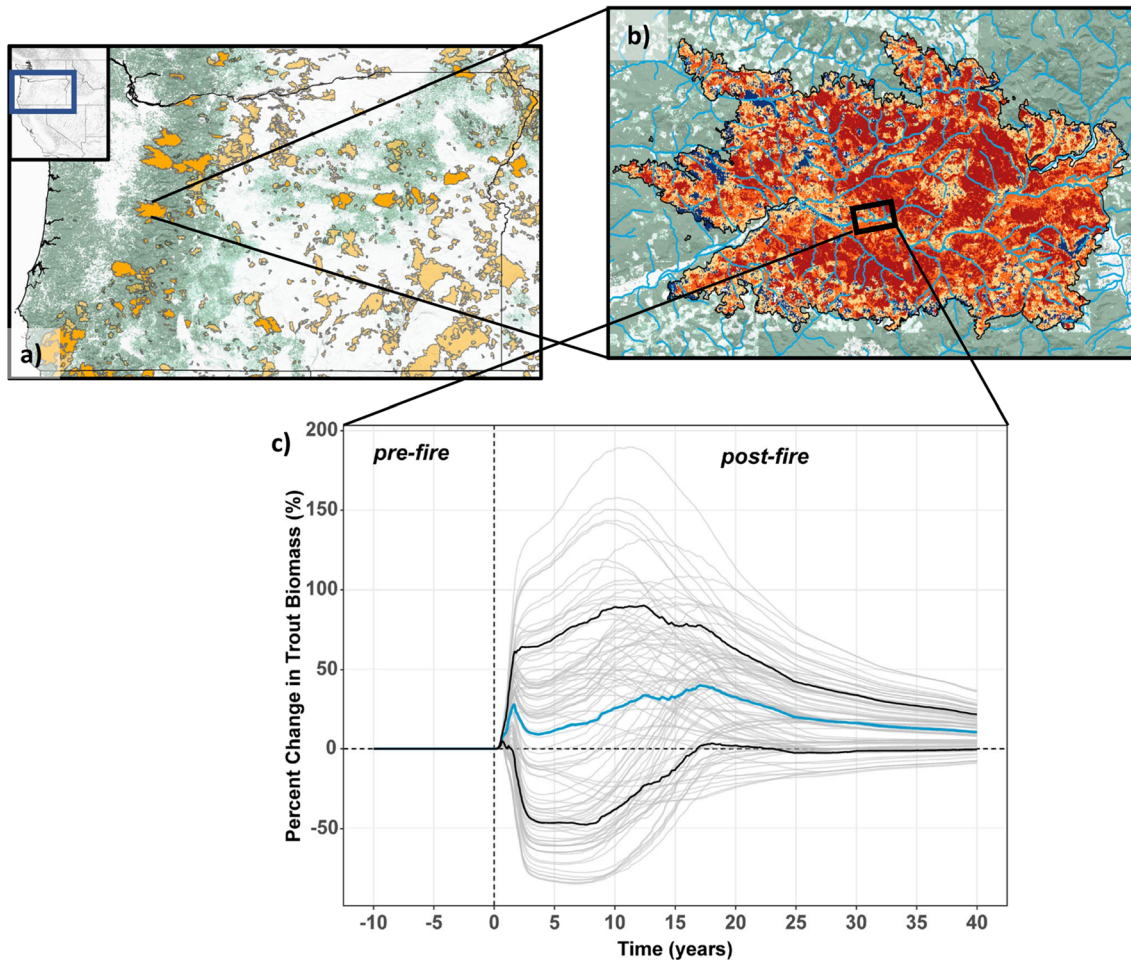
Our global sensitivity analysis estimated that fish biomass responses to fire had the potential to vary extensively due to the combination of background spatial heterogeneity and mixed-severity fire (Figure 7). In some cases, fish biomass exhibited a strong decreasing response to fire, with biomass decreasing by 5–85% relative to unburned forests (Figure 7). In other cases, fish biomass exhibited a strong increasing response (that is, biomass pulse), with biomass increasing by 0–180% relative to unburned forests (Figure 7). However, median estimates of trout biomass in response to wildfire in westside headwater streams indicated that fish were more likely to increase by an average of 20% (range: 0–40%) over time relative to unburned conditions (Figure 7). Median estimates of trout responses to wildfire fluctuated through time, peaking 15–20 years after fire, suggesting delayed fish responses to wildfire (Figure 7).

