MACROINVERTEBRATE RESPONSE TO WILDFIRE IN A WILD AND SCENIC RIVER

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ABSTRACT

MACROINVERTEBRATE RESPONSE TO WILDFIRE IN A WILD AND SCENIC RIVER

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Wildfires, intensified by anthropogenic influences, impose substantial impacts on freshwater ecosystems. In the Southwest USA, wildfire season is succeeded by monsoon season, introducing indirect disturbances, such as erosion, sediment transport, channel modification, and turbidity, induced by post-fire runoff. Leveraging pre-existing data from 2005 and 2006, we assessed the short-term (< one year) responses of aquatic macroinvertebrates to wildfire and subsequent flooding, focusing on changes in density, diversity, and community composition. The investigation revealed substantial decreases in invertebrate density and taxa richness, with a dynamic recovery pattern, suggesting complex interactions between habitat stability, sedimentation, and the adaptability of invertebrate taxa. To disentangle these interactions, we categorized sites along Fossil Creek into predicted disturbance categories, considering factors such as initial sediment loading, potential future sediment loading, riparian burn severity, and anticipated changes in peak flows. However, the observed responses of dependent variables did not conform to predicted disturbance groups based on upland watershed conditions, nor the distinctions between upstream and downstream sites. We observed an unexpected but positive response, both at and downstream of a confluence, where flow events increased resource transfer, enhanced invertebrate drift, and scoured woody debris. This study provides valuable insight into the post-wildfire response of aquatic invertebrates over short time scales, particularly in systems characterized by travertine deposition.

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INTRODUCTION

Natural disturbances, such as wildfires, play a multifaceted role in the physical, chemical, and biological dynamics that sustain the health, diversity, and resilience of ecosystems worldwide. Anthropogenic activities, however, such as land use changes and climate alterations, are causing wildfire size, severity, and frequency to exceed natural levels, pushing the limits of ecosystem recovery and resilience (Bixby et al., 2015; Sankey et al., 2017; Xu et al., 2020). While fire management and policy have traditionally emphasized the protection of human life, property, and terrestrial resources, wildfires also exert profound impacts on freshwater resources, aquatic and riparian habitats, and the biodiversity within (Bixby et al., 2015). Critical freshwater ecosystems experience some of the most pronounced effects from wildfires (Minshall, 2003).

Identified research gaps highlight the need for a comprehensive exploration of diverse fire scenarios, considering factors such as severity, extent, frequency, hydrology, catchment geomorphology, and aquatic conditions (Bixby et al., 2015). It is critical to investigate not only severe but also subtle, ecologically significant fire effects within the fire perimeter (Bixby et al., 2015). Moreover, the unpredictable timing and locations of wildfires limits the availability of pre-fire data, further complicating the study of ecosystem dynamics following a wildfire. This study contributes to understanding how fires affect rivers by examining wildfire impacts to a unique travertine ecosystem. Fossil Creek is a 23-km spring-fed, travertine stream, and one of only two Wild and Scenic rivers in Arizona. The distinct travertine morphology is characterized by the presence of terraces, steep waterfalls, and large pools, which create unique, high-quality habitats for macroinvertebrates and fish (Marks et al., 2006).

Extensive biotic monitoring of Fossil Creek began prior to and following a significant river restoration project involving removal of a hydroelectric dam and restoration of full river flows (Dinger, 2006; Weedman et al., 2005). The presence of extensive pre-fire data provides a unique opportunity to investigate the effects of wildfire and subsequent flooding on freshwater ecosystems. The Backbone Fire, ignited by lightning in the summer of 2021, burned approximately 41,924 acres, with areas experiencing vegetation losses ranging from 0% to greater than 90% (Lacroix & Paffett, 2021; Steinke & Jacobson, 2021). While patchy burn severity is not unique, the availability of diverse burn severity data within a single fire perimeter, alongside comprehensive in-stream pre-fire data, presents a unique research opportunity for quantifying the fire's impacts on Fossil Creek's biota.

Rivers can be likened to nature's diligent custodians, working tirelessly to "clean up" the impacts of the terrestrial upland environment. Through intricate hydrological processes, rivers serve as natural purifiers. The water removes suspended particles, sediments, and pollutants from the uplands, as it flows through substrates like gravel, sand, and vegetation (Cooper et al., 1919; Minshall, 1988). A river's filtration capacity depends on the type and amount of pollutants, the flow rate, the health of the riparian zone, and the composition of substrates within the river. Disturbances can disrupt this natural purification process, especially when the river becomes overwhelmed by excessive inputs (Benda et al., 2003; Bixby et al., 2015; Earl & Blinn, 2003; Minshall, 1988).

The effects of fire on rivers depend on upland vegetation burn severity, soil burn severity, and the magnitude of postfire flows following hydrological events (Earl & Blinn, 2003; Minshall, 2003; Gresswell, 1999). In burned catchments with exposed soil and unstable slopes, even relatively small storms and low rainfall intensities can produce significant flow events, leading to travertine degradation and increased rates of sediment transport and deposition into the river (Minshall, 2003; Gresswell, 1999; Benda et al., 2003; Verkaik et al., 2015; Tuckett & Koetsier, 2016; Pan et al., 2017; Fuller et al., 2011). As sediment accumulates, alterations in the river's geomorphology can occur, potentially shifting banks, filling in pools and riffles, and increasing substrate embeddedness (Gresswell, 1999; Benda et al., 2003; Minshall, 2003; Coombs & Melack, 2012; Ball et al., 2010; Silins et al., 2014). These changes can have cascading effects on the river's ecosystem, impacting microhabitats, oxygen levels, food sources, and overall water quality (Minshall, 2003; Bixby et al., 2015).

Aquatic macroinvertebrates are often used as an indicator species to monitor ecosystem changes because they are sensitive to environmental changes, occupy a variety of microhabitats, show wide ranges of tolerance to disturbances, and are large enough to be easily collected without being mobile enough to avoid disturbances (Hilsenhoff, 1988; ADEQ, 2007; 2015; Gaufin & Tarzwell, 195; Goodnight, 1973). Aquatic macroinvertebrates play a pivotal role in river food webs, serving as a primary food source for a wide range of aquatic organisms, including fish and amphibians (Vannote et al., 1980; Merritt & Cummins, 2007). A high density and diversity of invertebrates are essential for supporting food webs, bolstering resilience, and enhancing the custodial abilities of the river (Mihuc & Minshall, 1995).

The immediate effects of wildfire on freshwater ecosystems, including elevated water temperature, increased nutrient levels, and the deposition of ash and charcoal (Gresswell, 1999a; 1990b; Benda et al., 2003; Coombs & Melack, 2012; Minshall, 2003; Ball et al., 2010) can lead to substantial invertebrate mortality (Minshall et al., 1989; Minshall, 2003; Rinne, 1996; Tronstad et al., 2012; Verkaik et al., 2015; Minshall & Robinson, 1992; Minshall et al., 2001b; Spindler, 2004). Following those initial impacts, community composition may shift toward disturbance-adapted organisms if certain taxa take longer to recover or never re-establish populations (Minshall et al., 2001a; Spindler, 2004; Verkaik et al., 2015; Rinne, 1996). In contrast, macroinvertebrates can return to pre-fire conditions within one to two years, particularly in streams with minimal anthropogenic disturbances (Roby & Azuma, 1995; Minshall et al. 2001b). The recovery and resilience of aquatic macroinvertebrate communities after fire depends on the severity and extent of the fire, with post-fire flow events playing a crucial role in the recolonization dynamics by meditating food resources and available substrate for microhabitats (Roby & Azuma, 1995; Minshall et al. 2001b; Tuckett & Koetsier, 2016; Zweig & Rabeni, 2001; Statzner & Higler, 1986; Verkaik et al., 2015; Fuller et al., 2011).

As sediment input changes the river's geomorphology (Silins et al., 2014; Benda et al., 2003; Tuckett & Koetsier, 2016; Statzner & Higler, 1986; Growns & Davis, 1994; Ball et al., 2010), available substrate for invertebrate microhabitats is altered, resulting in reduced pool depth, embedded rifles becoming runs, and travertine armoring the riverbed. Frequently, the altered geomorphology reduces invertebrate habitat diversity, thereby decreasing invertebrate density and diversity (Mihuc & Minshall, 1995; Ball et al., 2010; Spindler, 2004; Silins et al., 2014; Rinne, 1996; Rabeni & Minshall, 1977). However, the deposition of fire-related debris and the movement of large boulders may also create new microhabitats, potentially increasing aquatic macroinvertebrate density and diversity (Silins et al., 2014; Benke et al., 2003; Duan et al., 2008; Harris et al., 2018).

The aquatic food web of Fossil Creek is supported by benthic algae and riparian leaf litter, both vital resources for macroinvertebrates (Compson et al., 2009; Dinger, 2006). Wildfires have the potential to significantly alter the integrity of this food web by damaging or killing riparian vegetation, thereby reducing inputs of riparian leaf litter into the stream (Earl &

Blinn, 2003). However, where riparian vegetation is severely damaged or destroyed by the fire, canopy coverage decreases, increasing light and temperature levels (Cooper et al., 2014; Beakes et al., 2014), potentially boosting primary productivity and increasing benthic algae production (Spencer et al., 2003; Vannote et al., 1980). An increase in primary productivity offers the potential for compensation from the loss of leaf litter inputs. Nonetheless, it is crucial to recognize that this potential compensation may be negated by fine sediment loading, potentially limiting primary productivity, and impeding the growth of new benthic algae (Betts & Jones, 2009; Tronstad et al., 2012; Mihuc & Minshall, 1995; Minshall et al., 2001a; Coombs & Melack, 2012; Sankey et al., 2017).

Evaluating a shift in the base of the food web can be achieved by monitoring changes in the composition of invertebrate functional feeding groups. If there is a shift from a leaf litter-based to an algae-based food web, an increase in the predator population driven by the ecosystem's enhanced productivity and the subsequent availability of a more abundant prey base would be expected. (Mihuc & Minshall, 1995; Ramírez & Gutiérrez-Fonseca, 2014; Minshall et al., 2001a; Cooper et al., 2021; Tronstad et al., 2012; Verkaik et al., 2015). This shift is also anticipated to result in increased populations of scrapers and herbivores, leading to a proportional decrease in collector species (Ramírez & Gutiérrez-Fonseca, 2014; Wallace & Webster, 1996; Rabeni & Minshall, 1977). If the input of external organic matter (allochthonous) and the production of organic matter within the ecosystem (autochthonous) are diminished due to fine sediment loading, we anticipate a decline in predator populations, as the food web sustains fewer prey.Additionally, the increased sediment load may smother the surfaces where algae typically thrive (Coombs & Melack, 2012), potentially reducing the populations of scrapers and herbivores (Lemly, 1982; Rabení et al., 2005). Conversely, collectors might increase in number, as the presence of newly suspended particles could offer them an expanded food source. For the same reason, filter feeders may increase unless high sediment loads clog their filtering mechanisms (Spindler, 2004; Statzner & Higler, 1986; Growns & Davis, 1994; Lenat et al., 1981). The recovery of stream macroinvertebrates after fire is linked to the rate at which riparian vegetation and geomorphological conditions recover (Minshall et al., 2001a; 2001b; Verkaik et al., 2015). However, their ability to return to their pre-fire state amid changing climate conditions remains uncertain, highlighting the need for a better understanding of how macroinvertebrates as this indicator group are affected as wildfire frequency and severity continue to increase (Prather et al., 2012; Cooper et al., 2021; Devkota et al., 2022; Mueller et al., 2020; Aspin et al., 2018; Boulton & Lake, 2008).

In this study, we asked three questions. 1) How did the Fossil Creek aquatic macroinvertebrate community respond to wildfire? 2) To what extent did the Fossil Creek aquatic macroinvertebrate recover over the subsequent year? 3) Do differences in the aquatic macroinvertebrate communities correspond to predicted disturbance groups based on sediment loading? We conducted a comprehensive assessment of the aquatic macroinvertebrate community at nine sites distributed along the river's length that varied in riparian burn severity and sediment loading. Dependent variables included density, diversity, tolerance, and functional feeding groups (Table 1). To address question one, we compared response variables to baseline data gathered before the fire, in 2005 and 2006. We predicted a decrease in invertebrate density, diversity, and a shift towards more tolerant taxa, compared to before the fire. To address questions two and three, we compared macroinvertebrate assemblages across sites that were categorized into three disturbance groups based on the range of fire effects observed in upland vegetation. We predicted that "most disturbed" sites will have the lowest density and diversity, and the highest proportions of tolerant taxa. Alternatively, it's possible that a site's predicted disturbance group, based on upland disturbance, may not directly correspond to conditions at that site. In this context, we considered a null hypothesis that disturbances occurring upstream may have a greater impact on downstream sites than disturbances in the upland watershed. We predicted dependent variables would differ among sites, with upstream sites experiencing higher density, diversity, and lower proportions of tolerant taxa than downstream sites as sediment flushing occurs. Results from this study will inform our understanding of how wildfire impacts aquatic macroinvertebrate communities in e4w3systems characterized by travertine deposition, contributing to the broader knowledge of ecosystem response to disturbances in unique environments.

METHODS

Study Site

Fossil Creek is a 23-km long, perennial, spring-fed stream in Arizona managed by the Coconino and Tonto National Forests (Figure 1). The abundance of unique recreation opportunities to swim, hike, canoe, cliff jump, and more attract national and international visitors. The watershed plays an important role in the traditional practices and spiritual wellbeing of Yavapai and Apache tribes, as it was one of the first places many families returned to after leaving reservations (CRMP, 2020). Spring water, high in calcium carbonate, forms travertine terraces and supports a diverse community of fish and macroinvertebrates (Dinger, 2006; CRMP, 2020). The recreational and cultural resources, unique geology, and diverse biotic assemblage of the river led to Fossil Creek's designation as a National Wild and Scenic River in 2009 (CRMP, 2020). The designation ensures the river is managed in a way that promotes the protection of free-flowing water and its unique resources (Perry, 2017; NPS, Wild & Scenic Rivers Act).

