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Effects of Wildfire on Interactions Among Nematode Parasites, Mayfly Hosts and Trout Predators

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ABSTRACT

1. Wildfire activity is increasing globally, highlighting the need to understand how fire disturbance affects species interactions. In particular, few studies have examined how fire influences interactions among parasites, hosts and predators in freshwater streams.
2. We characterised host–parasite and parasite–predator interactions involving nematode parasites (Family Mermithidae), mayfly hosts (Order Ephemeroptera) and trout predators (*Salvelinus fontinalis*, *Salmo trutta* and *Oncorhynchus clarkii*) at 8 burned and 8 unburned stream sites in the southern Rocky Mountains for 2 years following severe wildfires.
3. Mayfly density, infection probability, and density of infected mayflies (infected mayflies/m²) were all lower at burned sites 1 year after fire but returned to levels similar to unburned sites after 2 years. Density of infected mayflies increased with overall mayfly density; however, infection prevalence (%) ranged from 0% to 26% across burned and unburned streams, and there was no relationship between mayfly density and infection prevalence.
4. Based on dissections of > 20,000 mayflies, intermediate-size (4–6 mm) mayflies in the family Baetidae had the highest infection probability and were also the most common mayfly family and size class found in trout stomachs. Wildfire did not affect the number of mermithids consumed per trout, and infection prevalences of mayflies consumed by trout were significantly lower than in the benthos, suggesting predator-avoidance behaviour by infected mayflies.
5. Overall, our results suggest that mermithid nematode responses to fire reflected changes in host density, consistent with the single-host life cycle of mermithids. These results help integrate host–parasite–predator interactions into our understanding of disturbance ecology in freshwater streams, with implications for parasite roles in energy flow through food webs.

1 | Introduction

Freshwater ecosystems can be strongly altered by wildfires, which are increasing in frequency and severity (Liu et al. 2010; Westerling 2016; Higuera and Abatzoglou 2020). Fire can influence freshwater ecosystems by altering riparian vegetation,

hydrology and water quality, which can subsequently affect aquatic communities (reviewed by Bixby et al. 2015). The effects of fire-associated disturbance on stream biota can vary in magnitude and direction over time (Minshall et al. 1997). Fire followed by flooding and erosion can reduce aquatic macroinvertebrate abundance in the first year following fire, whereas the

effects of increased light and nutrients can increase primary and secondary productivity 2–10 years post-fire (Silins et al. 2014; Bixby et al. 2015; Swartz and Warren 2022). While considerable research has focused on how fire affects community structure and ecosystem processes in streams, less research has focused on how fire affects cryptic interactions, such as parasitism.

Species interactions involving parasites might be substantially modified by disturbances such as wildfire (reviewed by Albery et al. 2021; Donaldson et al. 2023). For instance, fire can directly affect parasite transmission by altering the survival of free-living parasite stages (Ortega 2018; Kaiser et al. 2021; Donaldson et al. 2023). Changes to host density following fire can indirectly alter infection prevalence and parasite abundance, particularly when transmission is density-dependent (Arneberg et al. 1998; Hossack et al. 2013; Lagrue and Poulin 2015). Environmental changes can also alter host phenology, growth and development, thereby altering the likelihood of successful transmission to certain host life stages (Cromwell 2018). Disturbances could also influence trophic interactions between parasites and predators, such as concomitant predation—when parasites are inadvertently consumed by a predator alongside the infected host (Johnson et al. 2010; Thieltges et al. 2013). Predation on parasites is prevalent in food webs and can have implications for parasite transmission and energy flow (Johnson et al. 2010; Thieltges et al. 2013); however, concomitant predation on parasites has not been studied in the context of disturbance ecology.

To address this knowledge gap, we examined how wildfire affects host–parasite and parasite–predator interactions, focusing on nematode parasites (Family Mermithidae), mayfly hosts (Order Ephemeroptera) and trout predators (*Salvelinus fontinalis*, *Salmo trutta* and *Oncorhynchus clarkii*) in freshwater streams. Mermithidae is a large family of parasitic nematodes that can infect a variety of invertebrate hosts, including mayflies (Nickle 1972; Poinar Jr and Benton Jr 1986). We focused on mayfly hosts due to their abundance in Rocky Mountain streams, major prey contributions to trout diets (Bozek et al. 1994) and mermithid nematode prevalences up to 80% (Cromwell 2018). Free-living adult mermithids overwinter in streams, mate and lay eggs that hatch the following spring (Hominick and Welch 1980). The free-living immature worm infects early-stage mayfly nymphs and influences mayfly physiology and behaviour, including sterilisation, sex reversal in males, and inducing oviposition behaviour in sterile males (Vance 1996a; Vance and Peckarsky 1997; Cromwell 2018). Mermithid infection can also suppress drift and swimming behaviours in mayflies, which can result in lower mayfly consumption rates in trout (Vance 1996b; Cromwell 2018); however, some contrasting studies have found an increased likelihood of drifting behaviour in infected mayflies (Williams et al. 2001). After maturing, the parasite emerges from the adult mayfly during oviposition, killing its host (Hominick and Welch 1980; Vance 1996a). Each mayfly can support only one individual mermithid, which typically fills the entire host abdomen in a mature infection (see Figure S2). The single-host life cycle of mermithids may suggest tight coupling between host and parasite population densities (Lagrue and Poulin 2015).

We hypothesised that wildfire would cause cascading changes in host–parasite–predator interactions in stream communities.

