UNIVERSITAT DE BARCELONA

Wildfire effects on macroinvertebrate communities in Mediterranean streams

Efectes dels incendis forestals sobre las comunitats de macroinvertebrats en rius mediterranis

Iraima Verkaik

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Wildfire effects on macroinvertebrate communities in Mediterranean streams

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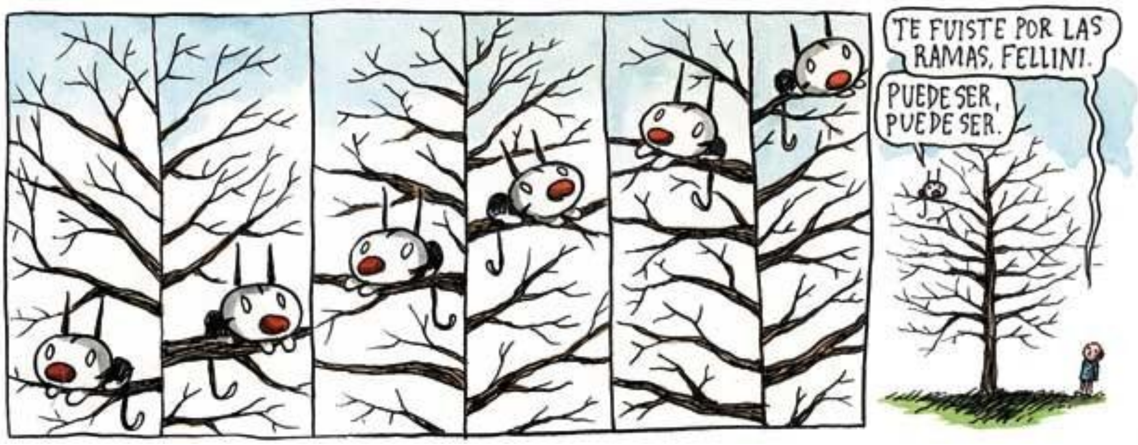
A los mismos 3 gatos, ahora con gatitos, y al mismo perro en el
mismo chiringuito que nos sigue esperando en la playa


"LAS IDEAS SON COMO LOS CONEJOS. USTED OBTIENE UN PAR, APRENDE A CUIDARLOS, Y MUY PRONTO TENDRÁ UNA DOCENA"
JOHN STEINBECK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Contents

General introduction

Fire as a natural disturbance

Wildland fire is a critical component in the terrestrial and atmospheric dynamics of our Earth system (Flannigan *et al.* 2009). This is not a recent story. During most of the Earth's history, fires have been integral to the evolution of flora and fauna, and responsive through feedback processes to changes in climatic and paleoatmospheric variations (Pausas & Keeley 2009). Burning in the last decades an average of 383 Mha annually (Schultz *et al.* 2008), wildfire is the natural disturbance that influences the bigger areas through out several regions (Lavorel *et al.* 2007). This becomes very clear when looking at the fires map from the European Space Agency (ESA), based on thermal infrared satellites images taken from July 1996 until August 2010 (Figure 1). Actually, wildfire is the key factor to understand many of the world's biomes distribution and fire-prone ecosystems structure and function (Bond & Keeley 2005). Fire also affects many fundamental ecosystem processes such as nutrient cycling (Turner *et al.* 2007), vegetation succession pathways (Turner *et al.* 2007; Brown & Smith 2010), and other disturbance patterns such as pest outbreaks (McCullough *et al.* 1998), hydrology (Shakesby & Doerr 2006), and erosion (DeBano *et al.* 1998; Shakesby *et al.* 2007).

In summary, fire has been playing a significant role in the natural global carbon cycle and in regulating terrestrial ecosystems and biodiversity (Whelan 1995). At the same time, fire has been also considered the main climate-triggered hazard that can threat ecosystems and human security (Dube 2009), because biomass burning plays the major role in global environmental changes, influencing atmospheric composition, climate systems, human health, and economic activities (Schultz *et al.* 2008). Annual costs of fire prevention and suppression in the US have reached nearly $3 billion annually in recent years (Marlon 2009), with increases of 11% per year on average (Schoennagel *et al.* 2009). Fire costs damages can be very high; as an example, recent Russian fires have been calculated in $15 billion (Wikipedia 2010, http://en.wikipedia.org/wiki/2010_Russian_wildifres, retrieved September 2010). Therefore, the interest in fire and its effects has become global and interdisciplinary due to influences, interactions, and feedbacks among fire, terrestrial, and atmospheric systems (Krawchuk *et al.* 2009). Although the physical process is theoretically simple, modern fire regimes are an ongoing focus in ecological research, nuanced by the role of humans who are changing the landscapes to be more or less flammable, and also lighten and extinguish fires (Lavorel *et al.* 2007; Chuvieco *et al.* 2008; Krawchuk *et al.* 2009).

Black years are becoming more common, and the recent fires in Russia (2010) are again a good example with more than 300 thousand of forest hectares burned (Nature news, doi:10.1038/news.2010.404, retrieved September 2010). Moreover, these black years are more recurrent in extended areas of the world. For example, in 1994 more than 2 million hectares burned in areas such as Mediterranean climate areas, South Australia, Russia and South America (Terradas 1996); in 1997-1998 the WWF entitled this period as “The Year the World Caught Fire” (Rowell & Moore 2000); in 2003 large fires burned South Eastern Australia, Western Canada, Mediterranean Europe and Southern California (Lavorel *et al.* 2007). All of them drew again considerable public and political attention to fire as a phenomenon through which ecological and human dynamics collide (Lavorel *et al.* 2007). The most recent example is the 50% rise in wheat prices partly as a consequence of the wildfires that occurred during the last summer of 2010 (BBC, http://www.bbc.co.uk/news/business-10851170, retrieved September 2010).

Some models already predict a higher recurrence in fires (Westerling *et al.* 2006), but the future trends of global fire activity (severity and recurrence) are varied and difficult to determine owing to the complex and non-linear interactions between weather, vegetation, and people (Flannigan *et al.* 2009). The uncontrolled and widespread wildfires that occurred in 1997 seemed to be a consequence of extreme dry conditions brought by El Niño that year (Levine 1999). Although weather forecasts predicted 1999 as a wet year, 18 months after some of the worst forest fires in the modern era, fires started again (Rowell & Moore 2000). Thus, in general, dry years enhance the fire consequences (Westerling & Swetnam 2003), and in the future an increase in the frequency and intensity of extreme droughts is expected (Houghton *et al.* 1996).

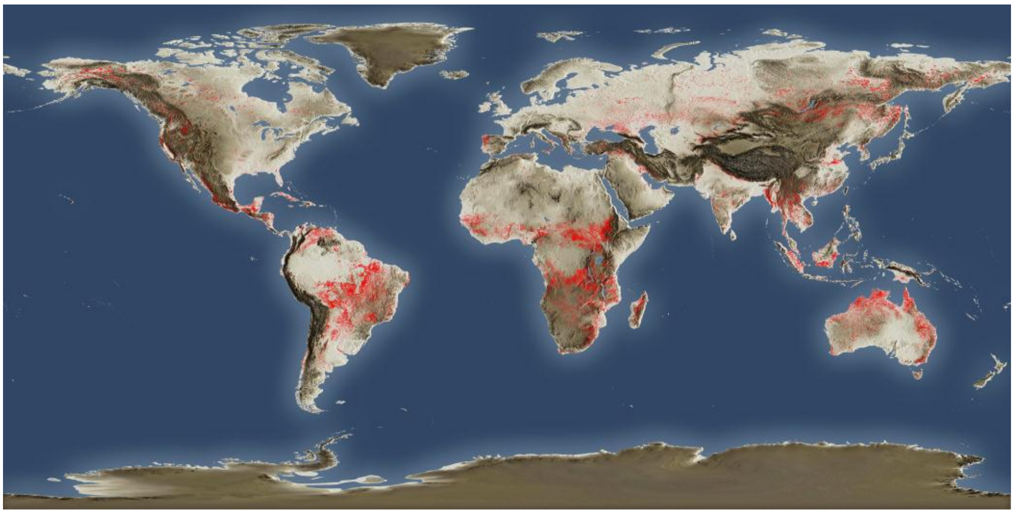


Figure 1. Fire global map based on the ESA global detection of hot spots with twin radiometer sensors (along track scanning radiometer and Envisat's advanced along track scanning radiometer) from July 1996 to August 2010. Temperatures exceeding 38.85ºC are classed as burning fires (taken from the ESA webpage retrieved September 2010, http://www.esa.int/esaCP/SEMGQSJOXDG_Protecting_0.html)

Wildfire effects on biological communities

Disturbance is defined as any event that disrupts ecosystem, community, or population structure which, and the same time, change resources, availability of substratum, and the physical environment (*sensu* Pickett & White 1985 in Resh *et al.* 1988). Wildfires thus represent a clear disturbance factor by removing all the biomass or by an alteration or simplification of the post-fire environment (Smith & Lyon 2000).

As mentioned earlier, the role of fire as a disturbance has been relatively well studied in terrestrial communities that live in the tropics (Goldammer & Seibert 1990; van der Werf *et al.* 2008), Mediterranean-type ecosystems (Moreno & Oechel 1994; Pausas 2004; Rodrigo *et al.* 2004), the Western of the United States (Agee 1998; Flannigan *et al.* 2009), Australia (Bradstock *et al.* 2002), and riparian ecosystems (Dwire & Kauffman 2003). However, until the last decades, studies about wildfire effects on communities that live in aquatic ecosystems were relative scarce (Minshall 2003).

The 'heartland' (*sensu* Shakesby & Doerr 2006) of research in fire impacts in aquatic ecosystems is located in the West of the United States, where research started to be conducted after the 1988 fires in the Yellowstone National Park. This provided a unique opportunity to study fire effects on several ecosystem processes in a natural laboratory (Schoennagel *et al.* 2009). A notable review of fire and aquatic ecosystems was published in 1999 by Gresswell. Later, in 2003, the Forest Ecology and Management journal dedicated two issues to the Effects of Wildland Fire on Aquatic Ecosystems in the West USA (Rieman *et al.* 2003), a compendium about fire effects in different topics: historical aspects, geomorphology and physico-chemical responses, biology of macroinvertebrates, amphibians, reptiles and fishes, concluding with key questions in fire as a tool in land use and the role of fire in the future climate change scenario.

Fire effects on aquatic ecosystems: lessons from the West of the US

In general, the effects of fire on aquatic ecosystems can be conveniently separated into direct and indirect influences (Minshall 2003). Direct effects such as atmospheric inputs or excessive heating are quick and have generally short-lived consequences for ecological processes and for biological communities (Minshall 2003; Hall & Lombardozzi 2008). On the other hand, indirect effects are more persistent, for example, an enhanced erosion, sediment transport and turbidity, all related to changes in channel morphology and instream habitat as a consequence of floods (Bisson 2003; Minshall 2003). The first runoff appears to be catastrophic (Gresswell 1999). The entrance of ashes and increased sediment loads is in general the reason of the disappearance of biota, including algae (Robinson *et al.* 1994), macroinvertebrates (Rinne 1996; Minshall 2003; Vieira *et al.* 2004), and fishes (Gresswell 1999).

In a midterm time frame, soil hydrophobicity is enhanced (Benda 2003; Shakesby & Doerr 2006) and overland flow may increase over time with higher erosion associated with high peak flows (Cerda & Doerr 2005). Wood and sediment is routed downstream by fluvial processes that form different aquatic habitats (Benda 2003; Miller *et al.* 2003; Minshall 2003), and the recruitment of new large woody debris to streams is expected (Arkle *et al.* 2010). Coarse sediment and wood is gradually depleted as they decay, break up, and are transported downstream before being replenished by new post-fire erosional episodes (Benda 2003; Miller *et al.* 2003).

In terms of biological communities, the midterm response to fire is usually quick: taxonomic richness, total abundance, and total biomass returns to its pre-fire conditions within months or during the first years (Roby & Azuma 1995; Minshall *et al.* 2001c). A shift towards a community dominated by macroinvertebrates disturbance-adapted strategists like Chironomidae, Baetidae, and Simuliidae seems to be a common response (Mihuc *et al.* 1996; Vieira *et al.* 2004; Mellon *et al.* 2008; Malison & Baxter 2010a). Usually fire enhances aquatic production over pre-fire conditions most likely as a consequence of faster algal growth in streams with removed canopy (Behmer & Hawkins 1986), higher temperatures, and increased delivery of inorganic nutrients such as nitrogen and phosphorus (Minshall *et al.* 1997; Spencer 2003). The qualitative changes in plant food resources (e.g. loss of riparian leaf detritus or increase in algae) occur mainly in low order streams or severely burned streams, and this is expected to alter the feeding guild composition of the macroinvertebrate community (Minshall *et al.* 1989). In general, shredders are expected to track the loss and subsequent recovery of allochthonous leaf detritus, and scrapers are expected to reflect the changes in autotrophic periphyton associated with the opening of the forest canopy and the release of nutrients (Minshall 2003) (Figure 2).

The correct assessment of the impact of fire requires an understanding of local site characteristics interpreted in the context of general conceptual frameworks of post-fire recovery patterns, because the macroinvertebrate community's response to fire is often individualistic and related to the generally stochastic nature of disturbance and the heterogeneity of environmental conditions and not all streams within the fire perimeter are affected equally (Minshall 2003). Differences in severities are common as fire behaviour in riparian areas often differ from the upland areas, because the riparian microclimate, moisture availability, and species composition result in different fuel loads (Dwire & Kauffman 2003). For example, Malison & Baxter (2010a) found a significantly higher secondary production in high-severe burned streams compared to control streams and low-severe burned streams. Therefore, in general, the relatively rapid recovery of stream macroinvertebrates is associated with the recovery pace of the riparian vegetation (25–50 years to full canopy development), which is fast compared to that of the catchment (100–300 years) (Minshall *et al.* 2001b; Minshall *et al.* 2001c).

Finally, over long timescales wildfire is the major cause of hydrological and geomorphological changes in fire-prone landscapes (Shakesby & Doerr 2006). Besides, it increases the channel complexity and habitat heterogeneity (Robinson *et al.* 2005). This landscape changes in habitat diversity, and changes in the types and amount of food resources are reflected in the structure and function of the stream flora and fauna (Minshall *et al.* 2004).

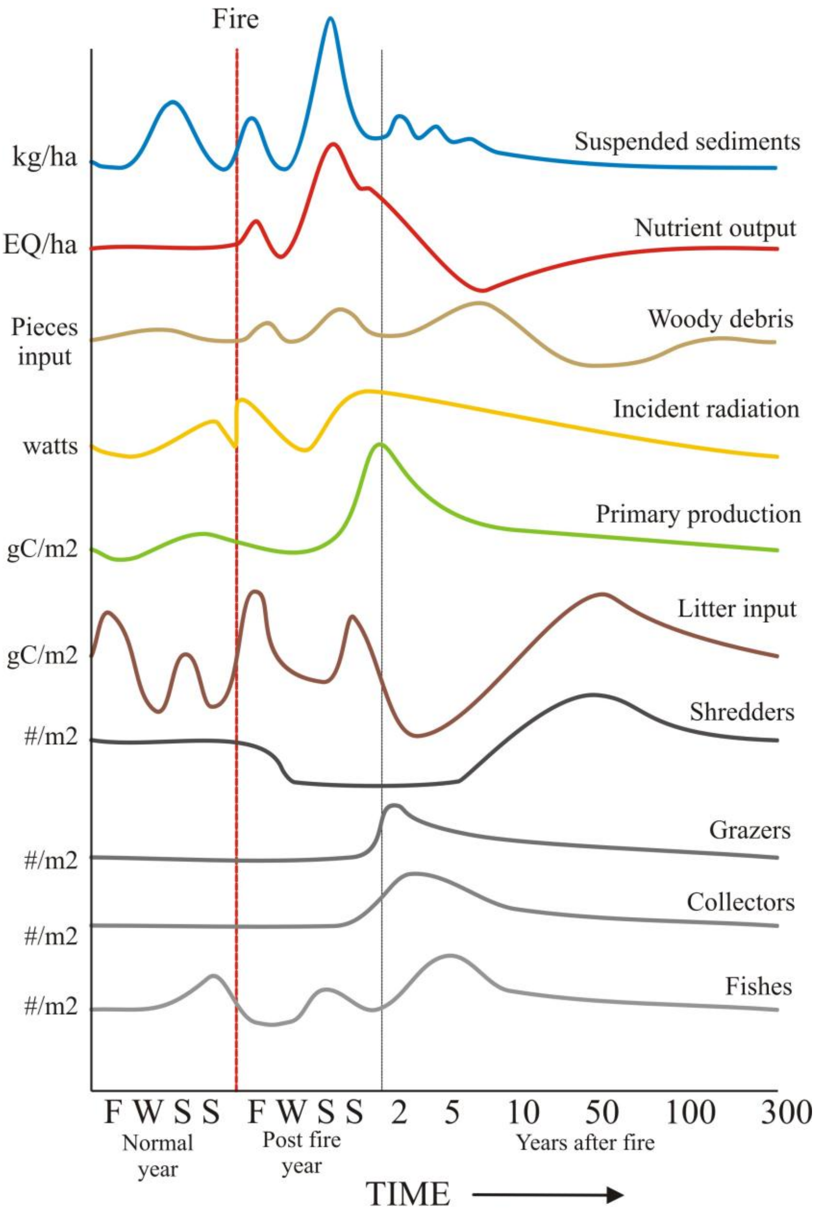


Figure 2. Hypothetical changes in physical, chemical, and biological characteristics following fire. The letters F, W, S, and S indicate fall, winter, spring, and summer, respectively (Adapted from Minshall *et al.* 1989 and Gresswell 1999).

Fire effects on aquatic ecosystems: what the rest of the world has contributed

Twenty years ago, Minshall *et al*. (1989) denoted about the small number of studies done about the effects of fire on aquatic biota. Since that date, the number of publications has increased answering several questions and bringing more uncertainties. One of the main gaps until now is how to generalize the observations of fire effects to a larger geographical range, especially where fire is also a common and recurrent disturbance, such as the Mediterranean climate areas. As mentioned, wildfires in this biome have been part of the evolutionary constraints of life history traits (Blondel &

Aronson 1999) shaping their biodiversity attributes (Pausas & Verdú 2008). Thus, while fire in terrestrial communities has been deeply studied (Trabaud & Prodon 1993; Terradas 1996), the studies in fire effect in aquatic communities from this climate area are few (Britton 1991; Bêche *et al.* 2005; Vila-Escalé 2009).

Similarly, the Southeast corner of Australia has one of the most bushfire-prone environments (Collett 2007; Lyon & O'Connor 2008; Seymour & Collett 2009), and the effect of bushfires has been largely studied on different Australian terrestrial ecosystems (Bradstock *et al.* 2002). In contrast, studies of bushfires effects on aquatic systems have been mainly focused on water chemistry (Townsend & Douglas 2004) and on changes in hydrology, soil erosion, sediment transport, and deposition (see list at Lane *et al.* 2006; Shakesby *et al.* 2007). Studies on the impact of wildfire on aquatic communities have just recently begun and have focused on benthic algal assemblages and fish population (Cowell *et al.* 2006; Lyon & O'Connor 2008). These studies, together with some preliminary unpublished reports on macroinvertebrates, were motivated after the large fire of 2003, which was regarded as the worst since 1939 (Victoria 2003; Crowther & Papas 2005). Two important points were highlighted: first, the 2003 fires occurred towards the end of a long drought, the worst in 100 years (Victoria 2004); and second, some of the wildfire affected areas were followed by high flood events (Victoria 2003; Lyon & O'Connor 2008). 2003 was also the year when a large fire burned part of the Sant Llorenç Natural Park in Catalonia (NE Spain), and research about fire effects on Mediterranean streams began. Similarly to Victoria, drought and floods are the seasonal common disturbances that shape the Mediterranean streams (Gasith & Resh 1999). As a consequence, the biological communities that live in these streams have to cope with the high environmental variability produced by such large disturbances, and it has been hypothesized that life cycles may be adapted to the long-term dynamics of these disturbances rather than to specific flow events (Lytle & Poff 2004).

Although some generalizations could be made about wildfires responses on stream biota, local factors like hydrology and climate should be somehow different (Minshall 2003), interacting with other common disturbances like floods and droughts. Also, different endpoints may be expected after the same time of recovery. Usually direct wildfire effects on aquatic communities could be almost negligible, but their indirect effects can initiate a suite of intense physical disturbances to streams, and interact with other disturbances like floodings that can reset recovery trajectories (Vieira *et al.* 2004) or seasonal droughts (Cowell *et al.* 2006) that can generate different responses by delaying the recolonization process (Arkle *et al.* 2010). Thus, the complex effects of one disturbance on ecological communities can be further complicated by subsequent perturbations within an ecosystem.

In lotic systems, the disturbances are regarded as an important topic that defines the equilibrium reached in the communities (Resh *et al.* 1988), where opposite factors such as stochastic vs. deterministic are interacting depending on the strength of the disturbance (Lepori & Malmqvist 2009). The response of the aquatic biota to large disturbance events should proportionately be characterised by two strategies: resistance and resilience (Gunderson 2000). The first is the degree to which the benthic fauna is reduced by the initial disturbance and the second, the rate of recovery both in absolute and relative terms (Marchant *et al.* 1991); the dynamics between both responses and the nature and strength of the disturbances will be influencing the stability of the communities (Lepori & Malmqvist 2009).

Main objectives

In August 2003, the Eastern sector of the Sant Llorenç del Munt i l'Obac Natural Park, an area with high recreational and conservation interest, suffered a major forest fire. Temperatures of 39ºC and 7% of relative humidity were the initial conditions that promoted the rapid propagation of fire, in 5 days 4543 hectares got burned affecting many habitats of natural interest, such as riverside woodlands, holm oak woods, and pine woods (Guinart 2007). Within this context, the main objective of this thesis was to study the midterm effects of wildfire on the macroinvertebrate communities in Mediterranean streams and compare the results with those of other biomes. Before this study was carried out, the effects of fire on one headwater stream were monthly studied for two years (Vila-Escalé 2009). However, the question was still if these responses in a single stream could be transposed to other Mediterranean streams or were present on a more extended time frame.

This research study was divided in four chapters, which are summarized in Table 1 with the following general objectives:

1) Study the midterm fire effects on the macroinvertebrate succession in one Mediterranean stream (Vall d'Horta) 30 months after a wildfire, with a monthly comparison of the macroinvertebrate communities between two local riparian canopy reaches (open due to fire vs. closed not burned canopies) that were affected differently by the fire (Chapter 1).
2) Document the annual changes in species composition after the fire in several streams of Sant Llorenç Natural Park, and compare the changes between the burned and control streams in a framework of large interannual variability of discharge (Chapter 2).
3) In order to expand the knowledge on fire effects in macroinvertebrate communities at larger spatial scales, another fire-prone area was studied. In

Victoria, SE Australia, the main objective was to study the midterm response of the structure (taxa number and abundance) and function (functional feeding groups) of the macroinvertebrate community in three streams located in catchments affected by bushfires after a decade of intense drought, which could result in different hydrological conditions (Chapter 3).

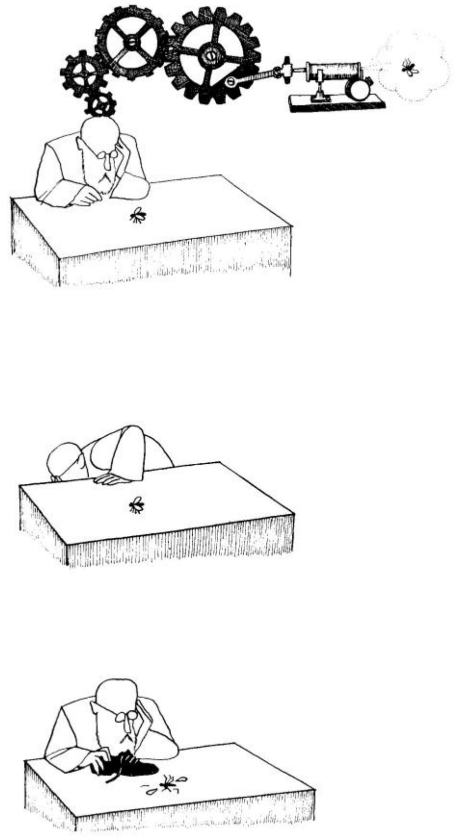
4) Finally, in order to test to what extent the macroinvertebrate's response to fire can be generalized beyond distinct regions, the main objective of this last chapter was to compare the responses of the composition and structure of the macroinvertebrate assemblages to wildfire in three fire-prone biomes with different biogeographical and climatic contexts (NW Mediterranean, SE Australia and NW United States) (Chapter 4).

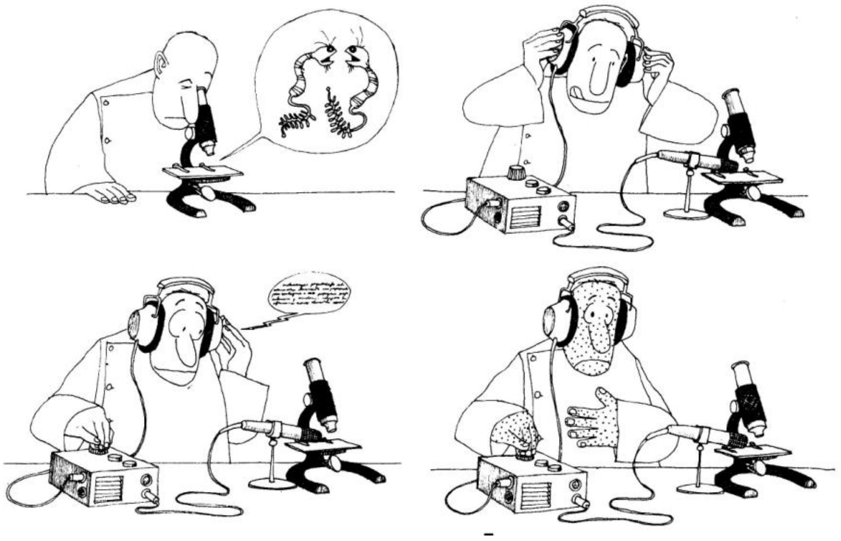
Table 1. Summary of the spatial and temporal scale addressed in each chapter.

Chapter	Scale	Time after wildfire	Sampling intensity
1	Reach	3 years	once/ month
2	Basin	2 months – 5 years	once/ year
3	Basin	9 months	once
4	Regions	9-11 months	once

Chapter 1

Midterm macroinvertebrate community response to different local riparian canopy affectation by a wildfire





Quino

Introduction

Based on the studies developed in the West of the US, one of the midterm effects of fire on a headwater catchment is related to the removal of the overstorey vegetation, reducing the organic matter allochthonous inputs and originating a sharp increase in the solar radiation incidence. Allochthonous detritus is a primary determinant of energy and organic matter dynamics in low order streams (Hynes 1975), and any significant change in its quality or quantity (e.g. terrestrial vs. aquatic vegetation) is likely to exert profound effects throughout the stream ecosystem. At the same time, an increase on the sediment levels and erosion of the stream channel, and a gradual decrease in nutrient loss from the watershed has been recorded in burned catchments (Minshall *et al.* 1997). These changes produced by fire will gradually diminish along with the recovery of the vegetation, both in the basin and in the riparian area, arriving to previous to fire net photosynthetic rates of terrestrial vegetation (Minshall *et al.* 1989). Accordingly, along with these physico-chemical alterations, some biological and ecological changes are expected as a response. In severe burned streams, an increase in sunlight penetration allows an increase of algal growth within the stream (Behmer & Hawkins 1986). An increment in the stream temperature is also expected. This coupled with the enhanced plant growth, is assumed to increase primary and secondary stream production. The qualitative changes in food resources following fire (e.g. loss of riparian leaf detritus or increase in algae) could be expected to alter the feeding guild composition of the macroinvertebrate community (Minshall *et al.* 1989). In general, shredders abundance and biomass are expected to track the loss and subsequent recovery of allochthonous leaf detritus, while scrapers are expected to reflect the changes in autotrophic periphyton associated with the opening of the forest canopy and the release of nutrients (Minshall 2003).

Fire behaviour in riparian areas often differ from the adjacent basin area, because the riparian microclimate, moisture availability, and species composition result in different fuel loads and moisture, generating more patchy and heterogeneous affectation (Dwire & Kauffman 2003; Pettit & Naiman 2007). In this sense, we can expect great local variability in the post-fire responses in streams depending on the burn severity, and this could be important. For example, studies developed in Idaho have shown significant differences in macroinvertebrate biomass and emergence from severe burned streams (i.e. total removal of the canopy) compared to reaches with a burned understorey vegetation (Malison & Baxter 2010a). In this context, there are no studies on midterm effects that have followed the macroinvertebrate succession in Mediterranean streams that have differences in local affectation of the canopies. Actually, the literature about wildfire effects on macroinvertebrates in the Mediterranean area is scarce (Britton 1991; Vila-Escalé 2009). Results have indicated that as in other areas severe floodings after fire change immediately the instream habitat conditions, affecting negatively the macroinvertebrate community (Vila-Escalé 2009) and enhancing post-fire erosion (Mayor *et al.* 2007). However, two years were enough for macroinvertebrate taxa number to arrive to pre-fire levels. This result seems quite surprising, because due to the repeated intense hydrologic disturbances that characterise Mediterranean streams, a reset of recovery patterns of the community after floodings in a burned catchment was expected (Vieira *et al.* 2004). On the other hand, the Mediterranean streams have been characterized as highly resilient (Bonada *et al.* 2007a), which can explain the rapid responses in macroinvertebrates results of Vila-Escalé (2009).

In this context, we hypothesize that local fire related differences in riparian cover will generate differences in the macroinvertebrate composition, and similar to other studies (Mellon *et al.* 2008; Malison & Baxter 2010a) we expect a higher macroinvertebrate abundance and biomass in the reach without riparian cover. Also, the predictable seasonal but strong variation in precipitation (Gasith & Resh 1999) will generate major floodings that will lower the density and biomass of macroinvertebrates. In the open canopy reach, we expect that floodings will greatly influence the community because of its greater reliance on periphyton resources (Biggs *et al.* 1999) which can be reduced by spates (Death & Zimmermann 2005). Similarly, at a habitat scale, floodings will mainly shape the stone habitat, affecting the periphyton that grows on it and indirectly the invertebrates that live on this habitat. On the other hand, the leaf litter will promote a higher stability in the macroinvertebrate community when present. The functionality of the community will depend first on the initial disturbance -floodings- but also the presence or not of further perturbations as successive floodings or drought that may mask the fire effects in the basin or the riparian area. Based on the study of Vila-Escalé (2009), we expect that, after the initial flooding, the community will be dominated by small invertebrates with >1 reproductive cycles per year, with a strong larval and adult dispersion, and higher abundance in filter and collector feeders. After three years and partial recovery of the basin and riparian area, we will expect a higher abundance of grazers and lower of shredders in the open canopy reach. The importance of severe dry conditions may be different in the open canopy compared to closed canopy reach that probably affect the permanence of water on the stream.

Methods

Study site

The Vall d'Horta river (42º1' N; 1º46' - Altitude: 475m asl) is located at the Natural Park Sant Llorenç del Munt in NE Spain. The main course is formed from the confluence of Pregona (700m asl) and Font del Llor (640m asl) small headwater creeks, at the Ripoll's basin, a Besòs river tributary (NE Spain). The climate is Mediterranean with irregular and intense rainfall, mostly in winter, but with some rainfall in spring and autumn, while summer is normally very dry. All meteorological data was taken from the nearest meteorological station to the study site (Sant Llorenç del Munt (X UTM: 419078 Y UTM: 4615060 altitude: 528m asl). The geology is predominantly calcareous (mainly sandstones), with some highly permeable substrates alternating with less permeable ones where springs are located.

Before the fire, the catchment was dominated by evergreen oak tress (*Quercus* ilex L.) and Aleppo pine (*Pinus halepensis* Miller), while the riparian area was a mixture of *Corylus avellana* L., *Cornus sanguinea* L., *Populus nigra* L., *Populus alba* L., and *Rubus ulmifolius* Schott. Flames heavily affected 67% of the catchment, and the riparian area resulted in a mixture of burned severities along the main stream. Resprouting species (e.g. *Quercus ilex* L.) or seeding species (e.g. *Pinus halepensis* Mill.) were present 30 months after the fire in the catchment. Riparian areas resulted also in a mixture of pre-fire vegetation. Furthermore, some areas along the stream were managed during the second post-fire year because of the fire severity and social interest of the area. The restoration included stabilization of some denuded riverbanks with high slopes and replantation of previous and new species like *Fraxinus angustifolia* Vahl, *Salix atrocinerea* Brot., *Sambucus nigra* L., *Amelancher ovalis* Medik. (Garcia & Sorolla 2007).

As a consequence of this mixture of burned severities and recoveries in the Vall d'Horta stream riparian areas, we were able to define two close stream reaches, each approximately occupying 35 m^2, within 6 Km^2 of the 67% burned catchment area: one with a completely burned riparian canopy cover and the other with a non fire affected and intact riparian canopy (called hereafter, respectively, Open (O) and Closed (C) canopy). Differences in solar radiation exposure in each one of the reaches were tested measuring the photosynthetically active radiation (PAR) above the stream water with a ceptometer (Decagon Sunfleck Ceptometer, Pullman, WA) during an eight-month-period. The open canopy presented significant higher values compared to the closed one (O: 491 ± 3 $\mu mol/m^2s$ vs. C: 199 ± 6 $\mu mol/m^2s$; KW: 13.95, p-value<0.0001). We also compared the PAR measures taken above the water stream to ones taken in the adjacent open field (635 ± 6 $\mu mol/m^2s$), and both canopies presented lower values of light incidence (closed and open reaches, respectively, KW: 2.60, p-value<0.0001 and KW: 1.94, p-value: 0.001).

Substrate and physicochemical habitat characteristics

Both study sites were monitored every four weeks during a 13-month-period (February 2006 to February 2007). Discharge (l/s) was estimated from depth, width, and water velocity measurements. Water temperature (ºC), percentage of saturated oxygen (%), pH, and conductivity (µS/cm) were measured *in situ* with a Multiline P4 VTW. Water samples were collected and processed at the laboratory. The turbidity was estimated with a nefelometric method (Hach model 2100P), and the Total Organic Carbon (TOC) was performed with a Shimadzu TOC-5000 analyzer (EPA 9090A, USEPA 1996). The water samples were filtered (250 ml through microfiber filters Whatman GF/F) to calculate the Total Suspended Solids (TSS, mg/l) and analyze the remaining chemical parameters. The Dissolved Organic Carbon (DOC) was performed like for the TOC. The chloride, nitrates, and sulphates were analyzed with an ionic chromatography (UV/V KONTRON model 332, EPA 9056); the reactive phosphorous was measured using a spectrophotometer (Shimadzu UV-1201) at 890 nm (Murphy & Riley 1962); the calcium, iron, potassium, and sodium were analyzed using a Perkin-Elmer Optima (3200 RL); and the alkalinity was measured using a titulation with sulphuric acid (0,02N) and phenolphthalein. The absorbance (a300) and fluorescence (f 450/500) emission values were measured as described in Vila-Escalé *et al.*(2007).

On each site, six to seven transects were fixed in order to map the distribution of the inorganic and organic substrate. Percentages of bedrock, stones, sediment, and leaf litter cover were estimated with a viewer of 20x20 cm; the aquatic vegetation cover was also estimated on each inorganic substrate; and the depth and the velocity was also recorded. With all these data, the cover characteristics of both reaches were estimated every four weeks. A surface of 1 cm^2 on three randomly selected stones were scraped and kept cold for chlorophyll-*a* measures. Once in the laboratory, and after defrosting, the samples were filtered (Whatman filters, GF/C 0.7 µm-pore size) and each filter was extracted in buffered acetone (90%) for 24 hrs before sonication (5 min). Chlorophyll-*a* was measured with a spectrophotometer (Perkin-Elmer, Lambda UV/VIS), following the methods described by Jeffrey & Humphrey (1975).

Aquatic vegetation and composition

Samples of submerged vegetation were taken and preserved in formalin 4% for group recognition. Subsequently, twelve main taxonomical groups were established that were able to distinguish from macroscopic identification in the field: 1. Macrophytes (*Rorippa nasturtium-aquaticum*, *Apium nodiflorum*, *Callitriche stagnalis*), 2. Briophytes, 3. *Chara* sp., 4. Cladophorales (*Cladophora* sp. and *Rhizoclonium* sp.), 5. *Vaucheria* sp., 6. Zygnematales (*Mougeotia* sp., *Spirogyra* sp., and *Zygnema* sp.), 7. *Hildenbrandia* sp., 8. Diatoms (*Melosira* sp., *Fragilaria* sp., *Cocconeis* sp, among others), 9. *Nostoc* sp., 10. *Scytonema* sp., 11. Oscillatoria (*Oscillatoria* sp., *Phormidium* sp. and *Lyngbia* sp.), and 12. Ulvals (*Enteromorpha* sp., *Monostroma* sp., *Oedogonium* sp., and *Ulothrix* sp.).

The cover of each taxonomical group was first estimated in percentages for each habitat (bedrock, stone and sediment) and then extrapolated at reach scale in each site and time.

Macroinvertebrate sampling

With the same periodicity, three macroinvertebrate replicate samples were collected from the three dominant habitats (individual stones, sediment, and leaf litter) and preserved in formalin 4%. The stone samples were taken washing three to five medium-sized stones in a 250 µm mesh that was placed downstream while lifting and cleaning the stone. To estimate the sampled surface area each stone was wrapped with aluminium foil which was finally weighted (regression determined empirically; r^2=0.99). Sediment samples were collected with a core of r= 5.6 cm. Leaf litter samples were collected from within a core of r= 19 cm. Macroinvertebrates were identified to the lowest possible taxonomic group and counted. Oligochaeta, Ostracoda, and Diptera were identified, respectively to order and family level. Once separated and identified, the body lengths were measured to the nearest 1 mm. If more than fifty individuals of a given taxon were found, at least three size groups were distinguished and twenty specimens of each were measured. Ash Free Dry Mass (AFDM) was calculated using length-weight relationships (Smock 1980; Meyer 1989; Benke *et al.* 1999). If an equation was not available for a taxon, it was substituted by one from the most similar taxon available.

Biological trait information for each taxon was collected from the literature (Tachet *et al.* 2000) and the proportion was calculated using the fuzzy information (Chevenet *et al.* 1994). Similar to Bonada *et al.* (2007a), a small group of biological traits were chosen based on hypothetical changes in functionality of the macroinvertebrate community as a result of disturbances present in Sant Llorenç (changes in canopy, flooding, and drought). The eight modality traits compared were: >1 reproductive cycles per year, strong adult and larval dispersers, shredders, scrapers, predators-piercers, deposit and filter collectors, and none resistance.

Data analysis

Non metric multidimensional scaling (NMDS) was used to analyze the physico-chemical parameters based on the Euclidian distances. To test the NMDS analysis significance, the Adonis pseudo-ratios were used to compare Canopy, Sampling, and their interaction.

Changes in macroinvertebrate community between canopies over time were explored at two hierarchical levels: reach level (open and closed canopy) and at habitat level (stone, sediment, and leaf litter).

First, we examined taxonomic composition, abundance, and biomass between seasons using an analysis of variance (ANOVA). Canopy and Sampling were treated as a fixed factor, and Replicate as a random factor in order to test differences in taxa number (S), diversity (Simpon's index – H'), density (n/m^2, n/reach), and biomass (gr/m^2, gr/reach). Afterwards, the differences between sampling months were tested with a paired Student t-test with the subsequent FDR correction (Benjamini & Hochberg 1995). The density and biomass data was log transformed to fit normality assumptions. The same procedure was done separately for each habitat: stone, sediment, and leaf litter.

To detect periods of similar composition in the macroinvertebrates dataset and to identify discontinuities we used chronological clustering (Legendre *et al.* 1985; Legendre & Legendre 1998), which is a non-hierarchical clustering technique based on a dissimilarity matrix (Bray-Curtis distance) that imposes a time constraint of temporal contiguity so that adjacent years cluster together. We used time-series analyses with three replicates for each sampling data, all part from the 'mvpart' package of the R statistics (R Development Core Team 2006). Afterwards, indicator values (IndVal, from the ‘labdsv’ package) and significance for each value were calculated for each taxa (Dufrêne & Legendre 1997), the groups used were the ones formed from the previous time constrained cluster analysis. NMDS ordinations were also performed, and the discontinuities are presented in each ordination graph with the significant taxa obtained from the IndVal analysis.

The modalities of the biological traits percentages were compared with paired student tested after the arcsinus of the square root transformation. Additionally, the biomass for scrapers and predators-piercers was also calculated, separating them in two groups according to the measured sizes: < and $\geq$500 µm. The root transformation was used to apply the paired Student t-test comparison. All statistical analyses were carried out using the R freeware package (R Development Core Team 2006).

