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Research article

Short-term effects of wildfire on high elevation stream-riparian food webs

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Understanding how wildfires affect food web structure and function remains an important challenge, especially at high elevations that historically have burned infrequently. In particular, fires may alter the magnitude of reciprocal cross-ecosystem subsidies, leading to indirect effects on aquatic and terrestrial consumers. We quantified characteristics of high-elevation (2500–3000 m) stream-riparian food webs at 10 locations in the southern Rocky Mountains less than one year following high-intensity, stand-replacing wildfires. Using a paired 'burned—unburned' stream survey design, we assessed benthic periphyton, aquatic macroinvertebrate community structure, trout population characteristics, trout stomach contents, inputs and emergence of insects to and from streams, and abundance of predatory riparian spiders that consume aquatic insects. Benthic macroinvertebrate density, flux of emerging aquatic insects, and riparian spider abundances were lower at burned sites. Fluxes of insect inputs entering the stream did not differ with burn status, despite the loss of riparian vegetation due to fire. Trout were somewhat less abundant, but larger on average at burned sites and did not differ in body condition. These results suggest mortality of smaller trout from fire disturbance and/or recolonization of burned sites by larger individuals. Trout showed subtle changes in diet composition with burn status, but no change in biomass or number of prey consumed. In general, burned sites showed greater variation in community characteristics than unburned sites, which may reflect differences in the timing and magnitude of post-fire flooding, erosion, and scouring of the stream bed. Taken together, our results suggest that short-term effects of fire disturbance strongly altered some food web responses, but others appeared relatively resilient, which is notable given the high severity of the wildfires in the study area.

Keywords: food web, macroinvertebrates, predator–prey interaction, reciprocal subsidy, wildfire

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Introduction

Recent increases in the frequency and extent of wildfires highlight the growing importance of understanding how fires affect food web structure and functioning (Abatzoglou and Williams 2016, McLauchlan et al. 2020). In some cases, wildfires strongly alter community composition and the magnitude of energy and nutrient fluxes through ecosystems, leading to successional changes lasting for decades (McLauchlan et al. 2020). In other situations, however, communities may show greater resistance (i.e. the ability to withstand wildfire) or resilience (i.e. rapid rate of recovery post-fire) (Donohue et al. 2016). Whether communities show large changes due to fire has been linked to characteristics of the fire disturbance itself (e.g. frequency, severity, and extent) and of the ecological community, including species traits and evolutionary history with fire (Turner et al. 1998).

Freshwater streams often show a number of related changes following wildfires, many of which are initially due to post-fire flooding, ash inputs, and debris flows that can cause mortality of aquatic organisms (Dunham et al. 2003, Minshall 2003). The time-scale of subsequent aquatic community changes after disturbance depends in part on dispersal ability, life history, reproductive potential, and the availability of refugia from disturbance (Van Looy et al. 2019, Jager et al. 2021). On medium time scales (e.g. 2–10 years post-fire), increased light and water temperatures, as well as nutrient inputs from the terrestrial environment, can collectively lead to positive bottom–up effects on stream productivity (Silins et al. 2014). Although these general expectations have received considerable support (Bixby et al. 2015), the specific time-scales of ecological changes can be challenging to predict, and are likely to vary with environmental context (Verkaik et al. 2015). As fires increasingly appear in areas that previously have burned infrequently, such as high elevation (i.e. subalpine) temperate forests (Sibold et al. 2006, Alizadeh et al. 2021), there is potential for post-fire changes that may diverge from expectations based on lower elevation streams. For instance, the steep gradients at high elevations are expected to increase post-fire erosion and decrease stream bed stability, particularly in areas with significant summer precipitation. Additionally, the lower temperatures, seasonally variable flow regimes (i.e. high peak flows during spring runoff) and generally more challenging environmental conditions at high elevation may prolong population recovery of stream organisms after disturbance (Jager et al. 2021). As a result, high elevation streams may be particularly prone to wildfire disturbance relative to lower elevation streams.

While considerable research has focused on shifts in stream community composition following wildfires, less work has quantified changes in food web functioning, including trophic interactions and resource subsidies between water and land. Stream and riparian habitats are intimately connected via the infall of terrestrial invertebrates into the stream and the emergence of aquatic insects to land (Nakano and Murakami 2001, Baxter et al. 2005). Reciprocal subsidies can be utilized by consumers in both environments, sometimes resulting in important population and community effects. A handful of studies have evaluated how wildfire disturbance affects stream–riparian subsidies, focusing on the mid-term (2–5 years) changes in emergence of aquatic insects to the terrestrial environment (Mellon et al. 2008, Malison and Baxter 2010, Harris et al. 2018). These studies found either no change or increased export of aquatic insects after high severity fires, likely owing to bottom–up effects on stream production after post-fire disturbance has subsided. Decreased inputs of terrestrial subsidies, including leaf litter and terrestrial invertebrates, five years after fire have also been observed at some of the same sites (Jackson et al. 2012). Studies that have examined both imports and exports of insects to and from streams after wildfires, and linked this to characteristics of both aquatic and riparian consumer populations, are relatively rare. In many mountain streams, trout and riparian spiders (Tetragnathidae) utilize cross-ecosystem insect subsidies (Benjamin et al. 2011), making them useful indicators of changes in food web functioning that may be affected by wildfires and post-fire disturbances (Koetsier et al. 2007, Jackson and Sullivan 2015). Additionally, while many post-fire studies on stream community ecology have evaluated mid-term effects, fewer have quantified change on shorter time scales (e.g. months post-fire). This period shortly after fire may be critical to setting the trajectory of later ecological change because it is when the surrounding terrestrial landscape and the stream environment are most susceptible to post-fire disturbance such as erosion and flooding.