We expected mayfly densities and mermithid infection levels to differ between streams in burned and unburned catchments due to fire-induced disturbances to the stream environment. We predicted that these responses would vary with time, with an initial decrease in mayfly density due to post-fire disturbance (e.g. scouring; Minshall 2003; Preston et al. 2023), followed by an increase in mayfly density over time due to increased stream productivity (i.e. ‘bottom-up’ effects from higher light and nutrients). Because mermithids have a single-host life cycle, we expected that increased mayfly density would lead to increased infection levels. Alternatively, wildfire could change host–parasite phenology, resulting in a timing mismatch between parasites and susceptible hosts (MacDonald et al. 2021; MacDonald and Brisson 2022). Elevated stream temperatures following canopy loss and increased solar insolation (Minshall et al. 1997; Dunham et al. 2007; Chen and Chang 2023) can accelerate mayfly development (Harper and Peckarsky 2006), limiting the time for larval mermithids to encounter early-stage mayflies and thus possibly reducing transmission success (Cromwell 2018). We also predicted that if fire disturbance increased the density of infected mayflies, more mermithids would be found in trout stomachs at burned sites.

2 | Methods

2.1 | Field Surveys

We surveyed 16 stream reaches in the Rocky Mountain region of northern Colorado for two summers (2021 and 2022) following wildfires that occurred in the summer and autumn of 2020 (Figure S1). Sampling campaigns were conducted during the same time period (July 18 to August 27) in 2021 and 2022 to minimise potential effects of seasonality on biotic variables. Eight of the stream reaches were within the Cameron Peak, East Troublesome and William Fork fires, which together burned over 169,000 ha of forest in northern Colorado (National Interagency Fire Center 2020). To serve as unburned references, we also surveyed 8 stream reaches that were outside the fire perimeters, were of relatively similar elevation and stream size, and were located near (< 13.5 km) the burned sites. All sites were between 2490 m and 3220 m in elevation and were 3rd to 4th order stream reaches. These sites were originally surveyed in 2021 as components of two research projects examining the effects of wildfire on Rocky Mountain streams (Preston et al. 2023; Kanno and Preston 2023), with ten (5 burned and 5 unburned) sites in the Arapaho and Roosevelt National Forest and six (3 burned and 3 unburned) within Rocky Mountain National Park (Figure S1).

At each site, we measured environmental variables related to fire severity and stream conditions. Elevation, latitude and longitude of each site were measured using a handheld GPS unit. Focal stream reaches measured either 50 m or 100 m in total length (see Table S1). We measured channel width and maximum depth every 10 m along the reach. We also recorded discharge using the midsection method at a representative point along each reach using a flowmetre (JDC Electronics, Hamm, Belgium). Turbidity was averaged across three locations along the reach using a handheld turbidimetre (Hanna Instruments, Woonsocket, Rhode Island). Water temperature, pH, dissolved oxygen and conductivity were measured at one location using a

YSI Pro 1020 (Yellow Spring Instruments, Yellow Springs, Ohio). To estimate the severity of fire effects on riparian vegetation, we measured canopy cover using a densiometre in the centre of the stream width and at evenly distributed intervals along the reach length (every 10 m for 50 m reaches and 20 m for 100 m reaches). Tree mortality percentage (blackened trees killed by fire) was estimated along the riparian corridor within 3 m of the stream reach. We also calculated the percentage of upstream catchment area burned using ArcGIS to compare upstream fire impacts between burned and unburned streams (see Data S1).

We also quantified mermithid nematodes, mayflies and trout stomach contents. To quantify mermithids and mayflies in the stream benthos, we collected replicate samples of macroinvertebrates from riffle sections of each stream reach using a Surber sampler (0.09 m² in area, 248 µm mesh). In 2021, we collected 5 replicate Surber samples at 10 sites and 3 replicate samples at 6 sites (see Table S1). In 2022, we collected 5 replicate samples at all sites. Macroinvertebrate samples were preserved in 80% ethanol until processed in the laboratory. To quantify mayflies and mermithids in trout stomach contents, we lavaged the stomachs of 17–32 individual trout (*Salvelinus fontinalis*, *Salmo trutta* and/or *Oncorhynchus clarkii* depending on the local composition; see Data S1 for composition and size distribution) that were collected via electrofishing (Smith-Root, LR-24, Vancouver, Washington) from 10 of the 16 sites in both 2021 and 2022 (5 of which were burned and 5 unburned; Table S1). We anaesthetised the fish with Aqui-S and non-lethally lavaged them to collect stomach contents. Gastric lavage involved flushing water into the trout's stomach using a wash bottle with an attached straw for larger fish, or a 60 mL syringe with a blunt 18-gauge needle for smaller fish. Stomach contents were collected onto a coffee filter and preserved in 80% ethanol before processing in the lab. The fish were released back into the stream upon recovering from anaesthesia.

2.2 | Quantifying Mermithid Infections

We screened 14,237 mayflies from Surber samples and 5093 from trout diet samples for mermithid infections. Mayfly nymphs were first identified to family, counted and measured to the nearest half millimetre from the anterior end of the head (excluding antennae) to the posterior of the abdomen (excluding cerci). Adult mayflies from trout stomachs were counted and measured but not identified to family due to identification uncertainty when partially digested. Under a microscope (8x-35x), we dissected mayflies using forceps to evaluate the presence/absence of mermithids. We dissected all mayflies larger than 1 mm, but after finding that mermithids infected only 0.13% of mayflies < 1 mm, we dissected only a subset ($n = 2361$ out of 4983 collected) below this size. While processing trout stomach contents, we found mermithids “loose” in the stomachs and not associated with mayflies, either because they had exited a host after being consumed or because they were consumed as a free-living adult in the benthos. We recorded these worms separately from those that were completely inside or partially inside consumed mayflies. For analyses of mermithids in trout stomach contents, we conservatively included only nematodes that were associated with a mayfly (see Data S1 for analyses including loose nematodes). This likely underestimated infection

prevalence in consumed mayflies; however, these underestimates should be consistent across sites, burn status and years.

