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Wildfire disturbance shapes the physical and biological condition of  
Pacific Northwest stream ecosystems

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**Abstract**

Wildfire disturbance shapes the physical and biological condition of  
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Wildfire constitutes one of the most influential processes affecting watershed conditions across the Pacific Northwest. Although the patterns and impacts of wildfire are well-described for terrestrial ecosystems, a comprehensive understanding of wildfire effects in aquatic ecosystems is still being developed. The occurrence of wildfire within stream catchments can greatly influence regimes in flow, temperature and organic material, but understanding how wildfire contributes to the natural variability of these processes at broader spatial and temporal scales is poorly understood. Additionally, multiple studies have documented biotic responses to wildfire within a single catchment or following an individual burn event, yet how these disturbances impact stream communities at the landscape scale is less well-documented. As wildfire activity continues to increase in the Pacific Northwest, there is a need to broaden our

understanding of stream-wildfire dynamics and quantify how these disturbances interact with the habitat and biota of riverine ecosystems in the region.

My thesis addresses these challenges by investigating the abiotic and biotic effects of wildfire for watersheds across the Pacific Northwest. In Chapter 1, we quantify the response of stream temperatures to wildfire using a pre-fire/post-fire comparison of annual thermal regimes collected at 18 watersheds across the region. Using a non-parametric effect size approach and constrained multivariate ordination, we describe the patterns and drivers of stream thermal response to wildfire in the first year following disturbance. Despite substantial variability at the reach scale in the response of most stream thermal metrics, we detected a regional increase in the number of warm events coupled with a decrease in the number of cold events in the first post-fire year, relative to historic conditions. Catchment precipitation, percentage of watershed burned and annual streamflow were identified as the most important predictors of responses across all facets of the thermal regime. Our results suggest that despite the importance of reach-scale conditions in driving the sensitivity of stream temperatures, regional-scale patterns are possible, indicating wildfire events can influence post-fire stream thermal dynamics across a wide variety of catchment conditions well into the post-disturbance period.

In Chapter 2, we compare the functional diversity between burned and unburned streams in a large number of catchments across the Pacific Northwest experiencing variable habitat conditions and wildfire histories. Using regression analyses, we compare three indices of functional diversity in streams experiencing recent and extensive wildfire, and identify habitat- and watershed-scale conditions most responsible for describing patterns within these indices. Values in functional richness and functional dispersion were largely similar between burned and

unburned streams, but total abundance was higher in streams that had experienced wildfire in the past year compared to unburned conditions. Values in stream temperature, substrate size and the amount of large woody debris were largely important in describing values in functional diversity, through which predictors did best depended on the wildfire history experienced at each site. Despite the potential for wildfire to play a major role in affecting community composition for individual watersheds, our analysis suggests that fine-scale habitat conditions play a more important role in structuring functional diversity across multiple catchments.

Collectively, our analysis provides insight into the interaction between wildfire and stream ecosystems in the Pacific Northwest and helps identify factors affecting the physical and biological condition in streams within a fire-prone landscape.

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# Chapter 1: Stream thermal responses to wildfire in the Pacific Northwest

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## 1.1 ABSTRACT

In the Pacific Northwest region of North America, wildfire disturbance has been identified as one of the most prevalent forces of ecological change in freshwater environments. Research has documented stream temperature responses to wildfire disturbance, but studies are often limited to individual watersheds or burn events, resulting in an incomplete understanding of how wildfires affect stream temperature at broader spatial scales and of which environmental and pyrological factors are important in predicting thermal responses. In this study, we quantified the impact of wildfires on stream temperature by analyzing long-term temperature monitoring data from 18 wildfire-affected streams across the Pacific Northwest. Using a non-parametric effect size approach, we quantified response patterns among 26 metrics describing different facets of the thermal regime (magnitude, variability, frequency and timing of stream thermal events) in the first post-fire year. We used multivariate ordination and spatially-explicit data on pyrological, hydrological and meteorological conditions to identify potential drivers of thermal sensitivity to wildfire effects in disturbed watersheds. The results revealed substantial variability in thermal responses at the site level, but in general, streams of the Pacific Northwest are prone to an increased frequency of warmer temperatures and a decreased frequency of cooler temperatures in the year following wildfire disturbance. Redundancy analysis identified that 30-55% of the variation in stream temperature responses was explained by pyrological, hydrological and meteorological conditions. Mean annual precipitation, percentage of watershed burned, and mean annual flow were primary factors shaping thermal response to wildfire, but the relative importance of these potential drivers was variable across facets of the thermal regime. In summary, our study provides new insight into the regional influence of wildfire on stream thermal regimes, and indicates that wildfire could exacerbate climate-induced warming in

streams. Further investigation of the interaction between wildfire, hydrology and climatic processes as well as enhanced stream network monitoring are necessary to effectively manage fresh waters in a future likely facing more severe and frequent wildfire activity.

## 1.2 INTRODUCTION

Wildfires have long been recognized as a primary agent of ecological change in freshwater ecosystems (Resh et al. 1988, Gresswell 1999). In the Pacific Northwest region of the United States, wildfire continues to be one of the most influential disturbance agents in terrestrial ecosystems (Hessburg & Agee 2003), but a comprehensive understanding of how wildfire affects freshwater ecological conditions is still under development (Reeves et al. 1995, Mote et al. 2003). Changes to stream habitat in wildfire-affected watersheds can range from mild to severe, causing varying levels of biotic response immediately following disturbance (Gresswell 1999, Burton 2005). At broad spatial and temporal scales, the patterns and drivers of riverine change following wildfire are complex, thus challenging our ability to generalize responses across watersheds (Bisson et al. 2003, Bixby et al. 2015). Consequently, regional scale assessments of wildfire disturbance to stream ecosystems are increasingly needed and simultaneously difficult to attain, due largely to the unpredictable nature of wildfire activity (Stanley et al. 2010, Bixby et al. 2015).

Stream temperature is a critical determinant of ecological status in freshwater ecosystems (Magnuson et al. 1979, Webb et al. 2008) and sensitive to both local habitat conditions and regional hydrometeorological patterns that can be affected by wildfire disturbance. The thermal budget of temperate streams is largely controlled by energy fluxes in solar radiation and heat exchanges between the stream channel and the surrounding environment (Webb & Zhang 1997, Moore et al. 2005). Fine-scale temperature patterns are also dependent on substrate conditions,

which can promote or inhibit the amount of friction between the streambed and channel flow and thus contribute to heat loss through bed conduction (Webb & Zhang 1997). By altering the magnitude of these energetic processes, factors such as riparian shading, substrate form and cold-water inputs can be important controls on stream temperatures at local scales (Johnson 2004, Dugdale et al. 2013, Lawrence et al. 2014). At regional scales, watershed geomorphology and climatic patterns tend to dictate inter-annual variability in stream temperature as well as the sensitivity to regional air temperature (Mayer 2012, Luce et al. 2014, Lisi et al. 2015). The broad range of conditions affecting stream temperature at multiple scales contribute to an intricate thermal landscape (Vatland et al. 2014, Steel et al. 2017). For example, stream thermal regimes of the Pacific Northwest can demonstrate substantial variability over space (Fullerton et al. 2015, Leach et al. 2017) while exhibiting unexpected trends over time (Arismendi et al. 2012). Wildfire disturbance interacts with many processes driving stream thermal dynamics at both local and regional scales, but an understanding of how this interaction influences thermal variability within streams is limited.

By influencing various morphological and hydrometeorological processes, wildfires can alter stream thermal dynamics in burnt catchments. Through destabilizing soils, contributing to sediment input and damaging riparian corridors, wildfire disturbance can induce changes to channel structure following subsequent precipitation events in the post-fire period (Meyer & Pierce 2003, Kleindl et al. 2015). Such changes can impact temperature patterns by influencing the degree of topographic shading to the stream channel (Isaak & Hubert 2001) and controlling stream thermal sensitivity to air temperatures (Lisi et al. 2015). Removal of riparian vegetation during wildfire also increases incipient solar radiation to wildfire-affected portions of the stream channel (Amaranthus et al. 1989, Beakes et al. 2014). Each of these mechanisms can alter

thermal regime patterns in the immediate and intermediate post-fire period (Johnson & Jones 2000, Beakes et al. 2014, Lisi et al. 2015).

In combination with other forms of habitat alteration, short-term changes to stream temperature following wildfire can play an important role in structuring stream communities. Wildfire has been shown to interact with post-fire hydrologic regimes to facilitate a rapid shift to autochthonous-based algal production and conditions that favor opportunistic, disturbance-adapted macroinvertebrate taxa (Mellon et al. 2008, Klose et al. 2015). Immediate increases in temperature can lead to local extirpation and reduction of thermally-suitable habitat for resident fish species (Gresswell 1999, Hitt 2003, Sestrich et al. 2011), though recolonization of fire-affected reaches can occur quickly (Howell 2006). Thermal impacts can persist for years following disturbance, where temperature differences in the post-fire period can influence variability in physiology and metabolic demands among burned and unburned stream reaches (Beakes et al. 2014). The inherent resilience within freshwater communities often facilitates their rapid recovery from disturbance, but the prevalence of wildfire events regionally can allow short-term impacts to manifest at larger spatial scales (Dunham et al. 2003, Minshall 2003). Factors such as fire severity, post-fire hydrologic patterns and geomorphic conditions are important controls on the biotic response to wildfire disturbance, but the relative contribution of stream temperatures in mediating these responses is largely unknown (Malison & Baxter 2010, Harris et al. 2015, Verkaik et al. 2015).

Identifying the specific facets of the thermal regime that are most sensitive to wildfire disturbance is challenging. Several studies have compared temperatures in wildfire-affected streams of the Pacific Northwest to temperatures prior to disturbance or to neighboring unburned reaches (Burton 2005, Dunham et al. 2007, Sestrich et al. 2011). The unpredictable nature of

wildfires and the geographic patchiness of temperature monitoring networks results in most data collection being opportunistic and relegated to sparse observations in the summer or autumn period immediately following disturbance (Romme et al. 2011), when stream thermal regimes of the Pacific Northwest are most variable. Although analyzing the full-year thermal regime for an entire river network is difficult, decomposing temperature time series into a suite of descriptive metrics enables us to quantify the response in multiple thermal facets of ecological interest (Steel et al. 2017). For example, daily maximum and average temperatures are tightly correlated with multiple landscape characteristics such as elevation, flow, and drainage area, and provide an indication of riverine health and integrity (Olden & Naiman, 2010). They have also been shown to be responsive to wildfire disturbance (Hitt 2003, Sestrich et al. 2011) and are frequently used in predicting the distribution of cold-water species in the region (Isaak et al. 2010, Benjamin et al. 2016). Given the multitude of ways that temperature impacts stream taxa and the range of facets that are of potential ecological interest, it is important to incorporate metrics describing the magnitude, variability, frequency, and timing of thermal events in streams over seasons and over entire years (Olden & Naiman 2010, Arismendi et al. 2013).

In general, post-fire conditions are characterized by higher stream temperature, but these responses are often transient and may vary substantially between river systems. Several studies have documented correlations between increases in stream temperatures and the proximity and severity of corresponding fires (Hitt 2003, Sestrich et al. 2011, Beakes et al. 2014); however, increases in temperature can be mitigated by hydrologic and geomorphic conditions. Results from several observational studies in the Pacific Northwest suggest that increased watershed size, streamflow, and distance from burn perimeter could promote greater thermal inertia and resistance to direct radiative heat transfer in wildfire-affected streams (Amaranthus et al. 1989,

Robinson et al. 2005, Mahlum et al. 2011). Analyses of stream temperatures following wildfire in the region have been limited to individual watersheds or burn events, making it unclear whether thermal responses manifest across larger spatial scales (Bisson et al. 2003).

Consequently, there is a need to identify the environmental conditions and disturbance attributes that drive thermal sensitivity to wildfire at the regional scale.

Here we leverage opportunistic data sets in which temperatures were measured prior to and immediately following wildfire disturbance to quantify wildfire effects on stream thermal regimes across the Pacific Northwest. We linked annual temperature time series from 18 recently burned watersheds with spatially-explicit data on wildfire severity and hydrometeorological conditions. We quantified regional stream temperatures through a suite of ecologically relevant metrics and used nonparametric methods to categorize thermal regime responses according to descriptors of magnitude, variability, frequency and timing. We then applied multivariate analyses to reveal the pyrological and environmental factors that amplify or dampen thermal responses to wildfire. Our analysis addressed the following questions: (1) what are the immediate impacts of wildfire on ecologically-relevant facets of stream thermal regimes? and (2) what are the relative roles of pyrological, hydrological and meteorological factors in describing stream thermal responses to wildfire? By considering a range of thermal responses to wildfire across multiple ecological systems, our study seeks to understand and quantify the impact of wildfire on riverine ecosystems across the inland Pacific Northwest.

## 1.3 METHODS

### 1.3.1 *Study system*

We used long-term temperature monitoring data from fire-affected catchments across the Pacific Northwest to analyze stream thermal regimes following wildfire disturbance.

Temperature monitoring sites were mapped through the NorWeST database (NorWeST Project; [www.fs.fed.us/rm/boise/AWAE/projects//NorWeST.html](http://www.fs.fed.us/rm/boise/AWAE/projects//NorWeST.html)), and data for each site were provided by a combination of federal (i.e. U.S. Forest Service Nez Perce-Clearwater National Forest, U.S. Geological Survey National Water Information System, NOAA Water Quality Baseline Environmental Monitoring Program, U.S. Bureau of Reclamation Hydromet) and state (i.e. Washington State Dept. of Ecology) agencies (Table 1.1). By intersecting temperature gauging stations with burn-severity maps provided by the Monitoring Trends in Burn Severity database (MTBS Project; <http://www.mtbs.gov/>) describing recent (2006-2012) wildfires in Washington, Oregon and Idaho, we identified 18 stream reaches with multi-year temperature monitoring data contained in watersheds affected by 16 wildfires for a total of 18 unique fire-gauge combinations (Table 1.1; Figure 1.1a). Thermal regimes in our analysis ranged from “stable cold” to “variable cool” conditions (Maheu et al. 2015; Supp. Figure 1.1a,b), and contributing watersheds were characterized by fire regimes of low, mixed and replacement severity with 5-to-60-year return intervals (Fire Regime Layer, LANDFIRE 2014, U.S. Dept. of the Interior, Geological Survey; <https://www.landfire.gov/index.php>), representing much of the gradients in hydrology and pyrogeography present in watersheds of the region (Figure 1.2).

Eight sites were in reaches that were either adjacent to, or contained in, the burn perimeter of their corresponding wildfire, whereas 10 were in reaches downstream from the burn perimeters of wildfires that occurred within their catchment. Fire-affected streams were distributed across 8 drainage basins defined as separate accounting units (HUC6 level) within the Watershed Boundary Dataset (WBD, U.S. Geological Survey), with the most fire-affected streams occurring in the Clearwater Basin of eastern Idaho (Figure 1.1b). Each reach was contained in a distinct sub-watershed (Table 1.1) with no two sites being flow-connected, thus

reducing the influence of spatial autocorrelation (Ganio et al. 2005). Stream reaches in our analysis ranged from high-order systems where wildfires burned a minimal proportion of the total watershed immediately upstream of the temperature monitoring gauge to first-order streams draining headwater systems that had up to 81% of watershed area burned (Figure 1.1c, d). Our selection of sites covered a wide range of potential fire impacts. This approach enabled us to compare watersheds with varying geomorphology and fire-histories, and identify important drivers of thermal responses to wildfire that are rarely analyzed at the landscape scale (Bixby et al. 2015).

### 1.3.2 *Temperature time series and landscape data*

Stream monitoring at our sites began anywhere from 3 to 57 years prior to the date of ignition of the corresponding wildfire, and ended 1 to 8 years after this date. From these full time series, we focused our analysis on temperature records beginning no earlier than 01 July 2000 and ending in the autumn period one year after the wildfire. We removed data from the summer period when burning began in order to separate thermal time series into periods during which streams were experiencing pre-fire and post-fire conditions (Table 1.1; Figure 1.2). The date of 01 July 2000 corresponds to a shift from a “warm” regime to a more dynamic period in the Pacific Decadal Oscillation (PDO; Mantua & Hare 2002), a factor driving hydro-meteorological patterns and wildfire activity in the Pacific Northwest (Vaccaro 2002, Hessler et al. 2004). We thereby selected a window of analysis within which there was a uniform climatological context. Within this window of analysis, we used all available data including time series of varying lengths, to maximize the number of observations and the number of sites in our analysis, thus improving our capacity for regional inference (Liermann & Roni 2008). We also focused our analysis on the first year post-fire, where physical responses to wildfire are thought to be most

pronounced (Minshall et al. 1989). For this analysis, we characterized ‘wildfire effects’ as responses in stream temperature beginning on the first day of sampling following the summer of the wildfire and continuing for one year after (Figure 1.3).

Raw temperature data were summarized into time series of minimum, average and maximum daily temperatures. Temperatures outside the range of -10 °C to 40 °C were detected and removed following Arismendi et al. (2013), and erroneous data due to temperature logger failure were eliminated by comparing temperature data across years (Sowder & Steel 2012). Finally, we removed data in which consecutive daily readings differed by more than 7.5 °C, a threshold chosen by the authors to distinguish recordings that appeared infeasible with respect to typical variability in temperatures. We restricted our analysis to time series which had temperature data for at least 75% of daily recordings within the temporal window of interest. Sites in our analysis experienced wildfire disturbance over a six-year period during which thermal metrics were quantified across multiple facets and temporal scales (Table 1.2). Our approach ensured that differences between pre-fire and post-fire temperatures would represent a response due to disturbance rather than an artifact of long-term thermal dynamics caused by regional climatic patterns.