Results

Precipitation and flow regime patterns

The daily precipitation before and during the studied period is presented in Figure 1.1 together with the flowing conditions of the stream that were characterized in four classes: flowing, connected and isolated pools, and dry. The initial period of sampling was characterized by high flow due to the elevated accumulated precipitation during the former autumn (293 mm). The precipitation of the following winter (131 mm) and spring (35 mm) was low and the isolation of pools started in the end of May which ultimately resulted in their total desiccation in the open canopy from June until September. The heavy late summer and autumn precipitations (together 642 mm) restored the flow conditions in both reaches but progressive disconnection of the pools occurred until the end of the sampled period, when rainfall resumed.

Physical habitat, chlorophyll-*a* and chemical parameters

Both reaches were very similar in terms of habitat availability (Figure 1.2). Sediment was the most frequent habitat (35 to 80% of streambed depending on the month). The highest values of bedrock and stones coverage were found during the high flow conditions (February, March, October and November 2006). As expected, the only significant differences were found for the leaf litter cover, which was significantly higher in the closed canopy compared to the open canopy (C: 18.5 ±3.0% vs. O: 4.3 ±0.7%; F-value: 32.8, p-value<0.0001), while the aquatic vegetation cover showed the opposite trend (C: 31.1 ±4.5% vs. O: 47.0 ±3.5%; F-value: 7.9, p-value: 0.013). The paired t-Student test showed that the chlorophyll-*a* measured in the open canopy was always significantly higher compared to that of the closed canopy (t-test: -3.07, p-value: 0.015, see Table 1.1).

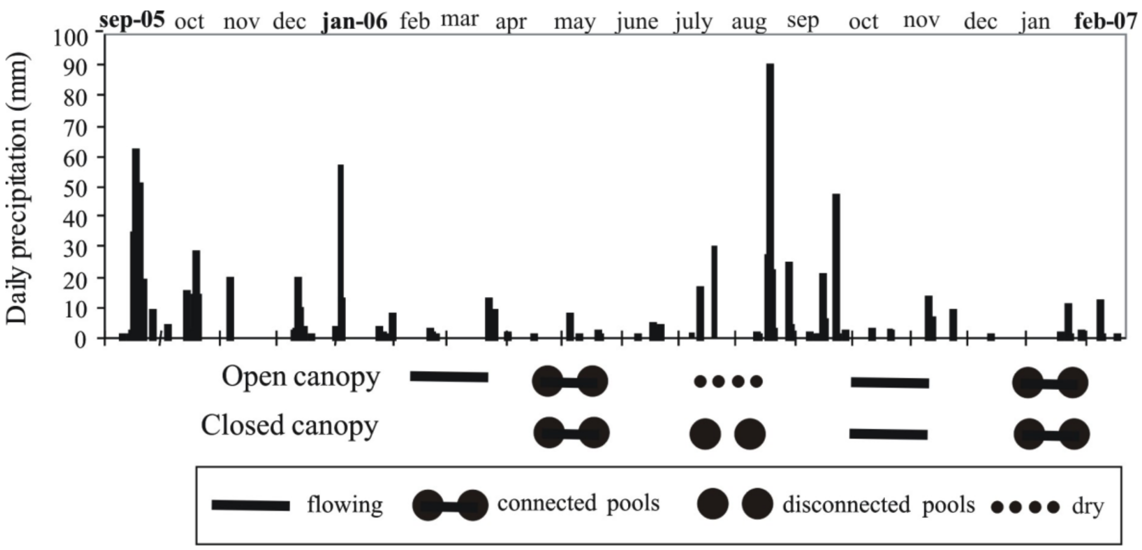


Figure 1. Daily precipitation just before and during the sampling period (September 2005 – February 2007). The flow conditions for each reach (open and closed canopy) are characterized in four types: flowing, connected and disconnected pools, and dry.

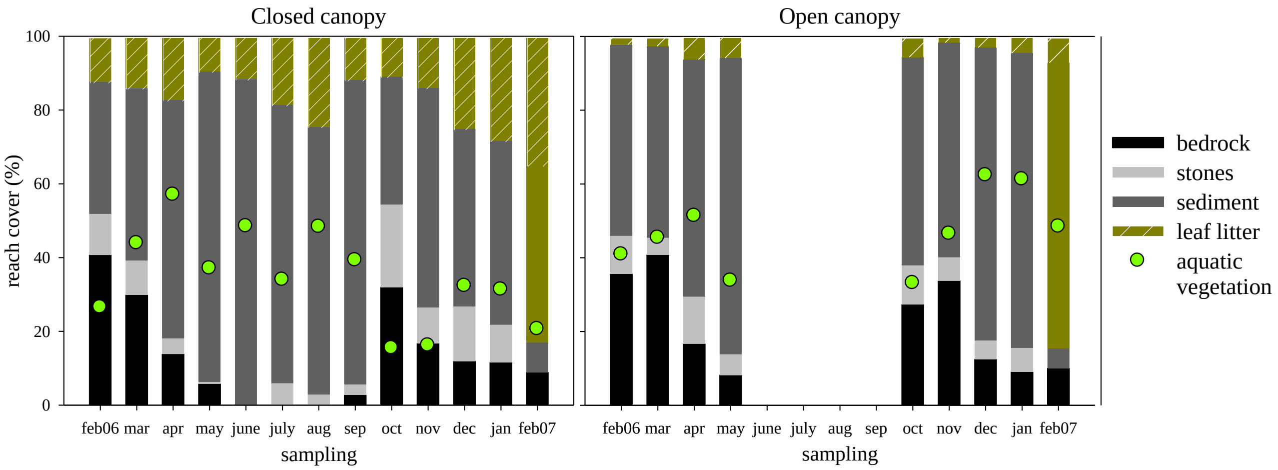


Figure 1.2. Streambed cover percentage of closed (left) and open (right) canopies during the sampling period. The cover was divided in bedrock, stones, sediment, and leaf litter. The aquatic vegetation cover was measured on the inorganic substrate.

Mean values of all the main physico-chemical parameters were calculated and grouped according to the flow conditions and are presented in Table 1.1. The Adonis comparison after the NMDS done with the Euclidian distance with the physico-chemical parameters (Figure 3) showed barely a significant difference between the reaches (F-value: 1.8; p-value: 0.046), with higher values of pH and oxygen in the open canopy (Table 1.1). On the other hand, the sampling time was highly significant (F-value: 3.8; p-value

<0.001) for almost all the physico-chemical parameters, while the interaction was not (F-value: 0.8; p-value >0.05). The samples were ordered following the time series period, as can be seen in the two dimensions graph (Figure 1.3), and thus indicating a relationship with flow condition, being the most different ones the summer samples of the closed canopy (open canopy was dry in the summer).

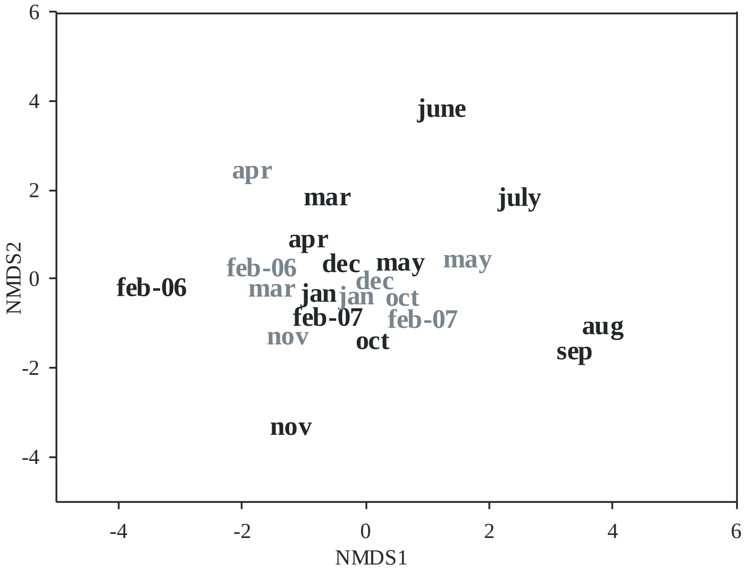


Figure 1.3. NMDS of the physico-chemical parameters based on the Euclidian distance of the closed (black) and open (grey) reaches.

Habitat and reach scale variability of aquatic vegetation cover and composition

Canopy cover determined the differences between reaches regarding the aquatic vegetation composition (Figure 1.4). In the closed canopy, the assemblage on sediment substrate was dominated by macrophytes accompanied by Cladophorales, *Chara* and/or Oscillatoriales and Zygnematales that depended on the month in relation with the hydrological cycle, with the more important presence of diatoms in the winter. Bedrocks and stones were covered by bryophytes, cladophorales, and less abundantly diatoms. In the open canopy all habitats were colonized by Chladophorales and Zygnematales, accompanied by diatoms in winter on the sediment and *Hildenbrandia* in the hard substrates all throughout the year. Total abundances varied along the year in each habitat and reach. In the closed canopy reach the algae on the sediment was more abundant in April just after floodings, matching with the sediment accumulation and when the temperature was rising (Figure 1.2 and Table 1.1). While for the open canopy reach, algae cover was homogenously high, except for the dry months (no cover) and just before and after this period (Figure 1.4).

Table 1.1. Mean ± standard error for the main physico-chemical parameters and chlorophyll-*a* measured in closed (left) and open (right) canopy. To simplify the table, month values were grouped according to the flow conditions in time (F: flowing, CD: Connected pools, DC: Disconnected pools, D: Dry).

	closed canopy					open canopy				
	feb-mar-06	apr-may	june-sep	oct-nov	dec-feb-07	feb-mar-06	apr-may	june-sep	oct-nov	dec-feb-07
Flow type	F	CP	DP	F	CP	F	CP	D	F	CP
Flow (l/s)	38.1 ± 9.0	6.5 ± 2.8	0.2 ± 0.2	18.0 ± 5.3	3.4 ± 0.9	29.3 ± 3.8	2.6 ± 1.4		17.2 ± 6.4	2.4 ± 1.3
Temperature (ºC)	11.9 ± 1.3	15.8 ± 1.3	19.2 ± 0.7	14.0 ± 0.4	7.8 ± 1.2	10.12 ± 1.2	18.7 ± 3.9		15.2 ± 0.2	9.0 ± 1.3
Oxigen (%)	96.2 ± 1.5	105.4 ± 7.0	60.8 ± 9.2	90.4 ± 3.7	88.2 ± 2.8	93.2 ± 4.0	105.5 ± 5.8		119.2 ± 3.7	105.5 ± 3.6
f 450/500	2.08 ± 0.03	1.99 ± 0.07	2.00 ± 0.05	2.02 ± 0.04	2.03 ± 0.02	2.04 ± 0.05	1.97 ± 0.05		2.02 ± 0.02	2.01 ± 0.04
a300	3.82 ± 0.27	5.87 ± 0.54	13.88 ± 1.55	6.98 ± 0.37	5.323 ± 0.51	3.51 ± 0.33	5.63 ± 1.17		5.48 ± 0.43	5.14 ± 0.47
TSS (mg/l)	3.12 ± 0.33	2.18 ± 0.23	5.61 ± 3.26	1.29 ± 0.36	2.74 ± 0.27	3.07 ± 0.47	2.43 ± 0.23		1.44 ± 0.08	2.24 ± 0.23
Turbidity (NTU)	2.36 ± 1.39	1.34 ± 0.41	2.36 ± 0.34	1.15 ± 0.26	1.52 ± 0.48	0.72 ± 0.25	1.51 ± 0.58		1.32 ± 0.40	1.66 ± 0.44
Conductivity (µS/cm)	656 ± 9	641 ± 15	546 ± 26	493 ± 24	445 ± 13	644 ± 9	627 ± 17		497 ± 13	427 ± 14
Sodium (mg/l)	6.62 ± 0.06	7.27 ± 0.20	8.84 ± 0.95	10.39 ± 1.80	7.26 ± 0.09	6.92 ± 0.43	8.23 ± 0.52		7.24 ± 0.22	8.22 ± 0.21
Potassium (mg/l)	0.81 ± 0.50	0.36 ± 0.21	1.29 ± 0.63	1.70 ± 0.37	0.33 ± 0.21	1.68 ± 0.79	3.78 ± 3.45		0.73 ± 0.14	0.28 ± 0.18
Iron (mg/l)	0.001 ± 0.001	0 ± 0	0.018 ± 0.006	0.060 ± 0.031	0.0017 ± 0.000	0.013 ± 0.013	0 ± 0		0.050 ± 0.023	0.001 ± 0.000
Chlorides (mg/l)	9.52 ± 1.44	12.48 ± 2.14	14.23 ± 2.67	14.25 ± 0.55	18.69 ± 1.01	7.84 ± 2.90	13.57 ± 3.22		14.92 ± 0.59	18.76 ± 0.60
Sulphates (mg/l)	21.63 ± 1.65	25.71 ± 0.44	15.74 ± 3.03	22.93 ± 2.05	27.00 ± 1.342	21.245 ± 6.36	28.46 ± 0.78		25.48 ± 0.99	29.35 ± 1.52
Calcium (mg/l)	85.84 ± 1.62	75.92 ± 3.50	84.05 ± 11.23	129.44 ± 24.01	84.21 ± 4.04	89.18 ± 0.57	61.40 ± 3.82		92.12 ± 7.39	78.57 ± 4.81
Alcalinity (µeq/l)	6.54 ± 0.07	6.84 ± 0.19	6.75 ± 0.26	6.96 ± 0.21	7.45 ± 0.16	6.63 ± 0.09	6.4 ± 0.19		7.09 ± 0.09	7.14 ± 0.18
pH	7.74 ± 0.08	7.90 ± 0.05	7.97 ± 0.16	7.91 ± 0.02	7.87 ± 0.03	7.96 ± 0.08	7.94 ± 0.07		8.12 ± 0.07	8.08 ± 0.03
Nitrates (mg/l)	0.62 ± 0.20	0.58 ± 0.16	0.11 ± 0.06	0.72 ± 0.08	0.72 ± 0.08	0.80 ± 0.19	0.35 ± 0.12		0.61 ± 0.21	0.32 ± 0.07
Phosphates (mg/l)	0.024 ± 0.017	0.018 ± 0.006	0.015 ± 0.005	0.009 ± 0.001	0.015 ± 0.001	0.010 ± 0.006	0.003 ± 0.002		0.009 ± 0.000	0.0113 ± 0.002
TOC	2.27 ± 0.21	3.21 ± 0.48	6.06 ± 0.61	2.90 ± 0.14	2.34 ± 0.16	2.27 ± 0.26	3.47 ± 0.87		2.58 ± 0.21	2.65 ± 0.11
DOC	2.19 ± 0.19	2.91 ± 0.42	4.69 ± 0.51	2.65 ± 0.17	2.14 ± 0.20	1.96 ± 0.04	3.03 ± 0.67		2.48 ± 0.17	2.26 ± 0.10
Chlorophyll (mg/cm^2)	2.86 ± 0.60	3.60 ± 2.23	4.86 ± 2.44	5.80 ± 0.78	10.91 ± 2.12	36.14 ± 22.84	14.82 ± 4.99		15.10 ± 9.35	22.03 ± 5.78

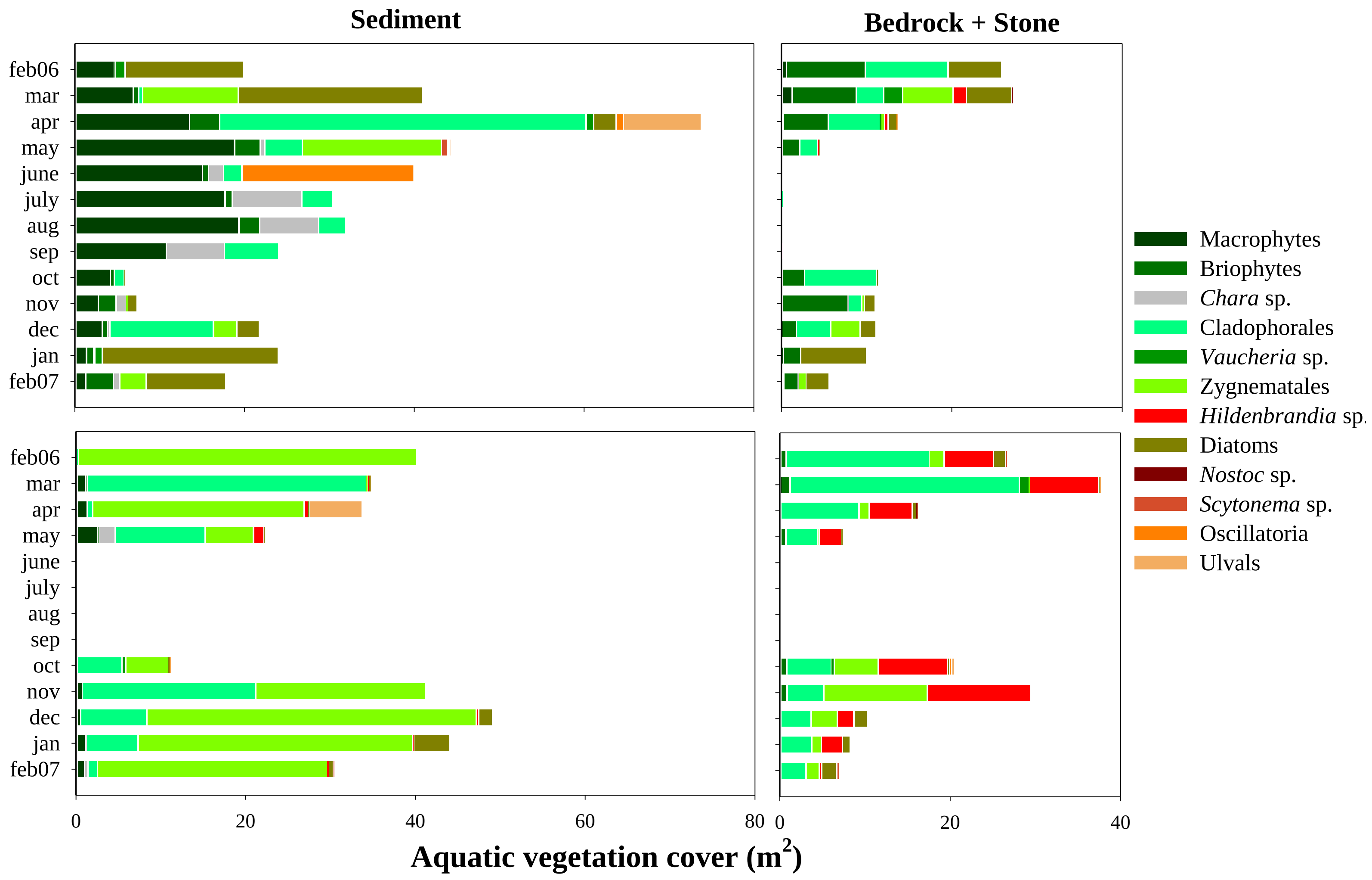


Figure 1.4. Aquatic vegetation cover (m^2) for the 12 taxonomical identified groups on each habitat (left= sediment and right= bedrock + stone) and reach (top= closed canopy and bottom= open canopy).

General composition and variability of the macroinvertebrate community

During the study, 64 insect genera were identified beside the 26 Diptera identified to a lower level (family or subfamily), and together with the Oligochaeta, Ostracoda, Hydracarina, and Acheta accounted for a total of 101 different taxa. 27 taxa were exclusively found in the closed canopy, while 9 taxa were exclusive from the open canopy (see Appendix 1). The dominance of Diptera, Oligochaeta, and Ostracoda was similar in both canopies, representing at least the 60% of the macroinvertebrate community, followed by Ephemeroptera and Mollusca being the last one an important group in the closed canopy reach during the dry months and in the open canopy only at the end of the sampling period.

At reach scale, riparian canopy affectation resulted in an important factor determining differences in taxa number, diversity, and macroinvertebrate densities, as well as biomasses per reach (Table 1.2). The paired t-Student comparisons are shown in Table 4. The open canopy presented a lower taxa number (C: 26 ±1 *vs.* O: 24 ±1), diversity (C: 0.89 ±0.03 *vs.* O: 0.74 ±0.03), and reach biomasses (C: 42.5 ±5.4 gr *vs.* O: 37.8 ±4.5 gr), while the opposite was found for the abundance (C: 4234 ±491 *vs.* O: 6798 ±792). Similarly, the time of sampling represented also a significant factor for the taxa number, diversity, and abundance, while the interaction was not significant in any case (Table 1.2). The highest taxa numbers were found in the months of April, December, and February 2007, while the lowest was found at the first sample and when the flow got restored (Figure 1.5a). Diversity was highest during the last four months of sampling (Figure 1.5b). The density peaked similarly to the taxa number, but April was the most significantly different in relation to the other months (Figure 1.5c). Total abundance per reach was only significantly different for sampling period (Table 1.2), with the higher values registered in April and the lowest in October (Figure 1.5e, Table 1.4). Following similar trends, the biomass had a peak in April in the closed canopy and at the end of the sampling period in the open canopy reach (Figure 1.5d, 1.5f), but neither canopy nor sampling were significant for biomass per square meter (Table 1.2).

Table 1.2. F-values from the analysis of variance testing for differences in canopy affectation and sampling time at reach scale for the taxa number (S), density (n/m^2), biomass (gr/m^2), reach density (n/reach), and reach biomass (gr/reach) (p-value: ***<0.001, **<0.01, *<0.05, ^{ns} not significant).

	S	H’	n/m^2	gr/m^2	n/reach	gr/reach
Canopy	**6.47 ***	**9.32 ****	**4.50 ***	3.06 ^{ns}	0.17 ^{ns}	**11.12 ****
Sampling	**2.78 ***	**5.82 *****	**4.56 ***	1.37 ^{ns}	**5.15 ****	1.67 ^{ns}
Canopy x Sampling	0.93 ^{ns}	1.79 ^{ns}	1.04 ^{ns}	0.73 ^{ns}	0.90 ^{ns}	0.72 ^{ns}

Comparing the three habitats, the leaf litter showed the highest taxa number while the sediment showed the lowest abundance. In the open canopy, the stone habitat presented higher abundances (C: 4731 ±1855 vs O: 10577 ±527), while in the closed canopy the leaf litter showed a higher taxa number (C: 18 ±1 vs. O: 15 ±1) and biomass (C: 0.49 ±0.12 vs O: 0.31 ±0.06gr/m^2) (Table 1.3). Consistent with the previous results from the exclusive taxa found in the closed canopy, half of them were registered in the leaf litter habitat only, represented mainly by Odonata, Coleoptera and Diptera. On the other hand, 6 from the 9 exclusive taxa found in the open canopy were found in the stone habitat represented mainly by EPT taxa. It was in this same habitat where the sampling was significant for the taxa number and abundance (Tables 1.3 and 1.4).

Table 1.3. F-values from the analysis of variance testing for differences in canopy affectation and sampling time separated by habitat (stone, sediment and leaf litter) for the taxa number (S), density (n/m^2), and biomass (gr/m^2) (p-value: ***<0.001, **<0.01, *<0.05, ^{ns} not significant).

	Stone			Sediment			Leaf litter		
	S	n/m^2	gr/m^2	S	n/m^2	gr/m^2	S	n/m^2	gr/m^2
Canopy	2.73 ^{ns}	**5.72 ***	0.01 ^{ns}	0.99 ^{ns}	0.91 ^{ns}	0.90 ^{ns}	**7.95 ***	0.02 ^{ns}	**5.44 ***
Sampling	**5.06 ****	**3.03 ***	1.16 ^{ns}	1.16 ^{ns}	1.46 ^{ns}	0.37 ^{ns}	1.65 ^{ns}	1.56 ^{ns}	0.95 ^{ns}
Canopy x Sampling	2.39 ^{ns}	0.77 ^{ns}	0.74 ^{ns}	1.02 ^{ns}	0.86 ^{ns}	0.31 ^{ns}	1.91 ^{ns}	0.56 ^{ns}	0.39 ^{ns}

Table 1.4. Paired Student t-test results from the comparison between months at a reach scale (top) and at habitat scale-stone (bottom). If there were significant differences between sampling, these were presented differently for taxa number (α), abundance per square meter (+), and abundance at reach scale (‡).

feb-06	mar	apr	may	oct	nov	dic	jan	feb-07	
▨	‡	α +	‡	+ ‡		α		α	feb-06
	▨	+ ‡		+ ‡	+ ‡				mar
		▨	‡	α + ‡	+ ‡	+ ‡	+ ‡	+ ‡	apr
			▨	+ ‡	+ ‡	‡			may
				▨	α	‡	α + ‡	α + ‡	oct
					▨				nov
						▨			dic
							▨		jan
								▨	feb-07

feb-06	mar	apr	may	oct	nov	dic	jan	feb-07	
▨	α	α +	α +	α +	α +	α +	α +	α +	feb-06
	▨	α	α			α +	α	α +	mar
		▨		α		+		α	apr
			▨	α				α	may
				▨		α +	α	α +	oct
					▨	α +	α	α	nov
						▨			dic
							▨	α	jan
								▨	feb-07

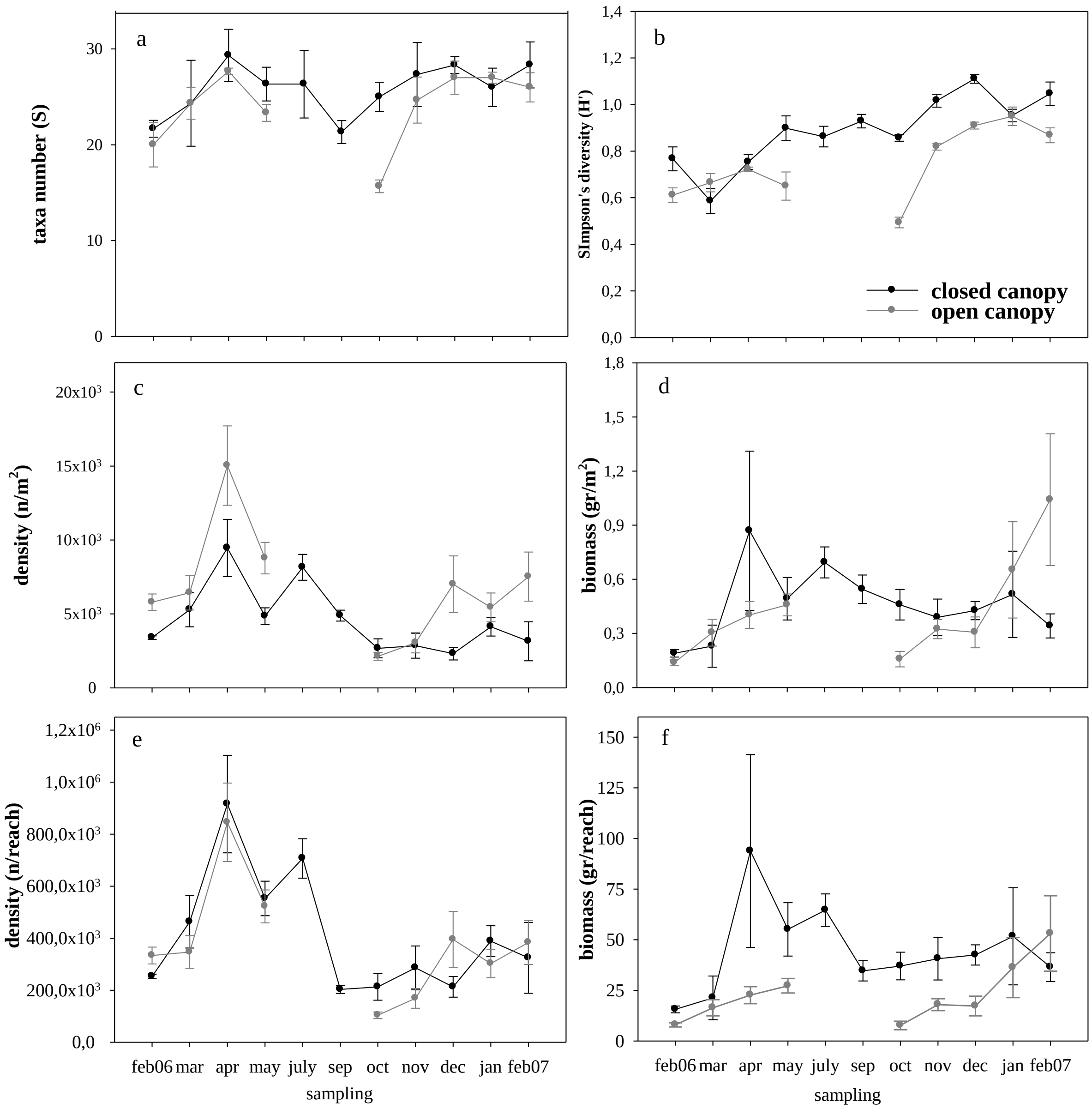


Figure 1.5. Mean ± standard error of the taxa number (a), Simpson’s diversity (b), density (c) and biomass (d) per square meter, and density (e), and biomass (f) at reach scale during the sampling period.

Temporal discontinuities in the community composition

Based on the time constrained cluster analysis, the discontinuities in the community ranged from three to six aggregations, and the habitats in the open canopy always presented more changes or species turnover compared to the closed canopy. May was the only month that represented consistently a temporal brake among assemblages in both canopies and in the three habitats (Figure 1.6).

In the stone habitat, three turnovers (four groups) could be recognised in the closed canopy while in the open canopy five turnovers were detected. Sampling months were similarly situated in both canopies except when the open canopy was dry (Figure 1.6).

18 taxa were significantly associated with time cluster groups, sharing almost half of the taxa that were associated to the same sampling months. For example, *Ephemerella* sp., *Galba* sp., and Oligochaeta were significantly related to the period of low flow, while *Baetis* sp., *Nemoura* sp., and *Habroleptoides* sp. were associated to winter (Figure 1.6). In the leaf litter habitat, similar number of changes were defined in the closed and the open canopy, but neither the sampling months were closely situated nor the significant shared taxa were found in similar sampling months. For example, *Mesophylax* sp. was associated to the spring group in the closed canopy, while in the open canopy it was significant related to the winter one. Similarly, *Agabus* sp. was found in the spring group of the closed canopy and just after the dry months during the recovery in the open canopy reach (Figure 6). Finally, in the sediment habitat, six clusters were defined in the open canopy reach while only three in the closed canopy (Figure 1.6). The associated taxa were mainly Chironomidae, Oligochaeta, and beetles from the Dytiscidae and Haliplidae families.

Community traits

Apparently, no large differences among reaches were observed for the selected biological traits (Figure 1.7). However, important changes in their proportion were found related to flooding recovery and during the dry months. A higher proportion of organisms that present >1 reproductive cycle per year were found in the open canopy (t-test: -5.6, $p<0.001$) and this percentage was higher just after the floodings, during February, March, November and October 2006 (Figure 1.7). In the closed canopy, during the dry months, a higher proportion of strong larval dispersers (t-test: 3.0, p: 0.006) and invertebrates with some type of resistance (t-test: -3.5, p: 0.016) against unfavourable conditions (e.g. eggs, cocoons, refuge, diapause, etc.) were found (Figure 1.7).

On the other hand, for the feeding types, the difference between canopies was clear in the shredders percentage (t-test: 6.8, $p<0.001$) and as expected, a higher value was found in the closed canopy (Figure 1.7). The dominant strategy in both canopies was the filterer-gatherer collector and no differences were found for this group of organisms (t-test: -1.0, $p>0.05$). The second most abundant strategy was the scrapers, which presented a higher abundance (t-test: -5.0, $p<0.001$) in the open canopy except when the reach was dry (Figure 1.7). The low flow conditions maintained not only a higher biomass but also bigger scraper invertebrates (≥500 μm). Finally, the predators-piercers did not represent an abundant strategy (in percentage); however, in the closed canopy it was significantly higher (t-test: 3.5, p: 0.002). Furthermore, in terms of biomass these differences disappeared between canopies, but bigger invertebrates >500 µm were generally more significant in the closed canopy (Figure 1.7).

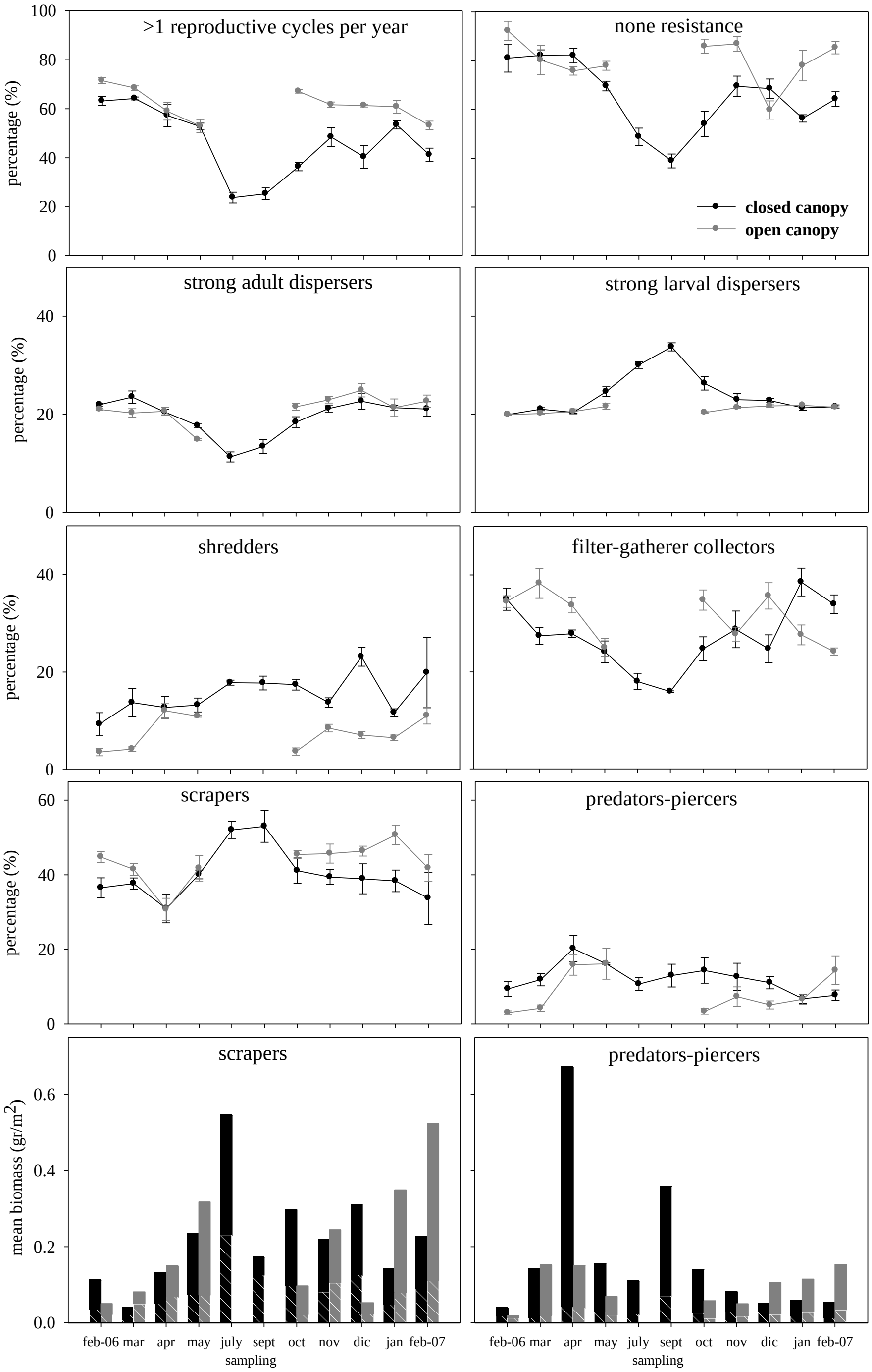


Figure 1.7. Closed and open canopy reaches are presented respectively in black and grey for the proportion (%) of the *a priori* chosen biological traits: >1 reproductive cycles per year, none resistance, strong adult and larval dispersers, shredders, filter-gatherer collectors, scrapers, and predators-piercers. The mean biomass (gr/m^2) from scrapers and predators-piercers is also represented differentiating small (<500µm) (in stripes) from the big invertebrates (>500µm) (solid colours).

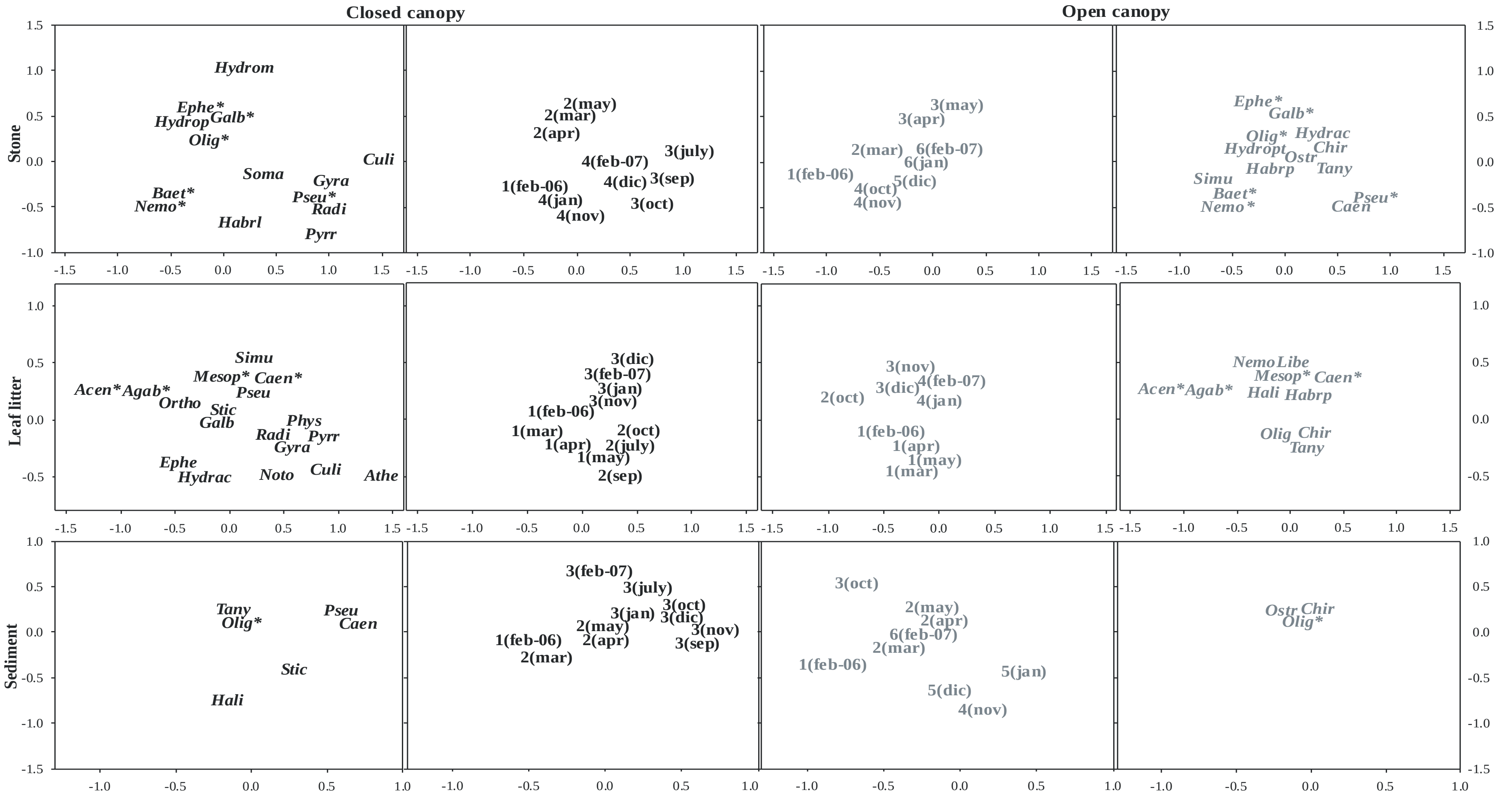


Figure 1.6. NMDS of the macroinvertebrate communities from closed (black, left) and open (grey, right) canopies from the three studied habitats considered independently: stone, sediment, and leaf litter, based on the Bray-Curtis distance. Sample assignation to time-constrained cluster analysis groups (one to six) are indicated together with the sample month. Besides each ordination, the significant taxa obtained from the IndVal analysis is plotted for each habitat and canopy. Shared significant taxa between the canopies are indicated with an asterisk.

Discussion

The importance of canopy cover

Invertebrate communities were strongly influenced by the riparian cover. Similar to other studies (Hawkins *et al.* 1982; Stone & Wallace 1998; Death & Zimmermann 2005), in Sant Llorenç the open canopy generated a higher abundance and differences in macroinvertebrate composition turnover, probably due to a greater algal cover and hence primary productivity (Zimmermann & Death 2002). Studies done in the west of the US have corroborated that midterm effects of the wildfire contribute to a greater density and emergence in the burned areas (Mellon *et al.* 2008; Malison & Baxter 2010a). However, in this study, peak densities were more associated to the recovery after floodings and also when the flow ceased in the closed canopy. This indicates the relevance of the effects of fire but also those of hydraulic conditions for the macroinvertebrate community. Hydrology (i.e. flood, drought) emerges as a very important factor in our stream governing the succession, as has been shown by other studies (Robinson & Minshall 1986; Zimmermann & Death 2002). An equivalent response has been shown by Acuña *et al*. (2005) in a Mediterranean stream not affected by fire, where the decline of density during the low flow months was attributed to the physicochemical changes associated to the fragmentation of the watercourse.

