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PRIMARY RESEARCH PAPER

Short-term changes in-stream macroinvertebrate communities following a severe fire in the Lake Tahoe basin, California

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Abstract Large and severe wildfires can dramatically alter terrestrial and aquatic ecosystems. We documented changes in benthic macroinvertebrate communities and physical habitat at two sites along Angora Creek, CA, USA for 2 years following a severe fire. Although post-fire years had low precipitation, canopy cover and bank stability declined dramatically following the wildfire (canopy cover: 88% pre-fire, 22% post-fire; stable bank: 93% pre-fire, 11% post-fire). Substrate also changed substantially, with fine sediment 8× more abundant post-fire and cobble 7× less abundant post-fire. We found no consistent changes in taxonomic richness or diversity following the fire, but post-fire densities and percentage of sensitive taxa were significantly reduced. We observed large reductions in relative abundances of shredder and scraper taxa, while collector-gatherer abundances increased. Community composition shifted away from pre-fire configurations, and continued to diverge in the second year following the fire. Scores from a regionally derived index of biotic integrity (IBI) were variable but overall much lower in post-fire samples and did not show recovery after 2 years. Overall, our study demonstrated substantial post-fire effects to aquatic ecosystems even in the absence of large flooding or scouring events, and showed that these effects can be transmitted downstream into unburned reaches.

Keywords Benthic · Subalpine streams · Wildfire ecology · Macroinvertebrates · Bioassessment

Introduction

Natural wildfire regimes play a critical role in terrestrial ecosystem health by maintaining diversity and promoting natural ecosystem function (Covington et al., 1994). The role of wildfire effects on aquatic ecosystems has received increasing attention in the last two decades as researchers seek to better understand how natural disturbances structure aquatic communities (Gresswell, 1999; Minshall, 2003). Changes in aquatic ecosystems following fire disturbance are often linked to indirect fire effects associated with a suite of variables including fire severity, extent of watershed burned, topography, geology, climate,

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timing of precipitation, hydrologic response, vegetation, stream size, and land-use history (Turner et al., 1998; Minshall, 2003; Vieira et al., 2004). These diverse factors, in conjunction with the unpredictability of wildfires and a frequent lack of pre-fire data, make it difficult to predict and evaluate the effects of wildfire on aquatic systems.

Benthic macroinvertebrates are commonly used as bioindicators in the evaluation of ecosystem processes and ecological change because their life histories allow them to integrate environmental conditions over time and thus reflect discrete, continuous, and cumulative changes within their environment (Rosenburg & Resh, 1993; McGeoch, 1998). When combined with information on physical and chemical parameters, a comprehensive bioassessment can provide valuable insight into the structure and function of an aquatic ecosystem.

In the past few decades, the use of benthic macroinvertebrate communities as bioindicators in evaluating the effects of disturbances has become increasingly popular (e.g., Rinne, 1996; Earl & Blinn, 2003). Previous studies have investigated the response of benthic macroinvertebrate communities to wildfire disturbances of differing intensities and extent of watershed area burned, but overall results have been inconclusive (e.g., Minshall et al., 1995; Roby & Azuma, 1995; Minshall et al., 2001b; Vieira et al., 2004).

This study investigated the short-term effects (1 and 2 years post-fire) of a catastrophic wildfire (Angora Fire) on the physical habitat and benthic macroinvertebrate communities of a small, sub-alpine stream in the Sierra Nevada, California, USA. This study is distinguished from previous studies due to the variety of montane landscapes affected within the watershed and the severe, localized nature of the fire. In addition, the existence of pre-fire data makes this a unique case study in the context of post-fire monitoring in subalpine and urbanized montane landscapes. Following the fire, an intensive post-fire, multi-agency monitoring program was established to track discharge and water quality (i.e., nutrient and sediments) within the affected watershed (Oliver et al., 2011). Our study was designed to enhance the resolution of the post-fire water quality monitoring program by incorporating bioassessment as a tool to investigate impacts on the aquatic ecosystem. Given the severe nature of the fire and the surrounding watershed characteristics including topography, soil and vegetation types, and varying levels of urbanization, we anticipated that (1) changes in physical habitat and food resources would favor post-fire colonization by opportunistic taxa with high dispersal and omnivorous feeding habits, (2) the largest effects would be apparent in the first year following fire, and (3) the succession trajectory of the community would largely depend on watershed responses such as the magnitude of runoff, erosion, and vegetation succession. Information from this study may be used to guide management for subalpine Sierra Nevada aquatic ecosystems that may experience greater wildfire impacts due to global climate change (Westerling et al., 2006).

Methods

Study area

The Angora Fire occurred from June 24 to July 2, 2007 on the southwest shore of Lake Tahoe, California and was the largest wildfire recorded within recent history (c. 100 years) in the Lake Tahoe basin (Fig. 1). The Angora Fire occurred under high winds and extremely dry fuel conditions and, as a result, was high in both severity and intensity (Murphy et al., 2007; Safford et al., 2009). Remote-sensing assessment of fire severity indicated that approximately 53% of the Angora Fire burned at high severity (>75% canopy mortality), 21% at moderate/mixed severity (25–75% mortality), and 26% at low severity (<25% canopy mortality) (Miller et al., 2009). The fire burned a total of 1,255 ha, the majority (~67%) located within the subalpine Angora Creek watershed.

Angora Creek is a perennial first-order stream originating from the Angora Lakes basin (2270 m). The stream enters the burn area ~100 m from the outlet of lower Angora Lake and flows down a steep area of coniferous forest for approximately 3.2 km before crossing into a lower-gradient meadow. The stream then enters an urban area (58 ha) for 1 km prior to exiting the burned area. Post-fire potential threats identified within the urban area included impacts of increased runoff from impervious surfaces and sedimentation (USFS, 2007). Below the burned area, the stream flows through a large meadow for an additional 1.2 km before joining the Upper Truckee River, which flows into Lake Tahoe.