We extracted DNA and sequenced a subset of mermithids to determine whether these parasites are likely to belong to a single or multiple species and if these putative species occurred in the benthic samples and trout stomachs. A ~1 kb fragment of the 18S rRNA gene was amplified following methods in Floyd et al. 2005, using Nem_18S_F and Nem_18S_R primers, which target an 18S gene region where most sequence variability tends to be found in nematodes. Sequences ($n = 18$; 11 benthic samples and 7 diet samples) were compared with deposited sequences in the NCBI GenBank (Benson et al. 2018) using Megablast (Boratyn et al. 2013). We aligned sequences and calculated estimates of divergence using MEGA11 (Tamura et al. 2021) and calculated the Kimura Two-Parametre pairwise distance (Kimura 1980) using default parameters. We then used a 0.01 ad hoc species delineation threshold to estimate the number of putative species detected from our 18 sequences (Macheriotou et al. 2019) (see Data S1 for detailed molecular methods).

2.3 | Data Analyses

We first examined how environmental characteristics varied between burned and unburned sites after wildfire. We tested whether elevation, upland burned area (% of contributing catchment), canopy cover, canopy mortality, pH, dissolved oxygen, turbidity (2021 only), conductivity (2021 only), channel width, channel depth or water temperature varied between burned and unburned sites in 2021 and 2022 using Two-Sample t-tests and Welch's Two Sample t-tests, as appropriate.

We tested whether wildfire altered benthic mayfly density (log-transformed mayflies/m²) using a linear mixed effect model (LME; “lme4” package in R) with an interaction between burn status (burned or unburned) and sampling year (2021 or 2022), and a random effect of site. We ran models with all mayflies combined, as well as separate models for each of the three most abundant families (Baetidae, Ephemerellidae and Heptageniidae) using individual Surber samples as replicates. We restricted analyses to mayflies > 1 mm because all mayflies above this size were dissected. Analyses incorporating all mayflies showed similar patterns and are reported in the Data S1.

We then assessed how host characteristics and burn status influenced mermithid infection in benthic mayflies. We first tested whether infection density (infected mayflies/m²) differed between burn status and year. We log-transformed infection density to meet normality assumptions and used an LME that included the main effects and interaction between burn status and year, and a random effect of site. Next, we examined which factors predicted individual mayfly infection status (infected/uninfected; “infection probability”) from Surber samples. Data from 14,231 individual mayflies were analysed using a binomial generalised additive mixed model (GAMM, “mgcv” package; Wood and Wood 2015) with fixed effects of mayfly size (nonlinear smoothing term), mayfly family (Baetidae, Ephemerellidae or Heptageniidae), an interaction between burn status and year, and a random effect of site. We performed a likelihood ratio test on nested models to generate one test statistic (and p-value) for the categorical mayfly family

variable. To test whether infection levels increased in response to host density, we used a linear mixed effects model with benthic mayfly density (log-transformed) as a predictor of either infection density or benthic infection prevalence (%), again incorporating site as a random effect. We also explored using upstream catchment burned area (a continuous variable) as a predictor instead of the categorical burn status variable (burned/unburned). Because results were generally similar with both approaches, we report model results using catchment burned area in the Data S1.

We next analysed how burn status influenced counts of mayflies and infected mayflies in trout stomachs using separate Poisson mixed effects models (GLMMs) with an interaction between burn status and year and a random effect of site. We also examined which factors predicted individual infection status in mayflies from trout diets, using a binomial GAMM with the same predictors as the model used for infection probability in the Surber samples ($n=3548$ individual mayflies). To test whether mayfly infection prevalence in stream benthos differed from the trout stomach contents, we used an LME model with site-level infection prevalence in trout diets as the response and site-level infection prevalence in Surbers as the predictor, including a random effect of site to account for multiple years of data. We also tested whether mayfly infection probabilities differed between the stream benthos and trout diets using a binomial GAMM with the fixed effect of sample type (Surber or trout stomach) and mayfly size (nonlinear smoothing term), and a random effect of site ($n=17,779$ individual mayflies). Because differences in infection prevalence between stomach contents and Surber samples could be due to trout preferentially feeding on certain size classes, we tested whether mayfly size (log-transformed to meet normality assumptions) differed by sample type using an LME, including site as a random effect. All analyses were performed in R version 4.2.2 (R Core Team 2023) and models were assessed for fit, outliers and dispersion using the “DHARMA” package (Hartig and Hartig 2017). We used the package “lmerTest” (Kuznetsova et al. 2017) to generate p-values for LMEs and report all mean values as mean \pm standard error.

3 | Results

3.1 | Environmental Variables

The 2020 wildfires impacted 65.7% (± 10.9) of catchment area upland to the burned sites, compared to 7.1% (± 2.8) of the unburned sites (Welch *t*-test, $t=5.19$, $p<0.001$). After the fires, streams in the burned areas had lower canopy cover (Welch *t*-test, [2021] $t=-3.20$, $p=0.015$, [2022] $t=-2.26$, $p=0.046$) and higher canopy mortality (Welch *t*-test, [2021] $t=5.19$, $p<0.001$, [2022] $t=6.38$, $p<0.001$) than unburned sites, with consistent findings in 2022 (Table S1). There were no differences in elevation, channel width, maximum channel depth, water temperature, stream turbidity, discharge, pH, conductivity or dissolved oxygen between burned and unburned sites at the time of sampling in 2021 or 2022 (all *p*-values >0.05 ; Table S2).