Regarding to the taxa number and diversity, contrary to what was expected from studies in other areas (Malison & Baxter 2010a), this Mediterranean stream revealed a decrease in the open canopy. Although open canopies has been characterized as good recipients for propagules and adult insect colonists (Binckley & Resetarits 2007), from the few studies that have looked the effects of light on taxa richness (Robinson & Minshall 1986; Death 2002; Zimmermann & Death 2002), no tendency has been revealed (Vinson & Hawkins 1998). Additionally, midterm wildfire effects have shown variable responses, and ultimately depend more on local characteristics of the catchment and how fire have affected it (Minshall 2003). From studies done in the Mediterranean (Vila-Escalé 2009), the taxa number achieved pre-fire levels two years after fire. However, the recovery of both taxa number and density in Mediterranean streams may be highly dependant on the hydrology of each year (Chapter 2), which in the Mediterranean can be very variable from year to year (Bêche & Resh 2007). Everything together could have contributed to the lower global diversity in the open canopy. Thus after the removal of the riparian canopy due to fire, the aquatic vegetation composition changed and probably favoured the evapotranspiration enhancing the pools dry-up. In addition, biomass was not significantly different between canopies. In this respect divergent responses have also been found in other midterm burned streams studies (Mellon *et al.* 2008; Malison & Baxter 2010a). Temporality was again an important issue in terms of biomass changes in Sant Llorenç, and canopies differed in the period of maximum accumulation: in the spring for the closed canopy and by end of the sampled period in the open canopy, which matches with the periods of high production (winter and spring) described in Mediterranean streams (Guasch & Sabater 1995). This is consistent with the study by Cardinale *et al.* (2005), where a positive relationship between the producer richness and the net production of biomass was demonstrated. Following the abatement of a disturbance, taxa recolonize and the diversity increases before the next disturbance event or until carrying capacity set the habitats productivity is reached (Death 2010). The dominant species in both reaches during the growth period were similar, and one of their traits is a very fast growth, a characteristic that ultimately confer them a high resilience to disturbances (Haddad *et al.* 2008). Thus, the high resilience of macroinvertebrates of Mediterranean streams to large disturbances (floods and droughts) is what could also explain the high resilience observed after other disturbances like wildfire.

Macroinvertebrates at a habitat scale

Consistent to the findings at a reach scale, the macroinvertebrate structure and funtions of the three types of habitats responded to a mixture of temporal changes and variation in aquatic vegetation cover. The algae growing on the stone and sediment habitats were the main bottom-up drivers on the invertebrates. Similar results were found in stream with clear-cut watershed where invertebrate responses depended on the type of substrate, being the cobbles-riffles the most affected habitat (Gurtz & Wallace 1984). Furthermore, the total aquatic vegetation cover was highest on the sediment habitat because this was the most abundant substrate in this stream during the growth seasons (April, May, January, and February 2007), confirming that epipelic algae represents one of the most important components in primary productivity in Mediterranean streams (Velasco *et al.* 2003). Although leaf litter was more important in the closed canopy and the algal cover on stone was higher in the open canopy, both substrates were not dominant and therefore their contribution at reach scale was lower compared to the sediment cover (Figure 4). The frequent changes in the macroinvertebrate community components reflected the dependence on the algae dynamics in structure (Melody &

Richardson 2004) and succession (Peterson & Stevenson 1992) as a result of the removal of the canopy and shaped also by disturbance events like floods and changes in environmental conditions like droughts. The changes in algae cover maintained the habitat heterogeneity (Ledger *et al.* 2008), which in turns affected direct consumers and viceversa (Hillebrand 2008). Consumer effects in aquatic systems are often context-dependent (Power *et al.* 2008), and predicting when consumers will alter rates of ecosystem function is complex. In a clear-cut Mediterranean stream, the bottom-up factors (e.g., nutrient concentrations and light) caused high rates of primary production (Sabater *et al.* 1998) and was then probably this algal abundance what could have outpaced grazing. However, the hydrological conditions may have altered the importance of organisms. For example, true scrapers like molluscs (e.g. *Radix* sp., *Physella* sp., *Gyraulus* sp.) were highly abundant during the summer in the closed canopy reach. On the other hand, the increase in abundance of these organisms in the open canopy started only after the flow got restored and algae and macroinvertebrate biomass peaked by the end of the sampling period. Although both reaches showed different times in scrapers biomass accumulation, the values obtained were similar. Other scrapers like some Chironominae were always significantly related to the spring season (high algae cover) in the open canopy, suggesting that this taxon was responding to the maximum of periphyton rather than controlling it (Wellnitz & Ward 1998).

The autumn floodings changed the conditions in both canopies but for different reasons and allowed the rapid colonization to opportunists. In the closed canopy reach, flood scoured the stream invertebrates and the periphyton reducing the effect of benthic consumers (Ludlam & Magoulick 2010), while in the open canopy the flow got restored and along with high light availability let to a quick growth of the periphyton (Velasco *et al.* 2003). The dominant taxa at this time are those typically found in denuded channels as blackflies, chironomids, and baetid mayflies, which often reach high densities early in the recolonization (Mackay 1992). After fires, these taxa represent the highest density (Minshall *et al.* 1989), biomass (Mellon *et al.* 2008), and emergence (Malison & Baxter 2010a). In this study, the high abundance of these taxa in both reaches and in all seasons indicates the occurrence of disturbances, including fire, in this type of streams. This is confirmed by the dominance in invertebrates with >1 reproductive cycle per year that are mainly generalist feeders (filter-gather collectors).

In this study, the responses to fire after three years seem to be limited to the midterm effects due to the absence of canopy in one of the studied reaches. Thus, higher abundance of leaf litter in the closed canopy brought stability to the community and accumulated a significant higher biomass and diversity. Shredders abundance was higher in the closed canopy, but situation seems to change at the end of the period, because taxa like *Habrophlebia* sp., *Mesophylax* sp., *Haliplus* sp., and *Stictonectes* sp. were significantly more abundant at the end of the sampling in the open canopy. However, the biomass was always significantly lower compared to the closed canopy. The leaf litter in the open canopy reach was low and above all dry out during the summer, thus the possibility for shredder taxa to grow and accumulate biomass in such an instable habitat is harsh (Kobayashi & Kagaya 2009). Other generalist feeders were also found which corroborates that spatial variations in taxa abundance often reflects the vagaries of colonization rather than true habitat preferences (Fonseca & Hart 2001).

During the summer, the scrapers rather than shredders were more abundant in the closed canopy. Furthermore, we also expected a high presence of predators during this time. However, the scraper biomass was highest during the total pool disconnection, while the maximum predator biomass was found just before and after this period. This result matches with the study by Chase *et al.* (2010), who found that predator communities in isolated mesocosmos had lower biomass and richness, while the herbivore biomass was higher in the same conditions compared to connected mesocosmos. Drying can reduce the abundance of larger, long-lived invertebrates (Chadwick & Huryn 2007) and concentrates organisms that compete for resources and avoid the exposition to predators (Magoulick & Kobza 2003).

Final remarks

30 months after the first pulse of nutrients due to post-fire precipitations, most of the physico-chemical parameters were not significantly different among the two canopy conditions studied in Sant Llorenç. Although some studies have shown differences in uptake lengths in nutrients in logged canopies (Sabater *et al.* 2000), it seems that the differences between canopies in a burned catchment were not enough, in this case, probably because both reaches were close. Post-fire erosion in burned Mediterranean streams is extremely enhanced during the first couple of years (Mayor *et al.* 2007). However, these nutrient flashes coming from an already drained catchment like the Vall d'Horta stream did not generate significant differences between canopies, which is probably also because both reaches were not that far from each other. As demonstrated by this data, temporality was more significant than fire and was responsible for the most

significant changes in species turnover during the study period. Temporary-river species are decoupled by frequent disturbances, and populations of these species are usually expanding and contracting as a consequence of habitat connectivity and diversity.

The indirect changes produced by the absence of canopy were highly significant in terms of differences in reaches in organic cover (aquatic vegetation and leaf litter). Similar to results described by Minshall *et al.* (1989), in Sant Llorenç macrophytes and moss cover were related to the closed riparian canopy, while the dominance of green algae was found in the open canopy. However, development of filamentous algal mats (e.g. *Cladophora*) was observed in both reaches reflecting the previous input of nutrients and light as has been described in other burned streams (Minshall *et al.* 1989). This importance of algae in the growth of invertebrates even in closed canopy areas has been previously shown (McCutchan & Lewis 2002). Temporality factor was also very important in the organic cover, and although we did not measure productivity, the aquatic vegetation cover and community reflected the relationship between disturbance and productivity (Lake 2000). In both canopies, floods and seasonal drought represented a key factor not only in the cover of organic matter but also in the structure and function of macroinvertebrate communities living in streams (Resh *et al.* 1988), with a reciprocal response between both levels (Wooton & Power 1993). The presence of consumers not only alters the mean biomass of the prey assemblage, but also affects the spatial heterogeneity of biomass distribution (Hillebrand 2008).

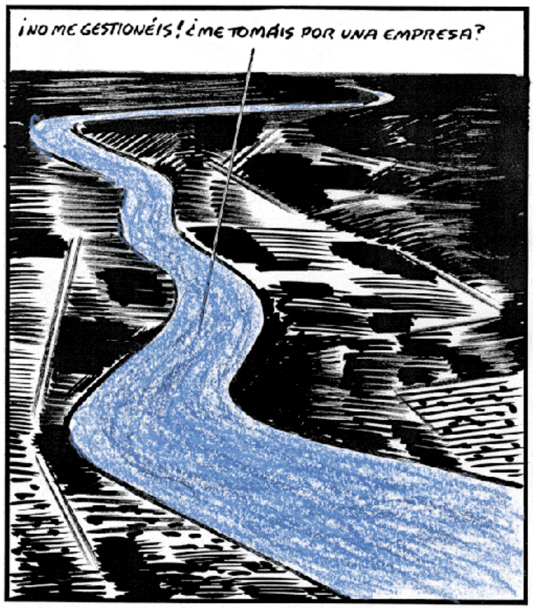
The response of assemblages to disturbance is influenced not only by extrinsic characteristics of the disturbance event, such as scale and environmental context, but also by the intrinsic biological traits of the organisms of interest (Lepori & Hjerdt 2006). Mediterranean streams are characterized by macroinvertebrates with high dispersion and colonization capabilities, reflecting the effects of seasonal discharge patterns and their high resilience to disturbances (Bonada *et al.* 2007a).

In summary, midterm fire effects in this Mediterranean stream affected significantly the invertebrate composition and abundance through indirect effects in the riparian cover. Analogous to the study by Fuller *et al.* (2008), the responses of the macroinvertebrate communities in the closed canopy reach showed more resistance to floods because pools of macroinvertebrates were present to recolonize rapidly. Also, the open canopy was more resilient to flood disturbance, as drought played a very important factor in this reach.

Chapter 2

Wildfire versus seasonal drought shaping a Mediterranean macroinvertebrate community


EL CLIMA CADA DÍA ESTÁ MÁS RARO:
EL AGUA ME LLEGA AL PECHO, PERO MIS PIES ESTÁN SECOS


¡NO ME GESTIONÉIS! ¿ME TOMÁIS POR UNA EMPRESA?

El Roto

Introduction

Mediterranean climate ecosystems are characterised by strong temporal and spatial heterogeneity of abiotic parameters (Touloumis & Stamou 2009), and therefore their biological communities have to cope with this high environmental variability. Furthermore, Mediterranean landscapes are highly dynamic, and disturbances such as wildfires are likely to be part of the evolutionary constraints of life history traits (Blondel & Aronson 1999), structuring the terrestrial communities (Bond *et al.* 2005) and shaping their biodiversity attributes (Pausas *et al.* 2008; Pausas & Verdú 2008). Simultaneously, the hydrologic regimes of the streams of such ecosystems vary from extreme flooding to periods of drought, which also affect the biological communities within the streams (Gasith & Resh 1999; Bonada *et al.* 2007a; 2008).

It is well known that forest fires affect the terrestrial ecosystem severely and directly, which in turns also affects the aquatic ecosystem that exists within it, reflecting the tight coupling between the two (Hynes 1975). As a consequence, wildfires can influence hillslope erosion, stream sedimentation, and the recruitment of large woody debris into streams (Benda 2003; Miller *et al.* 2003; Arkle *et al.* 2010). The timing and severity of erosion and sedimentation can differ by geography, geology, precipitation regime, and fire regime (Minshall 2003). Like in other biomes, in Mediterranean climate areas, soil hydrophobicity is generally enhanced during the first post-fire year (Shakesby *et al.* 2007; Tague *et al.* 2009). The overland flow may increase over time, and as a consequence, more erosion is associated with high peak flows (Cerda & Doerr 2005).

The recovery of the stream habitats following wildfires is related to successional changes in the regrowth of terrestrial vegetation and to decomposition characteristics of burned terrestrial organic matter in the catchment (Minshall *et al.* 1989). Over time, wood and sediment are routed downstream by fluvial processes that form different aquatic habitats (Benda 2003; Miller *et al.* 2003; Minshall 2003). Coarse sediment and wood are gradually depleted as they decay, break up, and are transported downstream before being replenished by new post-fire erosional episodes (Benda 2003; Miller *et al.* 2003). In a long-term view and at larger scales, the post-fire geomorphological impact should be viewed as a matter of soil redistribution rather than of simple net loss (Shakesby & Doerr 2006).

The effect of fires on the biological communities in the aquatic systems can also be partitioned into temporal components (Minshall 2003). The first effects are associated with the physical upheaval resulting from the flooding and mass movement, with accompanying channel alteration and sediment transport and deposition, which generally negatively affect the biota living in the streams, such as algae (Robinson *et al.* 1994), macroinvertebrates (Rinne 1996; Minshall *et al.* 1997; Minshall 2003; Vieira *et al.* 2004), and fishes (Gresswell 1999; Lyon & O'Connor 2008). Though the effect may be temporarily dramatic, the response of the macroinvertebrate community to fire is usually quick, and in terms of taxonomic richness, total abundance, and total biomass, it may return to its pre-fire conditions in a year or two (Roby & Azuma 1995; Minshall *et al.* 2001c). Nonetheless, after large wildfires, a shift towards a community dominated by disturbance-adapted strategists like Chironomidae, Baetidae and Simuliidae seems to be a common response (Mihuc *et al.* 1996; Vieira *et al.* 2004; Mellon *et al.* 2008; Vila-Escalé 2009; Malison & Baxter 2010a). The fire enhances the aquatic production over pre-fire conditions due to increased input and availability of light and nutrients (Minshall *et al.* 1989; Mellon *et al.* 2008; Malison & Baxter 2010a). However, the macroinvertebrate community’s response to fire is often individualistic and related to the generally stochastic nature of disturbance and heterogeneity of environmental conditions, as not all streams within the fire perimeter are affected equally (Minshall 2003). In general, the relatively rapid recovery of stream macroinvertebrates is more closely associated with the recovery of the riparian vegetation and flood plain conditions than with the more-distant portions of its catchment (Minshall *et al.* 2001a).

Above all, the characterisation of the major responses of the macroinvertebrate community after a fire has mostly taken place in the western United States, where the climate is quite different from the Mediterranean (Britton 1991; Bêche *et al.* 2005; Vila-Escalé 2009). Thus, although the story seems well known, the fauna that live in this climate area are subjected not only to scouring floods but also to the subsequent gradual reduction of flow or complete drying of the stream surface over the course of the dry season; this can produce different conditions than have been studied in other biomes (Gasith & Resh 1999; Bêche *et al.* 2005; Vila-Escalé 2009). Furthermore, depending on whether the year is wet or dry, the stream channel may dry up partially or completely (Williams 2006).

Droughts and floods represent the extremes of the hydrological continuum (Lake 2000) and are disturbances that differ markedly in the physical and chemical stresses that they impose on resident biota and in relation to the return time, duration and spatial extent of their impact (Humphries & Baldwin 2003). In Mediterranean rivers, droughts and floods are mainly seasonal and predictable (Gasith & Resh 1999), and life cycles may be adapted to the long-term dynamics of these disturbances rather than to specific flow events (Lytle & Poff 2004). Multivoltinism is the rule and short life cycles are favoured, particularly for those organisms with low migratory capacity (most of the highly abundant Ephemeroptera, Plecoptera and Trichoptera), and thus at least one generation will be ensured before a possible early drought at intermittent or permanent sites (Bonada *et al.* 2007b). Feminella and Hawkins (1995) also reported that antecedent hydrological conditions associated with riffle permanence largely governed macroinvertebrate assemblage structure, apparently due to their influences on the survival and recruitment of subsequent generations.

Catchment-scale disturbances, like fires, can have a midterm effect on the community's composition, providing an opportunity to explore the changes within it. Moreover, in the Mediterranean climate, there can also be simultaneous disturbances, such as floods and droughts, that may affect biological features of streams, including the succession of species, the seasonal influx of aerial colonisers, and temporal changes in the food base (Williams 2006).

The aim of this paper was to determine the midterm response of the macroinvertebrate communities of Mediterranean streams to a wildfire. The general objectives were to document the annual changes in species composition after the fire and to compare the changes between the burned and control streams in a framework of large interannual variability of discharge. Therefore, the specific objectives were to determine: i) How macroinvertebrate assemblages (in structure and function) and environmental variables respond immediately and at a midterm to fire; ii) Which environmental variables are associated with the macroinvertebrate response; iii) The resilience and/or resistance of macroinvertebrate communities in Mediterranean streams after a fire followed by a large flood and a severe seasonal drought during the first five post-fire years.

Material and Methods

Study Area

The study was carried out within the confines of the Natural Park Sant Llorenç de Munt, located in the region of Vallès Occidental (41º81'- 42º25' N; 1º71'- 1º69' E, Catalonia, NE Spain) (Fig. 2.1), a protected area characterised by a conglomerate landscape with Holm oak forest and Mediterranean shrubs, with a dominance of forest pines (Santos *et al.* 2009). By the beginning of the 20th century, the landscape was dominated by vineyards, but after the devastating *Phylloxera* plague, the fields were abandoned and replaced by a natural pine forest (Santos *et al.* 2009).

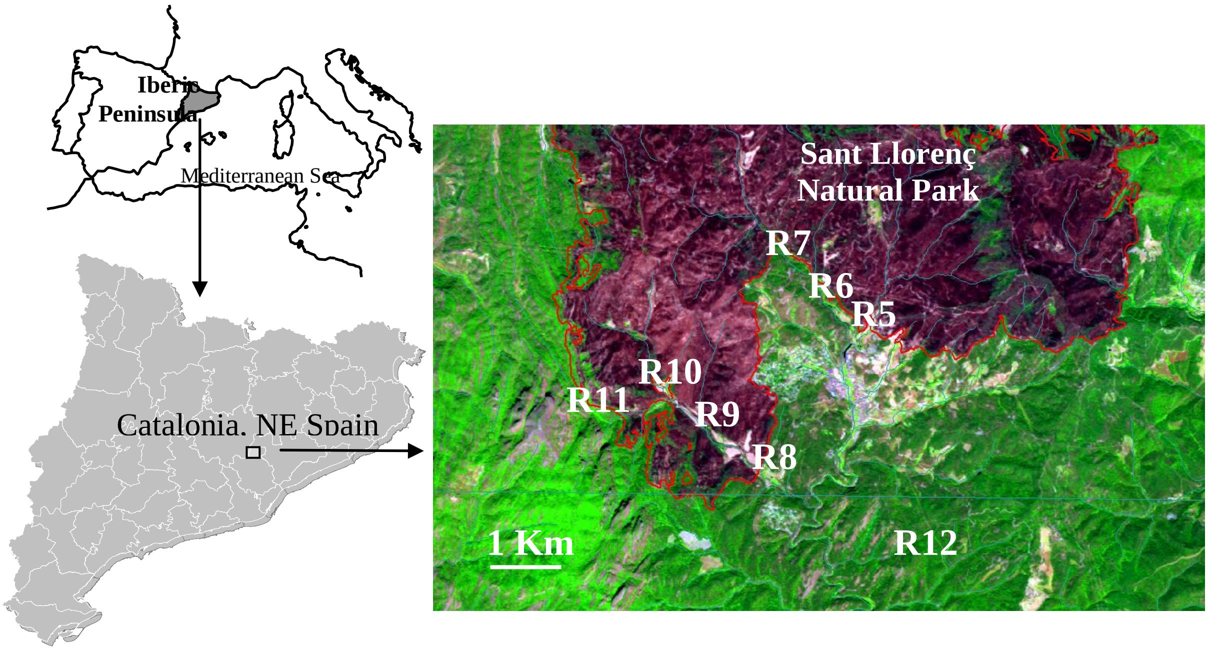


Figure 2.1. Situation of the sampling sites. The burned area is indicated by the darker colour.

The climate is Mediterranean, with mild winters and warm springs and summers. The hydrological regime is intermittent, and generally, there are large floods in autumn/winter and severe droughts in summer, depending on the large interannual variability in rainfall. The precipitation data (Fig. 2.2) were taken from the nearest meteorological station to the study site (Sant Llorenç de Munt 41º91’ N, 1º51’ E; altitude: 528m asl). The geology is mainly calcareous, with several intermediate levels of conglomerates resulting in the presence of permanent natural pools and zones that dry completely.

On August 10, 2003, the dry conditions of the previous months (the accumulated precipitation in spring was 8mm) combined with specific wind regimes resulted in an extensive crown fire of medium intensity (Paricio 2007). In four days, the total forested burned area totalled 4543ha, affecting the catchments of several streams. Two months after the fire, seven sampling sites were established in streams that were affected by the wildfire as well as two non-affected sampling sites that were used as controls (see Table 2.1, Fig. 2.1). All studied streams are tributaries of the Besòs River, and their catchments are mainly forested, dominated by *Pinus halepensis* Mill. with some minor areas where cereals are cultivated (<15%). The proportion of the catchment burned for each sampling point was estimated using aerial photographs with the software Idrisi 32

(ClarkLabs 1999). The six affected sites were each found to have more than 60% of their catchments burned (Table 2.1). As for the control sites, less than 3% of their catchments were burned. In order to study midterm effects on the chemistry of the water and the macroinvertebrate assemblages, we established a five-year monitoring programme. The first sampling was done in October 2003, two months after the fire and severe flooding (187mm of accumulated precipitation, Fig. 2.2), and the subsequent samplings were done in June and July of the following years, i.e., 2004, 2005, 2006, and 2007, referred to from now on by the year of each measurement. Each year was also classified as dry or wet based on the precipitation accumulated during the spring and during the entire year. As mentioned before, the driest spring was recorded in 2003, followed by 2006; the year that experienced the least accumulated precipitation was 2005 (Fig. 2.2). Thus, 2003, 2005 and 2006 were established as dry years. On the other hand, 2004 was the wettest year, and together with 2007, which registered values within the 95% confidence interval, was classified as a wet year.

Table 2.1. Sampling sites, their catchment areas and percentages burned.

Sampling site code	Sampling site location	Stream	Catchment area (Km^2)	% catchment burned
R5	St. Llorenç Savall	Ripoll	7.5	91.2
R6	Torrent de St. Miquel	Ripoll	6.8	94.2
R7	Torrent de la Sala	Ripoll	4.6	99.7
R8	Molí de la Roca	Vall d'Horta	8.8	65.8
R9	Oliveres	Vall d'Horta	7.6	74.0
R10	Can Brossa	Vall d'Horta	5.1	62.1
R11	Marquet de les roques	Vall d'Horta	0.9	2.9
R13	Font del Plàtan	Castelló	2.9	0

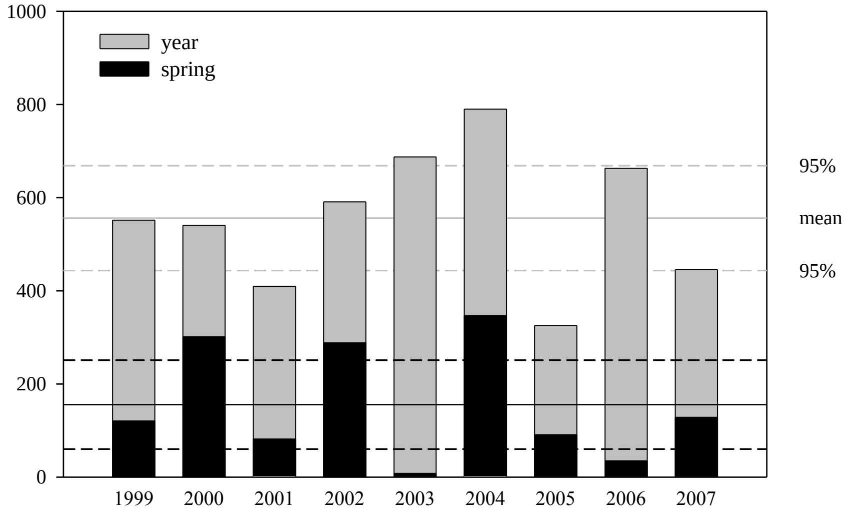


Figure 2.2. Total (grey bars) and spring (black bars) accumulated precipitation from October 1999 –2007, with the mean values and 95% confidence intervals represented. Data from the Sant Llorenç de Munt meteorological station.

Characterisation of the streams: Physico-chemistry, riparian quality, fluvial habitat and macroinvertebrate communities.

Water temperature (T, ºC), dissolved oxygen (O_2, mgO_2/l), pH and conductivity (Cond, µS/cm) were measured in situ with a Multiline P4 VTW. Discharge (Flow, l/s) was estimated from mean depth, transect width, and water velocity measurements recorded with a mini-air flow meter (Schilknecht miniAir). Water samples from 2003, 2004, and 2005 were frozen (-18ºC) and stored in the dark until analysis, while the water samples from 2006 and 2007 were collected and processed immediately. The turbidity (Turb) was estimated by a nefelometric method (Hach model 2100P), and the Total Organic Carbon (TOC) was calculated with a Shimadzu TOC-5000 analyser (EPA 9060A, USEPA, 1996). The water samples were filtered (250 ml through microfiber filters Whatman GF/F) to calculate the Total Suspended Solids (TSS, mg/l) and analyse the remaining chemical parameters. The Dissolved Organic Carbon (DOC) was measured as for the TOC. The ammonium (NH_4) content was measured using a FLOW SOLUTION IV spectrophotometer (ALPKEM, EPA 350.1). To calculate chloride (Cl), nitrates ($N\text{-}NO_3$), and sulphates (SO_4), ionic chromatography was employed (UV/V KONTRON model 332, EPA 9056); the reactive phosphorous ($P\text{-}PO_4$) was measured using a spectrophotometer (Shimadzu UV-1201) at 890 nm (Murphy & Riley 1962); the calcium (Ca), potassium (K), magnesium (Mg), sodium (Na) and manganese (Mn) were analysed using a Perkin-Elmer Optima (3200 RL). The alkalinity (Alk) was determined using a titulation with sulphuric acid (0.02 N) and phenolftaleina. The water absorbance (a300) and fluorescence (f450-500) emission values were measured as described in Vila-Escalé *et al.* (2007).

Furthermore, at each site, the riparian habitat was characterised in terms of four components: total riparian vegetation cover, cover structure, cover quality and channel alterations, following macroscopic indication as described for the QBR quality index in Munné *et al.* (2003). The fluvial in-stream habitat was characterised by the IHF (Index of Fluvial Habitability), which measures habitat heterogeneity and gives an idea of the physical diversity present in the stream and ultimately the suitability of the macroinvertebrate community (Pardo *et al.* 2002).

Multi-habitat samples for analysis of the macroinvertebrate community were taken using a 250-µm net with a kick-sampling method for a four-minute period. All samples were collected and fixed in formalin 4% until sorting, counting and identification. To estimate the macroinvertebrate abundances, all individuals per sample were counted, although sub-sampling was done when more than 200 individuals of one taxon (for example, Diptera families) were found. When possible, the macroinvertebrates were identified to the genus level using Leica MZ6 dissecting microscopes, except for Diptera and non-insect taxa, which were identified to either the order or the family level. After the identification, biological trait information for each taxon was collected from the literature (Tachet *et al.* 2000) and 12 biological traits were selected, with a total of 65 modalities to characterise them: body morphology (i.e., body size), life history (ovoposition, voltinism, life cycle duration, aquatic stages, respiration, resistance), mobility (i.e., dispersal capacity), and ecology (i.e., rheophily, locomotion, food, feeding habits).

Data Analysis

To compare the macroinvertebrate assemblages between burned and control streams, the number of taxa, the total abundance (individuals/sample), and the percentage of Chironomidae + Simuliidae + Baetidae were calculated. The number of species was also calculated using rarefaction curves with the lowest number of individuals (Hurlbert 1971) present for every year (respectively, 139, 2305, 313, 1144, and 2266). Afterwards, in order to compare the burned and control sites, the normality of the data was tested with the Shapiro-Wilkinson test. The total number of individuals was log (x+1) transformed, fitted to a normal distribution and compared via the Wilcoxon rank test. The other parameters measured were compared using the non-parametric Kruskal-Wallis test as the data did not fit a normal distribution.

Non-metric multidimensional scaling (NMDS) was used to represent similarities of macroinvertebrate communities between streams. The Bray-Curtis similarity coefficient was applied to analyse the taxonomic structure after the log (x+1) transformation. ANOSIM (Clarke & Warwick, 2001) was used to test the effect of fire and also of the nested year. To quantify the changes in the community, bubble graphics, an option on the PRIMER package where the relative abundances are plotted in the NMDS graph, were used. The vector-fitting routine (Oksanen *et al.* 2008) was used to examine which environmental variables were associated with the taxonomic ordinations. Vector-fitting illustrates which environmental variables may be contributing to the pattern of macroinvertebrate communities; the arrows indicate the direction and relative strength of the correlation (R^2 and significance) in ordination space.

A multivariate analysis was used to compare the biological traits or functional compositions of the communities. The taxa-trait matrix was first multiplied by the taxa abundances in each locality. The resulting site-trait array was transformed to the relative abundance of each trait category in each site and further processed by fuzzy correspondence analysis (FCA), as described by Chevenet *et al.* (1994). We examined if there were differences between the factors studied, in this case, fire (fire versus control sites), years (2003, 2004, 2005, 2006, and 2007) and dry and wet years, for which 2003, 2005, and 2006 were classified as dry years and the others as wet years (i.e., 2004 and 2007). Afterwards, Kruskal-Wallis was used to compare all of the traits separately for each factor to detect significant differences, and a false discovery rate correction was applied (Benjamini & Hochberg 1995). All statistical analyses were carried out using the R Freeware package (R Development Core Team 2006), except the bubble graphs and the SIMPER analysis, which were done with the PRIMER package version 6.1.2 (Clarke & Warwick 2001).

Results

None of the measured community structure parameters showed significant differences between the burned and the control streams or for any year (Table 2.2). The lowest rarefied taxa number was found in the samples from 2003 and 2005, followed by the 2006 sample. On the contrary, the highest rarefied taxa number was found in the 2007 samples followed by the 2004 sites, which also presented the highest abundance, especially for the burned streams (Table 2.2).

The NMDS in Figure 3a shows a clear separation of the community two months after the fire (2003) from the control streams and subsequent years. The ANOSIM comparison between burned and control streams was not significant (R: 0.11, p-value: 0.274), but if the year was nested, the difference became significant (R: 0.556, p-value: 0.001). The criterion of 40% similarity split the assemblages into six groups, where three of them were clearly separated: burned sites in 2003, control sites in 2003 and 2005, and burned sites in 2005 (Fig. 2.3b). Meanwhile, the overlapped group was represented by the other three groups, where each could be separated by: mixture of control sites, burned sites in 2004 and 2007, and burned sites in 2006 (Fig. 2.3b).

Table 2.2. Mean (± standard error) taxa number, abundance, rarefied taxa number, and percentage of Chironomidae, Simuliidae and Baetidae for all the control and burned sites for the 5 years of sampling (*p<0.05, **p<0.01, ***p<0.001, ^{NS}: non-significant).

Year	Community parameter	**Control**	**Burned**	**Kruskal-Wallis test**
2003	Taxa number	27 ± 4	21 ± 1	1.80 ^{NS}
	Rarefied taxa number	14 ± 4	14 ± 2	0.11 ^{NS}
	% Chiron+Simul+Baet	53 ± 23	63 ± 10	0.44 ^{NS}
	Abundance	1078 ± 785	683 ± 349	0.44 ^{NS}
2004	Taxa number	39 ± 1	39 ± 4	0.86 ^{NS}
	Rarefied taxa number	33 ± 5	25 ± 3	0.86 ^{NS}
	% Chiron+Simul+Baet	82 ± 6	75 ± 10	0.21 ^{NS}
	Abundance	5115 ± 2810	14289 ± 2059	3.42 ^{NS}
2005	Taxa number	16	15 ± 3	
	Rarefied taxa number	16	15 ± 3	
	% Chiron+Simul+Baet	76	49 ± 18	
	Abundance	313	5235 ± 1817	
2006	Taxa number	31 ± 6	28 ± 3	0.00 ^{NS}
	Rarefied taxa number	17 ± 1	21 ± 3	0.00 ^{NS}
	% Chiron+Simul+Baet	48 ± 27	30 ± 10	0.44 ^{NS}
	Abundance	7286 ± 2123	4774 ± 1044	1.00 ^{NS}
2007	Taxa number	33 ± 0	44 ± 3	1.78 ^{NS}
	Rarefied taxa number	29 ± 3	38 ± 3	1.78 ^{NS}
	% Chiron+Simul+Baet	78 ± 5	59 ± 7	2.78 ^{NS}
	Abundance	4085 ± 1502	4532 ± 1173	0.00 ^{NS}

Diptera, mainly Chironomidae, dominated all of the macroinvertebrate communities, independently of whether they were located in affected or unaffected streams. Simuliidae were present two months after the fire but were heavily affected by the 2005 and 2006 droughts (Fig. 2.3d). On the other hand, Culicidae, Ceratopogonidae and Stratiomyidae increased in abundance in 2005. In the case of the mayflies, Baetidae were mainly represented by two genera. *Baetis* sp. was present in 2003, and its dominance was clear in the wet years (2004 and 2007) but reduced in dry conditions (2005 and 2006) (Fig. 2.3e). The opposite pattern was shown by *Pseudocentroptilum* sp., being more abundant in 2005 and 2006 (dry years), although its appearances at the control sites do not seem related to its hydrology (Fig. 2.3h). The percentages of Chironomidae, Simuliidae and Baetidae did not show significant differences between the burned and control streams, although the highest percentage was found 10 months after the fire, in 2004 (Table 2.2). The orders most affected immediately after the fire were the Odonata and Mollusca, which showed an increase in their abundance during the following years (Fig. 2.3f shows Mollusca as an example). Caenidae and Leptophlebiidae were not only negatively affected by the fire, but their abundance also decreased during 2005 and 2006 (dry years) (Fig. 2.3g shows Caenidae as an example). Finally, no Coleoptera genera showed any variation and were present throughout all of the samples, showing a similar pattern as Chironomidae (Fig. 2.3c) and, along with the Diptera, presenting the highest number of taxa.

The environmental fittings for all years are presented in Figure 2.4. Similarly to the NMDS of all of the sites, the 2003 environmental fitting showed a clear separation by the fire, and seven chemical parameters were significantly related (>70%) to the affected sites: Total and Dissolved Organic Carbon, Total Suspended Solids, a300, f450/500, K, and flow (Fig. 2.4). The 2004 community resemblance was only related to sodium (99%). On the other hand, 2005 was correlated with the Total Organic Carbon (TOC, 88%), while in 2006, the phosphates, potassium, manganese and turbidity were related (>70%) (Fig. 2.4). The samplings in 2005 took place in totally disconnected pools in all sites, and in 2006 half of them were still connected but with a very low flow (<1 l/s). In 2007, the rarefied taxa number was the highest, and the distance between the communities was the closest compared to the other years. Furthermore, there was no chemical parameter related to the NMDS in 2007 (Fig. 2.4).

After testing for the effects of the fire by year, it became clear that the hydrology of a given year seems to be a key factor for the community structure, and the dry and wet years were also compared. The number of taxa was significantly higher in the wet years compared to the dry years (respectively, 40 ± 2 vs. 26 ± 2; K-W: 16.39, p-value<0.001), although the rarefied taxa number did not differ (K-W: 0.83, p-value >0.05). Finally, the abundance in the wet years was also significantly higher than that in the dry years (respectively, 7339 ± 1453 vs. 3368 ± 700; K-W: 5.56, p-value<0.05).

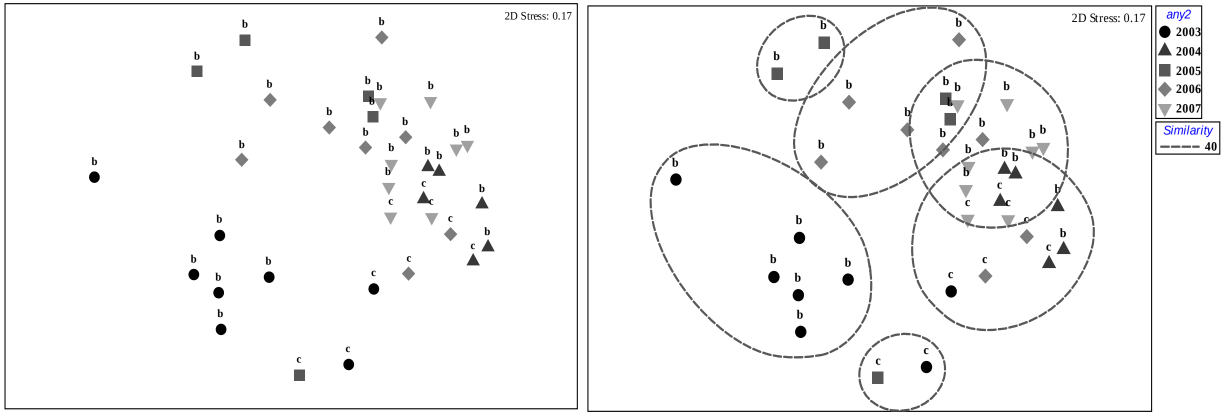
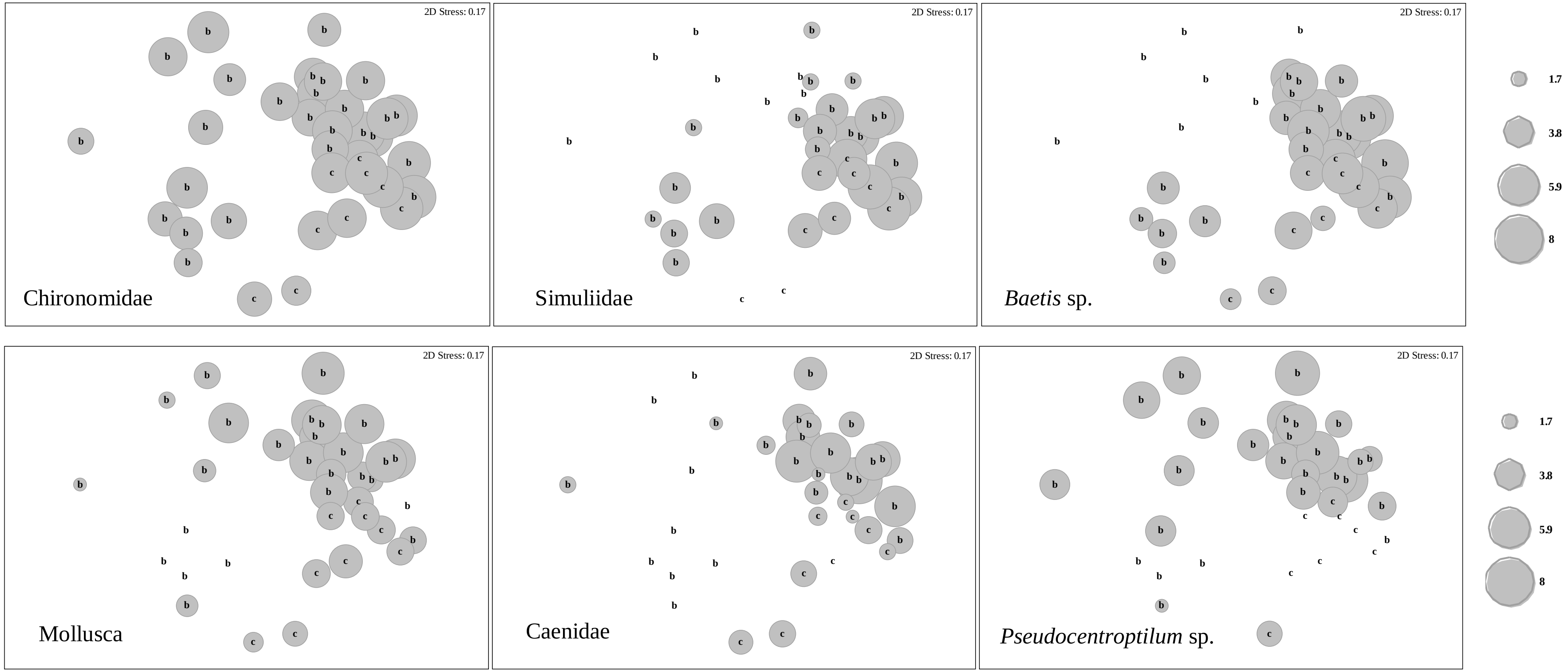


Figure 2.3. NMDS of the macroinvertebrate community based on the Bray-Curtis resemblance matrix and showing the 40% level of similarity (left). The transformed (log x+1) abundances for the different taxa and orders are represented (below) for: Chironomidae, Simuliidae, *Baetis* sp. Mollusca, Caenidae, and *Pseudocentroptilum* sp.