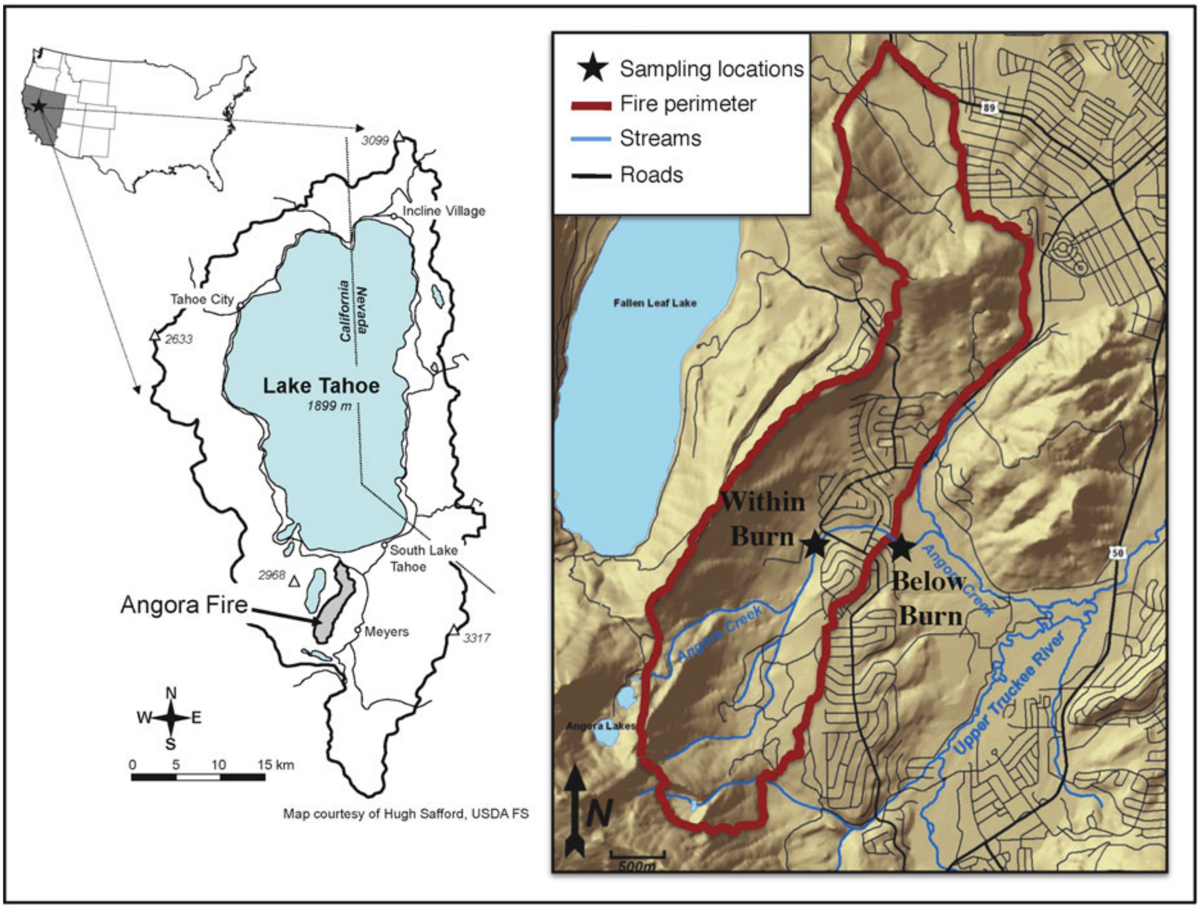

Fig. 1 Location of Angora Fire and sampling locations within the Angora Creek watershed

Mean annual temperature at the elevation of Lake Tahoe (1,898 m) is 6°C with a mean July temperature of 15°C and mean January temperature of −2°C. Precipitation varies as a function of elevation, with the majority of precipitation falling as snow between November and March. Pre-fire vegetation within the Angora Fire boundary was a mature mixed conifer forest, with riparian corridor vegetation such as alder (*Alnus incana*), aspen (*Populus tremuloides*), willow (*Salix* spp), sedges, and other forbs. Soils on steeper slopes are derived from granitic glacial till and have gravelly, loamy sand textures, while soils in lower elevation meadows are poorly drained, with gravelly loamy coarse sands grading to silt loams.

Two sites on Angora Creek were selected for benthic macroinvertebrate and physical habitat surveys (Fig. 1). These locations were chosen to capture stream conditions within and below the fire (Table 1), and to correspond with sites chosen as hydrologic and water quality monitoring stations (Oliver et al., 2011). Our uppermost site (designated "Within Burn") was located within the burned area, and represented conditions draining the undeveloped, severely burned upper watershed. In addition, there were pre-fire macroinvertebrate and habitat data from the Within Burn site, collected in 2002, which we used as a reference point for the effects of fire on in-stream and riparian habitat and community composition. The lower site (designated "Below Burn") was located just below the fire boundary (~100 m) to capture conditions in Angora Creek incorporating the entire burn area. The Below Burn site received drainage from both the burned upper watershed and the burned urban area, however, the area immediately surrounding the Below Burn site was unburned and composed largely of mixed conifer, with similar riparian species as described above. No pre-fire data were available for the Below Burn site.

Table 1 Sub-watershed characteristics for the two sampling sites

Site name	Landscape features	Area (ha)	% Total watershed	% Area burned	% Area burned high severity
Within Burn	Forested, high-gradient slopes, undeveloped	459	31	78	35
Below Burn	Urban and forest, variable gradient, extensive development	120	8	56	12

The Within Burn subwatershed represents the area of the watershed below Angora Lakes and the Below Burn subwatershed represents the area between the Within Burn and Below Burn sites. The remaining portion of the Angora Creek watershed (53%) remained largely unburned

The environmental setting of Angora Creek makes this stream especially vulnerable to wildfire impacts. Much of the watershed has a south or southeast facing aspect, and experiences earlier snowmelt, accompanied by dryer forest litter and soils. Slopes of the upper drainage area are quite steep (average slope 45–60%), but the lower portion of the drainage is comprised of low gradient meadows (average slope 0–5%) where sediment may accumulate. We compare physical and biological conditions before and after the fire at two sites on Angora Creek (slope ~2.3%). Reaches above the wildfire on Angora Creek were inappropriate for comparison or use as a control because they were not perennial, so we used an index of biological integrity (IBI), which defines the range of biological metrics for habitats with minimal exposure to human disturbance. The IBI used in our study was derived from regional reference streams of the eastern Sierra Nevada, including Angora Creek and other nearby streams in the Tahoe Basin, to set expectations and evaluate the biological potential of Angora Creek (Herbst & Silldorff, 2009).

