

Short-term effects of wildfire on Patagonian headwater streams

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Abstract. In March–April 2015, the El Cristo fire burned 1228 ha of mixed *Nothofagus* forest in Los Alerces National Park (Argentine Patagonia). We compared physicochemical variables and community structure of burned and unburned headwater streams. Sampling began shortly after the fire was extinguished and comprised periodic water quality assessments and four visits to collect periphyton and invertebrate samples (May, August, October and December). Water temperature, total dissolved solids, total suspended solids and specific conductance were significantly higher in burned sites, whereas nutrient and oxygen concentrations exhibited no major differences. Chlorophyll *a* (used as a surrogate for autotrophic periphyton biomass) also did not differ significantly. Macroinvertebrate richness, abundance and diversity showed no differences across sites, but taxonomic composition and densities of sensitive taxa were markedly lower at burned streams. Oligochaetes and amphipods, however, were significantly more abundant in the disturbed reaches. Analysis of functional feeding groups revealed that the relative abundances of shredders and collector-filterers were lower at burned sites, possibly reflecting a shift in detrital input.

Additional keywords: fire, functional feeding groups, low-order streams, macroinvertebrate communities, total suspended solids.

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Introduction

Wildfires are considered major agents of landscape change and their effects on terrestrial communities are instantly visually apparent. However, the profound influence wildfires exert on aquatic ecosystems, both directly and indirectly, is not as easily recognised (Lyon and O'Connor 2008). Fire has a stronger influence on headwater streams than on large rivers because a greater proportion of the catchment is burned, and the ratio between stream margin and water volume is higher (Mellon *et al.* 2008). Direct effects arise from increased water temperatures and alterations in water chemistry and food quality, whereas long-term changes include chemical responses and variations in the relative abundances of macroinvertebrate species (Robinson and Minshall 1991; Gresswell 1999; Neary *et al.* 2005; Koetsier *et al.* 2010). Return to pre-fire conditions typically follows overstorey vegetation recovery, usually occurring within a few years or decades (Rhoades *et al.* 2011).

Several post-fire processes increase the rates of riverbank and watershed erosion. In particular, the partial or complete removal of the protective cover (forest floor) leaves the soil susceptible to raindrop impact and reduces water storage, thus allowing erosive overland flow to occur more readily on the soil surface (Tronstad *et al.* 2013). Several researchers agree that this is one of the most important factors leading to increased post-fire erosion (Johansen *et al.* 2001; Shakesby and Doerr 2006;

Larsen *et al.* 2009). Furthermore, extreme heating can cause some soils to develop a hydrophobic layer, therefore creating a higher probability of surface runoff (DeBano 1981, 2000). Post-fire sediment yields are generally highest in the first year after burning, especially when the watershed has been exposed to large rainfall events immediately after the fire (Neary *et al.* 2005). The deleterious effects of high suspended-solid loads on stream macroinvertebrates have been well documented (Ryan 1991; Wood and Armitage 1997). High and sustained levels of sediment may cause permanent alterations in community structure, diversity, density, biomass, growth, and rates of reproduction and mortality. Impacts on individuals, populations and communities are expressed through alterations in local food webs and habitats (Henley *et al.* 2000). As stated by several authors (e.g. Ryan 1991; Wood and Armitage 1997; Wood *et al.* 2005), increased sediment concentrations (1) affect respiration owing to the deposition of silt on respiration structures, (2) alter feeding activities by impeding filter feeding and reducing the food value of periphyton, (3) increase drift owing to substrate instability, and (4) reduce habitat availability owing to clogging of interstitial space.

Riparian vegetation loss has additional effects on lotic environments. Severe wildfires can function like timber clearcuts, raising the temperature of the channel owing to direct heating of the water surface, which in turn can stimulate

biological activity (Kiffney *et al.* 2003). Increased algal production may result in a trophic cascade of more grazing aquatic macroinvertebrates and greater food availability to predators (Mellon *et al.* 2008). Detritus consumers (i.e. shredders), however, are expected to show the opposite response, resulting in a shift from heterotrophic- to autotrophic-based food webs (Minshall *et al.* 1997; Mihuc and Minshall 2005; Vieira *et al.* 2011; Tronstad *et al.* 2013). Moreover, water temperature (degree days) is recognised as one of the key factors shaping lotic ecosystems and determining life history characteristics of stream macroinvertebrates. Respiration, embryonic development, nymphal growth, emergence, terminal body size and survivorship of certain taxa are believed to be temperature-dependent (Wallace 1990; Demars *et al.* 2011; Li *et al.* 2013).

In Los Alerces National Park (LANP; north-western Patagonia), the peak fire season typically occurs during the summer months of December to March. This period coincides with low precipitation and air humidity, and the average daily temperature for this period is 14°C (Monjeau *et al.* 2006). Fire season is followed by a typically rainy winter, meaning that the denuding of watersheds by wildfire is followed by heavy precipitation and runoff into the streams. The El Cristo fire was an intense, unprescribed human-started fire, which burned through 1228 ha of native forest in LANP (March–April 2015). Fire frequency in the region has increased in the last years (Mohr Bell 2015). However, only a single study (Temporetti 2006) has investigated the responses of water courses to this type of disturbance. The present paper discusses the short-term effects of the fire on stream properties, macroinvertebrate assemblages and functional feeding groups in headwater streams. The data obtained from four affected sites was compared with information from reference streams. Given the critical importance of water courses as biodiversity hotspots, understanding the effects of fire is crucial to biodiversity conservation and protection (Bixby *et al.* 2015). We propose answering the following questions: (1) which were the main environmental changes in burned streams? (2) Did the macroinvertebrate faunas of burned reaches differ in terms of taxonomic composition and functional feeding groups from those of nearby undisturbed streams? And (3) how do the short-term effects of wildfire compare with previous research conducted in other regions of the world?

Methods

Study area

LANP lies in the north-west of Chubut province, Argentina, and incorporates 263 000 ha, of which 187 500 ha are a national park, and the remainder a national reserve (Kutschker *et al.* 2015). The national reserve was conceived as a buffer zone where regulated uses are permitted (e.g. livestock-raising and tourism) (Martin and Chehébar 2001). Climatically, the region belongs to a cold-temperate humid type; the mean annual temperature is 8°C and precipitation occurs mainly from April to October, with snow falling in winter (June to September). Summers are dry and warm (Monjeau *et al.* 2006). The area is characterised by abrupt relief, high snow-capped peaks and many glaciated valleys with large glacial lakes. The distribution of vegetation is controlled by two main factors: rainfall, which decreases abruptly from west to east (from 3000 to 800 mm), and

temperature, which decreases with altitude (de Pietri 1995). LANP has been classified into two phytogeographical provinces: Sub-Antarctic and High Andean (Cabrera and Willink 1980). Sub-Antarctic forests are dominated by pure or mixed stands of *Austrocedrus chilensis* (D. Don) Pic. Serm. and M.P. Bizzarri, *Fitzroya cupressoides* (Molina) I.M. Johnst., and several species of *Nothofagus*, whereas the High Andean Province is characterised by a mosaic of grasses, shrubs and forbs of limited cover like *Chusquea culeou* Desvaux and *Aristotelia chilensis* (Molina) Stuntz.