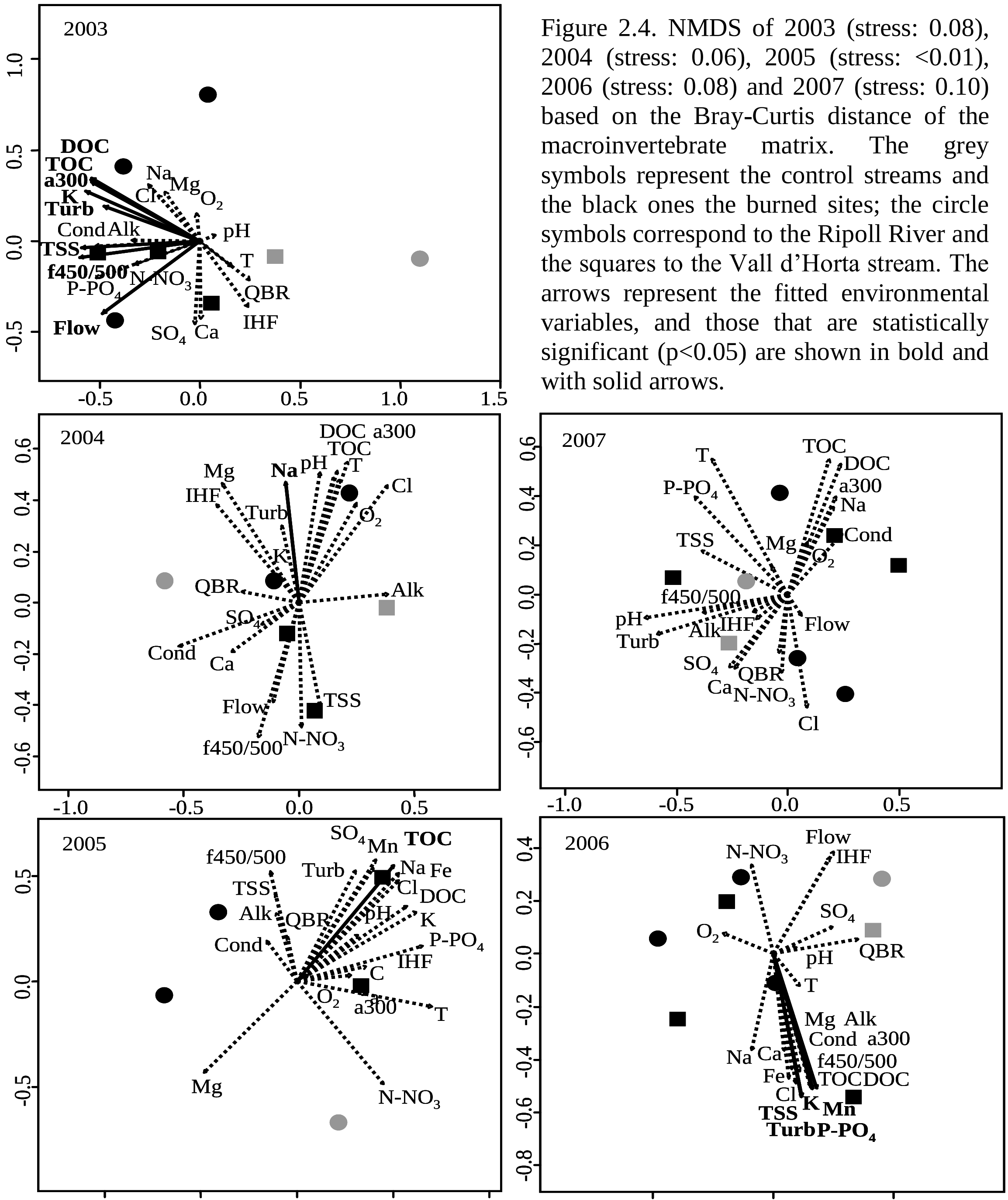


Figure 2.4. NMDS of 2003 (stress: 0.08), 2004 (stress: 0.06), 2005 (stress: <0.01), 2006 (stress: 0.08) and 2007 (stress: 0.10) based on the Bray-Curtis distance of the macroinvertebrate matrix. The grey symbols represent the control streams and the black ones the burned sites; the circle symbols correspond to the Ripoll River and the squares to the Vall d'Horta stream. The arrows represent the fitted environmental variables, and those that are statistically significant ($p<0.05$) are shown in bold and with solid arrows.

The dominant biological traits of the macroinvertebrates were taxa with larva and pupa aquatic stages, those with a higher aquatic passive dispersion and crawler habits in standing waters. Furthermore, the macroinvertebrates were dominated by sizes of <10 mm and with multivoltine or univoltine life cycles. The three factors tested by the fuzzy correspondence analysis (FCA) of biological traits all showed significant differences: a) fire (Obs: 0.07, p-value: 0.037), b) year (Obs: 0.20, p-value: 0.039) and c) wet-dry (Obs: 0.12, p-value: 0.003) (Fig. 2.5). When testing the separate biological traits for each factor and after the FDR correction, no significant difference by year was observed (Table 2.3). For the fire factor, a significantly higher percentage of macroinvertebrates that feed on living microphytes was found at the control sites compared to the burned ones (Fig. 2.6e). The wet-dry factor exhibited the longest list of differences between traits (Table 2.3). During the wet years, a higher percentage of oviposition in fixed clutches, crawlers, organisms that fed on living macrophytes, and organisms with no resistance were found (respectively, Figs. 2.6a, 2.6c, 2.6d and 2.6b). On the contrary, the dry years presented higher percentages of organisms with spiracle respiration, surface swimmers, living in null current, and feeding on macroinvertebrates (respectively, Figs. 2.6g, 2.6h, 2.6f, and 2.6i).

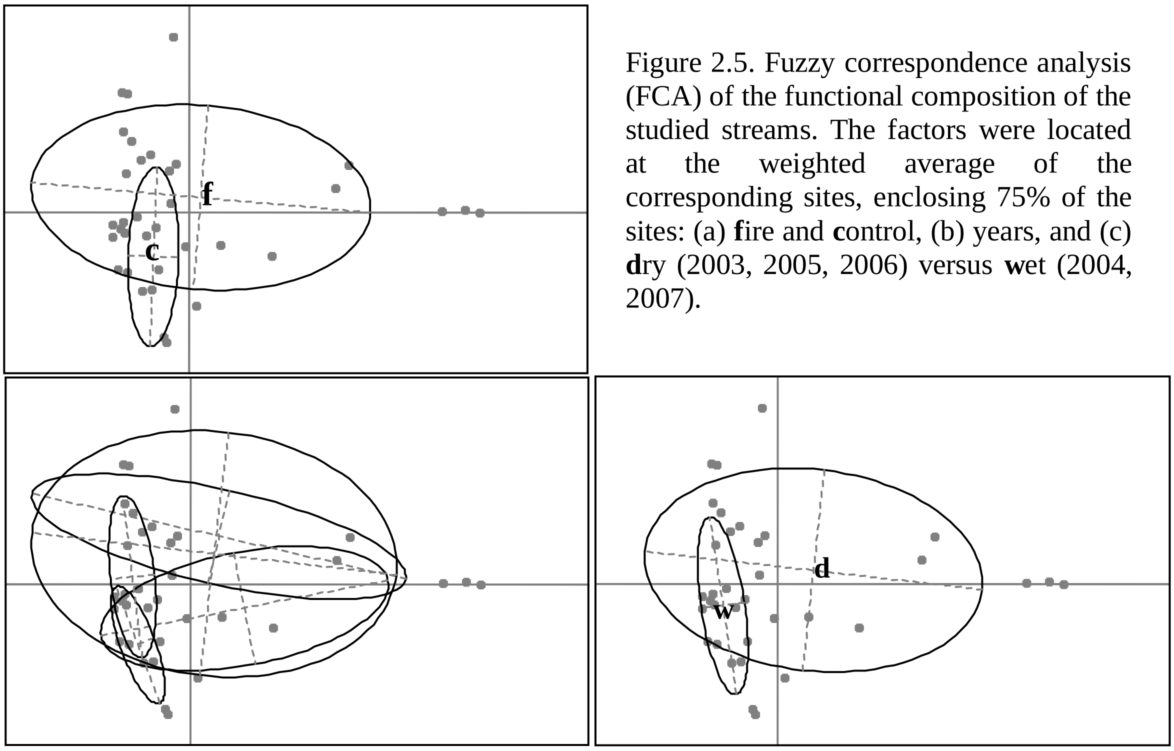


Figure 2.5. Fuzzy correspondence analysis (FCA) of the functional composition of the studied streams. The factors were located at the weighted average of the corresponding sites, enclosing 75% of the sites: (a) **f**ire and **c**ontrol, (b) years, and (c) **d**ry (2003, 2005, 2006) versus **w**et (2004, 2007).

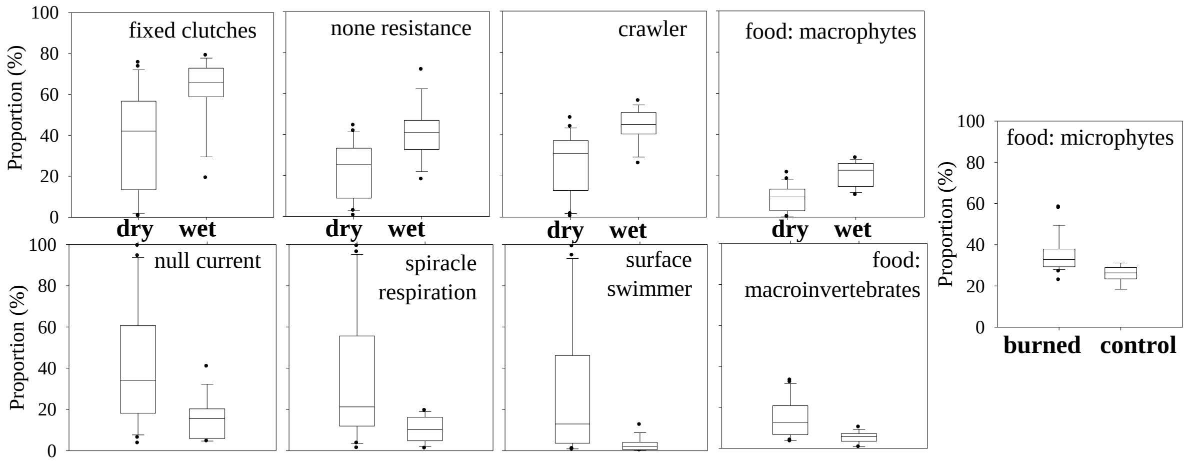


Figure 2.6. Proportion of the biological traits that were significant after the FDR correction between the wet versus dry years and burned versus control sites.

Table 2.3. Kruskal-Wallis values for the comparison between the modalities for the traits categories. Only the significant results are presented and in bold stand for the significant ones after the FDR correction, leaving unfilled all the others. 65 modalities were tested for each factor (fire, year and, wet-dry; *p<0.05, **p<0.01, ***p<0.001).

Traits		**fire**	**year**	**wet-dry**
Maximal size	>4-8 cm		10.77*	
Voltinism: Potential number of reproduction cycles per year	<1	3.86*		
	1	6.78**	10.28*	
	>1	4.47*	10.63*	
Aquatic stages	larva		10.08*	
	imago		13.12*	
Ovoposition	ovoviviparity	4.19*		
	isolated eggs, free		9.52*	4.94*
	clutches, cemented or fixed		10.30*	**8.78****
	clutches, free			4.94*
	clutches in vegetation		12.96*	
Resistance form	cells against desiccation			5.61*
	diapause or dormancy			5.72*
	none		13.03*	**11.57*****
Food	plant detritus ≥ 1 mm			4.79*
	living microphytes	**12.06*****		
	living macrophytes		17.63**	**17.43*****
	living macroinvertebrates		11.81*	**10.02****
Feeding habits	absorber	5.65*		
	scraper			4.50*
	filter-feeder	6.02*	13.93**	
	predator			4.36*
Respiration	tegument		10.33*	
	plastron		13.61**	
	spiracle		11.01*	**8.58****
Locomotion and substrate relation	flier		12.23*	
	surface swimmer		14.36**	**10.67****
	crawler		14.61**	**13.72*****
	interstitial	4.00*	13.77**	6.72**
	temporarily attached	6.02*	12.64*	4.36*
	permanently attached			4.86*
Rheophily (current velocity preferendum)	null		11.59*	**9.39****
	moderate (25-50 cm/s)	8.23**	10.90*	7.26**
	fast (> 50 cm/s)	5.83*	12.86*	6.90**

Discusión

Fire effects

The strongest effects of a wildfire on aquatic ecosystems are generally associated with the first post-fire precipitations (Bisson 2003), and a rapid recovery indicates that even dramatic changes may go undetected if sampling does not coincide with ash delivery (Earl & Blinn 2003). Likewise, a contemporaneous study done in the nearby area by Vila-Escalé (2009) also showed that the most dramatic impact was associated with the post-fire flooding, sediment transport and deposition immediately after the fire. In addition, two months after the fire almost all of the chemical parameters were re-established, except for a few variables, like the total and dissolved organic carbon, the total solids suspended, turbidity, phosphates, absorbance and fluorescence coefficient (Vila-Escalé 2009). Along the same lines, in our study the accumulated precipitation after the wildfire (35, 62, and 32 mm within 22 days and 50 mm of accumulated precipitation 2 weeks before the sampling) resulted in heavy rains. Correspondingly, two months after the fire almost the same variables (except the phosphates) were significantly related to the taxonomic ordination, showing again that the absorbance and fluorescence coefficients can function as post-fire indicators (Vila-Escalé *et al.* 2007; Vila-Escalé 2009).

Regarding the macroinvertebrate community, Vila-Escalé (2009) reported one *Hydrometra* sp. 12 days after the fire; two and three months after the fire, the macroinvertebrate community was represented by 9 and 20 families, respectively, compared to the previous 39. After two months, the density was reduced by 65%, but just a month later it was only reduced by 14% relative to pre-fire levels. In our study, two months after the fire, the comparisons between the burned and control community structural measures were not significant. This indicates a rapid response from the macroinvertebrate community, as expected in Mediterranean streams (Gasith & Resh 1999; Vila-Escalé 2009). However, the community was not the same: the snails were one of the more negatively affected groups, consistent with the results of Vila-Escalé (2009). Similarly, a study in the same area by Santos *et al.* (2009) also showed a negative effect of the fire on the richness of terrestrial gastropod assemblages four years after the perturbation. In their study, they chose terrestrial snails as an appropriate group for which to evaluate post-fire response because of their dependence on vegetation and moisture and their low mobility. It is this low mobility and limited dispersion that also explains the classification by Vila-Escalé (2009) of aquatic snails (i.e., Lymnaeidae, Ancylidae, Planorbidae) as less resilient than all other aquatic macroinvertebrates. Likewise, *Ancylus fluviatilis* was also classified as less resilient after flooding in a Mediterranean stream (Acuña *et al. 2005)*

One year after the fire (2004), there was a slightly higher abundance of taxa with disturbance-adapted strategies (i.e., Chironomidae, Simuliidae, and Baetidae), a response which has also been reported in other studies not only after fires (Minshall

2003; Vieira *et al.* 2004; Mellon *et al.* 2008; Vila-Escalé 2009), but also after droughts (Boulton & Lake 1992c; Reznickova *et al.* 2007).

In summary, the fire and the post-fire flooding seemed to have weakly affected the structure of the macroinvertebrate community, but the composition changed. The group of biological traits also showed significant differences. The only significant difference in biological traits corresponded to a higher abundance of macroinvertebrates that fed on microphytes (i.e., diatoms, microscopic algae, biofilms, etc.) in burned sites, which could be a response to an increased input and availability of light and nutrients (Minshall *et al.* 1989).

In addition, the dry conditions before the fire seemed to have a stronger effect, affecting the control streams in addition to the burned sites, because the difference in the response of the structure of the community was clear and stronger between dry and wet years than between burned and control sites.

Severe seasonal drought effects

In the process of drying of an ephemeral stream, Dahm *et al.* (2003) reported lower dissolved organic carbon, phosphorous and nitrogen inputs, and Williams (2006) described that this pattern is followed by lower microbial activity, with a shift from predominantly heterotrophic to autotrophic processes. Additionally, in Mediterranean streams, leaf fall can also take place during the summer, and too much accumulation of this material can lead to anoxic conditions (Boulton 2003). In our study, the physicochemical variation was the greatest during 2003 (after the drought, fire and post-fire flooding). However, the flow cessation in 2005 and 2006 also caused a change in physicochemical and habitat conditions that seemed to impose a threshold on the macroinvertebrate community. Hence, 2005 and 2006 showed the lowest taxa number and rarefied number compared to the wet years (2004 and 2007). Similar to the pattern described by Acuña *et al*. (2005) in an intermittent Mediterranean stream, high dispersal taxa (e.g., Dytiscidae) with low dissolved oxygen requirements (e.g., Chironomidae, Stratiomyidae) and semi-aquatic or air-breathing taxa (e.g., Notonectidae, Gerridae) were found. Above all, the community was dominated by Diptera, followed by Coleoptera and Heteroptera, but this is not surprising as the samples were taken from intermittent streams during summer, a typical characteristic of macroinvertebrate communities for this time of the year (Rieradevall *et al.* 1999).

The difference between biological traits measured in wet and dry years was very significant, and this indicates a change in the functionality of the community as a consequence of large changes in habitat conditions (no flow and isolated pools).

Mixed effects: fire + severe seasonal drought

In summary, as in the study of the three regions of California by Bêche and Resh (2007), the majority of the temporal variation in the composition and abundance of the macroinvertebrate community can be explained by short-term climatic patterns, and in our study by annual differences in precipitation and spring precipitation. In general, during 2003, 2005 and 2006, the taxonomic richness might have declined, leading to niche selection, so the large disturbances (pre-fire drought, fire, flooding and severe seasonal drought) determined the prevalence of some taxa, filtering out species that lacked suitable traits (Chase 2007).

Resilience appears to be the predominant strategy: small macroinvertebrates, multivoltine life cycle and high dispersion were favoured. This is consistent with other studies that state the importance of resilience rather than resistance in intermittent streams (Boulton & Lake 1992c; Vieira *et al.* 2004; Acuña *et al.* 2005; Vila-Escalé 2009) and in desert streams (Stanley *et al.* 1994).

Some patterns were observed during the post-disturbance recolonisation processes, for example, higher richness of aquatic beetles among the burned streams. The distributions of aquatic beetles have been considered to be more strongly influenced by chance colonisation than by habitat suitability (Fairchild *et al.* 2003), and this could mean that disturbances like the fire and the flooding led to easier colonisation by aquatic beetles. However, there was also site-to-site variation because they are in part idiosyncratic, depending on the community composition before the disturbance and the distance of the nearest sources of colonists (Robinson *et al.* 2000). The disturbance-driven shifts that arise abruptly and vary in intensity, such as droughts (Chase 2007) and fires, might cause swings from stochastic (in the absence of disturbance) to deterministic (in the presence of disturbance) community assembly, with intermediate conditions pre-empted (Lepori & Malmqvist 2009). However, this study lacks true replication of the burned and unburned treatments and must be viewed as a simple comparison study.

As emphasised by Robinson *et al.* (2005), time plays an important role in determining the response to the generally large-scale disturbance resulting from fire. Furthermore, extreme disturbance events such as the prolonged and extreme droughts are often not captured in ecological studies (Bêche & Resh 2007). However, we think we captured two of them in our five-year study, and this could be just a hint of the future situation in a changing global climate. Conversely, the role of natural droughts is to maintain a temporal mosaic of habitats and diversity in aquatic environments (Boulton 2003), as shown in Mediterranean streams around the world (Bonada *et al.* 2008). However, extreme disturbance events result in both qualitatively and quantitatively different effects on ecosystems, indicating thresholds for severe events (Bêche & Resh 2007).

Nowadays there is much concern about the linkages between the climate, humans, and vegetation and the critical fire factor, as all of it is sensitive to global change (Piñol *et al.* 1998; Lavorel *et al.* 2007; Pausas *et al.* 2008). Especially on the northern (European) rim of the Mediterranean, industrialisation and rural exodus have led to the abandonment of many fields, increasing the cover and continuity of early succession species (many of which are very flammable, like pine woodlands) and changing the landscape pattern and the fire regime (Moreira *et al.* 2001; Pausas 2004). Thus, although the Mediterranean Basin forests may be strongly resilient to fire (i.e., shrublands and oak forest), some parts of the current landscapes, which are products of a long human history with questionable land policies, are relatively sensitive to fires, and in such conditions, disasters or ecosystem degradation (e.g., soil losses, strong vegetation changes) are possible (Pausas *et al.* 2008). Likewise, the aquatic communities in this climate generally show a very high resilience (Gasith & Resh 1999). But hydroclimatic models predict that climate change would increase the frequency and severity of floods and droughts across Europe (Folke *et al.* 2004). In addition, the increasing population in the already densely populated Mediterranean Basin and hence the scarcity of water must also be considered (Prat & Manzano 2009). As in many other ecosystems, the new perspective recognises that resilience can be and has been eroded and that the self-repairing capacity of ecosystems should no longer be taken for granted (Gunderson 2000; Folke *et al.* 2004; Bond *et al.* 2008).

Chapter 3

Effects of bushfire on structural and functional parameters of macroinvertebrate communities in Victorian creeks affected by a decade of drought

Michael Leunig

Introduction

The south-east corner of Australia has one of the most bushfire-prone environments (Collett 2007; Lyon & O'Connor 2008; Seymour & Collett 2009) and this is not a recent story as fire has been an integral part of this environment even before European settlement (Jurskis 2005). In this context, the effects of bushfires has been largely studied on different Australian terrestrial ecosystems (Bradstock *et al.* 2002) and are known to play a significant role in structuring terrestrial plant communities (Whelan 1995). Furthermore, the studies of bushfires effects in the aquatic systems have been mainly focused on water chemistry (Townsend & Douglas 2004) and on the changes in hydrology, soil erosion, sediment transport and deposition (see list at Lane *et al.* 2006; Shakesby *et al.* 2007). The studies of the impact of wildfire on the aquatic communities have just recently begun to get more attention in benthic algal assemblages and fish population (Cowell *et al.* 2006; Lyon & O'Connor 2008). These studies, together with some preliminary unpublished reports on macroinvertebrates, were motivated after the large fire of 2003, regarded as the worst since 1939 (Victoria 2003; Crowther & Papas 2005). Two important points were highlighted: first, the 2003 fires occurred towards the end of a long drought, the worst in 100 years (Victoria 2004), and second, some of the wildfire affected areas were followed by high flood events (Victoria 2003; Lyon & O'Connor 2008).

Equivalent to studies done in other biomes (Minshall 2003), it is the first runoff, i.e. entrance of ashes and increased sediment loads, the reason of the disappearance of the biota, including algae (Robinson *et al.* 1994), macroinvertebrates (Rinne 1996; Minshall 2003; Victoria 2003; Vieira *et al.* 2004; Crowther & Papas 2005; Vila-Escalé 2009) or fishes (Gresswell 1999; Lyon & O'Connor 2008).

Generally, in a midterm time frame, i.e. after the first runoff and post-fire year indirect effects (Minshall *et al.* 2004), the soil hydrophobicity is enhanced (Shakesby *et al.* 2007; Tague *et al.* 2009), and it also takes place changes in the hillslope erosion, stream sedimentation, and recruitment of large woody debris to streams (Benda 2003; Miller *et al.* 2003; Arkle *et al.* 2010). From the studies primarily undertaken in the western United States, a basic change in the detrital food quality will be consequence of the reduction of allochthonous resources in post-fire streams (Mihuc & Minshall 1995) and in general, shredders are expected to track this lost (Minshall 2003) as has been showed in Mediterranean streams (Chapter 1). Wildfire has also the potential to stimulate aquatic productivity (Mellon *et al.* 2008; Malison & Baxter 2010a), most likely as a consequence of the faster algal growth in streams with removed canopy, higher temperatures, or increased delivery of inorganic nutrients such as nitrogen and phosphorus (Minshall *et al.* 1997; Spencer 2003) and scrapers are expected to reflect this changes (Minshall 2003). In contrast, the reports of the midterm effects of bushfires in south east Australia showed different results and were inconclusive (Crowther & Papas 2005; Russell *et al.* 2008). It is evident that the effect of bushfires on the south east Australian stream-riparian ecosystems respond to local factors like in other biomes (Minshall 2003) and additionally bushfire effects are difficult to separate from other disturbances like floods or droughts, which are considered part of the natural disturbances in Australian streams (Lake 1995).

Drought is a recurring theme in Australia being the world's driest continent after Antarctica (Lake 1995). And the most recent event, the so called 'millennium' drought, ten consecutive years of below average rainfall has been affecting most of the southern and eastern Australia (Bond *et al.* 2008).

In lotic systems the disturbances are inherent properties (Resh *et al.* 1988), and act as a filter to set the stage for subsequent colonization, succession and community assembly (Poff 1997). The complex effects of one disturbance on ecological communities can be further complicated by subsequent perturbations within an ecosystem (Arkle *et al.* 2010). So although direct wildfire effects on aquatic communities are almost negligible, their indirect effects can initiate a suite of intense physical disturbances to streams (Gresswell 1999), and interact with other disturbances like floodings that can reset recovery trajectories (Vieira *et al.* 2004) or seasonal droughts that can generate different responses by delaying the recolonization process (Cowell *et al.* 2006).

The response of the aquatic biota to large disturbance events should proportionately be characterised by two strategies: resistance and resilience (Gunderson 2000), the degree to which the benthic fauna is reduced by the initial disturbance (i.e. resistance of the fauna) and the rate of recovery (i.e. resilience of the fauna) both in absolute and relative terms (i.e. relative to control densities of taxa or individuals) (Marchant *et al.* 1991). And the dynamics between both responses and the nature and strength of the disturbances will be influencing the stability of the communities (Lepori & Malmqvist 2009).

In this context, the main objective was to study the midterm response of the structure (taxa number and abundance) and function (functional feeding groups) of the macroinvertebrate community, from three Victorian streams located in catchments affected by bushfires after a decade of intense drought which can result in different hydrological conditions. Moreover, our results could be important not only because fire is a major large-scale disturbance in many biomes (Whelan 1995; Lavorel *et al.* 2007), but also for the fire scenario with an increase in their number (Williams *et al.* 2001) and a decrease in the annual runoff (Chiew & McMahon 2002) for the next decades.

Study site and Methods

The study area is located in central Victoria State, Australia (Figure 3.1) at the north of the Hume Freeway, which separates the 'hill country' of the Strathbogie Ranges from the 'flats' of the Goulburn River floodplain (Downes *et al.* 2006). The fire season 2006/07 in Victoria commenced north-east of the region in early December and this was prompted by exceptionally dry conditions in the grip of a decade of long drought (Smith 2007; Bond *et al.* 2008; Crowther *et al.* 2008). The longest fires (69 days) in Victoria's history were recorded, impacting more than 1.2 million hectares of private and public land, including parts of the upper catchments of the Goulburn and Ovens rivers (Smith 2007).

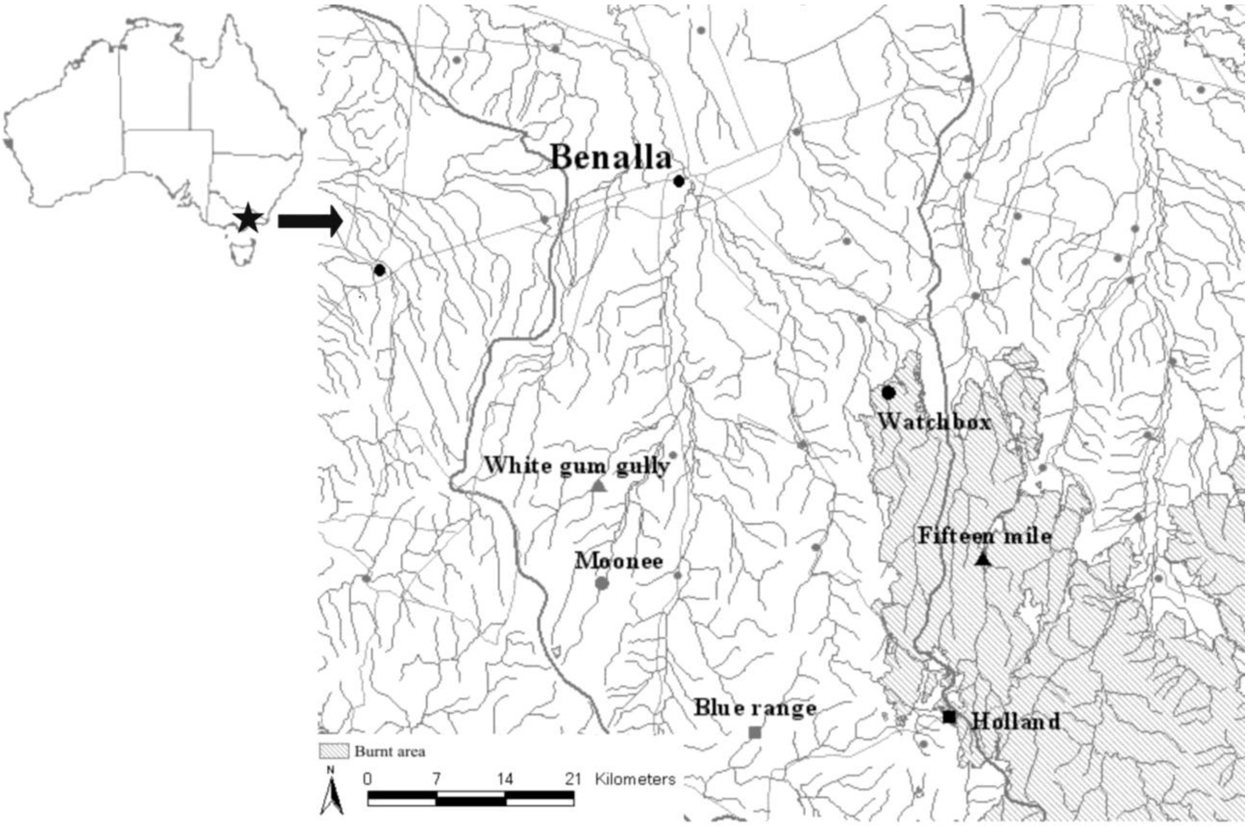


Figure 3.1. Map of the study location with the six creeks.

In October 2007, nine months after the bushfires, six creeks were chosen using fire maps provided by the Department of Sustainability and Environment (DSE Victoria): three burnt (Burnt= B) and three unburnt (Control= C). In order to choose the creeks we considered important: 1) Select low order streams as headwater catchments tend to burn more intensely and completely than do larger size streams (Minshall 2003); 2) Select very close streams in order to minimize the geologic differences and maximize climatic conditions, 3) Select streams affected by the same fire and 4) Sample the same number of control streams − defined as a place similar as possible in all respects to the impacted site, except for the presence of the putative impact (Downes *et al.* 2002). The main characteristics of these creeks are presented on Table 3.1. The percentage of the catchment burned was calculated using maps provided by DSE Victoria and sites were considered burnt if at least 60% of the catchment was impacted by fire. Furthermore, to be certain from the differences at reach scale the comparison between burned and control sites scale was done measuring at one bank of the river the percentage of bare soil in 30 plots of 1x1 m, with a result of a significant difference between burned and control sites (Burned 38±1% vs. Control 11±4%; F: 35.04, p-value 0.0041), although the total riparian cover of the stream at the reach was not different (Burned 44±12% vs. Control 54±5%; F: 0.48, p-value 0.5276).

Table 3.1. Main characteristics of the six creeks sampled (B = Burned, C= Control).

Creek	Location	Catchment —area (km^2)	Lithology	Discharge (l/s)	Burned?	% Burned catchment	Altitude (m asl)
B – Watchbox creek	36º41926′ S 146º10696′ E	Broken —31.3	sandstone	2	Yes	86.3	400
B – Holland creek	36º55089′ S 146º15991′ E	Broken —9.0	sandstone	16	Yes	60.1	380
B- Fifteen mile creek	36º48240′ S 146º16560′ E	Ovens —60.7	sandstone	215	Yes	96.2	483
C- Moonee creek	36º51020′ S 145º56417′ E	Broken —26.0	granites	14	No	0	420
C- Blue Range creek	36º56114′ S 146º05736′ E	Broken —16.7	sandstone	25	No	0	420
C- White gum gully creek	36º47236′ S 145º54861′ E	Broken —23.5	granites	36	No	0	503

The fire history of each catchment was based on the data and maps of the Department of Sustainability and Environment (Victoria) from 1970-2007. None of the sites has been affected by bushfires between these dates. Nevertheless, prescribed fires were undertaken in the catchments of Watchbox and Moonee creeks. 2.6% of the Watchbox catchment was burned in 2004, while in Moonee Creek 6.8% was burned before 1982 and afterwards 1.1% in 1992 and 0.9% in 2007. However, the total of the affected catchment was less than 9%, far less than the area considered where fire may be an important disturbance to streams (40%, Minshall 2003). Moreover, studies on streams in catchment submitted to prescribed burning have shown almost no impact on the aquatic macroinvertebrate community (e.g. Britton 1991; Bêche *et al.* 2005; Munro *et al.* 2009).

The sampled creeks corresponded to second order in the Australian region 3 which is characterized by a rainfall of 600-1200mm and correspond to an area of intermittent streams (Wells *et al.* 2002), which flows in winter/spring (June/November) and often form disconnected pools in summer/autumn (December-May). Daily weather data was obtained from the SILO Data Drill (Jeffrey *et al.* 2001): rainfall, maximum and minimum air temperature, radiation and potential evapotranspiration. The data is based on the Bureau Meteorology records which interpolates spatially daily climate sequences (http://www.longpaddock.qld.gov.au/silo/index.html). We used the rainfall as a surrogate of the stream flow although the relationship between the amount of water that reaches the catchment and rainfall is not linear, and even less during the long dry period at the time of sampling (Murphy & Timbal 2008). In the figure 3.2 is presented the mean rainfall and potential evapotranspiration (mm) of the burned and control sites from 2003 until 2009.

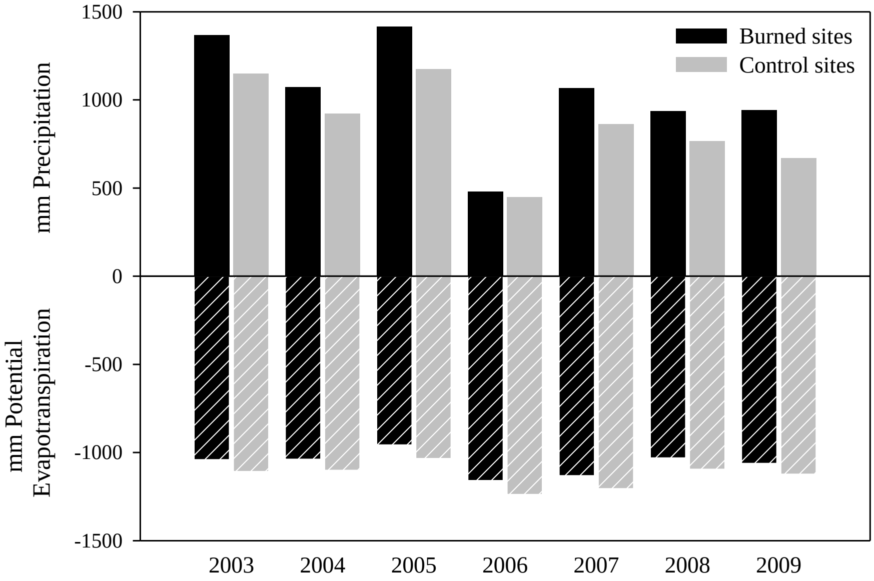


Figure 3.2. Mean milimeters accumulated of Precipitation and potential evapotranspiration (mm, negative numbers) from 2003-2009 for the burned and control sites. Data was obtained from the SILO Data Drill based on the records of the meterorological stations of the Australian Bureau of Meteorology.

At the time of the study, the six creeks consisted of a shallow channel (mean width 1.5-3.2m, mean depth 8-30cm) with alternating pools and riffles (max. velocity 110 cm/s). At every site ten transects were defined to estimate visually the substrates covers divided in inorganic (percentages of bedrock, boulders, cobbles, pebbles, gravels, sand and clay-silt) and organic (percentages of macrophytes, filamentous algae, mosses, roots, small, and large woody debris). Riparian cover was measured by calculating the density of trees (ind/m^2). Shrubs and understorey cover were estimated using 10 random 1x1m plots where the percentages of herbs-grasses, bare soil, and, twigs-coarse wood were recorded. The riparian forest of all creeks was dominated by *Eucalyptus* spp.

Water temperature (ºC), pH, turbidity (NTU), Total Suspended Solids (TSS, mg/l) and conductivity (µS/cm) were measured with a multi-parameter probe (Horiba Instruments Inc, Irvine, CA). Discharge (l/s) was measured using a Marsh-McBirney, Flo-Mate (Model 2000) portable flowmeter. In order to measure the water nutrients content, 500 mL of water samples were taken, frozen (-18ºC) and stored in the dark until analysis. Phosphate, ammonium and nitrate were measured using a spectrophotometer at 890, 655 and 500 nm, respectively (Hach Methods 8048, 8337 and 8192).

At each site sweep samples of macroinvertebrates of three riffles and three pools were taken using a 250µm net. Sweeps were taken for three minutes with similar effort of sampling for each. All the samples were subsequently fixed in 70% ethanol. To estimate the macroinvertebrate abundances all individuals per sample were counted, although sub-sampling was done when more than 200 individuals of one taxon (for example, Diptera families) were found. When possible, the macroinvertebrates were identified to genus (using Leica MZ6 and MZ8 dissecting microscopes). Chironomidae were identified to subfamily level and the other Diptera and non-insect taxa to either order or family level. All identified taxa were assigned to a functional feeding groups (Hawking *et al.* 2009).

After the samples were sorted, the remaining organic and inorganic fractions were processed to provide an estimate of the coarse organic particles content. Samples were dried for 48h in a 60ºC oven, weighted and then combusted in a muffle furnace at 500ºC for 3h, and weighed again.

Data Analysis

To compare the macroinvertebrate communities between burnt and control sites the taxonomic richness and the total abundance (individuals/sample) were computed.

Because of the different sizes of samples, the number of species was also calculated using rarefaction curves' with the lowest number of individuals present (929); i.e. the expected species richness in a subsample of n individuals selected at random from a sample containing N individuals and S species (Hurlbert 1971). Afterwards the burned and control sites were compared with the non-parametric Kruskal-Wallis test, as the data did not fit a normal distribution. The total number of individuals was compared with the Wilcoxon rank test after a log (x+1) transformation. The normality was tested with the Shapiro-Wilkinson test.

The percentages of the functional feeding groups were compared with a nested ANOVA, having Burned as the main factor and Creek as the nested one. The percentages data were transformed as the arcsinus of the square root to fit normal distribution.

Non-metric multidimensional scaling (NMDS) was used to represent similarities of macroinvertebrate communities between creeks. The Bray-Curtis similarity coefficient was applied to analyze taxonomic structure and habitat preferences, while Euclidian distance was used in functional feeding groups analysis to include the joint absences (Hose *et al.* 2005). To test the NDMS analysis significance, the distances between the creeks affected by fire and the control creeks were compared with Adonis. The significance test of Adonis is calculated with pseudo-F ratios based on sequential sums of squares from permutations of semimetric and metric distance matrices, and it was chosen because it prevails as a more robust analysis of variance compared to the ANOSIM that uses the rank of order of dissimilarity values (Oksanen *et al.* 2008). Moreover, a nested Adonis test with two fixed factors can be performed compared to other broader used as ANOSIM test where it is not available in current statistical software. The factors tested were: Burned as the principal factor and Creek as the nested factor. The Habitat was treated as an independent factor and hence the interaction was also tested (between Burned and Habitat).