Field and laboratory procedures

Sampling occurred in June, July, and August for two summers following the fire (2008 and 2009). At each site, benthic macroinvertebrates (BMI) were collected from riffle habitat within a 100 m reach by disturbing a 30×30 cm^2 area of substrate in front of a 250 μm *D*-ring net. Rocks and other substrates were overturned and gently brushed to dislodge individuals and allow them to be carried by the current into the net. A total of eight individual replicates were collected and composited for each 100 m reach. Invertebrate samples were picked by hand and stored in 90% ethanol. In the laboratory a Folsom plankton splitter (Wildlife Supply Company, Buffalo, NY) was used to obtain subsamples with a minimum count of 500 individuals for identification. The remaining fraction of the unprocessed sample was sorted by hand for large and rare organisms. Invertebrates were identified with a dissecting microscope at 10× magnification to the lowest feasible taxonomic level (usually genus).

Physical habitat assessments were conducted in August of each year. Throughout the 2-year study, sites were outfitted with automated samplers (ISCO 6710; Teledyne Isco Inc., Lincoln, NE, USA) and instrumented to record stage, velocity, temperature, conductivity, and turbidity (Campbell CR10X; Campbell Scientific, Logan, UT, USA). During each sampling event we measured pH and dissolved oxygen with a handheld meter (YSI 556 meter; YSI, Yellow Springs, OH, USA). A transect was established at each sample location, and major categories of in-stream substrate type (categories: fines (<0.06 mm), sand (0.06–2 mm), gravel (2–63 mm), or cobble (63–250 mm)) and substrate cover (categories: algae, aquatic vegetation, aquatic moss, wood, detritus, leaves, roots, or bare) were identified at five evenly distributed points across the channel and recorded in terms of percent abundance for each transect. Percent abundances for each transect were then averaged for the entire sample reach by site and year. Riparian vegetation type (categories: herb, bush, deciduous tree, evergreen tree), percent cover (using a densitometer), and bank stability (categories: stable, vulnerable, eroding) were identified and recorded at each of five transects spaced at 20 m increments throughout the 100 m sampling reach, and then averaged to determine mean values by site and year.

Most studies on wildfire and stream interactions lack pre-fire data. Fortuitously, Angora Creek was sampled prior to the fire in August 2002 at the Within Burn site as part of a project aimed at developing a regional index of biotic integrity (Herbst & Silldorff, 2009). In addition, climate and hydrologic conditions were similar in 2002 to the two post-fire years investigated here, allowing for greater confidence in the comparability between datasets despite the 6 year gap between pre-and post-fire samples. Pre-fire sampling included collection of five samples of three individual replicates from riffle habitats, as well as physical habitat surveys as described above. All pre-fire invertebrate samples were subsampled to 250 individuals each, enumerated, and identified using the same methods described above.

Community composition

Taxa were assigned a functional feeding group category (predator, shredder, grazer, filterer, and collector) and tolerance value (TV), which represents the relative sensitivity to perturbation and/or stressors based on previous data from Barbour et al. (1999). Metrics of community composition were determined for each sample, including benthic macroinvertebrate (BMI) density, taxa richness, EPT (orders Ephemeroptera, Tricoptera, and Plecoptera) richness, percentage of sensitive taxa, and percentage of specific functional feeding groups. BMI communities were evaluated for diversity (within sites) and similarity (between sites). Species diversity was evaluated using the Shannon index (H'). All univariate comparisons of differences between means at each site between post-fire years were conducted using paired *t* tests or nonparametric Kruskal–Wallis ANOVA on ranks. BMI communities tend to show high intra- and inter-annual temporal variability (Resh & Rosenberg, 1989), and because all pre-fire data used in this study were collected in August, direct community comparisons to pre-fire data are made using only the August post-fire samples in 2008 and 2009. The pre-fire sampling technique also used a lower minimum count of 250 individuals for each replicate (versus 500 for post-fire samples), so we chose to make all comparisons using the average value determined from all 5 pre-fire replicates.

Nonmetric multidimensional scaling (NMS) of Sørensen dissimilarity matrices was used to examine the composition (species occurrence and abundance) of the BMI community before and after fire, and to assess how composition was related to physical habitat parameters. To evaluate differences between a priori sample groups, a multi-response permutation procedure (MRPP) was used to test the hypotheses of (1) no difference between pre-fire (Aug 2002: $n = 5$) and post-fire samples (Jun–Aug 2008, 2009: $n = 6$) at the Within Burn site and (2) no difference between the Within Burn samples (Jun–Aug 2008, 2009: $n = 6$) and Below Burn samples (Jun–Aug 2008, 2009: $n = 6$). MRPP quantifies within-group agreement and distinctness (see Mielke et al., 1981). Indicator species analysis (ISA) was used to determine which BMI taxa were associated with each of the three sample groups: (1) pre-fire Within Burn ($n = 5$), (2) post-fire Within Burn ($n = 6$), and (3) post-fire Below Burn ($n = 6$). The statistical significance of each indicator value (IV) was tested using a Monte Carlo randomization with 5,000 runs. All multivariate nonparametric statistical analyses were conducted using the software program PC-ORD Version 5.10 (McCune & Mefford, 2006).

Eastern sierra-index of biological integrity

The Eastern sierra-index of biological integrity (ES-IBI) is a multimetric index developed to aid in long-term monitoring strategies for the Lahontan region of the Sierra Nevada (Herbst & Silldorff, 2009). The ES-IBI integrates aquatic invertebrate bioassessment data compiled from streams within the ES (including the Tahoe basin and Angora Creek) to define reference-standard conditions and determine responses to stressors. The ten metrics included in the ES-IBI are: (1) a modified Hilsenhoff index, the richness values of (2) all taxa, (3) Ephemeroptera, (4) Plecoptera, (5) Trichoptera, (6) Acari, and the relative abundances of (7) Chironomidae, (8) tolerant taxa, (9) shredders, and (10) the dominant three taxa. To evaluate community responses and overall stream habitat suitability following the Angora Fire, pre- and post-fire community data were evaluated using the ES-IBI. The use of a regional reference condition reduces error associated with comparing impaired conditions to only a few local reference streams. The ES-IBI values determined from test sites can be compared with the range of reference values to designate stream condition in terms of regulatory standards (Herbst & Silldorff, 2009).