Using a paired 'burned–unburned' stream survey design, we quantified aspects of stream–riparian food webs in the southern Rocky Mountains in Colorado less than one year following high intensity, stand replacing fires that burned in 2020. Several aspects of the focal wildfires were unique, including that they burned until late in the season (December), at high elevations (up to 4000 m), were exceptionally large, including the two largest fires in Colorado state history (>78 000 ha each), and although of mixed severity, produced large, contiguous patches of high severity burn. We focused on analyzing benthic macroinvertebrate composition, resource subsidies of insects between the stream and riparian habitats, trout population characteristics, trout diets, and abundance of riparian spiders that consume aquatic insects.

We tested several key predictions about the effects of wildfire on high elevation stream–riparian food webs. While prior studies indicate that in some cases population recovery of stream invertebrates is rapid, we predicted that the environmental conditions at high elevation – including steep gradients, low temperatures, and seasonal stream flow regimes – would prolong the recovery process, and thus invertebrates may have lower abundance, biomass, and richness at burned sites (Minshall 2003). Similarly, we expected lower abundance of trout at burned sites due to mortality from disturbance, including post-fire flooding and channel destabilization (Dunham et al. 2003). For both fish and invertebrates, we expected that population recovery may be underway, but incomplete at the time of our surveys less than one year after fire. If macroinvertebrates had not yet fully recovered, we predicted reduced emergence of invertebrates at burned sites, potentially causing indirect reductions in riparian spiders that consume aquatic insects (Kato et al. 2003). Depending on the timing of recovery of riparian habitats, we further expected to see a reduced magnitude of terrestrial insect subsidies entering the stream at the burned sites because riparian vegetation structure has been correlated with inputs of terrestrial insects to streams (Wipfli 1997, Kawaguchi and Nakano 2001).

Material and methods

Stream surveys

We surveyed five pairs of streams in late July and August of 2021 in the northern Colorado Rockies within the Arapaho and Roosevelt National Forests (Fig. 1a). Three of the burned sites were within the perimeter of the Cameron Peak Fire, one was within the East Troublesome Fire, and one was within the Williams Fork Fire (see the Supporting information for characteristics of the three fires, and Fig. 1b for site images). Each burned site was paired with an adjacent unburned site outside of the fire perimeter. At each site, we calculated the percentage of upstream watershed area that had been burned (Supporting information). We also visually estimated local tree mortality along the riparian corridor (% of trees killed by fire). To characterize the stream environment, we measured stream widths, depths, discharge, chlorophyll a from periphyton, canopy cover, adjacent burn severity, water chemistry (dissolved oxygen, pH, water temperature, conductivity), and turbidity at each site at the time of the survey (see the Supporting information for additional details on environmental variables measured). We attempted to select sites that were similar in elevation, aspect, stream size and valley classification (Carlson 2009) between the burned and unburned pairs. To test this assumption, we assessed whether the burned and unburned sites differed in elevation, wetted width, maximum depth, or discharge using paired t-tests. There were no significant difference in these environmental variables (all $p > 0.05$; Supporting information for mean values). Trout species composition at all sites included nonnative brook trout *Salvelinus fontinalis* and/or brown trout *Salmo trutta*, except for one site that supported cutthroat trout *Oncorhynchus clarkii* (see the Supporting information for species compositions).

Macroinvertebrates were sampled using benthic Surber samplers, emergence traps and pan traps. Five Surber samples (0.09 m^2 in area, 248 μm mesh each) were evenly spaced along each reach in approximately the center of the stream, focusing on riffle habitat. We deployed three emergence traps and three pan traps within each reach on the same day as surveys were conducted. Traps of both types were collected after approximately 70 h (range = 66–72 h). Emergence traps (Cadmus et al. 2016) were 0.37 m^2 in area (see the Supporting information for images of emergence and pan traps) and incorporated an opening at the top that directed insects into a Nalgene bottle of 80% ethanol. Emergence traps were situated in relatively calm water, typically below a riffle. For pan traps, we used shallow plastic bins 0.30 m^2 in area supported on frames of PVC plastic tubing (Supporting information).