3.2 | Host Responses

Mayfly density was lower at burned sites (741.4 ± 136.3 mayflies/ m^2) compared to unburned sites (1004.6 ± 117.7 mayflies/ m^2) in the first year after fire (LME, Burn*Year, $t=2.35$, $p=0.020$), but not in the second year after fire (Burn: 1228.6 ± 184.2 ; Unburned: 1260.6 ± 189.3 mayflies/ m^2). This pattern was driven largely by Baetidae, which had lower densities at burned sites in the first year, but comparable densities 2 years after fire (Figure 1A; LME, Burn*Year, $t=2.99$, $p=0.003$). Heptageniidae density was lower at burned sites (282.9 ± 53.6 mayflies/ m^2) than at unburned sites (326.2 ± 30.1 mayflies/ m^2) regardless of year, but this difference was not statistically significant (Figure 1C; LME, Burn, $t=1.62$, $p=0.126$); however, heptageniid density significantly decreased with increasing percentage of upland burned area (see Data S1). There was no effect of burn status, year or their interaction on Ephemerellidae density (Figure 1B; LME, Burn*Year, $t=0.56$, $p=0.574$). The majority of mayflies in benthic samples were baetids (59.9% overall) followed by heptageniids (26.3%),

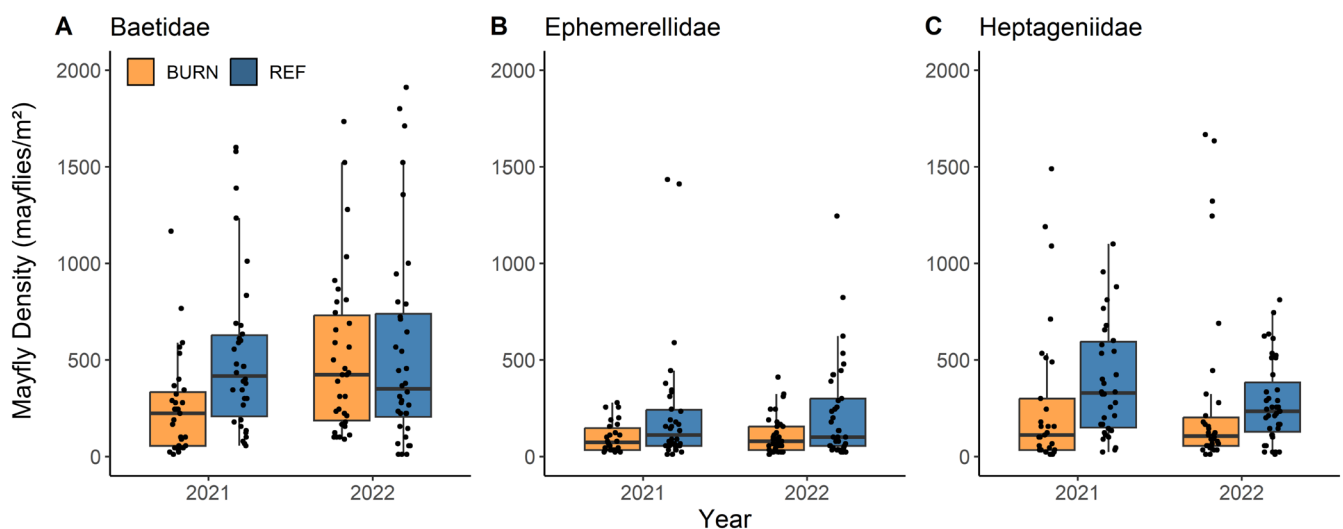


FIGURE 1 | Mayfly density of the three most abundant mayfly families, (A) Baetidae, (B) Ephemerellidae and (C) Heptageniidae at burned (orange) and unburned (blue) sites surveyed one and 2 years (2021 and 2022) after wildfire. For all boxplots, the thick horizontal lines represent the median, boxes represent interquartile range and whiskers represent minimum and maximum values of Surber-level density. Outlier values >2000 mayflies/ m^2 are not shown on the Baetidae plot. Data do not include mayflies ≤ 1 mm in size.

ephemerellids (13.7%) and other rare families (Leptophlebiidae, Ameletidae; <1%). The size distribution of benthic mayflies was strongly right-skewed, regardless of burn status or year (mean 2.8 ± 0.02 mm) (Figure 5).

3.3 | Infection Patterns in the Benthos

Genetic sequencing of 18 mermithid specimens detected at least five putative species based on Kimura Two-Parametre pairwise distances (Table S4). Up to three putative species were detected at the same site (Little Beaver Creek) and one presumed species was found infecting more than one mayfly family (Baetidae and Heptageniidae) (see Tables S3 and S4). Sequencing confirmed that nematodes were mermithids; however, none matched named genera or species in the NCBI GenBank database (Table S3).

Mermithid infection varied with mayfly attributes and site factors. Across all sites and years, infection prevalence averaged 6.3% (± 0.6), with a mean of 59.2 (± 5.8) infected mayflies per square metre of streambed. Infection density at burned sites (23.9 ± 4.8 infected mayflies/m²) was lower than at unburned (58.2 ± 9.3 infected mayflies/m²) sites in 2021 (LME, Burn*Year, $t = -3.00$, $p = 0.003$), but was similar to unburned sites in 2022 (Figure 2A). Infection density increased with mayfly density (Figure 3A; LME, $t = 7.54$, $p < 0.001$); however, infection prevalence (%) was not related to mayfly density (Figure 3B; LME, $t = 0.11$, $p = 0.912$).

At burned sites, the infection probability of benthic mayflies was lower in the year following fires but higher after 2 years (Figure 2B; binomial GAMM, Burn*Year, $z = -3.77$, $p < 0.001$). Average infection prevalence at burned sites rose from 4.0% (± 0.9) in 2021 to 8.5% (± 1.6) in 2022. Infection probability differed between mayfly families (Likelihood Ratio Test, $F = 269.92$, $p < 0.001$). Infection prevalence was highest in Baetidae (10.0% $\pm 1.9\%$), followed by Ephemerellidae (3.6% $\pm 0.9\%$) and Heptageniidae (3.1% $\pm 0.7\%$) (Figure S3). Mayfly size was a strong predictor of infection (binomial GAMM, Size, $\text{ChiSq} = 230.80$, $p < 0.001$), with infections most common in intermediate-size mayflies (~4–6 mm) (Figure 4A).

3.4 | Mayflies and Mermithids in Trout Diets

Trout stomachs contained an average of 9.68 (± 4.72) mayflies, with no difference in the average number of consumed mayflies per trout between burned or unburned sites or across years (Poisson GLMM, Burn*Year, $z = 1.13$, $p = 0.261$). Most (69.5%) nymphal mayflies in trout stomachs were Baetidae, and 20.2% of mayflies found in trout stomachs were adults. Sequencing data indicated that mermithids in trout stomachs were among the same taxa found in mayflies from the benthos (Tables S3 and S4).