Results

Environmental variables

Relative to the 26-year precipitation mean of 117 cm, both pre- and post-fire years were drier than average

(102 cm in 2002; 79 cm in 2008; 103 cm in 2009). Precipitation data indicate that hydrologic conditions were especially similar between pre-fire and the second year following fire (data acquired from SNOwpack TELemetry stations; USDA-NRCS). Post-fire hydrology and water quality response for each site is not covered extensively here, but see Oliver et al. (2011) for additional information. Stream water discharge was consistently higher at the Below Burn site (average was 60 and 37% higher than discharge at Within Burn in 2008 and 2009, respectively), and was greater overall in the second year following fire. Physical habitat varied between sites due to effects from the fire (i.e., canopy loss, vegetation type) as well as site-specific differences in hydrology, water quality (Table 2), and stream geomorphology (Table 3). Comparisons between sites reveal that the Within Burn site exhibited higher water temperatures ($t = 3.53$, $P < 0.01$), and lower EC ($t = -6.66$, $P < 0.001$) and pH ($t = -3.43$, $P < 0.05$) than the Below Burn site. Stream flow velocity was higher at the Below Burn site ($t = -3.32$, $P < 0.05$), especially in 2009.

Comparisons between pre- and post-fire years show dramatic differences in physical habitat characteristics

Table 2 Summary of mean water velocity and water quality measurements on Angora Creek recorded during sampling events

	Pre-fire, 2002	2008		2009	
	Within Burn	Within Burn	Below Burn	Within Burn	Below Burn
Velocity (m/s)	1.7	0.5 (±0.4)	0.5 (±0.3)	0.3 (±0.1)	0.4 (±0.1)
Temperature (°C)	9.0	16.8 (±4.0)	15.0 (±2.8)	17.1 (±3.2)	14.2 (±3.5)
Conductivity (μS/cm)	51.8	28.9 (±5.4)	51.4 (±13.6)	32.5 (±16.5)	66.0 (±29.9)
pH	7.2	6.7 (±0.3)	7.2 (±0.2)	6.7 (±0.2)	7.0 (±0.2)
Dissolved oxygen (mg/L)	8.9	8.4 (±0.5)	8.3 (±0.2)	6.8 (±0.1)	7.1 (±0.3)

Values are mean ± standard deviation. Pre-fire samples were taken only during the month of August

Table 3 Physical habitat data from pre- and post-fire physical habitat surveys

	Pre-fire, 2002	2008		2009	
	Within Burn	Within Burn	Below Burn	Within Burn	Below Burn
% Riparian cover	87.9	21.7 (±2.6)	21.3 (±7.1)	21.3 (±3.2)	20.0 (±5.0)
% Banks undercut and/or eroding	26.7	89.9 (±4.4)	15.0 (±4.3)	88.3 (±3.6)	23.0 (±4.72)
% Banks stable	93.3	10.1 (±4.2)	85.0 (±4.4)	11.2 (±2.4)	77.0 (±8.08)
Substrate					
% Fines (<0.06 mm)	4.0	32.8 (±5.5)	5.8 (±2.5)	30.8 (±6.2)	ND
% Sand (0.06–2 mm)	25.3	32.2 (±2.5)	43.9 (±6.0)	ND	34.3 (±9.3)
% Gravel (2–63 mm)	25.3	28.7 (±1.5)	50.3 (±8.5)	69.2 (±6.2)	65.1 (±9.4)
% Cobble (63–250 mm)	45.3	6.5 (±1.5)	ND	ND	ND
Substrate cover					
% Algae	8.0	43.3 (±8.0)	17.9 (±7.5)	18.8 (±6.3)	12.8 (±8.2)
% Aquatic vegetation	ND	25.0 (±6.0)	31.5 (±6.6)	69.2 (±12.5)	37.8 (±10.6)
% Wood	17.3	18.6 (±11.5)	3.3 (±5.8)	ND	ND
% Aquatic moss	13.3	ND	12.5 (±2.5)	6.3 (±6.2)	ND
% Leaves	2.7	ND	ND	ND	ND
% Bare/other	4.0	13.2 (±2.6)	39.2 (±1.4)	12.3 (±12.3)	41.0 (±15.5)

For uniform comparison across years, all physical habitat data were collected during the month of August. Values are mean ± standard deviation

ND not detected

(Table 3). Riparian cover decreased at the Within Burn site from 88% to a mean of 21%, with the majority of post-fire cover consisting of burned, large woody debris within the stream channel. The geomorphology of the stream also changed following fire. In the first year post-fire (2008) the Within Burn site had largely unstable, eroding, and undercut banks, which were predominately unvegetated and lacked canopy cover. The small amount of vegetation present post-fire at the Within Burn site consisted of immature willows, grasses, and forbs. In contrast to the Within Burn site, the Below Burn stream banks were significantly more stable ($t = -21.89$, $P < 0.001$), with fewer undercut or eroding banks ($t = 23.79$, $P < 0.001$) and the canopy was composed of large conifers, mature willows, grasses, and forbs. Cobble was the most abundant substrate type at the Within Burn site in 2002, followed by gravel and sand. Following the fire, cobble was nearly absent from the Within Burn site while fine sediments greatly increased. The Below Burn site also lacked cobble substrate in 2008 and 2009, but did not have the fine sediment cover observed post-fire at the Within Burn site ($t = 10.46$, $P < 0.001$). Instead, gravel and sand were the dominate substrate types, with significantly more sand at the Below Burn site than the Within Burn site ($t = -4.03$, $P < 0.01$). In addition, the percentage of algal and aquatic vegetation cover increased dramatically following the fire at the Within Burn site, although only the algae increase was significant ($t = 2.82$, $P < 0.05$).