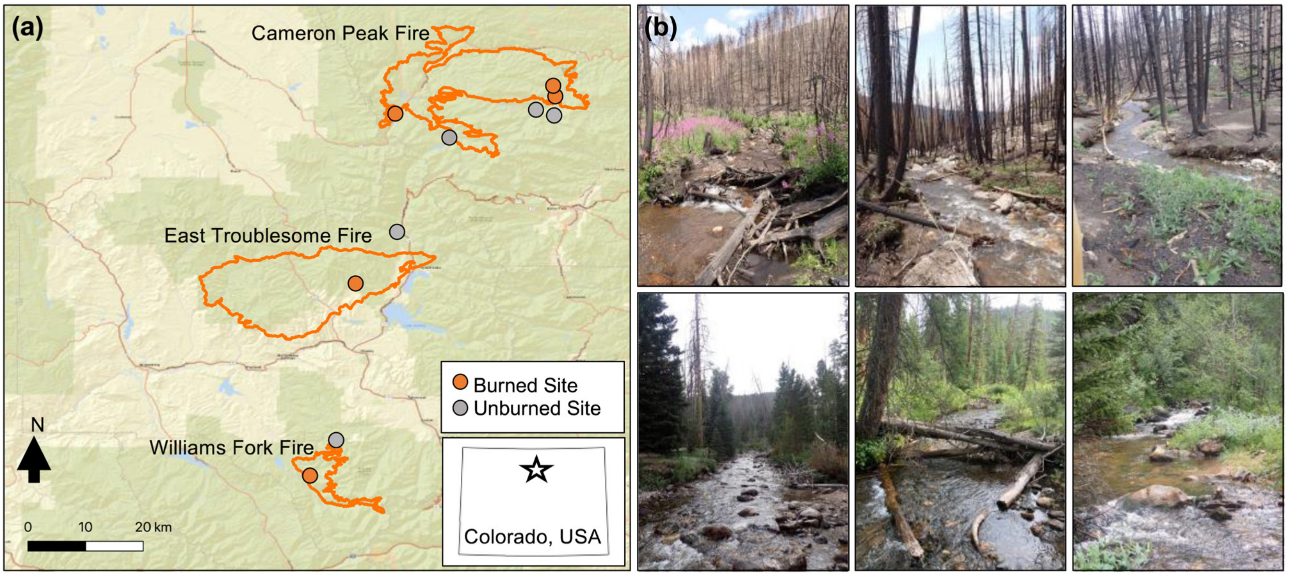

Figure 1. The study location showing the paired stream sites and the fire perimeters of the Cameron Peak, East Troublesome and Williams Fork fires (a). The bottom right inset on the map shows the location of the study area within Colorado, USA. The panels at right show images of three example pairs of stream reaches, with burned sites on the top row and their unburned pair on the bottom row (b). From top left to bottom right, the sites are Trail Creek, Kinney Creek, Fish Creek, Bowen Gulch, Keyser Creek and Pennock Creek. See the Supporting information for additional images of the survey sites showing burn severity and stream characteristics.

Pan traps were situated in shallow water at the edge of the streams and were filled with stream water and approximately 5 ml of unscented dish soap. Insects were removed from pan traps using a handheld dipnet (750 µm mesh) and preserved in 80% ethanol.

To survey riparian spiders, we followed methods described in Benjamin et al. (2011). Spiders were surveyed along a 50 m reach that was undisturbed by electrofishing, either immediately upstream or downstream of the electroshocking survey reach. Because the focal spiders are nocturnal, spider surveys were initiated at night after 21:00 h. Two observers wearing headlamps, one on each side of the stream, recorded all visible spiders within approximately 1 m of the wetted stream edge and up to 2.5 m in height. Based on their morphology, spiders were identified as Tetragnathidae, Araneidae, or 'other' for individuals that could not be identified (<2% of all spiders; Supporting information). Prior studies indicated that detection probabilities using these survey methods were > 90% (Benjamin et al. 2011). Because spider abundances may be related to habitat availability for web-building, we also quantified the density of branches along each stream reach (focusing on branches < 5 cm diameter and > 50 cm in length). Branch density was estimated in categories (0, 1–5, 6–25, 26–50, >50 branches) for every 2 m along both sides of the 50 m reach (Benjamin et al. 2011). We used the midpoint of each category as the estimated branch density. For the highest branch density category, we used 75 as the midpoint. Branch density data for a single site (South Fork Poudre) were lost, resulting in a comparison between four unburned and five burned sites.

We quantified trout relative abundance, population size structure, body condition and stomach contents. At each site, we conducted a single-pass survey using a backpack electroshocker within a designated 50 m stream reach. The selected reaches were composed primarily of riffle and run habitats, which helped standardize habitat conditions between sites (habitat images in the Supporting information). All trout caught were anesthetized with Aqui-S, nonlethally lavaged for stomach contents, measured for total length (nearest mm) and weight (nearest 0.1 g), and then released after recovery from anesthesia. Fish were lavaged using either a laboratory wash bottle with an affixed plastic straw (for larger fish) or a 60 ml syringe with a blunt 18 gauge needle (for smaller fish). Fish stomach contents were preserved in 80% ethanol until processing in the laboratory. At some sites, we collected fewer than three trout in the designated reach, so we continued electroshocking upstream and downstream of the reach until we obtained 20–30 trout for diet analyses (mean = 27; Supporting information). We calculated trout relative abundance within each reach as the number of fish caught per minute of the electroshocker running. The number of people electroshocking (n = 4) and number of backpack electroshockers (n = 1) were standardized within the reach at each site. At one site (Corral Creek), problems with the electroshocker affected shocking efficiency, so we omitted this site from estimates of trout relative abundance but included it for all other analyses.