### DISCUSSION

In this study, we applied a food web simulation model to explore the multiple pathways through which fires influence aquatic ecosystems and ultimately top predators such as fish (Davis and others 2013; Bellmore and others 2017; Geary and others 2020). Model simulations revealed that wildfire can have diverse effects on aquatic ecosystems that varied extensively with fire severity, over time, and across trophic levels and fish species. In addition, sensitivity analyses helped identify potential drivers of fish responses to wildfire and provided estimates of the potential variation in fish responses due to landscape heterogeneity. Although model simulations were not meant as precise predictions that represent specific watersheds or discrete points in time, these generalized insights hold heuristic value for researchers and managers alike as they can improve understanding that can help develop new conceptual models, generate hypotheses, guide future empirical studies, and act as decision support tools (Power 2001; Davis and others 2013; Bellmore and others 2017).

### Aquatic Ecosystem Responses to Fire Varied Extensively with Fire Severity

Model simulations indicated that aquatic ecosystem responses to wildfire varied extensively with the severity of fire, demonstrating that variation in fire characteristics can be an important factor influencing how wildfires may affect fish and aquatic communities over time (Malison and Baxter 2010a, b; Jackson and others 2012; Cooper and others



**Figure 7.** Wildfires can add patches of spatial heterogeneity to forested landscapes across and within fire perimeters that affect aquatic ecosystems through space and time. As streams flow through these burned landscapes, they navigate a mosaic of fire severity and time since fire, each with its own distinct series of short and long-term effects on aquatic systems. As a result, aquatic ecosystems likely integrate conditions across this fire mosaic as they flow downstream. Given that shifting fire regimes are projected to increase the spatial extent, frequency, and severity of fires in Pacific Northwest forests, so too will aquatic systems respond. Here we examined how heterogeneity in fire severity may influence ecological responses using a global sensitivity analysis. We simulated the range of potential trout biomass responses to fire using a Latin hypercube approach that randomly selects the severity of each fire effect ( $n = 8$ ) for 100 runs to get an indication of the distribution of possible outcomes. Gray lines show the individual runs, the blue line shows the median response, and the black lines show standard deviation. **A** Map of the state of Oregon, USA. Polygons are fire perimeters from Monitoring Trends in Burn Severity (MTBS) database from 1984 to 2019 in light orange, 2020 wildfires that hit Oregon in dark orange. **B** Inset map shows mosaic of burn severity of the Holiday Farm Fire in western Cascades, Oregon that burned in 2020. **C** Results of global sensitivity analysis showing the potential change in trout biomass.

2015). Model simulations suggest that each trophic level of the stream food web exhibited distinct response trajectories to fire. For example, the potential biomass of basal resources and invertebrates that relied on terrestrial resources (detritivores and terrestrial invertebrates) tended to decrease post-fire, and the magnitude and duration of their responses increased with fire severity. These patterns support key tenets of disturbance ecology that ecological responses should scale with

disturbance severity (Montgomery 1999; Turner 2010). Moreover, these modeled responses align with post-fire observations in basal resources and invertebrates from empirical studies in California and Idaho watersheds that found stronger responses to high severity fire than low severity fire (Malison and Baxter 2010a, b; Jackson and others 2012; Cooper and others 2015). In contrast, algae and fish displayed more complex responses to fire severity scenarios; low and moderate fire

severity tended to increase invertebrate and fish biomass that peaked at different periods of time post-fire, whereas high severity fire initially decreased invertebrate and fish biomass that were followed by delayed increases. Due to the infrequent, high severity fire regime characteristic of westside forests in the PNW (Reilly and others 2017), there are few empirical studies to compare these results to. Research so far points to immediate to short-term post-fire increases in fish biomass, even after high severity fire, however longer-term responses remain unknown (Heck 2007; Swartz and Warren 2022; Coble and others 2023, 2024). Our model simulations appear to align with observations by Burton (2005) and Howell (2006) that documented short-term declines in fish biomass to high severity fire over time tend to be followed by eventual increases in fish productivity in Idaho and NE Oregon watersheds. As a result, our model simulations highlight that fish and aquatic ecosystem responses in westside headwater streams are likely to be diverse and depend on the combination of post-fire effects that emerge (for example, post-fire storm events or debris flows that can drive initial post-fire fish declines).