We collated spatially-explicit data on pyrological, hydrological and meteorological conditions in each catchment to investigate the role of hydrogeomorphology, wildfire conditions and climate in shaping stream thermal sensitivity to wildfire effects. Watersheds of fire-affected stream reaches were delineated in a Geographic Information System (ESRI ArcGIS Desktop 2017) using the National Hydrography Database (NHDPlus v.2; <http://www.horizon-systems.com/NHDPlus/>) and a digital elevation model provided through the National Elevation Dataset ([NED, U.S. Geological Survey; https://lta.cr.usgs.gov/NED](https://lta.cr.usgs.gov/NED)). We extracted data on

median elevation of the stream reach, average watershed slope and estimated mean annual flow (abbr. *ELEV*, *SLOPE*, and *FLOW*, respectively), all of which are central drivers of stream temperatures at the regional scale (Isaak & Hubert 2001, Lisi et al. 2015, Dunham et al. 2007, Caissie 2006). We included mean annual catchment precipitation (abbr. *PRECIP*) by averaging predictions for annual precipitation across each pre-fire sampling year for each watershed, using spatially-explicit precipitation data provided by the PRISM database (PRISM Climate Group, Oregon State University; <http://prism.oregonstate.edu>). Capturing long-term precipitation patterns allowed us to estimate the propensity for debris flows, channel reformation and subsequent temperature alterations in the year following disturbance as well as provided a coarse proxy for soil moisture, vegetative conditions and potential evapotranspiration within each catchment.

We used burn-severity mosaics provided by MTBS to quantify fire disturbance in reaches and analyze the spatial relationship between wildfire perimeters and stream networks. Wildfire conditions were quantified through three variables: the percentage of watershed burned (abbr. *PERBURN*), a binary variable indicating whether the stream reach was within or adjacent to the burn perimeter of the corresponding wildfire (abbr. *FIREADJ*), and a burn severity index calculated as the average difference in Normalized Burn Ratio values (dNBR) across all 900 m<sup>2</sup> parcels of catchment area affected by wildfire, where “Unburned” conditions correspond to 0 and “High” burn severity conditions correspond to 3, following severity measurements used within MTBS assessments (abbr. *FIRESEV*). We considered this combination of pyrological variables sufficient to quantify the extent, proximity, and intensity of wildfire damage to stream reaches, characteristics that have been shown to influence the response of stream temperatures to immediate and upstream effects of wildfire (Beakes et al. 2014, Mahlum et al. 2011). A

comparison of fire return intervals within catchments showed that our analysis captures a wide gradient of wildfire regimes present in watersheds across the Pacific Northwest. Collectively, this suite of predictors captures a broad characterization of wildfire and watershed conditions that can influence temperatures in fire-disturbed stream reaches.

### 1.3.3 *Statistical analysis*

We summarized temperature time series by calculating 26 metrics describing the magnitude, variability, frequency and timing of stream thermal events across seasonal and annual periods (following Olden & Naiman 2010, Arismendi et al. 2013, Steel et al. 2016). A larger suite of metrics was initially constructed to categorize potential impacts of wildfire on stream thermal regimes and to consider those impacts with the most direct biological consequences. The final set of metrics was then chosen from this larger suite following a principal component analysis (PCA) on pre-fire metric values to reduce redundancy among metrics (Table 1.2). We maintained metrics that were computationally accessible and important for stream ecological processes in order to readily inform the management of freshwater streams in fire-prone areas of the Pacific Northwest. For instance, we analyzed seasonal and annual summaries of maximum weekly maximum temperatures (MaxWTMax ; Table 1.2) because this metric has well-defined thresholds pertaining to state water quality standards (WA Dept. of Ecology Water Quality Standards, Section 173-201A-200; <http://www.ecy.wa.gov/programs/wq/wqhome.html>; Oregon Administrative Rules for Water Quality, Section 340-041-0028; [http://sos.oregon.gov/archives/Pages/oregon\\_administrative\\_rules.aspx](http://sos.oregon.gov/archives/Pages/oregon_administrative_rules.aspx)) and has been recently used in modeling the distribution of aquatic biota in stream networks of the Pacific Northwest (Isaak et al. 2010, Benjamin et al. 2016). We also ensured our metrics included facets that have been previously documented to respond to wildfire events and post-fire conditions, such as

average and maximum temperatures in the autumn period immediately following wildfire (Hitt 2003, Sestrich et al. 2011). By incorporating multiple components of the thermal regime, our final suite of metrics measures a number of important facets in temperature that are sensitive to physical conditions affected by wildfire and relevant to biological processes in streams of the region.

We used descriptive statistics and non-parametric analyses to compare thermal metrics in the year following wildfire to pre-fire conditions. We quantified responsiveness to wildfire disturbance by formulating an effect size  $\delta$  defined by the difference between the post-fire metric value and the pre-fire average value, scaled by the standard error in pre-fire values:

$$\delta = \frac{X_{Fire} - \overline{X_{Pre}}}{\frac{S_{Pre}}{\sqrt{n_{Pre}}}}$$

This formulation was motivated by the standard construction of a Student's t-statistic, although it does not follow a traditional parametrized distribution due to the dependent and non-normal error structure present in stream temperature time series. Utilizing a non-parametric effect size approach allowed us to incorporate stream temperature data of varying resolution and length. Our approach was well-suited for exploratory analyses and provided a robust estimation of disturbance impact in absence of typical normality assumptions (Nakagawa & Cuthill 2007). Effect size values can be interpreted as the immediate impact of wildfire to a thermal regime metric relative to its pre-fire variability, with values near zero indicating minimal effect of wildfire and negative or positive values indicating a relative decrease or increase in a thermal metric following disturbance, respectively. We calculated across-site averages ( $\bar{\delta}$ ) to describe regional patterns in thermal responses and estimated uncertainty by constructing and plotting 95% bootstrapped confidence intervals for average effect sizes of each metric. We supplemented

our effect size analyses with paired-difference comparisons between pre- and post-fire metric averages over all sites using Monte Carlo permutation testing based on 99,999 replicates.

We used redundancy analysis (RDA; Rao 1964) to summarize patterns of variation in thermal effect sizes and relate these patterns to descriptors of pyrological, hydrological and meteorological conditions. Redundancy analysis is a canonical ordination approach that applies principal component analysis to a set of fitted response values found through multiple linear regression, in order to optimally and linearly relate a set of dependent variables to a set of explanatory variables (Legendre & Legendre, 2012). In our analysis, separate response matrices composed of thermal effect sizes ( $\delta$ ) for four component groups of thermal metrics (magnitude, variability, frequency and timing) were regressed against a predictor matrix composed of potential drivers of stream thermal sensitivity to wildfire disturbance (*ELEV*, *SLOPE*, *FLOW*, *PERBURN*, *FIREADJ*, *FIRESEV* and *PRECIP*). Fitted regression responses were then subjected to PCA. Distributions for mean annual flow, percentage of watershed burned and elevation were log-transformed to ensure normality in residual errors for multiple regression. Relationships between the thermal metrics and environmental and disturbance predictor variables were assessed using ordination triplots constructed from the first two constrained axes. Each ordination was compared using unadjusted redundancy statistics ( $R^2_{Y|X}$ ; Borcard et al. 2011), and the relative importance of watershed characteristics (*ELEV*, *SLOPE* and *FLOW*), wildfire conditions (*PERBURN*, *FIREADJ* and *FIRESEV*) and annual precipitation (*PRECIP*) were measured by calculating each predictors contribution to canonical axes. All data processing and statistical analyses were conducted in R (R Core Team 2017; <https://www.R-project.org/>) with ordination analyses conducted using the *vegan* package (Oksanen et al. 2017).

## 1.4 RESULTS

### 1.4.1 *Wildfire effects on stream thermal regimes*

Thermal responses in the year following wildfire were highly variable across streams (Figure 1.4). A substantial increase in daily average or maximum conditions in the autumn following wildfire across all sites was not detected (AvgWTAvg.Aut:  $\bar{\delta} = 1.4057$ , MaxWTMax.Aut:  $\bar{\delta} = -0.9134$  respectively; Figure 1.4a), although a few sites did experience warmer temperatures immediately following disturbance. Many streams experienced an increase in average winter temperatures after wildfire (AvgWTAvg.Win:  $\bar{\delta} = 1.1763$ ) followed by a decrease in both average and minimum temperatures the following spring (AvgWTAvg.Spr:  $\bar{\delta} = -1.3461$ , MinWTMin.Spr:  $\bar{\delta} = -1.3139$  respectively). Average and maximum temperatures in summer had effect sizes evenly distributed around 0, whereas metrics measuring variability in average temperatures and the daily range in temperatures during summer had a coherent though non-significant response (VarAvg.Sum:  $p = 0.1506$ , AvgRange.Sum:  $p = 0.3848$ ) suggesting a decrease in thermal variation following wildfire ( $\bar{\delta} = -1.6160$ ,  $\bar{\delta} = -0.9340$ , respectively; Figure 1.4b). Metrics of thermal variance in other seasons had effect size distributions and confidence intervals that did not differ from 0 for most sites (Figure 1.4b). Metrics measuring the frequency and timing of annual thermal events generally had limited response to wildfire effects; effect size distributions and confidence intervals for metrics measuring the frequency of days when moving averages of maximum daily temperatures exceeded 16 °C, 18 °C and 20 °C (MWMT16, MWMT18, and MWMT20 respectively) were tightly clustered around 0 (Figure 1.4c), as were distributions for metrics measuring the timing of absolute minimum and maximum temperatures (AnnMin.Ann, AnnMax.Ann respectively) and the 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> quartile of the cumulative temperature distribution (CTD25.Ann, CTD50.Ann, and CTD75.Ann respectively; Figure 1.4d).

Metrics measuring the occurrence of relatively cold and warm events throughout the year demonstrated the strongest response to wildfire effects (Figure 1.4c). These metrics used daily minimum and maximum temperature regimes standardized over all observations to measure the frequency of days falling above or below a threshold of one standard deviation (see Table 1.2, Arismendi et al. 2013 for more details). Effect size distributions for both metrics indicated a consistent shift across sites in the year following wildfire. For metrics measuring the frequency of cold events (*ColdEvents.Ann*), the mean effect size was  $\bar{\delta} = -5.6579$ , corresponding to an average decrease of approximately 8 “cold” days in the year following wildfire. By contrast, metrics measuring the occurrence of warm events (*WarmEvents.Ann*) increased following wildfire, with a mean effect size of  $\bar{\delta} = 3.1455$  corresponding to an average increase of approximately 3 “warm” days in the post-fire year. A decreased frequency of cold events and increased frequency of warm events in the post-fire year occurred at most sites, and bootstrapped confidence intervals and permutation tests indicated a significant shift in pre-fire and post-fire metric distributions overall (*ColdEvents.Ann*:  $p = 0.00039$ , *WarmEvents.Ann*:  $p = 0.00189$ ).

#### 1.4.2 *Correlates of stream thermal sensitivity to wildfire*

Pyrological, hydrological and meteorological predictors were all important in explaining variation in thermal responses. Across all metric groups, variables for precipitation and wildfire conditions tended to be the strongest predictors of thermal responses; annual average precipitation amounts within each catchment (*PRECIP*) and percentage of watershed burned (*PERBURN*) had high eigenvalue contributions to constrained variance in each ordination of thermal responses (Figure 1.5a, Figure 1.6). Of the hydrogeological variables, mean annual flow (*FLOW*) was the strongest predictor of thermal responses, although stream reach elevation (*ELEV*) was also an important predictor, particularly in the ordination of variability and

frequency metrics (Figure 1.5b, c). Fire severity (*FIRESEV*) and adjacency (*FIREADJ*) were the least important predictors for variability and frequency metrics, but had a stronger linear relationship to responses in magnitude metrics and especially timing metrics (Figure 1.5). Watershed slope (*SLOPE*) and reach elevation were more important in explaining thermal effect sizes in variability and frequency metrics.

The degree to which pyrological, hydrological and meteorological factors explained temperature responses to wildfire varied across facets of the thermal regime (Figure 1.6). Timing metrics had the strongest linear relationship with environmental predictors, with almost 55% of variation in thermal effect size responses explained by pyrological, hydrological and meteorological conditions ( $R_{Y|X}^2 = 55\%$ ). Redundancy statistics for magnitude and frequency metrics were somewhat lower, showing around a third of all variability captured by constrained axes ( $R_{Y|X}^2 = 38\%$ ,  $R_{Y|X}^2 = 30\%$ , respectively). Metrics measuring variability in stream temperatures had a stronger linear relationship with predictors, with 42% of variation in effect size responses explained. Ordination within each groups of metrics indicated a measurable portion of unstructured variation in thermal responses that did not respond linearly to environmental and disturbance gradients captured by our predictor variables.

The temporal scale of each thermal metric was partially responsible for determining its position in multivariate space. Streams that experienced responses in minimum, average and maximum temperature during autumn and winter (Figure 1.6a, M1-M4) were associated with watersheds with higher average slope and catchment precipitation. Metric response in summer temperatures, on the other hand, was more correlated to mean annual flow (Figure 1.6a, M7-M8). Metrics measuring thermal variance during autumn were located in the first quadrant in the ordination space of all variability metrics (Figure 1.6b, V1-V2), indicating an association with

streams in watersheds that had higher average slope, annual flow, and more area burned. The frequency of cold events in the post-fire thermal regime was positively correlated with percentage of watershed burned and weakly correlated with streamflow (Figure 1.6c, F1). Conversely, the frequency of warm events was negatively correlated with watershed slope and positively correlated with elevation, flow and catchment precipitation (Figure 1.6c, F2). Ordination of timing metrics showed that changes in the timing of absolute minimum temperatures was strongly associated to stream reach adjacency to wildfire (Figure 1.6d, T1), while the timing of maximum conditions and portions of the cumulative temperature distribution were more associated with patterns in precipitation, elevation and watershed slope (Figure 1.6d, T2-T5).

## 1.5 DISCUSSION

Our study revealed variable thermal responses to wildfire across streams of the inland Pacific Northwest. We did not detect a regional increase in average and maximum temperatures after wildfires despite reports of such effects in finer-scale stream studies (Hitt 2003, Dunham et al. 2007, Sestrich et al. 2011). We did, however, find a consistent increase in the frequency of relatively “warm” days, and a decrease in the frequency of “cold” days, in the year following disturbance. Multivariate analyses showed that catchment precipitation, fire extent and mean annual flow were broadly important in explaining variability in thermal responses, thus contributing to a more complete understanding of how pyrological and climatic processes influence stream thermal sensitivity to wildfire. Our results help articulate the potential mechanisms driving thermal responses to wildfire and can inform freshwater management by moving beyond individual streams and burn events and instead advancing a region-wide perspective that is only possible due to large-scale monitoring efforts (Isaak et al. 2017).

### 1.5.1 *Regional responses of stream temperature to wildfire*

The change in the frequency of “warm” and “cold” periods in streams was the most prevalent difference between pre-fire and post-fire thermal regimes. All but two of our sites experienced a decreased frequency of days where standardized temperatures were relatively cooler (ColdEvents.Ann), whereas close to three-quarters of sites experienced an increased frequency of days where standardized temperature were relatively warmer (WarmEvents.Ann). The paired response in these two metrics illustrates a unidirectional trend towards more frequent warm events occurring in the post-fire annual thermal regime, and suggests that wildfires and post-fire conditions could make streams more prone to experiencing anomalously high temperatures, relative to recent conditions. Although similar responses have been documented in streams of the region and attributed to warming trends due to the effects of climate change (Isaak et al. 2012, Arismendi et al. 2013), differences in the timing of wildfire across sites and our focus on responses in the immediate post-fire window makes it unlikely that these results are an artifact of climate-induced warming. We conclude that wildfire and post-fire conditions are at least partially responsible for the change in the frequency of cooler and warmer thermal events for streams represented in our analysis.

Wildfire extent within the catchment was identified as an important correlate to change in the number of cold events. Conversely, hydrogeological conditions were more important in explaining responses in warm events while being largely independent of wildfire characteristics. The occurrence of cold and warm events is relegated to the winter and summer portions of the annual thermal regime, respectively. Streams in heavily-burned catchments of varying hydrogeological condition appear susceptible to decreases in the number of cold events during winter, possibly due to increased solar radiation reaching the stream or to changes in channel

structure following precipitation events during winter that prevent frequent cold spells. In summer, however, the response in the number of warm events appears to be structured by streamflow, elevation and precipitation patterns. These analyses suggest that the relative importance of wildfire extent and hydrogeological conditions in determining stream thermal responses may be seasonally dependent.

Our regional study did not detect a consistent increase in average and maximum temperatures in the autumn period immediately following wildfire, a result that contrasts with finer-scale studies analyzing disturbed streams in the region (Amaranthus et al. 1989, Hitt 2003, Sestrich et al. 2011). Some streams in our analysis did experience higher temperatures in the immediate post-fire window, but increases in average temperatures did not always correspond to increases in maximum temperatures. Additionally, our analysis did not indicate a consistent pattern in the conditions driving these responses; some sites which experienced immediate warming occurred in headwater systems downstream of high-severity fire whereas others occurred in mainstem systems adjacent to low-severity burn areas. We conclude that the phenomenon of higher temperatures immediately following wildfire is not ubiquitous and instead depends on watershed conditions and climatic contexts. Given the variability in stream thermal regimes (Fullerton et al. 2015, Steel et al. 2017) and the inherent complexity in the spatial relationship between wildfire regimes and riverine networks (Dunham et al. 2007), we contend that our understanding of stream responses to wildfire should be more nuanced than expectations of higher temperatures.