We used a vector-fitting routine (R vegan package: Oksanen 2008) to examine which environmental variables were associated with the taxonomic and functional feeding group ordinations. Vector-fitting illustrates which environmental variables may be contributing to the pattern of macroinvertebrate communities; the arrows indicate the direction and relative strength of the correlation (R^2 and significance) in ordination space. The environmental variables included were: temperature (T), pH, conductivity (Cond), turbidity (Turb), TSS, nitrate, ammonium, phosphate, flow, habitat cover:

%bedrock, %boulder, %cobble, %pebble, %gravel, %sand, %clay/silt, %macrophytes (macrop), %filamentous algae (algae), %moss, %roots, %small woody debris (SWD), and %large woody debris (LWD), riparian cover: %cover (cover_p), %herbs (herbs.grasses), %bare soil, %twigs, tree density, and organic content of the samples: dry organic material (gr.OM) and ash free dry mass (afdm). Mantel tests were used to examine the correlations between the dissimilarity matrixes.

Separate Kruskal-Wallis analyses were done to test the Burned and Habitat factors for each taxa that represented >1% in abundance. The taxa with a significant difference were plotted in the taxonomic data NMDS with the species scores. This was done through the wascores function, which stands for the calculation of Weighted Averages scores of species either for ordination configuration or for environmental variables. All the analyses were carried out using R package (R Development Core Team 2006).

Results

Taxonomic composition

Macroinvertebrate taxa richness at the control sites was significantly higher compared to the burned ones (C: 41 ±4 vs. B: 26 ±1; Kruskal-Wallis test: 7.57, p-value 0.006). The same pattern was observed with the rarefaction curves at N=929 (C: 37 ±4 vs. B: 17 ±1; Kruskal-Wallis test: 12.79, p-value <0.001). Total abundance data, individuals per sample, also showed significant differences (Wilcoxon test: 81, p-value <0.001), with a higher number in the burned sites compared to the unburned sites (C: 1541 ±212 vs. B: 6164 ±539, Table 3.2).

Table 3.2. Taxa richness, number of rarefacted taxa and number of individuals at the six study sites.

Creek	Taxa richness, S (μ ± se)	Number of rarefacted taxa, n= 929 (μ ± se)	N (μ ± se)
B – Watchbox	25 ± 2	18 ± 1	7278 ± 871
B – Holland	25 ± 1	16 ± 1	5702 ± 665
B – Fifteen mile	28 ± 2	18 ± 1	5512 ± 1162
C – Moonee	44 ± 2	36 ± 2	2222 ± 342
C – Blue Range	27 ± 1	26 ± 2	1165 ± 173
C – White gum gully	51 ± 4	48 ± 4	1235 ± 208

Looking separately at the different orders, the control sites generally had a higher number of taxa compared to the burned sites (Figure 3.3a). The number of EPT taxa was the highest at Moonee and White gum gully and represented at least 18% of the community, while at the burned sites did not arrive to 3% (Figure 3.3a). The most common families of the EPT orders, found at all creeks were Leptophlebidae, Baetidae, Gripopterygidae, Hydrobiosidae, Philopotamidae and Hydroptilidae. The families found exclusively at the control creeks were the Caenidae, Hydropsychidae, Leptoceridae, and different genera from the Baetidae family, mainly of the genus *Centroptilum* sp. There were no Odonata or Megaloptera found at the burned sites, though abundances at control sites were very low (Fig 3.3b). Elmids were the most common beetle family found in all the creeks, predominantly *Austrolimnius* sp. which was more abundant at the control sites (C: 68 ±18) compared to burned sites (B: 14 ±6).

Diptera was the most abundant order found across all creeks, especially at burnt sites (Figure 3.3b). The Chironomidae was the most abundant family, with a range of 50-73% at the burned sites and 23-58% at the control ones. The Aphroteniinae subfamily was only found at the control creeks. The Simuliidae was the second most relative abundant family representing 21 and 24% of the community at Holland and Fifteen mile creeks. At Watchbox creek was less than 1% compared to the mean of 9± 4% of the control creeks. The second highest order found at the burned sites was the Oligochaeta, representing almost half of the community in Watchbox creek (Figure 3.3b).

NMDS generated from the macroinvertebrate taxonomic data revealed an apparent separation between the burned and control creeks (Figure 3.4), confirmed by significant difference from the Adonis comparison. Creeks within burnt and unburnt categories also showed significant differences (see Table 3.3). Chironominae, Orthocladiinae, Simuliidae, Naididae, *Taschorema* complex (Hydrobiosidae) and *Dinotoperla* sp. (Gripopterygidae) were more abundant at the affected streams and marked clearly the separation between burned and control streams (Figure 3.4).

From the 29 environmental variables tested with the taxonomic data, 13 were significant and are shown in the graph (Figure 3.4; MANTEL test 0.3958, p-value: 0.005). The riparian measures showed significant correlations of at least 60% (p-values <0.003). Herb, grasses and riparian cover percentage and tree density were related to the control sites. In constrast, the percentage of bare soil was related to the burned sites (Figure 3.4). The medium size instream habitat type cover: cobbles, pebbles and gravel percentages were strongly related (>77%) with the Watchbox creek, a burned site (Figure 3.4), while the sand and macrophytes percentages were related to the control sites however mainly to the Blue range creek. The organic material was more related to Moonee and White gum gully creeks. Finally, nitrate and conductivity were related to Watchbox creek.

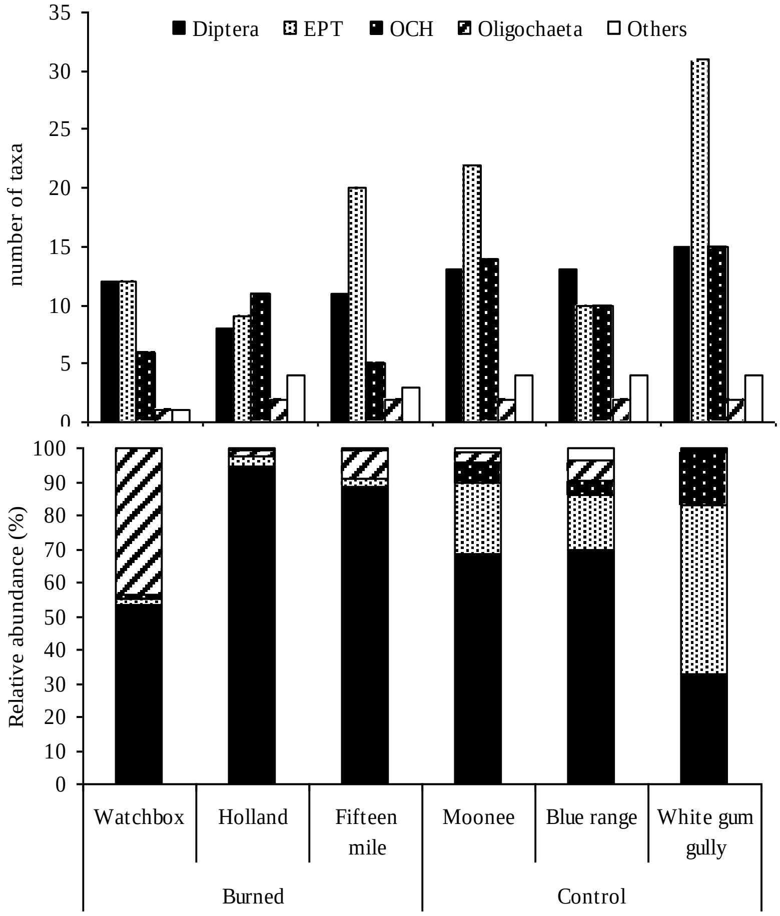


Figure 3.4. Number of taxa (a) and relative abundances (b) of the major taxa sampled at the six creeks. EPT: sum of Ephemeroptera, Plecoptera, and Trichoptera; OCH: sum of Odonata, Coleoptera, and Heteroptera; Others: sum of Megaloptera, Mollusca, and Ostracoda.

Habitat associations

Habitat associations for some taxa were clear in some creeks and fire (Burned factor) was also important, but the interaction between them was not (Table 3.3). From the 37 taxa that represented more than 1% in abundance, 15 taxa presented significant habitat preferences (Table 3.4). Generally, the riffles supported a greater abundance for most of the taxa, while in the pools just 4 taxa were more abundant: Chironominae, Tanypodinae, *Centroptilum* sp. and *Necterosoma* sp. On the other hand, *Riekoperla* sp., *Illiesoperla* sp., *Dinotoperla* sp. and Simuliidae were associated to riffles of three streams, Holland and Fifteen mile creeks (burned) and Blue range creek (control), but not to the others. Watchbox creek was the only site that the pools and riffles did not follow the general pattern, and the riffles where localized close to the pool samples (Figure 3.5).

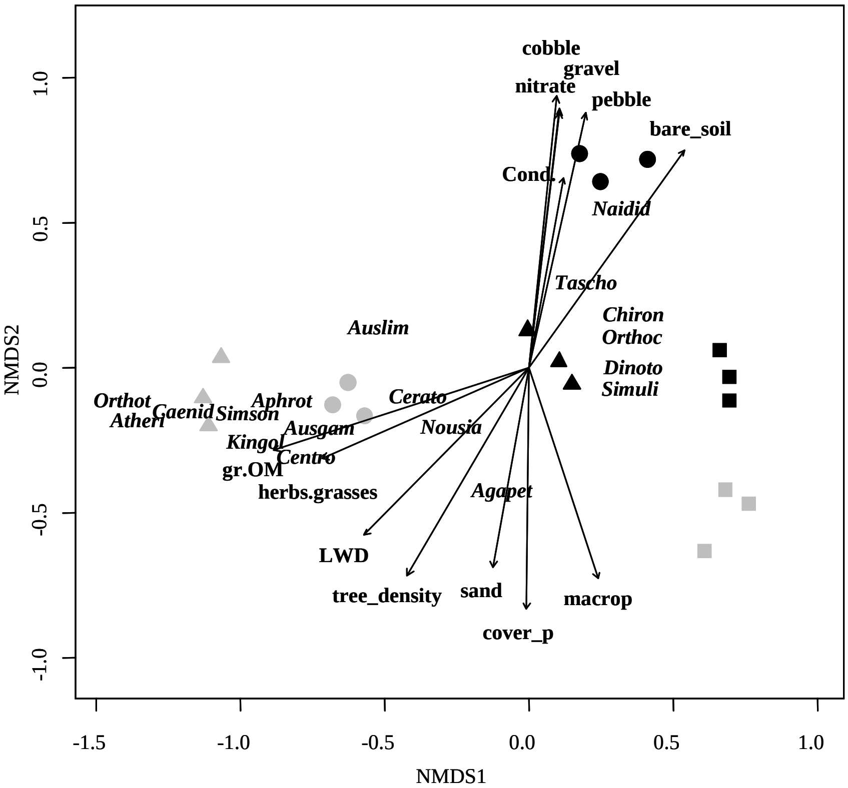


Figure 3.4. Control vs. burned sites representation in a non-metric MDS ordination based on the Bray-Curtis resemblance matrix of the macroinvertebrate taxonomic data (stress 0.07). The grey symbols represent the control creeks (circle: Moonee creek, square: Blue range creek, triangle: White gum gully creek) and the black symbols the burned ones (circle: Watchbox creek, square: Holland creek, triangle: Fifteen mile creek). The significant taxa are plotted and the acronyms key is on Table 3.4. The arrows represent the fitted environmental variables that were significant, and the length of the arrow shows the magnitude of the correlation.

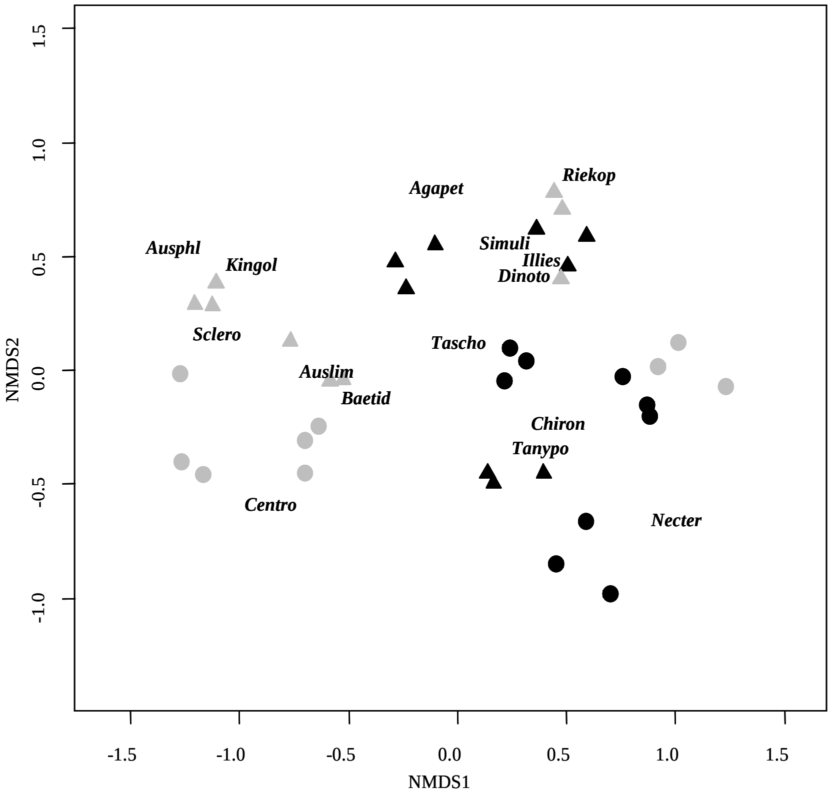


Figure 3.5. Pool vs. riffle representation in a non-metric MDS ordination based on the Bray-Curtis resemblance matrix of the macroinvertebrate taxonomic data across all the creeks and habitats. The grey symbols represent the control creeks and the black symbols the burned ones. The circles are the pool and the triangles the riffle samples (stress: 0.14). The significant taxa is plotted and the acronyms key is on Table 3.4.

Table 3.3. F, R^2 and p values of the Adonis comparison based on the variance of the dissimilarities from the taxonomic, habitat and feeding group matrixes. The factors treated in all analyses were Burned, as the main factor and Creek, as the nested one. The Habitat was treated as independent factor (*p<0.05, **p<0.01, ***p<0.001, ^{NS}: non-significant p>0.05).

	Taxa		**Habitat**		**Feeding group**	
	F	**R^2**	**F**	**R^2**	**F**	**R^2**
Burned	18.11***	0.45	24.93***	0.31	25.01***	0.60
Burned (Creek)	1.59***	0.40	2.25***	0.28	1.09***	0.26
Habitat	--	--	6.85***	0.09	--	--
Burned x Habitat	--	--	3.37 ^{NS}	0.04	--	--
Residuals	--	0.15	--	0.28	--	0.14

Table 3.4. Kruskal-Wallis values for the taxa with a higher >1% abundance in order to test the differences between the burned and habitat factor (*p<0.05, **p<0.01, ***p<0.001, ^{NS}: non-significant p>0.05).

Taxa	**Acronym used**	**Factor: Burned**		**Factor: Habitat**	
Agapetus sp.	*Agapet*	12.44	***	13.83	***
Antiporus sp.		0.54	^{NS}	1.89	^{NS}
Aphroteniinae	*Aphro*	4.51	*	0.13	^{NS}
Athericidae	*Ather*	6.33	*	3.34	^{NS}
Austrogammarus sp.	*Ausgam*	4.43	*	2.52	^{NS}
Austrolimnius sp.	*Auslim*	4.37	*	6.08	**
Austrophleboides sp.	*Ausphl*	1.62	^{NS}	4.36	*
Baetid genus 2 sp.	*Baetid*	0.10	^{NS}	4.33	*
Caenid genus C sp.	*Caenid*	8.06	**	0.02	^{NS}
Centroptilum sp.	*Centro*	8.06	**	6.92	**
Ceratopogonidae	*Cerato*	4.41	*	0.16	^{NS}
Chironominae	*Chiron*	7.74	**	5.48	*
Cyprettinae		0.06	^{NS}	2.64	^{NS}
Dinotoperla sp.	*Dinoto*	5.28	*	21.41	***
Glyptophysa sp.		3.37	^{NS}	3.17	^{NS}
Herpetocypridinae		2.53	^{NS}	1.27	^{NS}
Hydrochus sp.		0.31	^{NS}	1.89	^{NS}
Illiesoperla sp.	*Illies*	0.72	^{NS}	9.83	**
Kingolus sp.	*Kingol*	6.04	*	8.04	**
Naididae	*Naidid*	10.39	**	0.27	^{NS}
Necterosoma sp.	*Necter*	0.09	^{NS}	4.42	*
Notalina sp.		3.38	^{NS}	0.00	^{NS}
Nousia sp.	*Nousia*	4.15	*	0.45	^{NS}
Orthocladiinae	*Orthoc*	12.79	***	0.08	^{NS}
Orthotrichia sp.	*Orthot*	4.76	*	0.30	^{NS}
Oxyethira sp.		0.00	^{NS}	0.62	^{NS}
Platynectes sp.		1.88	^{NS}	0.48	^{NS}
Podonominae		1.87	^{NS}	3.39	^{NS}
Psychodidae		0.20	^{NS}	1.10	^{NS}
Riekoperla sp.	*Riekop*	0.05	^{NS}	3.85	*
Sclerocyphon sp.	*Sclero*	6.59	*	4.33	*
Simuliidae	*Simuli*	3.95	*	17.85	***
Sinsonia sp.	*Simson*	5.41	*	0.82	^{NS}
Smicrophylax sp.		3.37	^{NS}	1.28	^{NS}
Tanypodinae		2.82	^{NS}	7.87	**
Taschorema complex	*Tascho*	6.87	**	8.95	**
Tubificidae		0.24	^{NS}	0.11	^{NS}

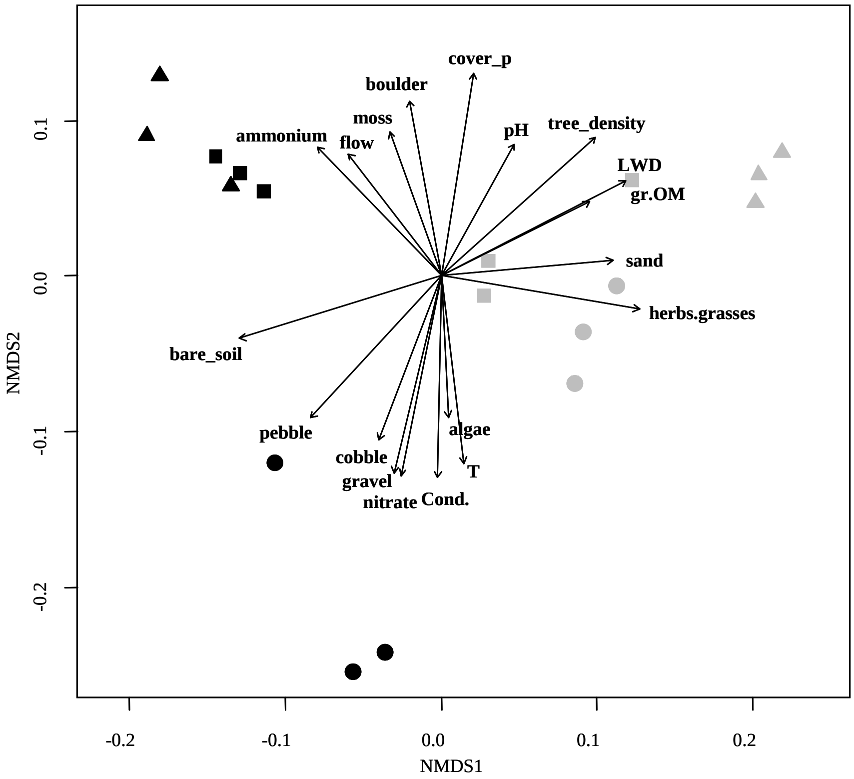


Figure 3.6. Representation of the functional feeding group data based on the Euclidian distance resemblance matrix in a non-metric MDS ordination (stress 0.02). The grey symbols represent the control creeks (circle: Moonee creek, square: Blue Range creek, triangle: White gum gully creek) and the black symbols the burned ones (circle: Watchbox creek, square: Holland creek, triangle: Fifteen mile creek). The arrows represent the fitted environmental variables that were significant, and the length of the arrow shows the magnitude of the correlation

Functional feeding groups

Relative abundances for three of five functional feeding groups showed significant differences between burnt and control/unburnt sites (Table 3.5). The percentage of shredders was 12.4 % lower at the control creeks while the opposite was found for the predators and scrapers percentages. The biggest difference was found in the percentage of scrapers that was 10 times higher at the control creeks compared to the burned ones (Table 3.5). The variance of the Creeks was significant for all the variables.

The NMDS generated from the functional feeding group data is shown in figure 3.6. The Burned factor was again significant and explained the 60% of the variance (Table 3.3). A similar pattern was obtained for the vector fitting compared to the taxonomic ordination, 19 environmental variables were significant and showed a correlation of at least 45% (Figure 3.6; MANTEL test 0.3474, p-value: 0.009). The significant riparian measures were again creek cover percentage, herb and grasses cover percentage and tree density, related to control sites, and the bare soil percentage, related to burned sites (Figure 3.6). The cobbles, pebbles, gravel and algae cover percentages were related to

Watchbox creek. And the same trend for nitrate, conductivity and temperature, associated to this creek (Figure 3.4). The sand percentage, large woody debris and organic material associated to the sample were correlated to the control sites. Finally, moss and boulder percentages, flow, and ammonium were related to Holland and Fifteen mile creeks (Figure 3.6).

Table 3.5. F values for the nested ANOVA (main factor: Burned, nested factor: Creek) comparing the five functional feeding groups considered in this study. The relative abundances (% ± standard error) of the burned and control creeks are presented (*p<0.05, **p<0.01, ***p<0.001, NS: non-significant p>0.05).

Functional feeding group	**Burned**	**Mean ± s.e.**		**Burned (Creek)**
	F	**C**	**B**	**F**
Gathering collectors	3.98	21.1 ± 1.9	31.7 ± 8.0	7.16**
Filtering collectors	0.54	11.9 ± 1.1	15.4 ± 3.7	41.97***
Shredders	4.79*	**34.1** ± 2.6	**46.5** ± 5.9	3.42*
Scrapers	327.69***	**25.2** ± 3.8	**2.3** ± 0.2	16.31***
Predators	25.88***	**7.7** ± 1.3	**4.1** ± 1.0	14.35***

Discussion

The importance of fire

Nine months after the bushfire affected the Victorian creeks sampled in this study the macroinvertebrate communities were different compared to the control ones. The burned sites had lower number of taxa but four times the number of individuals. Even though some taxa were unique at the control creeks it seems that the main differences were due to the abundance of common taxa, correspondent to Orthocladiinae, Naididae, Simuliidae, Chironominae, *Dinotoperla* sp. and *Taschorema* complex. The change of the composition in the macroinvertebrate communities after a wildfire have been shown in previous studies (Minshall *et al.* 1997; Minshall *et al.* 2001a) where commonly there is a shift and a dominance of early colonists and opportunistic species with short life cycles (Minshall 2003). The midterm effects of fire on the macroinvertebrate assemblage corresponds to an increase in number and biomass of opportunistic macroinvertebrates like Chironomidae, Simuliidae and Baetidae (Minshall *et al.* 1989), and a higher density of insects emergence (Mellon *et al.* 2008; Malison & Baxter 2010a). In Australian streams, stonefly nymphs such as *Dinotoperla thwaitesi* have been reported as proficient recolonists (Boulton & Lake 1992b) and many hydrobiosids are able to deposit considerable numbers of eggs over a relatively short period (e.g. 111 600 eggs in 10 days, (Reich & Downes 2003), which could eventually explain the higher density in the burned creeks of these two taxa.

The effect of the fire was not only clear on the structure but also on the function. The fire explained 60% of the difference found between the burned and control functional feeding groups, indicating the importance in the change of the resources after the fire. The organic matter inputs after the fire are altered, and the generalist herbivore-detritivore taxa with broad physical habitat preferences appear to be best adapted for the conditions found in post-fire streams (Mihuc & Minshall 1995, 2005). In this study, the percentage of the gathering collectors was higher at the burned creeks but the main factor was not significant. We also expected a decrease in the shredders proportion simultaneously with the disappearance of the woody debris and leaves packs in the burned stream. This is consistent with the higher percentage in large woody debris and organic material found in the control creeks but the proportion of shredders was larger at the burned sites. On the other hand, the largest difference found was in the scrapers proportion; the control was ten times higher compared to the burned sites. And this seems to be contradictory. However, as found by Boulton (1991) and Maamri *et al.* (1997) in drying streams, the scrapers rather than shredders were more important in litter breakdown. Then it seems that the breakdown of the higher organic material found in the control creeks (LWD and gr.OM) could be done mainly by the scrapers. Besides, in the study by Gama *et al.* (2007) in Portugal the alteration of the quality of allochthonous inputs in post-fire streams did not seem to determine changes in ecosystem functioning in a short term. Moreover, the breakdown of fire exposed leaves of *Eucalyptus* sp. was clearly promoted by fungi and accelerated by physical fragmentation (Gama *et al.* 2007). This could indicate that even the entrance of partly burned organic material, mainly *Eucalyptus* sp., could also be used by the shredders or the scrapers.

Nevertheless, the classification of the macroinvertebrate taxa in just one functional feeding groups (as we did in this study) has been criticized before (Mihuc & Minshall 2005). Furthermore, as reviewed by Closs & Lake (1994) analysis of large and detailed food webs have suggested that features such as long food chains and omnivory may actually be more common than has been previously observed. And indeed, in a more recent study done in Victorian streams, the primary consumers appeared to be opportunistic generalists dependent on allochthonous detritus (mainly *Eucalyptus* sp. throughout the year) and the associated biofilm, regardless of their primary mode of feeding (Reid *et al.* 2008). As reviewed by some authors this type of food webs may confer high resistance and resilience to disturbance (Fisher & Likens 1973; Closs & Lake 1994; Reid *et al.* 2008). This could suggest that even there is a change in the organic material that is entering the creek after a fire; the omnivory prevails before and after the fire.

The importance of hydrological conditions and instream habitat

Although fire may have direct effects on aquatic communities, the most important effects are related to those produced by the subsequent floods (Minshall *et al.* 1989; Minshall *et al.* 1997; Minshall *et al.* 2001a; Victoria 2003; Robinson *et al.* 2005). And after a fire, with a higher percentage of bare soil and less vegetation as in the cases of the burned sites of this study (respectively, 38% and 0.031±0.015 trees/m^2) the erosion and sedimentation would be greater, as showed in other studies (Nakamura *et al.* 2000; Bisson 2003). However, the post-fire erosion rates in eucalypt forests compared to other areas (e.g. Chaparral scrub or Coniferous forest) seem to be less severe in geomorphological terms (e.g. erosion rates, water repellency) although this will locally depend on the hill slope conditions and post-fire rainfall events (Shakesby *et al.* 2007).

In our study area, a 40% of variance after the fire was explained through the creek factor which indicates that: first, individual rivers can have their own community patterns even in geographically adjacent ones (Lloyd *et al.* 2005) and second, the responses may largely depend on local factors (Minshall 2003). This means that although the precipitation, mean temperature, radiance, and potential evapotranspiration indicated similar conditions at the whole study area, local differences may still take place. For example, at the sampling time, the streambed of Watchbox creek was still completely covered by ashes which ultimately indicated that they were still not washed out. Additionally, it has been stated that ashes are a predominant source of nitrogen among other nutrients (Belillas & Rodà 1993) and was Watchbox the creek that presented the highest conductivity and nitrate values (respectively, 110.2 μS/cm and 4.1 mg/l) and the lowest flow (2 l/s). Furthermore, Watchbox recorded the highest percentage of Oligochaeta (59% compared to 19% of mean of the other creeks); a taxa which is generally enhanced by flow reduction (Dewson *et al.* 2007). On the other hand, all the other sites presented higher flow (16-225 l/s) and no ash in the streambed (on the affected sites) what suggest higher precedent runoff. Thus the differences of Watchbox creek with the other burned creeks have to be due to the lower importance of indirect effects because the lower stream flow produced between the moment of fire and the date when the site was sampled.

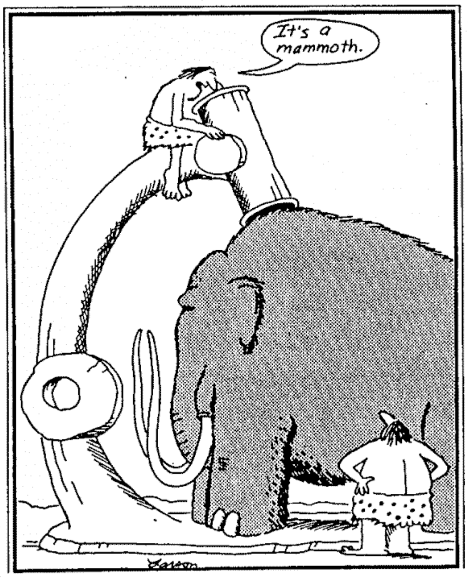
What it seemed also interesting is that when separated by habitats Fifteen mile and Holland (burned) and Blue range (control) creeks shared quite a lot of common taxa. The riffles of these three creeks were characterized by Simuliidae, *Dinotoperla* sp., *Riekoperla* sp. and *Illiesoperla* sp. All these taxa are known by their high capacity of recolonization (Boulton & Lake 1992b). Although Blue range creek was not affected by the fire, it showed a percentage of bare soil of 20% in the riparian zone which was higher compared to the other control sites. And perhaps this let to a higher entrance of sediments (after higher precipitations) which could have affected the macroinvertebrate community. This is confirmed partly by the reduction of *Austrolimnius* spp. in this creek (abundant in the other two control creeks), because as reported by Doeg & Koehn (1994) an extreme reduction of larvae and adults of this genera was produced in a study after sediment releases from a small retaining weir from a tributary of the Yarra River.

Final remarks

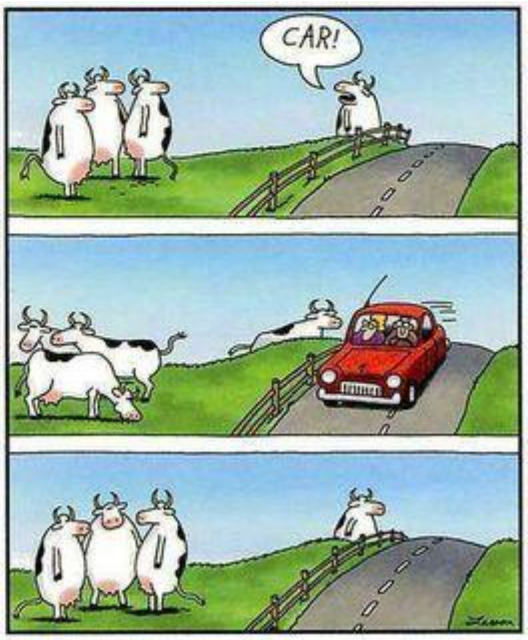
Australian aquatic fauna and flora are characterized by the high prevalence of both resistance and resilience traits, reflecting the evolutionary significance of drought as a selective pressure on aquatic biota and ecosystems (Boulton 2003; Bond *et al.* 2008). After a large disturbance such as bushfire, there was a negative impact on the structure of macroinvertebrate communities but, as expected, there was a rapid recovery response. Nine months after the bushfire the macroinvertebrate community was shaped by wildfire that interacted differently with flooding or drought, depending on the creek. The future climatic conditions in south east Australia predicts a decrease in annual run-off which ultimately means lower flow and a higher probability of more severe bushfires. It seems then important to study the response of high resilient communities, like the macroinvertebrates, to a higher recurrence of disturbances and see if the high capacity self repairing system will be responding with the same resilience.

Chapter 4

Effects of wildfire on stream macroinvertebrate assemblages in three biomes: do climate and hydrology mediate responses?



Early microscope



Gary Larson

Introduction

The ‘heartland’ (Shakesby & Doerr 2006) of research in fire impacts on aquatic ecosystems is located in the Western United States. The main effects found in this region have been described previously in the introduction of this thesis. Twenty years ago, Minshall *et al.* (1989) was concerned at the small number of studies done on the effects of fire on the aquatic biota. Since then the number of publications has increased dealing with several questions and raising additional ones. One of the major existing gaps is how to generalize the observations of fire effects to a larger geographical range.

In order to test to which extent the macroinvertebrate response to fire found can be generalized beyond the western US, the main objective of this work was to compare the responses of the composition and structure of macroinvertebrate communities to wildfire in three fire-prone biomes with different biogeographical and climatic contexts (NW Mediterranean, SE Australia and NW United States) using comparable methods and a unique sampling team. According to the findings of previous authors (e.g. Chapter 3), we hypothesized that 9 -11 months after fire: (i) macroinvertebrate taxa number would be unchanged or only moderately lower at the burned streams compared with control streams; (ii) we expected to find large differences between both group of streams in taxonomic composition, with a higher similarity of communities among burned streams and a higher spatial variance compared to unburned streams; and (iii) the abundance of macroinvertebrates would be higher at the burned streams, with a few species dominating, while there would be more rare taxa at the control streams. Above all, we expected that the responses of the macroinvertebrate communities in burned streams compared to those in unburned streams will be more rapid in the Mediterranean biome compared with those in the other two biomes followed by Australia, and then the NW United States because of longer history of floodings and drought conditions of the two former biomes.

Methods

Study site

Macroinvertebrate data were collected in three study areas: (i) northwest of the United States, in central Idaho within the Payette National Forest in the South Fork of the Salmon River (**IDH**: 44º42'41''- 44º54'44'' N, 115º41'04''- 115º45'21'' W), (ii) southeast Australia, in Victoria in the Goulburn and Ovens catchments (**VIC**: 36º25'9''- 36º33'40''

S, 145º32'55''- 146º6'25'' E), and (iii) northeast Spain, in the Natural Park of Sant Llorenç de Munt in Catalonia in the headwater streams of the Besòs and Llobregat rivers (**CAT**: 46º7'2''- 46º10'9'' N, 41º34'48''- 42º30'59'' E) (Figure 4.1). Fire is a common disturbance in all these three areas, generally occurring during the dry hot season and maintaining a mosaic of areas with different post-fire vegetation (Table 4.1). On the other hand, the main differences among the three are the climatic characteristics and hence the vegetation, and the stream hydrologic regime. Although Victorian streams have been previously described in Chapter 3 and those of Sant Llorenç in Chapter 1 and 2, here we summarize their conditions oin order to be compared with the Idaho streams.

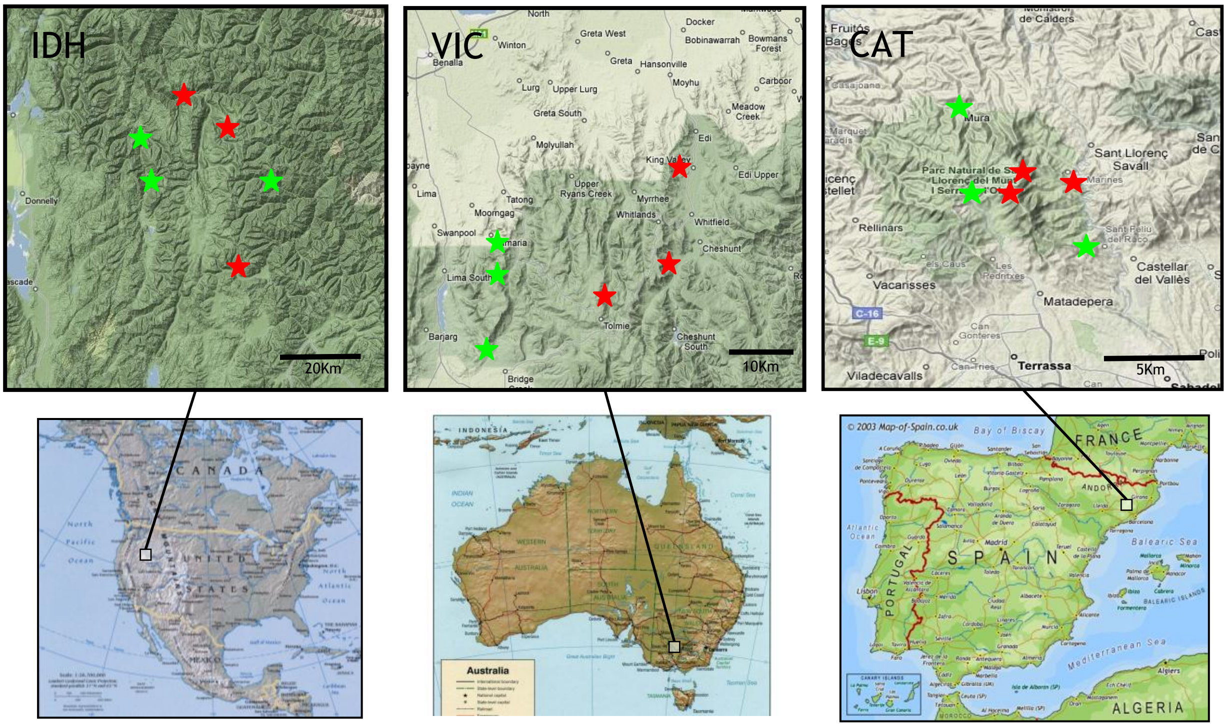


Figure 4.1. Map of the locations of the streams studied in each biome. Burned creeks are showed in red and control creeks in green.

1) IDH is characterized as having a cold-temperate climatology, located between mean elevations of 1228 – 1689 m. The majority of the annual precipitation occurs as snow, resulting in peak flows during spring and early summer (May and June) and generally remaining at baseflow from midsummer through autumn (July to September). The flow of the stream in the South Fork of the Salmon River (central Idaho) goes through steep valleys with forested slopes of primarily *Pseudotsuga menziesii*, *Pinus ponderos*, *Picea engelmanii*. Open areas of grass and sagebrush (*Artemisia tridentata*) are common in the drier slopes. Riparian forests are characterized by *Alnus incana*, *Cornus sericea*,

Acer glabrum, *Salix* and *Betula occidentalis*. The wet areas of the streams ranged in size from 2.5-10.8 m and a mean depth of 18.7 cm.

The most recent information of the fire history in the Idaho study area was available in the National Atlas (http://www.nationalatlas.gov/index.html, retrieved December 2009) which indicates that there has been no fire among the streams between 1995 –2000. Information from years 1740 – 1900 using charcoal and scar studies indicates a high fire recurrence of 8 to 32 years (Heyerdahl *et al.* 2008). In 1910 the largest fires of Idaho could have affected, at least partly, the area. Fire suppression can be seen after this period, but fires again commenced after the 90's with different fires (e.g. the Chicken Fire in 1994, the Diamond Fire in 2000, etc.) but none affecting the study area until 2007. At the beginning in the fall of 2006 and continuing into the spring of 2007, the precipitation tended to be about 50 percent of the long-term averages reported by several Idaho weather stations (e.g. Boise, Cascade, Stanley) (Western Regional Climate Center 2008; Graham *et al.* 2009). As a result, in April 2007 a moderate drought existed in central Idaho and it increased to very extreme in July. In this situation, lighting ignited multiple fires and the one called the East Zone Complex fire, that started at the end of July until mid September 2007, and burned more than 95000 ha (Tily 2008) including the catchment areas of our study site.

2) VIC sites have a warm-temperate climate. Their elevations were between 380 – 503 m. The forests are mainly dominated by different species of *Eucalyptus*. The streams are intermittent with flow in winter/spring (June/November) and low flow and cease-to-flow resulting in a series of disconnected pools in summer/autumn (December/May). The channel profile was mainly shallow with a mean width of 1.5-3.2 m and depth of 8-30 cm. Information on the fire history of Victoria came from maps of the Department of Sustainablity and Environment (DSE) from 1970 to 2007 and this information revealed that none of the stream catchments were burned during this time. Nevertheless, prescribed fires occurred in Watchbox and Moonee streams catchments in some years (1992, 2004, 2007) burning a total of 2.6% and 8.8% of the catchment, respectively. Before 1970, more precise data are not available but from maps and information from the DSE, the 1938-39 and 1851 'Black Thursday' fires could have affected the areas as they burned more than 2 and 5 million hectares respectively. If this is true then the large fires recurrence is between 65 – 90 years. The fire season 2006/07 in Victoria commenced northeast of the region in early December and was heightened by exceptionally dry conditions of a severe megadrought (Smith 2007; Bond *et al.* 2008;

Crowther *et al.* 2008). The longest fires (69 days) in Victoria's history were recorded, having impacted more than 1.2 million hectares of private and public land, including parts of the upper catchments of the Goulburn and Ovens Rivers (Smith 2007).

3) CAT contains intermittent streams in a Mediterranean climate, characterized by wet winters and hot dry summers with large floods in winter/autumn and severe seasonal droughts in summer (Gasith & Resh 1999). The catchment forests are dominated by *Pinus halepensis* and *Quercus ilex*, while the riparian forest by *Corylus avellana*, *Cornus sanguinea*, *Populus nigra*, *Populus alba*, and *Rubus ulmifolius*. The Sant Llorenç Natural Park in Catalonia has a long history of wildfires, with 667 fires recorded between 1965 and 2003 (Santos *et al.* 2009). However, most of the fires were quickly extinguished, including the one in 1994 that burned 143 ha and affected part of the study site, a total of 15.8% of the Vall d'Horta stream. In August of 2003, the dry conditions of the previous months combined with specific wind regimes resulted in an extensive crown fire of medium intensity (Paricio 2007). In four days, the total forested burned area was of 4543 ha which included most of our study area.