Six study sites, consisting of 50-m reaches, were selected in six fishless headwater streams ranging from 553 to 587 m above sea level (asl) in elevation. Sites were classified into three groups based on their location. Reference streams (R; $n = 2$) were located entirely outside the burned area; within-burn streams (WB; $n = 3$) were located within the fire perimeter, and a single below-burn site (BB; $n = 1$) was located downstream of the riparian burned area (Fig. 1). An unbalanced design was unavoidable given the availability and accessibility of streams within and outside the fire perimeter. Care was taken in choosing burned and reference sites comparable in channel morphology, discharge and riparian vegetation. Reference and below-burn sites had an undisturbed riparian zone, with high canopy cover (>60%) and generally a well-structured community; the riparian vegetation was dominated by native species (see previous paragraph), and the understorey consisted of grasses and herbs. Within the fire perimeter, riparian vegetation was severely affected (i.e. stand-replacing fire).

Sampling

Sampling began in May 2015, 2 weeks after the fire was extinguished. The six streams were visited seasonally during 2015 (May, August, October and December) for site characterisation and for periphyton, nutrient and macroinvertebrate sampling. Additionally, water temperature, pH, specific conductance, salinity, oxygen saturation, dissolved oxygen and total dissolved solids (TDS) were measured 11 times throughout the year using a Hach sensION multiparametric probe; total suspended solids (TSS) were measured gravimetrically from water samples (Elosegui and Butturini 2009).

Wet width was determined using a laser distance meter, current velocity was measured by timing a float as it moved over a distance of 5 m (average of three measurements), and average depth was estimated from five equally spaced measurements with a calibrated stick along three transverse profiles across the channel. Discharge was obtained by combining depth, width and current velocity (Gordon *et al.* 2004). The following classification of substratum particle sizes (modified Wentworth scale) was used: (1) sand (diameter <0.2 cm), (2) gravel (0.2–6 cm), (3) pebble (6–12.8 cm), (4) cobble (12.8–25 cm), and (5) boulder (>25 cm). For nutrient assessment, three water samples were collected below the water surface, kept at 4°C and transported to the laboratory for analysis. Nitrate (NO_3^-), nitrite (NO_2^-), ammonia (NH_4^+) and soluble reactive phosphate (SRP) were determined using standard methods (APHA 1999). Attributes of the riparian vegetation were examined once (December) at each site employing an adaptation of the QBR index (qualitat del bosc de ribera or riparian corridor quality index; Munné *et al.* 2003) for Patagonian streams: the QBRp (Kutschker *et al.* 2009). This

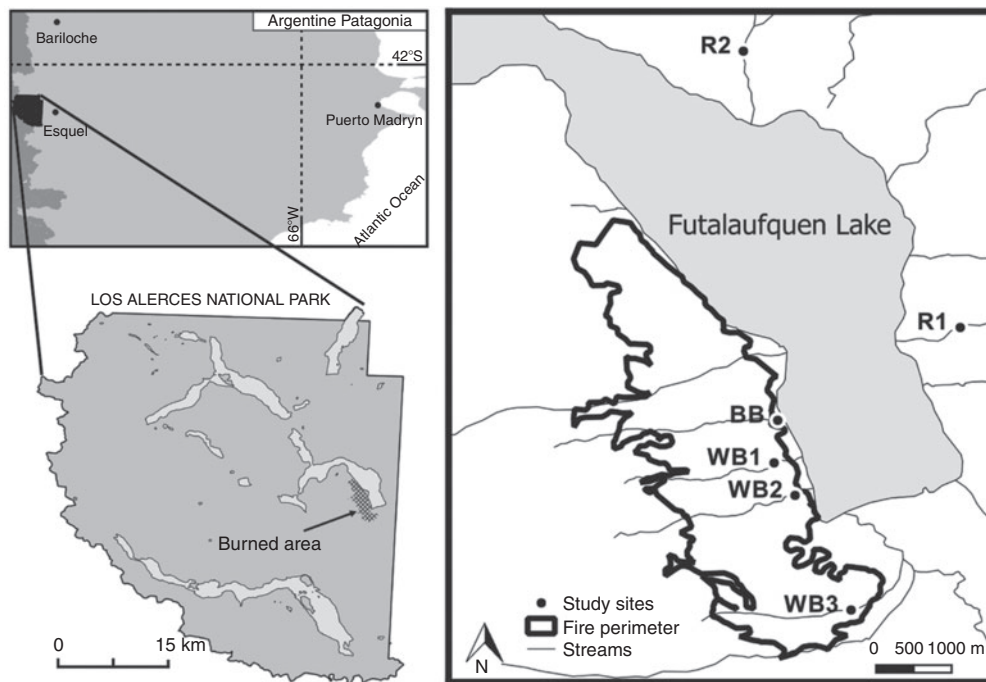


Fig. 1. Location of the El Cristo fire and sampling locations within the Los Alerces National Park. WB = within-burn; BB = below-burn; R = reference.

index evaluates the quality of the riparian corridor and considers four parameters (1) degree of cover; (2) structure, and (3) quality of the vegetation; and (4) degree of naturalness of the channel. The total QBRp score ranges from 0 to 100 points; values below 25 indicate extreme degradation whereas values over 90 indicate a good quality riparian forest. Summer represents the ideal period for this type of assessment because vegetation cover is at its peak and deciduous species are easy to identify. Habitat quality was evaluated using the habitat condition index (HCI) for high gradient streams proposed by Barbour and others (1999), which evaluates the ability of the stream's physical habitat to support a given fauna. This method ranks 10 channel features from 0 to 20. A score of 200 points indicates that the river is in its best possible condition.

Three periphyton samples were collected from riffles at each site. Each sample consisted of the scraped material from three randomly selected rocks. Samples were preserved in water from the site and cooled while transported in dark containers to the laboratory, where they were filtered on Whatman GF/F filters. Chlorophyll *a* was extracted from filters in 90% acetone and measured spectrophotometrically with pheophytin correction according to standard methods (APHA 1999; Hauer and Lamberti 2007). We were unable to collect periphyton samples at site WB3 because we found no suitable rocks nearby. Quantitative macroinvertebrate samples were taken with a modified Surber sampler (250- μ m pore size) with a 0.09-m² sampling area. At each site, three subsamples from riffles ($n = 3$) were collected along a 50-m reach. Owing to the size of the study streams, pool habitats were poorly represented and, thus, were not considered here. All samples were fixed with 4% formaldehyde and sorted under 5 \times magnification in the laboratory. Invertebrates were

stored in 70% ethyl alcohol. Individuals were identified to the lowest possible taxonomic level, usually species or genus but family for some groups, for example, Oligochaeta and some Diptera. Functional feeding groups (FFGs) were assigned using available references (Merritt and Cummins 1996; Domínguez and Fernández 2009). Whenever literature assigned two or more FFGs to a single taxon, gut content analysis and expert opinion were employed to choose the most relevant one. Abundance data from the three benthic subsamples were pooled together and used to calculate different community descriptors, including rarefied taxa and EPT (Ephemeroptera, Plecoptera and Trichoptera) richness, total density and Shannon's diversity index. Percentage and total density of each FFG were also obtained. Benthic organic matter, collected in conjunction with macroinvertebrate samples, was classified into fine particulate organic matter (FPOM, 250–1000 μ m) and coarse particulate organic matter (CPOM >1000 μ m), wood, leaves, bryophytes and charcoal. All fractions were dried (50°C, 24 h) and weighed on an electronic balance to ± 0.003 g.