### Aquatic Ecosystem Responses to Fire are Highly Dynamic through Time

Temporal trajectories as provided by model simulations showed that initial post-fire responses did not always tell the whole story of how fire effects were likely to play out through time. Instead, model simulations suggested that fire effects on aquatic ecosystems can be highly dynamic as time passes and the watershed recovers. As predicted, model simulations indicated that fire effects frequently recovered over time following the trajectories of riparian and instream conditions programmed into the model, indicating evidence of aquatic ecosystem resilience to fire across multiple trophic levels (Lewis and others 2014). More surprisingly, however, model simulations also revealed complex emergent responses to fire, especially at the higher trophic levels. These complex dynamics were likely due to physical fire effects interacting with the post-fire responses of the lower trophic levels. Although our model simulations were shorter in duration than the conceptual models of Minshall and others (1989) and Gresswell (1999), our temporal trajectories showed substantial overlap. Similar to Minshall and Gresswell, our model simulation suggested that even when fire led to initial decreases in biomass of fish and aquatic invertebrates for the first 8–15 years,

like under high severity fire scenarios, those initial negative effects were frequently followed by delayed increases in biomass emerging 10–15 years post-fire. Most empirical fire studies tend to focus on short-term fire effects and so understanding of longer-term effects remains limited (Bixby and others 2015). However, Romme and others (2011) evaluated post-fire responses 20 years after the Yellowstone fires of 1988, finding that many attributes of aquatic ecosystems had started to recover or fully recovered within that time frame. Moreover, studies by Burton (2005) and Rosenberger and others (2015) observed that fire enhanced fish populations and habitat conditions 5–10 years after severe fire in central Idaho watersheds. These results highlight the complementary value of models which can forecast potential responses through time (Davis and others 2013).

### Aquatic Ecosystem Responses to Fire Varied Widely in Direction

Despite recent literature reviews that have emphasized the potential impacts of wildfire on water quality and aquatic ecosystems (Sievers and others 2017; Paul and others 2022; Erdozain and others 2024), our model simulations varied extensively in their direction, spanning a range of what might be perceived as “positive” or “negative.” As a result, although there may be a tendency in the literature, magnified by public perception, to highlight the perceived negative influence of wildfire impacts to watersheds (that is, decreasing the abundance of stream organisms), our model simulations suggest that this is not a foregone conclusion. The direction of aquatic ecosystem responses to fire in westside headwater streams frequently depended on trophic level. Overall, model simulations support the notion that periodic disturbance like fire may not be problematic at the individual reach or watershed scale, and instead that increased ecological heterogeneity may even enhance aquatic ecosystem productivity relative to unburned forests (Lepori and Hjerdt 2006; Malison and Baxter 2010a, b). In fact, evidence of aquatic ecosystem vulnerability to fire as described by persistent decrease in potential biomass by our conceptual trajectories in Figure 2 was relatively rare. Of the trophic levels we included in the model, terrestrial resources and primary consumers that relied on those terrestrial resources (detritivores and terrestrial invertebrates) were most likely to decrease in potential biomass post-fire. However, even those terrestrial resources and their consumers tended to recover over time. Instead, model



simulations suggested evidence of mixed responses or increases in potential biomass post-fire across multiple trophic levels including periphyton, algivores, and fishes. Moreover, food web diagrams showed that overall food web responses were often positive (that is, biomass increased) under low severity fire at short-term intervals and high severity fire after longer-term intervals. Collectively, model simulations highlighted that fire in forested headwater streams in the PNW are unlikely to lead to persistent lower-productivity levels, even after severe fire, illustrating the potential resilience of aquatic ecosystems (Lewis and others 2014; Jager and others 2021). However, these results are an outcome of our assumed fire effects on environmental inputs to the model (for example, riparian cover, temperature, turbidity, and so on; Figure 3), which are likely to be much more stochastic in real systems and highly context dependent and should be viewed as conceptual models or hypotheses of responses that could emerge with wildfire.