Due to the opportunistic nature of our analysis and the distribution of wildfire and stream monitoring efforts across the Pacific Northwest, we do not expect our results to completely characterize thermal responses experienced by all fire-affected streams of the region. Our

analysis looked for regional responses in temperature in the year following disturbance, and was not designed to detect highly localized temperature changes. As such, reach-scale thermal responses occurring at hourly or daily periods are not as well-described in our approach as in other studies measuring temperatures within individual watersheds or after a single burn event (Hitt 2003, Mahlum et al. 2011). Additionally, low-order streams at high elevation were underrepresented in our analysis, as were streams in catchments experiencing fire return intervals of more than 60 years (Figure 1.2). Thermal responses to wildfire may be unique in high-elevation catchments, given that streams in these systems often have higher sensitivity to air temperatures and the effects of solar radiation (Holsinger et al. 2014, Lisi et al. 2015). Nevertheless, our focus on long-term thermal dynamics in fire-affected watersheds experiencing variable hydrologic and geomorphic conditions was able to capture responses in temperature that have not been documented in previous studies. Combining fine-scale observational studies that address specific uncertainties in disturbance responses with regional analyses that integrate multiple data sources and describe general patterns in environmental variability will be essential in developing a more complete understanding of stream-wildfire interactions.

Characterizing general thermal response patterns to stochastic wildfire disturbance at a regional scale is difficult, but can be made more tangible by utilizing multiple data sources and adopting exploratory statistical approaches. Many previous studies have taken advantage of in-place temperature monitoring networks to compare short-term responses in stream temperature of burned and unburned reaches (Dunham et al. 2007, Mahlum et al. 2011, Beakes et al. 2014). Other studies have used correlative approaches and remote-sensing data to track long-term patterns of stream temperatures and channel structure at broader spatial resolutions (Isaak et al. 2010, Kleindl et al. 2015). Although each of these approaches provides valuable insight into the

trajectory of physical processes in streams in the post-fire period, there is a need for analyses that can explain how responses at the reach scale might manifest over space to determine regional response patterns. Our analysis attempted to bridge this gap by combining broad-scale remote-sensing data on burn severities with site-level data retrieved from a regional network of stream temperature monitoring agencies in order to help inform the management of freshwater streams in fire-prone watersheds.

### 1.5.2 *Environmental correlates of thermal response to wildfire*

Our work contributes to a larger body of research suggesting that stream thermal response to wildfire is highly site-specific. Effect size responses ranged widely across stream sites, especially for metrics measuring the magnitude and variability of post-fire temperatures, and there was notable variation in the explanatory power of our predictor variables among metrics measuring different components of the thermal regime. Nevertheless, regional scale patterns in the drivers of thermal response to wildfire did emerge in our analysis. In particular, catchment precipitation, percentage of watershed burned and mean annual flow were all important determinants of disturbance responses across sites and within different thermal regime components. Previous studies have shown that stream warming during wildfire can be highly localized (Dunham et al. 2007, Mahlum et al. 2011) and that temperature increases following burn events may be mitigated by intact riparian shading downstream of burned areas (Amaranthus et al. 1989) or thermal inertia due to high flows (Minshall et al. 1997, Robinson et al. 2005). Results of our study suggest that streamflow can act as an important control on wildfire-induced warming, but that high wildfire extent might influence thermal dynamics across a broad range of hydrological contexts.

Regional wildfire patterns and the distribution of monitoring effort across river networks contain a high degree of spatial structure that is important to consider when interpreting our results (Agee 1998, Strobl & Robillard 2008). The importance of wildfire extent and streamflow likely reflects mechanisms occurring at finer-scales that are not explicitly captured in our analysis, such as changes in riparian shading and channel morphology. For example, long-term studies have shown the importance of regional precipitation patterns (Meyer & Pierce 2003, Mote et al. 2003) and watershed morphology (Lisi et al. 2015) in guiding thermal sensitivity in streams. This speaks to the wide range of factors influencing stream thermal dynamics at varying spatial scales and at different times of the post-fire recovery period. Our broad stream temperature dataset allowed us to explain response patterns along multiple environmental and pyrological gradients, but explaining stream thermal responses in specific ecotones and watersheds with unique fire histories remains an important task (Bixby et al. 2015). Understanding stream-wildfire dynamics and adapting management to best practices will require incorporating the role of drivers operating at different spatial scales (Bisson et al. 2003) as well as structuring monitoring networks to be most efficient in answering key questions about in-stream processes (Marsha et al. 2018).

The nature of hydrometeorological regimes in the Pacific Northwest likely contribute to a complex interaction between factors driving increased wildfire activity and regional patterns in stream temperature. In the Western U.S., increased soil hydrophobicity following wildfire occurrence has been shown to be a major contributor to annual streamflow (DeBano 2000, Hallema et al. 2018), and increased flows following the first precipitation event in the post-fire period could potentially lead to higher thermal inertia of stream temperatures. Additionally, climate-induced increases in air temperatures have shown to be a driver of correlation between

annual wildfire activity and the timing of spring snowmelt (Westerling et al. 2006). Given the potential for increased snowmelt to decrease stream thermal sensitivity to air temperatures in high-latitude streams (Lisi et al. 2015), it may be that snowmelt and regional precipitation patterns could buffer streams from higher temperatures in years when wildfires are more likely to occur. Although thermal regimes at our sites did not illustrate a shift in the timing of extrema or cumulative temperatures that might be expected with earlier snowmelt (Luce et al. 2014), we found that average annual precipitation was important in describing responses in stream temperature during the post-fire period. As the Pacific Northwest moves towards a climate dictated by more variable precipitation (Mote & Salathé 2010) and a fire regime consisting of larger, more severe and frequent wildfires (Abatzoglou & Williams 2016), advancing a more comprehensive understanding of the interactions between climate, fire activity and hydrologic dynamics will be essential for effective management.

### 1.5.3 *Biotic implications of wildfire effects on thermal regimes*

Changes to water temperature, in combination with other alterations in stream habitat, can greatly affect stream biota in the post-fire period. Stream temperature is widely acknowledged as a critical determinant in the life history, behavior and spatial distribution of freshwater species (Ward & Stanford 1982, Caissie 2006), suggesting that short-term responses such as those examined in our analysis could cause wildfire disturbance to play a role in structuring stream communities at the landscape scale. Our study did not attempt to characterize biotic responses within fire-affected streams, but did document changes in the distribution of stream temperatures to favor increased periods of warmer temperatures over cooler ones in the first post-fire year. Regional responses such as these could have substantial ecological impact by altering the distribution of suitable thermal habitat and affecting energetic demands on thermally-

sensitive stream biota in fire-prone landscapes. Combining sampling efforts at the reach scale with data on landscape processes and disturbance regimes will be an essential step in constructing a more holistic understanding of stream biotic responses to wildfire.

Evaluating the composition of stream macroinvertebrate communities provides an effective way to measure the ecological impacts of wildfire. The relative contribution of stream temperatures in facilitating biotic responses to fire is difficult to quantify, but multiple studies have documented mild to significant increases in temperature co-occurring with decreased diversity and increased biomass in macroinvertebrate communities in fire-affected streams of the Pacific Northwest (Minshall et al. 2001, Mellon et al. 2008). Studies in the Salmon River Basin, Idaho, have shown similar response patterns occurring several years after disturbance, with wildfire-affected reaches exhibiting higher temperatures and favoring r-strategist taxa (Chironomidae, Baetidae, and Simuliidae) compared to unburned reaches (Malison & Baxter 2010, Harris et al. 2015). These studies have also illustrated the importance of precipitation-driven erosion events in controlling the magnitude of ecological responses, suggesting that the factors driving thermal responses in streams could also be responsible for controlling biotic productivity in the post-fire recovery period. Although general disturbance theory predicts an immediate disturbance response followed by a gradual return to pre-fire conditions (Mihuc & Minshall 2005), hydrometeorological variability could mitigate initial responses and dampen the rate of recovery in stream communities (Arkle et al. 2010, Rugenski & Minshall 2014). This underscores the potential for short-term thermal changes to propagate over space and structure the composition of stream communities well into the post-fire period.

Our results indicated that not all streams are prone to increased temperatures immediately following wildfire, but that a shift towards warmer temperatures relative to recent conditions is

common in the first post-fire year. Short-term temperature responses such as these have the potential to influence phenological dynamics of communities inhabiting fire-disturbed reaches, especially during life-history stages where individuals are more sensitive to alterations in temperature. Research on coastal streams of central California showed that even a short-term temperature increase of 0.6 °C a year following wildfire contributed to higher metabolic demand and lower density in steelhead and rainbow trout individuals in burned pools (Beakes et al. 2014). Similarly, individual-based models describing bioenergetics and demography demonstrated that rainbow trout in wildfire-disturbed streams could experience faster growth and heightened levels of inter-species competition driven by warmer temperatures (Rosenberger et al. 2015). Less obvious changes in temperature can also impact phenological patterns; a laboratory study of embryonic development in Chinook salmon showed that changes in thermal variability could affect emergence timing and development at emergence (Steel et al. 2012). In summary, understanding how climate change and shifting wildfire regimes can interact with temperature to impact physiological conditions of freshwater species remains a major challenge (Beer & Anderson 2013).

The potential for wildfire to alter stream thermal regimes also has important implications for modeling the spatial distribution of fish species in the Pacific Northwest. Warming stream temperatures have corresponded to the range expansion of warm-water invasive species in the region (Lawrence et al. 2014), and recent studies utilizing mechanistic models have illustrated the potential for wildfire-induced warming to exacerbate the effects of climate change in driving discrepancies in thermal habitat (Isaak et al. 2010, Falke et al. 2014). For example, spatial stream network models were used to show that higher temperatures due to wildfire were partially responsible for increasing the extent of thermal habitat for rainbow trout populations in the Boise

River Basin of Idaho, while decreasing thermal habitat for bull trout (Isaak et al. 2010). In another study, mechanistic models of stream habitat conditions paired with Bayesian network analysis showed that wildfire could potentially improve habitat quality for Chinook salmon in the Wenatchee River subbasin of Washington through increased channel complexity caused by large woody debris inputs in the post-fire period (Flitcroft et al. 2015). Although modeling results in this analysis indicated that increased stream temperatures due to wildfire were likely to negatively impact juvenile Chinook individuals in some areas, those areas where high-severity fire were likely to occur were already considered unsuitable stream habitat. The ability to model the distribution of thermal habitat across entire stream networks makes mechanistic approaches invaluable for providing insight into the nature of wildfire impacts, but such efforts require validation through opportunistic studies or controlled experiments that can provide a more detailed explanation of the patterns and drivers of stream temperature in fire-affected catchments.

## 1.6 CONCLUSION

Characterizing the role of wildfire in shaping stream habitat conditions at the landscape scale remains a pressing and challenging goal in stream ecosystem management (Bixby et al. 2015). Our analysis illustrated that wildfire can impact ecologically-relevant facets of stream temperature at the regional scale, through altering the frequency of relatively cool and warm periods of the post-fire thermal regime. We identified the contribution of various pyrological, hydrological and meteorological factors in determining thermal responses, identifying important environmental drivers to thermal sensitivity in burnt catchments. The coherent regional responses found in our analysis provide important insight into the processes connecting stream thermal dynamics, wildfire events and ecological conditions in streams of the Pacific Northwest.

Further investigation into the role of wildfire in contributing to natural thermal variability will be essential to the management and conservation of stream ecosystems in the region.

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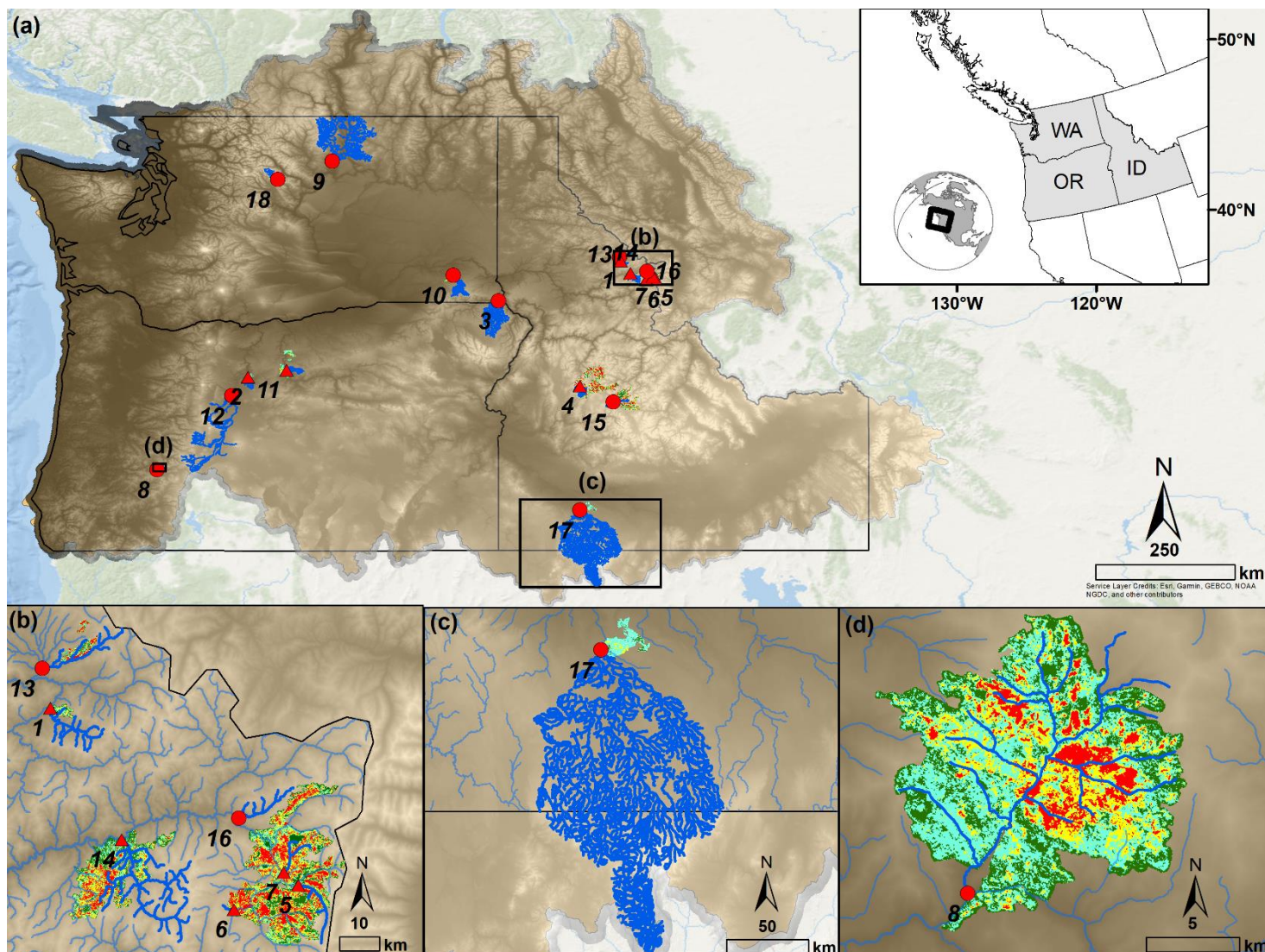
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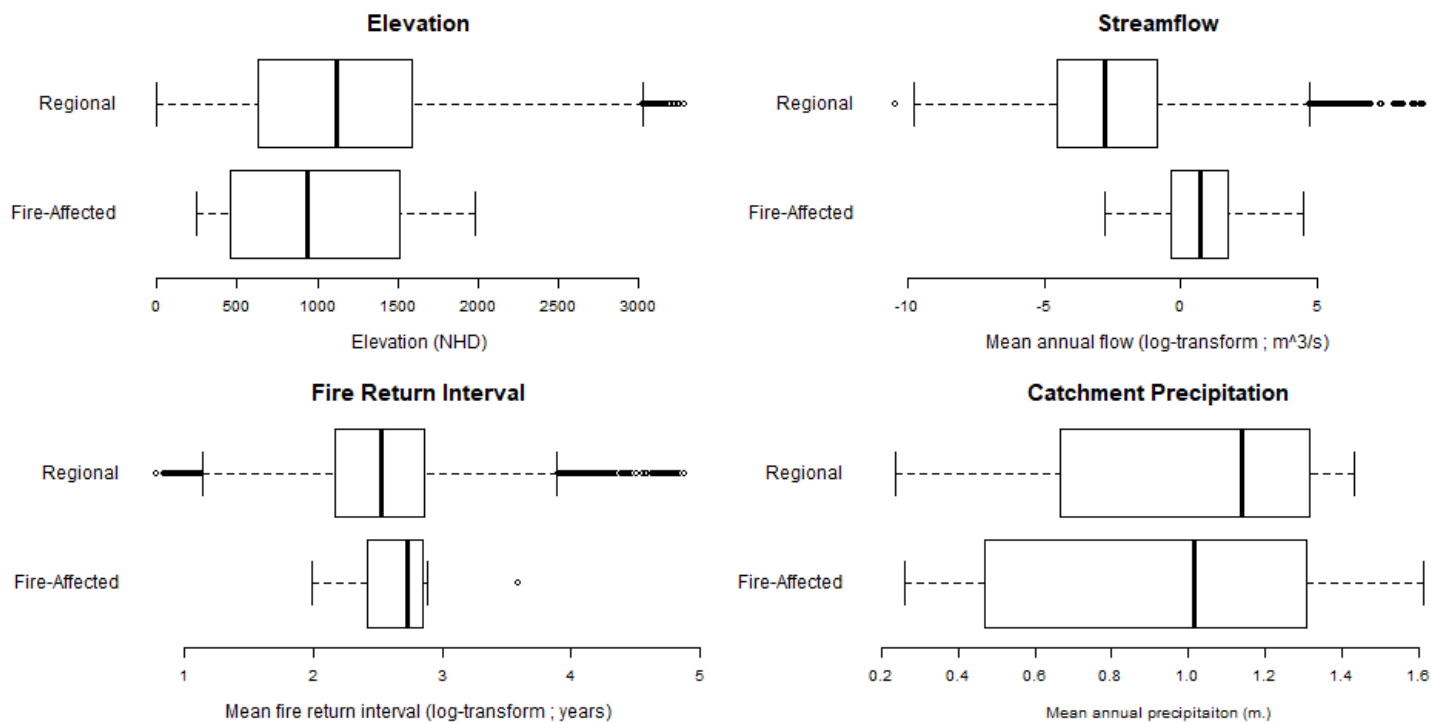
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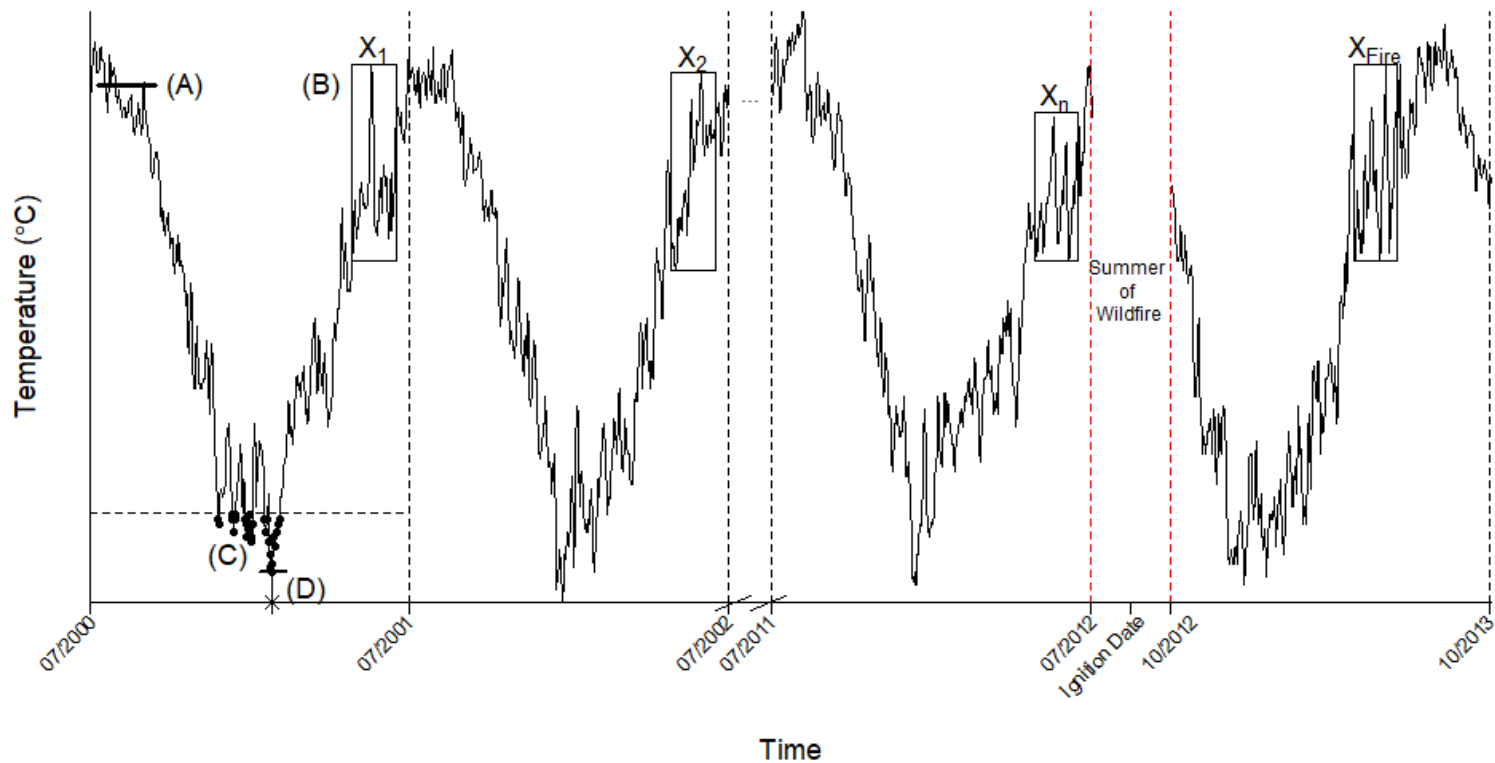
## 1.9 FIGURES &amp; TABLES