From 1909 to 2005 most of Fossil Creek's flow was diverted for hydroelectric power production (CRMP, 2020; Compson et al., 2009; Marks et al., 2006). In 2004 - 2005 federal and state agencies partnered to restore the river by decommissioning the dam, removing non-native fish species, building a fish barrier, restoring natural flow, and stocking native fish species above the fish barrier (CRMP, 2020; Compson et al., 2009; Marks et al., 2006). Recreation is the main human land use today, and the Forest Service regulates visitation during the high-use season. (Coconino NF, Fossil Creek CRMP: Background and History; Brown, 2019).

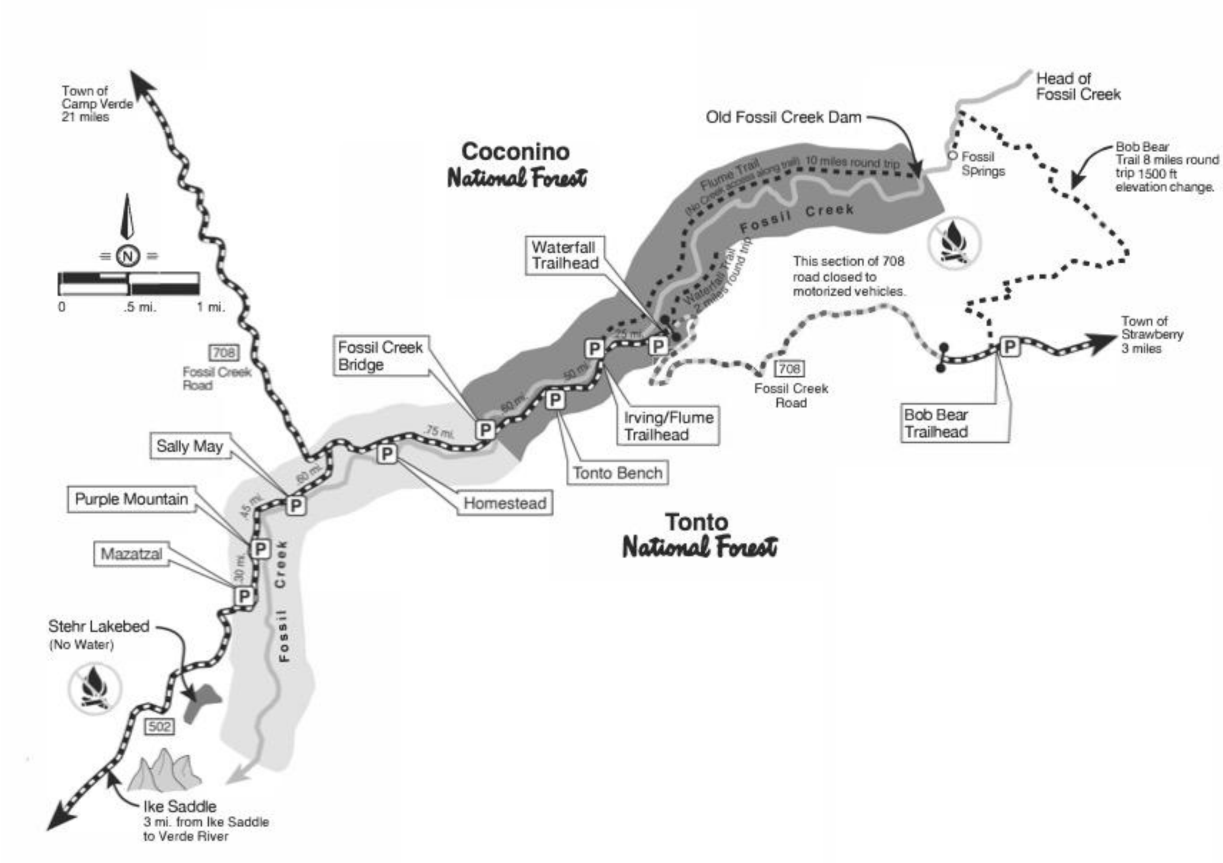

Figure 1: Map of Fossil Creek recreation sites and surrounding National Forest.

Backbone Fire

The Backbone Fire was ignited by a lightning strike and persisted from June 16, 2021 to July 19, 2021, affecting an estimated 41,924 acres of public land. A diverse array of vegetation was affected, including pinyon-juniper woodlands, grasslands, chaparral, and riparian vegetation (Lacroix & Paffett, 2021; Steinke & Jacobson, 2021). Characteristics of this fire align with the historical low-frequency, high-intensity fire regime of pinyon-juniper woodlands in the Southwest (Sankey et al., 2017; Baker & Shinneman, 2004; Schuss man et al., 2006). Due to rocky, less productive soils found in pinyon-juniper woodlands, and low infiltration rates, fires of this category are often limited to individual patches of fuel, spreading only under conditions of drought, and sustained high winds (Baker & Shinneman, 2004; Schussman et al., 2006; Floyd et al., 2000). This results in a mosaic of soil burn severities (Figure. 2). Two percent of the Fossil Creek watershed experienced high burn severity, 34% moderate burn severity, 54% low burn severity and 10% very low or unburned severity (Lacroix & Paffett, 2021). Sites with moderate and high soil burn severity exhibit soil repellency, which inhibits water infiltration for the first 2-5 years (Lacroix & Paffett, 2021). Water-repellent soils combined with a loss of protective vegetative ground cover usually accelerates soil erosion and water runoff on slopes greater than ~15% (Lacroix & Paffett, 2021), In the Fossil Creek watershed, 80% of soils within the burn were on slopes greater than 15% (Steinke & Jacobson, 2021). Erosion potential of soils affected by the Backbone Fire was estimated to be 7.2 tons/acre/year, delivering up to 911 cubic yards/square mile (Lacroix & Paffett, 2021; Steinke & Jacobson, 2021).

The US National Forest Service has identified natural recovery as the preferred treatment for this fire because fire-adapted shrub species are expected to regenerate and protect the soil from accelerated erosion and runoff within 3 years (Lacroix & Paffett, 2021). In the meantime, storm events are likely to cause accelerated water runoff and erosion, resulting in sediment delivery downslope. Sediment delivery into the river can be expected to cause aggradation, down cutting, and/or widening of stream channels (Coombs & Melack, 2012). The severity of sediment delivery at individual sites along the river is governed by upper watershed conditions, including the slope class and soil burn severity (Lacroix & Paffett, 2021; Earl & Blinn, 2003; Minshall, 2003; Gresswell, 1999).

Of particular concern are the remarkable values of Fossil Creek Wild and Scenic River (Fossil Creek CRMP). Riparian vegetation mortality varied along the river, but most concerning is the Boulder Creek drainage—a tributary to Fossil Creek—which experienced 100% mortality of riparian trees (Lacroix & Paffett, 2021). Boulder Canyon is the first watershed along the river that is large enough to substantially impact overall flows in Fossil Creek. Sally May, further downstream, is the second.

The Backbone burn scar area, including the entirety of Fossil Creek, was closed to public recreation for over a year due to flooding and safety concerns (Lacroix & Paffett, 2021). During this period, we had the opportunity to study the natural response of Fossil Creek to a range of sediment loading and predicted disturbances.

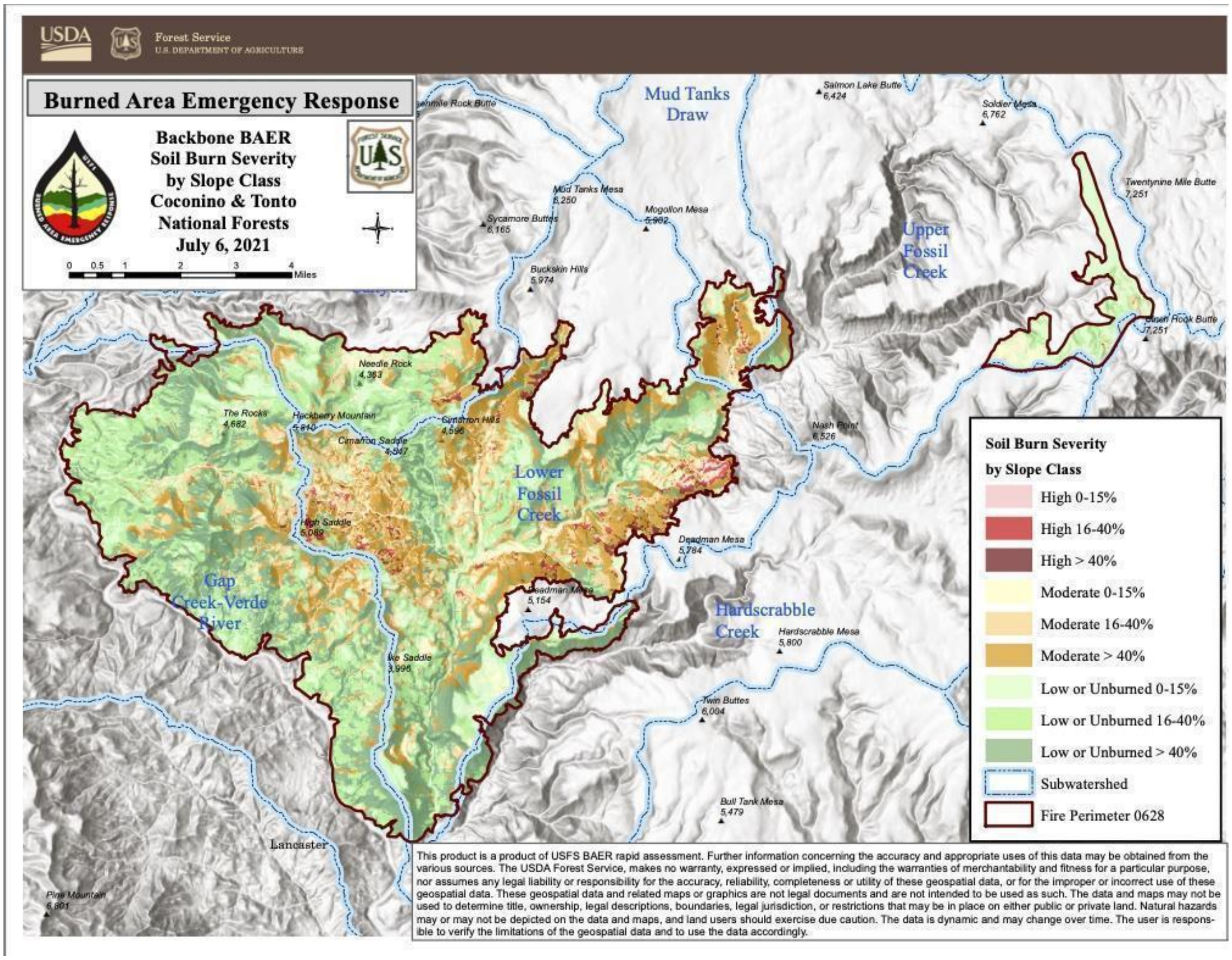

Figure 2: Map of soil burn severity for the Backbone fire by the National Forest Service Burned Area Emergency Response Teams (Lacroix & Paffett, 2021).

Site Selection

We sampled nine sites at two time points that varied in observed and predicted fire disturbances (Figure 3). The nine sites were categorized into three predicted disturbance groups based on the amount of initial sediment loading observed: future sediment loading potential, riparian burn severity, and predicted changes to peak flows. Future sediment loading potential was based on post-fire erosion potential of upstream watersheds, determined by Soil Burn Severity (SBS) and slope of the terrain. Watersheds within the Backbone Fire perimeter that have a slope greater than 15% and moderate or high SBS are at highest risk for water runoff and erosion, indicating potential for high sedimentation where the watershed basin drains into the river at our sites (Lacroix & Paffett, 2021). For this study, sites with upland slope of 15%- 40% with moderate soil burn were considered to have moderate sediment loading potential, while sites with upland slopes 15%- 40% with high soil burn or > 40% slope and moderate or high soil burn severity were considered to have high sediment loading potential. Riparian Burn Severity was the percentage of riparian Basal Area (BA) lost due to the fire at each site, determined by the US Forest Service Burned Area Emergency Response (BAER) team (Lacroix & Paffett, 2021). Burn severity is categorized as low (< 50% BA lost), moderate (< 90% BA lost) or severe (> 90% BA lost). Predicted changes to peak flows for 2-, 5-, and 100-year floods were modeled by USFS hydrologists considering slope class, soil burn severity, and the river's geomorphology. Changes were classified as minimal (less than 100% increase), significant (100%-200% increase), very significant (200%-800% increase) or extreme (> 800% increase). These factors were considered to categorize each site as least disturbed, moderately disturbed, or most disturbed in relation to each other.

At each site, three Surber samples were collected, except for the two samples taken below the fish barrier during the summer sampling period. In total, there were 53 samples. Sites were compared based on location along the river, predicted disturbance categories, and season. We conducted a before-and-after analysis using count data from a previous study on the Fossil Creek invertebrate community. The study examined the impact of flow restoration on macroinvertebrates in Fossil Creek, Arizona, which had experienced over a century of flow diversion (Dinger, 2006). The pre fire dataset included six sampling sites, where invertebrates were haphazardly sampled using five replicate Surber samples at each site, across two time points, resulting in a total of 60 samples (Dinger, 2006).