Data analysis

Several factors, including time, influence the effects of wildfire on aquatic ecosystems. However, we were forced to use a comparative, univariate analytical framework because low replication reduced the statistical power to detect differences with a multivariate approach; furthermore, the single below-burn site was excluded from statistical analyses owing to lack of replicates. The effects of the two remaining categories (reference, within-burn) on physicochemical and biological variables were tested using a series of single-factor Kruskal-Wallis tests, where streams were the unit of replication. Associations

between environmental variables and community descriptors (e.g. total density, rarefied taxa richness) were tested with Spearman rank correlation. The distribution pattern of the sampling units (SU: *site* × *date*), based on environmental characteristics, was analysed using principal component analysis (PCA; Ter Braak and Smilauer 1998).

Results

Environmental variables

The main characteristics of the sampled reaches are presented in Table 1. The range of discharge was narrower (from 0.005 to 0.33 m³ s⁻¹) at within- and below-burn sites. At most sites, the substrate particle size was mainly large and small cobbles, although gravel was also present at sites WB2 and WB3.

As expected, stream shade was higher at canopied sites (both reference and below-burn). This resulted in a significantly lower water temperature at reference sites in comparison with that registered at within-burn sites (Kruskal–Wallis, *P* < 0.005) (Fig. 2). Mean specific conductance ranged between 14.8 and 409 μS cm⁻¹, within-burn sites having significantly higher conductivity values than reference sites (Kruskal–Wallis, *P* < 0.005); salinity showed a similar pattern (Kruskal–Wallis, *P* < 0.005). Variables commonly linked to watershed erosion (i.e. TSS, TDS) were markedly higher at within-burn sites. A strong increase in mean TSS values in the water column was detected at within-burn sites (Kruskal–Wallis, *P* < 0.005), particularly at site WB3, where mean TSS values were 20 times higher than reference values. Oxygen saturation (%SAT) and dissolved oxygen (OD) contents did not differ significantly across stream categories (Kruskal–Wallis, *P*_{%SAT} = 0.63; *P*_{OD} = 0.21). Nutrient concentrations were not meaningfully affected by the fire, as no significant differences were observed between sites.

QBRp scores showed that within-burn sites had strong riparian alterations, whereas below-burn and reference sites showed no signs of fire disturbance (Fig. 3). Values of riparian vegetation coverage, structure and quality approached 0 at site WB3, because both the understorey and the canopy were completely consumed by the fire. In contrast, some dead trees still remained standing at the other two within-burn sites. HCI was optimal at sites BB and R1, suboptimal at R2, and marginal at all within-burn sites. The main alteration detected in the studied reaches was riverbank erosion due to the lack of vegetation cover. Mean amounts of chlorophyll *a* (considered indicative of the actual periphyton standing crop) were highly variable at the below-burn site (Fig. 4); chlorophyll *a* levels showed a substantial increase during August and October, followed by a major reduction in December. Conversely, chlorophyll *a* production remained constant at all time intervals at within-burn sites, while it progressively decreased at reference sites during the same time period. Differences among within-burn and reference sites, however, were not statistically significant (Kruskal–Wallis, *P* = 0.8). Within-burn sites contained significantly larger quantities of CPOM, FPOM and charcoal than reference sites (Kruskal–Wallis, *P* < 0.05) (Table 2). In contrast, leaves and woody debris showed no significant differences between reaches. Bryophytes dry mass was significantly lower at within-burn sites and no bryophytes were found at the WB2 and WB3 sites during the study.

Table 1. Environmental variables registered at the six studied sites

Data are annual means, ranges are given in parentheses. Only statistically significant relationships are shown (*P* < 0.005 for Kruskal–Wallis test); site BB was not included in the analysis owing to lack of replicates. TDS = total dissolved solids; TSS = total suspended solids; SRP = soluble reactive phosphorus. Sample size was *n* = 4 for water velocity, discharge, substrate size, NO₂, NO₃, NH₄ and SRP; *n* = 11 for water temperature, specific conductance, TDS, TSS, salinity, pH, dissolved oxygen and oxygen saturation; and *n* = 12 for chlorophyll *a*; L, pebble = large pebble; S, pebble = small pebble

Site Variable	WB1	WB2	WB3	BB	R1	R2	Relationship
Water velocity (m s ⁻¹)	0.2 (-)	0.3 (0.11–0.5)	0.14 (0.12–0.18)	0.72 (0.6–0.85)	0.61 (0.4–0.85)	1.03 (0.3–1.7)	R > WB
Discharge (m ³ s ⁻¹)	0.07 (0.01–0.25)	0.1 (0.008–0.3)	0.01 (0.005–0.01)	0.22 (0.11–0.33)	0.38 (0.14–0.72)	1.07 (0.06–1.71)	R > WB
Substrate size	L, pebble, s, pebble	S, pebble, gravel	S, pebble, gravel	L, pebble, s, pebble	L, pebble, s, pebble	L, pebble, s, pebble	-
Water temperature (°C)	8.56 (5.7–14.4)	7.97 (5.6–12.4)	10.34 (7.7–15.4)	7.01 (4.4–13.5)	5.39 (3.7–8.8)	4.63 (2.2–8.6)	WB > R
Specific conductance (μS cm)	58.5 (46–110)	62.8 (46.6–120)	237.47 (111.1–409)	63.69 (40.9–78)	19.08 (14.8–23.2)	19.36 (14.83–25.9)	WB > R
TDS (mg L ⁻¹)	40.5 (33.7–77.5)	44.63 (33.8–88)	165.59 (79.6–259)	46.42 (25.6–54.1)	14.49 (10.4–19.15)	14.6 (9.9–18.5)	WB > R
TSS (mg L ⁻¹)	6.47 (0.2–14.2)	6.49 (1.94–14)	23.28 (0.14–52.78)	4.47 (0.6–31.4)	1.89 (0.21–5.26)	1.84 (0.26–3.67)	WB > R
Salinity (‰)	0.15 (0.1–0.2)	0.16 (0.1–0.2)	0.2 (0.1–0.3)	0.17 (0.1–0.3)	0 (-)	0 (-)	WB > R
pH	7.17 (5.58–7.97)	7 (5.63–7.79)	6.85 (5.76–7.55)	7.31 (6.2–7.83)	7.35 (6.24–8.02)	7.21 (5.76–8)	-
Dissolved oxygen (mg L ⁻¹)	11.13 (7.54–15.6)	11.24 (8.12–14.44)	10.72 (5.2–14.3)	12.06 (7.75–20.7)	12.81 (9.22–16.66)	12.96 (10.05–16.2)	-
Oxygen saturation (%)	93.42 (63–115.3)	94.29 (67.5–115.3)	92.63 (44.8–116.6)	96.83 (63.5–118.1)	99.22 (70.3–118.1)	100.75 (75.3–117.1)	-
Chlorophyll <i>a</i> (μg cm ⁻²)	0.17 (0.098–0.3)	0.16 (0.05–0.23)	-	0.54 (0.087–0.88)	0.36 (0.029–0.71)	0.2 (0.044–0.47)	-
NO ₂ (μg L ⁻¹)	23.33 (10–40)	26.66 (20–40)	30 (20–40)	20 (-)	16.66 (10.0–20.0)	20 (-)	-
NO ₃ (μg L ⁻¹)	4106.66 (3080–4840)	4363.33 (2970–6160)	3520 (3080–4400)	3520 (2640–4840)	3626.66 (2960–4400)	3666.66 (3080–3960)	-
NH ₄ (μg L ⁻¹)	26.66 (10–60)	6.66 (0–10)	10 (0–20)	6.66 (0–10)	16.66 (10–30)	10 (0–20)	-
SRP (μg L ⁻¹)	343.33 (20–870)	616.66 (40–1670)	486.66 (20–1410)	310 (60–770)	136.66 (40–240)	233.33 (90–310)	-