Sample processing

Macroinvertebrates from Surber samples were identified to family, while macroinvertebrates from trout stomach contents, emergence traps, and pan traps were identified to either family or order (Ward et al. 2002, Merritt et al. 2008). Macroinvertebrates from trout stomach contents, emergence traps, and pan traps were also assigned as either 'aquatic', indicating they have one or more aquatic life stages, or 'terrestrial', indicating they have no aquatic life stage. Invertebrates identified to order generally included adult life stages of certain taxa (e.g. Diptera) and invertebrates from trout stomachs that were partially digested and had lost key features (lists of taxa and taxonomic resolution in the Supporting information). A subset of 10 intact invertebrates of each taxon from each sample were measured for body length to the nearest 0.5 mm. We then used published length-to-mass regressions to estimate dry biomass for individual invertebrates (Benke et al. 1999, Sabo et al. 2002), which was then summed for each Surber to obtain biomass per unit area.

Analyses

We used a categorical burn status variable ('burned' or 'unburned') as the main predictor in analyses. This variable described local reach-scale burn severity and was well-correlated with percent of upstream watershed burned (Supporting information). For responses that involved comparison of a mean value between burned and unburned sites we used either paired t-tests (for response variables of paired sites when sample sizes were equal) or Welch's t-tests (when sample sizes were unequal and variance differed between groups; used only for fish relative abundance and branch density). When response variables included repeated measurements within a site, we used linear mixed effects models (LMEs) or generalized linear mixed effects models (GLMMs) with a random intercept term for site identity (Zuur et al. 2009). To analyze trout body condition, we calculated residuals from a linear regression of log-body mass (grams) against log-body length (mm) using fish from all sites. Residuals from this regression were used as the response variable to evaluate effects of burn status on body condition. To visualize differences in the composition of macroinvertebrates in benthic samples and in trout stomach contents, we used non-metric multidimensional scaling (NMDS) followed by permutational multivariate analysis of variance (PERMANOVA) with Bray–Curtis dissimilarity on abundance data, using the *adonis* function in the R package 'vegan' (www.r-project.org, Oksanen et al. 2013). For both types of data, we included burn status and site identity as predictor variables in the PERMANOVA, using either Surber samples or individual trout as replicates. All analyses were conducted in R ver. 4.2.1 (www.r-project.org).

Results

Burned and unburned sites showed significant differences in some environmental variables, but not all. At burned sites, 100% of the riparian trees along the survey reach were killed by fire, while no tree mortality from fire was observed at the unburned sites (Supporting information). The percentage of upstream watershed area burned averaged 83% at the burned sites, compared to 9% at the unburned sites (Supporting information). Conductivity was higher on average at the burned sites (mean = 57 μS cm^{-1}) compared to the unburned sites (mean = 32 μS cm^{-1}) (paired t-test, t = 3.45, p = 0.03). Turbidity was also ~ 2× higher at burned sites (mean = 6.5 NTU) relative to the unburned sites (mean = 2.9 NTU), but the difference was not statistically significant (paired t-test, t = 2.00, p = 0.11). Other water chemistry variables (pH, dissolved oxygen, water temperature) and chlorophyll-a from periphyton were relatively similar across burn status on the date of the surveys (paired t-tests, all $p > 0.05$; Supporting information).

Burned and unburned sites showed subtle differences in some aspects of benthic macroinvertebrate community structure. Total macroinvertebrate density was 2× higher at unburned compared to burned sites (LME, t = 2.57, p = 0.03; Fig. 2a). Five of six Orders showed lower mean densities at the burned sites (including Coleoptera, Diptera, Ephemeroptera, Oligochaeta, Plecoptera and Trichoptera), although these taxon-specific differences were not statistically significant due to high variation at the site level (Supporting information). Macroinvertebrate biomass was similar across the burned and unburned sites (LME, t = 0.79, p = 0.45; Fig 2b). Taxonomic richness averaged 19.8 families at burned sites (±2.03 SE) and 23.8 families (±0.97 SE) at unburned sites and this difference was not statistically significant (Poisson GLMM, z = 1.66, p = 0.10; Fig. 2c). Burned sites showed greater heterogeneity in composition in ordination space (Supporting information). Overall macroinvertebrate composition was influenced by burn status (PERMANOVA, $p < 0.001$, $r^2 = 0.09$) as well as individual site identity (PERMANOVA , $p < 0.001$, $r^2 = 0.48$). Differences in composition were caused in part by reductions in Coleoptera, Diptera, Ephemeroptera, Oligochaeta and Plecoptera at burned sites, particularly at Fish Creek and Little Beaver Creek, which had the most divergent communities (Supporting information).