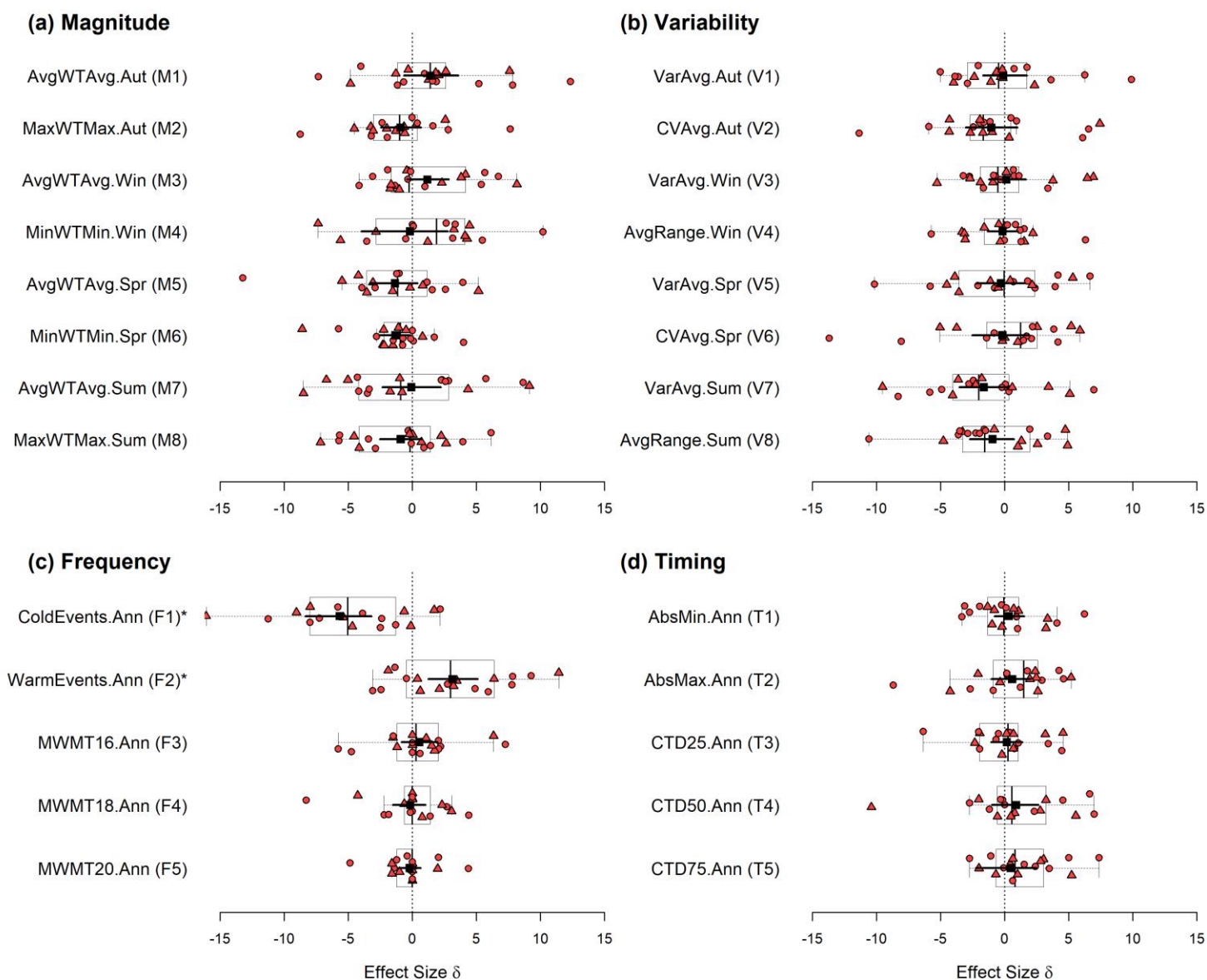
**Figure 1.1 – Distribution of fire-affected temperature monitoring gauges in the Pacific Northwest.** (a) Map showing the distribution of temperature monitoring gauges within the inland Pacific Northwest. Sites are numbered according to their description in Table 1, where circles denote sites downstream of fire perimeters and triangles denote sites within or adjacent to fire perimeters (b) Sites 1, 5, 6, 7, 13, 14 and 16 were located within the Nez Perce-Clearwater National Forest of the Clearwater Basin in Idaho. Insets (c) and (d) are provided to illustrate the range in hydrologic conditions and burn configurations captured in our analysis, characterized by higher-order systems with minimal wildfire extent ((c) Bruneau River, ID affected by the East Rock Fire, August 2012) to low-order systems with high wildfire extent ((d) Boulder Creek, OR affected by the Rattle Fire, August 2008).



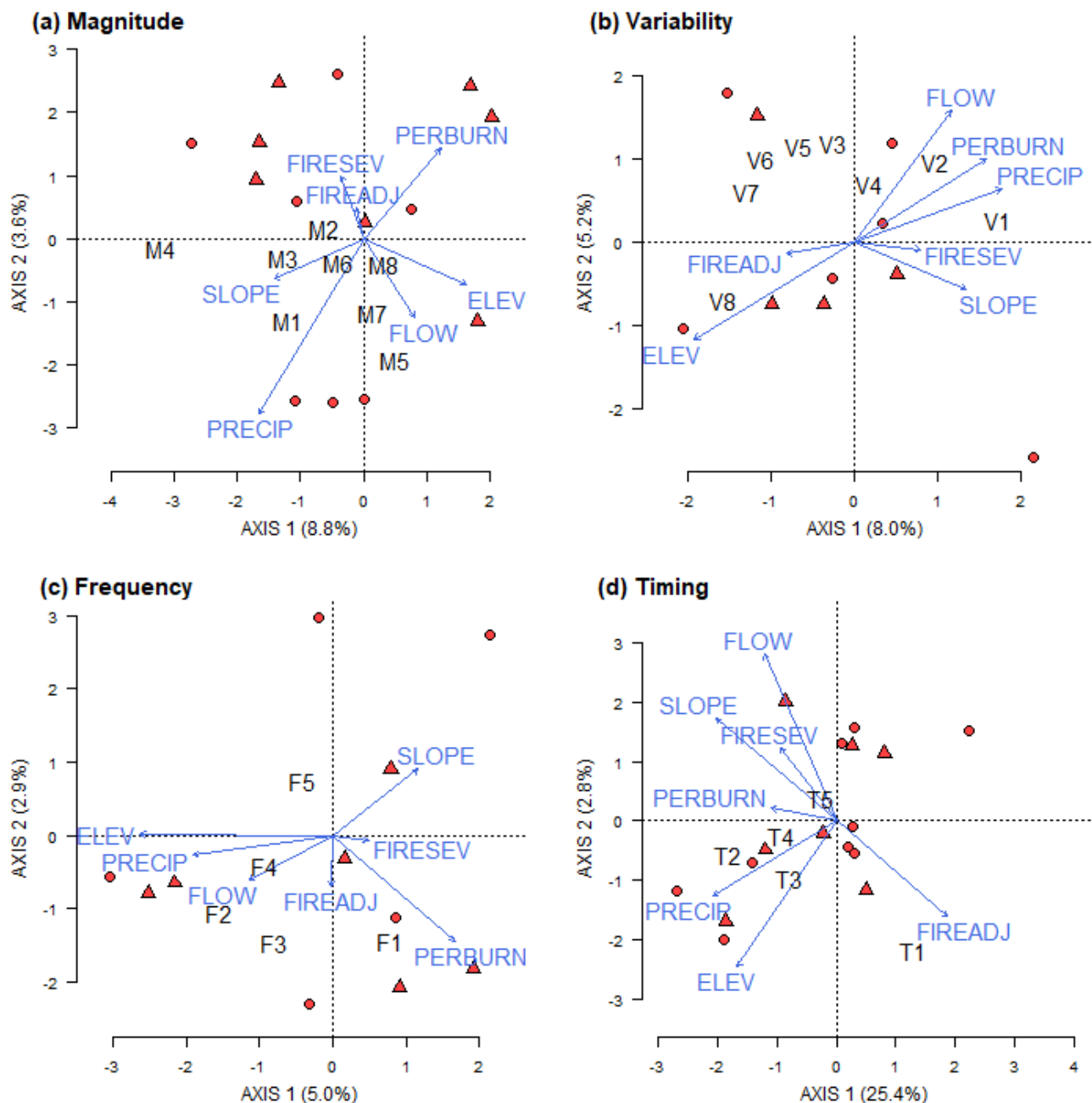
**Figure 1.2 – Comparison of abiotic conditions within catchments.** Distributions of modelled elevation, streamflow, fire return interval and average annual catchment precipitation experienced by watersheds in our analysis and regionally across the Pacific Northwest. Distributions of streamflow and fire return interval are log-transformed for illustrative purposes. Elevation and streamflow data are derived from the National Hydrography Database (NHDPlus v.2; <http://www.horizon-systems.com/NHDPlus/>), fire return interval values from the LANDFIRE database (Fire Regime Layer, LANDFIRE 2014, U.S. Dept. of the Interior, Geological Survey; <https://www.landfire.gov/index.php>), and annual average precipitation estimates from the PRISM database (PRISM Climate Group, Oregon State University; <http://prism.oregonstate.edu>).



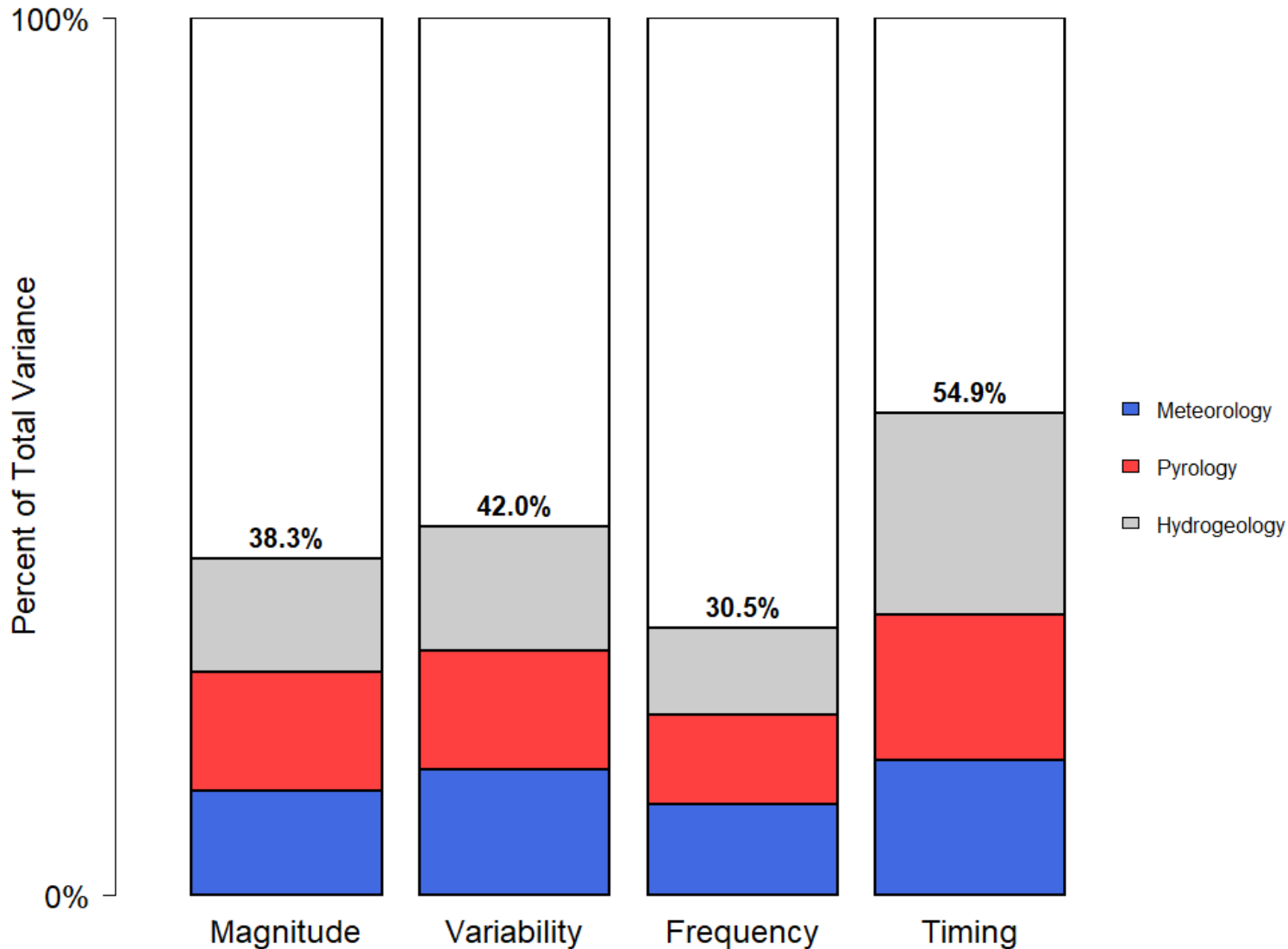
**Figure 1.3 – Decomposition of thermal regime.** Conceptual figure describing decomposition of annual thermal regimes into metrics measuring the (A) magnitude, (B) variability, (C) frequency and (D) timing of thermal events across the year. Here, the pre-fire observations from 2000 to 2012 ( $X_1, X_2, \dots, X_n$ ) are compared to the metric value in the post-fire year ( $X_{Fire}$ ) through the effect size  $\delta$  described in the text (see Methods).