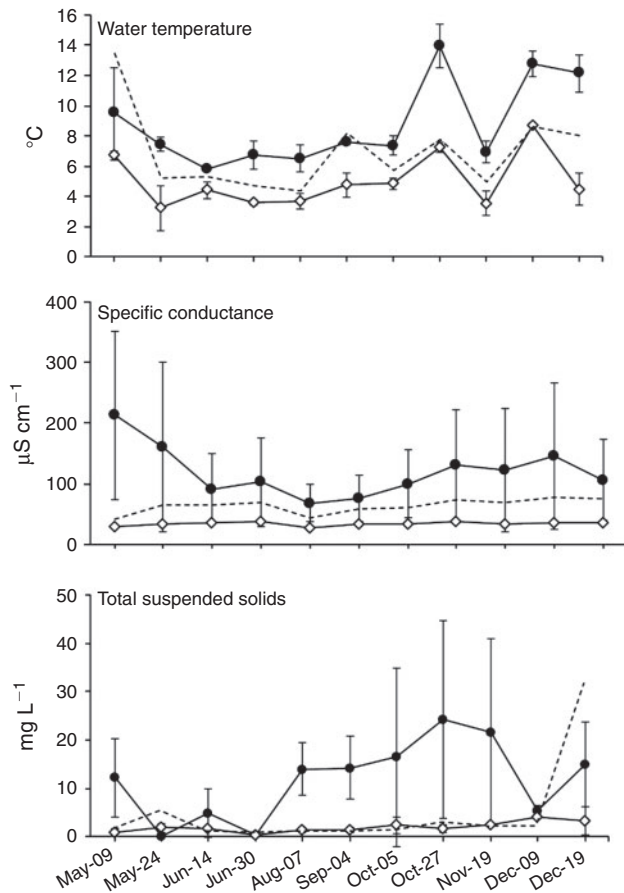


Fig. 2. Mean temporal variation of selected environmental variables at the six studied sites. Error bars represent standard deviation between replicates. Sample size was $n = 3$ for within-burn sites (closed circles), $n = 1$ for the below-burn site (dashed line), and $n = 2$ for reference sites (open diamonds).

PCA of environmental data showed that the first and second axis explained 74 and 14% of the variability of the SUs respectively. PCA1 described a clear environmental gradient, with reference SUs on the positive end of the axis, and within-burn SUs on the negative side. Reference streams were characterised by high dissolved oxygen levels and low TSS, salinity, specific conductance and water temperature values, whereas within-burn streams were associated with high levels of TSS, specific conductance, water temperature and salinity (Fig. 5). Most of the below-burn sampling units showed an intermediate position, located on the lower-left quadrant, and were associated with high chlorophyll *a* values (Fig. 5).

Macroinvertebrates

We collected a total of 53 taxa from all sites, of which 50 were insects from six orders: Coleoptera, Diptera, Ephemeroptera, Mecoptera, Plecoptera and Trichoptera. The groups Oligochaeta (*Lumbricidae* sp.), Turbellaria (*Cura* sp.) and Amphipoda (*Hyalella araucana*) comprised the rest of the community. Diptera was the most abundant taxon across the five streams (48 to 67%), with the exception of site WB3, where oligochaetes accounted for 65% of the community (Fig. 6). Likewise, the

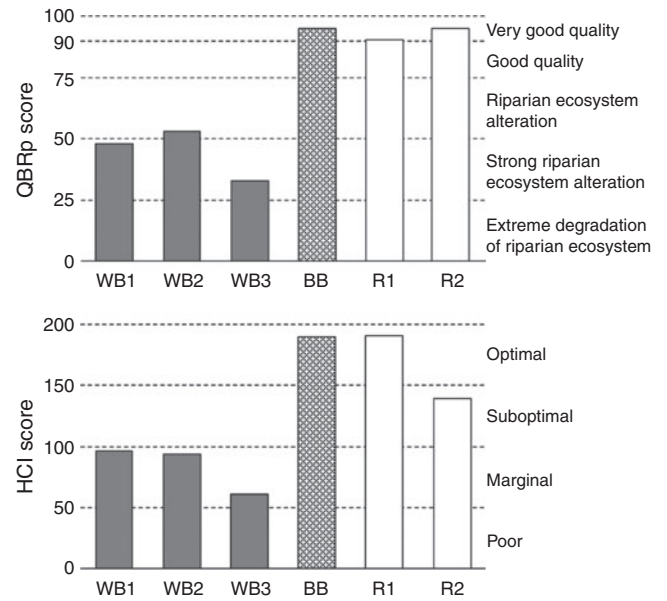


Fig. 3. Riparian corridor quality index (upper), and habitat condition index (lower) at the six studied sites. WB = within-burn; BB = below-burn; R = reference.

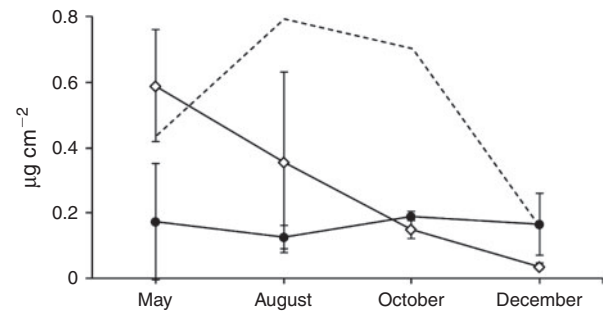


Fig. 4. Temporal variation of mean chlorophyll *a* concentration in periphyton samples. Error bars represent standard deviation between replicates. Sample size was $n = 6$ for within-burn sites (closed circles), $n = 3$ for the below-burn site (dashed line), and $n = 6$ for reference sites (open diamonds).

greatest taxa richness occurred in the order Diptera, which contained representatives of 24 taxa, followed by Trichoptera (17), Plecoptera (4) and Ephemeroptera (4) (see Appendix 1).