Burn status had variable effects on insect fluxes, but strongly influenced abundance of riparian consumers. No difference could be detected in inputs of either aquatic insects (LME, t = −0.63, p = 0.54) or terrestrial insects (LME, t = 0.24, p = 0.81) into the streams due to burn status (Fig. 2d). Fluxes of emergent aquatic insects out of the stream averaged 0.91 mg m^{-2} h^{-1} (±0.30 SE) at burned sites, compared to 2.2 mg m^{-2} h^{-1} (±0.68 SE) for unburned sites (LME, z = 1.72, p = 0.12; Fig. 2d). Riparian spider abundance at unburned sites was 4.6 times the abundance at burned sites (paired t-test, t = −3.45, p = 0.02; Fig. 2e). The difference in spider abundance was caused mostly by Tetragnathidae spiders. Araneidae spiders

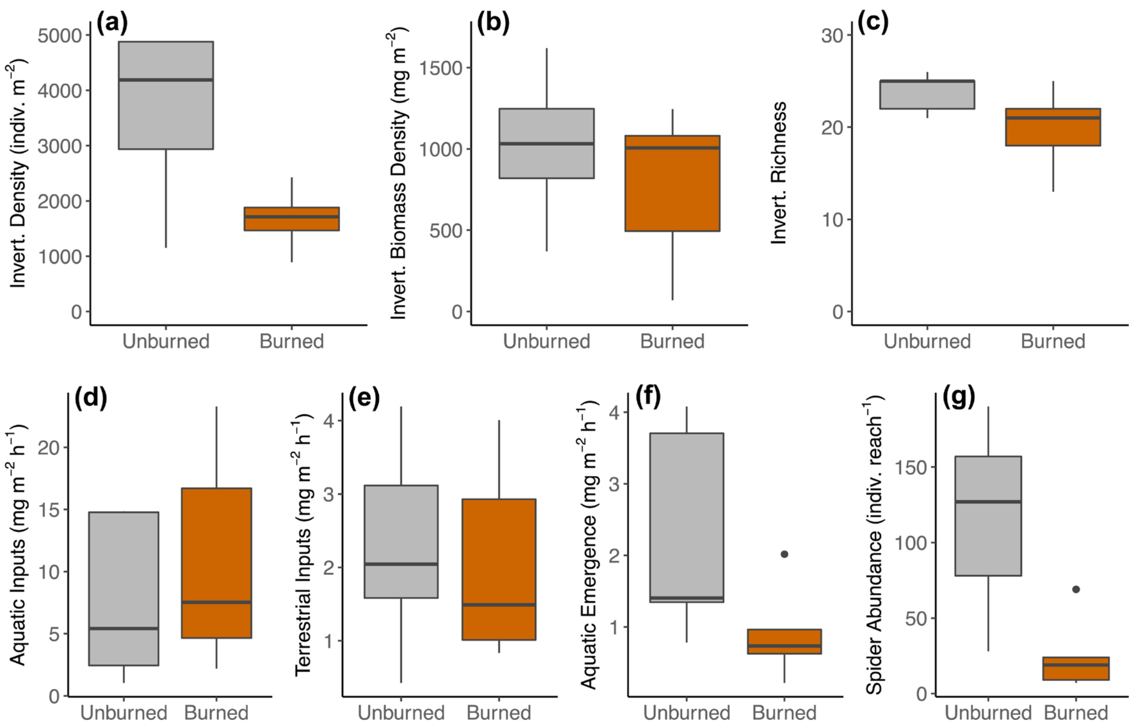

Figure 2. Benthic macroinvertebrate density (a), biomass (b), and taxonomic richness (c) at burned and unburned sites. Macroinvertebrates were identified to the level of family for richness estimates. The bottom left panel shows fluxes of aquatic insects entering the stream (d), followed by terrestrial insects entering the stream (e), and aquatic insects emerging out of the stream (f). Insect fluxes are expressed as milligrams per square meter of stream surface per hour. Note the differences in y-axes. The bottom right panel shows abundances of riparian spiders per 50 m stream reach that was surveyed (g). On all box plots, horizontal lines show the median, the box shows the interquartile range, and the whiskers are the minimum and maximum values. Outliers are shown as points.

showed the same pattern but with much lower overall abundances (Supporting information). Branch densities per 50 m reach averaged 636 at the unburned sites and 275 at the burned sites (Welch's t-test, $t = -2.18$, $p = 0.09$).