### Sensitivity Analyses Identified Driving Mechanisms and Estimated Potential Variation in Fish Responses to Wildfire

Sensitivity analyses revealed that fire may have diverging effects on fish and aquatic ecosystems that simultaneously push and pull the system in different directions. For example, post-fire increases in solar radiation, shifts in riparian canopy composition toward higher quality deciduous species, increases in streamflow, and increases in nutrients all led to increased fish biomass (Jackson and others 2012; Silins and others 2014; Emelko and others 2016; Musetta-Lambert and others 2017). On the other hand, post-fire reductions in terrestrial resources, increases in stream temperature and sediment concentrations (turbidity) all led to decreased fish biomass (Beakes and others 2014; Rust and others 2019; Preston and others 2023). These are well documented empirically in the literature (Gresswell 1999; Bixby and others 2015; Gomez Isaza and others 2022), however, what is unique about the modeling approach applied here is that the whole-system structure can help tease apart the relative influence of each of these mechanisms to one another, both individually and collectively (Bellmore and others 2017; Whitney and others 2020; Benjamin and others 2022). As a result, our food web model identified the direction and relative strength that each individual fire effect may have on fish, and how that may vary among fish species. In this light, model simulations re-

vealed that the potential drivers of fish vulnerability to fire may be largely similar, yet the relative magnitude of influence varied between fish species, highlighting that fire effects are often species dependent (Reale and others 2021). This is likely due to the unique physiological and ecological niches occupied by the two fish species included in the model (Amundrud and Srivastava 2016; Benjamin and others 2022). For example, sculpin, as benthic predators, were especially sensitive to fire effects that affected primary production such as post-fire reductions in riparian shading, increases in turbidity, and increases in phosphorus that likely interacted to boost aquatic productivity across multiple trophic levels (Silins and others 2014; Emelko and others 2016). Trout, in contrast, relied on a mix of terrestrial and aquatic invertebrates (Falke and others 2020; Benjamin and others 2022), and so were more likely to be vulnerable to losses in terrestrial resources, which could explain the smaller post-fire trout biomass responses relative to sculpin. Collectively, our sensitivity analyses suggested that unique combinations of trophic and physical drivers could lead to the distinct fish responses to fire as depicted in the model (Benjamin and others 2022). These combinations could be explored in more detail to fully appreciate their species-specific responses to wildfire.

Sensitivity analyses also indicated that post-fire fish responses had the capacity to range widely, suggesting there is unlikely to be a singular fish response to fire across the landscape, even within a single context (for example, forested headwater streams of the PNW). Wildfires add patches of spatial heterogeneity to forested landscapes across and within fire perimeters that can enhance aquatic ecosystem productivity through space and time (Lepori and Hjerdt 2006; Jackson and others 2015; Verkaik and others 2015). As streams flow through these burned landscapes, they experience a mosaic of fire severity and time since fire, each with its own distinct series of short and long-term effects on aquatic systems. Upstream fire effects can also propagate downstream with the advective flows of water, nutrients, and organic matter (Power and Dietrich 2002). Although our global sensitivity analysis did not account for all sources of spatial variability across the landscape that may contribute unique responses to wildfire (for example, watershed structure and orientation, underlying geology, and so on), our sensitivity analysis provided an approach that attempted to capture the potential range in fish responses to fire that may emerge due to spatial heterogeneity in fire and watershed conditions within forested

headwater streams in the region. However, many fishes likely integrate conditions across this fire mosaic as they move across riverscapes, tracking shifting foraging and growth opportunities through time (Rossi and others 2024). As a result, our model simulations may underestimate the potential range in post-fire fish responses in westside headwater streams. More attention is needed to unpack how shifting fire regimes and expected shifts in spatial heterogeneity could influence aquatic systems; heuristic tools like food web modeling are essential to better understand and predict these aquatic system responses.

### Management Implications, Model Limitations, and Future Directions

As wildfires increasingly affect river networks due to global climate and land cover change (Halofsky and others 2020; Ball and others 2021), it raises pressing concerns for resource managers in many regions including western North America. For example, following recent high severity fires in westside forests of the PNW (e.g., 2020 Labor Day fires in western Oregon), there has been a renewed interest by researchers and resource managers to understand and predict the impacts of wildfire on fish and their habitats in this region (Reilly and others 2022). Although the severity of these fires was not uncharacteristic of the historical fire regime (Reilly and others 2022), because fires have not occurred in this region in recent recorded history, the implications of fires for fish remain poorly understood. Resource managers are frequently tasked with the responsibility of making decisions about how to manage landscapes and land use activities without adversely affecting sensitive species that inhabit those landscapes. As a result, decisions are often made with imperfect information regarding how a species functions or responds to disturbance (Bascompte 2010). There is a tendency to rely on empirical studies to guide this decision making; however, empirical studies are not always available or come with constraints that may limit their insights. Empirical studies following the 2020 fires are just starting to emerge (for example, Coble and others 2023), but can only characterize the immediate post-fire effects so far. In these situations, food web simulation models like the ATP that can incorporate the multiple pathways that fire impacts aquatic ecosystems can play an important role (Power 2001). Although these models do not necessarily provide precise predictions of what *will* happen, they can act as heuristic tools that improve understanding of *what*

*could* happen and *how* it may happen through time (Power 2001; Davis and others 2013; Bellmore and others 2017, 2019). Moreover, when paired with sensitivity analyses, they can help identify potential mechanisms responsible for driving ecosystem responses to fire. In turn, simulation results can also be viewed as testable hypotheses that can guide management and empirical data collection in an adaptive management framework (Power 2001). This is important as fire regimes are expected to continue to shift with climate change (Hagmann and others 2021).