So the three areas have in common that after and in very dry years they suffered from intense and extensive fires that burned most of the studied catchments and they were all sampled at a similar time (9-11 months) after the fire.

Sampling design and sample collection

A total of eighteen streams were sampled, six streams at each biome, half of which were affected by fire (Table 4.2). Sampling was done between nine and eleven months after fire. Sampling across the three biomes consisted in choosing a minimum of a 50- m reach on each stream for collecting: water samples, fluvial and riparian habitat measures, and macroinvertebrates. Water temperature (T, ºC) and conductivity (µS/cm) were measured *in situ*. Discharge (l/s) was estimated from mean depth, transect width, and water velocity measurements recorded with a flow meter. The fluvial in-stream habitat was characterised by the IHF (Index of Fluvial Habitability), which measures habitat heterogeneity and gives an idea of the physical diversity present in the stream and ultimately the suitability of the macroinvertebrate community (Pardo *et al.* 2002). The canopy cover was visually estimated as a percentage of the stream channel shaded by vegetation.

We followed the community sampling protocols for each biome. The macroinvertebrates were collected using a 250µm net and fixed in formalin (4%) in

Catalonia and ethanol (90%) in Idaho and Victoria. Once in the laboratory, dissecting microscopes Leica MZ6 were used to separate and identify specimens to genus level, except for Diptera and non-insect taxa which were identified to family/sub-family or order level, respectively. The macroinvertebrates were counted although sub-sampling was done when more than 200 individuals of one taxon (for example, Diptera families) were found. Three to five replicate Surber net ($929cm^2$) were taken in Idaho, whereas in Victoria and Catalonia three replicate of 4 minute multihabitat kick-sampling were taken. The replicates in two streams in Catalonia (Gallifa and Mura) were taken on different dates starting the first sample on May 14th until the last sample was taken on July 30th.

Table 4.1. Summary of the main characteristics of the three biomes studied.

Biome/ Characteristics	IDAHO	VICTORIA	CATALONIA
Climate	Cold-temperate	Warm-temperate	Mediterranean
Mean min-max annual temperature (°C)	0.1 – 15.3	7.6 - 20.8	8.8 – 25.5
Mean annual precipitation (mm)	950	817	650
High flows	Early spring	Extreme winter	Highest peak in winter and lowest in summer
Peak of leaf fall	Autumn	Summer, dominated by: bark, branches, fruit capsules	Summer and Autumn
Catchment use	Forestry	Forestry and some parts agriculture	Forestry and agriculture until 1956
Catchment vegetation	*Pseudotsuga menziesii*, *Pinus ponderosa*. Lawson, *Picea engelmanii*, *Artemisia tridentata*.	*Eucalyptus*	*Pinus halepensis*. and *Quercus ilex*.
Riparian vegetation	*Alnus incana*, *Cornus sericea*, *Acer glabrum*, *Salix* and *Betula occidentalis*.	*Casuarina*, *Leptospermum*, *Melaleuca*, *Pomaderris aspera*.	*Corylus avellana*, *Cornus sanguinea*, *Populus nigra*, *Populus alba*, and *Rubus ulmifolius*.
Common disturbances	Peak runoff in spring	Floods, droughts	Floods, seasonal droughts
Other less predictive disturbances	Fire	‘Millennium’ drought >10years, fire	Fire
Date of the fire	August 19th - September 9th 2007	January 11th 2007	August 10th 2003
Sampling date	July 31st – August 1st 2008	October 8 – 9th 2007	May 14th – July 30th 2004

Table 4.2. Main characteristics and *in situ* measures of the sampled streams.

	Control (C)			**Burned (B)**		
			IDAHO STREAMS			
	Blakmare	Goat	Phoebe	Dollar	Camp	Buckhorn
Location	44°48'43" N 115°45'21" W	44°45'20" N 115°41'04" W	44°54'15" N 115°42'34" W	44°42'41" N 115°42'38" W	44°53'23" N 115°42'14" W	44°54'44" N 115°45'10" W
Area (km^2)	4.9	17.2	17.4	24.7	28.7	48.8
Elevation (m)	1689	1472	1256	1548	1256	1228
Discharge (l/s)	690	272	48	349	53	1276
Specific discharge (km^2 l/s)	141.71	15.84	2.76	14.12	1.85	26.16
Catchment burned (%)	10	75	85	80	10	10
Temperature (°C)	10.7	14.1	12.7	9.2	11.1	15.5
Conductivity (µS/cm)	38	51	86	40	68	38
Orientation	E	W	E	E	W	E
			VICTORIAN STREAMS			
	Moonee	Watchbox	Holland	Fifteen mile	Blue range	White gum gully
Location	36°30'37" S 145°33'51" E	36°25'9" S 146°6'25" E	36°33'3" S 146°9'36" E	36°28'57" S 146°9'56" E	36°33'40" S 146°3'27" E	36°28'20" S 145°32'55" E
Area (km^2)	26.0	31.3	9.0	60.7	16.7	23.5
Elevation (m)	420	400	380	483	420	503
Discharge (l/s)	14	2	16	215	25	36
Specific discharge (km^2 l/s)	0.54	0.06	1.78	3.54	1.50	1.53
Catchment burned (%)	0	86.3	60.1	96.2	0	0
Temperature (°C)	10.7	17.6	11.1	8.1	13.4	11.7
Conductivity (µS/cm)	42	110	25	31	60	37
Orientation	N	N	W	N	W	NE
			CATALONIAN STREAMS			
	Mura	Gallifa	Vall d'Horta	Ripoll	Font del Llor	Castelló
Location	46°9'58" N 41°34'48" E	46°9'52" N 42°30'59" E	46°8'19" N 42°1'12" E	46°9'43" N 42°6'30" E	46°8'35" N 41°49'2" E	46°6'56" N 42°10'58" E
Area (km^2)	2.8	2.9	7.6	7.5	0.9	2.9
Elevation (m)	540	560	510	487	520	520
Discharge (l/s)	150	13	17	5	1	1
Specific discharge (km^2 l/s)	53.71	4.49	2.27	0.69	0.97	0.31
Catchment burned (%)	0	84	66	91	3	0
Temperature (°C)	17.7	18.0	20.0	24.5	19.6	18.1
Conductivity (µS/cm)	563	690	619	616	564	647
Orientation	W	S	SE	S	E	W

Additionally, in Idaho, three to five rocks were scraped in order to estimate the chlorophyll-*a* content of the periphyton, which was extracted following standard methods: in 10-ml of methanol, filtered through Watman GF/F 4.7cm filters, and measured using a spectrophotometer (model ThermoSpectronic Genesys 5) (APHA

1995). Furthermore, at this biome, the macroinvertebrate biomass was also calculated after drying the sample (105 °C for at least 24 hours) and weighing all insects (to nearest 0.001g).

Species diversity and composition

We calculated the observed taxonomic richness and the total abundance (individuals/sample) for each stream. Because of the different sizes of samples, the number of species was standardized using rarefaction curves' with the lowest number of individuals present for each biome (IDH: 217, VIC: 929, and CAT: 2291); i.e. the expected species richness in a subsample of n individuals selected at random from a sample containing N individuals and S species (Hurlbert 1971). The burned and control sites were compared with an ANOVA, but for the data that did not fit a normal distribution the non-parametric Kruskal-Wallis test was used. Normality was tested with the Shapiro-Wilkinson test.

In order to compare the species composition and diversity of two or more assemblages in taxonomic and ecological research, similarity (overlap) and/or dissimilarity (turnover, beta diversity, or distance) indices provide quantitative basis of assessment (Magurran 2004). However, the choices of transformation and of dissimilarity measures have important consequences for interpreting results. In this study, we used two qualitative indices (Jaccard and Sørensen) and two abundance-based indices (Bray-Curtis and Chao) (Chao *et al.* 2006). For the first the Jaccard index was used. The second index used, the Sørensen index, has been used as a flexible measure of beta diversity calculated as average distance (dissimilarity) from an individual site to the group centroid (Anderson *et al.* 2006). The Bray-Curtis index was used with squared root transformed abundance data. Finally, the Chao index was also calculated which is also based on the abundance data, but takes into account the number of unseen species pairs and it has been recommended when there is a possibility of not having sampled all the species. Adonis was used to test the effect of fire, stream and replicates for each biome. The significance test of Adonis is calculated with pseudo-F ratios based on sequential sums of squares from permutations of semimetric and metric distance matrices, and it was chosen because it prevails as a more robust analysis of variance compared to the ANOSIM that uses the rank of order of dissimilarity values (Oksanen *et al.* 2008).

Rank/abundance or Whittaker plots were compiled for the three biomes because as they have been reported to effectively illustrate changes after an environmental impact

(Magurran 2004). All statistical analyses were carried out using the R freeware package (R Development Core Team 2006), except the rank/abundance plots which were done with the PRIMER package version 6.1.2 (Clarke & Warwick 2001).

Results

The combined data from all the biomes together showed that the control streams not only had a significantly higher stream cover (B: 66 ±3 vs. C: 76 ±3 %; F: 5.69, p-value: 0.03) but also a higher fluvial habitat index (B: 51 ±5 vs. C: 65 ±4; F: 4.79, p-value: 0.04). The chlorophyll-*a* levels measured in Idaho streams were slightly higher in burned streams (0.36µg/cm^2 ±0.03) than in the control streams (0.25µg/cm^2 ±0.03), but this difference was not significant (F: 1.14, p=0.30).

The richness of macroinvertebrate taxa 9-11 months after the fire was lower in the burned streams in Idaho and Victoria but not in Catalonia (Table 4.3). The biggest difference was found in Victoria where the control streams had 30% more taxa compared with the burned streams. In general, the macroinvertebrate abundances in burned streams were higher than those of control streams although this difference was only significant in the Victorian streams (Table 4.3). The percentage of Chironomidae, Simuliidae and Baetidae was significantly higher in burned streams in Victoria and Idaho; but not in Catalonia where this percentage was high in both control and burned streams, are among the highest across the streams of the biomes (Table 4.3).

Table 4.3. Mean (± standard error) taxa richness, rarefied taxa number, abundance, Fisher diversity for control and burned streams in each biome. The Kruskal-Wallis test value from the control and burned comparison is presented (*p<0.05, **p<0.01, ***p<0.001, NS: non-significant).

Biome	**Community parameter**	**Control (C)**	**Burned (B)**	**Kruskal-Wallis test**
Idaho	Taxa richness	34 ± 1	30 ± 1	**4.57 ***
	Rarefied taxa number (n=218)	26 ± 1	22 ± 1	**11.28 *****
	Abundance	702 ± 64	826 ± 144	0.63 ^{NS}
	%Chironomidae+Simuliidae+Baetidae	36.7 ± 2.0	50.5 ± 3.6	**6.75 ****
Victoria	Taxa richness	40 ± 4	26 ± 1	**6.19 ***
	Rarefied taxa number (n=930)	36 ± 4	17 ± 1	**12.79 *****
	Abundance	1548 ± 641	6174 ± 1624	**12.79 *****
	%Chironomidae+Simuliidae+Baetidae	55.7 ± 6.1	77.4 ± 7.2	**5.48 ***
Catalonia	Taxa richness	38 ± 2	37 ± 2	0.00 ^{NS}
	Rarefied taxa number (n=2291)	32 ± 2	26 ± 2	3.27 ^{NS}
	Abundance	5411 ± 2565	10142 ± 1896	2.82 ^{NS}
	%Chironomidae+Simuliidae+Baetidae	76.1 ± 4.6	80.1 ± 5.3	1.07 ^{NS}

When comparing the community composition at a presence-absence level (Jaccard index) the fire showed a significant effect in all the three biomes and in Victoria the highest variance of macroinvertebrate community was explained by fire (38%). Furthermore, the permanova test showed the burned streams presented a higher variance compared to the control streams (Fig. 4.2a). Across all biomes, the stream was also a significant factor but Idaho presented the lowest variance (13% in Catalonia compared to 23% in Victoria) (Fig. 4.2a).

The results of Adonis on Sørensen dissimilarity index showed that fire and stream, again, were significant. The permanova test showed that the distances were similar for Catalonia and Victoria, while in Idaho the distances (i.e. dissimilarity) were smaller and the burned streams were significantly more similar compared to the control streams (Fig. 4.2b). And, contrary to the results obtained in the Jaccard index, the variances across the control streams were higher compared with the burned streams (Fig. 4.2b). The Chao index bases its similarity on the number of unseen species pairs, giving more weight to the rare taxa. For Idaho, fire and stream were highly significant and showed the lowest dissimilarities. In Victoria the variance was significantly higher in control streams compared with the burned ones, but the dissimilarity was more similar to that of the Catalonian streams (Fig. 4.2d). The percentage of the rare taxa (<5%) was similar between control and burned streams however across the biomes, Idaho streams showed the lowest percentage (C: 13% vs. B: 14%), followed by Victorian streams (C: 23% vs. B: 27%), and Catalonian streams the highest was found (C: 38% vs. B: 41%).

The higher dominance in Catalonian streams of few taxa in comparison with the other two biomes can be seen in the cumulative dominance plot (Fig. 4.3c). The control and burned Catalonian streams showed a similar trend and moreover, the relative abundance of rare taxa (<5%) was also equal (C: 90% vs. B: 90%). A similar tendency was seen in the burned streams of Victoria (Fig. 4.3d) which separated clearly from the control streams, and the relative abundance of rare taxa again corroborates this result (C: 67% vs. B: 90%). Finally, it seemed that, compared to the other biomes, the dominance of few taxa was more balanced in Idaho streams, and the relative abundance of rare taxa was also the lowest found (C: 55% vs. B: 62%).

The cumulative species rank plot based on the macroinvertebrate biomass in Idaho (Fig. 4.3b) showed some separation between control and burned streams compared to the one based on abundance (Fig. 4.3a). And, although the burned streams presented a higher biomass (113.6mg ±23.0) compared with the control streams (84.0mg ±13.8), this difference was not significant (F: 0.73, p=0.40).

Similarity based on the Bray-Curtis index showed that fire had a significant effect on the macroinvertebrates communities from the three biomes; with the variance explained in Victoria being the highest (Fig. 4.2c). The similarities among the burned and control streams were similar in Idaho and Catalonia, while in Victoria the burned streams showed significantly higher similarities and homogeneity compared to the control streams (Fig. 4.2c). In general, for any distance metric, the greatest dissimilarities across all the biomes were mainly in the Catalonian streams although they were similar between control and burned streams (Table 4.4). In contrast, Idaho streams usually showed the highest similarity and variance and in Victoria the response was always opposite between control and burned streams.

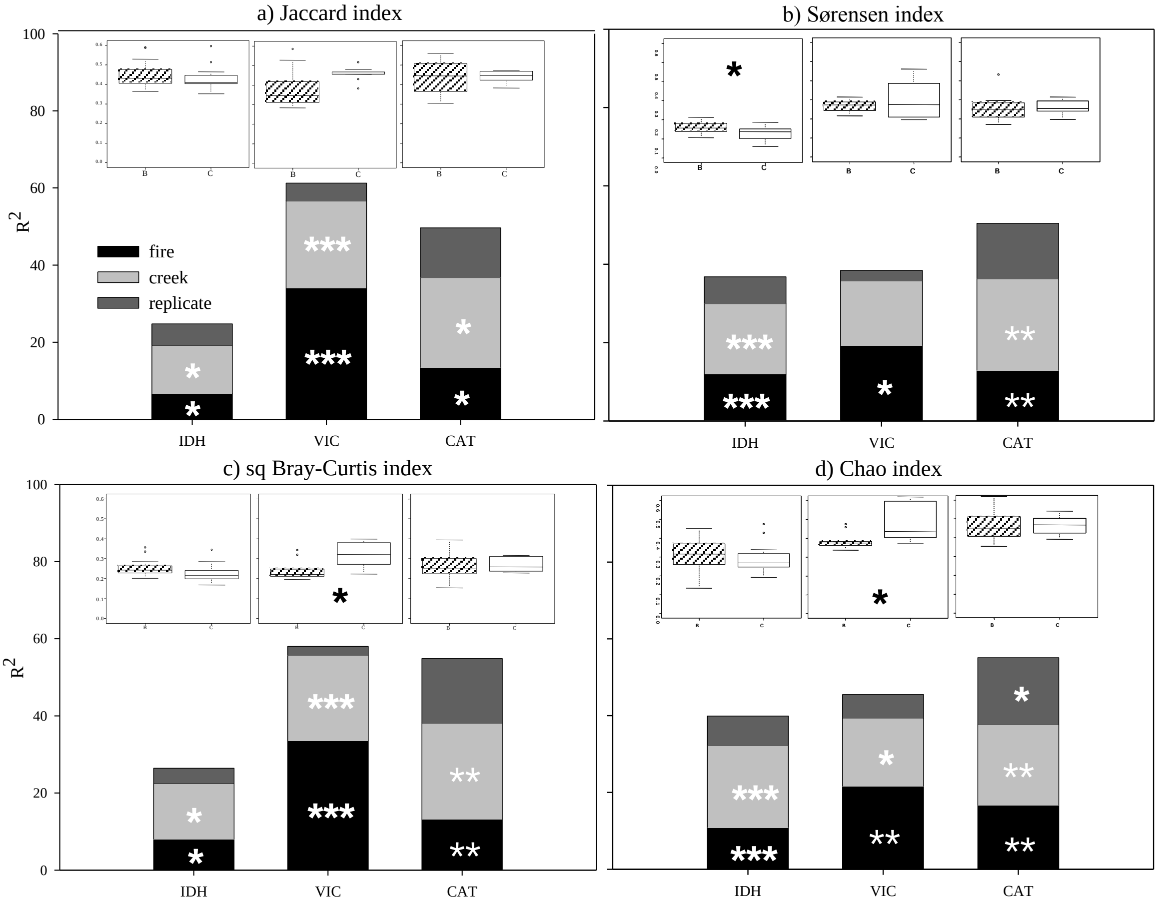


Figure 4.2. Variation explained (R^2) from the analysis of dissimilarities after the Adonis comparison. Four dissimilarities indices were tested: Jaccard (a), Sørensen (b), Bray-Curtis with a square root transformation of the data (c), and Chao (d) in each biome (IDH, VIC, and CAT). The factor used was nested as follows: Fire/Stream/Replicate which are presented, respectively, in black, grey and dark grey; if there were significant differences asterisks are presented in each rectangle (*** $p<0.001$, ** $p<0.01$, * $p<0.05$, no asterisk means no significant differences). In the upper part of each figure the mean and the variance of the similarities in burned (stripes) and control (blank) sites are plotted and were tested for each biome (* $p<0.05$).

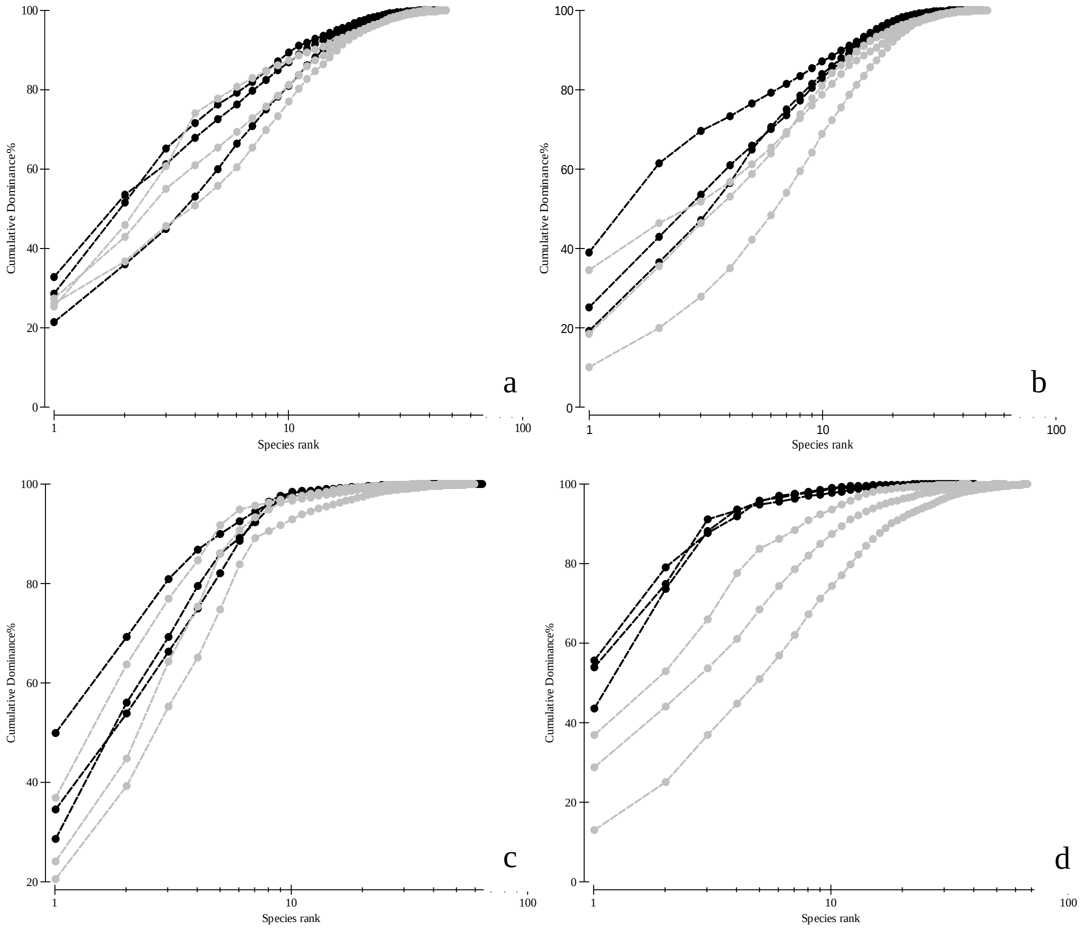


Figure 4.3. Cumulative rank species plot for the macroinvertebrate community from the streams based in abundance in Idaho (a), Catalonia (c) and Victoria (d). The same graph but based in the biomass is only available in Idaho (b). The grey symbols represent the control streams and the black ones the burned sites.

Table 4.4. Summary of the results of the macroinvertebrate communities, ones that showed significant differences are shown in bold.

	Hypothesis	Results
Richness	Burned < Control	**VIC > IDH** CAT
Abundance	Burned > Control	**VIC** IDH, CAT
Composition:	Factors:	
Jaccard	Fire	**VIC > CAT > IDH**
	Stream	**VIC = CAT > IDH**
	Variance: Burned > Control	**CAT = VIC > IDH**
Sørensen	Fire	**VIC > CAT > IDH**
	Stream	**CAT > IDH**
	Variance: Burned > Control	
Chao	Fire	**VIC > CAT > IDH**
	Stream	**IDH > CAT = VIC**
	Variance: Burned > Control	**CAT = IDH**
Bray-Curtis	Fire	**VIC > CAT > IDH**
	Stream	**CAT > VIC > IDH**
	Variance: Burned > Control	**CAT**

Discussion

Macroinvertebrate taxa number, abundance and composition changes

In general, the responses of the macroinvertebrate communities in the burned streams were similar across all the biomes (Table 4.4), but with some differences that suggest that contextual factors may play a key role in determining community structure. The only biome that accorded with all our initial hypotheses was in Victoria.

Fire in Victorian streams showed clearly that almost 30% of the taxa were adversely affected, and the post-fire dominance of few taxa and the increases in abundance, suggested an increase in production as indicated in other studies after wildfires (Minshall *et al.* 2004; Mellon *et al.* 2008; Malison & Baxter 2010b). These results could have been a consequence of the maintenance of the ash in the streambed as they were still not washed out after nine months; this ash accumulation was no doubt due to the continuation of low flows in the ‘millennium’ drought. In general, peak concentrations in nitrogen and phosphorus have been reported immediately after wildfires (Gresswell 1999; Spencer 2003). The addition of wood ash in Swedish streams after logging has been reported as being beneficial as it helps to mitigate the acidification found in these streams and it contributes nutrients as calcium, potassium, sodium, etc. but also potentially toxic metals, like cadmium, zinc, copper and lead (Aronsson & Ekelund 2008). Similarly, Vila-Escalé *et al*. (2007) also reported inputs of polycyclic aromatic compounds in a stream after a wildfire, which could be potentially toxic for aquatic organisms as bioaccumulation.

Control streams in Victoria showed had high beta diversity for macroinvertebrates, as expected as a result of long history of droughts and floods. Our results suggest that continued drought may result in loss of resilience of the community and a severe reduction in beta diversity in Victorian streams.

In contrast, the responses of the macroinvertebrates in Catalonia did not support most of the initial hypotheses. 11 months after fire, there were no significant differences in terms of richness or abundance, and also the highest percentage of *r*-strategist taxa was found, indicating the response of taxa to repetitive disturbances that reside in this type of streams. Mediterranean streams are physically, chemically and biologically shaped by sequential, predictable, seasonal events of flooding and drying over an annual cycle (Gasith & Resh 1999). The macroinvertebrate communities that live in these streams are constrained by this predictable seasonal variation (Bonada *et al.* 2007a). In terms of traits, the macroinvertebrates show a high dispersional and colonization capabilities

(Bonada *et al.* 2007a) with also high flexibility depending on the seasonality shifting from dry to wet years (Bêche & Resh 2007), which all together confers high resilience after disturbances.

Furthermore, the Catalonian streams also showed a high variability in the Chao distance, not only in streams but also in replicates. A possible cause could be that in one of the streams we used time for space substitution as replicates. However, this high variability is also comprehensible in terms of community recovery trajectories after a disturbance (i.e seasonal drought, floodings). It has been described that recolonization of disturbed reaches could be similar in early successional stages but differences in general emerge later attributed to the composition of the surrounding regeneration pool (Allison 2004). Contrary to responses found in Victoria, in the Catalonian streams large floods occurred just after the fire, which also affected the control streams (Vila-Escalé 2009).

Finally, in Idaho, fire slightly reduced the macroinvertebrate taxa number and the change in relative composition was fairly small, so, in general, the community was only moderately affected by the fire. In Idaho streams, the canopy opening was detected in the burned streams but the subsequent increase in radiation and hence chlorophyll-*a* was not found. Similar responses has been reported among these lines (Gresswell 1999). In the Idaho streams there were no differences, in either macroinvertebrates abundances or in biomass, indicating that there was not a big change in basal resources, or at least at the time of sampling. Furthermore, Idaho streams showed also the most similarity in their taxa distribution compared to the ones in the other biomes. This could mean that peak spring runoff covered fire effects. In this sense, the most significant differences measured with the Sørensen index were found in Idaho, which means that all the macroinvertebrate assemblages were more similar among them, and ultimately indicates a lower beta diversity. A study by Robinson *et al*. (2000) in pristine streams in central Idaho showed that variance during five years in macroinvertebrate abundance was low, indicating the importance of repeated snow peak related disturbances even in burned catchments.

In summary, although fire effects are present in all these systems, their importance varied accordingly to the intensity of other conditions unrelated to fire.

Post-fire erosion and changes in the instream habitat

After a wildfire the major changes in the aquatic habitat closely depend on the intensity and amount of the post-fire runoff and the type and areal extent of catchment vegetation burned, as these ultimately trigger the indirect effects of fire (especially through erosion) on the aquatic system (Minshall 2003). The magnitude of post-fire flows will largely determine the condition of the biota, the level of consumable resources (e.g. living space and food) and the condition of the habitat (Lake 2000). So after explaining specifically the direct responses of the macroinvertebrates it is necessary to consider how fire interacts with the local physical processes, for example the post-fire erosion and recovery in burned catchments. Although we did not measure directly the responses in the catchment we could make some assumptions from the type of climate and hydrology for each biome and support it with the literature. The formulated prediction is then that climate, via its effects on hydrology and riparian vegetation, will cause differences between the streams located in the three biomes in terms of: a) recovery of the basin after the disturbance; b) changes in the inputs dynamics and storage of allochthonous organic matter; and c) the seasonal patterns of hydrology.

According to Robinson *et al.* (2000) the pristine streams in central Idaho showed that the variation in terms of habitat (measured as coefficient of variation) is relatively small. However, after a fire the situation changes and produces greater annual variation in habitat conditions and in macroinvertebrate community (Arkle *et al.* 2010). Furthermore, years with high peak flows associated with a big snow accumulation or localized rainstorms can reset the recovery trajectories in the macroinvertebrate communities (Vieira *et al.* 2004). This variation is expected to decline with the recovery of the coniferous forests and riparian canopy. Above all, after a wildfire the morphology of the stream changes, but the major physical alterations generally do not occur immediately. Althoug post-fire precipitation does occur, it is the magnitude of high-intensity rainstorms or the rate snow-pack runoff that determine the major runoff events. This happened in Cache stream in Yellowstone National Park, where heavy major channel changes took place three years after the 1988 wildfire (Minshall *et al.* 2004). In consequence, fires, snow and storms act together as a set of stochastic temporal drivers that alter the susceptibility and trigger sediment fluxes over a landscape (Miller *et al.* 2003), and it seems that in Idaho this often does not occur immediately after wildfires.

In contrast to these relatively predictable conditions in Idaho, the streams in Mediterranean regions are characterized by high interannual variability in the intensity and frequency of floods, as well as by periods of intermittent flow (Gasith & Resh 1999). After the dry summer, autumn is generally characterised by heavy rainfalls which could change the instream habitat. Following wildfire, this is compounded by a bare catchment having severily reduced water retention and infiltration, resulting in extremely enhanced runoff and sediment yield into the stream (Mayor *et al.* 2007). Although not all the Mediterranean vegetation respond positively after a fire (Pausas 2004; Rodrigo *et al.* 2004) and the post-fire conditions (mainly precipitation) can drive the pace on the recovery of vegetation, these terrestrial ecosystems are commonly considered resilient to fire (Pausas *et al.* 2008). This means that even though the erosion will be higher in burned catchments (Mayor *et al.* 2007), the biggest changes in the instream habitat will occur just after the first post-fire rains. This was corroborated by the intensive sampling done by Vila-Escalé (2009) in Gallifa (burned stream in Catalonia) were the most dramatic impact was associated with the post-fire flooding, sediment transport and deposition 2-8 weeks after the fire.

The intermittency of the streams also characterizes the hydrology in Victoria and summer storms are also frequent so we had expected a similar response as in Catalonian streams. The post-fire recovery of eucalypt vegetation in southeast Australia tends to more rapid than in native coniferous of Mediterranean forests (Shakesby *et al.* 2007). Much of the eucalypt forest vegetation tends to lead to a rapid build-up of leaf cover after fire through regrowth from epicormic and lignotuber shoots (e.g. Morrison & Renwick 2000 in (Shakesby *et al.* 2007). This provides not only a direct cover of the stream but a quicker supply of allochtonous resources. We expected big changes in the instream habitat however, as mentioned before, the consequences of this ‘millennium’ drought created low connectivity and maintenance of the ash in the streambed which can explain the main direct fire effects in Victoria compared to the other two biomes studied. So, in general, we did not see a drastic change in the habitat because of the rapid regeneration of the catchment and riparian vegetation.

Resilience to fire?

It is broadly appreciated that variation in diversity can be both a cause and a consequence of variation in community productivity or resource density, or that both directions may act simultaneously (Hughes *et al.* 2007). We found that disturbance severity increased the species loss; but also the other direction, thus an effect of diversity on the response after a disturbance. In this sense, the burned Victorian streams showed the lowest diversity although we expected a higher resilience. It seems then that the combination of drought and fire acted together reducing the capacity of self-resilience. This corroborates the observation that the resilience of a community strongly depends on which species are initially present and the degree of disturbance (Allison 2004).

Fires can cause dramatic changes in the structure and function of terrestrial (Lavorel *et al.* 2007) and aquatic ecosystems (Gresswell 1999). Additionally, fire is enhanced by many factors, including drought, which seems to be a very severe disturbance and less predictable (Boulton & Lake 2008). In general, it is always difficult to separate them, and it seems that in a climate change context, they will come together more often. The macroinvertebrate communities have been cataloged as highly resilient but, with more prolongued and severe disturbances, this resiliency may be overwhelmed. Furthermore, it is important to continue studying the effects of large scale disturbances like wildfire for long periods of time (Minshall *et al.* 1997; Turner *et al.* 2003), in order to establish the trajectories, end points, and mechanisms of recovery by aquatic ecosystems and to determine the effects of global climate change on them.

General Discussion

The main purpose of this thesis was to enlarge the geographical knowledge on the responses of macroinvertebrate communities after wildfires, with special emphasis on Mediterranean streams. Based on the review done by Gresswell (1999), a summary of mainly published results of fire effects on macroinvertebrates, including this thesis, is presented in Table 3. In general, the indirect effects of wildfires on macroinvertebrate reduce their density and in some cases taxa richness. However, response intensity depends on local factors like severity of the wildfire, post fire precipitation, hydrology, geology, and time. Thus, fire is a stochastic disturbance, but depending on the conditions before, during and after the wildfire the response could be enhanced or not relevant. As of the results of this thesis, the responses varied in severity starting in Victoria, Idaho, and finally Catalonia (Chapter 4).

The 2003 wildfire in Sant Llorenç Natural Park (Catalonia) represented an opportunity to study fire effects in the whole area because it initiated a set of changes in terrestrial and aquatic ecosystems within a Mediterranean context. The main results are summarized chronologically in the periods studied: short- and mid-term.

The first short-term results indicated a generalized negative effect on all the sectors studied; therefore to speed the regeneration of the affected area, a series of multidisciplinary projects was started (Guinart 2007). Similar to other areas (Shakesby & Doerr 2006), soil hydrophobicity was enhanced and a greater erosion combined with heavy post-fire precipitations transported high amounts of ash and aromatic compounds into the streams (Vila-Escalé *et al.* 2007). Effects of fire on flora were immediately deleterious, and terrestrial communities got burned while the aquatic communities were completely dragged after the first floodings. This result corroborated the idea that floods in aquatic systems and fires in terrestrial systems have been identified as an analogous major reset mechanism (Wagener *et al.* 1998). This means that, on one hand, floods in streams rearrange habitats, transport stored carbon and nutrients, and displace or kill many resident organisms; and on the other, fire is the major analogous reset mechanism that affects terrestrial systems and soils, removing superficial organic matter.

Regarding fauna, changes in habitat conditions, depletion of resources and possibly toxic conditions just after the fire negatively affected the aquatic, semi-aquatic, and terrestrial organisms (Guinart 2007; Engstrom 2010). In the streams of Sant Llorenç, two months after the fire, the number of macroinvertebrate taxa was lower in the burned streams compared to the control ones, but for most streams the differences were not significant (Chapter 2). Composition changed severely, and the most affected macroinvertebrates corresponded to the orders mollusca and odonata, taxa that has been characterized as slow resilient after drought (Acuña *et al.* 2007) or flooding in intermittent streams (Vila-Escalé 2009).

As for midterm results, after one year, the macroinvertebrate taxa number was the same between control and previous data, but the composition was different and the abundance was three times in burned streams (Chapter 2). Dominance of Chironomidae, Baetidae, and Simuliidae was generalized in all streams. Other fauna like salamanders, frogs, and toads were detected but far from the pre-fire diversity and abundance. Similarly, the wintering birds were reduced in 76% while the nesting birds in 52% (Herrando & Baltà 2005). One of the most severe affected were bats because from the previous 17 species detected in the Vall d'Horta stream, one year after fire, in 2004, only one was censed (Serra-Cobo 2005). Similarly, fishes also were badly affected. The two authocthonous fishes found before the fire, two years later, *Barbus meridionalis* was found in 42% of the potential distribution and *Squalis cephalus* was found in four stations from thirteen sites in Ripoll River, and has been no longer recolonized Vall d'Horta stream (Sostoa *et al.* 2006). Besides wildfire effects, it seems that recovery is difficult by the presence of barriers downstream and the presence of allochthonous species (Guinart 2007).

In general, it seems then that one year after the fire some taxa showed a rapid response, which confirms the high resilience of Mediterranean ecosystems. However, regeneration is not always the rule (Rodrigo *et al.* 2004; Pausas *et al.* 2008). Many key factors can pace the response, although one of them is post-fire precipitation and 2004 was a humid year. Furthermore, the fire did not affect all the area homogeneously, and patches of unburned vegetation are crucial for the regeneration of burned areas (Ordóñez *et al.* 2005). For example, aerial images detected some unburned coniferous islands in Sant Llorenç (Lobo 2005), and their regeneration was common in the neighbourhood of these areas. Similarly, riparian areas were also patchily burned because of the higher moisture that characterizes these areas, which in turns generates severely burned riparian areas and other more intact areas, both in the same burned catchment. Effectively, three years after fire, closed vs. open riparian canopy reaches in a burned Mediterranean stream resulted in highly significant differences in the organic cover, and the macroinvertebrate composition and turnover responded to differences in cover, but also to hydrology (Chapter 1). While the aquatic vegetation cover was higher in the open canopy, the leaf litter was higher in the closed one. Similar to studies in the West of the US (Minshall *et al.* 2004), macrophytes and moss cover were related to the closed riparian canopy while the dominance of green algae was found in the open canopy. However, development of filamentous algal mats (e.g. *Cladophora*) were observed in both reaches, reflecting the enhanced entrance of nutrients and light that has been described in burned streams (Minshall *et al.* 2004). Temporality factor was also very important in the organic cover, and it has been previously described as an important driver in the organic matter dynamics in Mediterranean streams (Acuña *et al.* 2004). Although we did not measure productivity, the algae cover and community reflected the relationship between disturbance and productivity (Lake 2000). In both canopies, disturbances (floods and seasonal drought) represented a key factor, not only in the organic cover (Hillebrand 2008) but also in the structure and function of macroinvertebrate communities living in streams (Boulton & Lake 1992a; Acuña *et al.* 2005), with a reciprocal response between both levels (Wootton 1998).

Four years after the fire in Sant Llorenç, a study in the fauna of terrestrial ecosystem by Santos *et al.* (2009) found 257 species belonging to diverse groups: molluscs, ants, heteropters, vegetation beetles, ortopters, reptiles, birds, carnivores, and bats. It was observed that 18% of the species were exclusively found in control sites compared to a 17% in the burned sites. While 22% of the taxa were considered generalists and were found in both sites and varied habitats. It seemed that the taxa found in burned sites were mainly fliers and herbivore feeding-type. On the other hand, taxa found in the control sites were the ones normally found in Mediterranean climate ecosystems.

The response of the composition and abundance of the macroinvertebrate aquatic community in the burned Mediterranean streams after the same elapsed time responded more to the temporal variation in hydrology (annual and spring precipitation) than to fire (Chapter 2), which is a response that has been described previously in other intermittent streams (Acuña *et al.* 2005; Bêche & Resh 2007). In general, during 2003, 2005, and 2006, the taxonomic richness might have declined, so the different large disturbances determined the prevalence of some taxa leading to niche selection, filtering out species that lacked suitable traits (Chase 2007) for the conditions of those years.

The dry-year constraint results from the Mediterranean streams were also consistent with the results from the bushfire effects on macroinvertebrates in Victorian streams, because 9 months after the initial disturbance, the 10-year-of-below-average rainfall 'millennium' drought was still occurring (Chapter 3). Even though a rapid response was expected, the maintenance of ash on the streambed and the low flow generated a negative impact on the structure of macroinvertebrate communities, especially in one site. Across all three studied biomes, the burned Victorian streams presented the lowest diversity (Chapter 4). Australian aquatic fauna and flora are characterized by the high prevalence of both resistance and resilience traits, which reflect the evolutionary significance of drought as a selective pressure on aquatic biota and ecosystems (Boulton 2003; Bond *et al.* 2008). It seems then that the combination of drought and fire acted together to reduce the capacity of self-resilience, which means that the resilience of the community strongly depends on what species are initially present and the degree of disturbance (Hughes *et al.* 2007). The main results of the comparison of wildfire effects on macroinvertebrate communities in streams in Idaho, Victoria and Catalonia are summarized in Figure 3.

Long-term studies on fire are few, and one that is still under exploration is the area affected by the 1988 Yellowstone National Park Fires (USA). So far, the main conclusions indicate that fires are not just a devastating disturbance, although large and infrequent disturbances like wildfires can produce durable changes in physical and biological structure (Foster *et al.* 1998). Stand-replacing fires are an important source of landscape heterogeneity, which create a spatial variation (product of different burned severities and unburned patches) that diversifies the ecosystem function (Turner *et al.* 2003). Similarly, periodic large-scale disturbances of aquatic ecosystems are inevitable and often beneficial over long periods (Bisson 2003). When a wildfire affects an area, the surrounding streams will also respond to physical and ecological processes occurring over the terrestrial landscape (Hynes 1975). This dynamic view accepts patterns of disturbance and recovery across a landscape as a process needed for an interconnected mosaic of diverse, changing habitats and communities (Bisson 2003).