Community comparisons

Following the fire, the average density of individuals declined at both sites, although density increased at the Below Burn site during the first post-fire August (2008) (Fig. 2). In the first year following fire, taxa richness and EPT richness at the Within Burn site were similar to pre-fire levels, however, both declined in the second year. While the difference in EPT richness in the second year post-fire was largely due to a sharp decline in the number of Plecoptera taxa, Ephemeroptera also declined. In comparison to pre-fire levels, the percentage of sensitive taxa decreased from 40 to 30% at the Within Burn site in the first year following fire and remained low for the duration of post-fire sampling.

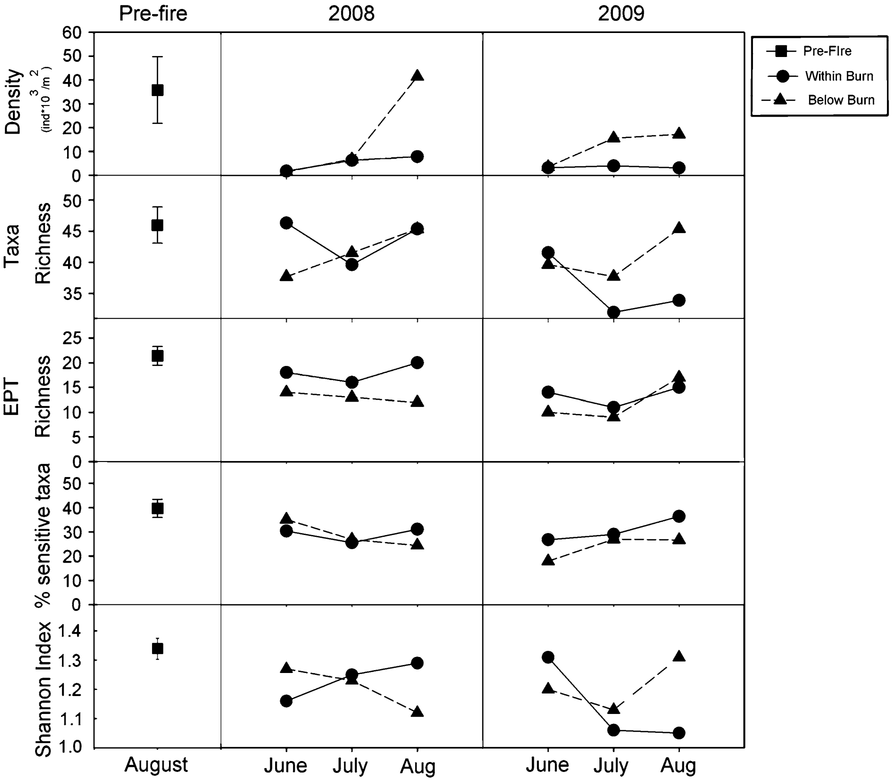

Fig. 2 Density of individuals, total taxonomic richness, EPT richness, percent abundance of sensitive taxa, and Shannon diversity index for pre-fire (2002, within the future burn site) shown as mean and 95% confidence interval of five intervals, and following the fire (2008 and 2009) at Within Burn and Below Burn sites

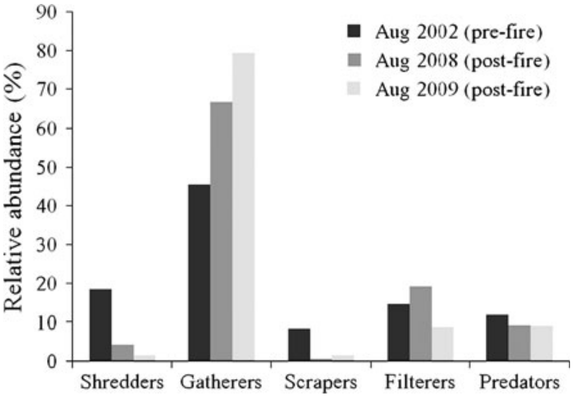

Fig. 3 Mean relative abundances of benthic macroinvertebrate functional feeding groups from Within Burn samples before (August 2002) and after (August 2008 and 2009) the Angora Fire

Comparisons of diversity and community metrics for post-fire samples showed no statistical differences between years or sites. Shannon diversity was similar for both years at each of the two sites when averaged across months, but differed when considering only August samples. Shannon diversity declined from its pre-fire value ($H' = 1.34$) in August 2008 ($H' = 1.29$) and then continued to decline in August 2009 ($H' = 1.05$).

Comparisons of pre-fire versus post-fire August samples at the Within Burn site revealed a large shift in functional feeding group composition (Fig. 3). Pre-fire samples showed a more even distribution of functional feeding groups and much higher relative abundances of shredders and scrapers than either of the post-fire years. In comparison with pre-fire samples, collector-gatherers increased following the fire by 145 and 172% in 2008 and 2009, respectively. Collector-filterers increased from pre-fire abundances by 30% in 2008, but then decreased from pre-fire levels by 58% in 2009. Shredder populations decreased following the fire, particularly in the first year (2008) when percent abundance declined 77% relative to pre-fire samples. Predator abundance was also slightly higher in pre-fire samples, and declined by about 30% in both years post-fire.

When averaged across the 3 months of each post-fire year, collector-gatherers were the dominant functional feeding group at the Within Burn site (relative abundances: 57% in 2008, 72% in 2009). The second most abundant functional feeding group was the collector-filterer group (26% in 2008, 16% in 2009). In 2008, the remaining functional feeding groups were shredders (8%), predators (8%), and scrapers (1%). However, in the second year following fire (2009), the relative abundance of shredders and scrapers both declined to <1% while the percent abundance of predators increased slightly to 11%.

The Below Burn site was also largely composed of collector-gatherers in both years following fire when averaged across the 3 months (48% in 2008, 55% in 2009). In 2008, the Below Burn site had a greater number and more even distribution of collector-filterers (16%), scrapers (8%), shredders (8%), and predators (17%) than the Within Burn site. In 2009, scrapers and shredders decreased to <1 and 3%, respectively, while filterers increased to 26%. Predator percent abundance decreased slightly in 2009, but overall remained fairly similar across both years.