Infection probability of mayflies in trout stomachs did not differ between burned and unburned streams (binomial GAMM, Burn, $z = 1.80$, $p = 0.072$). Burn status also had no effect on the number of mermithids consumed per trout through concomitant predation (Poisson GLMM, Burn, $z = 1.43$, $p = 0.153$). Overall, infection prevalence of mayflies in trout stomachs was positively associated with infection prevalence of mayflies in benthic samples (Figure 4B; LME, $t = 2.53$, $p = 0.023$); however, infection probability of mayflies

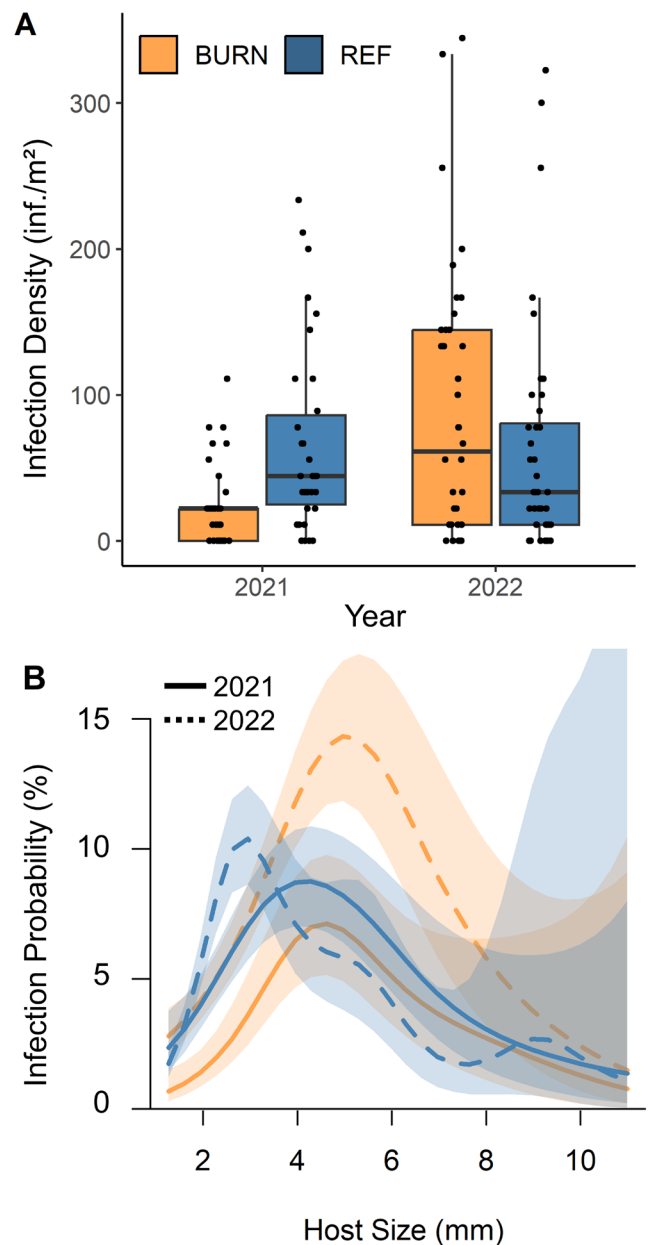


FIGURE 2 | (A) Infection density (number of infected mayflies/m²) within burned (orange) and unburned (blue) streams surveyed one and two years (2021 and 2022) after wildfire. For all boxplots, the thick horizontal lines represent the median, boxes represent interquartile range and whiskers represent minimum and maximum values of Surber-level density and prevalence values. (B) Infection probability of mayflies collected from burned (orange) and unburned (blue) streams one-year (2021, solid lines) and two-years (2022, dashed lines) after fire by host size (mm). Shaded region represents 95% confidence band. Host size greater > 11 mm is omitted from the (B) graph due to low sample size. Data do not include mayflies ≤ 1 mm in size.

in trout diets was significantly lower than in Surber samples (Figure 4A; binomial GAMM, $z = 10.03$, $p < 0.001$). Mean infection prevalence in trout diets ($1.42\% \pm 0.39\%$) was 3.2 times lower than observed in the stream benthos ($4.63\% \pm 0.68\%$). Trout preferentially consumed larger mayflies (LME, $t = 67.03$, $p < 0.001$), with trout diets having normally distributed mayfly sizes centered around intermediate-sized mayflies (5.3 ± 0.03 mm) compared to benthic samples having a right-skewed distribution of mayfly sizes