It is important to keep in mind that our modeling approach was intended to be heuristic, aimed at improving our understanding of the potential impacts of wildfire on fish and their ecosystem. Therefore, estimates provided by model simulations are not suggesting the precise amount of fish biomass that will occur after wildfire, but rather, the potential dynamic response trajectories that may emerge after fire. As a result, model simulations are more useful when considered as conceptual models and testable hypotheses.

We developed this model for a single context—small headwater streams in westside forests of the PNW, as headwater streams make up most of the stream length in river networks and because headwater streams are more likely to be sensitive to changes in riparian forests (Minshall and others 1997; Power and Dietrich 2002; Davis and others 2013). However, given that wildfire effects likely vary depending on the background conditions and spatial context of where a fire takes place (Verkaik and others 2015), it is important to keep in mind that results produced in the model do not necessarily apply to all locations (Whitney and others 2020). Along those lines, we have developed an interactive version of the model to facilitate further understanding: (<https://exchange.iseesystems.com/public/david-roon/wildfire-effects-on-aquatic-ecosystems-model>). The interactive version of this model allows researchers and resource managers to explore how different combinations of fire effects may interact to affect aquatic responses across multiple trophic levels through time. Understanding how aquatic ecosystems are likely to respond to fire is essential as it can guide decision making before any post-fire management or restoration takes place. To illustrate the utility of the interactive version of the model, we have shared an example in the model interface that explores how trout biomass responded to two different alternative post-fire riparian recovery scenarios—one simple and one more complex. As a result, model simulations presented in this analysis

and the interactive version of the model are likely relevant to those interested in a variety of common management and restoration actions that often follow wildfire events such as salvage logging (Reeves and others 2006), instream floodplain or channel restoration (Pugh and others 2022), or post-fire forest restoration such as thinning or prescribed and cultural burning (Beche and others 2005; Barros and others 2018; Hessburg and others 2021). Users can set model parameters tailored to the combination of fire effects of their interest and explore the potential implications for fish and aquatic ecosystems. Understanding how fish and aquatic ecosystems likely respond to fire is an essential first step that can provide context before post-fire management actions take place, determine whether post-fire restoration actions are necessary, or prioritize post-fire restoration strategies (Bellmore and others 2017; Whitney and others 2020).

Expanding the applications of the approach introduced here could further address the complex pathways through which wildfire influences aquatic ecosystems. The current version of the model focuses on local, reach-scale effects of wildfire on aquatic and riparian forest conditions. Expanding the spatial scale of the model would allow future simulations to explore the spatial variation in aquatic ecosystem responses to wildfire within and across watersheds and the potential mechanisms driving those responses. For example, applying the model to represent different positions along the river continuum including larger river systems, and the unique thermal and flow regimes characteristic of different ecoregions of the PNW could provide a broader understanding of fire effects on aquatic ecosystems and the mechanisms driving those responses. Along those lines, making the model more spatially explicit to look at spatial variation within a watershed could allow for exploration of how fire effects in different locations propagate longitudinally downstream throughout a stream network (Nichols and others 2024). Moreover, the addition of other fire effects not yet included in the model such as large wood inputs (Coble and others 2023), physical habitat structure (Flitcroft and others 2016; Pugh and others 2022), or debris flows (Reale and others 2021) could make the model more broadly applicable to those interested in the implications of wildfire on the physical processes in watersheds. Because the model acts as a flexible template, the model can be easily adapted to explore a wide variety of questions related to fire. However, tradeoffs emerge when including additional complexity to models that can limit

interpretation of responses. Nevertheless, future modeling simulations can expand upon the framework initiated here to further explore fire effects on aquatic ecosystems across the region.

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## DATA AVAILABILITY

Data for this publication are available through the Open Science Framework at: <https://doi.org/http://doi.org/10.17605/OSF.IO/8E9K4>

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