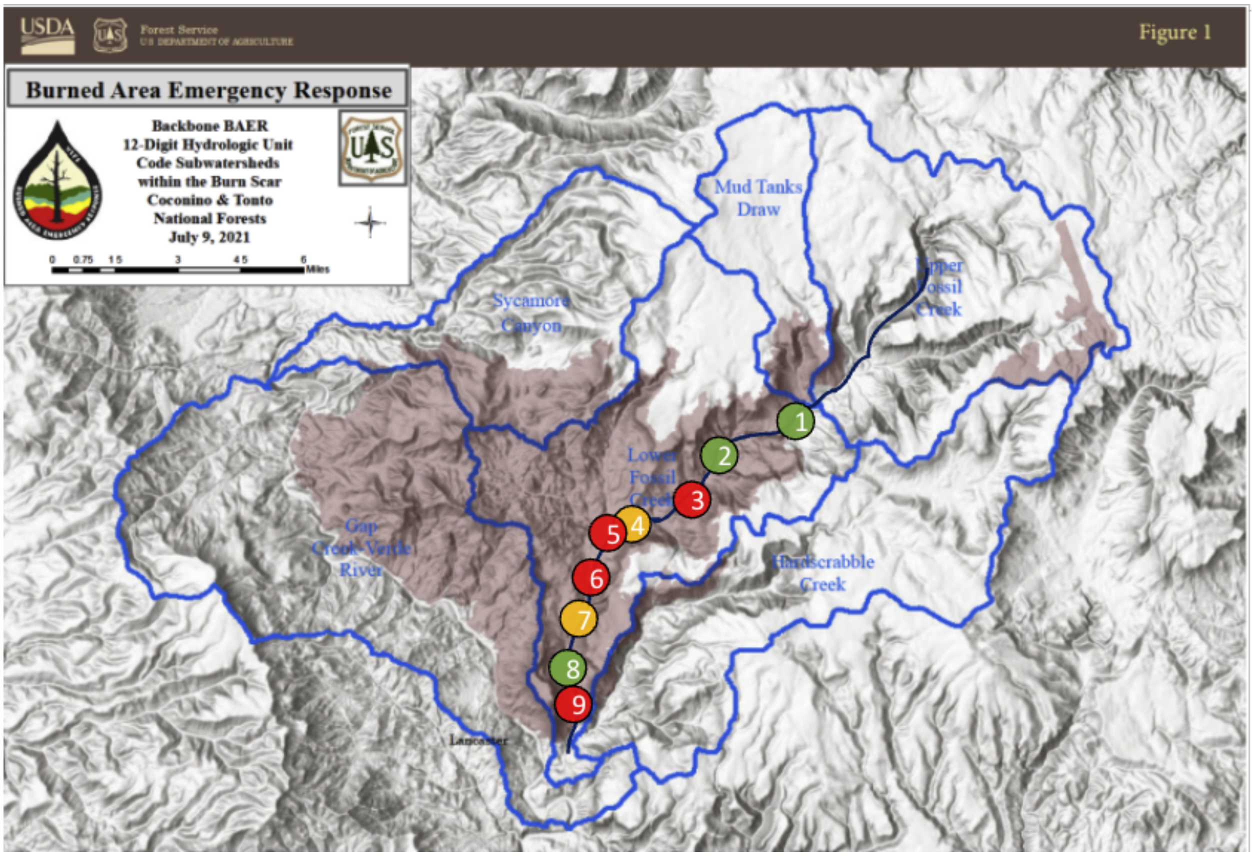

Figure 3: Map of nine sample sites along Fossil Creek within the backbone burn perimeter. Color denotes fire disturbance category. Green = Least disturbed, Yellow = Moderately disturbed, Red = most disturbed. Numbers represent sites from upstream to downstream (Lacroix & Paffett, 2021). 1: Spring (SP), 2: Waterfall (WF), 3: Tonto Bench (TB), 4: Above Boulder Canyon (ABC), 5: Below Boulder Canyon (BBC), 6: Sally May (SM), 7: Mazatzal (MAZ), 8: Above Fish Barrier (AFB), 9: Below Fish Barrier (BFB).

Invertebrate Sampling

This study took place Spring (April) and Summer (June-July) of 2022. Riffles were sampled for benthic invertebrates using a Surber sampler (250 µm mesh size, 0.093 m^2). Substrate was agitated and scrubbed for about one minute or until the entire sample area was affected. Samples were preserved in 95% ethanol. In the lab, samples were filtered through a 250µm mesh sieve. Invertebrates were sorted from associated substrates under low-power magnification using a LEICA EZ4 dissecting microscope. Identification was performed to genus, except for Chironomidae (keyed to family) and Oligochaeta (keyed to order), using standard taxonomic references (Pennak, 1955; Thorp & Rogers, 2014; Merritt & Cummins, 1996) as well as online resources (Macroinvertebrate Identification Key 2017). Invertebrates were counted and reported as density (# of individuals per m^2).

Invertebrate Community Analysis

To visualize and analyze community composition differences among invertebrate assemblages after the wildfire, we conducted Non-Metric Multidimensional Scaling (NMDS) ordinations using the Bray-Curtis dissimilarity matrix of taxa count data. Stress was less than 0.25. Invertebrate abundances were standardized to species maximum to equalize the importance of each taxon and converted to a similarity matrix using the Bray-Curtis similarity index. Significance of grouping was tested using an Analysis of Similarity (ANOSIM) statistical test in R using the packages vegan (Oksanen et. al., 2022), dplyr and plyr (Wickham et al., 2011).

Dependent Variables

We analyzed the response variables density, diversity, tolerance, and the relative abundance of functional feeding groups (Table 1). Dependent variables were calculated per sample with means and standard error values calculated based on the comparison being made. For example, when comparing between sampling periods, the Spring sampling period means and standard errors were calculated from all 27 samples taken in the spring season from all sites. Site means and standard errors were calculated from 6 samples, taken in both the spring and the summer. For the pre/post fire comparisons, means and standard errors were calculated from 60 pre fire samples and 53 post fire samples for one value that is representative of the entire river.

The variables total taxa richness and the Arizona Index of Biological Integrity (AZ IBI) will only be used to compare pre and post fire conditions and were calculated differently than other variables. Count data was aggregated by sampling period and metrics were calculated per time point rather than per sample to reach the minimum 500 individuals per sample required by the index. Mean and standard error values were calculated from three pre -fire samples and two post-fire samples.

The Arizona Index of Biological Integrity (IBI) for warm water streams (located below 5000 ft elevation) developed by Arizona Department of Environmental Quality (ADEQ) was used in this study. This index is a multi-metric index selected for responsiveness to disturbance in four categories: richness, composition, tolerance, and functional feeding groups (ADEQ IBI Technical Report). Sample values are compared to reference values that represent ecological conditions and greatest associated diversity for a region. Metric scores are computed by comparing the sample values to reference values. Formulas to calculate the IBI metrics follow.

This formula is applied to the following metrics with the reference value in parentheses next to it:

$$1.\quad Metric\ Score = \frac{Sample\ Value}{Reference\ Value}\ x\ 100$$

1. Total taxa richness (37)
2. Number of Ephemeroptera taxa (9)
3. Number of Trichoptera taxa (9)
4. Number of Diptera taxa (10)
5. Percent Ephemeroptera (70)
6. Percent scrapers (23.7)

7. Number of scraper taxa (7)

These formulas are applied to tolerant metrics two and three, whose values are expected to increase with disturbance.

2. Hilsenhoff Biotic Index (4.89)

$$Metric\ Score = \frac{10 - \ Sample\ Value}{10 - Reference\ Value}\ x\ 100$$

3. Percent dominant taxon (19.1)

$$Metric\ Score = \frac{100 - \ Sample\ Value}{100 - \ Reference\ Value}\ x\ 100$$

The final IBI is an average of the metric scores, with higher scores indicating healthier stream ecosystems and lower scores indicating degradation or impacts from human activities, like pollution, habitat destruction, and flow regime alterations (Gerritsen et al., 2017; ADEQ, 2015). IBI scores calculated from this study will not be used for official water quality assessment by the Department of Environmental because Fossil Creek violates the site condition requirement "not dominated by bedrock or travertine deposits" (ADEQ, 2007). However, these values will be used for future comparisons of Fossil Creek to itself.

We chose to calculate a second index, the Hilsenhoff Biotic Index (HBI), which is a weighted average of tolerance values for each sample (Hilsenhoff, 1987; 1988) and is calculated as:

$$HBI\ = \sum \quad (\frac{ni\ x\ ti}{N})$$

where n_i = number of individuals counted for species i, t_i = tolerance value for species i, and N is the total number of individuals in a sample. The tolerance values for invertebrates in our samples were sourced from the Arizona Department of Environmental Quality (ADEQ, 2022) and range from 0 to 10, with 0 indicating intolerance to organic pollution and 10 indicating high tolerance to organic pollution. Where genus-level tolerance values were not available, we used the tolerance level for the corresponding family. In instances where no tolerance values were available for a taxon, we excluded the taxon.

Statistical Analysis

All assumptions of normality and equal variances were rigorously tested, and the data successfully passed these tests. To address question one, the significance of the response variables to the wildfire was assessed using the Welch's Two Sample t-test, comparing pre- and post-fire variable means. Density and taxa richness were transformed using (Log x+1) to normalize the distribution of data. Additionally, Cohen's D, with pooled variance and a 95% confidence interval, was calculated to evaluate the magnitude of the wildfire's impact on response variables. Effect sizes, measured using Cohen's D, provide insights into the changes that might not be statistically significant but are biologically relevant (Nakagawa & Cuthill, 2007; Goulet-Pelletier & Cousineau, 2018). Following standard practice, the effect size was considered to be small when D = 0.2, medium when D = 0.5, and large when D = 0.8 and above (Nakagawa & Cuthill, 2007). We considered any effect size above 0.5 to have had a meaningful ecological impact.

To answer questions two and three, a two-way analysis of variance (ANOVA) was conducted, examining differences among seasons and the three predicted disturbance groups. A two-way ANOVA analyzes differences among group means while considering the simultaneous effects of two independent variables. Density was transformed using (Log x+1) to normalize the distribution of data. To assess the viability of the alternative hypothesis, that disturbances occurring upstream may have a greater impact on downstream sites than disturbances in the upland watershed, a subsequent analysis was performed, examining the interaction among seasons and the nine sites. When significant differences were detected from the 2-way ANOVA, the Tukey Honestly Significant Difference (HSD) test with Bonferroni correction was employed. This approach identifies specific groups that contribute to observed variations, enabling a more detailed understanding of the impact over time. A significance level of 0.05 was used for all statistical tests. All calculations, figures, and statistical analyses were performed using R (Posit Team, 2023).

RESULTS

Density

The Backbone Wildfire had a meaningful impact on macroinvertebrate density (Cohen's D = 0.75), resulting in a decrease of over 50%, from ~ 2,300 individuals per square meter before the fire to ~1,000 individuals after the fire ($p < 0.001$) (Figure 4, Figure 5, Table 2). Following the wildfire, changes in invertebrate density among sites were significant ($p = 0.02$), with one site being significantly different from three others according to post hoc tests. Despite a mean increase of invertebrate density from spring to summer, five of the nine sites experienced a decrease (Appendix 4). The sites that experienced a decrease were the three most upstream sites after the springs (WF, TB and ABC), and the two most downstream sites (AFB and BFB). In an instance of rapid and unexpected recovery, we observed a large increase in density between spring and summer at the most disturbed site, Below Boulder Canyon (BBC), where the density increased by over 1,300 individuals (Figure 5).

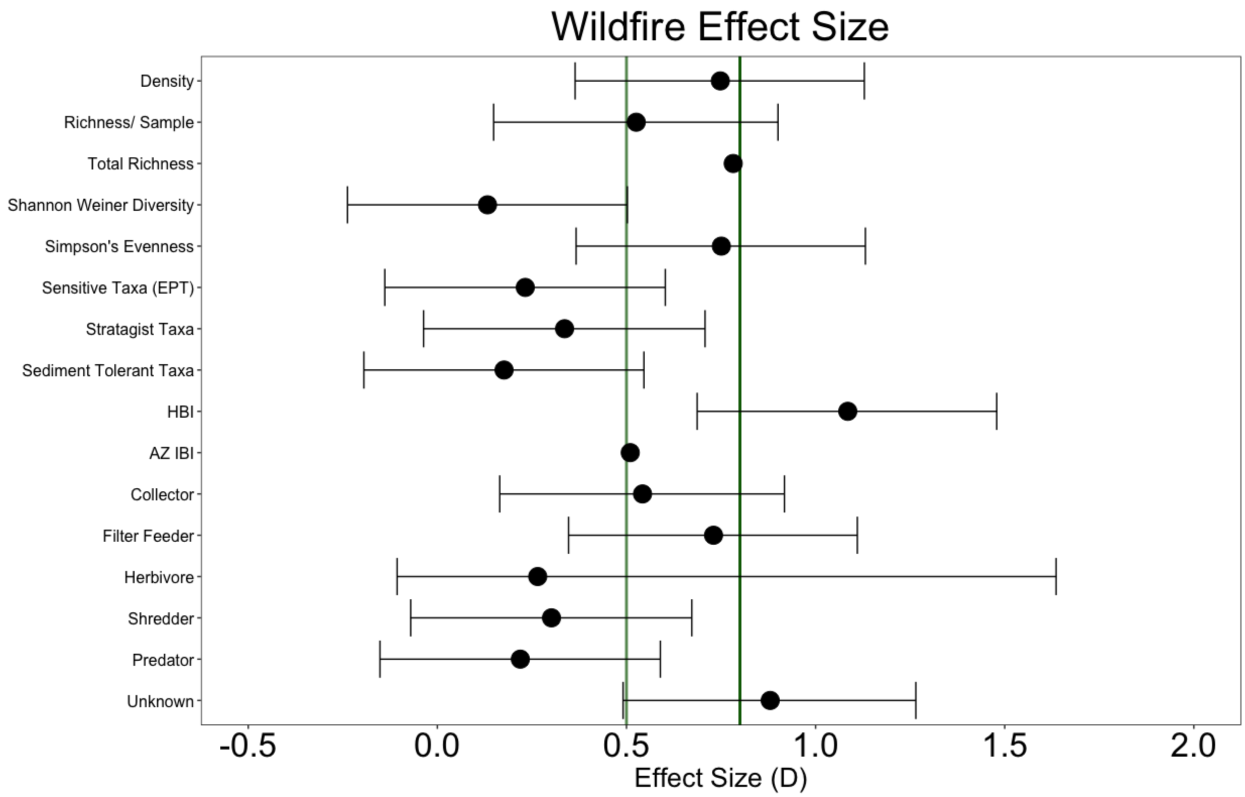

Figure 4: Standardized effect size (Cohen's D) for each response variable, representing the magnitude of the difference between pre- and post-fire means. Error bars indicate 95% confidence intervals of the mean difference between groups. First line at D = 0.5 indicates medium effect and second line at D = 0.8 indicates a large effect