Mean trout relative abundance was over 3× higher at burned sites compared to unburned sites but this difference was not statistically significant (Welch's t-test, $t = 2.25$, $p = 0.10$; Fig 3a). Trout were significantly larger, on average, at burned sites (mean body length = 184 mm) compared to unburned sites (mean = 134 mm) (LME, $t = -3.31$, $p = 0.01$). Burned sites had few juvenile fish below 120 mm, which were relatively common at the unburned sites (Fig. 3b). Trout body condition did not differ significantly between the burned and unburned sites (LME, $t = -2.10$, $p = 0.07$), although the mean (log) body mass residuals were positive at the burned sites (mean = 0.04) and negative at the unburned sites (mean = −0.03) (Supporting information). At burned sites, there were slightly higher proportions of Diptera and Oligochaeta in trout stomach contents (Fig. 4, Supporting information). Both burn status (PERMANOVA , $p < 0.001$, $r^2 = 0.02$) and site identity (PERMANOVA, $p < 0.001$, $r^2 = 0.14$) had significant effects on overall diet composition, with site identity explaining more variation. There was not a significant difference in the number of prey per fish between burned and unburned sites (LME, $t = -1.03$, $p = 0.33$) and total prey biomass per fish was also similar between burned and unburned sites (LME, $t = -1.54$, $p = 0.16$). A comparable percentage of prey from trout stomachs were terrestrial in origin at unburned (18.2%) and burned sites (18.6%). On average, trout contained 48 diets items (min = 1, max = 728) and we identified 58 unique prey taxa, most to family (Supporting information).

Discussion

Prey resource subsidies connecting adjacent ecosystems have been increasingly recognized to play important roles in structure and functioning of recipient food webs (Polis et al. 2004). In many ecosystems, there is relatively little understanding of how ecosystem subsidies will be affected by global change (Larsen et al. 2016). This is especially true for high elevation ecosystems, which may be particularly susceptible to disturbances following wildfires. In the present study, we quantified aspects of stream-riparian food webs in relation to wildfire disturbance, including subsidies of insects between water and land. Our findings suggest that while some components of the food web were strongly altered in the short-term (e.g. riparian spiders), other responses showed greater resistance or resilience on the timescale of our surveys after fire (e.g. composition of prey consumed by individual trout). In general, many of the observed differences between the burned and unburned sites were consistent with expected short-term effects of post-fire flooding, erosion, and channel instability. These findings differ from prior work on wildfire and stream ecosystem subsidies, which has generally found positive bottom–up effects of fire on stream productivity, but on longer post-fire time-scales than our surveys (Mellon et al. 2008, Malison and Baxter 2010, Harris et al. 2018). Our findings in relation to this previous work may reflect both the timing of flooding disturbance at our sites, as well as unique characteristics of the high-elevation streams in our study.

At most or possibly all of the burned sites in our study there was channel-mobilizing flooding during the summer of 2021, which likely caused ongoing disturbances that led to faunal losses not long before our surveys. Post-fire flooding and erosion are able to eliminate or greatly reduce macroinvertebrate densities (Minshall 2003, Tuckett and Koetsier 2018). Some macroinvertebrate taxa (e.g. Ephemeroptera, Diptera), are expected to recover fastest after disturbance, likely owing to their rapid dispersal and early maturity (Anderson 1992, Minshall et al. 2001, Vieira et al. 2004). If macroinvertebrate populations had recovered, we would have expected to see higher densities of these taxa at burned sites, and yet we found no evidence for increases in Diptera or Ephemeroptera. Interestingly, unlike total density, macroinvertebrate biomass was not different between burned and unburned sites, potentially because chironomid midges, which have a relatively small individual biomass compared to many other taxa, showed the greatest reduction in density

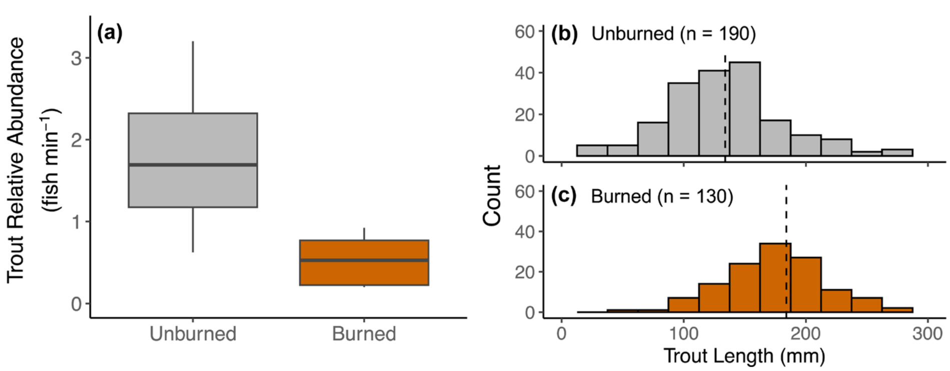

Figure 3. Relative abundance of trout (fish caught per minute of electroshocking) at burned and unburned sites (a). Horizontal lines show the median, the box shows the interquartile range, and the whiskers are the minimum and maximum values. To the right are histograms showing size structure of trout at the unburned (b) and burned (c) sites. Sample sizes of trout are indicated at the top of both histograms.