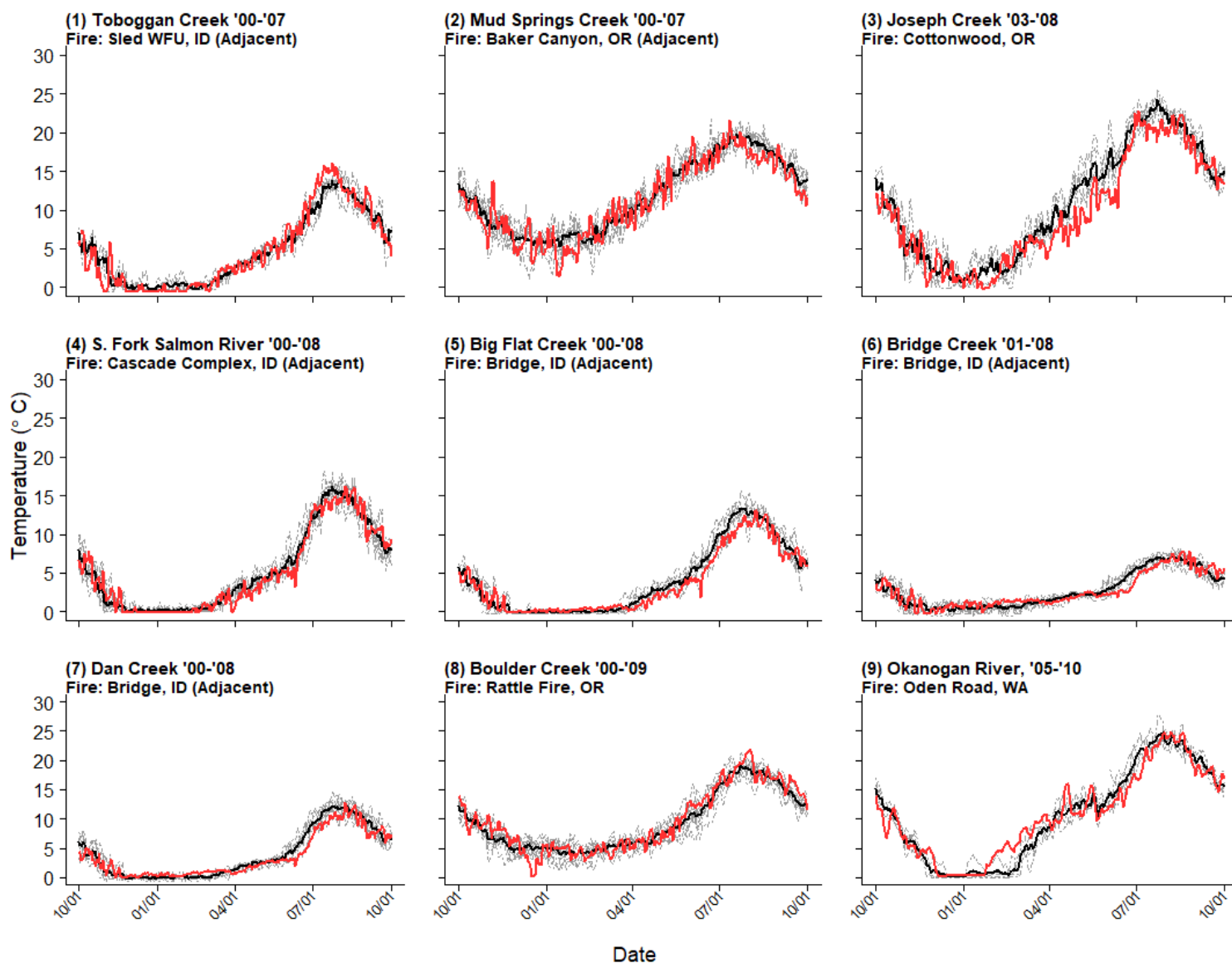
**Figure 1.4 – Distribution of thermal effect sizes.** Distribution of effect sizes for metrics measuring the **(a)** magnitude, **(b)** variability, **(c)** frequency, and **(d)** timing of thermal events in wildfire-affected streams. Metric names and codes are explained in Table 1.2. Points indicate the effect size at a single site, where circles denote sites downstream of fire perimeters and triangles denote sites within or adjacent to fire perimeters. Boxplot whiskers extend to 1.5 times the interquartile range, with crosses denoting observations outside this range. Black boxes and lines show the average effect size and bootstrapped 95% confidence interval. “\*” indicates a significant difference between pre-fire and post-fire averages at the  $\alpha = 0.01$  level.



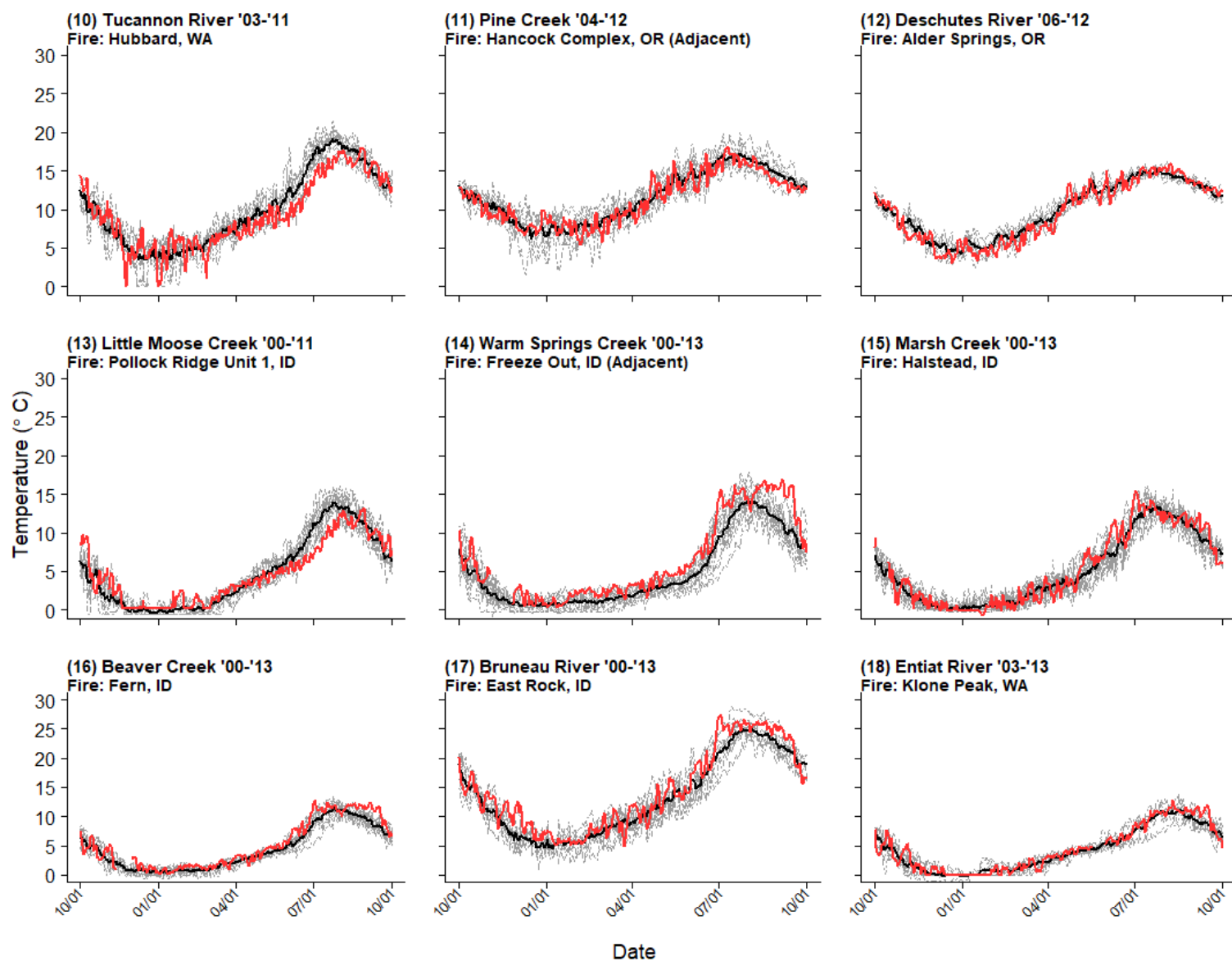
**Figure 1.5 – Correlation triplots from redundancy analysis.** Correlation triplots from redundancy analyses showing the ordination of effect sizes measuring the (a) magnitude, (b) variability, (c) frequency and (d) timing of stream thermal events in the post-fire year. Triplots are constructed using the first two constrained axes, with the proportion of variance explained by each axis shown in parentheses. Sites are shown as points based on the weighted averages of species scores (WA scores), where circles denote sites downstream of fire perimeters and triangles denote sites within or adjacent to fire perimeters. Metrics are plotted according to their normalized eigenvector contributions to canonical axes (i.e. “species scores”), and depicted by their corresponding index (Table 1.2). Environmental and pyrological predictors are fit to the ordination and shown as vectors, with the magnitude scaled according to their contribution to the constrained axes.



**Figure 1.6 – Decomposition of ordination variance.** Comparison of the degree of fit within each ordination of each thermal metric group. The total redundancy statistic for each ordination ( $R^2_{Y|X}$ ) is shown on the y-axis. Constrained variation was decomposed into groups of predictors capturing conditions in hydrogeology (*ELEV*, *SLOPE*, and *FLOW* shown in dark gray), pyrology (*PERBURN*, *FIREADJ* and *FIRESEV*, shown in gray) and meteorology (*PRECIP*, shown in light gray). Unconstrained variation is shown in white.



**Supplementary Figure 1.1a – Annual thermal regimes (Sites 1-9).** Annual thermal regimes of daily average temperatures from 01 October to 30 September for Sites 1-9. Gray lines depict pre-fire thermal regimes. Black lines show the average pre-fire thermal regime across all sampling years, and red lines show the thermal regime in the first post-fire year. “Adjacent” designates those sites which were adjacent to or contained within their corresponding wildfire perimeter.



**Supplementary Figure 1.1b – Annual thermal regimes (Sites 10-18).** Annual thermal regimes of daily average temperatures from 01 October to 30 September for Sites 10-18. Gray lines depict pre-fire thermal regimes. Black lines show the average pre-fire thermal regime across all sampling years, and red lines show the thermal regime in the first post-fire year. “Adjacent” designates those sites which were adjacent to or contained within their corresponding wildfire perimeter.

**Table 1.1 – Temperature monitoring sites.** Stream temperature monitoring sites and corresponding wildfires across the Pacific Northwest (ID = Idaho, OR = Oregon, WA = Washington). Site locations are depicted in Figure 1.1. Watersheds for each site are listed by their hydrologic unit codes (HUC12) provided within the Watershed Boundary Dataset (USGS). Agencies responsible for conducting stream temperature monitoring are described further in the text. Recording periods indicate the subset of total time series used in the analysis for quantifying pre-fire and post-fire thermal regimes.

Site	Wildfire Name & State	Ignition Date	Stream Name	HUC12	Monitoring Agency	Recording Period
1	Sled WFU, ID	08/16/06	Toboggan Creek	170603070205	USFS Nez Perce-Clearwater NF	07/01/00 – 09/30/07
2	Baker Canyon, OR	08/29/06	Mud Springs Creek	170703070403	USBR Pacific Northwest Region Hydromet	07/01/00 – 09/30/07
3	Cottonwood, OR	07/13/07	Joseph Creek	170601060607	WA State Dept. of Ecology	07/01/03 – 09/30/08
4	Cascade Complex (Monumental), ID	07/17/07	S. Fork Salmon River	170602080406	NOAA Water Quality Baseline Environmental Monitoring Program	07/01/00 – 09/30/08
5	Bridge, ID	07/18/07	Big Flat Creek	170603030203	USFS Nez Perce-Clearwater NF	07/01/00 – 09/30/08
6	Bridge, ID	07/18/07	Bridge Creek	170603030204	USFS Nez Perce-Clearwater NF	01/01/01 – 09/30/08
7	Bridge, ID	07/18/07	Dan Creek	170603030206	USFS Nez Perce-Clearwater NF	07/01/00 – 09/30/08
8	Rattle, OR	08/17/08	Boulder Creek	171003010801	USGS NWIS	07/01/00 – 09/30/09
9	Oden Road, WA	08/21/09	Okanogan River	170200062205	USGS NWIS	07/01/05 – 10/01/10
10	Hubbard, WA	08/26/10	Tucannon River	170601070608	WA State Dept. of Ecology	07/01/03 – 09/30/11
11	Hancock Complex, OR	08/01/11	Pine Creek	170702040408	USGS NWIS	04/01/04 – 09/30/12
12	Alder Springs, OR	09/22/11	Deschutes River	170703011104	USGS NWIS	01/01/06 – 10/01/12
13	Pollock Ridge Unit 1, ID	09/21/10	Little Moose Creek	170603070302	USFS Nez Perce-Clearwater NF	07/01/00 – 09/30/11
14	Freeze Out, ID	08/08/12	Warm Springs Creek	170603030403	USFS Nez Perce-Clearwater NF	07/01/00 – 09/30/13
15	Halstead, ID	07/27/12	Marsh Creek	170602050305	NOAA Water Quality Baseline Environmental Monitoring Program	07/01/00 – 09/30/13
16	Fern, ID	08/08/12	Beaver Creek	170603030208	USFS Nez Perce-Clearwater NF	07/01/00 – 09/30/13
17	East Rock, ID	08/06/12	Bruneau River	170501021306	USGS NWIS	07/01/00 – 09/30/13
18	Klone Peak, WA	09/08/12	Entiat River	170200100202	WA State Dept. of Ecology	10/01/03 – 09/30/13

**Table 1.2 – Suite of thermal regime metrics.** Suite of thermal regime metrics constructed from annual time series of daily minimum, average and maximum temperatures. Metric codes refer to the name of the metric followed by the season which it applies to; for instance, AvgWTAvg.Aut corresponds to average weekly average temperatures in autumn. Metric codes refer to labels shown in Figure 1.4, and metric indices are used to distinguish position in multivariate ordination triplots in Figure 1.5.

<b>Component (Index)</b>	<b>Metric (Code)</b>	<b>Description</b>	<b>Season (Code)</b>
Magnitude (M1 – M8)	Minimum weekly minimum temperature (MinWTMin)	Minimum of all weekly (7-day) moving averages of minimum daily temperatures	Autumn, 10/01 – 12/31 (Aut)
	Average weekly average temperature (AvgWTAvg)	Average of all weekly (7-day) moving averages of average daily temperatures	Winter, 01/01 – 03/31 (Win)
	Maximum weekly maximum temperature (MaxWTMax)	Maximum of all weekly (7-day) moving averages of maximum daily temperatures	Spring, 04/01 – 06/30 (Spr) Summer, 07/01 – 09/30 (Sum)
Variability (V1 – V8)	Variability of daily average temperatures (VarAvg)	Empirical variance of daily average temperatures	Autumn, 10/01 – 12/31 (Aut)
	CV of daily average temperatures (CVAvg)	Coefficient of variation of daily average temperatures	Winter, 01/01 – 03/31 (Win)
	Average daily range in temperatures (AvgRange)	Average of daily range in temperatures	Spring, 04/01 – 06/30 (Spr) Summer, 07/01 – 09/30 (Sum)
Frequency (F1 – F5)	Frequency of cold and warm events (ColdEvents, WarmEvents)	Frequency of events (in days) when daily minimum / maximum temperatures standardized by across-year average and standard deviation are less than – 1 / greater than 1	Annual, 07/01 – 06/30 (Ann)
	Frequency of 16, 18, and 20 °C MWMT events (16MWMT, 18MWMT, 20MWMT)	Frequency of events (in days) when maximum weekly maximum temperatures exceed 16, 18, and 20 °C	
Timing (T1 – T5)	Timing of absolute minimum and absolute maximum temperatures (AbsMin, AbsMax)	Timing of the absolute minimum and maximum daily temperatures annually	Annual, 10/01 – 09/30 (Ann)
	Timing of 25 <sup>th</sup> , 50 <sup>th</sup> and 75 <sup>th</sup> percentile of CTD (CTD25, CTD50, CTD75)	Timing of the 25 <sup>th</sup> , 50 <sup>th</sup> , and 75 <sup>th</sup> percentile of the annual cumulative temperature distribution.	