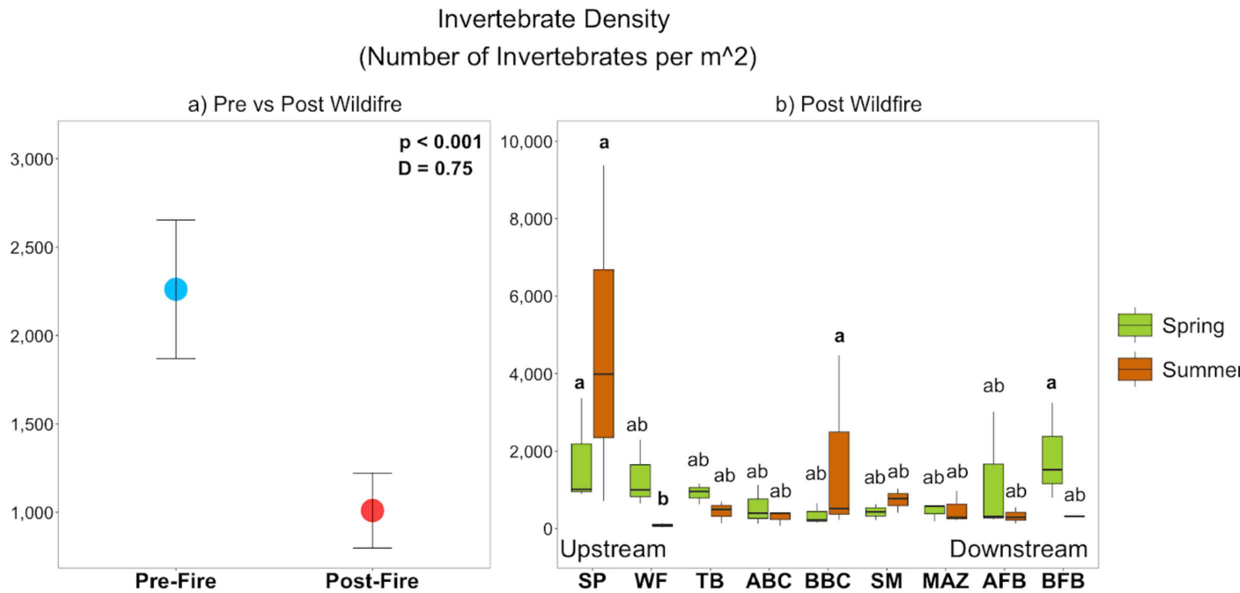

Figure 5:Comparison of mean invertebrate density. 5a) before and after the fire, n = 113. Welch t-test p-value and Coehn's D effect size value is shown top right. Significant values at $\alpha = 0.05$ and meaningful values at $D > 0.5$ are indicated in bold. 5b) Boxplot comparing sites during Spring and Summer, n = 53. Letters indicate results from the Tukey-Kramer post-hoc test, with different letters representing statistically significant differences between groups ($p < 0.05$).

Invertebrate Diversity

Wildfire-induced changes were observed for total taxa richness (D = 0.78), taxa richness per sample (D = 0.53), and Simpsons' Evenness Index (D = 0.75) (Figure 3, Table 3). Mean total taxa richness decreased by 25% from 48 unique taxa pre fire to 36.5 post fire. This decrease was not statistically significant (p = 0.38); however, the medium effect size implies the decrease was influenced by the wildfire. From spring to summer, total richness increased from 32 unique taxa to 41. Richness per sample decreased from ~11 unique taxa to ~9 post fire (p = 0.006). The response of taxa richness after the wildfire was influenced by an interaction between season and site (p = 0.05), with only two sites, WF and MAZ in the summer, showing significant differences from each other (Figure 6). Although mean taxa richness per sample increased with time, from the spring to the summer, there were instances of decreased richness at four sites (Appendix 4).

Other than Tonto Bench (TB), sites that experienced decreased density over time also experienced decreased richness.

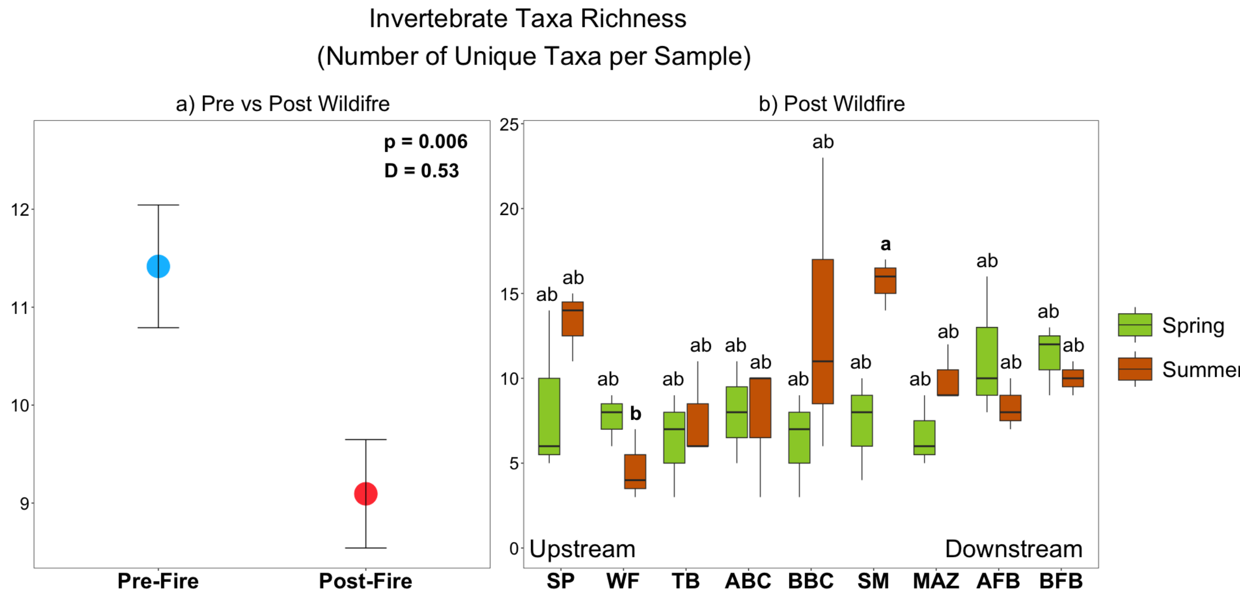

Figure 6: Comparison of mean invertebrate taxa richness per sample. 5a) before and after the fire, n = 113. Welch t-test p-value and Coehn's D effect size value is shown top right. Significant values at α = 0.05 and meaningful values at D > 0.5 are indicated in bold. 5b) Boxplot comparing sites during Spring and Summer, n = 53. Letters indicate results from the Tukey-Kramer post-hoc test, with different letters representing statistically significant differences between groups ($p < 0.05$).

Simpson's Evenness Index increased, as predicted, from 0.27 before the fire to 0.35 after the fire ($p < 0.001$). Following the wildfire, the distribution of taxa was influenced by an interaction between season and site ($p < 0.001$) (Table 5). There were only two sites significantly different from each other, and sites that experienced a decrease in density from spring to summer also experienced an increase of taxa evenness (Figure 7). In contrast to predictions, the Shannon-Weiner Diversity Index, which accounts for both richness and evenness, showed minimal change ($p = 0.48$, D = 0.13). While taxa richness decreased and evenness increased, the small change in the Shannon Weiner Diversity Index could indicate that some species rebounded strongly, compensating for the decrease in richness. Encouragingly, Shannon Weiner Diversity increased over time, from spring to summer, exhibiting a positive response to season ($p < 0.001$), with downstream sites being generally more diverse than upstream ones ($p < 0.001$) (Figure 8). Overall, these changes indicate a shift towards a more homogenous invertebrate assemblage at Fossil Creek following the wildfire, with variable impacts observed at individual sites.

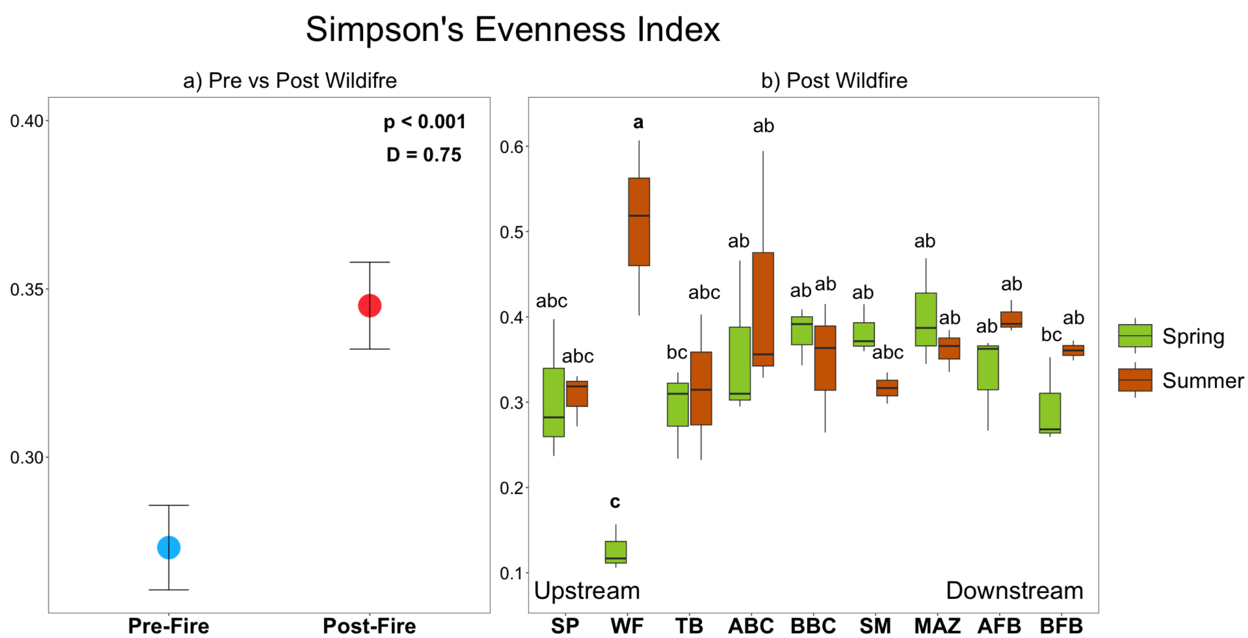

Figure 7: Comparison of mean Simpson's Evenness Index. 7a) before and after the fire, n = 113. Welch t-test p-value and Coehn's D effect size value is shown top right. Significant values at $\alpha = 0.05$ and meaningful values at $D > 0.5$ are indicated in bold. 7b) Boxplot comparing sites during Spring and Summer, n = 53. Letters indicate results from the Tukey-Kramer post-hoc test, with different letters representing statistically significant differences between groups ($p < 0.05$)

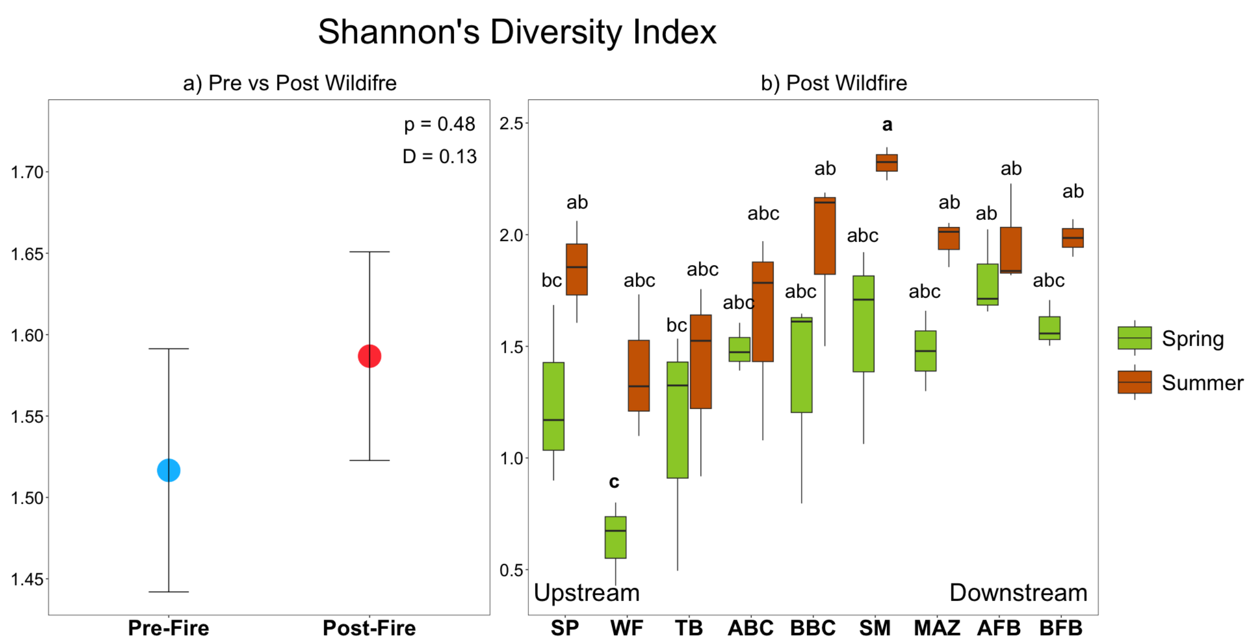

Figure 8: Figure 8: Comparison of mean Shannon's Diversity Index. 8a) before and after the fire, n = 113. Welch t-test p-value and Coehn's D effect size value is shown top right. Significant values at $\alpha = 0.05$ and meaningful values at $D > 0.5$ are indicated in bold. 8b) Boxplot comparing sites during Spring and Summer, n = 53. Letters indicate results from the Tukey-Kramer post-hoc test, with different letters representing statistically significant differences between groups ($p < 0.05$).