Comparisons of the ecological processes between terrestrial and aquatic ecosystems suggest similarities but also differences as showed in Sant Llorenç. The action of water seems to be the most important descriptor (Grimm *et al.* 2003), which in turn leads the differences in the temporal scale and temporal pace of ecosystem processes. The consequences of wildfire occur at faster rates in the aquatic ecosystems, because of differences in consumer strategies, growth rates, sizes, and stoichiometry of organisms in aquatic and terrestrial ecosystems (Nowlin *et al.* 2008).

In this sense, resource pulses like hurricanes and insect outbreaks, indicate that, depending of the inputs, they are transmitted more rapidly to aquatic systems (Nowlin *et al.* 2008). Although wildfire is not a resource pulse *per se*, the indirect effects could be considered as resource pulses. For example, post-fire precipitations could represent an infrequent entrance of accumulated nutrients (Yang *et al.* 2008) that result in a “pulse” flux of higher emergence of aquatic insects (Malison & Baxter 2010b). This large input is not strange as interfaces between terrestrial-aquatic are classified as hot biogeochemical spots (McClain *et al.* 2003). In Sant Llorenç, even though the emergence was not measured, one year after the fire the macroinvertebrate abundance was the highest. Also, some other fauna aquatic or species that live nearby streams, like bats, are gradually recovering. Other studies have shown the importance of all these connexions among different levels (Baxter *et al.* 2005; Arnan 2006). As mentioned earlier, after the 2003 fire, several actions were performed in order to help with rapid regeneration.

Since the 2003 wildfire, two meetings from the Sant Llorenç Natural Park have been held. As expected, half of the conferences in 2005 were related to fire and in 2009, although less represented, there was still some research devoted to the burned area. The main results in terrestrial ecosystems have concluded that there were no significant differences in vegetation regeneration between the different applications (e.g. cutting of burned feet, forest pruning, reuse of the woody material, removal of invasive species) (Pañella 2009). On the contrary, the different railroads that were opened after the fire to get the machinery through that was needed for cutting trees, pruning the forest, and removing dead branches generated more soil erosion, and this is actually what could severely affect landscape regeneration and the aquatic ecosystems. In this sense, the recovery of aquatic ecosystems the water availability is crucial and, as described in Chapter 2, the midterm effects of fire are highly dependant on this, which was ultimately what generated differences among years.

Climate change is expected to alter the geographic distribution of wildfire, a complex abiotic process that responds to a variety of spatial and environmental gradients. These new patterns of burning are the result of complex interactions between climate, vegetation, and people. How future climate change may alter global wildfire activity, however, is still largely unknown (Krawchuk *et al.* 2009). Fires can cause dramatic changes in the structure and functioning of terrestrial and aquatic ecosystems (Gresswell 1999). Additionally, fire is enhanced by many factors, including drought, which has proved to be a very severe disturbance in streams and less predictable (Boulton & Lake 2008). In general, it is always difficult to separate them, and it seems that in a climate change context, they will come together more recurrently. Macroinvertebrate communities have been catalogued as highly resilient, but with more prolonged and severe disturbances this cannot be taken for granted. Furthermore, it is important to continue studying the effects of large scale disturbances like wildfire for long periods of time (Minshall *et al.* 1997; Turner *et al.* 2003), in order to establish trends, end points, and mechanisms of recovery by aquatic ecosystems and to determine the effects of global climate change on them.

Nowadays, there is much concern about the linkages between climate, humans, vegetation, and the critical fire factor, as all of them are sensitive to global change (Folke *et al.* 2004). Especially in the Northern (European) rim of the Mediterranean, industrialisation and rural exodus have led to the abandonment of many fields, which has increased the cover and continuity of early succession species (many of which are very flammable, like pine woodlands) and has changed the landscape pattern and the fire regime (Pausas *et al.* 2008). Thus, although the Mediterranean Basin forests may be strongly resilient to fire (i.e., shrublands and oak forest), some parts of the current landscapes, which are the result of a long human history with questionable land policies, are relatively sensitive to fires, and in such conditions, disasters or ecosystem degradation (e.g., soil losses and strong vegetation changes) are possible. Likewise, the aquatic communities in this climate generally show a very high resilience (Gasith & Resh 1999). However, hydroclimatic models predict that climate change will increase the frequency and severity of floods and droughts across Europe. In addition, the increasing population in the already densely populated Mediterranean Basin and hence the scarcity of water must also be considered (Prat & Manzano 2009). As in many other ecosystems, the new perspective recognises that resilience can be and has been eroded and that the self-repairing capacity of ecosystems should no longer be taken for granted (Gunderson 2000; Folke *et al.* 2004; Bond *et al.* 2008).

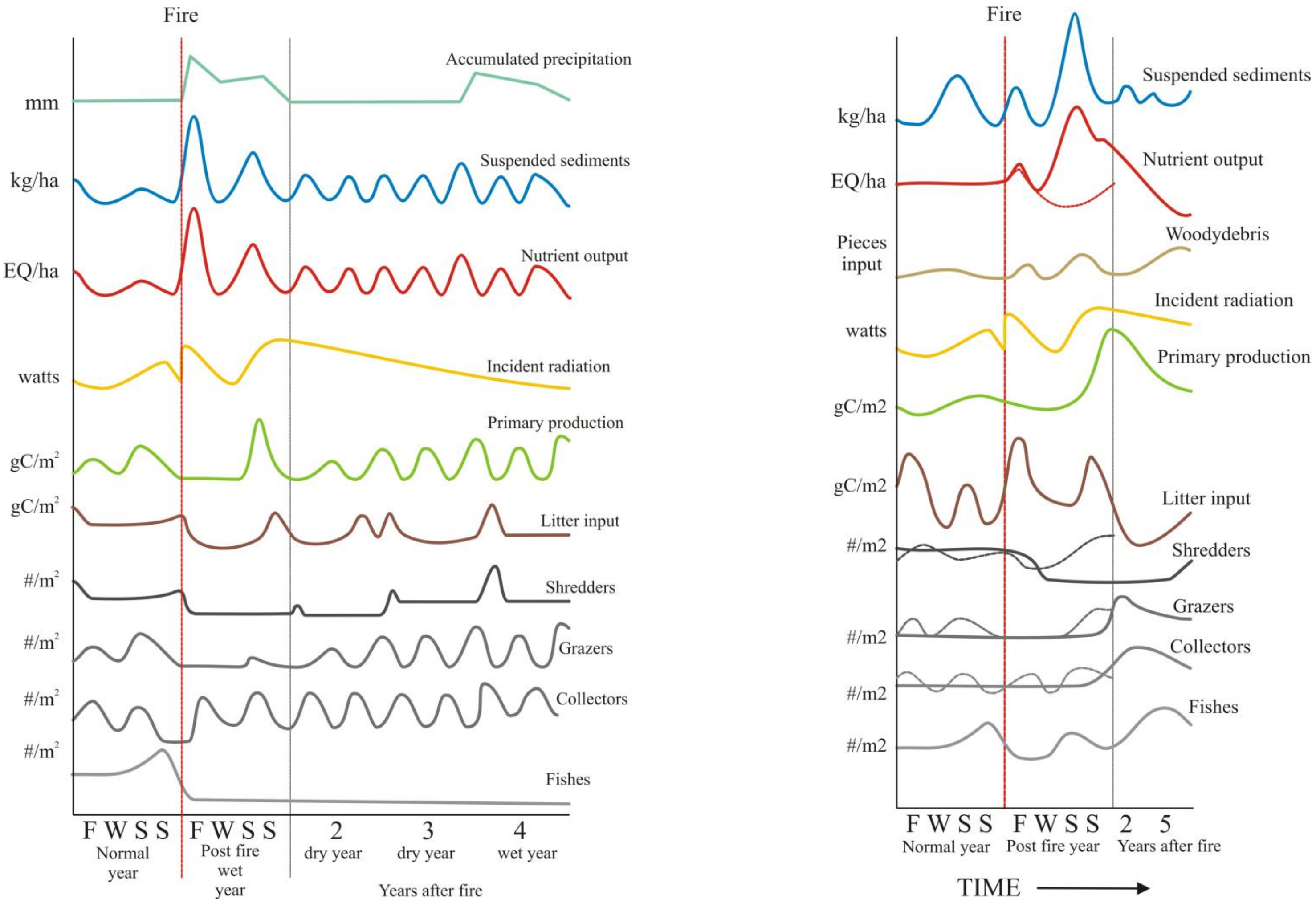


Figure 3. Hypothetical changes in physical, chemical, and biological characteristics 5 years following wildfire in Mediterranean streams (left) compared to streams from Western US (right, solid lines) and SE Australia (right, dashed lines). The letters F, W, S, and S indicate fall, winter, spring, and summer, respectively (Adapted from Minshall *et al.* 1989 and Gresswell 1999).

Table 3. Summary of the references of studies done of fire effects in macroinvertebrate communities of lotic ecosystems. Main results of this thesis are also included (Adapted from Gresswell 1999).

Source	Fire size (type)	Spatial scale	Time scale	Location	Comments
(Lotspeich *et al.* 1970)	101000 ha (wf)	4 streams (9 sites)	1 year	Dennison River, AK	No statistically significant change detected in benthic aquatic fauna attributed to the effects of fire
(Stefan 1977)	1100 ha (wf)	1 stream (order 3; 22 sites)	1 year	White Cap Wilderness, ID	Numbers of Plecoptera varied on artificial substrates among above-burn, burn, and below-burn sites; above-burn site adjacent to the burn had higher amounts of chlorophyll on periphyton samplers
(Albin 1979)	200 ha (wf)	2 streams (order 1-2)	3 months	Yellowstone NP	Benthic insects abundant during and after fire, and no dead insects observed
(Albin 1979)	481-506 ha (3 wf)	2 streams (2120-3930 ha) (7 sites)	35 years	Yellowstone NP	Greater abundance and diversity in burned watershed 35 years following fire
(La Point *et al.* 1983)	26000 ha (wf)	11 streams (290-29880 ha) (order 1-5)	3 years	Middle Fork Salmon River, ID	Episodic storm events influenced composition of resident macroinvertebrate fauna; taxonomic richness, evenness, and diversity declined in burned watersheds; dominant functional feeding group was different in the burned watersheds
(Roby 1989)	800 ha (wf)	2 streams (825 ha) (6 sites)	9 years	Plumas Nacional Forest, CA	Increase in density and decrease in diversity 1 year postfire; differences with unburned control stream remained after 9 years; four other watersheds showed similar patterns up to 23 years following fire

Source	Fire size (type)	Spatial scale	Time scale	Location	Comments
(Minshall *et al.* 1990)	26000 ha (wf)	1 stream (10900 ha) (order 4-5; 2 sites)	10 years	Middle Fork Salmon River, ID	Increase in abundance 1 year postfire
(Richards & Minshall 1992)	26000 ha (wf)	5 streams (order 1-5)	1-5 years	Middle Fork Salmon River, ID	Species richness was greater in reference streams than disturbed streams. Disturbed streams were more similar one to another and showed an increasing trend in richness over time.
(Jones *et al.* 1991)	322000 ha (wf)	6 streams (order 4-6)	3 years	Yellowstone NP	Macroinvertebrate abundance, species richness, and diversity increased except in the Gibbon and Madison rivers where abundance, biomass, and richness declined somewhat; shift toward groups that utilize autochthonous food sources
(Lawrence & Minshall 1994)	>200000 ha (wf)	22 streams (order 1-4; 22 sites)	2 years	Yellowstone NP	Fire severity and distance of burn from channel were correlated with macroinvertebrate species diversity; streams with greatest disturbance had lowered diversity, but after 2 years these streams had higher macroinvertebrate diversity
(Roby & Azuma 1995)	(wf)	2 streams (one burned and cone lose unburned reaches)	3 weeks – 11 years	California	Three weeks after fire benthic invertebrate density and taxa richness was lower compared to control stream. Three years after fire the density was significantly higher in burned reach. Shannon diversity of the burned reach was significantly lower than the unburned reach throughout the 11 year period-study. However, after three years the differences were not significant.

Source	Fire size (type)	Spatial scale	Time scale	Location	Comments
(Mihuc *et al.* 1996)	292000 ha (wf)	5 streams (140–18,000 ha)	4 years	Yellowstone NP	Physical changes in stream habitat and alteration of resource availability were the primary factors that affected the postfire response of individual taxa
(Rinne 1996)	(wf)	3 streams (order 1)	1 month – 3 years	Tonto Nacional Forest, Arizona	Aquatic macroinvertebrate densities in affected streams declined near to zero within a month after the fire, but recovered to 25%-30% of prefire diversity in two of the streams 1 year later, and continued to fluctuate postfire.
(Minshall *et al.* 1997)	292000 ha (wf)	20 streams (order 1–4; 10 sites)	5 years	Yellowstone NP	Species appeared to respond individualistically; species with relatively short generation times and that disperse through drift appeared to be favoured following fire
(Minshall *et al.* 2001b)	26000 ha (wf)	5 streams (Order 1-5)	10 years	Middle Fork of the Salmon Stream	Taxa richness and total abundance tended to be lower in burned than in reference streams, but tended to converge near the end of the study. Total biomass and that of the scraper, filterer, and miner functional groups usually were greater in the burned streams.
(Vieira *et al.* 2004)	6500 ha (wf)	1 stream (order 1)	BACI (2 years before and 6 years after)	Capulin NM	Taxon richness and community composition were less resilient to post fire hydrologic disturbances. Composition in the burned streams still differed from pre-fire and reference stream compositions after 6 years post fire. A unique assemblage, dominated by taxa with strong larval and adult dispersal was established after the flash floods abated.

Source	Fire size (type)	Spatial scale	Time scale	Location	Comments
(Bêche *et al.* 2005)	26 ha (pf)	1 stream (order 1)	BACI (7 years before and 1 year after)	Dark Canyon	Macroinvertebrate community composition but not density, richness, or diversity was affected 10–19 d post-fire; composition recovered within 1 year.
(Hall & Lombardozzi 2008)	56000 ha (wf)	8 streams (order 2-3)	1-2 years	San Isabel National Forest, CO	Streams in the burned area contained fewer benthic macroinvertebrate taxa compared to unburned streams during the year after the fire, and contained lower invertebrate densities and biomass compared to reference streams 2 years post-fire.
(Mellon *et al.* 2008)	2000 ha (wf)	2 streams	2 years	Colville National Forest, WA	There were significantly higher macroinvertebrate densities in burned than control sites. Macroinvertebrate biomass was greater at burned sites only from emergence samples; in benthic and drift samples there was no significant difference between burned and control sites. Diversity was lower in the burned catchments dominated by chironomid midges.
(Vila-Escalé 2009)	4543 ha (wf)	1 stream (order 1)	BACI (5 years before and 3 months – 2 years after)	Catalonia, Spain	Burned stream response to fire was categorized in three periods. During the first 9 months after fire a reduced taxa number and abundance was found, but taxa was catalogued as highly resilient and persistent. Before the second year, the taxa number was similar to control stream and pre-fire samples, characterized as temporarily favoured taxa. After the second year the less resilient taxa arrived but the community was not the same as before.

Source	Fire size (type)	Spatial scale	Time scale	Location	Comments
(Arkle *et al.* 2010)	60610 ha (wf)	6 streams (order 2-3)	1-4 years	Big creek and South Fork Salmon River	Streams in more severely burned catchments exhibited increasingly dynamic macroinvertebrate communities and did not show increased similarity to reference streams over time.
(Malison & Baxter 2010a)	60610 ha (wf)	9 streams (order 2-3)	5-10 years	Middle Fork of the Salmon River, ID	Sites that experienced high severity wildfire had the greatest biomass of r-strategist and generalists primary consumers including Chironomidae, Baetidae, and Simuliidae. Moreover, a significantly greater flux of adult aquatic insect emerged at sites that experienced high severity fire versus low severity burned and unburned sites.
Verkaik (2010)	4543 ha (wf)	1 burned stream, 2 reaches with differences in local riparian affectation (order 2)	3 years, monthly sampling	Sant Llorenç Natural Park, Catalonia	The heterogeinity of fire burning in the riparian area was still clear in a burned Mediterranean stream. Closed vs. open canopies showed a clear difference in aquatic vegetation and leaf litter cover. During the sampling year the macroinvertebrate communities varied with the changes in aquatic vegetation cover, demonstrating the reliance of consumers in primary production. However, temporality was a very important factor that changed the resources and the macroinvertebrate community turnover.
Verkaik (2010)	4543 ha (wf)	2 burned streams, 2 control streams (order 1-2)	2 months – 5 years	Sant Llorenç Natural Park, Catalonia	Two months after the fire the taxa number and diversity were lower in burned streams compared to control streams; nor was it the subsequent years. On year after the fire the abundance in the burned streams was 3 times higher compared to control streams. The macroinvertebrate community changed and was highly related to the spring and annual precipitation, and the biological traits fluctuating from humid to dry characteristics.

Source	Fire size (type)	Spatial scale	Time scale	Location	Comments
Verkaik (2010)	1200000 ha (wf)	3 burned, 3 control streams	9 months	Victoria, SE Australia	9 months after the bushfire and during the 'millennium drought' there was a significant effect of fire on the macroinvertebrate community. The burned creeks presented shifts in the abundance of common taxa at the burned sites (Orthocladiinae, Naididae, Simuliidae, Chironominae, *Dinotoperla* sp. and *Taschorema* complex). A higher percentage of shredders was found at the burned sites, while scrapers were codominant at control creeks.
Verkaik (2010)	Catalonia- 4543 ha, Victoria- 1200000 ha, Idaho- 95000 ha (wf)	9 burned, 9 control streams (order 1-3)	9 – 11 months	Victoria, Idaho, Catalonia	Comparison of macroinvertebrate communities in the three biomes showed important differences that were related to climate and hydrology. Study streams in Victoria (SE Australia) experienced a drought of >10yr and low flows that encompassed the time the study. Streams in Idaho (NW USA) experienced high peak runoff the spring after wildfire. Those in Catalonia (NE Spain) experienced strong floods immediately after the fire. Significant negative effects of wildfire on macroinvertebrate taxa were observed except in Catalonia. Across all biomes, invertebrate assemblages of burned streams had greater dominance of *r*-strategist insects (e.g., Chironomidae, Simulidae, Baetidae) than in control streams. In Catalonia and Idaho, the combined effect of wildfire and floods also appeared to increase these taxa, but these were also apparently affected by flood timing. These comparisons suggest that the occurrence and timing of flood and drought may mediate fire effects on macroinvertebrates.

Conclusions

1. Three years after the wildfire in Sant Llorenç there were still differences in two close riparian areas that burned differently. The absence of riparian vegetation promoted a significant difference in aquatic vegetation and leaf litter covers, which in turn also influenced the macroinvertebrate communities. In the open canopy, the higher macroinvertebrate abundance reflected the increase in algal cover, thus probably the primary productivity, and their reliance in this resource. However, the temporality of Mediterranean streams may also interact with fire affecting the resources and habitat and thus the aquatic macroinvertebrates richness and abundance. Macroinvertebrate turnover during the sampled period mainly relied on the algal cover and the temporality, reflecting the relationship between disturbance and productivity. The open canopy dried-up during the summer probably as a result of an enhanced evapotranspiration with a higher light income in the reach. Once the flow was restored, the recolonization was fast and followed similar trends compared to the closed canopy.
2. The macroinvertebrate community of streams in the Sant Llorenç Natural Park showed a high resilience to the effects of a fire disturbance, initiating a fast recovery just two months after the fire. Although one year after abundance was the highest, there were no differences in taxa richness after few months, nor in the subsequent years. The macroinvertebrate communities' structure and function on the subsequent years after the fire was highly dependent on the hydrology of each year, which can be very variable. This fact was clear when the macroinvertebrate community was restablished in 2007 after the severe seasonal droughts of 2005-2006, showing their high resilience (characteristic of Mediterranean streams).

3. The effects of fire on the streams of SE Australia showed a significant negative impact on taxa number and a higher abundance compared to the control streams. Our results show that the 'millennium' drought that affected part of SE Australia modulated the bushfire effects on macroinvertebrate communities in Victorian streams.
4. Compared to other biomes (SE Australia and NW USA), in the Mediterranean streams the abundance of *r*-strategy taxa was highest, which reflects the recurrent disturbances that affect this type of streams and the high resilience of aquatic macroinvertebrate communities.

   Although some generalizations about the wildfire effects can be extended from the studies done in the West of the US, it seems that they will depend on hydrology and timing of other disturbances like drought or flooodings can enhance or mitigate fire effects on macroinvertebrate communities. One of the main differences in post-fire effects in the Mediterranean catchments is that big floodings generally occur few weeks after a wildfire, while in other biomes effects could be delayed by drought (SE Australia) or by the hydrologic characteristics from the stream itself (NW USA).
5. There is a high concern about the future effects of fires on several ecosystems of the world as burning of large areas will become more frequent. Furthermore, future climate models predict prolonged droughts, a disturbance that enhances fire disturbance. How both disturbances will interact is still not clear. For now, it seems that in the Mediterranean system given the repeated frequency of disturbances (floods, and seasonal droughts), the recovery of aquatic macroinvertebrate communities is relatively fast, but uncertainties about how this will be in the future are great.

Introducción general

El fuego como perturbador natural

Los incendios forestales representan un componente clave en la dinámica tanto de los ecosistemas terrestres como de la atmósfera (Flannigan *et al.* 2009). Esto no es una historia reciente. Durante la mayor parte de la historia de la Tierra, los incendios han sido parte integral de la evolución de la flora y la fauna, que han respondido a través de procesos de retroalimentación a los cambios en las variaciones climáticas y atmosféricas (Pausas & Keeley 2009). Durante las últimas décadas se ha quemado un promedio anual de 383 millones de hectáreas (Schultz *et al.* 2008), por lo que el fuego es el agente perturbador que más influye en diferentes zonas de la biosfera terrestre y que afecta a un área mayor (Lavorel *et al.* 2007). Esto se hace evidente a nivel mundial al observar el mapa de imágenes térmicas infrarrojas tomadas por satélites de la Agencia Espacial Europea (ESA) desde julio de 1996 hasta agosto de 2010 (Figura 1). Los incendios forestales son un factor clave para entender muchos de los biomas del mundo, así como la estructura, función y distribución de los ecosistemas propensos a incendios (Bond & Keeley 2005). De la misma manera, el fuego también afecta los procesos fundamentales de los ecosistemas, como el ciclo de nutrientes (Turner *et al.* 2007), la sucesión de la vegetación (Turner *et al.* 2007; Brown & Smith 2010) y otras perturbaciones tales como los ataques de plagas (McCullough *et al.* 1998), la hidrología y la erosión. En resumen, el fuego desempeña un papel importante en el ciclo global del carbono y en la regulación de los ecosistemas terrestres y su biodiversidad (DeBano *et al.* 1998; Shakesby *et al.* 2007).

Al mismo tiempo, el fuego ha sido también considerado como una gran amenaza para los ecosistemas y las sociedades humanas (Dube 2009). Esto se debe a que la combustión de biomasa tiene un papel importante en los cambios globales ambientales, que influyen en la composición atmosférica, la climatología, la salud humana y las actividades económicas (Schultz *et al.* 2008). Los costes anuales en prevención y extinción de incendios en EE.UU. han llegado a casi 3.000 millones de dólares anuales en los últimos años (Marlon 2009), con aumentos en un 11% promedio annual (Schoennagel *et al.* 2009). Los costes de los daños por los fuegos en otras áreas pueden ser también muy elevados. Por ejemplo, los recientes incendios ocurridos en agosto de 2010 en Rusia se han calculado en 15.000 millones dólares (Wikipedia 2010, http://en.wikipedia.org/wiki/2010_Russian_wildifres, consultado en septiembre de 2010). Por ello, el fuego y sus efectos tienen un interés global e interdisciplinario, debido a sus influencias, interacciones y retroalimentaciones con los sistemas terrestres y la atmósfera (Krawchuk *et al.* 2009). Si bien el proceso de combustión es teóricamente sencillo, los regímenes modernos de incendios son difíciles de clasificar ya que están sujetos a la acción humana, que ha cambiado la flamabilidad de los paisajes así como la recurrencia de incendios asociada a las variaciones en la tasa de extinción de fuegos (Lavorel *et al.* 2007; Chuvieco *et al.* 2008; Krawchuk *et al.* 2009).

Años catalogados como devastadores debido a la acción del fuego son cada vez más comunes, y nuevamente un buen ejemplo, es que ocurrió en Rusia este año (2010) con más de 300.000 hectáreas de bosque quemados (Nature news, doi:10.1038/news.2010.404, consultado en Septiembre de 2010). Los años devastadores son también más recurrentes. Existen varios ejemplos: en 1994, se quemaron más de dos millones de hectáreas en diversas áreas, como la cuenca mediterránea, el sur de Australia, Rusia y América del Sur (Terradas 1996). Durante 1997-1998, la WWF caracterizó este período como "el año en que se quemó el mundo" (Rowell & Moore 2000); y en el 2003 ocurrieron grandes incendios en el sureste de Australia, el oeste de Canadá, Europa Mediterránea y el sur de California (Lavorel *et al.* 2007). Los incendios generan irremediablemente una considerable atención pública y política respecto al fuego, contrastando su papel como un fenómeno natural con la dinámica humana, que en consecuencia resulta afectada (Lavorel *et al.* 2007). El ejemplo más reciente, es el aumento del 50% en los precios del trigo en parte como consecuencia de los incendios que se produjeron el pasado verano de 2010 (BBC, http://www.bbc.co.uk/news/business-10851170, consultado en Septiembre de 2010).

Algunos modelos predicen una mayor recurrencia en los incendios actuales (Westerling *et al.* 2006), pero las tendencias futuras de la actividad global de incendios (severidad y recurrencia) son variadas y difíciles de determinar debido a las interacciones complejas y no lineales entre el clima, la vegetación y las actividades de los seres humanos

(Flannigan *et al.* 2009). Así, los incendios forestales no controlados y generalizados que se produjeron en 1997 parecían ser una consecuencia de la sequía extrema derivada de El Niño (Levine 1999). Por otra parte, aunque las previsiones meteorológicas predijeron un año húmedo en 1999, dieciocho meses después tuvieron lugar algunos de los peores incendios forestales en la era moderna (Rowell & Moore 2000). De esta manera, los años secos aumentan el riesgo y la propagación del fuego (Westerling & Swetnam 2003), y como los modelos climáticos predicen un aumento en la frecuencia e intensidad de las sequías extremas también parece que lo harán los incendios (Houghton *et al.* 1996).

El fuego como agente perturbador de las comunidades biológicas

La perturbación se define como cualquier evento que altere un ecosistema, una comunidad o la estructura de una población y que, al mismo tiempo, cambie los recursos, la disponibilidad de sustrato y el ambiente físico (*sensu* Pickett & White 1985 in Resh *et al.* 1988). Los incendios forestales representan un factor de perturbación claro por eliminar la biomasa o alterar y simplificar el hábitat después del incendio (Smith & Lyon 2000).

Como se mencionó anteriormente, el papel del fuego como perturbador se ha estudiado relativamente bien en las comunidades terrestres de los trópicos (Goldammer & Seibert 1990; van der Werf *et al.* 2008), los ecosistemas de tipo mediterráneo (Moreno & Oechel 1994; Pausas 2004; Rodrigo *et al.* 2004), el oeste de EE.UU (Agee 1998; Flannigan *et al.* 2009), Australia (Bradstock *et al.* 2002) y algunos ecosistemas ribereños (Dwire & Kauffman 2003). Sin embargo, hasta las últimas décadas, los estudios sobre los efectos de los incendios forestales en las comunidades que habitan en ecosistemas acuáticos son escasos (Minshall 2003).

El 'corazón' (*sensu* Shakesby & Doerr 2006) de la investigación en efectos de los incendios en los ecosistemas acuáticos se encuentra en el oeste de los Estados Unidos, donde se dio inicio a estos estudios tras los incendios de 1988 que azotaron el Parque Nacional de Yellowstone. Esto proporcionó una oportunidad única para estudiar los efectos del fuego en varios procesos de los ecosistemas en un laboratorio natural (Schoennagel *et al.* 2009). Una revisión notable de fuego como perturbador en los ecosistemas acuáticos (basados esencialmente en estudios en esta zona) se publicó en 1999 por Gresswell. Después, en 2003, la revista *Forest Ecology and Management* dedicó dos volúmenes a los efectos de los incendios forestales en los ecosistemas acuáticos en el oeste de EE.UU. (Rieman *et al.* 2003), generando así un compendio sobre los efectos del fuego en diversos temas: aspectos históricos, la geomorfología y respuestas físico-químicas, la biología de macroinvertebrados, anfibios, reptiles y peces. Los estudios concluyen con preguntas futuras sobre el fuego, tanto en relación a su papel como herramienta en la gestión del territorio como a sus futuros efectos en los ecosistemas en un escenario de cambio climático.

Efectos del fuego sobre los ecosistemas acuáticos: lecciones del oeste de EE.UU

En general, los efectos del fuego en los ecosistemas acuáticos pueden separarse convenientemente en directos e indirectos (Minshall 2003). Los efectos directos, como los aportes atmosféricos o aumento de temperatura, son rápidos y tienen consecuencias generalmente de corta duración en las comunidades biológicas y en los procesos ecológicos (Minshall 2003; Hall & Lombardozzi 2008). Por otra parte, los efectos indirectos son más persistentes, como por ejemplo, una mayor erosión o el aumento del transporte de sedimentos y turbidez asociado a los cambios en la morfología del canal y el hábitat fluvial consecuencia de las inundaciones después del incendio (Bisson 2003; Minshall 2003). A primera vista, los primeros efectos indirectos parecen ser catastróficos (Gresswell 1999). La entrada de cenizas y el aumento de la carga de sedimentos son en general los causantes de la desaparición de la biota, que incluye algas (Robinson *et al.* 1994), macroinvertebrados (Rinne 1996; Minshall 2003; Vieira *et al.* 2004) y peces (Gresswell 1999).

A mediano plazo, la hidrofobicidad del suelo es mayor (Benda 2003; Shakesby & Doerr 2006), y el flujo superficial puede aumentar con el tiempo con una erosión mayor en momentos de caudal alto (Cerda & Doerr 2005). La entrada de sedimentos irá disminuyendo y la entrada de material forestal formará diferentes hábitats acuáticos a través de diferentes procesos fluviales (Benda 2003; Miller *et al.* 2003; Minshall 2003). Se prevé que la aportación de madera irá en aumento (Arkle *et al.* 2010) en la medida que los pies quemados se pudran, se rompan y sean transportados aguas abajo (Benda 2003; Miller *et al.* 2003).

En cuanto a las comunidades biológicas, las respuestas al fuego a mediano plazo suelen ser rápidas: la riqueza taxonómica, la abundancia y la biomasa total volverán a su situación anterior al fuego en pocos meses o durante los primeros años (Roby & Azuma 1995; Minshall *et al.* 2001c). Un cambio en la composición de una comunidad dominada por macroinvertebrados con estrategias adaptadas a la perturbación como

Chironomidae, Simuliidae y Baetidae parece ser una respuesta común (Mihuc *et al.* 1996; Vieira *et al.* 2004; Mellon *et al.* 2008; Malison & Baxter 2010a). Por lo general, el fuego aumenta la producción primaria en comparación con las condiciones previas al incendio, probablemente como consecuencia de la aceleración del crecimiento de algas en los ríos que responden a su vez a la remoción de cobertura ribereña (Behmer & Hawkins 1986), temperaturas más altas y un mayor aporte de nutrientes inorgánicos, como nitrógeno y fósforo (Minshall *et al.* 1997; Spencer 2003). Debido al cambio cualitativo en los recursos alimenticios (por ejemplo, la pérdida del aporte de material alóctono de la ribera y a su vez el incremento de algas), se espera que la composición de los grupos funcionales, interpretado a través del modo de alimentación de los macroinvertebrados, registre este cambio (Minshall *et al.* 1989). Como consecuencia del fuego y los cambios posteriores, se predice que los más afectados sean los trituradores debido a la baja disponibilidad de hojarasca, mientras que un incremento en los raspadores reflejará los cambios derivados del aumento en el perifiton consecuencia de la apertura de la cobertura ribereña y la entrada de nutrientes (Minshall 2003) (Figura 2).

La evaluación correcta del impacto del fuego requiere un enfoque en las características locales, ya que la respuesta de macroinvertebrados a la perturbación producida es a menudo local y está relacionada con la naturaleza estocástica de las perturbaciones y la heterogeneidad de las condiciones ambientales de la región. En este sentido, incluso dentro de un mismo perímetro de acción del fuego, no todas las zonas se queman en igual grado de severidad y ello influenciará en los efectos posteriores (Minshall 2003). Además las diferencias en niveles de severidad son comunes en las zonas ribereñas ya que son áreas con un microclima más húmedo que las áreas aledañas a la cuenca (Dwire & Kauffman 2003). Por ejemplo, Malison y Baxter (2010a) encontraron una producción secundaria significativamente mayor en ríos severamente quemados en comparación con ríos control y con ríos no tan severamente afectados. Así que, en general, la recuperación relativamente rápida de los macroinvertebrados acuáticos se asocia con la recuperación local de la vegetación ribereña (se calculan unos 25-50 años para el desarrollo total del follaje), que generalmente es más rápida en comparación con a la regeneración de la vegetación de la cuenca (unos 100-300 años) (Minshall *et al.* 2001b; Minshall *et al.* 2001c).

Por último, a largo plazo los incendios forestales se consideran como uno de los principales causantes de cambios hidrológicos y geomorfológicos de los ecosistemas asociados con el fuego (Shakesby & Doerr 2006). Asimismo, son áreas donde se ha observado un aumento de la complejidad del canal y de la heterogeneidad del hábitat (Robinson *et al.* 2005). Esto puede repercutir en cambios en el paisaje, en la diversidad de hábitat y en la cantidad y tipos de recursos alimenticios, que finalmente se verá reflejado en la estructura y función de la flora y fauna de los ecosistemas acuáticos (Minshall *et al.* 2004).

Efectos del fuego sobre los ecosistemas acuáticos: lo que se sabe del resto del mundo

Hace veinte años, Minshall *et al* (1989) ya habían señalado el escaso número de estudios realizados sobre los efectos del fuego sobre la biota acuática. Desde entonces, el número de estudios y publicaciones han ido en aumento, que si bien han respondido algunas preguntas han generado otras incertidumbres. Una de las principales dudas hasta hoy en día es cómo generalizar las observaciones de los efectos del fuego a un rango geográfico más amplio que los EE.UU., especialmente en áreas donde el fuego también es un factor recurrente, como por ejemplo, las zonas de clima mediterráneo. Como se ha mencionado anteriormente, los incendios forestales en este bioma han moldeado la evolución de los caracteres biológicos (Blondel & Aronson 1999) y han conformado sus atributos de biodiversidad (Pausas & Verdú 2008). Sin embargo, mientras el fuego en las comunidades terrestres se estudiado profundamente (Trabaud & Prodon 1993; Terradas 1996), los estudios sobre el efecto del fuego en las comunidades acuáticas en este clima son muy escasos (Britton 1991; Bêche *et al.* 2005; Vila-Escalé 2009).

Del mismo modo, en el sudeste de Australia, descrita como una de las regiones más propensas a incendios forestales (Collett 2007; Lyon & O'Connor 2008; Seymour & Collett 2009), los efectos del fuego han sido objeto de amplios estudios en diferentes ecosistemas terrestres de la región (Bradstock *et al.* 2002). Por el contrario, los estudios sobre los efectos de los incendios forestales en los sistemas acuáticos se han centrado principalmente en la química del agua (Townsend & Douglas 2004), la hidrología, la erosión del suelo, el transporte de sedimentos y su deposición (ver lista en (Lane *et al.* 2006; Shakesby *et al.* 2007), y sólo recientemente se han realizado estudios sobre el impacto de los incendios forestales sobre las comunidades acuáticas considerando las comunidades de algas bentónicas y de peces (Cowell *et al.* 2006; Lyon & O'Connor 2008). Estos estudios, junto con otros informes preliminares no publicados sobre macroinvertebrados, se iniciaron después del gran incendio ocurrido en 2003, considerado como el peor desde 1939 (Victoria 2003; Crowther & Papas 2005). Los primeros resultados arrojaron dos consideraciones importantes. En primer lugar, los incendios de 2003 se produjeron hacia el final de una larga sequía, la peor en 100 años (Victoria 2004), y segundo, algunas de las zonas afectadas por los incendios forestales fueron sufrieron inmediatamente después inundaciones (Victoria 2003; Lyon & O'Connor 2008).

El año 2003 coincidió también con el momento en que un gran incendio quemó parte del Parque Natural de Sant Llorenç en Cataluña (noreste de España), y fue esta la ocasión para iniciar una investigación multidisciplinar sobre los efectos del fuego, con especial interés en los ríos mediterráneos (Gasith & Resh 1999). Una de las características más importantes de los ríos mediterráneos es la fuerte estacionalidad hidrológica, presentando sequías durante el verano y fuertes inundaciones principalmente en el otoño. Las comunidades biológicas que viven en este tipo de ríos tienen que hacer frente a esta variabilidad, y se ha formulado la hipótesis de que los ciclos de vida están adaptados a una dinámica a largo plazo y no a eventos puntuales de inundaciones (Lytle & Poff 2004).

Como se ha mencionado anteriormente, a pesar de que algunas respuestas de macroinvertebrados ante los incendios forestales podrían generalizarse, los factores locales como la hidrología y el clima podrían generar diferencias en las respuestas (Minshall 2003) y podrían ser importantes las interacciones con otras grandes perturbaciones como sequías o inundaciones. Si los efectos indirectos del fuego inician una serie de cambios intensos en los ríos, la suma de otras perturbaciones como inundaciones (Vieira *et al.* 2004) podrían o bien restablecer la trayectoria de recuperación (Arkle *et al.* 2010) o bien generar respuestas diferentes al retrasar el proceso de recolonización como las sequías estacionales (Cowell *et al.* 2006). Así, los efectos de una perturbación en las comunidades biológicas de los ríos podrían ser más complejos debido a las perturbaciones posteriores dentro del mismo ecosistema.

En los sistemas lóticos, las perturbaciones son consideradas como un filtro importante que define el equilibrio alcanzado en las comunidades (Resh *et al.* 1988), donde interactúan factores opuestos (estocásticos *vs.* determinísticos) en función de la intensidad de la perturbación (Lepori & Malmqvist 2009). La respuesta de la biota acuática a eventos perturbadores de gran proporción está caracterizada por dos estrategias: la resistencia y la resiliencia (Gunderson 2000). La primera es el grado en que la fauna bentónica se reduce por la perturbación inicial, y la segunda, es la tasa de recuperación de especies tanto en términos absolutos como relativos (Marchant *et al.* 1991). La dinámica entre ambas respuestas y la naturaleza y la fuerza de las perturbaciones presentes durante el período de recuperación influirán en la estabilidad de las comunidades (Lepori & Malmqvist 2009).

Objetivos y resúmenes

En agosto de 2003, el sector oriental del Parque Natural de Sant Llorenç del Munt i l'Obac, una zona con alto interés recreativo y de conservación, sufrió un incendio forestal severo. Las condiciones iniciales, con temperaturas de 39 ºC y 7 % de humedad relativa, promovieron una rápida propagación del fuego, y en 5 días se quemaron 4543 hectáreas que afectaron diversos hábitats de gran interés natural (como bosques de ribera, encinares, bosques de pinos y ríos) (Guinart 2007). Previo al estudio que se presenta aquí se investigaron los efectos del fuego en un río mediterráneo cercano al parque natural con una periodicidad mensual a lo largo de dos años (Vila-Escalé 2009). Sin embargo, la pregunta continuaba siendo si las respuestas obtenidas en un solo río podrían generalizarse a otros ríos mediterráneos y si estas se mantenían a una escala de tiempo mayor.

En este contexto, el objetivo principal de la tesis ha sido estudiar los efectos a mediano plazo de los incendios forestales sobre las comunidades de macroinvertebrados de los ríos mediterráneos y comparar los resultados con los de otros biomas. Para ello, se realizó un diseño que se presenta en la Tabla 1, cuyos resultados se presentan en cuatro capítulos que abordan estudios a diferentes escalas espaciales y temporales.

Tabla 1. Resumen de las escalas temporales y espaciales de los capítulos presentados en la tesis.

Capítulo	Escala	Tiempo después del incendio	Intensidad de muestreo
1	Localidad	3 años	Mensual
2	Cuenca	2 meses – 5 años	Anual
3	Cuenca	9 meses	Una vez
4	Regional	9-11 meses	Una vez

A continuación se presentan los títulos, objetivos generales planteados y su resolución en cada uno de los capítulos, así como sus respectivos resúmenes de resultados y conclusiones.

Capítulo 1: **Respuesta de la comunidad de macroinvertebrados a mediano plazo en dos localidades afectadas de manera diferente en la cobertura ribereña por los efectos de un fuego intenso.**

> Objetivo: Estudiar los efectos del fuego a medio plazo sobre la sucesión de macroinvertebrados en un río Mediterráneo (Vall d'Horta) 30 meses después de un incendio forestal, comparando mensualmente las comunidades de macroinvertebrados entre dos localidades cercanas con bosques de ribera afectados de manera diferente por el fuego (cobertura severamente afectada *vs*. cobertura no afectada por el fuego).