Assemblages at reference sites were mainly composed of dipterans and EPT taxa. Amphipods were absent from R1 and R2, although they were well represented at sites WB1 (30%) and WB2 (30%). The remaining groups, Mecoptera, Coleoptera and Turbellaria, were the least abundant, with combined percentages ranging between 0 and 4%. Invertebrate density ranged from 100 to 3155 individuals m^{-2} , with the mean value being 1034 for within-burn, 1211 for below-burn, and 892 for reference sites. Mean taxa richness was greater in reference streams (7.71) than in below-burn (6.75) or within-burn sites (6.01) (see Appendix 1). Four taxa, *Dactylophlebia carnulenta*, *Tipula* sp., *Paratrichocladius* sp. and *Nannochorista* sp., were found exclusively in fire-affected streams (both WB and BB sites). Shannon's

Table 2. Benthic organic matter collected at the six studied sites

Data are annual means (g m^{-3}), percentages of the total amount are given in parentheses. Only statistically significant relationships are shown ($P < 0.005$ for Kruskal–Wallis test); site BB was not included in the analysis due to lack of replicates. Sample size was $n = 4$. WB = within-burn; BB = below-burn; R = reference. FPOM = fine particulate organic matter; CPOM = coarse particulate organic matter

	WB1	WB2	WB3	BB	R1	R2	Relationship
Bryophytes	1.13 (0.8)	0	0	6.87 (9.25)	1.68 (5.4)	4.09 (9.94)	R > WB
Leaves	10.65 (7.54)	7.59 (9.14)	3.37 (0.72)	12.92 (17.41)	3.86 (12.41)	4.95 (12.05)	–
Wood	37.61 (26.62)	18.48 (22.24)	71.64 (15.32)	25.07 (33.79)	16.72 (53.69)	25.44 (61.89)	–
Charcoal	16.88 (11.95)	26.48 (31.87)	70.53 (15.09)	4.15 (5.59)	0	0	WB > R
FPOM	39.59 (28.02)	23.46 (28.24)	177.51 (37.96)	10.61 (14.3)	5.44 (17.49)	3.33 (8.11)	WB > R
CPOM	35.41 (25.06)	7.06 (8.5)	144.52 (30.91)	14.59 (19.66)	3.43 (11.02)	3.29 (8.01)	WB > R

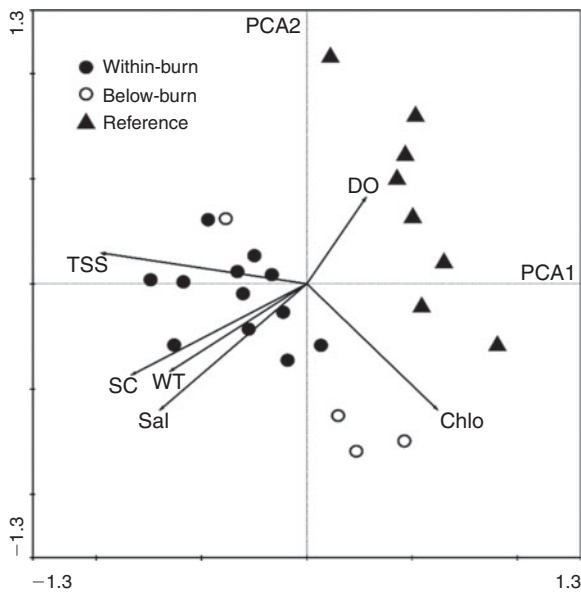


Fig. 5. Plot of principal component analysis (PCA) axes 1 and 2 for environmental data of 24 sampling units ($\text{site} \times \text{date}$). Percentage of total variation as follows: PCA1 = 74%; PCA2 = 14%. Chlo = chlorophyll α ; DO = dissolved oxygen; Sal = salinity; SC = specific conductance; TSS = total suspended solids; WT = water temperature.

diversity was lower for within-burn streams (1.38) than below-burn or reference sites (1.55 and 1.38 respectively). Differences in density, rarefied taxa richness and Shannon were not significant (Kruskal–Wallis, $P_{\text{abundance}} = 0.33$; $P_{\text{richness}} = 0.25$; $P_{\text{diversity}} = 0.54$). EPT relative abundance was significantly lower at within-burn than reference sites (all dates combined), whereas the non-insect taxa (NIT) showed the opposite response (Kruskal–Wallis, $P_{\text{EPT}} < 0.005$; $P_{\text{NIT}} < 0.005$). Spearman correlation analysis indicated that EPT abundance decreased with TDS, salinity and FPOM, whereas NIT showed a positive correlation with the same variables. NIT also increased with TSS, water temperature, CPOM and charcoal (Table 3).

In terms of trophic structure, WB1 and WB3 were characterised by communities amply dominated by collector-gatherers (WB1 = 71%; WB3 = 88%), mostly *Hyallela araucana* and *Lumbricidae* sp. WB2 exhibited an approximately even distribution of collector-filterers (53%) and collector-gatherers

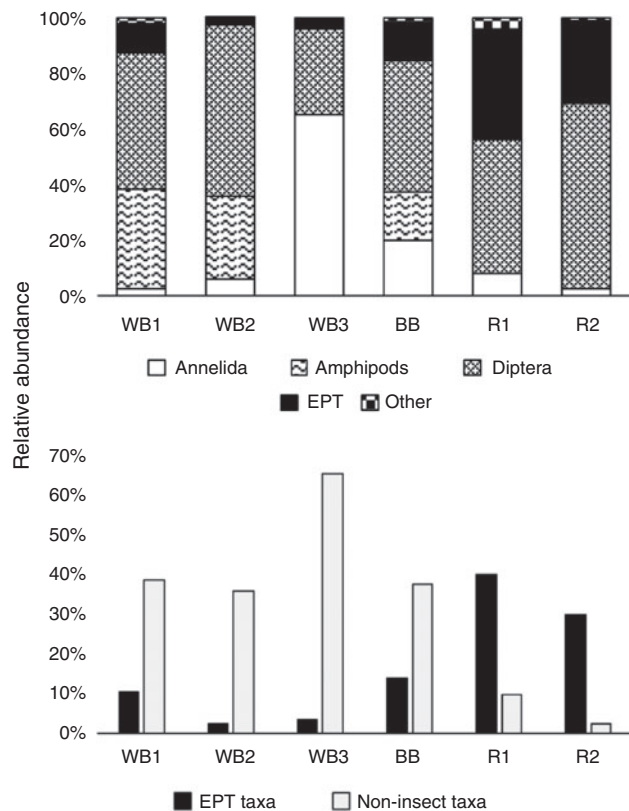


Fig. 6. Relative abundance of major macroinvertebrate taxa (upper) and relative abundance of Ephemeroptera, Plecoptera and Trichoptera taxa (EPT) and non-insect taxa (lower) in the six studied reaches ($n = 4$). ‘Other’: Turbellaria, Coleoptera and Mecoptera. WB = within-burn; BB = below-burn; R = reference.

(44%). BB showed a similar pattern to WB2, but with a slightly higher percentage of shredders and scrapers (Fig. 7).

At reference sites, shredder abundance was significantly higher, reaching 27% of the total density at R1 (Kruskal–Wallis, $P = 0.005$); conversely, collector-gatherer numbers were significantly lower at the same sites (Kruskal–Wallis, $P = 0.04$). Collector-filterers were the predominant group, accounting for 41 and 67.5% of the total density at sites R1 and R2 respectively. Predators were present in all six streams, although in low numbers (0.8 to 5%).