Tolerant Taxa

A measure of ecosystem health specific to Arizona streams, the Index of Biological Integrity (IBI), decreased as predicted, from ~84 before the wildfire to ~77 after ($p = 0.56$, $D = 0.51$). Contrary to predictions, however, HBI decreased from ~ 6.0 before the wildfire to ~ 5.2 after the fire ($p < 0.001$), indicating the stream is less disturbed by organic pollution than before the fire ($D = 1.09$) (Figure 9). Highlighting the community's resilience, the wildfire did not result in significant changes to the proportion of strategist taxa ($p = 0.07$, $D = 34$), or sediment tolerant taxa ($p = 0.35$, $D = 18$; Table 2).

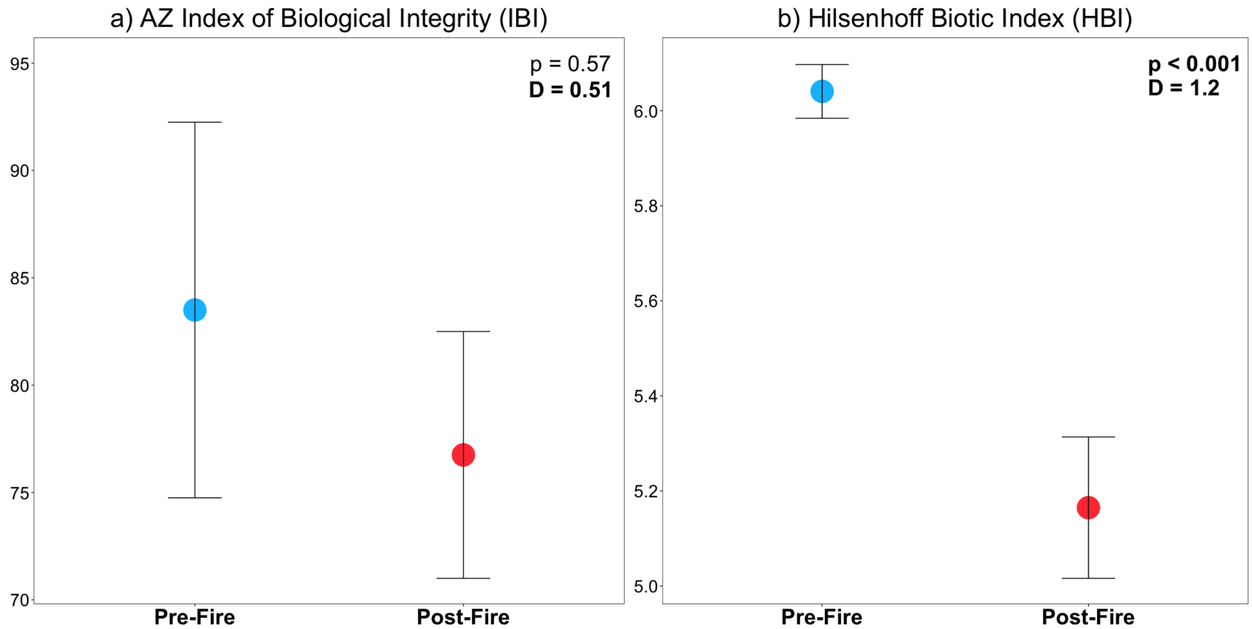

Figure 9: Comparison of mean a) Arizona Index of Biological Integrity, n = 5 and b) Hilsenhoff Biotic Index (HBI), n = 113, before and after the fire. Welch t-test p-value and Coehn's D effect size value is shown top right. Significant values at $\alpha = 0.05$ and meaningful values at $D > 0.5$ are indicated in bold.

Following the wildfire, there were significant changes over time, as the community responded to post wildfire disturbances (Table 5). Tolerance variables responded to season based on distance downstream, with the split occurring between site 4 (Above Boulder Canyon, ABC) and site 5 (Below Boulder Canyon, BBC). HBI scores decreased from spring to summer at the first four upstream sites, while the lower five sites experienced an increase ($p = 0.005$). This result indicates recovery and a shift towards a more sensitive invertebrate community at upstream sites but the opposite downstream (Figure 10). In contrast, upstream sites exhibit a significantly higher proportion of sediment-tolerant taxa ($p= 0.002$) compared to downstream sites in the spring, but these differences level out over time (Figure 11). Encouragingly, both the proportion of sediment-tolerant taxa ($p = 0.002$) and strategist taxa ($p < 0.001$) significantly decreased from spring to summer, suggesting sediment flushing and reduced disturbance over time (Figure 11). Notably, the exception to this trend was observed at the most disturbed site, Below Boulder Canyon (BBC), where the proportion of sediment-tolerant taxa increased from 10% in the spring to 15% in summer. This result aligns with expectations because below Boulder Canyon is located at a confluence and has continued to experience sedimentation with each flow event. Overall, tolerance metrics indicate a less impacted invertebrate community downstream than upstream.

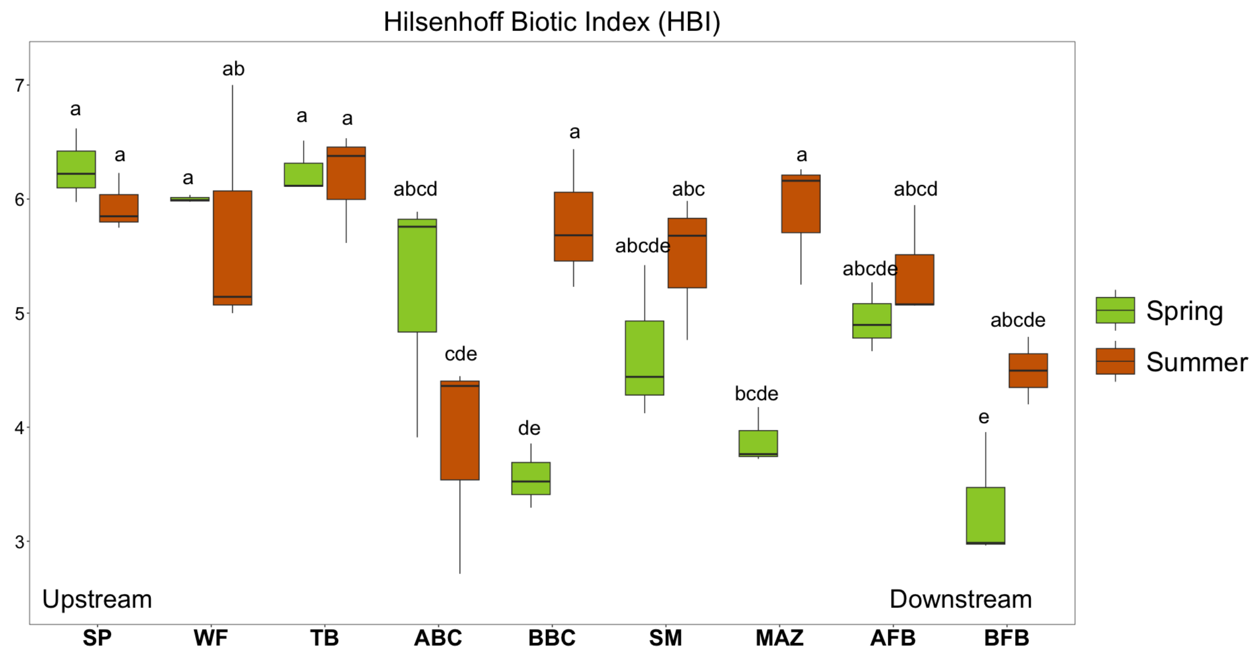

Figure 10: Boxplot comparing the Hilsenhoff Biotic Index among sites during Spring and Summer, n = 53. Letters indicate results from the Tukey-Kramer post-hoc test, with different letters representing statistically significant differences between groups ($p < 0.05$).

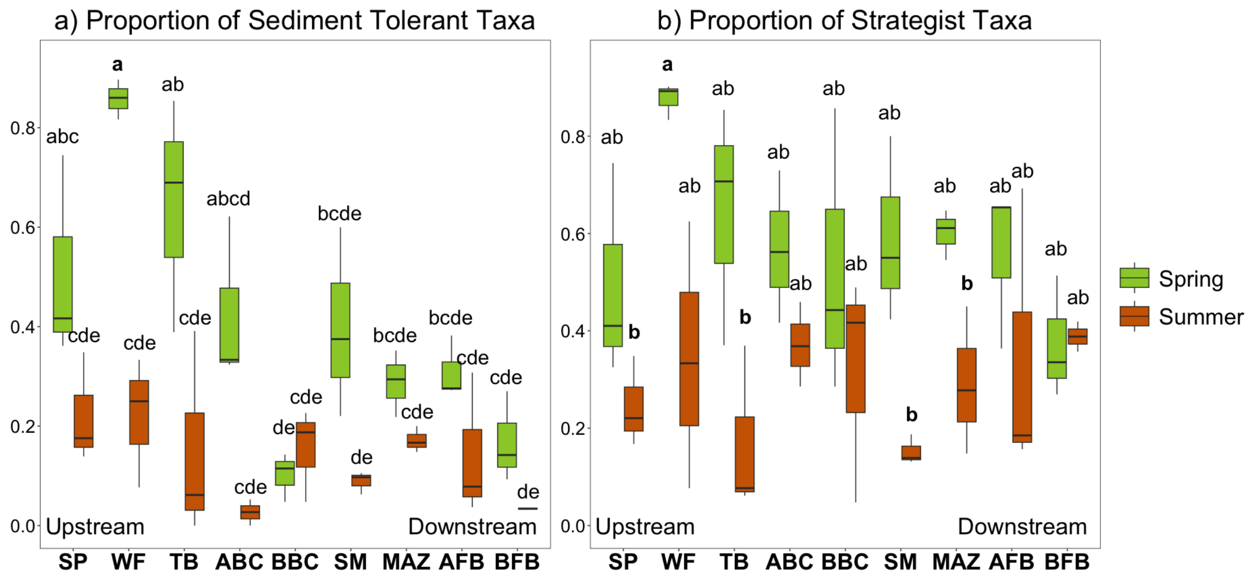

Figure 11: Boxplots comparing tolerance variables a) Proportion of sediment tolerant taxa and b) Proportion of Strategist Taxa among sites during Spring and Summer, n = 53. Letters indicate results from the Tukey-Kramer post-hoc test, with different letters representing statistically significant differences between groups ($p < 0.05$).

Some tolerance variables, including the Hilsenhoff Biotic Index (HBI) ($p < 0.001$), and the proportion of sediment-tolerant taxa ($p = 0.02$) responded to the predicted disturbance groups; however, the direction was unexpected (Table 4). Contrary to predictions, the least disturbed group had the highest mean HBI score of ~5.7 and the highest proportion of sediment tolerant taxa at 38%, indicating a more impacted community compared to the other groups. It is more likely however, that the tolerance variables responded to differences among sites rather than a site's predicted disturbance group. Two of the three "Least Disturbed" sites are the most upstream and could have dominated the disturbance grouping significance tests, which are based on mean values.

Functional Feeding Groups

The wildfire significantly influenced the mean relative abundance of some of the functional feeding groups, indicating a potential restructuring of the community (Figure 12). Collectors increased by 13% ($p = 0.004$, $D = 0.54$) while filter feeders decreased by 17% ($p < 0.001$, $D = 0.73$). Scrapers also decreased by 5%, though the difference was not significant or ecologically meaningful ($p=0.2$, $D = 0.23$). There was minimal change in the proportions of predators, herbivores, and shredders. The mean relative abundances of functional feeding groups changed over time (Figure 13). Collectors ($p < 0.001$) and Herbivores ($p = 0.01$) increased from spring to summer, while Filter Feeders ($p < 0.001$), Scrapers ($p = 0.01$), and Predators decreased. An interaction between season and site was observed for the proportion of Scrapers. Overall, there were higher proportions of scrapers downstream than upstream, with a mean decrease of 5% in the proportion of scrapers from the spring to summer, influenced by decreases greater than 13% at just three sites (Appendix 4).