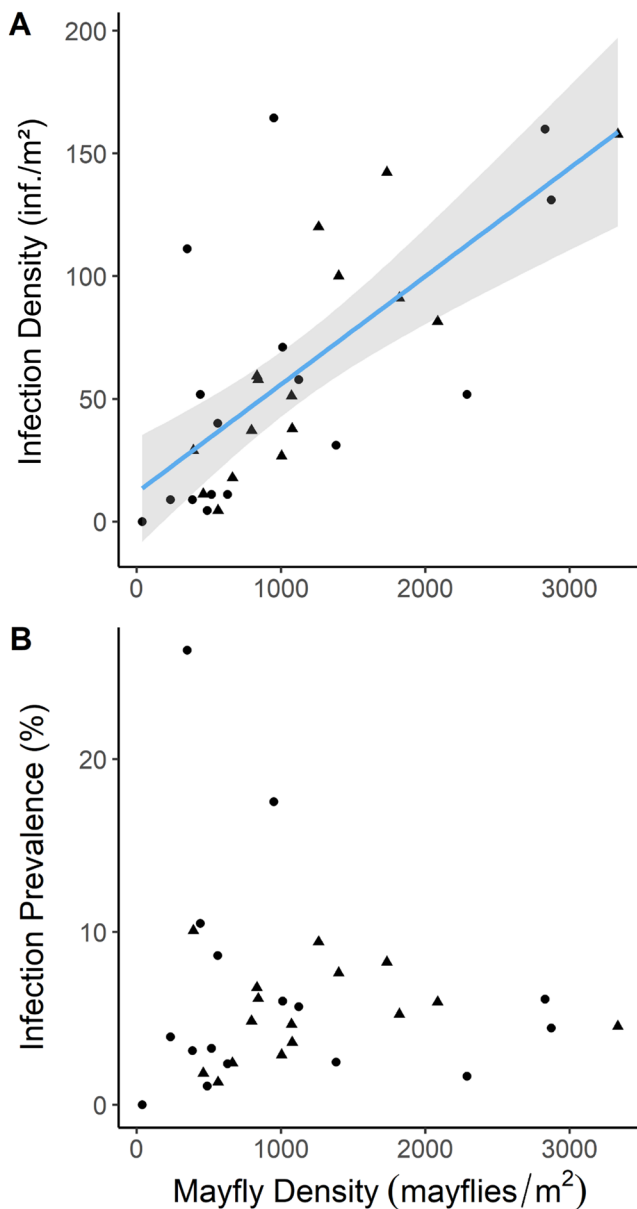


FIGURE 3 | Comparison of mermithid infection patterns to site-level mean mayfly density at burned (circles) and unburned (triangle) sites across years. Y-axes of the scatterplots represent site-level means for (A) infection density (number of infected mayflies/m²) and (B) infection prevalence (percentage of infected mayflies out of total mayflies) at each stream site. A linear regression line with 95% confidence interval is shown for the significant relationship ($p < 0.001$) between (A) infection density and log-transformed mayfly density. Data do not include mayflies ≤ 1 mm in size.

(2.8 ± 0.02 mm) (Figure 5). Infection prevalence of adult mayflies consumed by trout was low, at only 0.012% (13 out of 1100 adult mayflies).

4 | Discussion

Wildfire activity is increasing in many regions (Westerling et al. 2006; Higuera and Abatzoglou 2020), underscoring the need to investigate how freshwater communities will be affected in fire-prone areas. Most research on how wildfires affect stream

communities has focused on free-living biota (Bixby et al. 2015), overlooking the parasite interactions that can account for numerous food web links in aquatic ecosystems (Marcogliese and Cone 1997; Lafferty et al. 2006). We hypothesised that fire disturbance would affect mermithid parasites via changes in mayfly population characteristics, and that this response would vary over time since fire. We also expected that fire effects would alter parasite–predator interactions between trout and mermithid parasites through changes in rates of concomitant predation. We found that fire initially reduced mayfly density, resulting in decreased infection density; however, it did not significantly alter parasite–predator interactions.

Mayfly densities at burned sites initially decreased, but then recovered to levels comparable to unburned sites by 2 years post-fire. Previous research has shown that aquatic macroinvertebrates in burned stream catchments can recover or even increase as early as one to 2 years after fire (Caldwell et al. 2013; Vieira et al. 2004; Mellon et al. 2008). Two years after fire, post-fire erosion and flooding could have subsided in frequency or magnitude, allowing mayflies to reestablish. Recolonization rates appear to be taxon-specific, as we found Baetidae densities recovered within 2 years, while less abundant Heptageniidae and Ephemerellidae did not follow this trend. Rarer taxa may exhibit less predictable population responses to disturbance, as smaller populations are more vulnerable to demographic stochasticity (May 1973). Differences in population recovery could also reflect life-history differences. Populations of aquatic macroinvertebrates that can reproduce and disperse quickly may increase rapidly after disturbance subsides (Minshall et al. 2001; Minshall 2003; Mellon et al. 2008; Malison and Baxter 2010). Baetids, which can produce multiple generations per year (Clifford 1982), can recover or increase in burned streams within a year after fire (Vieira et al. 2004); however, heptageniids, which typically only have one generation per year (Clifford 1982), can take four to 8 years to recover from fire (Martens et al. 2019; Vieira et al. 2004). Moreover, temporal mismatches are possible between host phenology and fire occurrence in mayflies with only one generation per year, depending on how the timing of the wildfire aligns with annual reproduction. Compared to baetids, we did not observe as dramatic a decline and subsequent recovery in heptageniids and ephemereids, which could be related to the life stage at which the fires occurred. In turn, these host-specific responses to disturbance likely mediated the parasite responses observed in our study.

Wildfire altered mermithid infection over the two-year study period, likely due to changes in host abundance. Mirroring changes in mayfly density, infection density decreased shortly after fire, but then recovered after 2 years. The strong positive relationship between mayfly density and infection density suggests that changes in mermithid populations are associated with host density. Similar coupling between host population density and parasite density has been documented in other freshwater communities (Lagrange and Poulin 2015). Conversely, we did not find a relationship between infection prevalence and mayfly density. A de-coupling of infection prevalence from host density may be advantageous to mermithids, as it could stabilise parasite populations regardless of host densities. In a previous study, the prevalence of trematode parasites in long-lived (5–7 years) aquatic snail hosts remained surprisingly stable despite severe wildfires (Svatos et al. 2023). Some