Community analysis

NMS ordination analysis of all sites and samples resulted in a 2-D solution (stress = 12.6%, instability <0.0001, $P = 0.02$). Upon examination of the resulting ordination, it appeared that two sampling dates (June & July 2008) at the Below Burn site were quite different from the other samples. Outlier analysis confirmed that these Below Burn samples were statistically different from all other samples (standard deviation > 2.0). Based on this information and the results from MRPP, physical habitat analysis, and community metrics we chose to run a separate NMS analysis examining pre-fire versus post-fire communities for all sample dates at the Within Burn site only.

NMS ordination analysis of the pre- and post-fire samples at the Within Burn site resulted in a 2-axis solution (stress = 4.83%, instability <0.0001, $P < 0.01$) with clear separation of samples in community space based on effects of fire (Axis 1) and the month of sampling (Axis 2) (Fig. 4). The ordination explained 93% of the variation in the original community matrix, with axis 1 explaining the majority of the variation in community composition among samples (axis 1 $R^2 = 0.55$, axis 2 $R^2 = 0.38$). Many environmental variables were correlated with the unburned to burned sample gradient described by Axis 1, including percent cobble ($r = -0.93$), percent leaves ($r = -0.91$), water velocity ($r = -0.91$), percent fines ($r = 0.90$), and percent aquatic vegetation ($r = 0.90$).

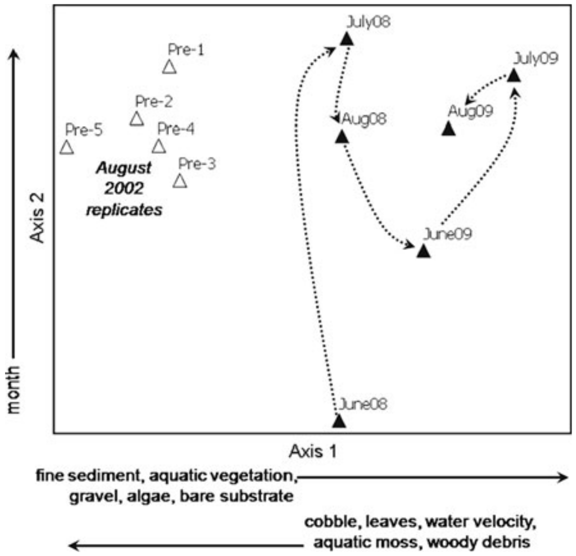

Fig. 4 NMS ordination of pre-fire versus post-fire sample community composition. *Hollow triangles* represent samples collected pre-fire, *solid triangles* indicate samples taken post-fire, and *dotted vectors* connect sequential samples post-fire. All samples shown are from the Within Burn site. *Vectors* and text below the axes indicate the environmental variables that were highly correlated with axes 1 and 2. *Vectors* pointing to increasing values along an axis represent positively correlated environmental variables, while *vectors* pointing to decreasing values along an axis represent negatively correlated environmental variables

MRPP tests revealed that BMI communities in pre- and post-fire samples were distinct from one another ($A = 0.198$; $P < 0.001$). There was no clear distinction between post-fire communities at the Within Burn and Below Burn sites ($A = 0.030$; $P = 0.066$), indicating that the fire had a larger effect on community composition than geographic or fine-scale habitat differences between the Within and Below Burn sites.

Indicator species analysis identified 22 significant ($P < 0.05$) indicators of pre-fire Within Burn samples, six significant indicators of post-fire Within Burn samples, and 1 significant ($P < 0.05$) and five marginally significant ($P < 0.1$) indicators of post-fire Below Burn samples (Table 4). Pre-fire Within Burn indicator taxa were a diverse group of mainly shredders, predators, scrapers, and gatherers, and were sensitive, intolerant taxa (mean Tolerance Value (TV) = 2.8). Post-fire Within Burn indicator taxa were much more tolerant (mean TV = 6.0) and were omnivores, gatherers, filterers, and predators. The only highly significant post-fire Below Burn indicator taxon was the omnivorous caddisfly *Micrasema* ($P < 0.05$), while the remaining significant taxa ($P < 0.1$) were a small group of omnivores, predators, and gatherers. In general, post-fire Below Burn indicator taxa were fairly tolerant (mean TV = 5.8).

ES-IBI

The ES-IBI scores indicate a loss in biological integrity following the Angora Fire (Fig. 5). The pre-fire mean IBI score was 89.5 (SE ± 0.8), and falls within the range of values used to designate streams as "unimpaired and acceptable" or "very good" (IBI > 80.4; Herbst & Silldorff, 2009). In the first year post-fire, the mean IBI score at the Within Burn site dropped to 67.5 (SE ± 6.2), which is designated as "unimpaired and intermediate" or "good" (IBI 63.2–80.4). The IBI score decreased further at the Within Burn site in the second year post-fire, with a mean score of 50.6 (SE ± 3.8), which qualifies as "impaired and partial supporting" or "poor" condition (IBI 42.2–63.2). The Below Burn site had relatively similar IBI values for both years, 58.3 (SE ± 2.4) in the first year and 52.8 (SE ± 12.5) in the second year. Interestingly, while the overall mean for the Below Burn site was low in the second year post-fire, the August sample did show a large increase (reaching IBI = 78), indicating that conditions in Angora Creek at the Below Burn site had improved by August 2009.

Discussion

Large disturbances, such as wildfire, are key drivers of spatial and temporal heterogeneity and can alter ecosystem state and succession trajectories (White & Pickett, 1985). The Angora Fire was a severe wildfire that resulted in altered flow regimes and increased nutrient and sediment concentrations within Angora Creek (Oliver et al., 2011). Our investigation of BMI communities and physical habitat characteristics in Angora Creek indicates that the fire also profoundly affected the stream ecosystem, shifting the structure, and function of the BMI community away from pre-fire conditions. While there were no notable trends in BMI community differences between the Within Burn and Below Burn sites, it is likely that both of these locations experienced effects from the fire, although the particular stressors at each site may have varied.