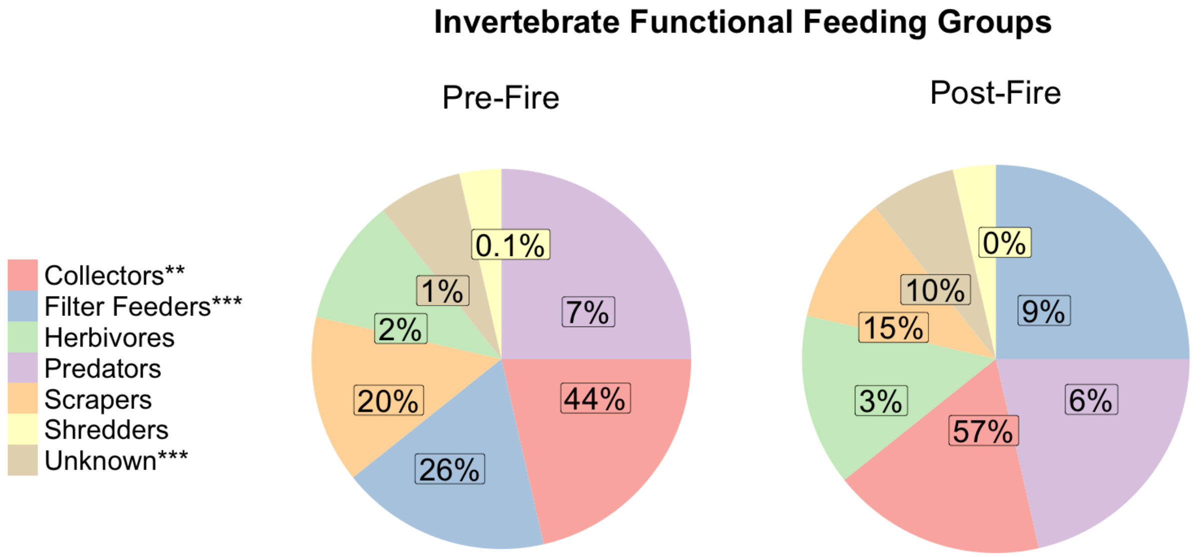

Figure 12: Comparisons of the mean relative abundances reported as percentages, of functional feeding groups before and after the fire, n = 113. Significant p-values at $\alpha = 0.05$ are indicated with stars: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

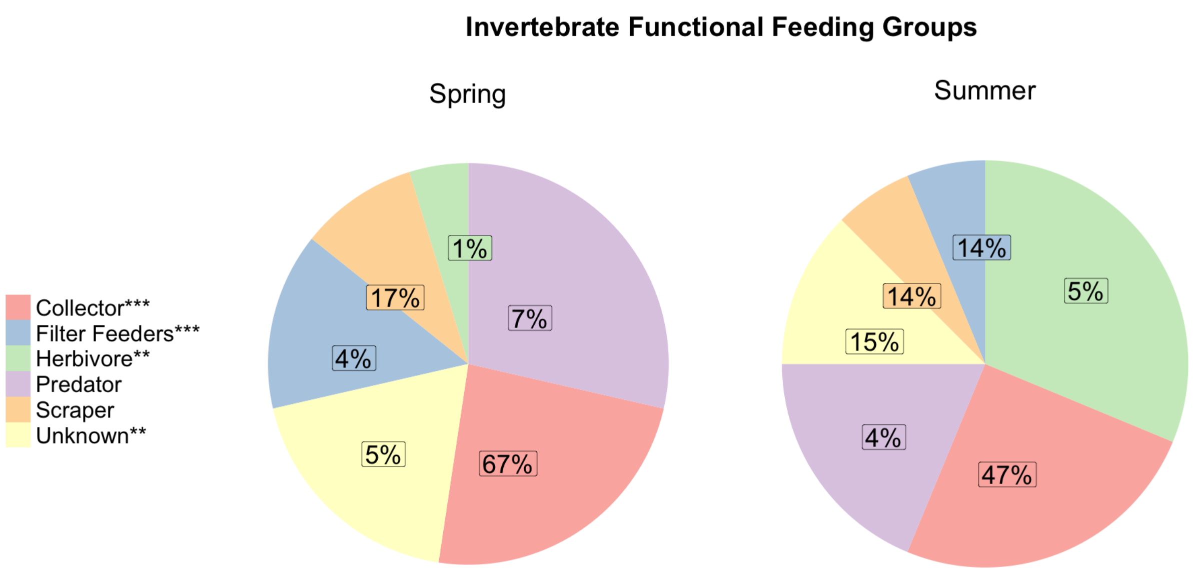

Figure 13: Comparisons of mean relative abundances, reported as percentages, of functional feeding groups in the spring and summer, n = 53. Significant p-values at $\alpha = 0.05$ are indicated with stars: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Post Wildfire Community Composition

A post-wildfire NMDS analysis confirmed shifts in the community compositions of invertebrate communities from spring to summer that were expected as density and diversity changed. The analysis revealed clear seasonal differences (Figure 14), with an unexpected shift from spring to summer (Figure 15). In spring, the three most upstream sites were more similar to each other than other sites ($p < 0.001$). However, by summer, compositions shifted among sites, demonstrating that the three most upstream sites became more similar to the others. This convergence suggests a seasonal homogenization in invertebrate community compositions, where the three most upstream sites, initially distinct in spring, became more akin to the broader pattern observed across all sites during the summer months.

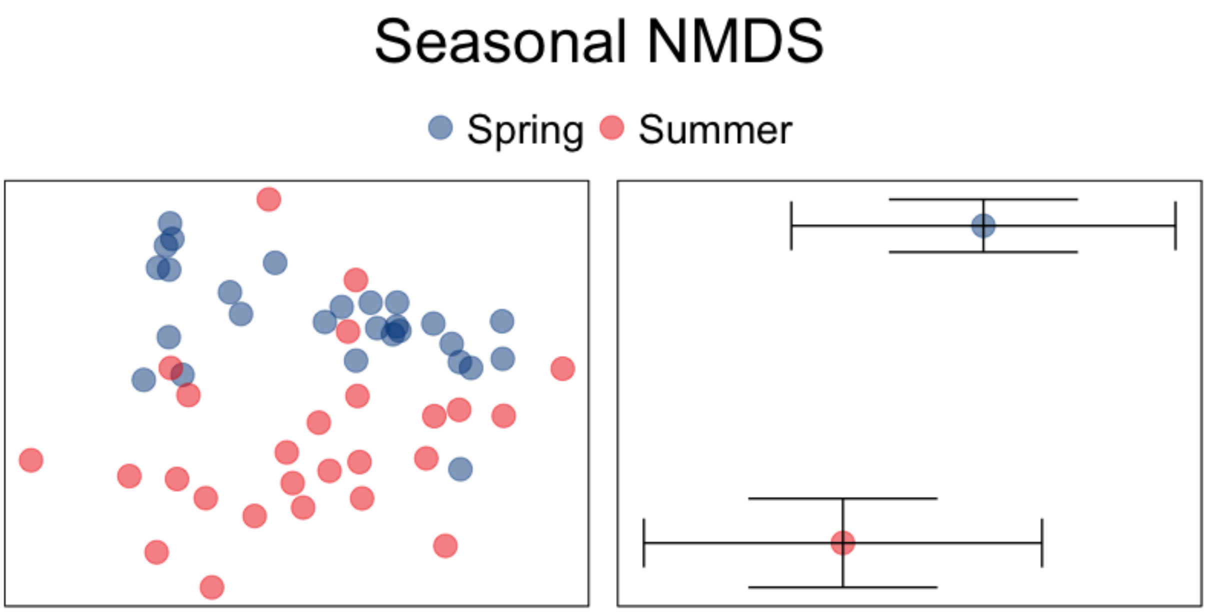

Figure 14: Non-Metric Multidimensional Scaling (NMDS) Analysis of invertebrate community composition differences between Spring and Summer sampling periods, n = 53. 8a: Each replicate sample is represented as a discrete point. 8b: Centroids of invertebrate assemblages between spring and summer with error bars that depict the variation within the respective sampling period. ANOSIM analysis p-value is shown top right. Significant values at $\alpha = 0.05$ are indicated in bold.

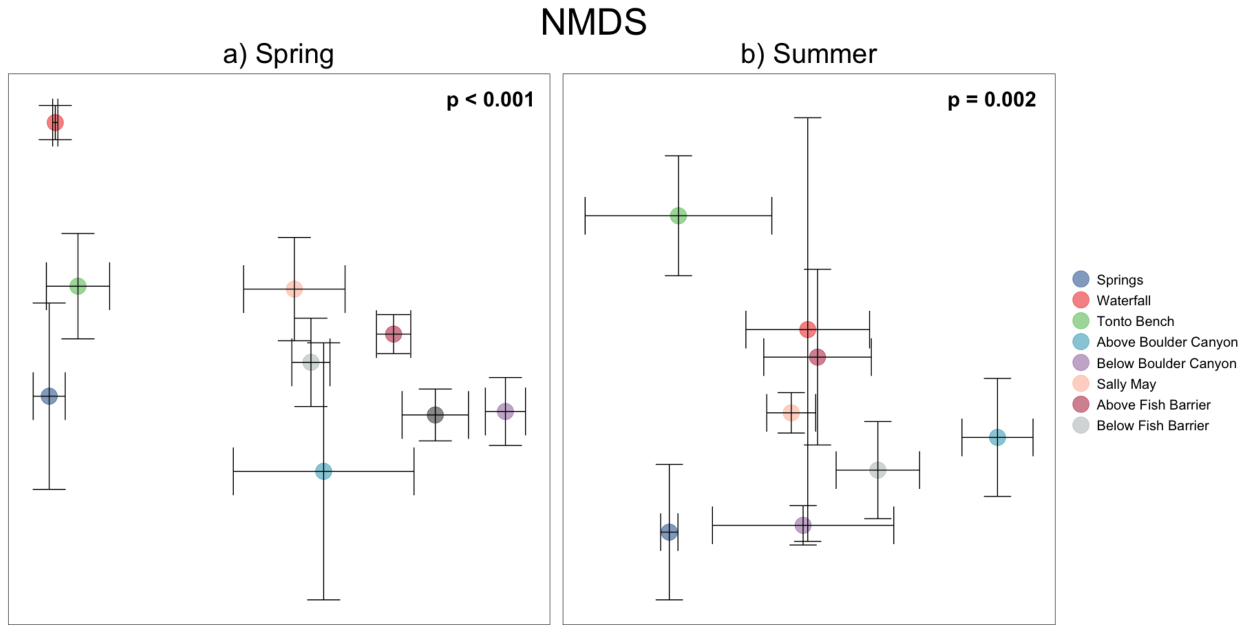

Figure 15: Non-Metric Multidimensional Scaling (NMDS) analysis of invertebrate community composition differences among sites in the a) Spring, n = 27 and b) Summer, n = 26. Centroids of invertebrate assemblages with error bars depict the variation within the respective sampling period. ANOSIM analysis p-value is shown top right. Significant values at $\alpha = 0.05$ are indicated in bold.

DISCUSSION

Invertebrate Community Response

The Backbone Wildfire brought about substantial alterations to Fossil Creek's invertebrate community, highlighting the severity of this disturbance on the whole ecosystem. In this study, we capitalized on pre-existing invertebrate count data collected in 2005 and 2006 to compare data collected soon after the burn. Given safety concerns in the aftermath of the wildfire, our initial sampling took place nine months post-burn. During this period, discernible changes in overall density, diversity, and the composition of tolerant taxa likely stemmed from indirect wildfire effects, including erosion, sediment transport, channel modification, and turbidity initiated by runoff post-fire (Gresswell, 1999; Minshall, 2003; Minshall et al., 1989; Tronstad et al., 2012; Verkaik et al., 2015).

Invertebrate mortality was high, represented by significant decreases in invertebrate density compared to pre-fire data. This decrease highlights the detrimental effects of the wildfire on invertebrate populations, an effect likely attributed to burial from sediment loading (Minshall et al., 1989; Minshall, 2003; Rinne, 1996; Tronstad et al., 2012; Verkaik et al., 2015; Minshall & Robinson, 1992; Minshall et al., 2001b; Spindler, 2004). Our results are similar to the findings by Rinne (1996), who studied the short-term impacts of wildfire in the Tonto National Forest, Arizona, noting a sharp decline in aquatic macroinvertebrate densities post-fire, reaching only 25-30% of pre-fire diversity after one year and exhibiting continued fluctuations.

Through the development of a statewide invertebrate bioassessment, the Arizona Department of Environmental Water Quality found that macroinvertebrate communities are sensitive to burial and to substrate parameters, such as particle size and embeddedness (Spindler, 2001; Spindler, 2004). Stream environments recently disturbed by high sediment input support fewer microhabitats due to high embeddedness, which can affect population size and community composition (Spindler, 2004; Duan et al., 2008). In this study, we noted a decrease in species richness, coupled with an increase in taxa evenness, indicating a shift towards a more homogeneous community structure. This result is consistent with findings from a study investigating stream invertebrate community responses to wildfire that reported diminished taxa richness and abundance in burned watersheds (Mihuc & Minshall, 1995).

Although taxa richness decreased and evenness increased, we observed a marginal change in the Shannon Weiner Diversity Index. This can be attributed to increased abundance of disturbance-adapted taxa that play a crucial role in ecosystem recovery following environmental perturbations (Rader; 1997; Mihuc & Minshall, 1995). We expected the post wildfire community to respond with increased proportions of strategist taxa and sediment-tolerant taxa. However, our findings deviate from similar studies (Spindler, 2004; Mihuc & Minshall, 1995; Tronstad et al., 2012; Verkaik et al., 2015; Harris et al., 2015), as we observed insignificant changes in the proportions of these taxa. We did see resilience to disturbance through increased abundances of terrestrial mites (Trombidiformes) and Ephemeroptera adapted to high flows, including *Cameleobaetidius sp*. Baetidae, Heptageniidae, and Leptohyphidae (Appendix 5) (Jacobus et al., 2019, Rader; 1997; Harris et al., 2015; Harris et al., 2018). *Cameleobaetidius sp*. Baetidae and Heptageniidae, with tolerance values of four (ADEQ, 2022), exhibit sensitivity to pollution, explaining the unexpected decline in the Hilsenhoff Biotic Index (i.e., apparent improved water quality). The Arizona Index of Biological Integrity decreased as predicted compared to the pre-fire phase; though not significantly different, the effect size indicated the change was due to the wildfire. Post-wildfire values remain high enough to be considered "attaining reference conditions," implying mild impacts 9 months after disturbance (ADEQ, 2015; 2007).

The proportion of macroinvertebrates in various functional feeding groups shifted after the Backbone fire. We report a significant decrease in filter feeders met by an increase of collector-gatherers. These results mirror a study indicating that elevated sediment levels lead to higher proportions of collector-gatherers and lower proportions of filterers and scrapers (Rabení et al., 2005). Collectors are often abundant in stream ecosystems with low flow, where fine particles are abundant (Ramírez & Gutiérrez-Fonseca, 2014). This group benefits from particles that sink to the bottom because they feed on the bottom, whereas filter feeders feed from the water column and their gills can be clogged by the sediment (Ramírez & Gutiérrez-Fonseca, 2014; Wallace & Webster, 1996; Lemly, 1982).