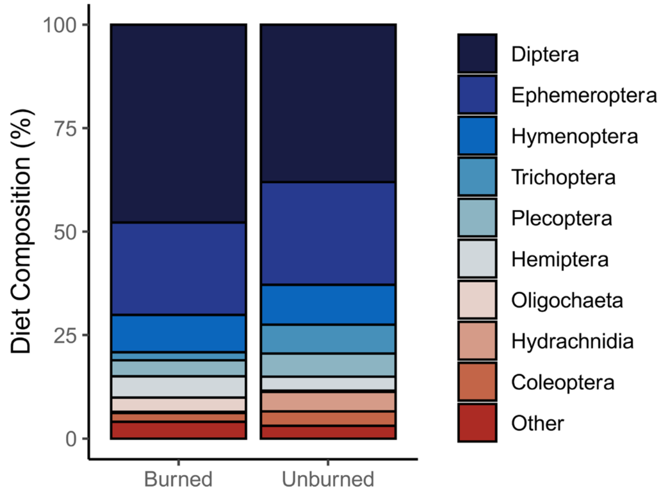

Figure 4. Composition of diet items observed in the stomachs of trout at burned and unburned sites. In addition the nine orders in the legend, the 'Other' category contains 49 additional rare invertebrate taxa, most identified at the family level. See the Supporting information for a complete list of taxa observed in trout stomach contents.

(and were the most abundant taxa numerically in samples). The high intensity of the fires in our surveys, coupled with the relatively high elevations and steep slopes, may lead to a prolonged recovery period relative to lower-elevation areas and lower intensity fires. Floods and associated movement of debris and ash were documented in late winter after the fires (e.g. Little Beaver Creek; White et al. 2022) and were particularly pronounced in late summer of 2021 when we observed flooding events at Little Beaver Creek and at Kinney Creek. Isolated high-intensity flooding events have continued into summer 2022, two years post-fire. These ongoing disturbances are likely to create a mosaic of stream conditions over space, leading to heterogeneity in the relative state of recovery or disturbance of stream communities within specific burned watersheds (Matthaei and Townsend 2000).

We found some evidence for reduced relative abundance of trout and shifts in trout size structure at the burned sites. At unburned sites, trout relative abundance was approximately 3x the values at unburned sites. This difference was not statistically significant in our analyses, which may stem from the modest sample size of sites rather than lack of a biologically meaningful difference. Evidence for this viewpoint comes from additional surveys conducted in Rocky Mountain National Park in summer of 2021 within the Cameron Peak Fire scar, which indicated that trout abundance declined compared to pre-fire surveys (Kanno et al. unpubl.). The reductions in trout relative abundance in our study were most notable for small fish, including young-of-year, which were largely absent from the burned sites, but abundant at most of the unburned sites. This pattern may be the result of 1) large fish being more resistant to fire-associated disturbance and persisting after the fires, 2) larger fish re-colonizing first from refugia outside the burned reaches, or both mechanisms. Previous research indicates that larger fish are more likely to move long distances than smaller fish (Gowan and Fausch 1996), suggesting that the shift towards larger fish was unlikely to be caused by emigration of small fish from the study reaches. When trout populations of conservation concern are limited to headwaters with steep gradients and confined valleys, post-fire debris flows can pose a significant conservation threat (Sedell et al. 2015). Die-offs of salmonids after fire and flooding disturbance have been reported in other regions, although population recovery is typically rapid if unimpacted refugia exist (Propst and Stefferud 1997, Rieman et al. 1997, Roghair et al. 2002, Dunham et al. 2003). If habitats are fragmented, however, then fish recovery may be slow, emphasizing the importance of connected metapopulations (Dunham et al. 2003, Jager et al. 2021). On longer timescales after fire, trout in streams that experienced wildfire may have faster growth rates and reach larger sizes due to increased food availability from bottom–up effects and warmer temperatures (Silins et al. 2014, Rosenberger et al. 2015). Future monitoring will be needed to determine when and if such effects occur in our study region.

We observed subtle differences in trout diet composition, but the number of prey items, the total prey biomass per fish, and the proportion of aquatic versus terrestrial prey were not different between burned and unburned sites. Given the reduction in benthic macroinvertebrate density, it is notable that trout did not appear to be consuming fewer prey items at the burned sites. This may be related to the fact that trout relative abundance was also lower at burned sites, leading to comparable (or even greater) food availability per individual fish. Body condition did not differ with burn status, suggesting that trout at burned sites were consuming comparable amounts of prey to unburned sites. The similar proportions of aquatic versus terrestrial prey in trout stomach contents at burned and unburned sites is also surprising given the total loss of tree canopy cover and the strong reduction in riparian vegetation at the burned sites. On longer time scales (five years post-fire), previous studies have found fewer terrestrial and more aquatic prey consumed by trout at burned sites (Koetsier et al. 2007). Inputs of terrestrial prey are generally correlated with riparian vegetation structure (Wipfli 1997, Kawaguchi and Nakano 2001, Rosenberger et al. 2011). At the time of our surveys, the riparian vegetation at the burned sites was, in some cases, nearly completely absent (Supporting information). Although our sampling of insect fluxes was relatively limited in time and space, we did not find conclusive evidence for differences in terrestrial insect inputs at the burned and unburned sites. We also did not find evidence for differences in the proportion of terrestrial prey in trout stomachs. It is possible that there was rapid recovery of terrestrial insect populations after fire, or alternatively, that additional sampling would have allowed us to detect a difference. Furthermore, terrestrial insects may come from longer distances away from the stream (e.g. unburned areas) and trout may also selectively prey on terrestrials (Saunders and Fausch 2018). One terrestrial prey subsidy that was abundant in trout stomachs at the burned sites were terrestrial earthworms, which likely respond differently to fire than terrestrial insects. This prey type may enter streams in high numbers at burned sites due to increased erosion and runoff, particularly after rain events.