Table 3. Spearman's rank correlation coefficients relating environmental variables and community parameters

Only statistically significant values are shown ($P < 0.005$). WT = water temperature; SC = specific conductance; TDS = total dissolved solids; TSS = total suspended solids; Sal = salinity; Sat = oxygen saturation; Chlo = chlorophyll *a*; Brio = bryophytes; FPOM = fine particulate organic matter; CPOM = coarse particulate organic matter; Ch = charcoal; Vel = water velocity; Dis = discharge; SRP = soluble reactive phosphorus; EPT = Ephemeroptera, Plecoptera, and Trichoptera; NIT = non-insect taxa; P = predators; Sh = shredders; Sc = scrapers; CG = collector-gatherers; CF = collector-filterers

	WT	SC	TDS	TSS	Sal	Sat	Chlo	Brio	FPOM	CPOM	Ch	Vel	Dis	NO ₃ ⁻	NH ₄ ⁺	SRP
Richness	-	-	-	-	-	-	-	0.50	-	-	-	-	-	-0.43	-	-
Density	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diversity	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
%EPT	-0.63	-	-0.65	-	-0.74	-	-	-	-0.49	-	-0.69	0.63	0.66	-	-	-
%NIT	0.57	0.75	0.73	0.52	0.61	-	-	-	0.55	0.44	0.58	-0.47	-0.42	-	-	-
%P	0.52	-	-	0.42	-	-	-	-	-	-	-	-	-	-	-	-
%Sh	-	-0.63	-0.64	-0.42	-0.47	-	-	0.50	-0.51	-	-0.60	0.65	0.65	-	-	-
%Sc	-	-0.43	-0.43	-	-	-	-	0.66	-0.43	-	-0.59	0.45	-	-0.46	-	-0.42
%CG	0.62	0.53	0.53	0.53	-	-	-	-	0.54	-	0.45	-	-	-	-	-
%CF	-0.65	-0.43	-0.41	-0.53	-	-	-	-	-0.52	-	-0.41	-	-	-	-	-
P richness	0.42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sh richness	-	-0.66	-0.65	-0.56	-	-	0.50	-	-0.61	-0.52	-0.59	0.47	-	-	-	-
Sc richness	-	-0.45	-0.45	-0.41	-0.48	-	0.43	0.65	-0.52	-	-0.60	0.45	0.41	-	-	-
CG richness	0.57	-	-	-	-	-0.42	-	-	-	-	-	-	-	-	-	-
CF richness	-	-	-	-0.41	-0.41	-	0.43	0.50	-0.47	-	-0.57	-	-	-	-	-

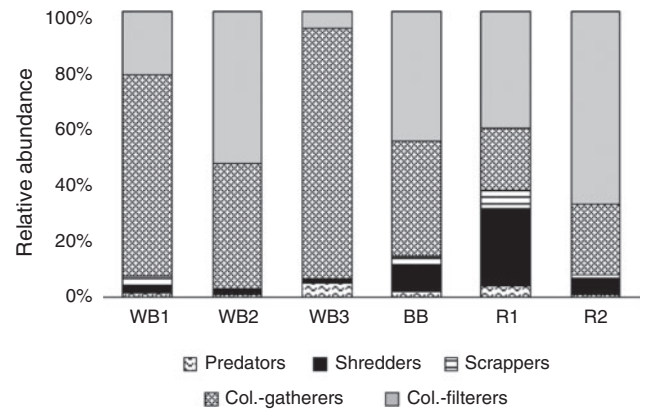


Fig. 7. Relative abundance of functional feeding groups at the six studied reaches ($n = 4$). WB = within-burn; BB = below-burn; R = reference.

Discussion

Environmental variables

Stream ecosystems' response to fire tends to be highly individualistic, primarily depending on post-fire precipitation, hillslope and burn severity (Minshall *et al.* 2001a, 2001b). For example, prescribed burns are small in extent and have minimal effects on stream chemistry, which include minor increases in nutrient concentrations within days after burning (Beche *et al.* 2005; Elliot and Vose 2006; Hall and Lombardozzi 2008). Alterations caused by large-scale catastrophic fires, however, have been reported to last several years, or even decades (Minshall *et al.* 2001a, 2001b; Mahlum *et al.* 2011; Romme *et al.* 2011).

Our knowledge of the immediate impact of the El Cristo fire is based on measurements and direct observations of six reaches during the first 8 months following burning. Numerous environmental variables were significantly different between within-burn and reference sites, particularly those associated with a lack of vegetation cover and increased stream-bank erosion. Although the lack of replicates prevented us from including the single below-burn site in the statistical analyses, we believe it is worth mentioning that environmental variables showed a clear pattern across the three stream categories, with below-burn values being consistently lower than those registered in within-burn reaches, but larger than those corresponding to reference sites. This would suggest that the buffer effect of riparian forest is evident in some physicochemical and community variables and highlights the importance of including these environments in future studies.

In agreement with previous studies, our periodic water quality assessment registered higher water temperatures at within-burn sites (Minshall *et al.* 1997; Minshall 2003; Mellon *et al.* 2008; Rhoades *et al.* 2011). Of all components of the stream heat budget, the loss of shading vegetation and the concomitant increase in solar radiation are the most likely mechanisms for the observed differences (Dunham *et al.* 2007). Mahlum and collaborators (2011) showed that wildfires have a long-lasting effect on water temperature, as maximum stream temperature remained high and showed no signs of returning to pre-fire norms even 7 years after a fire in the

Bitterroot River Basin (USA). Such trends are expected to continue under most climate change models.

Post-fire floods can influence stream ecosystem metabolism by mobilising and transporting organic matter and macroinvertebrates to downstream areas. Although debris flows are a common phenomenon in burned watersheds (Harris *et al.* 2015), none were registered during the first year after the fire. Nevertheless, it will be important to monitor the occurrence of such disturbances, because they are known to alter recovery trajectories of fire-affected streams. For example, flows can cause extensive channel scouring, which can remove or bury riparian vegetation, prolonging ecosystem recovery compared with that of a burned but unscoured stream (Tuckett and Koetsier 2016).

Sediment yield was also higher at within-burn sites, as indicated by increased specific conductance, salinity, TSS and TDS. Authors have attributed these differences to multiple factors, including soil water-repellency (DeBano 2000), soil sealing by sediment particles (Larsen *et al.* 2009), splash erosion (Shakesby and Doerr 2006) and loss of surface cover. In our work, lack of vegetation cover was reflected in low QBRp scores, and was likely linked to the high TSS and TDS values registered at within-burn sites. Many bamboo sticks and fallen limbs were observed bridging streams or forming channel obstructions (debris dams) that possibly altered water flow and acted as retention mechanisms (Bilby 1981). High sediment concentrations are a common feature in catchments affected by fire (Gresswell 1999; Bixby *et al.* 2015, and references therein). For example, Roby and Azuma (1995) found that transported sediment in a burned reach remained higher than reference values even 10 years after the fire. Similarly, Coombs and Melack (2013) reported unusually high concentrations of suspended sediments in streams draining burned Californian watersheds, which generally coincided with peaks in the hydrograph.