Invertebrate Community Recovery

The post-wildfire response paints a dynamic picture with site-specific responses varying based on reduced stability of postfire instream habitat (O'Neill et al., 1989). We report decreased invertebrate density and taxa richness at five of the nine sites across Fossil Creek, accompanied by increased taxa evenness at four of those five sites, from spring to summer. This is consistent with other studies reporting decreased macroinvertebrate abundance and richness following fire (Rinne, 1996; Minshall et al., 2001b; Earl & Blinn, 2003). However, at three highly disturbed sites, we observed an opposite trend than above, with increased invertebrate density and taxa richness, and a decrease in taxa evenness. The sites were Below Boulder Canyon (BBC), Sally May (SM), and Mazatal (MAZ). The upper watershed of these sites is sloped greater than 40% and experienced high vegetation mortality and soil burn severity, increasing the likelihood of erosion and sedimentation, negatively affecting the invertebrate community as flow events continued to occur (Lacroix & Paffett, 2021).

One study investigated the effects of wildfire and variations in peak streamflow on macroinvertebrate communities, uncovering dynamic changes over time primarily driven by sediment, large woody debris, and riparian cover (Arkle et al., 2010). Similar to the influence noted by Arkle et al. (2010), we report increased proportions of sediment-tolerant taxa by over 50% at one site, Below Boulder Canyon (BBC). This confluence was appropriately named, with boulders ranging from the size of a basketball to a car and 100% mortality of trees. With each flow event, the inputs of large woody debris and sediment of various sizes improved habitat heterogeneity at Boulder Canyon and the following two downstream sites (Harris et al., 2018; Benke & Wallace, 2003). While this result is not the norm (Rinne, 1996; Minshall et al., 2001a; Earl & Blinn, 2003), there are other studies that have reported increased invertebrate density in burned tributaries due to debris flow (Albin, 1979; Roby & Azuma, 1995; Gresswell, 1999). One study reported greater taxa richness, and 1.5x greater invertebrate abundance in burned streams compared to reference streams (Silins et al., 2014).

The responses of Shannon Weiner Diversity and the Hilsenhoff Biotic index paint a simpler picture. In just three months, diversity increased at every site, with mean values increasing with distance downstream. The Hilsenhoff Biotic Index decreased in three months, representing decreased pollution, at sites upstream of Boulder Canyon and increased pollution below. This separation was associated with changes in the proportion of sediment-tolerant taxa with high tolerance values at these sites, specifically Chironomidae (6) and Oligochaeta (8) (ADEQ, 2022). It is likely flow events increased resource transfer, enhanced invertebrate drift, and scoured woody debris downstream, thereby increasing downstream microhabitats and invertebrate diversity and sensitivity (Harris et al., 2015; Silins et al., 2014; Arkle et al., 2010).

Significant changes in relative abundances of functional feedings groups from spring to summer represent modifications of substrate, thereby affecting microhabitats for aquatic macroinvertebrates (Rabeni & Minshall, 1977; Minshall, 1988). In this study, we report a significant increase in the proportion of herbivores from spring to summer, suggesting aquatic vascular plant growth over time (Merritt & Cummins, 2007; Wallace & Webster, 1996; Ramírez & Gutiérrez-Fonseca, 2014). Vascular plants are often more prominent in slower-moving sections of streams, where plants can establish root systems (Webster & Benfield, 1986). While the presence of these plants tends to increase the retention of fine-sediment loading (Jones et al., 2010), we also report a significant increase of filter feeders matched by a significant decrease of collector-gatherers, which have been correlated with decreased suspended particles over time

(Rabení et al., 2005; Lemly, 1982). The proportions of scrapers exhibit variable changes among sites, without a discernible pattern.

Both our disturbance-grouping hypothesis and our alternative hypothesis, that disturbances occurring upstream may have a greater impact on downstream sites than disturbances in the upland watershed, were not supported. Few response variables responded to the predicted disturbance groups, leading to the conclusion that upper watershed conditions do not explicitly govern in-stream conditions (Table 4). It is likely the significant variables were responding to site-specific rain events, rather than the broader disturbance categories. This could be because rainfall is frequently very localized and would have varying impacts on flow rates based on upper watershed conditions (Comrie & Broyles, 2002; Arkle et al., 2010; Harris et al., 2015). In contrast to our alternative hypothesis, the observed response of dependent variables did not conform precisely to anticipated distinctions between upstream and downstream sites. Instead, downstream patterns were notably shaped by the severe disturbance at Boulder Canyon, the largest ephemeral tributary into Fossil Creek, resulting in a nuanced mix of expected and unexpected variable responses. This study provides valuable insights into the post-wildfire, short-term response of aquatic macroinvertebrates, with recovery patterns suggesting complex interactions between habitat stability, sedimentation, and the adaptability of invertebrates.

TABLES

Table 1: Invertebrate response variables

Category	Metric	Definition	Expected Response to Disturbance
Density	Density	Number of invertebrates per meter squared, standardized from abundance	Decrease
Diversity	Richness per Sample	Number of unique taxa in a sample of standard size	Decrease
	Total Richness	Number of unique taxa across entire river	Decrease
	Shannon's Diversity	Measure of species diversity that takes into account both the number of species present and their relative abundances	Decrease
	Simpson's Evenness	Measure of how evenly the individuals of a community are distributed among different taxa	Decrease
Tolerance	Hilsenhoff Biotic Index (HBI)	Abundance-weighted average tolerance of invertebrate assemblage in sample of standard size	Increase
	Arizona Index of Biological Integrity	Measure of invertebrate responsiveness to disturbance standardized for Arizona streams	Decrease
	Proportion of Strategist Taxa	Relative abundance of Chironomidae, Simuliidae, and Baetidae compared to total abundance	Increase
	Proportion of Sediment Tolerant Taxa	Relative abundance of Oligochaetes and Chironomidae compared to total abundance	Increase
Functional Feeding Groups	Proportion of each group	Relative abundance of taxa in each functional feeding group compared to total abundance (Filter Feeders, Scrapers, Collectors, Herbivores, Shredders, Predators and unknown)	Variable

Table 2: Mean ± SE values and the results from Welch's two-sample t-tests for response variables. Pre-fire (2005, 2006) and post-fire (2022). Significant p-values at α = 0.05 are indicated in bold.

Response Variable	Mean ± S.E.		df	t	p-value	95% Confidence Interval	
	Pre Fire	*Post Fire*				*Lower*	*Upper*
Density	2261 ± 392	1009 ± 212	109.72	3.97	< 0.001	0.42	1.26
Richness per Sample	11.4 ± 0.6	9.1 ± 0.5	108.11	2.78	0.006	0.06	0.36
Total Richness	48 ± 10.1	36.5 ± 4.5	2.67	1.04	0.382	-26.21	49.21
Shannon Weiner Diversity Index	1.59 ± 0.06	1.52 ± 0.07	110.13	-0.71	0.477	-0.27	0.12
Simpson's Evenness Index	0.27 ± 0.01	0.35 ± 0.01	110.10	-3.99	< 0.001	-0.11	-0.04
Proportion of Strategist Taxa	0.37 ± 0.03	0.43 ± 0.03	110.54	-1.81	0.074	-0.21	0.01
Proportion of Sediment Tolerant Taxa	0.23 ± 0.03	0.28 ± 0.03	109.28	-0.94	0.352	-0.13	0.05
HBI Index	6.04 ± 0.06	5.16 ± 0.15	66.93	5.50	< 0.001	0.56	1.19
AZ IBI	83.5 ± 8.7	76.75 ± 5.8	2.99	0.64	0.565	-26.65	40.15
Proportion of FFG Collector	0.44 ± 0.03	0.57 ± 0.03	109.98	-2.92	0.004	-0.224	-0.043
Proportion of FFG Filter Feeder	0.26 ± 0.04	0.09 ± 0.02	79.19	4.05	< 0.001	0.085	0.249
Proportion of FFG Scraper	0.20 ± 0.03	0.15 ± 0.02	100.84	1.27	0.206	-0.027	0.122
Proportion of FFG Predator	0.07 ± 0.01	0.06 ± 0.009	106.44	1.19	0.238	-0.012	0.047
Proportion of FFG Herbivore	0.02 ± 0.005	0.03 ± 0.009	79.63	-1.36	0.177	-0.036	0.007
Proportion of FFG Shredder	0.001 ± 0.0003	0	59.00	1.70	0.094	-0.0001	0.001

Proportion of FFG Unknown	0.01 ± 0.005	0.10 ± 0.02	60.56	-4.43	< 0.001	-0.124	-0.047

Table 3: Mean ± SE values, sample size, Cohen's D Effect Size, and 95% Confidence Interval for response variables, Pre-fire (2005, 2006), and Post-fire (2022). Meaningful effect sizes at D = 0.05 are indicated in bold.

Variable	Mean ± S.E.		n	Cohen's D	Effect Size	Effect Size 95% Confidence Interval	
	Pre Fire	*Post Fire*				*Lower*	*Upper*
Density	2261 ± 392	1009 ± 212	113	0.75	Medium	0.36	1.13
Richness per Sample	11.4 ± 0.6	9.1 ± 0.5	113	0.53	Medium	0.15	0.90
Total Richness	48 ± 10.1	36.5 ± 4.5	5	0.78	Medium	-1.16	2.61
Shannon Weiner Diversity Index	1.59 ± 0.06	1.52 ± 0.07	113	0.13	Trivial	-0.24	0.50
Simpson's Evenness Index	0.27 ± 0.01	0.35 ± 0.01	113	0.75	Medium	0.37	1.13
Proportion of Strategist Taxa	0.37 ± 0.03	0.43 ± 0.03	113	0.34	Small	-0.04	0.71
Proportion of Sediment Tolerant Taxa	0.23 ± 0.03	0.28 ± 0.03	113	0.18	Trivial	-0.19	0.55
HBI Index	6.04 ± 0.06	5.16 ± 0.15	113	1.09	Very Large	0.69	1.48
AZ IBI	83.5 ± 8.7	76.75 ± 5.8	5	0.51	Medium	-1.36	2.30
Proportion of FFG Collector	0.44 ± 0.03	0.57 ± 0.03	113	0.54	Medium	0.165	0.918
Proportion of FFG Filter Feeder	0.26 ± 0.04	0.09 ± 0.02	113	0.73	Medium	0.347	1.110
Proportion of FFG Scraper	0.20 ± 0.03	0.15 ± 0.02	113	0.23	Small	-0.138	0.604
Proportion of FFG Predator	0.07 ± 0.01	0.06 ± 0.009	113	0.22	Small	-0.152	0.589
Proportion of FFG Herbivore	0.02 ± 0.005	0.03 ± 0.009	113	0.27	Small	-0.106	1.636

Proportion of FFG Shredder	0.001 ± 0.0003	0	113	0.30	Small	-0.0705	0.673
Proportion of FFG Unknown	0.01 ± 0.005	0.10 ± 0.02	113	0.88	Large	0.491	1.265

Table 4: Results from Two-Way ANOVA testing influence of predicted disturbance groups (Least Disturbed, Moderately Disturbed and Most Disturbed), seasons (Spring and Summer) and their interaction on each response variables. Significant p-values at α = 0.05 are

Response Variable	Source	DF	F ratio	p value
Density	Season	1	2.32	0.13
	Disturbance Groups	2	0.43	0.65
	Season x Disturbance Group	2	1.44	0.25
Taxa Richness	Season	1	3.28	0.08
	Disturbance Groups	2	0.11	0.89
	Season x Disturbance Group	2	3.06	0.06
Shannon Weiner Diversity	Season	1	16.15	< 0.001
	Disturbance Groups	2	1.01	0.37
	Season x Disturbance Group	2	0.35	0.71
Simpson's Evenness	Season	1	5.34	0.03
	Disturbance Groups	2	0.9	0.42
	Season x Disturbance Group	2	4.94	0.01
Hilsenhoff Biotic Index (HBI)	Season	1	4.24	0.04
	Disturbance Groups	2	8.76	< 0.001
	Season x Disturbance Group	2	1.53	0.23
Proportion of Strategist Taxa (Chironomidae, Simuliidae & Baetidae)	Season	1	32.56	< 0.001
	Disturbance Groups	2	0.75	0.48
	Season x Disturbance Group	2	1.45	0.25
	Season	1	28.98	< 0.001

Proportion of Sediment Tolerant Taxa (Oligochaete & Chironomidae)	Disturbance Groups	2	4.29	0.02
	Season x Disturbance Group	2	0.8	0.46
Proportion of FFG Filterers	Season	1	14.51	< 0.001
	Disturbance Groups	2	1.68	0.2
	Season x Disturbance Group	2	1.21	0.31
Proportion of FFG Scrapers	Season	1	0.38	0.54
	Disturbance Groups	2	11.22	< 0.001
	Season x Disturbance Group	2	0.51	0.6
Proportion of FFG Collectors	Season	1	14.14	< 0.001
	Disturbance Groups	2	0.61	0.55
	Season x Disturbance Group	2	1	0.37
Proportion of FFG Herbivores	Season	1	7.86	0.01
	Disturbance Groups	2	0.64	0.53
	Season x Disturbance Group	2	0.27	0.76
Proportion of FFG Predators	Season	1	2.81	0.1
	Disturbance Groups	2	5.54	0.01
	Season x Disturbance Group	2	0.78	0.46
Proportion of FFG Unknown	Season	1	6.84	0.01
	Disturbance Groups	2	1.45	0.25
	Season x Disturbance Group	2	0.92	0.4

Table 5: Results from Two-Way ANOVA testing influence of nine sites (listed upstream to down: Springs, Waterfall, Tonto Bench, Above Boulder Canyon, Below Boulder Canyon, Sally May, Mazatal, Above Fish Barrier, Below Fish Barrier), seasons (Spring and Summer) and their interaction on each response variables. Significant p-values at $\alpha = 0.05$ are indicated in bold.