The reduction in riparian spider densities at burned sites may have been caused by more than one mechanism. Riparian tetragnathid spider densities are positively correlated with the magnitude of aquatic insect emergence at a stream (Kato et al. 2003, Benjamin et al. 2011). This led us to hypothesize that reductions in insect emergence from fire disturbance could cause reductions in riparian spider abundance. It is also possible that direct effects of the fires on spider mortality or indirect effects associated with changes in habitat underlie the differences in spider numbers between burned and unburned sites. The burned sites had abundant standing dead trees and shrubs, which presumably provided ample spider habitat. Dead trees in or along the stream tended to have the highest concentrations of spiders at the unburned sites, suggesting that living vegetation is not required for web-building. If branch habitat was not a limiting factor, it may have been the rate of spider re-colonization after mortality from fires that led to reduced spider abundances. Previous research has found that araneid spiders along temperate streams in northern Japan consume largely terrestrial prey, whereas tetragnathid spiders consume mainly aquatic prey (Kato et al. 2003). In our study, both tetragnathid and araneid spiders showed lower abundances at the burned sites. If the two taxa consume different prey, this result may suggest a colonization or habitat-related mechanism could underlie the observed pattern. We did not assess prey composition of spiders, however, to test this idea. A previous study on tetragnathid spiders from California found no difference in abundance at burned and unburned sites, with fires having burned between 2 and 15 years before the surveys (Jackson and Sullivan 2015). In northern Idaho streams, however, spider densities increased 5–6 years after severe fire, in association with increases in insect emergence (Malison and Baxter 2010). These findings suggest that spider abundances may increase over time at the burned sites in our study system, particularly as benthic invertebrates fully recover, potentially reversing the pattern we observed less than one year after the fires.

Our field survey design had a few limitations that should be considered in interpreting the results. First, the time-scale of our surveys limits inferences to short-term effects of fire disturbance (less than one-year post-fire). Several mechanisms by which fire can alter stream ecosystems require longer time scales to become evident, including positive bottom–up effects caused by increases in light and nutrients (Silins et al. 2014) and increased input of wood as dead trees fall and enter the steam (Vaz et al. 2015). Surveys conducted in additional years following the fires will be valuable to understand how the initial patterns reported here change over time. Second, our fish surveys were conducted using single-pass electroshock surveys, which can correlate strongly with abundance estimates from multi-pass electroshocking when capture probabilities are high (Hanks et al. 2018). Although multipass methods or mark–recapture would allow more precise estimates of population sizes, we have no evidence that capture probabilities were lower at the burned sites, making it unlikely that the patterns in fish abundance were due to methodological biases alone. Third, surveys limited to one time-point over the summer may have affected our ability to detect effects of wildfire for certain responses. In particular, the timing of insect emergence is sensitive to variation in stream temperature, which could lead to shifts in insect phenology across burned and unburned sites. Additional measurements of insect fluxes at multiple time points over summer and fall, and more replicates over space within the stream reach, would be especially useful in this regard.

Moving forward, it will be informative to survey the same sites over longer time-scales (e.g. 5–10 years post-fire) to document how the responses measured here change with recovery of the terrestrial landscape. As sediments stabilize and flooding events subside, we expect that the increased light availability and nutrients will lead to enhanced benthic primary and secondary production, possibly reversing many of the trends measured one year after fires. However, the timescale of stream community changes and the persistence of additional disturbances into the future is uncertain. The dynamics of disturbance in high-elevation streams after fire may range from a single pulse disturbance event to a series of chronic disturbances due to repeated flooding or debris flows. In some cases, a legacy of fire effects on stream–riparian ecosystems could persist for decades after fire (Minshall 2003). The resulting variation in food web- and ecosystem properties, over both space and time, can generate some desirable outcomes, possibly leading to enhanced beta diversity (i.e. the 'pyrodiversity begets biodiversty hypothesis'; Jones and Tingley 2022). On the other hand, conservation threats to small, isolated populations in fragmented habitats (Dunham et al. 2003) and alterations to ecosystem services (e.g. water provisioning) make fires a growing management challenge. While knowledge of fire effects on food web structure and functioning has grown considerably (McLauchlan et al. 2020), changes in land management and anthropogenic climate change are resulting in alterations to fire regimes, making it important to further quantify effects of fire on food web functioning across diverse ecosystems. Our results contribute towards this aim by documenting short-term responses of high elevation stream–riparian food web structure and function to fire disturbance.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mcvdnck5b (Preston et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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