Contrary to our expectations, the El Cristo fire appeared to have minimal impact on dissolved oxygen. We believe larger differences between sites would have been detected if the study had been continued through the summer, when temperature increases (the highest mean daily temperature registered during the studied period was 21°C).

Fire kills vegetation and alters soil chemistry, which results in reduced nutrient uptake. Consequently, nutrients such as phosphorus are often washed into the channel by rainfall (Bixby *et al.* 2015). Our study streams, however, did not exhibit statistical differences in nutrient concentrations. Our observations were inconsistent with results from several studies that report significant nutrient increases following wildfire (Gresswell 1999; Smith *et al.* 2011). It is possible that the interval between measurements (2 months) precluded the detection of a short-lived peak in nutrient concentration associated with precipitation (Spencer *et al.* 2003; Coombs and Melack 2013). Such a hypothetical short-lived increase could have been related to the steep slope of the watershed, and the very high precipitation during the first months after the fire (i.e. rapid mobilisation of available phosphorus and nitrogen). The high precipitation combined with the steep hydrologic gradient imposed by the relief can produce substantial surface water flow (Rock and Mayer 2007). This may have rapidly transported the soluble forms of phosphorus and nitrogen into the receiving water body

(Futalauquen Lake), leading to a shorter duration of elevated concentrations of these nutrients. Owing to the short-term nature of the study, revegetation (i.e. vegetation uptake) is likely to have had a negligible effect on nutrient concentration. Although several physical and biogeochemical factors are thought to influence nutrient concentration in burned streams (e.g. precipitation, amount of organic matter available for nitrification) (Bladon *et al.* 2014), the magnitudes of these processes were not studied here, and warrant further investigation.

As canopy opens significantly after fire, we expected higher autotrophic periphyton biomass in within-burn streams. Light availability is often the main factor limiting primary production in forested watersheds, as reflected by numerous studies that report an increase in primary production following canopy removal (e.g. Robinson *et al.* 1994; Hill *et al.* 1995; Minshall *et al.* 1995, 1997; Kiffney *et al.* 2003). Nevertheless, we did not observe higher chlorophyll *a* concentrations at within-burn sites, possibly because the negative influence of increased suspended sediments overrode the positive effect of increased light levels. Sediment suspension has been previously identified as an important cause of habitat degradation, altering penetration of light and reducing photosynthesis, damaging tissues owing to abrasion, preventing attachment to the substrate of algal cells, and smothering and eliminating periphyton (Ryan 1991; Wood and Armitage 1997; Henley *et al.* 2000). de Pietri and colleagues (2015) argued that the complexities in the effects of disturbance, light and nutrient levels on algal biomass account for some of the variable results observed in previous studies, which range from negative, to none, to positive algal responses to fire (e.g. Bêche *et al.* 2005; Koetsier *et al.* 2010; Malison and Baxter 2010; Oliver *et al.* 2012). For example, Minshall and colleagues (2001c) found a 3-fold increase in chlorophyll *a* during the first 2 years following wildfire, whereas Earl and Blinn (2003) reported a shift in diatom assemblage, but no significant differences in periphyton biomass. Others have proposed top-down regulation as a hypothesis to explain the apparent lack of algal response to increased light penetration (Hill *et al.* 1992), although this is probably not the case.

Macroinvertebrates

Our results show that streams affected by the El Cristo fire differed substantially in invertebrate assemblage composition, although invertebrate density, diversity and rarefied taxa richness exhibited no significant variation. Studies from the northern hemisphere have also reported mixed responses in macroinvertebrate communities in the first years after wildfire (Gresswell 1999; de Pietri *et al.* 2015). EPT populations were markedly low in within- and below-burn streams, where they constituted relatively small proportions of the total density ($\leq 10\%$ vs $\geq 30\%$ in reference sites). The combination of higher temperatures, altered organic matter supply and increased sediment concentrations could explain the low abundance of these sensitive insects (Richardson and Danehy 2007; Richardson 2008). In contrast, NIT attained levels $\geq 37\%$ at the same sites (i.e. lower EPT/NIT ratio), reaching maximum density at WB3 (65% of the community), perhaps through the release from competition or increases in fine sediment. These results are not unexpected based on observations of *Hyaella* species and oligochaetes thriving in sediment-laden environments and burned

watersheds (Ryan 1991; Suedel and Rodgers 1994; Minshall *et al.* 1997; Wood and Armitage 1997). The influence of suspended sediments on freshwater invertebrates is well documented (e.g. Wood and Armitage 1997; Henley *et al.* 2000). Moreover, several studies have linked changes in community composition to fire-related erosion and sedimentation. Oliver and colleagues (2012) reported a substantial post-fire change in substrate composition, with fine sediment being eight times more abundant. Similarly to our observations, the authors found no consistent changes in taxonomic richness or diversity but noted that post-fire densities and percentage of sensitive taxa were significantly reduced. Meanwhile, Malison and Baxter (2010) showed that sites with high-severity fires had the greatest biomass of r-strategists (i.e. Chironomidae and Simuliidae). Although we did not account for changes in biomass, we did find higher abundances of these fast-growing taxa in the disturbed reaches. In contrast, the biomass of total macroinvertebrates and shredders was higher in a fire-affected stream in north-eastern Spain, with sediment having a negligible effect on leaf breakdown, as reported by Rodríguez-Lozano and colleagues (2015).

Differences in functional structure among categories suggest alterations in food resources, which is consistent with previous results from the northern hemisphere (Minshall *et al.* 1997; Rodríguez-Lozano *et al.* 2015). Burned streams are expected to become more autotrophic as solar inputs are greater and water temperatures higher than before the fire (Robinson *et al.* 2005). At within-burn sites, community composition was dominated by generalist taxa (collector-gatherers, collector-filterers), whereas reference streams exhibited a more even distribution of FFGs. Collector-gatherers were well represented at all six sites but were particularly dominant at WB1 and WB3. Two species were classified as collector-filterers, *Gigantodax minor* (Diptera, Simuliidae) and *Smicridea annulicornis* (Trichoptera, Hydroptichidae). Their abundance was substantially lower at sites WB1 and WB3. These invertebrates rely on cephalic fans and net-spinning to capture suspended organic particles, so it is likely that increased suspended solids may have affected feeding efficiency by clogging the filter mechanisms, as stated by Grown and Davis (1994), and Tronstad and colleagues (2012). Lower detrital food quality, resulting from inputs of burned material, is also thought to adversely affect primary consumers, particularly collectors (Earl and Blinn 2003). This is supported by Mihuc and Minshall (1995), who found that only one taxon, of 11 examined, could utilise burned organic matter as a food source. Shredders were an important component of the community at reference sites, particularly in R1 (27% of the total individuals). This is a common feature of headwater streams, which depend more on allochthonous leaf detritus as basal resources, and less on primary production (Richardson and Danehy 2007). Previous studies suggest that the significantly lower number of shredders observed at within-burn sites was a predictable response to the loss of riparian vegetation (Minshall *et al.* 2001a; Mihuc *et al.* 1996). Vieira and colleagues (2004) also noted that shredder stoneflies were strongly affected by wildfire, and did not recover after 6 years, indicating that wildfires may have long-term impacts on shredder assemblages. We expected increased primary production in burned streams, cascading to greater densities of scrapers. Instead, and in agreement with other reports (Minshall *et al.* 2001a; Vieira

et al. 2004), scraper abundance was lower at within-burn sites (although not significantly). These insects require clean substrate surfaces on which to graze, and a sediment layer may inhibit periphyton growth or prevent access to the food source (Rabeni *et al.* 2005; Oliver *et al.* 2012). Others have proposed that primary consumer (i.e. scraper) abundance should not be necessarily associated with increased periphyton because predators crop surplus secondary production (top-down control) (Wootton and Power 1993). However, our data do not support this hypothesis because predators were not abundant at any of the six studied reaches.