Table 4 Indicator species analysis results for pre- and post-fire Within Burn samples and post-fire Below Burn samples

Group	Species name	IV	*P*	FFG
Pre-fire (Within Burn)	Capniidae	100	<0.01	Shredder
	Rhyacophila sibirica grp.	100	<0.01	Predator
	Dugesia tigrina	92	<0.01	Predator
	Pericoma	90	<0.01	Gatherer
	Yoraperla	87	<0.01	Shredder
	Stempellinella	87	<0.01	Gatherer
	Aturus	81	<0.01	Predator
	Malenka	80	<0.01	Shredder
	Cultus	80	<0.01	Predator
	Anagapetus	80	<0.01	Scraper
	Heteroplectron californicum	80	<0.01	Shredder
	Rhyacophila betteni	80	<0.01	Predator
	Feltria	80	<0.01	Predator
	Cinygmula	80	0.01	Scraper
	Zapada	75	<0.01	Shredder
	Stempellina	74	0.01	Gatherer
	Tvetenia bavarica	71	0.01	Gatherer
	Paraleptophlebia	67	<0.01	Gatherer
	Bezzia-Palpomyia	61	<0.01	Predator
	Cinygma	60	0.02	Scraper
	Dolophilodes	60	0.02	Filterer
	Diphetor hageni	58	0.04	Gatherer
Post-fire (Within Burn)	*Rheocricotopus*	85	<0.01	Omnivore
	Thienemanniella cf. *xena*	83	<0.01	Gatherer
	Pisidium	80	<0.01	Filterer
	Eukiefferiella claripennis	67	0.02	Omnivore
	Isoperla	59	0.04	Predator
	Simulium	56	0.05	Filterer
Post-fire (Below Burn)	*Micrasema*	75	<0.01	Omnivore
	Parametriocnemus	58	0.07	Gatherer
	Lebertia	53	0.06	Predator
	Narpus concolor	50	0.07	Gatherer
	Eukiefferiella brevicalar grp.	50	0.07	Omnivore
	Larsia	45	0.06	Predator

IV indicator value, *P* significance of IV, *FFG* functional feeding group

For example, as a result of the lower elevation within the watershed and local soil characteristics, substrate at the Below Burn site was sandier, and its position below the burned urbanized area resulted in higher stream flow, colder temperatures, and more impaired post-fire water quality conditions in comparison to the Within Burn site (see Oliver et al., 2011). The differences between the two sites emphasize the need for careful site selection as the Below Burn site likely experienced a combination of effects from different habitat characteristics, as well as upstream fire and urban effects.

The Angora Fire resulted in large changes to the physical habitat of Angora Creek, which were reflected in shifts in BMI community composition away from pre-fire values. Although the Angora Fire severely burned a large extent of the watershed area, the first year following the fire had low precipitation (79 cm, relative to the 26-year average of 117 cm), whereas the second year following fire had higher

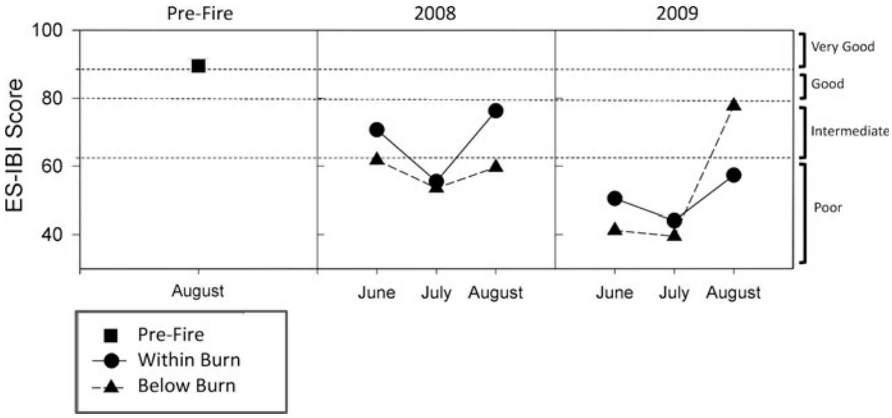

Fig. 5 Eastern ES-IBI scores for Within Burn and Below Burn sites. *Dotted lines* represent thresholds for various levels of stream ecosystem condition

precipitation (103 cm) and stream discharge, and resulted in a higher amount of sediment transport (Oliver et al., 2011). In comparison to pre-fire conditions, temperatures were also higher in Angora Creek as a result of both lower summer stream flow and canopy loss leading to greater solar insolation. These factors increase stress to certain taxonomic groups and can shift abundances within the BMI community. We observed declines in density and percentage of sensitive species immediately following the fire, and declines in Shannon diversity and EPT taxa richness in the second year following the fire, which were likely a result of the higher discharge and sediment loads in that year. These findings are corroborated by numerous other studies that have documented short-term decreases in BMI density, taxa richness, and diversity following severe wildfire and hydrological disturbance (e.g., Roby & Azuma, 1995; Earl & Blinn, 2003; Hall & Lombardozzi, 2008). However, our study demonstrates that significant changes in BMI communities can be observed even without large post-fire flooding and also that these effects can be transmitted downstream to unburned reaches.

Notable short-term changes in the relative abundances of functional feeding groups following the fire further indicated shifts in the availability of resources and habitat. Community composition became increasingly dominated by opportunistic taxa with strong larval dispersal capable of exploiting a variety of feeding strategies over a wide range of aquatic conditions. The most abundant of these taxa were gatherers, opportunistic omnivores that feed using a variety of methods. More specialized feeders, such as shredders and scrapers, decreased in abundance. These observations are consistent with previous studies where fire effects were shown to alter functional feeding group abundances and favor community dominance by trophic generalists (Mihuc & Minshall, 1995; Minshall et al., 2001a; Vieira et al., 2004). These results also support general predictions about functional feeding groups, which suggest that shredders will respond to the loss of riparian canopy.