Response Variable	Source	DF	F ratio	p value
Density	Season	1	3.26	0.08
	Site	8	2.79	0.02
	Season x Site	8	2.76	0.02
Taxa Richness	Season	1	4.44	0.04
	Site	8	1.73	0.13
	Season x Site	8	2.22	0.05
Shannon Weiner Diversity	Season	1	27.2	< 0.001
	Site	8	5.08	< 0.001
	Season x Site	8	0.81	0.6
Simpson's Evenness	Season	1	7.98	0.01
	Site	8	1.45	0.21
	Season x Site	8	5.94	< 0.001
Hilsenhoff Biotic Index (HBI)	Season	1	9.06	0.005
	Site	8	9.98	< 0.001
	Season x Site	8	5.58	< 0.001
Proportion of Strategist Taxa (Chironomidae, Simuliidae & Baetidae)	Season	1	33.85	< 0.001
	Site	8	0.97	0.48
	Season x Site	8	1.15	0.35
Proportion of Sediment Tolerant Taxa (Oligochaete & Chironomidae)	Season	1	62.61	< 0.001
	Site	8	6.49	< 0.001
	Season x Site	8	4.01	0.002
Proportion of FFG Filterers	Season	1	13.09	0.001
	Site	8	0.75	0.65
	Season x Site	8	0.89	0.54
Proportion of FFG Scrapers	Season	1	0.5	0.48
	Site	8	8.02	< 0.001
	Season x Site	8	3.19	0.01
Proportion of FFG Collectors	Season	1	15.62	< 0.001

	Site	8	0.62	0.75
	Season x Site	8	1.69	0.13
Proportion of FFG Herbivores	Season	1	6.95	0.01
	Site	8	0.57	0.8
	Season x Site	8	0.62	0.76
Proportion of FFG Predators	Season	1	3.02	0.09
	Site	8	2.68	0.02
	Season x Site	8	1.13	0.37
Proportion of FFG Unknown	Season	1	7.29	0.01
	Site	8	1.4	0.23
	Season x Site	8	1.04	0.43

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APPENDICIES

Appendix 1: Mean ± SE values of response variables for predicted disturbance groups between seasons, n = 3

Season	Spring	Summer	Spring	Summer	Spring	Summer
Disturbance Group	Least Disturbed	Least Disturbed	Moderately Disturbed	Moderately Disturbed	Most Disturbed	Most Disturbed
Density	1420 ± 390	1701 ± 1045	953 ± 322	374 ± 93	563 ± 115	975 ± 447
Taxa Richness	9.11 ± 1.24	8.78 ± 1.37	8.67 ± 0.99	9.13 ± 0.95	6.67 ± 0.90	12.22 ± 1.96
Shannon Weiner Diversity	1.23 ± 0.19	1.73 ± 0.12	1.52 ± 0.04	1.84 ± 0.11	1.34 ± 0.16	1.89 ± 0.17
Simpson's Evenness	0.25 ± 0.04	0.40 ± 0.03	0.35 ± 0.03	0.39 ± 0.03	0.33 ± 0.02	0.35 ± 0.02
Hilsenhoff Biotic Index (HBI)	5.74 ± 0.22	5.67 ± 0.22	4.13 ± 0.35	4.77 ± 0.41	4.82 ± 0.41	5.81 ± 0.20
Proportion of Strategist Taxa (Chironomidae, Simuliidae & Baetidae)	0.64 ± 0.08	0.31 ± 0.07	0.51 ± 0.05	0.35 ± 0.04	0.59 ± 0.07	0.21 ± 0.06
Proportion of Sediment Tolerant Taxa (Oligochaete & Chironomidae)	0.56 ± 0.09	0.19 ± 0.04	0.29 ± 0.05	0.08 ± 0.03	0.38 ± 0.09	0.13 ± 0.04
Proportion of FFG Filterers	.04 ± 0.03	0.21 ± 0.04	0.03 ± 0.01	0.14 ± 0.05	0.04 ± 0.02	0.09 ± 0.05
Proportion of FFG Scrapers	0.07 ± 0.03	0.07 ± 0.03	0.30 ± 0.06	0.23 ± 0.04	0.15 ± 0.05	0.13 ± 0.04
Proportion of FFG Collectors	0.75 ± 0.05	0.46 ± 0.07	0.59 ± 0.05	0.47 ± 0.06	9.66 ± 0.08	0.47 ± 0.07
Proportion of FFG Herbivores	0.01 ± 0.01	0.08 ± 0.04	0.01 ± 0.00	0.06 ± 0.03	0.00 ± 0.00	0.04 ± 0.01
Proportion of FFG Predators	0.07 ± 0.03	0.02 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.11 ± 0.03	0.08 ± 0.03
Proportion of FFG Unknown	0.07 ± 0.03	0.17 ± 0.04	0.04 ± 0.03	0.07 ± 0.03	0.05 ± 0.02	0.19 ± 0.08

Appendix 2: Mean ± SE post fire values of response variables for the first four sites upstream between seasons, n = 3.

Season	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer
Site	Springs (SP)	Springs (SP)	Waterfall (WF)	Waterfall (WF)	Tonto Bench (TB)	Tonto Bench (TB)	Above Boulder Canyon (ABC)	Above Boulder Canyon (ABC)
Density	1756.5 ± 803.5	4691.1 ± 2525.7	1314.7 ± 500.8	86.2 ± 31.1	915.9 ± 157.0	445.4 ± 163.7	553.2 ± 299.4	294.5 ± 109.6
Taxa Richness	8.33 ± 2.85	13.33 ± 1.20	7.67 ± 0.88	4.67 ± 1.20	6.33 ± 1.76	7.67 ± 1.67	8.00 ± 1.73	7.67 ± 2.33
Shannon Weiner Diversity	1.25 ± 0.23	1.84 ± 0.13	0.63 ± 0.11	1.38 ± 0.19	1.12 ± 0.32	1.40 ± 0.25	1.49 ± 0.06	1.61 ± 0.27
Simpson's Evenness	0.31 ± 0.05	0.31 ± 0.02	0.13 ± 0.02	0.51 ± 0.06	0.29 ± 0.03	0.32 ± 0.05	0.36 ± 0.05	0.43 ± 0.08
Hilsenhoff Biotic Index (HBI)	6.27 ± 0.19	5.94 ± 0.15	6.00 ± 0.02	5.71 ± 0.64	6.25 ± 0.13	6.18 ± 0.28	5.19 ± 0.64	5.19 ± 0.64
Proportion of Strategist Taxa (Chironomidae, Simuliidae & Baetidae)	0.49 ± 0.13	0.25 ± 0.05	0.88 ± 0.02	0.35 ± 0.16	0.64 ± 0.14	0.17 ± 0.10	0.57 ± 0.09	0.37 ± 0.05
Proportion of Sediment Tolerant Taxa (Oligochaete & Chironomidae)	0.51 ± 0.12	0.22 ± 0.06	0.86 ± 0.02	0.22 ± 0.08	0.64 ± 0.14	0.15 ± 0.12	0.43 ± 0.10	0.03 ± 0.02
Proportion of FFG Filterers	0.00 ± 0.00	0.21 ± 0.10	0.01 ± 0.00	0.22 ± 0.08	0.00 ± 0.00	0.17 ± 0.15	0.01 ± 0.00	0.11 ± 0.06
Proportion of FFG Scrapers	0.01 ± 0.01	0.01 ± 0.00	0.02 ± 0.01	0.05 ± 0.05	0.00 ± 0.00	0.03 ± 0.02	0.11 ± 0.10	0.33 ± 0.05
Proportion of FFG Collectors	0.76 ± 0.07	0.39 ± 0.15	0.88 ± 0.02	0.51 ± 0.14	0.86 ± 0.07	0.37 ± 0.16	0.72 ± 0.08	0.42 ± 0.07
Proportion of FFG Herbivores	0.02 ± 0.02	0.07 ± 0.04	0.00 ± 0.00	0.13 ± 0.13	0.00 ± 0.00	0.01 ± 0.01	0.00 ± 0.00	0.11 ± 0.09
Proportion of FFG Predators	0.04 ± 0.04	0.04 ± 0.02	0.04 ± 0.02	0.00 ± 0.00	0.08 ± 0.04	0.11 ± 0.07	0.02 ± 0.01	0.04 ± 0.02
Proportion of FFG Unknown	0.16 ± 0.07	0.28 ± 0.06	0.05 ± 0.02	0.09 ± 0.05	0.05 ± 0.04	0.30 ± 0.24	0.13 ± 0.06	0.00 ± 0.00

Appendix 3: Mean ± SE post fire values of response variables for the last five sites upstream between seasons, n = 3.

Season	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer	Spring	Summer
Site	Below Boulder Canyon (BBC)	Below Boulder Canyon (BBC)	Sally May (SM)	Sally May (SM)	Mazatzal (MAZ)	Mazatzal (MAZ)	Above the Fish Barrier (AFB)	Above the Fish Barrier (AFB)	Below the Fish Barrier (BFB)	Below the Fish Barrier (BFB)
Density	344.8 ± 157.8	1738.5 ± 1369.3	427.4 ± 121.3	739.9 ± 181.3	452.6 ± 134.7	492.1 ± 239.9	1188.9 ± 914.4	326.9 ± 119.6	1853.4 ± 725.6	317.9 ± 16.2
Taxa Richness	6.33 ± 1.76	13.33 ± 5.04	7.33 ± 1.76	15.67 ± 0.88	6.67 ± 1.20	10.00 ± 1.00	11.33 ± 2.40	8.33 ± 0.88	11.33 ± 1.20	10.00 ± 1.00
Shannon Weiner Diversity	1.35 ± 0.28	1.94 ± 0.22	1.56 ± 0.26	2.32 ± 0.04	1.48 ± 0.10	1.97 ± 0.06	1.80 ± 0.11	1.96 ± 0.13	1.59 ± 0.06	1.99 ± 0.08
Simpson's Evenness	0.38 ± 0.02	0.25 ± 0.04	0.38 ± 0.02	0.32 ± 0.01	0.40 ± 0.04	0.36 ± 0.01	0.33 ± 0.03	0.40 ± 0.01	0.29 ± 0.03	0.36 ± 0.01
Hilsenhoff Biotic Index (HBI)	3.56 ± 0.16	5.78 ± 0.35	4.66 ± 0.39	5.48 ± 0.37	3.89 ± 0.15	5.89 ± 0.32	4.94 ± 0.18	5.36 ± 0.29	3.30 ± 0.33	4.50 ± 0.30
Proportion of Strategist Taxa (Chironomidae, Simuliidae & Baetidae)	0.53 ± 0.17	0.32 ± 0.14	0.59 ± 0.11	0.15 ± 0.02	0.60 ± 0.03	0.29 ± 0.09	0.56 ± 0.10	0.34 ± 0.17	0.37 ± 0.07	0.39 ± 0.03
Proportion of Sediment Tolerant Taxa (Oligochaete & Chironomidae)	0.10 ± 0.03	0.15 ± 0.05	0.40 ± 0.11	0.09 ± 0.01	0.29 ± 0.04	0.17 ± 0.02	0.31 ± 0.04	0.14 ± 0.08	0.17 ± 0.05	0.03 ± 0,02
Proportion of FFG Filterers	0.05 ± 0.05	0.00 ± 0.00	0.06 ± 0.03	0.10 ± 0.04	0.05 ± 0.03	0.20 ± 0.10	0.12 ± 0.06	0.19 ± 0.06	0.05 ± 0.01	0.11 ± 0.11
Proportion of FFG Scrapers	0.29 ± 0.08	0.15 ± 0.09	0.15 ± 0.07	0.21 ± 0.05	0.32 ± 0.04	0.16 ± 0.06	0.11 ± 0.10	0.11 ± 0.06	0.46 ± 0.08	0.17 ± 0.08
Proportion of FFG Collectors	0.53 ± 0.17	0.60 ± 0.11	0.59 ± 0.11	0.45 ± 0.04	0.61 ± 0.03	0.49 ± 0.14	0.62 ± 0.11	0.48 ± 0.13	0.42 ± 0.07	0.54 ± 0.14
Proportion of FFG Herbivores	0.00 ± 0.00	0.04 ± 0.01	0.00 ± 0.00	0.05 ± 0.03	0.00 ± 0.00	0.04 ± 0.02	0.00 ± 0.00	0.03 ± 0.03	0.02 ± 0.01	0.00 ± 0.00

Proportion of FFG Predators	0.07 ± 0.06	0.04 ± 0.03	0.17 ± 0.01	0.08 ± 0.03	0.01 ± 0.01	0.03 ± 0.01	0.14 ± 0.05	0.03 ± 0.03	0.05 ± 0.02	0.02 ± 0.01
Proportion of FFG Unknown	0.05 ± 0.05	0.17 ± 0.04	0.03 ± 0.02	0.11 ± 0.01	0.00 ± 0.00	0.08 ± 0.04	0.00 ± 0.00	0.14 ± 0.09	0.00 ± 0.00	0.17 ± 0.06

Appendix 4: Mean ± SE values of response variables for seasons, n = 6.

Response Variable	Spring	Summer
Density	978 ± 179	1041 ± 394
Taxa Richness	8.15 ± 0.62	10.08 ± 0.9
Shannon Weiner Diversity	1.36 ± 0.08	1.82 ± 0.08
Simpson's Evenness	0.32 ± 0.02	0.37 ± 0.02
Hilsenhoff Biotic Index (HBI)	4.9 ± 0.23	5.44 ± 0.18
Proportion of Strategist Taxa (Chironomidae, Simuliidae & Baetidae)	0.58 ± 0.04	0.29 ± 0.03
Proportion of Sediment Tolerant Taxa (Oligochaete & Chironomidae)	0.41 ± 0.05	0.14 ± 0.02
Proportion of FFG Filterers	0.04 ± 0.01	0.15 ± 0.03
Proportion of FFG Scrapers	0.17 ± 0.03	0.14 ± 0.02
Proportion of FFG Collectors	0.67 ± 0.04	0.47 ± 0.04
Proportion of FFG Herbivores	0.01 ± 0.003	0.06 ± 0.02
Proportion of FFG Predators	0.07 ± 0.01	0.04 ± 0.01
Proportion of FFG Unknown	0.05 ± 0.02	0.15 ± 0.03