Conclusion

Wildfires affect aquatic ecosystems in numerous and complex ways, as suggested by several environmental and community differences found in our study. In general, larger effects tend to be observed in small, low-order streams similar to those studied here, because headwater catchments tend to burn more completely than do those surrounding larger streams. The return of lotic communities and abiotic parameters to the original pre-fire conditions will ultimately depend on the recovery of riparian and terrestrial vegetation in the drainage basin. The high year-to-year variability in post-fire recovery reported for other streams (Minshall *et al.* 1997) provides strong arguments for monitoring burned water courses over an extended period of time. Although we acknowledge the short-term nature of our study, it does represent an important snapshot of post-fire conditions in the first year following fire and provides a basis for future research on long-term stream recovery.

It is important to note that the scientific literature on fire-induced changes is dominated by research from the northern hemisphere, particularly regions where wildfire is a common and natural disturbance. This appears not to be the case in Patagonia, as abundant climatological evidence points to the warming and drying trend during the second half of the 20th century as one of the main factors influencing fire occurrence (Holz and Veblen 2011). Climate and weather patterns are among the many factors that contribute to the impact of wildfires on stream conditions (Gresswell 1999; Minshall *et al.* 2001a). Consequently, streams in different regions, or even in nearby catchments, may exhibit different responses. The challenge remains, therefore, somehow to develop an explanatory model equally applicable to different types of ecosystems across the globe. Surely, increasing research in understudied regions would be a first step in the right direction. Enhanced availability of data from a wide variety of biomes would enable us to undertake more thorough meta-analyses (see Verkaik *et al.* 2015) to look for generalities in the responses of aquatic habitats to fire.

Conflicts of interest

The authors declare no conflicts of interest.

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Appendix 1. Presence or absence, functional feeding group, mean total density, mean rarefied richness and mean Shannon's diversity of benthic macroinvertebrate taxa where 'X' indicates presence

Mean total density standard deviation in parenthesis. WB = within-burn; BB = below-burn; R = reference; FFG = functional feeding group; CF = collector-filterer; CG = collector-gatherer; P = predator; Sc = scraper; Sh = shredder

Taxa	FFG	WB	BB	R
Dugessidae				
<i>Cura</i> sp.	P	X	X	X
Lumbricidae				
<i>Eiseniella</i> sp.	CG	X	X	X
Hyalloleidae				
<i>Hyallolella araucana</i> (Gross and Peralta)	CG	X	X	
Austroperlidae				
<i>Klapopteryx</i> sp.	Sh			X
Gripopterygidae				
<i>Aubertoperla illiesi</i> (Froehlich)	Sh	X	X	X
Notonemouridae				
<i>Austronemoura chilena</i> (Aubert)	Sh	X		X
Diamphipnoidae				
<i>Diamphipnoa</i> sp.	Sh		X	X
Leptophlebiidae				
<i>Meridialaris chiloeensis</i> (Demoulin)	CG	X	X	X
<i>Dactylophlebia carnulenta</i> (Pescador and Peters)	CG	X		
Baetidae				
<i>Andesiops ardua</i> (Lugo-Ortiz and McCafferty)	Sc	X	X	X
Nesameletidae				
<i>Metamonoius</i> sp.	Sc	X		X
Hydropsychidae				
<i>Smicridea annulicornis</i> (Blanchard)	CF	X	X	X
Hydrobiosidae				
<i>Rheochorema</i> sp.	P		X	
<i>Rheochorema tenuispinum</i> (Schmid)	P	X	X	X
<i>Neopsilochorema</i> sp.	P			X
<i>Cailloma pumida</i> (Ross)	P			X
Limnephilidae				
<i>Monocosmoecus</i> sp.	Sh	X	X	
<i>Austrocosmoecus hirsutus</i> (Schmid)	Sh	X	X	
Sericostomatidae				
<i>Myotrichia murina</i> (Schmid)	Sh	X	X	X
<i>Parasericostoma cristatum</i> (Flint)	Sh	X	X	X
<i>Parasericostoma ovale</i> (Schmid)	Sh			X
Hydroptilidae				
<i>Metrichia patagonica</i> (Flint)	Sc			X
<i>Metrichia neotropicalis</i> (Schmid)	Sc			X
Polycentropodidae				
<i>Polycentropus</i>	P	X		X
Philorheithridae	P		X	
Helicophidae				
<i>Austrocentrus valgiformis</i> (Flint)	Sc	X	X	X
Leptoceridae				
<i>Brachysetodes</i> sp.	Sh	X		X
Glossosomatidae				
<i>Scotiotrichia ocreata</i> (Mosely)	Sc	X		X
Simuliidae				
<i>Gigantodax minor</i> (Wygodzinsky and Coscaron)	CF	X	X	X
Dixidae	CG		X	
Tipulidae	P			X
<i>Tipula</i> sp.	Sh		X	
Limoniidae				
<i>Hexatoma</i> sp.	P		X	X
<i>Molophilus</i> sp.	CG	X	X	X
Chironomidae				

(Continued)

Appendix 1. (Continued)

Taxa	FFG	WB	BB	R
<i>Parametriochnemus</i> sp.	CG	X	X	X
<i>Eukiefferiella</i> sp.	CG	X		X
<i>Paratrichocladus</i> sp.	CG	X		
<i>Parapetrocladius</i> sp.	CG	X		
Orthoclaadiinae sp.	CG			X
<i>Orthocladus</i> sp.	P	X		X
<i>Ablabesmyia</i> sp.	CG	X		X
Tanypodinae sp.	CG	X		X
Podonominae sp.	CG	X	X	X
Athericidae	Sc			X
Blephariceridae				
<i>Edwardsina</i> sp.	Sh			X
Ephydriidae				
Ephydriidae sp1.	CG	X	X	X
Ephydriidae sp2.	CG		X	
Ceratopogonidae	P	X	X	X
Empididae				
<i>Empididae</i> sp1.	P	X		X
<i>Empididae</i> sp2.	P		X	
<i>Empididae</i> sp3.	P		X	X
Tabanidae	P	X		X
Nannochoristidae				
<i>Nannochorista</i> sp.	P			X
Scirtidae	CR	X	X	X
Elmidae				
<i>Luchoelmis</i> sp.	Sc	X	X	X
Mean total density (individuals m ⁻²)		3103 (81.87)	1210 (767.8)	1785 (65.39)
Mean rarefied taxa richness		6.01 (1.7)	6.75 (2.22)	7.71 (2.45)
Mean Shannon's diversity		1.38 (0.17)	1.55 (0.51)	1.68 (0.47)