## Chapter 2: Stream macroinvertebrate community response to wildfire

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## 2.1 ABSTRACT

In the Pacific Northwest of the United States, wildfire plays a critical role in driving stream ecosystem dynamics through structuring physical habitat conditions and affecting in-stream biotic communities. Although various observational studies have characterized stream biotic responses to wildfire in the context of single burn events or individual watersheds, few studies have investigated how wildfire influences community structure in streams at broader spatial scales. Here we utilize an extensive monitoring dataset to examine the role of wildfire, fine-scale habitat conditions and watershed characteristics in structuring the functional diversity of stream macroinvertebrate communities in the Pacific Northwest. Burn severity maps of recent and extensive wildfires affecting stream catchments prior to sampling were collated to compare burned and unburned stream communities in 153 different fire-stream combinations. We used multivariate regression and nonmetric multidimensional scaling to explore variation within three indices of functional diversity through variables capturing fine-scale habitat conditions, watershed characteristics and wildfire occurrence across stream communities. Our analysis reveals that functional diversity is largely similar between streams experiencing recent and extensive wildfire and unburned streams, but that recent wildfire occurrence is a significant predictor of macroinvertebrate abundance. Overall our analysis provides insight into the components of wildfire activity and stream habitat conditions that describe patterns in stream macroinvertebrate diversity at the landscape scale.

## 2.2 INTRODUCTION

The role of disturbance in structuring stream macroinvertebrate communities has been a focus of research in freshwater ecology for decades (Resh et al. 1988, Poff 1992). In the Northwestern United States, wildfire represents the most prevalent disturbance regime to structure watershed conditions (Hessburg & Agee 2003), and as such plays an important role in influencing aquatic habitat conditions experienced by stream communities regionally (Bisson et al. 2003). Freshwater macroinvertebrate communities are largely structured by conditions in flow, temperature, geomorphology and organic matter inputs (Karr 1991, Li 2001), and as such may be sensitive to wildfire-induced alterations of these regimes. Studies contrasting community structure in burned and unburned streams have shown that fire can increase the presence of r-strategist, disturbance-adapted taxa for years following disturbance (Mellon et al. 2008, Harris et al. 2015). Wildfire activity often interacts with precipitation events, patterns in streamflow and temperature to influence community composition in burnt catchments (Arkle et al. 2010, Rugenski & Minshall 2014), but efforts to characterize the importance of these variables in driving aquatic diversity at broader spatial scales are lacking (but see Bixby et al. 2015, Verkaik et al. 2015). Understanding the role of wildfire activity as an environmental pressure in Western U.S. stream ecosystems constitutes an important goal to freshwater conservation in a future where fire activity is expected to become increasingly frequent and severe (Schoennagel et al. 2017, Stavros et al. 2014).

The periodic occurrence of wildfire creates heterogeneity in the post-fire recovery state of stream ecosystems across the Pacific Northwest. Wildfire-induced changes in stream physical conditions are largely dependent on pyrological characteristics like burn severity, extent of catchment burned and the proximity of stream reaches to fire perimeters (Amaranthus et al.

1989, Dunham et al. 2007), as well as hydrologic regimes and climatic patterns in the post-fire period (Arkle et al. 2010, Rugenski & Minshall 2014). These changes and their consequent biotic responses are often most pronounced in the immediate and intermediate post-fire period (Minshall 2003), with stream communities often quickly returning to pre-disturbance levels (Death 2010, Stanley et al. 2010). Nevertheless, ecological conditions in streams draining burned and unburned catchments can diverge for years following wildfire, both in the physical attributes of stream habitats (Robinson et al. 2005) and in the composition of primary consumers (Mihuc & Minshall 2005) and the responses of taxa at higher trophic levels (Beakes et al. 2015). Despite the potential for wildfire to drive a mosaic of stream habitat conditions over longer temporal periods and at broad spatial scales (Kleindl et al. 2015), we have an incomplete understanding of how fire influences stream biota (Bixby et al. 2015), and studies measuring the post-fire trajectory of stream communities have been largely opportunistic and relegated to a select few watersheds for only a few years following disturbance (Mellon et al. 2008, Arkle et al. 2010). Large-scale stream habitat monitoring projects and remote sensing data on wildfire occurrence provide the opportunity to understand major gradients in wildfire across watersheds and understand which facets of disturbance are most important in structuring stream communities.

Physical habitat conditions play a fundamental role in determining the distribution and diversity of freshwater taxa in streams, and so understanding how wildfire influences these conditions at broader spatial scales is an important goal in the management of freshwater ecosystems. Wildfire causes the destruction of organic material and the destabilization of soils in the upland and riparian areas of a streams catchment (DeBano 2000, Dwire & Kauffman 2003). Following post-fire precipitation events, these mechanisms can contribute to an influx of sediment and organic material to the stream channel (Minshall 1989, Dahm et al. 2015), and can

decrease the amount riparian shading leading to higher levels of incipient radiation reaching the stream channel (Beakes et al. 2015, Webb & Zhang 1997). Such responses contribute to the long-term patterns in temperature, organic material and flow that occur in fire-prone watersheds (Kleindl et al. 2015, Dunham et al. 2007, Isaak et al. 2010, Harris et al. 2015), and thus impact stream taxa that utilize temporal patterns in these physical regimes (Minshall et al. 2001, Verkaik et al. 2015). Watersheds across the Pacific Northwest are widely variable in wildfire regimes and hydrologic conditions however, and disturbance responses in stream communities are likely structured by site-specific conditions at the reach scale as well as broader-scale patterns in climatic and hydrogeomorphic conditions (Rugenski & Minshall 2014, Bixby et al. 2015). As such, characterizing the role of fire as a disturbance agent to stream ecosystems requires an understanding of how stream habitat conditions at multiple spatial scales vary across catchments with varying fire histories.

Quantifying the role of wildfire in structuring stream communities is inherently difficult, but can be made more manageable by characterizing taxa in terms of their functional attributes, or traits. Functional traits are often used as a means to describe general patterns across ecological communities (McGill et al. 2006), and indices of functional diversity have been increasingly utilized in explaining biotic responses to disturbances in freshwater ecosystems (Mouillot et al. 2013, Boersma et al. 2016). Characteristics such as life-history, morphology and ecological habits are driven by numerous environmental regimes in hydrology, temperature, nutrients and vegetation dynamics, allowing these forces to act as filters on functional diversity at multiple scales (Karr 1991, Poff 1997). All of these processes are affected by wildfire occurrence (Hallema et al. 2018, Dunham et al. 2007, Harris et al. 2015), and abiotic responses to fire can contribute to conditions favoring generalist taxa (Mihuc & Minshall 1995) with high dispersal

ability and multivoltine life-cycles (Vieira et al. 2004, Minshall 2003), as well functional feeding groups that benefit from the increased ratio in autochthonous-to-allocthonous based productivity commonly observed in recently burned streams (Cooper et al. 2015, Klose et al. 2015). Although these abiotic response patterns provide the potential for wildfire to act as a landscape filter on functional diversity in streams, the variability in wildfire characteristics and hydrogeomorphic conditions in watersheds, as well as the inherent complexity in the interaction of these two components, make individual observational studies unable to identify general response patterns from those specific to individual burn events. Thus, studies identifying functional responses to wildfire events across multiple catchments can provide useful insight into the importance of wildfire as a filter on stream communities at the landscape scale.

In this study, we investigated the role of wildfire in structuring the functional diversity of stream macroinvertebrate communities in watersheds across the Northwest United States. By utilizing an extensive set of data on stream habitat conditions and macroinvertebrate community counts collected over 1086 sites in the Columbia River Basin for the past 14 years, we describe the relative contributions of wildfire occurrence, hydrogeomorphology and fine-scale habitat variables in explaining biotic responses to disturbance in stream insect communities. Using a database of functional traits and spatially-explicit burn severity maps, we compared functional diversity of macroinvertebrate communities in unburned streams to streams which experienced recent and extensive fire prior to sampling. Our analysis addressed the following questions: (1) how does wildfire affect the functional composition of stream communities across the Pacific Northwest, and (2) which stream habitat conditions and wildfire disturbance characteristics are responsible for changes in stream community composition in the post-fire period? Our work

seeks to contribute to a broader understanding of the role of wildfire in shaping stream community composition at the landscape scale.

## 2.3 METHODS

### 2.3.1 *Study area, stream habitat and wildfire data*

Data for our analysis included 1086 sites across six states (Washington, Oregon, Nevada, Utah, Idaho and Montana) and 14 basins within the Columbia River drainage of the Pacific Northwest (Figure 2.1). Sites were distributed over 11 ecoregions including areas within the Cascade and Rocky Mountains and sagebrush steppe in the Columbia and Snake River Plateau (Level III designations; Omernik & Griffith 2014). Sampling locations ranged in elevation from 400 m. to 2500 m., within first- to fourth-order streams draining catchments with areas of 0.90 km<sup>2</sup> to 151.35 km<sup>2</sup>. Catchments received between 0.27 m to 1.97 m. per year on average based on long-term climatic patterns (PRISM Climate Group, Oregon State University; <http://prism.oregonstate.edu>), placing catchments in the range of arid to mesic conditions (Irvine et al. 2015). Fire regimes within our catchments captured much of the variability in pyrological conditions that are present throughout the Pacific Northwest. Most catchments were contained in high-elevation systems including Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii*) and Ponderosa pine (*Pinus ponderosa*) among others, with catchments having a history of low, mixed and replacement severity wildfires.

Stream habitat and macro-invertebrate data were collected through the PACFISH/INFISH Biological Opinion (PIBO) Monitoring Program, a broader study evaluating the status and trend of aquatic and riparian conditions in streams located in catchments on land that was primarily (> 50%) managed by federal agencies (Bureau of Land Management (BLM) and the U.S. Forest Service (USFS); Kershner et al. 2004). Subwatersheds were selected for

sampling using a generalized random tessellation stratified design (Kershner et al. 2004) and had management histories that were grouped into “reference” conditions where livestock grazing, road densities and dredging and mining activities were minimal, to “managed” conditions. Sites were repeatedly sampled during specific years between 2001 to 2016 (with sampling temporarily ceasing in 2012), for a total of 2596 sampling occurrences. Stream habitat and macroinvertebrate sampling was done using a well-established protocol that was adaptive and intended to reduce measurement error (Kershner et al. 2004, Archer et al. 2004). *A priori* power analyses were used to determine the sample size and site distribution necessary in order to detect change in most stream habitat attributes at finer and broader spatial scales (Henderson et al. 2005, Archer et al. 2004), providing an exceptional opportunity to measure the response of stream benthic communities to habitat conditions and wildfire disturbance across the Columbia River Basin.

Physical conditions in streams were characterized using a combination of reach-scale sampling data and spatially-explicit hydrological and climatic datasets to measure the role of habitat and watershed characteristics in structuring functional composition in benthic communities. Stream habitat monitoring data included information on stream reach structure, streambed particle size, and the distribution large woody debris. Stream temperature was measured hourly from 15 July to 31 August for each sampling year, and a weekly moving average of daily maximum temperatures (MWMT) was calculated to summarize stream thermal conditions. Streamflow conditions at each site were measured with estimated mean annual flow from the National Hydrography Database (NHDPlus v.2; <http://www.horizon-systems.com/NHDPlus/>) and precipitation in each catchment was estimated using historical averages from the PRISM database (PRISM Climate Group, Oregon State University;

<http://prism.oregonstate.edu>). Percent of catchment land-cover that was forested was derived using the National Land Cover Database (NLCD; Xian et al. 2011).

We used GIS and burn-severity maps provided by the Monitoring Trends in Burn Severity database (MTBS Project; <http://www.mtbs.gov/>) to determine the history of wildfire disturbance across sites. For each catchment which experienced wildfire, we calculated the percentage of watershed burned and minimal overland distance of each wildfire perimeter to sampling site using the ‘raster’ (Hijmans 2017) and ‘sf’ (Pebesma 2018) packages in R (R Core Team 2018; <https://www.R-project.org/>). Burn severity was summarized through a spatial average of values in the difference of Normalized Burn Ratios (dNBR) within each fire-affected portion of disturbed catchments, where 0 corresponds to “Unburned” and 4 corresponds to “High Severity” conditions (Roberts et al. 2008). We then analyzed distributions of each of these pyrologic metrics to understand the gradient in wildfire events experienced by sites in our analysis. Analyzing these characteristics allowed us to describe the recentness, extent and severity of wildfire at each site and select those streams where wildfire-induced impacts to macroinvertebrate communities were thought to be most detectable.

Our analysis identified a total of 351 fires which affected catchments in the study area from 2000 to 2015. From these fires, there were 187 fire-reach combinations where a fire burned at least 5% of a given catchment prior to sampling. We focused our analysis on a subset of 153 sampling occurrences from this total regional distribution that fell into three categories: reaches that had been recently burned (less than one year prior to stream sampling; n = 80), reaches that had been heavily burned (had at least 50% of catchment area burned by wildfire; n = 92), and reaches that had been recently and heavily burned (within catchments that had at least 50% of area burned less than one year prior to sampling; n = 19, Figure 2.2). All fires in our analysis

were less than 5 km. upstream from their respective stream reaches, and 93 reaches were located within the burn perimeter of their corresponding wildfire. This selection of sites allowed us to compare streams within catchments experiencing varying wildfire histories, allowing us to identify how burn severity, proximity and time since fire contribute to biotic responses in stream communities.

### 2.3.2 *Macroinvertebrate community and traits data*

Macroinvertebrate sampling at each reach was conducted followed protocols recommended by the Center for Monitoring and Assessment of Freshwater Ecosystems at Utah State University (USU, Hawkins et al. 2003). Species were analyzed and identified by the BLM/USU National Aquatic Monitoring Center, providing raw data on macroinvertebrate communities for each sampling reach (Miller & Judson 2011). We removed all ambiguous and non-insect taxa from the analysis and summarized counts of individuals to the nearest taxonomic level for which trait information was available. Counts for taxa at coarser taxonomic levels than family, or taxa for which trait data were unavailable, were distributed to their children based on relative abundances at each reach (DPAC method, Cuffney et al. 2007). In total we summarized individuals across 221 genera, 6 subfamilies and 63 families for a total of 290 operational taxonomic units (OTUs).

To explain the functional composition of stream insect communities, we utilized a trait database initially constructed by Poff and others and updated to include macroinvertebrate taxa common to the Pacific Northwest (Poff et al. 2006, Poff et al. 2010, Pyne & Poff 2017). Ten traits were selected that described the life history, morphology, mobility and ecology of stream insects across 34 different trait states (Table 2.1). This selection of traits yielded a potential of 104,976 unique combinations of functional trait states, or functional trait niches (FTNs) in total,

of which 207 were present among taxa within our analysis. These traits were selected after a review of studies describing the functional composition of stream communities in fire-affected watersheds (Table 2.1; Minshall 2003, Verkaik et al. 2013, Vieira et al. 2004, Mellon et al. 2008), and we used these studies to construct hypotheses concerning the distribution of traits in fire-affected communities (Table 2.1). We also conducted a non-metric multidimensional scaling (NMDS) analysis on the full set of trait data to construct a suite of traits that minimized redundancy in functional space. Thus, the traits analyzed in our study were likely to respond to wildfire-induced changes in stream abiotic conditions while providing an efficient representation of multidimensional functional space.

### 2.3.3 *Taxonomic/functional diversity indices and regression analyses*

We calculated three indices of functional diversity across our study reaches to explain the role of habitat conditions and wildfire in explaining community composition in streams. Total abundance (abbr. *Tab*) was to describe broad scale patterns of biomass and diversity in streams. We also used two recently described indices describing characteristics of trait-space: functional richness (abbr. *FRich*) and functional dispersion (abbr. *FDisp*). Functional richness measures the hypervolume of trait space occupied by species in a community (Villegger et al. 2008); because our trait database consisted only of ordinal traits, this corresponded to the number of unique trait combinations at a given site for our analysis. Functional dispersion is the multivariate analogue of mean absolute deviation in trait space, and is closely related to Rao's quadratic entropy (Laliberte & Legendre 2010). Indices were calculated by computing a dissimilarity matrix using Gower's distance (Gower 1971) weighted by the number of trait states (Laliberte & Legendre 2010) for macroinvertebrate communities at each site, and then performing principal coordinate analysis (PCoA) and using ordination axes to explain trait space. Each of these indices has been

used extensively to describe disturbance impacts in freshwater communities (Boersma et al. 2016, Mouillot et al. 2013) and provide a characterization of broad scale taxonomic patterns as well as the magnitude and variability in functional composition of disturbed and undisturbed communities.

We conducted a paired comparison of functional diversity indices among burned and unburned sites to measure the importance of wildfire and stream habitat conditions in structuring stream communities. Burned reaches were paired with unburned reaches that were sampled either at the same site prior to fire disturbance or at a different site within the same region (Forest Service District or BLM Field Office/Resource Area) and with a similar management history as the burned site. We then fit regression models and conducted ordination analyses for each fire history category (“recently burned”, “heavily burned”, and “recently and heavily burned”) using paired burned and unburned sites, and evaluated the ability for fire occurrence to describe the response of functional diversity indices. A supplementary principal component analysis (PCA) found that values in streamflow, temperature, substrate size and frequency of large woody debris were not highly structured by wildfire occurrence among this subset of sampling reaches (Figure 2.3). As such, this pairing allowed us compare macroinvertebrate community structure across streams experiencing similar hydrologic and climatic conditions, and maximized the probability of detecting and describing a biotic response due to wildfire.