In contrast to previous observations where increased light availability and nutrient flux following canopy loss tended to favor periphyton growth, and thus increase scraper abundances (Minshall et al., 2001c), we observed a severe decline in scraper abundance in Angora Creek for both years following the fire. The increase in fine sediment deposition following the fire may have inhibited periphyton growth necessary to support higher scraper abundances. The abundance of filterer groups also declined in the second year following fire. While filterers are also considered generalist feeders, these groups tend to have more specific food source requirements, and require adequate flows for transporting food sources (Hawkins & Sedell, 1981). In addition, detritus particle size may also play a role in supporting the abundance of certain filterer taxa (Drake, 1984). Increased stream flow has the capacity to transport larger particle sizes, therefore detritus dynamics in the second year following fire may have been less favorable for filterer groups than conditions during the lower-flow year immediately following fire. Alternatively, higher snowpack and a larger volume of snowmelt flushing in the second year may have depleted the standing stock of suitable detritus early in the season (Stubblefield et al., 2007) resulting in a deficit of food resources for filterers later in the summer.

Changes in BMI community composition result from the interaction of species, species traits, environmental variables, and hydrologic conditions (e.g., Townsend, 1989; Poff, 1997). Ordination and MRPP tests of Angora Creek community samples illustrated that post-fire communities were very distinct from pre-fire communities at the Within Burn site, despite significant seasonal variability in post-fire samples. In addition, the trajectory of BMI communities following the fire continued to diverge from pre-fire configurations along NMS axis 1 until August 2009, the second year after the fire. Habitat factors that were strongly correlated with this shift in community structure (e.g., reduced cobble and woody debris cover, increased fine substrate and algae cover) imply that Angora Creek was still experiencing indirect effects from the fire after 2 years. The continued divergence of the BMI community from pre-fire conditions and deteriorating in-stream biotic conditions indicate that the resilience of BMI communities to environmental stress in Angora Creek may have declined further in the second year, although that decline may have begun to reverse during our last sampling period (August 2009). Longer-term studies have observed that in small streams with well-managed and intact watersheds, divergence from pre-fire conditions may persist from 1 to 10 years, and high within-year variability may continue for an unknown (>15 years) length of time (Roby & Azuma, 1995; Mihuc et al., 1996; Minshall et al., 2001b, c). We report significant community changes for at least 2 years following the Angora fire, but further sampling is needed to determine if recovery indeed began in August 2009.

Numerous individual species contributed to the strong community distinction between pre- and post-fire samples at the Within Burn site. Perhaps unsurprisingly, many of the 22 pre-fire indicator taxa are sensitive EPT species including a number of shredders such as the stoneflies *Yoraperla*, *Malenka, Zapada,* and Capniidae, and the caddisfly *Heteroplectron californicum.* Thus, shredder stoneflies appear to be especially sensitive to wildfire-driven stream disturbance. Nemourid stoneflies, such as *Malenka* and *Zapada*, were eliminated from a New Mexico stream following a severe wildfire and post-fire floods, and remained rare for at least several more years despite the abatement of severe floods (Vieira et al., 2004). At Angora Creek, only six taxa were indicative of post-fire Within Burn samples, including three midge taxa (Chironomidae) and the blackfly *Simulium*; none of these taxa were shredders or scrapers, but rather were omnivores, gatherers, filterers, and predators. Both midges and blackflies have been previously identified as opportunistic taxa that can reach quite high densities immediately following riparian wildfires (both taxa: Vieira et al., 2004; midges: Mihuc et al., 1996; Minshall et al., 2001c) and these increased densities may last for several years (Malison & Baxter, 2010). However, unlike previous studies where increased predator populations were associated with increased productivity and density of primary consumers such as Chironomidae and *Simulium* (Malison & Baxter, 2010), we observed only a slight increase in predator populations in the second year following fire. The only sensitive post-fire indicator taxon at Angora Creek was the stonefly *Isoperla*. Vieira et al. (2004) noted that although *Isoperla* abundance was severely reduced immediately following fire, they were prominent community members soon after post-fire floods abated. Since Angora Creek did not experience significant flooding immediately following the fire, perhaps *Isoperla* was able to establish much quicker in the post-fire Within Burn reach.

The decline in the ES-IBI of Angora Creek over the 2 years following the Angora Fire indicated that, in comparison to pre-fire conditions, Angora Creek exhibited degraded conditions and reduced biological integrity. While we acknowledge that local reference sites can sometimes provide useful information for comparisons, they can also be problematic due to particular differences between sites that limit extrapolation and the ability to calculate variance estimates (Reynoldson et al., 1995). In this analysis, changes at Angora Creek were compared both to the state of the stream before fire, and to regional reference streams that represent a variety of habitat types, encompassing the range of variations expected for least-impaired reference conditions in the region. While certain individual metrics of community composition indicate deviation from pre-fire conditions, and in some cases high variability between months and years, overall the average values of individual metrics were not statistically different from 2008 to 2009. The large decrease from the pre-fire ES-IBI scores and seasonal changes in 2008–2009 indicates that the multi-metric index may be more informative about recovery than single metrics.

Changes in environmental conditions and resource availability within a stream following wildfire can be highly variable due to inherent differences between individual streams and watersheds (Vieira et al., 2004; Pettit & Naiman, 2007; Jackson et al., 2009). In general, larger effects tend to be observed in small, first-order streams, similar to Angora Creek (Minshall et al., 2001b, c; Hall & Lombardozzi, 2008). This study provides information on the short-term effects of a severe fire on high-elevation aquatic benthic macroinvertebrates in the context of low precipitation years. While we acknowledge the short-term nature of our study, it does represent an important snapshot of post-fire conditions and initial recovery, or lack thereof, in the first 2 years following the severe Angora fire. We demonstrate that post-fire BMI communities and physical habitat can shift dramatically from pre-fire conditions despite the lack of post-fire flooding disturbance, which is often determined to be the primary driver of post-fire biotic community responses. Since wildfire often occurs suddenly and without warning, researchers should design studies that can be rapidly implemented to track community responses to these unpredictable events (e.g., Lindenmayer et al., 2010) within and below burned areas and should utilize multi-metrics like indices of biological integrity when available. To effectively reintroduce wildfire as a natural process to Sierra Nevada ecosystems, it is necessary to consider the potential short- and long-term effects of fire on high-elevation headwater streams and the impact of these events on the overall resilience and recovery of aquatic ecosystems.

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