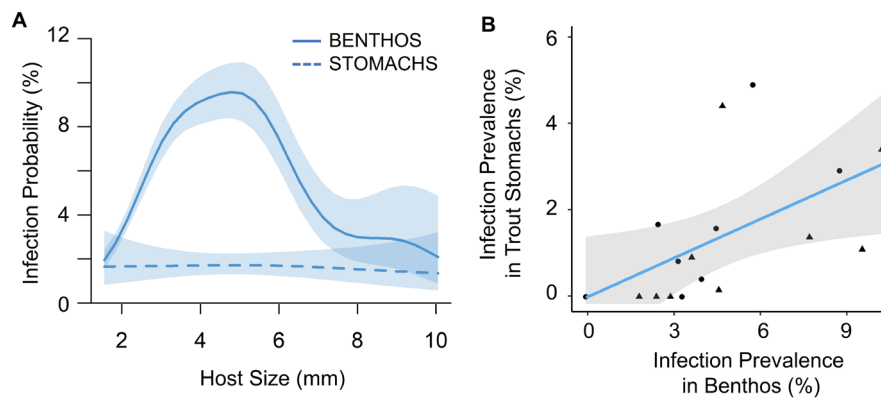


FIGURE 4 | (A) Infection probabilities of benthic mayflies (solid line) compared to those found in trout stomach contents (dashed lines) by host size (mm). Infection probabilities for mayflies > 10 mm are omitted from the figure due to low sample size. Shaded region represents 95% confidence band. (B) Comparison of site-level mayfly infection prevalences (percentage of infected mayflies out of total mayflies collected) between trout stomach contents (y-axis) and Surber samples (x-axis) from burned sites (circles) and unburned sites (triangles). A linear regression line with 95% confidence interval is shown representing the positive relationship ($p=0.023$) between variables. Data do not include mayflies ≤ 1 mm in size.

parasite responses to wildfire can be mediated by host-density dependence, as seen with mermithids, but further investigation is warranted into how this response may be contingent on specific host–parasite life history, such as host longevity or parasite life cycle complexity.

At both burned and unburned sites, infection prevalence in Baetidae mayflies was higher than in Ephemerellidae or Heptageniidae. This is consistent with previous studies that found mermithids to be common in baetids but seemingly absent from heptageniids (Flecker and Allan 1988). Differing infection levels could be due to differences in host behaviour or physical defences that limit the larval mermithids success in burrowing into the abdomen of a mayfly and thus infecting its host. For example, prevalence of mermithid infection is lower in mosquito species with higher activity levels, thicker cuticles and physiological resistance to nematode development (Petersen 1975). Physical characteristics, like the Heptageniidae’s flattened body and the Ephemerellidae’s abdominal spines, may possibly provide physical defences against infection compared to Baetidae, although this has not been studied. Additionally, differences in foraging and predator-avoidance behaviours of Baetidae compared to Ephemerellidae (Peckarsky 1996) may influence the likelihood of interactions with larval mermithids and subsequent infection. Finally, higher infection prevalence in Baetidae could be due to parasite adaption to infect the most abundant host (Lively and Dybdahl 2000), a pattern observed in other nematode-host systems (Arneberg et al. 1998).

The high infection prevalence observed in intermediate-sized mayflies from benthic samples may be due to several mechanisms. Smaller and younger mayflies may have low infection prevalence due to less exposure time compared to older individuals (Anderson and Gordon 1982; Pritchard and Zloty 1994). Lower prevalence in larger, older hosts could be from mayflies clearing infections, though this seems unlikely in this system (Cattadori et al. 2005). More likely, parasite-induced host mortality may cause lower observed infection prevalence in older mayflies, as seen in other aquatic hosts (Thomas et al. 1995; Knudsen et al. 2002). Notably, half of mermithid-infected

mayflies fail to fully develop, prematurely killing both the parasite and mayfly host (Vance and Peckarsky 1996). Another mechanism that may be limiting infection prevalence in large mayflies is that parasite infection itself may limit host growth (Pritchard and Zloty 1994). Parasitized Baetidae mayflies are generally smaller with less flight muscle than unparasitized individuals in late nymphal development stages, due to depletion of host resources (Vance and Peckarsky 1996; Cromwell 2018). Infection also delays mayfly development and emergence (Vance and Peckarsky 1996), which may contribute to the low infection prevalence we observed in adult mayflies. Size-specific host infection probability may affect parasite–predator interactions in predators that exhibit size-based consumption of mayflies, leading to food web consequences.

Mayfly infection probability and number of consumed mermithids in trout diets were unaffected by fire, despite decreased mayfly infection in the benthos one year post-fire. The mechanisms underlying this consistency of infected mayfly consumption are unclear, but infection levels of mayflies in the trout diets may have been too low to detect differences between burned and unburned sites. Trout at burned sites were larger on average than trout at unburned sites (Preston et al. 2023), thus ontogenetic shifts in trout diet preference had the potential to influence parasite consumption (Prati et al. 2020); however, we did not see any evidence of this in the current study. Accounting for size and family, mayflies in trout stomachs were less frequently infected than those in the benthos, suggesting that infected mayflies are less likely to be consumed by trout. This result is consistent with previous field studies and proposed mechanisms of predator-avoidance behaviours of infected mayflies (Vance 1996b; Cromwell 2018). Mermithid infection has been previously shown to reduce mayfly drifting and swimming behaviour compared to uninfected individuals (Vance 1996b; Cromwell 2018). Meanwhile, uninfected mayflies are known to reduce their drifting behaviour in response to fish predator cues (McIntosh and Peckarsky 1999); therefore, drift suppression would be considered a “predator-avoidance” behaviour. Parasites are known to alter host behaviour and physiology, which can, in turn, affect trophic interactions involving the host (Lafferty and