We quantified the relationship between habitat characteristics at the reach- and watershed-scale and functional diversity indices using multivariate regression models, and examined the additional role of wildfire disturbance in explaining functional diversity using likelihood ratio tests. Within each category of fire history, we constructed multivariate Gaussian models of environmental conditions at the reach- and watershed-scale (Table 2.2) to explain

distributions for each functional diversity index, where burned and unburned sites made up an equal proportion of observations. We used backwards selection based on Akaike's Information Criterion (AIC) to select the most parsimonious model to act as a "null model" in explaining functional diversity. We then included a binary indicator of fire occurrence to test for improved model fit using an F-test based on the ratio in the residual sum of squares at the  $\alpha = 0.10$  level, and allowed this factor to enter the model if the resultant model achieved a lower AIC value than the previous null model. We plotted standardized regression coefficients and associated confidence intervals to depict the relationship between stream habitat and watershed conditions and taxonomic and functional diversity indices. Our approach allowed us to describe which environmental factors were most important in describing patterns in functional diversity across our sites while also providing a robust means of testing for the influence of wildfire occurrence in structuring stream communities.

## 2.4 RESULTS

We found that functional diversity indices were similar across sites experiencing recent and extensive wildfire disturbance (Figure 2.4). Average values in total abundance, functional richness and functional dispersion were largely similar between unburned reaches and reaches within catchments that had experienced recent wildfire, extensive wildfire, or both. Sites that experienced recent wildfire did show a decrease in the variability of total abundance compared to unburned sites and sites within catchments that were heavily burned more than one year prior to sampling. The distribution of functional richness indicated that burned and unburned sites were each represented by a similar number of functional trait niches, around 28 unique. The distribution of functional dispersion among sites was also largely similar between burned and unburned stream reaches.

Total abundance of stream taxa was driven by different factors between sites experiencing recent and extensive wildfire disturbance. Total abundance was positively associated with wildfire disturbance in recently burned sites (Figure 2.5;  $F = 6.4366$ ,  $p < 0.05$ ), but not in sites that were heavily burned multiple years prior to sampling or immediately following wildfire (Figure 2.5). Mean annual flow and stream elevation were also positively correlated with abundance in recently burned sites. However, finer-scale habitat variables were selected as the best predictors of abundance in streams that had been heavily burned both recently and in years past; in particular, large woody debris was negatively correlated with total taxa abundance for “heavily burned” and “recently and heavily burned” reaches.

The spatial scale of predictors also played an important role in explaining the response in functional diversity indices. Functional richness increased with temperatures for both recently and heavily burned sites (Figure 2.5). Sites that were recently burned, however, had functional richness values that were positively correlated with finer-scale predictor variables of substrate size and amount of woody debris, whereas heavily burned sites had functional richness values more associated with coarser scale watershed characteristics, including reach elevation and average precipitation amounts within the catchment. Interestingly, sites that experienced wildfire disturbance that was both recent and extensive were best explained by a mix of these variables. Functional dispersion was also positively correlated with temperature, and decreased with higher levels of large woody debris in sites experiencing a high percentage of watershed burned. The average predictive ability of models of functional richness and dispersion were fairly similar ( $R^2_{\text{Avg}} = 0.1798$  and  $R^2_{\text{Avg}} = 0.1981$ , respectively).

## 2.5 DISCUSSION

Our analysis found that streams across the Pacific Northwest had similar distributions in functional diversity regardless of the history of wildfire within their catchments. The distribution of functional richness, as well as the functional dispersion within trait space, were largely similar in streams experiencing different wildfire histories compared to unburned conditions in the region, and wildfire occurrence was not a significant predictor of these indices in almost all regression models. Nevertheless, some disturbance responses were apparent; fire occurrence was a significant predictor of total abundance in streams that were recently burned, and corresponded to an increase in the magnitude and decrease in the variability of abundance at these sites, a finding consistent with other studies on disturbance responses in the region (Mellon et al. 2008). Sites within catchments that experienced extensive wildfire disturbance multiple years before sampling had macroinvertebrate abundances more correlated with finer-scale habitat variables, such as large woody debris counts and substrate size. This suggests that patterns of abundance in fire-affected communities could be largely dictated by broad scale drivers in the immediate post-fire window before returning to being associated with habitat conditions at a finer scale in the years following disturbance.

Against our expectations, indices of functional diversity showed limited responses to both recent and extensive fire disturbance. The number of unique trait combinations at a given site, captured by functional richness, was largely predicted by finer-scale variables in watersheds that experienced recent fire disturbance, but coarser-scale variables in sites that had previous fire disturbance and were heavily burned. Responses in functional dispersion showed the opposite pattern, however, with values in recently burned sites being structured by stream slope while those in heavily burned sites were structured by substrate size and the amount of large woody-

debris. Fire occurrence was not a strong predictor of functional diversity among any of our sites, but understanding drivers of functional diversity in the context of post-fire recovery of stream ecosystems can provide useful insight into how disturbance regimes impact stream communities at the landscape scale. The differences in the drivers of both functional indices within our sites demonstrates the need to characterize multiple components of trait space in characterizing disturbance impacts (Mouillot et al. 2013, Boersma et al. 2016).

Across multiple response indices and within sites experiencing varying wildfire histories, we found stream temperature and large woody debris inputs to be the most important predictors of functional diversity in streams. Higher temperatures were associated with decreases in taxonomic richness, but increases in functional richness and dispersion, suggesting that increased stream temperatures led to a few number of taxa occupying a broader region of functional space among our sites. The importance of temperature in structuring macroinvertebrate composition has been analyzed for aquatic ecosystems of Northern Europe, but to our knowledge our results are the first documenting the importance of temperature in structuring stream communities in the Pacific Northwest. Conversely, responses in stream communities to large woody debris inputs are well-documented, and suggest that changes in organic material may not affect community composition on a site-by-site basis but could play a role in structuring stream communities at broader spatial scales (Carlson et al. 1990, Limly & Hilderbrand 2000). Wildfire disturbance in conjunction with post-fire precipitation events can alter stream thermal patterns and contribute to organic material subsidies in burnt catchments (Dunham et al. 2007, DeBano 2000, Meyer & Pierce 2003), and thus possibly facilitate the role of wildfire in indirectly influencing community responses years after disturbance events. Developing a better understanding of the complexities in regional patterns in stream temperature (Steel et al. 2017) and processes driving organic input

at larger spatial and temporal scales (Harris et al. 2015) will be an important step in conserving functional attributes in a future of increased fire activity.

Although our approach provides the rare opportunity to gain insight into regional responses of stream macroinvertebrate communities during the post-fire period, it is important to consider the dynamics between these communities and wildfire events when contextualizing our results. The shift in wildfire regimes throughout the Western North America (Johnstone et al. 2016) as well as the analytic limitations in using remote-sensing burn severity data (Kolden et al. 2015) generate uncertainty in the classification of fires having severe ecological impact, both in terrestrial and aquatic ecosystems. Additionally, macroinvertebrate communities are inherently variable, and can be thought of as being in some state of post-disturbance succession and driven by mechanisms of dynamic equilibrium (McCabe & Gotelli 2000, Arkle et al. 2010). Thus, understanding how infrequent and stochastic events like wildfire affect the functional make-up of these communities over streams experiencing variable habitat conditions, flow regimes, and meteorological patterns is difficult. Detecting a functional response in macroinvertebrate communities to wildfire may rely on methodologies like a before-after control impact (BACI) design in order to understand how post-disturbance dynamics are altered in burned streams relative to unburned streams and capture the temporal variability inherent in these communities. Further research into wildfire-impacts to stream macroinvertebrates should give consideration to the full history of fire activity in study areas as well as consider the regional variability in functional composition of streams in fire-prone landscapes.

Our results suggest that while wildfire might have dramatic impacts to stream communities in specific watershed contexts, disturbance responses across streams experiencing different habitat conditions, hydrology and climatic patterns are more variable. We quantified

disturbance through analyzing responses in biotic indices to recent and extensive wildfire events, but it is likely that characterizing other facets of disturbance, such as burn severity and seasonality of fire, is also necessary to fully explain variability in biotic responses. Wildfire has been a dominant disturbance regime to structure forest ecosystems in the Northwest U.S. for millennia, and as such all streams are in some state of post-fire recovery (Minshall 2004). Additionally, a number of recent studies have demonstrated that wildfire-induced impacts to macroinvertebrate communities are largely determined by patterns in post-fire streamflow regimes, both in the Pacific Northwest (Rugenski & Minshall 2014, Arkle et al 2010) and globally (Verkaik et al. 2015). Fully characterizing the role of wildfire in structuring biotic conditions in streams will require a more thorough understanding of the processes linking patterns in climate, hydrologic conditions and wildfire occurrence at regional scales.

## 2.6 CONCLUSION

Our analysis utilized a vast collection of data on stream habitat conditions, macroinvertebrate communities and burn severity maps of wildfire to describe the factors of stream habitat and wildfire responsible for driving freshwater functional diversity in the Pacific Northwest. We found that streams experiencing recent and extensive wildfire disturbance had functional diversity values that were largely similar to unburned streams, but that total abundance increased following recent wildfire disturbance. Stream temperature and fine-scale habitat variables were identified as the most important predictors of taxonomic and functional diversity, and the spatial scale of predictors that explained variability in diversity indices varied between streams experiencing different wildfire histories. The surprising stationarity of stream diversity indices following wildfire suggests that stream communities can be highly resilient to fire disturbance except in the immediate post-fire window, and that fine-scale habitat variables

are largely important in structuring community composition in streams. These results suggest that while burn events within individual watersheds may play an important role in dictating short-term patterns in stream community composition at local scales, stream habitat conditions play a larger role than recent disturbance in structuring communities at the landscape scale.

Broad-scale studies on stream habitat and macroinvertebrate communities will become increasingly important in order to understand the processes driving freshwater biotic conditions in a fire-prone landscape.

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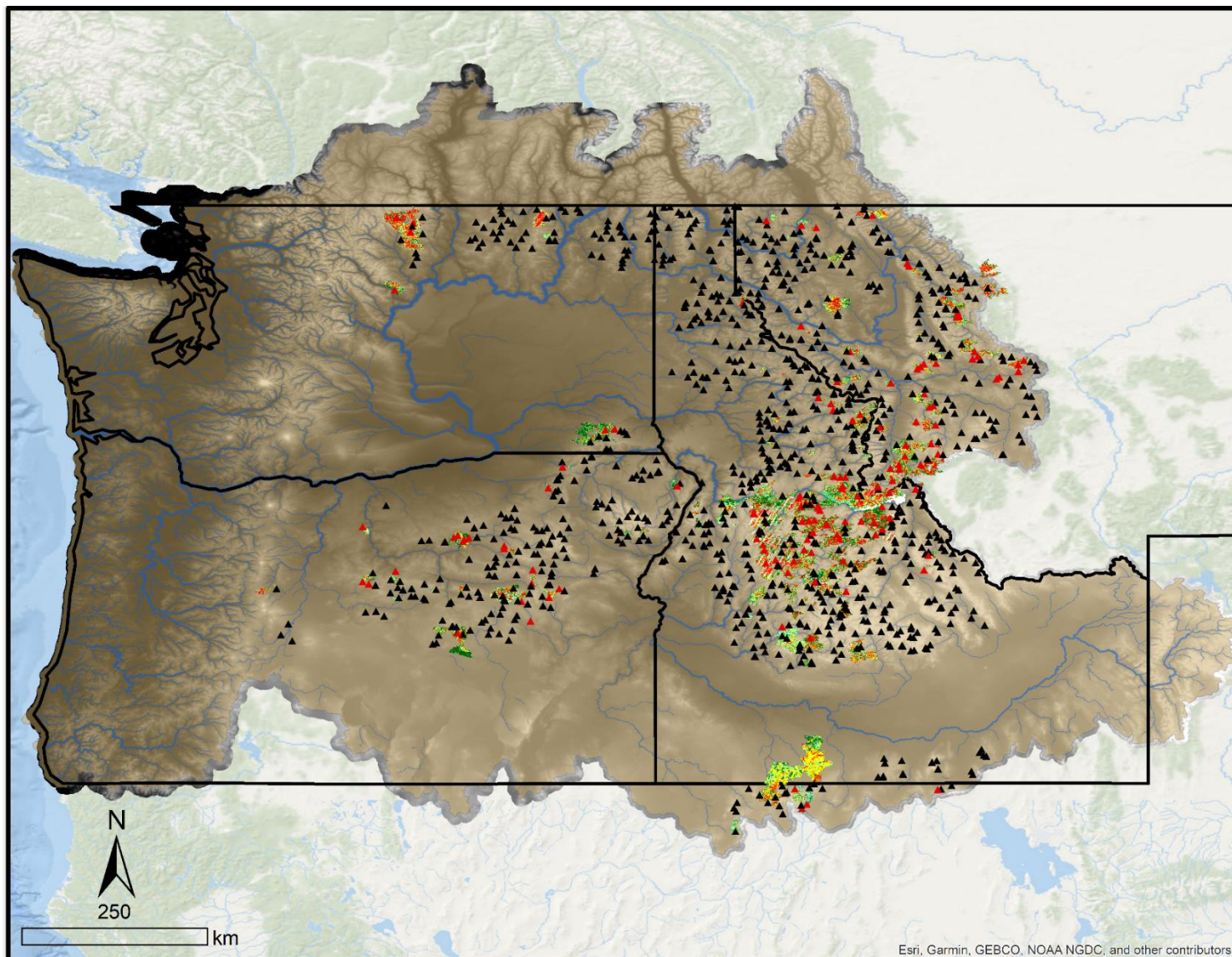
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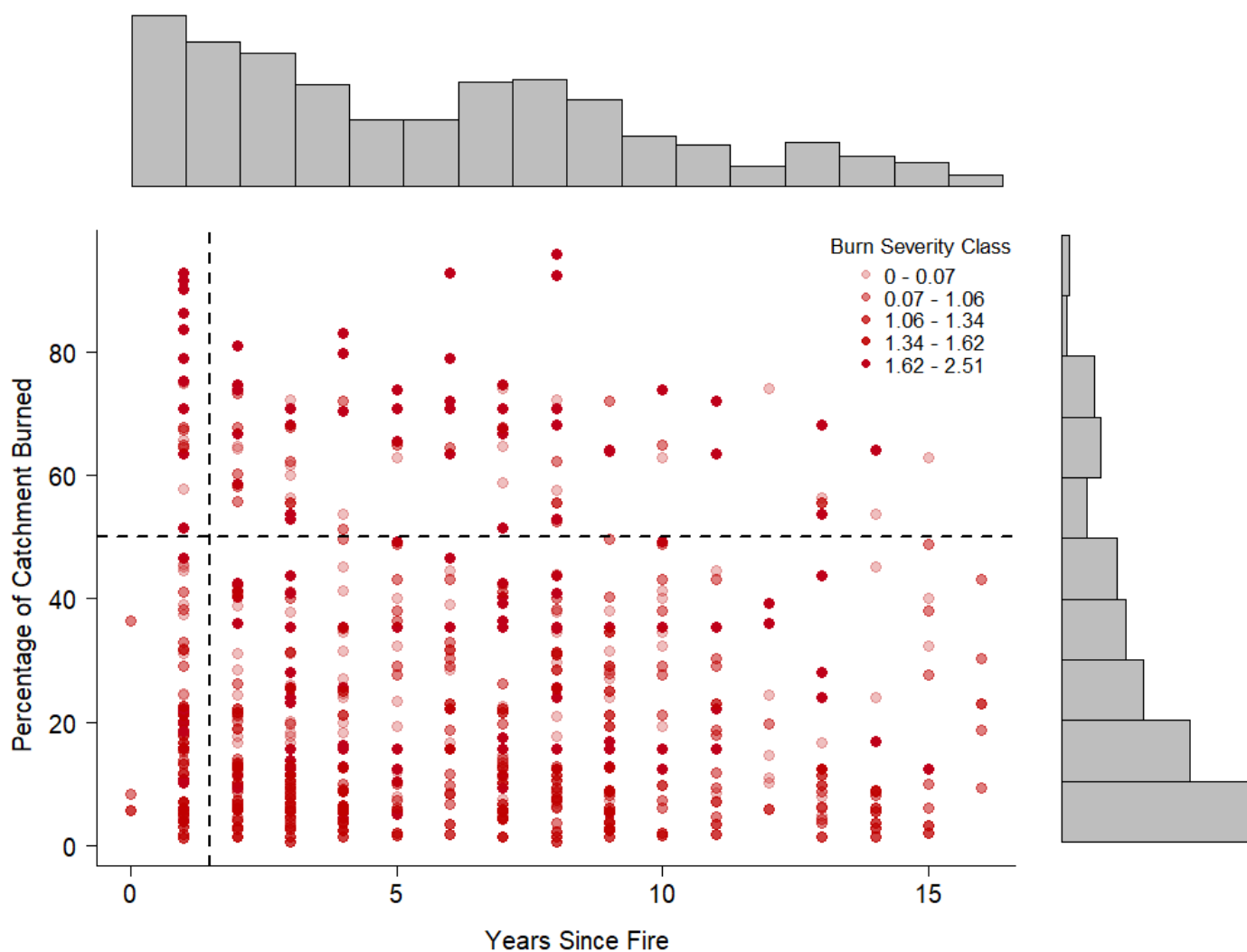
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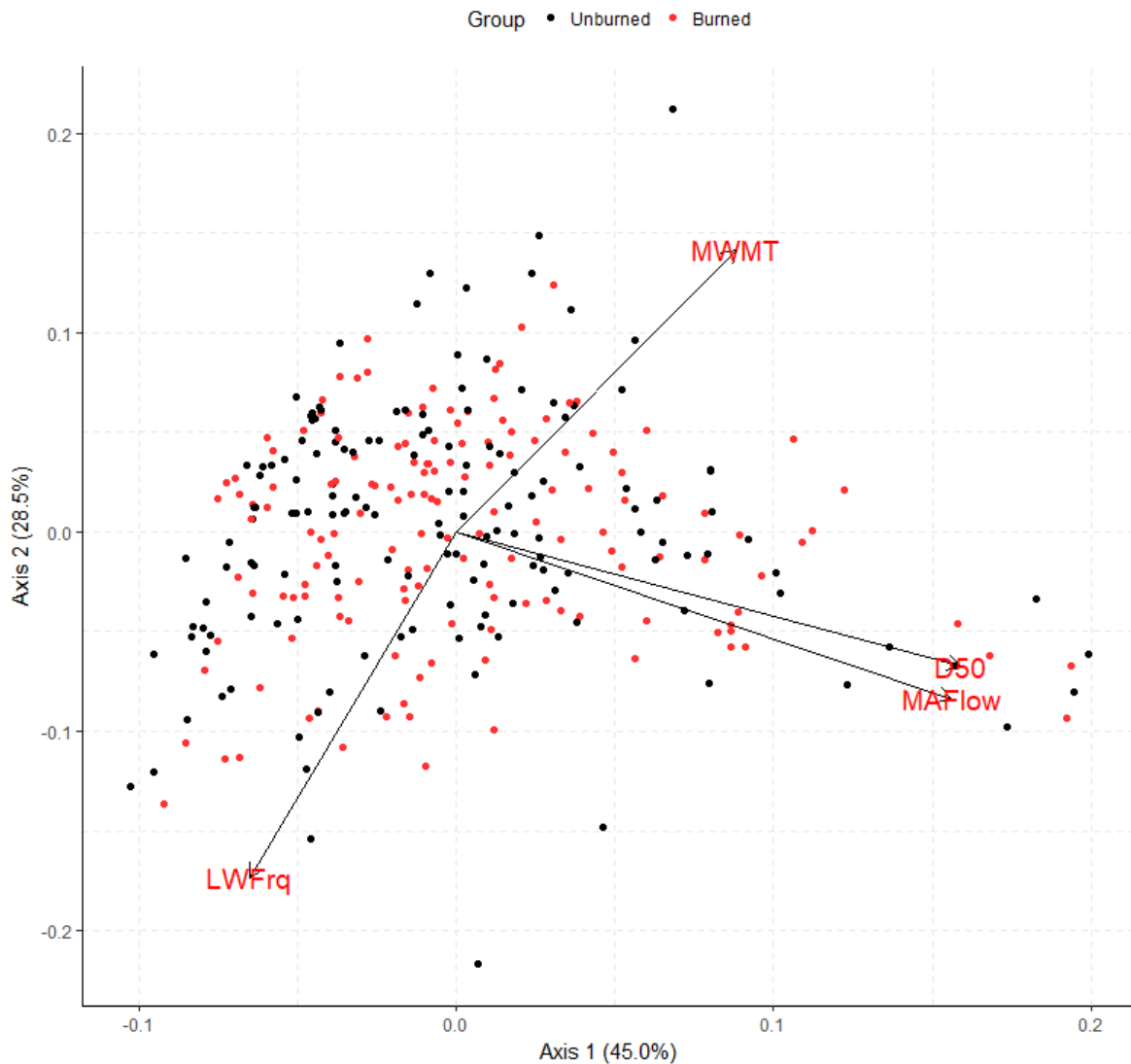
## 2.9 FIGURES &amp; TABLES