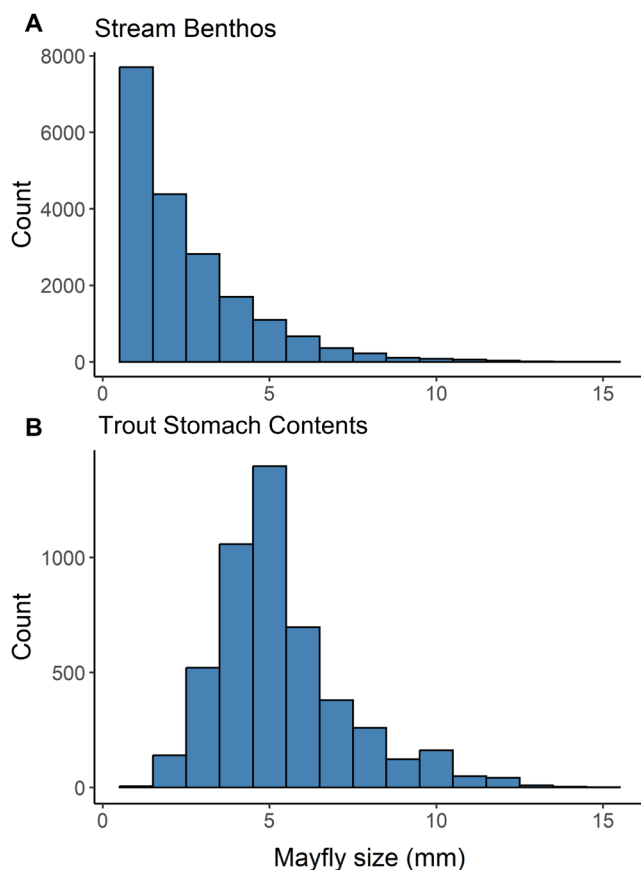


FIGURE 5 | Counts of mayflies collected from (A) benthic stream samples and (B) trout stomach contents by size class (rounded to nearest whole millimetre).

Morris 1996; Shaw et al. 2009; Sato et al. 2012a). Parasite-induced changes to host behaviour or physiology that reduce concomitant predation by trout should increase parasite fitness (Vance and Peckarsky 1997) and have been detected in a range of other host–parasite systems (Gutierrez et al. 2022). Despite negative consequences for the parasite, parasites can be valuable food resources for stream predators; therefore, changes to parasite–predator interactions can potentially affect energy flow within the stream community. Parasites, including nematodes, can be rich in lipids and glycogen (Łopieńska-Biernat et al. 2006; Ponton et al. 2005) and can contribute significant biomass to aquatic food webs, sometimes exceeding the biomass of aquatic insects or top predators (Kuris et al. 2008; Preston et al. 2021). However, predator-avoidance behaviours of mermithid-infected hosts might limit contributions of parasites to trout diets via concomitant predation. In another study system involving nematomorphs in streams, the availability of nematomorph-infected crickets to trout predators had widespread effects on community and ecosystem-level processes, including altering trout predation on benthic invertebrates, production of benthic algae, and leaf decomposition rates (Sato et al. 2012a). Whether any similar community-level consequences occur due to nematode infection in mayflies is unclear but deserves further study.

Bottom-up effects of increased stream productivity post-fire (Silins et al. 2014; Bixby et al. 2015; Swartz and Warren 2022) may be contributing to the recovery of mayfly and mermithid

abundances after 2 years. Riparian tree removal and subsequent canopy opening can increase both mayfly density and nematode parasite density 2–4 years after disturbance (Lagrué et al. 2018). This supports the prediction that bottom-up processes, including increased light and primary production, drive wildfire effects on mayfly populations. We also predicted that temperature changes in streams could create a mismatch between host phenology and parasite infection, but we did not find evidence to support this prediction. Elevated stream temperatures have been previously shown to accelerate mayfly development, decreasing the window of opportunity for mermithids to infect mayfly hosts, with negative implications for nematode transmission (Cromwell 2018). Fire effects on stream canopy cover and channel morphology can elevate water temperatures in streams for years after fire disturbance (Dunham et al. 2007; Chen and Chang 2023). Our understanding of the relative effects of environmental changes and host-phenology changes on infection outcomes is unclear and would benefit from experimental studies that test these factors in isolation.

Mayflies in both benthic and trout diet samples hosted a diverse assemblage of mermithids. Among only 18 nematode sequences, we observed five putative mermithid species, none of which matched named genera or species in the NCBI GenBank database. The closest matches (>95% similarity) to known sequences in GenBank resulted in nothing specified closer than the family level (i.e. “Mermithidae sp.”). The 5–6 putative mermithid species we detected likely underestimate mermithid diversity in this system, as we sequenced less than 2% of our nematode samples and used a relatively short sequence in the relatively conservative 18 s rRNA region. Our detection of undescribed mermithid diversity is consistent with other studies (Sato et al. 2012b; Tripodi and Strange 2018). For example, Sato et al. (2012b) found at least seven mermithid species at two stream sites in Japan, several of which could not be matched to genera or species by molecular sequencing. The vast amount of undescribed mermithid diversity highlights the need for more taxonomic work on mermithids, given their high prevalence in arthropod populations, impacts on hosts and ecosystem processes (Preston et al. 2016; Sato et al. 2012b) and their potential for biocontrol and integrated pest management (reviewed by Kumar et al. 2023). Although sequencing all collected nematodes was beyond the scope of this current project, exploring the genetic diversity of this system is worthy of future research.

Our study improves our understanding of aquatic host–parasite interactions and community-level responses to environmental disturbance. Previous research on parasites with aquatic insect hosts has been narrowly focused on a few host taxa and individual-level host responses, with less than 10% of studies involving parasite interactions with mayflies (Ephemeroptera), stoneflies (Plecoptera) or caddisflies (Trichoptera) and less than 4% of studies measuring population or community-level effects of host–parasite interactions (reviewed by Kohler 2008). Parasites serve ecologically important roles in communities, including as regulators of host populations (Kohler and Wiley 1992) and as key members in food webs (Lafferty et al. 2006; Thielges et al. 2013). As wildfires continue to increase in intensity, potential, and frequency globally (Westerling et al. 2006; Liu

et al. 2010; Higuera and Abatzoglou 2020), it is necessary to understand how fire effects both free-living and parasitic interactions, as well as how this influences energy flow in stream communities.

Author Contributions

Conceptualisation: E.C.S., D.L.P. Developing methods: D.L.P., E.C.S., M.P.F., Y.K. Conducting the research, writing: all authors. Data analysis, data interpretation: E.C.S., S.B.W. Preparation of figures and tables: E.C.S.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be made freely available at datadryad.org upon publication. Genetic sequences of our mermithid samples are publicly available in the NCBI GenBank under the accession numbers PQ522263 through PQ522282.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.