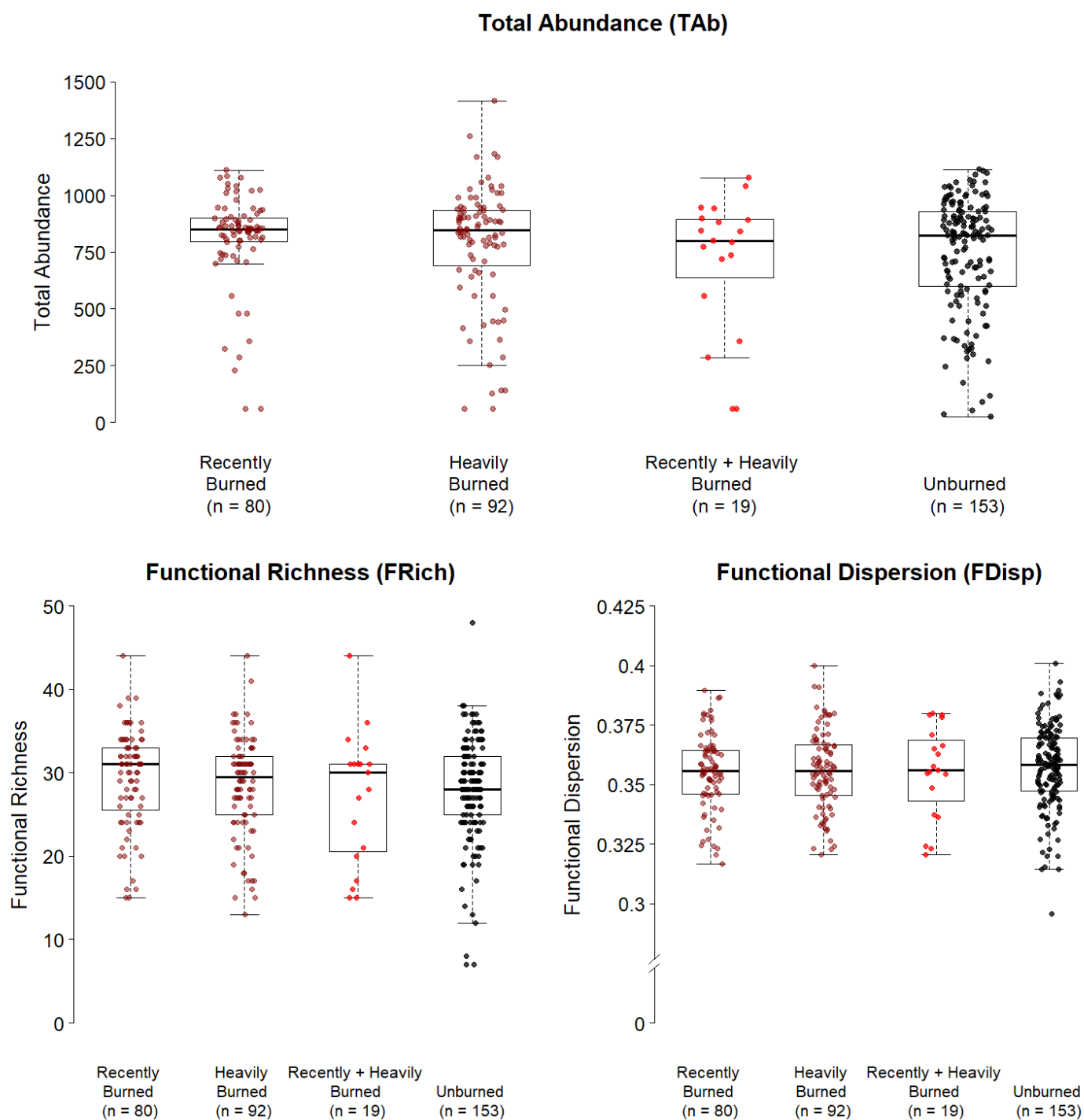
**Figure 2.1 – Map of PIBO sampling sites.** Map of PIBO sampling sites where stream monitoring occurred. Sites that experienced a wildfire which affected at least 5% of their catchment before sampling occurred are depicted in red, while unburned sites are shown in black. Fires affecting burned sites are shown by their burn severity maps.



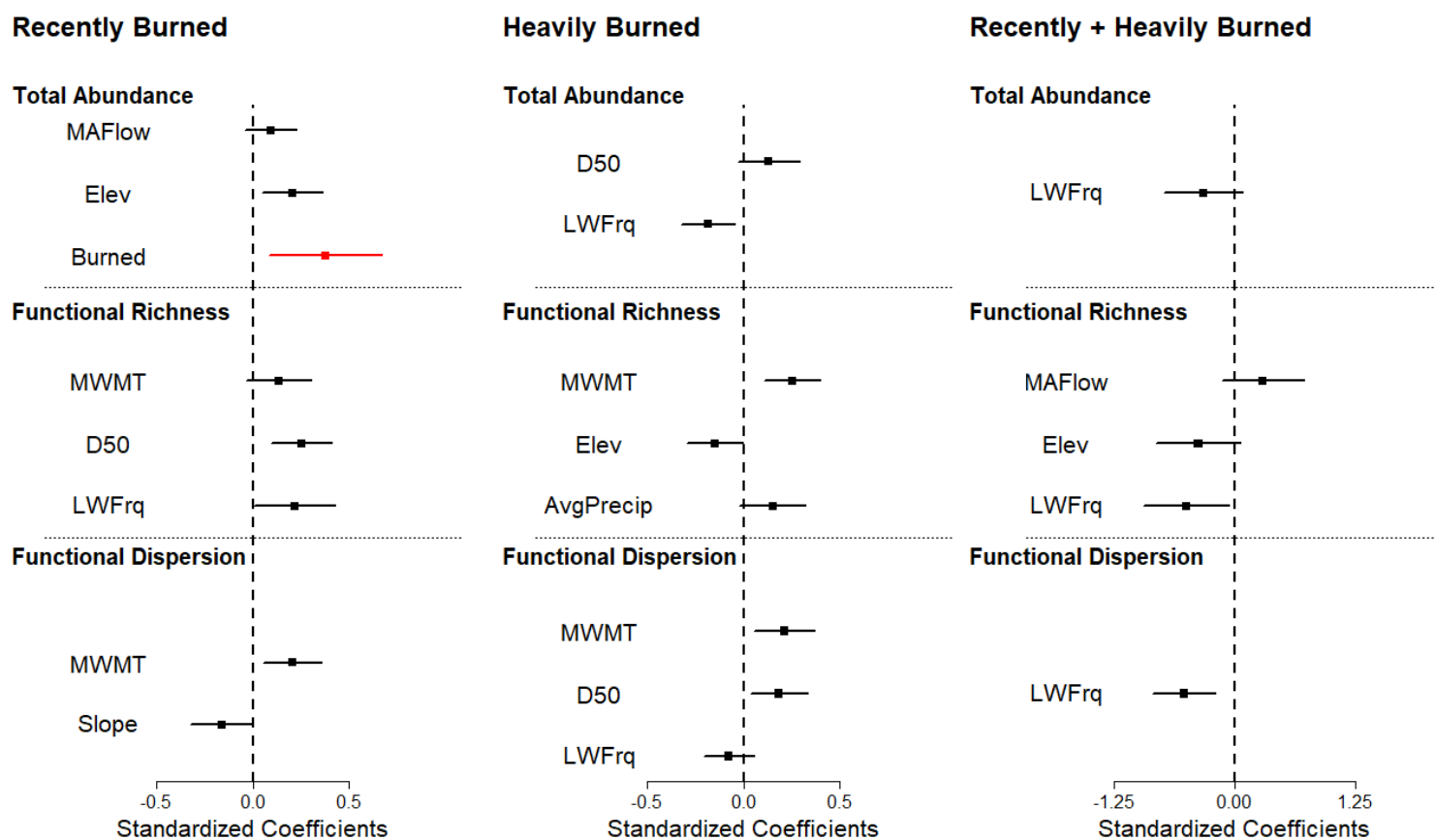
**Figure 2.2 -- Wildfire gradient across affected PIBO sites.** Scatter plots showing the relationship between the years since fire occurrence and percentage of watershed burned for all wildfire-sampling occurrence combinations. Reaches in the 2<sup>nd</sup>, 3<sup>rd</sup> and 4<sup>th</sup> quadrants were used in fitting regression models (see Section 2.3.4), with lines indicating thresholds used to select stream reaches where disturbance responses are believed to be most pronounced. Marginal histograms show the distribution of each variable represented by the corresponding axis. Points are colored according to the value of the burn-severity index for each fire (see Section 2.3.2).



**Figure 2.3 – PCA of stream habitat conditions.** Biplot of principal components analysis on four fine-scale habitat variables used in regression analyses – streamflow (MAFlow), temperature (MWMT), substrate size (D50) and frequency of large woody debris (LWFrq). Burned reaches are shown in blue, which unburned reaches are shown in red. Values in parentheses show the amount of variation explained by each principal axis.



**Figure 2.4 – Distribution of functional diversity indices.** Distribution of functional diversity indices (total abundance, functional richness and functional dispersion) across sites which were recently burned (< 1 year prior to sampling), sites which were heavily burned (> 50% of catchment), and both. Points represent the functional diversity value for a given site.



**Figure 2.5 – Distribution of standardized regression coefficients.** Depiction of standardized regression coefficients for continuous variables used in constructing null models functional diversity indices among sites which were recently burned, heavily burned, and both. “Burned” represents a categorical variable indicating whether a site burned or not. Predictors were chosen for each model using backward & forward selection with AIC. Boxes denote standardized regression coefficient with lines showing 95% confidence interval.

**Table 2.1 – Description of stream macroinvertebrate functional traits.** Description of traits used in computing functional diversity indices, as shown in Poff et al. 2006. Trait states were encoded using categorical levels, and descriptions are provided for each. Hypothesized responses show the expected response in taxa of a given trait space following wildfire and post-fire conditions, based on a review of the literature. References describe literature describing functional trait response to wildfire disturbance.

<b>Traits (Code)</b>	<b>Category</b>	<b>States</b>	<b>Hypothesized Response</b>	<b>References</b>
<b>Tropic habit (Trop)</b>	Ecology	Collector-Gatherer Collector-Filterer Herbivore (scraper, piercer, and shredder) Predator (piercer and engulfer) Shredder (detritivore)	Herbivore (grazer) (+) Collector-Filterer (+) Herbivore (shredder) (-)	Minshall 2003 Verkaik et al. 2013 Vieira et al. 2004
<b>Thermal preference (Ther)</b>	Ecology	Cold stenothermal or cold eurythermal Cool/warm eurythermal Warm eurythermal	Warm eurythermal (+) Cold stenothermal or cold eurythermal (-)	Mellon et al. 2008 Minshall 2003
<b>Body size at maturity (Size)</b>	Morphology	Small (< 9 mm.) Medium (9-16 mm.) Large (> 16 mm.)	Small (+) Large (-)	Verkaik et al. 2013 Vieira et al. 2004
<b>Body shape (Shpe)</b>	Morphology	Streamlined (flat, fusiform) Not streamlined (cylindrical, round of bluff)	Streamlined (+) Not streamlined (-)	Minshall 2003 Vieira et al. 2004
<b>Female dispersal (Dispersal)</b>	Mobility	Low (< 1 km. flight before laying eggs) High (> 1 km. flight before laying eggs)	High (+) Low (-)	Minshall 2003 Verkaik et al. 2013 Vieira et al. 2004
<b>Occurrence in drift (Drift)</b>	Mobility	Rare (catastrophic only) Common (typically observed) Abundant (dominant in drift samples)	Abundant (+) Rare (-)	Mellon et al. 2008 Minshall 2003 Vieira et al. 2004
<b>Voltinism (Volt)</b>	Life history	Univoltine (1 reproductive generation/year) Bi- or multi-voltine (>1 reproductive generation/year)	Bi- or multi-voltine (+) Univoltine (-)	Minshall 2003 Verkaik et al. 2013
<b>Life span (Life)</b>	Life history	Very short (<1 week) Short (<1 month) Long (> 1 month)	Very Short (+) Long (-)	Verkaik et al. 2013

**Table 2.2 – Distribution of habitat- and watershed-scale predictor variables.** Description of stream reach variables used in regression modelling. Mean and range are reported for continuous variables, while factor levels are reported for categorical variables. Variable codes correspond to predictors shown in Figures 2.3 and 2.5. Source indicates agency responsible for data and whether data was compiled through sampling or modeled.

<b>Variable (Code)</b>	<b>Units (Transformations)</b>	<b>Source (Methodology)</b>	<b>Mean &amp; Range / Levels</b>
<b>Elevation (Elev)</b>	m.	Pacfish/Infish Biological Opinion Monitoring Program (Measured)	1500 (458 – 2367)
<b>Reach slope (SLOPE)</b>	m./m.	National Hydrography Dataset (Estimated)	0.0342 (0.0015 – 0.1259)
<b>Estimated mean annual flow (MAFlow)</b>	m <sup>3</sup> /s (log-transform)	National Hydrography Dataset (Estimated)	0.66570 (0.0187 – 4.0115)
<b>Median particle size (D50)</b>	m. (square-root transform)	Pacfish/Infish Biological Opinion Monitoring Program (Measured)	0.0482 (0.0020 – 0.2100)
<b>Frequency of large woody-debris (LWFrq)</b>	Count (log-transform)	Pacfish/Infish Biological Opinion Monitoring Program (Measured)	314.9 (0 – 1548)
<b>Estimated annual average precipitation (AvgPrecip)</b>	m./year	PRISM Climate Group (Measured)	0.9463 (0.3680 – 1.7340)
<b>Maximum weekly maximum temperatures (MWMT)</b>	°C	Pacfish/Infish Biological Opinion Monitoring Program (Measured)	15.904 (9.3430 – 31.6710)
<b>Percent of catchment forested (ForestedC)</b>	Percentage (quadratic-transform)	National Land Cover Database (Estimated)	80.43 (18.80 – 99.72)
<b>Management history in catchment (Mgmt)</b>	Categorical	Pacfish/Infish Biological Opinion Monitoring Program	Managed Reference
<b>Federal region (Region)</b>	Categorical	Pacfish/Infish Biological Opinion Monitoring Program	USFS Region 1 USFS Region 4 USFS Region 6 BLM (Idaho) BLM (Montana)
<b>Year of sampling (Year)</b>	Categorical	Pacfish/Infish Biological Opinion Monitoring Program	1 – 16 (Corresponding to years since 2000)