Resumen

Uno de los efectos más importantes de los incendios forestales en los ecosistemas acuáticos es la eliminación del bosque de ribera, y consecuencia de ello el cambio significativo en la entrada de material alóctono en el río. Un aumento de exposición a la radiación directa en el río con una mayor entrada de nutrientes desde la cuenca quemada trae como consecuencia un aumento en el crecimiento de algas y, así, un aumento en la productividad primaria. El río de Vall d'Horta, situado en el Parque Natural de Sant Llorenç (Cataluña), fue afectado heterogéneamente a lo largo de su curso principal por el fuego de 2003. Elegimos dos localidades cercanas pero con dos grados diferentes de afectación por el fuego en el bosque de ribera: una zona severamente quemada y otra no afectada, ambas localizadas en la misma cuenca quemada (67%). El objetivo principal fue comparar estas dos localidades y estudiar la respuesta a mediano plazo de los efectos de incendios en las comunidades de macroinvertebrados a lo largo de doce meses. No se encontraron diferencias significativas en los parámetros físico-químicos entre ambas localidades. Como era de esperar, el porcentaje de hojarasca fue cuatro veces mayor en la localidad con el bosque de ribera cerrado en comparación con la localidad abierta, mientras que la vegetación acuática (principalmente algas) mostró la tendencia opuesta. En la localidad sin cobertura de ribera se registró una mayor abundancia promedio de macroinvertebrados, probablemente consecuencia del aumento en la cobertura de algas. Asimismo, se encontró una menor diversidad y número de taxones en comparación con la localidad cerrada posiblemente porque la localidad

abierta se secó completamente durante los meses de verano. En general, los caracteres biológicos reflejaron los cambios asociados a los cambios en la cobertura de algas y hojarasca, aunque también se asociaron a los cambios de hidrología a lo largo del año, sobretodo en la localidad abierta. Los efectos indirectos del fuego reflejaron un efecto a mediano plazo sobre el ecosistema acuático debido a la ausencia de la cobertura de ribera, que también pudo haber influido en una mayor evapotranspiración de las pozas en verano, lo cual refleja también la importancia de la estacionalidad de ríos, que es uno de los factores más importantes en la dinámica de los ríos mediterráneos.

Capítulo 2: **Incendio forestal *vs.* Sequía estacional ¿Quién moldea la comunidad de macroinvertebrados en un río mediterráneo?**

> Objetivo: Estudiar los cambios anuales en la composición de especies después del incendio en varios ríos afectados por el incendio y comparar los cambios entre los ríos quemados con ríos control en un marco de gran variabilidad interanual de la precipitación.

Resumen

Los ecosistemas de clima mediterráneo están caracterizados por una alta recurrencia de los incendios. Sin embargo, pocos estudios se han centrado en el estudio de los efectos de esta perturbación en las comunidades biológicas que viven en los ríos de sus cuencas. Estos ecosistemas además están afectados por una variabilidad estacional e interanual muy marcada en la precipitación y la temperatura, y, como consecuencia, los ríos de estos climas se caracterizan por soportar inundaciones y también sequías estacionales de duración variable dependiendo del año, por lo que los cursos de agua pueden secarse parcial o completamente durante varias semanas o meses. El objetivo de este capítulo fue determinar la respuesta a mediano plazo de la estructura y función de las comunidades de macroinvertebrados de ríos mediterráneos después de un incendio forestal durante los primeros cinco años post-incendio y su relación con los cambios hidrológicos. Dos meses después del incendio, el número de taxones en los ríos afectados por el fuego era menor en comparación con los ríos control. Sin embargo, esta diferencia no fue significativa, como tampoco lo fue en los años siguientes. También se observó un incremento en la abundancia un año después del incendio en los ríos que se quemó su cuenca, pero esta diferencia no fue significativa. Entre los organismos presentes, los moluscos y odonatos fueron los órdenes más perjudicados inmediatamente después del incendio y que más tardaron en recuperar su presencia y abundancia en los ríos cuya cuenca se quemó. Los caracteres biológicos de las comunidades de macroinvertebrados estudiados con un análisis de correspondencia difusa (FCA) revelaron una diferencia significativa entre los ríos control y quemados.

Por otra parte, las diferencias entre los años secos y los húmedos fueron altamente significativas, registrándose abundancias y riquezas de taxones más altas durante los años húmeros del período estudiado. El análisis FCA también mostró una clara separación entre los años secos y húmedos, y ciertamente las diferencias más significativas entre los rasgos biológicos estuvieron relacionadas más con las condiciones hidrológicas de cada año que con el hecho de que el río estuviera afectado por un incendio o no.

En general, las comunidades de macroinvertebrados mostraron una respuesta rápida al fuego. Las sequías derivadas de los años secos demostraron ser una perturbación severa para los macroinvertebrados, tanto en los ríos quemados como en los controles, aunque las comunidades mostraron nuevamente una alta resiliencia con recuperación de su estructura y función en los años húmedos.

Los futuros modelos de precipitaciones predicen que en un contexto de cambio climático, las inundaciones y sequías aumentarán la frecuencia y magnitud en toda Europa. Es por ello que surgen muchas dudas con respecto a si esta capacidad de resiliencia alta de estos ecosistemas se podrá mantener en el futuro.

Capítulo 3: **Efectos de los incendios forestales sobre los parámetros estructurales y funcionales de las comunidades de macroinvertebrados en los ríos de Victoria (Australia) previamente afectados por una década de sequía.**

> Objetivo: Con el fin de ampliar el conocimiento de los efectos del fuego en las comunidades de macroinvertebrados a mayores escalas espaciales, se muestreó otra área propensa a incendios: Victoria, al sureste de Australia. El objetivo principal fue estudiar la respuesta a mediano plazo de la estructura (número de taxa y abundancia) y la función (grupos funcionales según su modo de alimentación) de la comunidad de macroinvertebrados de tres ríos localizados en las cuencas afectadas por un incendio forestal y después de una década de sequía intensa.

Resumen

Son escasos los estudios del efecto del fuego en las comunidades de macroinvertebrados en otras áreas diferentes del oeste de EE.UU. Sin embargo, comienzan a ser de interés especialmente en biomas propensos al fuego, como el mediterráneo y el sureste de Australia. Los efectos de los incendios forestales en las comunidades de macroinvertebrados pueden separarse convenientemente a nivel cronológico siendo en general las primeras precipitaciones post-incendios las que afectan negativamente los organismos acuáticos. Es por esto que a veces resulta difícil separar los efectos de los incendios forestales de otras perturbaciones como las primeras inundaciones o como la sequía que suele producirse antes del incendio, lo cual aumenta el riesgo de propagación o la severidad del mismo y sus efectos posteriores. Y son generalmente estas perturbaciones, las inundaciones y las sequías, las que interactúan con el efecto del fuego y modulan la respuesta de la comunidad de macroinvertebrados frente a los incendios forestales (como hemos visto en el capítulo 2 de esta tesis). El objetivo de este capítulo fue entonces estudiar las comunidades de macroinvertebrados (estructura y función) de tres ríos de Victoria afectados por fuego y por una década intensa de sequía.

Para el estudio de estas interacciones, se muestrearon nueve meses después de un incendio forestal ocurrido en 2007 en Victoria (SE Australia) seis ríos, tres de ellos afectados por el fuego y tres no afectados que fueron utilizados como control, todos localizados en una zona afectada por una década de sequía denominada como la “sequía del milenio”— diez años consecutivos de precipitaciones inferiores a la media. Los resultados mostraron que hubo un efecto significativo de los incendios en la comunidad de macroinvertebrados. Las principales diferencias se debieron a un aumento en la abundancia de los taxones comunes (los más resilientes) en los sitios quemados (Orthocladiinae, Tubificidae, Simuliidae, Chironominae, *Dinotoperla* sp. y grupo *Taschorema*), aunque también algunos taxones se encontraron únicamente en los ríos control, mostrando que el efecto incendio fue negativamente significativo. Contrariamente a lo que se esperaba, se encontró un mayor porcentaje de macroinvertebrados trituradores en los sitios quemados, mientras que los raspadores fueron codominantes en los ríos control. Esto podría indicar, por una parte, la importancia de la omnivoría en estos invertebrados, tal y como se ha descrito en los ríos de Victoria, aunque también sugiere el poco conocimiento de las estrategias tróficas que se tiene de los organismos de los ríos australianos.

Las respuestas de los macroinvertebrados después del fuego variaron en los diferentes ríos, probablemente como consecuencia de las diferentes condiciones hidrológicas después del incendio, incluso entre algunos de los quemados, ya que la ausencia de lluvias post-incendio en una de las cuencas la diferenciaba significativamente de las otras dos, que sí habían sido lavadas, mostrando otra vez la importancia de las condiciones locales.

Si bien la fauna de macroinvertebrados en general mostró, como en el caso de Cataluña, una alta resistencia y resiliencia después del fuego, se cuestiona si esta respuesta será la misma en un futuro con alteraciones en el régimen de incendios en combinación con sequías más prolongadas.

Capítulo 4: **Efectos de los incendios forestales en las comunidades de macroinvertebrados en tres biomas: ¿son respuestas moduladas por el clima y la hidrología?**

> Objetivo 4: El último capítulo aborda una comparativa de la respuesta de la comunidad de macroinvertebrados después de un incendio forestal en tres biomas diferentes. El objetivo principal de este capítulo fue comparar las respuestas de la composición y estructura de las comunidades de macroinvertebrados a los incendios forestales en tres biomas donde el fuego es un perturbador común pero con diferentes contextos biogeográficos y climáticos (noreste del Mediterráneo, sureste de Australia SE y noroeste de Estados Unidos).

Resumen

Las comunidades de macroinvertebrados suelen responder rápidamente durante el primer año después de un incendio forestal, y su composición post-incendio está dominada por taxones adaptados a perturbaciones. Sin embargo, las diferencias en climatología e hidrología pueden modular las respuestas de estas comunidades. El objetivo principal de este capítulo fue comparar las respuestas de las comunidades de macroinvertebrados después de 9-11 meses del fuego en tres biomas diferentes, Idaho (noroeste EE.UU), Victoria (sureste Australia) y Cataluña (noreste España), y estudiar la importancia del clima y la hidrología en los cambios producidos post-incendio 9-11 meses depués.

Hidrológicamente las condiciones fueron también muy diferentes, ya que en Victoria, una sequía de 10 años mantuvo los caudales de los ríos en valores mínimos, lo cual coincidió con el momento de muestreo de este estudio, mientras que en Idaho, el muestreo de los ríos se realizó después de las inundaciones asociadas al deshielo primaveral. Finalmente, los ríos de Cataluña experimentaron grandes inundaciones después del incendio forestal debidos a intensas tormentas. En general, se encontraron en el momento del muestreo importantes efectos negativos de los incendios forestales en la estructura y composición de las comunidades de macroinvertebrados, que fueron menos claras en los ríos de Cataluña, donde las diferencias fuego-control eran casi inexistentes. El dominio de insectos adaptados a perturbaciones de estrategia *r* (por ejemplo, Chironomidae, Simuliidae, Baetidae) fue generalizado en todos los ríos afectados por el fuego. En Cataluña e Idaho, el efecto combinado entre los incendios y las inundaciones ocurridas posteriormente también pareció aumentar la abundancia de estos taxones. Estas comparaciones refrendan la idea de que otras perturbaciones como las inundaciones y las sequías influyen y modelan las respuestas de los efectos del fuego sobre los macroinvertebrados acuáticos, y de esta manera pueden producir efectos diferentes a lo largo del tiempo de recuperación post-incendio.

Discusión general

El objetivo general de esta tesis era aumentar el conocimiento en un ámbito geográfico amplio sobre las respuestas de las comunidades de macroinvertebrados después de incendios, con especial énfasis en ríos mediterráneos y a una escala temporal de mediano plazo (entre 1 y 5 años). Basándonos en el resumen hecho por Gresswell (1999), se presentan en la Tabla 3 los principales resultados publicados hasta el presente de lo que se conoce sobre los efectos del fuego sobre macroinvertebrados, incluyendo al final los resultados de los capítulos de esta tesis. En general, los efectos indirectos de los incendios son los causantes de una reducción en la riqueza y en la densidad de macroinvertebrados. Sin embargo, la intensidad de la respuesta depende de factores locales como la severidad del incendio, la precipitación post-incendio, la hidrología, la geología y el tiempo transcurrido. El fuego es por lo tanto un perturbador estocástico, pero dependiendo de las condiciones antes, durante y después de un incendio la respuesta será más o menos relevante porque afecta la composición, estructura y funcionalidad de la comunidad de macroinvertebrados acuáticos. Como pudo observarse en esta tesis, las respuestas de macroinvertebrados acuáticos variaron en su severidad comenzando por Victoria, seguida de Idaho y finalmente de Cataluña (Capítulo 4).

El incendio forestal de 2003 ocurrido en el parque natural de Sant Llorenç (Cataluña) representó una oportunidad para estudiar los efectos del fuego en toda el área. De esta manera se iniciaron diversos seguimientos para estudiar la respuesta de ecosistemas terrestres y acuáticos en el contexto mediterráneo. Los resultados principales se resumen cronológicamente en los períodos estudiados: corto y mediano plazo.

Los primeros resultados a corto plazo indicaron un efecto negativo generalizado en todos los sectores estudiados. Con el objetivo de acelerar la regeneración del área afectada, se iniciaron una serie de proyectos multidisciplinarios poco después del incendio (Guinart 2007). Como en otras áreas (Shakesby & Doerr 2006), la hidrofobicidad del suelo aumentó y se observó una mayor erosión asociada a las grandes precipitaciones que tienen lugar después del incendio, aportando altas cantidades de ceniza y compuestos aromáticos en los ríos (Vila-Escalé *et al.* 2007). Los efectos del fuego sobre la flora tanto terrestre como acuática fueron inmediatamente perjudiciales, por una parte el material orgánico terrestre se redujo a cenizas y a aportes atmosféricos mientras que las comunidades del ecosistema acuático fueron arrastradas totalmente después de las primeras inundaciones. Este resultado corroboró la idea de que las inundaciones en sistemas acuáticos y los fuegos en sistemas terrestres se han identificado como mecanismos análogos importantes de reinicio de la sucesión ecológica (Wagener *et al.* 1998). En cuanto a la fauna, los cambios en las condiciones del hábitat, el cambio de recursos y las condiciones tóxicas después del fuego probablemente afectaron a los organismos acuáticos, semi-acuáticos y terrestres (Guinart 2007; Engstrom 2010). En los ríos de Sant Llorenç, dos meses después del incendio, el número de taxa de macroinvertebrados fue inferior en los ríos afectados por el fuego; sin embargo, no fue significativamente diferente de los ríos control tampoco fue diferente en los años siguientes (Capítulo 2). Pero la composición cambió completamente y los macroinvertebrados más afectados correspondieron a los moluscos y odonatos, taxa que se ha caracterizado como poco resiliente después de sequías (Acuña *et al.* 2007) e inundaciones en ríos intermitentes (Vila-Escalé 2009).

Después de un año, se observó que el número de taxones de macroinvertebrados de ríos quemados no fue significativamente diferente de los ríos control, si bien la composición aún no era la misma y la abundancia fue tres veces mayor en los ríos quemados (Capítulo 2). La dominancia de Chironomidae, Baetidae y Simuliidae fue generalizada en todos los ríos estudiados. Otra fauna como salamandras, ranas y sapos fueron capturados después del fuego aunque la diversidad y abundancia distaron mucho de los que había previo al incendio. De la misma manera, las aves invernantes se redujeron en un 76% y las aves nidificadoras en un 52% (Herrando & Baltà 2005). Uno de los organismos más afectados fueron los murciélagos, ya que de las 17 especies censadas en la Vall d'Horta antes del incendio, en 2004, un año después del fuego, sólo se censó un murciélago (Serra-Cobo 2005). Otros grupos de organismos gravemente afectados fueron los peces. De las dos especies autóctonas que se encontraban antes del incendio, 2 años más tarde el *Barbus meridionalis* se pescó tan solo en un 42% de su potencial geográfico, y el *Squalis cephalus* se pescó en cuatro de las trece estaciones en el Ripoll no habiéndose encontrado ningún ejemplar en el arroyo de Vall d'Horta (Sostoa *et al.* 2006). Además de los efectos negativos del incendio sobre los peces parece que su recuperación es difícil en un río con alta presencia de barreras y presencia de especies alóctonas (Guinart 2007). En general, un año después del incendio ciertos taxones mostraron una respuesta rápida, lo que confirma la alta resiliencia de los ecosistemas mediterráneos. Sin embargo, la regeneración no es siempre la regla (Rodrigo *et al.* 2004; Pausas *et al.* 2008). Y varios factores son importantes para que se observe una regeneración exitosa, siendo uno de ellos la precipitación después del fuego (2004 fue un año húmedo). Asimismo, el fuego no afectó homogéneamente todo el perímetro del incendio, y las islas no quemadas son cruciales para la regeneración de áreas quemadas (Ordóñez *et al.* 2005). Por ejemplo, las imágenes aéreas tomadas después del incendio detectaron algunas islas de coníferas no quemadas en Sant Llorenç (Lobo 2005) y la regeneración fue común en las zonas aledañas. Esta afectación heterogénea ocurre comúnmente en los bosques de ribera debido a su microclima, lo cual genera diferentes grados de combustión. De esta manera es fácil encontrar localidades afectadas de forma diferente en el bosque de ribera en la misma cuenca (Capítulo 1).

En este sentido, tres años después del fuego, dos localidades, una con cobertura ribereña y otra sin cobertura (totalmente quemada), generaron diferencias significativas en la cobertura orgánica, y la composición y sucesión de macroinvertebrados respondió no sólo a las diferencias en cobertura sino también a la hidrología (Capítulo 1). Similar a los estudios en el oeste de los EE.UU. (Minshall *et al.* 2004), los macrófitos y los musgos estuvieron relacionados con localidades cerradas, mientras que la dominación de algas verdes fue encontrada en las localidades más abiertas. Sin embargo, en ambas zonas se observó un desarrollo de algas filamentosas (e.g. *Cladophora*), lo que refleja el gran aporte de nutrientes desde la cuenca y una mayor entrada de luz (Minshall *et al.* 2004). La temporalidad también fue un factor muy importante en la dinámica de la cobertura orgánica, y esto se ha descrito previamente como determinante en la dinámica de la materia orgánica en los ríos mediterráneos (Acuña *et al.* 2004). Si bien no medimos la producción primaria, la cobertura y la biomasa de algas y los cambios en la comunidad reflejaron la relación entre perturbación y productividad (Lake 2000). En ambas localidades, las perturbaciones (inundaciones y sequía estacional) representaron un factor clave no sólo en la cubierta orgánica (Hillebrand 2008) sino también en la estructura y la función de las comunidades de los macroinvertebrados que viven allí

(Boulton & Lake 1992a; Acuña *et al.* 2005), con respuestas recíprocas entre ambos niveles (Wootton 1998).

Cuatro años después del fuego en Sant Llorenç, un estudio de la fauna del ecosistema terrestre de Santos *et al* (2009) identificaron 257 especies pertenecientes a grupos diversos como moluscos, hormigas, heterópteros, escarabajos, ortópteros, reptiles, pájaros, carnívoros y murciélagos. Se encontró que un 18% de la especies fueron exclusivas de las zonas control en comparación con 17% de las zonas quemadas. Mientras que un 22% de los taxones eran considerados generalistas y comunes de ecosistemas mediterráneos. La mayor parte de los organismos encontrados en las zonas quemadas eran voladores y herbívoros.

La respuesta de la composición y abundancia de la comunidad acuática de macroinvertebrados de ríos mediterráneos transcurrido el mismo tiempo respondió más a la variación temporal en hidrología (precipitación acumulada anual y primaveral) que al fuego (Capítulo 2), una tendencia que se ha descrito en otros ríos intermitentes (Acuña *et al.* 2005; Bêche & Resh 2007). Durante 2003, 2005 y 2006 (años secos), la riqueza taxonómica disminuyó, fueron entonces las diferentes perturbaciones (siendo el fuego uno de estos factores perturbadores) las que determinaron el predominio de ciertos taxones, eliminando las especies que carecían de caracteres biológicos favorables (Chase 2007).

Estos resultados que relacionaban la importancia de la sequía con el fuego en los ríos mediterráneos fue mucho más evidente en el estudio de los ríos de Victoria, ya que 9 meses después del incendio, las cenizas aún se mantenían en la hábitat fluvial de alguno de los ríos, probablemente como consecuencia de la década de sequía que estaba padeciendo (Capítulo 3). Si bien se esperaba una respuesta rápida de los macroinvertebrados, el impacto de las perturbaciones sobre la comunidad en los ríos de cuenca quemada fue negativo en términos de biodiversidad y abundancia, especialmente en uno de los ríos muestreados. En relación a la comparación entre biomas, los tres ríos quemados de Victoria fueron los que presentaron la diversidad más baja (Capítulo 4). La fauna acuática y la flora australiana están caracterizadas por el predominio de los rasgos de resistencia y resiliencia, lo cual refleja la significación evolutiva de la sequía como presión selectiva (Boulton 2003; Bond *et al.* 2008). Parece ser entonces que la combinación en primer lugar de la sequía y luego del fuego redujo la capacidad de resiliencia de estos ríos, lo que puede sugerir que la capacidad de resiliencia de una comunidad depende en gran medida de qué especies están inicialmente presentes y de la severidad de la perturbación (Hughes *et al.* 2007).

Los resultados principales de la comparación de los efectos de incendios forestales sobre las comunidades de macroinvertebrados de ríos en Idaho, Victoria y Cataluña se resumen en la Figura 3.

Los estudios a largo plazo de los efectos del fuego son pocos, si bien la gran área afectada por los fuegos de 1988 en el Parque Nacional de Yellowstone continúa estando bajo estudio. Las conclusiones principales indican hasta ahora que los fuegos no son únicamente una perturbación devastadora, si bien en este caso este tipo de perturbación, intensa e infrecuente, puede producir cambios duraderos en la estructura física y biológica (Foster *et al.* 1998). Los fuegos recurrentes son una fuente importante de heterogeneidad del paisaje que crea una variación espacial (producto de la diferencia en la severidad y la presencia de zonas no quemadas) que diversifican la función del ecosistema (Turner *et al.* 2003). De forma similar, las perturbaciones con una gran escala espacial y temporal en los ecosistemas acuáticos son inevitables y a menudo beneficiosas (Bisson 2003). Cuando un incendio forestal afecta un área, los ríos que drenan por esta área responderán a los procesos físicos y ecológicos que ocurren en el ecosistema terrestre (Hynes 1975). Esta visión dinámica es un modelo de paisaje donde las perturbaciones y recuperaciones son importantes como un proceso necesario para mantener un mosaico interconectado entre hábitats y comunidades diversas y cambiantes (Bisson 2003).

Las comparaciones de los procesos ecológicos entre los ecosistemas terrestres y acuáticos sugieren semejanzas pero también diferencias, y así lo fue también en Sant Llorenç. La acción del agua parece ser el factor diferencial más importante (Grimm *et al.* 2003), marcando las diferencias en la escala espacial y aumentando el ritmo temporal de los procesos del ecosistema. Las consecuencias del incendio parecen ocurrir a velocidades más rápidas en los ecosistemas acuáticos, debido a diferencias en estrategias, tasas de crecimiento, tamaños y estequiometría de los organismos consumidores en ambos ecosistemas (Nowlin *et al.* 2008).

En este sentido, pulsos de recursos como los huracanes o plagas de insectos indican que, dependiendo del tipo de recurso, serán transmitidos más rápidamente a los sistemas acuáticos (Nowlin *et al.* 2008). Aunque los incendios no estén catalogados como pulsos de recursos, los efectos indirectos podrían considerarse como uno de ellos. Por ejemplo, las precipitaciones después del incendio podrían representar un pulso infrecuente de nutrientes acumulados (Yang *et al.* 2008), y un aumento en la emergencia de insectos acuáticos podría también considerarse como un "pulso" (Malison & Baxter 2010b). Esta gran productividad entre ambos ecosistemas no es algo nuevo, ya que la interfase entre terrestre-acuático ya ha sido clasificada como un punto biogeoquímico caliente (McClain *et al.* 2003). En Sant Llorenç, aunque la emergencia no fue estudiada, un año después del fuego la abundancia de macroinvertebrados fue máxima. Adicionalmente, la fauna acuática o la que vive en los corredores del río, como por ejemplo los murciélagos, se está recuperando gradualmente. De forma similar, otros estudios han mostrado la importancia de todas estas conexiones entre diversos niveles (Baxter *et al.* 2005; Arnan 2006).

Desde el incendio forestal de 2003 se han celebrado dos conferencias del Parque Natural de Sant LLorenç. Como era de esperar, en el 2005 la mitad de las conferencias que se presentaron estaban relacionadas con el incendio y en 2009, aunque menos representada, se indicó que se continuan realizando investigaciones en el área afectada. Hasta ahora, los resultados principales en los ecosistemas terrestres han concluido que no hay diferencias significativas en la regeneración de la vegetación entre las diversas áreas modificadas después del incendio (i.e. corte de pies quemados, poda del bosque, reutilización del material arbolado y retiro de especies invasoras) (Pañella 2009). Por el contrario, los diversos caminos que fueron abiertos después del incendio para poder acceder a diferentes zonas con maquinarias para cortar árboles, el raleo del bosque y la remoción de ramas muertas generaron una mayor erosión. Es este resultado lo que podría afectar seriamente la regeneración del paisaje y los ecosistemas acuáticos. Asimismo, para la recuperación de los ecosistemas acuáticos es crucial la disponibilidad de agua, y, como se observó en el capítulo 2, los efectos a medio plazo del fuego dependieron altamente de la precipitación anual, así que es la disponibilidad de agua lo que marcó las diferencias entre años.

Se espera que el cambio climático altere la distribución geográfica de regímenes de incendios, un proceso abiótico complejo que responde a una variedad de gradientes espaciales y ambientales. Estos nuevos modelos de incendios son el resultado de interacciones complejas entre el clima, la vegetación y las poblaciones humanas. Cómo se alterará la actividad global del fuego sigue siendo en gran parte desconocida (Krawchuk *et al.* 2009). Los incendios pueden causar cambios importantes en la estructura y el funcionamiento de los ecosistemas terrestres y acuáticos (Gresswell 1999). Además, el fuego es promovido por muchos factores, incluyendo la sequía, un perturbador muy severo en ecosistemas acuáticos y menos predecibles (Boulton & Lake 2008). Es generalmente difícil separar las diferentes perturbaciones, y parece que en un contexto de cambio climático vendrán junto con una mayor recurrencia. Si bien las comunidades de macroinvertebrados se han catalogado como muy resilientes, con perturbaciones más prolongadas y más severas esto podría no ser una respuesta suficiente para compensar los cambios producidos. Asimismo, es importante continuar estudiando los efectos de las perturbaciones a gran escala como los incendios forestales por mayores períodos de tiempo (Minshall *et al.* 1997; Turner *et al.* 2003), para establecer las trayectorias y los mecanismos de la recuperación de los ecosistemas acuáticos y determinar los efectos del cambio global sobre ellos.

Existe hoy en día mucha preocupación por los acoplamientos entre el clima, los seres humanos, la vegetación y el fuego, y cómo las relaciones se verán afectadas con el cambio global (Folke *et al.* 2004). En la zona más septentrional de la cuenca mediterránea, la industrialización y los éxodos rurales han llevado al abandono de muchos campos, lo cual aumenta la cubierta y la continuidad de comunidades primarias de la sucesión (que son altamente inflamables, como los pinares) y ha cambiado el modelo y el régimen del fuego del paisaje (Pausas *et al.* 2008). Así, aunque los bosques de la cuenca mediterránea pueden ser resilientes (i.e., matorrales y encinares), algunas zonas de los paisajes actuales, que son productos de una larga historia de la humanidad y su interacción con el paisaje existente, son relativamente sensibles a los fuegos, y en tales condiciones, los desastres o la degradación del ecosistema (i.e., pérdidas del suelo o cambios fuertes de la vegetación) son posibles. Asimismo, las comunidades acuáticas en este clima muestran generalmente una resiliencia muy alta (Gasith & Resh 1999). Sin embargo, los modelos hidroclimáticos predicen que el cambio climático aumentaría la frecuencia y la severidad de inundaciones y de sequías a través de Europa. Además, con la población en aumento en una ya densa cuenca mediterránea, también debe considerarse la escasez del agua (Prat & Manzano 2009). Como en muchos otros ecosistemas, la nueva perspectiva reconoce que la resiliencia podría verse afectada y que la capacidad auto reparadora de los ecosistemas podría ponerse en riesgo (Gunderson 2000; Folke *et al.* 2004; Bond *et al.* 2008). La inexistencia de estudios a largo plazo de los efectos del fuego en los ríos mediterráneos nos privará seguramente de poder dar una respuesta concreta a los cambios que se avecinan en el futuro.

Conclusiones

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1. Tres años después del incendio forestal de Sant Llorenç se encontraron diferencias significativas entre dos localidades cercanas dentro de la misma cuenca quemada pero con diferencias en la cobertura del bosque de ribera. La ausencia de la cobertura ribereña generó una diferencia significativa en las coberturas de vegetación acuática y hojarasca, que a su vez también influyó en las comunidades de macroinvertebrados. En la localidad expuesta, la mayor abundancia de macroinvertebrados reflejó el aumento de la cobertura de algas y, probablemente, de la producción primaria y la dependencia de los consumidores sobre este recurso. Sin embargo, la temporalidad de los ríos mediterráneos también interactuó con el fuego, lo cual afectó los recursos y el hábitat y, por tanto, la riqueza de macroinvertebrados acuáticos y su abundancia.

   Los cambios de composición de macroinvertebrados durante el período de muestreo dependió principalmente de la cobertura de algas y de la temporalidad, lo que confirmó la relación entre las perturbaciones y la productividad. La localidad expuesta se secó durante el verano, probablemente como resultado de una mayor evapotranspiración, debido a una mayor entrada de luz solar. Una vez que se restauró el flujo en otoño, la recolonización fue rápida y registró tendencias similares a las observadas en la localidad cerrada.
2. La comunidad de macroinvertebrados de los ríos del Parque Natural de Sant Llorenç mostró una alta resistencia a los efectos del fuego, ya que dos meses después del incendio comenzó una rápida recuperación. Si bien un año después la abundancia fue la más alta, no hubo diferencias en la riqueza de taxones después de algunos meses, ni tampoco en los años siguientes. La estructura de las comunidades de macroinvertebrados y su función en los años siguientes después del incendio dependió significativamente de la hidrología de cada año, que en el Mediterráneo puede ser muy variable. Este hecho fue evidente, ya que

la comunidad de macroinvertebrados se restableció en 2007 después de las severas sequías padecidas en 2005-2006, lo que reflejó su alta capacidad de resiliencia, característica propia de los ríos mediterráneos.

3. Los efectos de los incendios forestales en los ríos del sureste de Australia mostraron un impacto negativo en el número de taxones y una mayor abundancia en comparación con los ríos control. Estos resultados muestran que la sequía del "milenio" que afectó parte del sureste de Australia moduló los efectos de incendios forestales en las comunidades de macroinvertebrados en los ríos de Victoria, y que este bioma tenía por otra parte una riqueza específica menor. La ausencia de lluvias después del incendio se reflejó de forma clara especialmente en uno de los ríos que mostró una comunidad muy diferente, lo cual indica la importancia de los efectos indirectos del fuego en los macroinvertebrados.
4. En comparación con otros biomas (sureste de Australia y noroeste de EE.UU.), en los ríos mediterráneos las abundancia de los taxones de estrategia *r* fueron las más altas y reflejaron las perturbaciones recurrentes que afectan a este tipo de ríos y la alta resiliencia de las comunidades de macroinvertebrados acuáticos. A pesar de que se pueden realizar algunas generalizaciones acerca de los resultados obtenidos del oeste de EE.UU., parece que la hidrología y el momento de otras perturbaciones como la sequía o inundaciones puede aumentar o mitigar los efectos del fuego en comunidades de macroinvertebrados. Una de las principales diferencias en los efectos después del incendio en los ríos mediterráneos es que la gran inundación generalmente ocurre pocas semanas después del incendio, mientras que los efectos en los otros biomas puede retrasarse por la sequía (SE Australia) o por las características hidrológicas del río (noroeste EE.UU.).
5. Existe una gran preocupación sobre los efectos futuros de los incendios en los ecosistemas de diversas regiones del mundo, ya que grandes áreas se quemarán con una mayor frecuencia. Por otra parte, los futuros modelos climáticos predicen sequías más prolongadas, alteración que podría aumentar los incendios. Cómo van a interactuar ambas perturbaciones es todavía un interrogante. En el ecosistema mediterráneo, por la alta frecuencia de las perturbaciones (inundaciones y sequías estacionales), las comunidades de macroinvertebrados acuáticos se recuperan relativamente rápido, pero hay grandes incertidumbres si se mantendrá esto en un futuro.

Bibliography

Acuña V., Giorgi A., Munoz I., Uehlinger U. & Sabater S. (2004). Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology*, 49, 960-971.

Acuña V., Giorgi A., Muñoz I., Sabater F. & Sabater S. (2007). Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean stream. *Journal of North American Benthological Society*, 26, 54-69.

Acuña V., Muñoz I., Giorgi A., Omella M., Sabater F. & Sabater S. (2005). Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects. *Journal of the North American Benthological Society*, 24, 919-933.

Agee J. (1998). The landscape ecology of western forest fire regimes. *Northwest Science*, 72, 24-34.

Albin D.P. (1979). Fire and stream ecology in some Yellowstone tributaries. *California Fish and Game*, 65, 216-238.

Allison G. (2004). The influence of species diversity and stress intensity on community resistance and resilience. *Ecological Monographs*, 74, 117-134.

Anderson M., Ellingsen K. & McArdle B. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683-693.

Arkle R.S., Pilliod D.S. & Strickler K. (2010). Fire, flow and dynamic equilibrium in stream macroinvertebrate communities. *Freshwater Biology*, 55, 299-314.

Arnan X. (2006). Dinàmica postincendi i interaccions entre plantes i formigues mediterrànies. PhD thesis dissertation. In: *Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia*. Universitat Autònoma de Barcelona. Barcelona, p. 161.

Aronsson K. & Ekelund N. (2008). Limnological effects on a first order stream after wood ash application to a boreal forest catchment in Bispgården, Sweden. *Forest Ecology and Management*, 255, 245-253.

Baxter C.V., Faush K.D. & Saunders W.C. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, 50, 201-220.

Bêche L.A. & Resh V.H. (2007). Short-term climatic trends affect the temporal variability of macroinvertebrates in California 'Mediterranean' streams. *Freshwater Biology*, 52, 2317-2339.

Bêche L.A., Stephens S.L. & Resh V.H. (2005). Effects of prescribed fire on a Sierra Nevada (California, USA) stream and its riparian zone. *Forest Ecology and Management*, 218, 37-59.

Behmer D.J. & Hawkins C.P. (1986). Effects of Overhead Canopy on Macroinvertebrate Production in a Utah Stream. *Freshwater Biology*, 16, 287-300.

Belillas C.M. & Rodà F. (1993). The Effects of Fire on Water-Quality, Dissolved Nutrient Losses and the Export of Particulate Matter from Dry Heathland Catchments. *Journal of Hydrology*, 150, 1-17.

Benda L.M., D.; Bigelow, P.; Andras, K. (2003). Effects of post-wildfire erosion on channel environments, Boise River, Idaho. *Forest Ecology and Management*, 178, 105-119.

Benjamini Y. & Hochberg Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57, 289-300.

Benke A., Huryn A., Smock L. & Wallace J. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society*, 18, 308-343.

Biggs B., Smith R. & Duncan M. (1999). Velocity and sediment disturbance of periphyton in headwater streams: biomass and metabolism. *Journal of the North American Benthological Society*, 18, 222-241.

Binckley C. & Resetarits W. (2007). Effects of forest canopy on habitat selection in treefrogs and aquatic insects: implications for communities and metacommunities. *Oecologia*, 153, 951-958.

Bisson P.A.R., B.E.; Luce, Ch.; Hessuburg, P.F.; Lee, D.C.; Kershner, J.L.; Reeves, G.H.; Gresswell, R.E. (2003). Fire and aquatic ecosystems of westerns USA: current knowledge and key questions. *Forest Ecology and Management*, 178, 213-229.

Blondel J. & Aronson J. (1999). *Biology and wildlife of the Mediterranean region*. Oxford University Press, USA.

Bonada N., Dolédec S. & Statzner B. (2007a). Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology*, 13, 1658-1671.

Bonada N., Rieradevall M., Dallas H., Davis J., Day J., Figueroa R., Resh V.H. & Prat N. (2008). Multi-scale assessment of macroinvertebrate richness and composition in Mediterranean-climate rivers. *Freshwater Biology*, 53, 772-788.

Bonada N., Rieradevall M. & Prat N. (2007b). Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. *Hydrobiologia*, 589, 91-106.

Bond N.R., Lake P.S. & Arthington A.H. (2008). The impacts of drought on freshwater ecosystems: an Australian perspective. *Hydrobiologia*, 600, 3-16.

Bond W. & Keeley J. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, 20, 387-394.

Bond W., Woodward F. & Midgley G. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, 165, 525-538.

Boulton A. & Lake P. (1992a). Benthic organic matter and detritivorous macroinvertebrates in two intermittent streams in south-eastern Australia. *Hydrobiologia*, 241, 107-118.

Boulton A.J. (1991). Eucalypt leaf decomposition in an intermittent stream in south-eastern Australia. *Hydrobiologia*, 211, 123-136.

Boulton A.J. (2003). Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology*, 48, 1173-1185.

Boulton A.J. & Lake P.S. (1992b). The Ecology of two Intermittent Streams in Victoria, Australia .2. Comparisons of Faunal Composition between Habitats, Rivers and Years. *Freshwater Biology*, 27, 99-121.

Boulton A.J. & Lake P.S. (1992c). The Ecology of two Intermittent Streams in Victoria, Australia .3. Temporal Changes in Faunal Composition. *Freshwater Biology*, 27, 123-138.

Boulton A.J. & Lake P.S. (2008). Effects of drought on stream insects and its ecological consequences. In: *Aquatic Insects: Challenges to Populations* (eds. Landcaster J, Briers RA & Macadam C). Royal Entomoligcal Society of London, CAB International Wallingford, UK, pp. 81-102.

Bradstock R.A., Williams J.E. & Gill A.M. (eds.) (2002). *Flammable Australia: the fire regimes and biodiversity of a continent*. Cambridge University Press, Cambridge.

Britton D.L. (1991). The benthic macroinvertebrate fauna of a South African Mountain stream and its response to fire. *South African Journal of Aquatic Science*, 17, 51-64.

Brown J. & Smith J. (2010). Wildland fire in ecosystems: effects of fire on flora. In: *Technical Report RMRS-GTR-42* (ed. Department of Agriculture FS, Rocky Mountain Resear Station) Odgen, UT, p. 257.

Cardinale B., Palmer M., Ives A. & Brooks S. (2005). Diversity-productivity relationships in streams vary as a function of the natural disturbance regime. *Ecology*, 86, 716-726.

Cerda A. & Doerr S.H. (2005). Influence of vegetation recovery on soil hydrology and erodibility following fire: an 11-year investigation. *International Journal of Wildland Fire*, 14, 423-437.

Clarke K.R. & Warwick R.M. (2001). Changes in marine communities: an approach to statistical analysis and interpretation. In: PRIMER Package.

ClarkLabs (1999). Idrisi32 Software. In: Clark University Worcester, MA, USA.

Closs G.P. & Lake P.S. (1994). Spatial and Temporal Variation in the Structure of an Intermittent-Stream Food-Web. *Ecological Monographs*, 64, 1-21.

Collett N.G. (2007). Effect of fire retardant application on heathland surface-dwelling families of the Order Coleoptera (beetles) in Victoria, Australia. *Forest Ecology and Management*, 253, 232-243.

Cowell A.L., Matthews T.G. & Lind P.R. (2006). Effect of fire on benthic algal assemblage structure and recolonization in intermittent streams. *Austral Ecology*, 31, 696-707.

Crowther D., Lyon S. & Papas P. (2008). The response of threatened aquatic invertebrates to the 2006 fire in north-eastern Victoria. In: Department of Sustainability and Environment, Heidelberg, Victoria, p. 40.

Crowther D. & Papas P. (2005). Determining the impact of fire on invertebrate communities in alpine streams in north-east Victoria. In: Department of Sustainability and Environment, Melbourne, p. 23.

Chadwick M. & Huryn A. (2007). Role of habitat in determining macroinvertebrate production in an intermittent-stream system. *Freshwater Biology*, 52, 240-251.

Chao A., Chazdon R., Colwell R. & Shen T. (2006). Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics*, 62, 361-371.

Chase J., Burgett A. & Biro E. (2010). Habitat isolation moderates the strength of top-down control in experimental pond food webs. *Ecology*, 91, 637-643.

Chase J.M. (2007). Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 17430-17434.

Chevenet F., Dolédec S. & Chessel D. (1994). A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31, 295-310.

Chiew F. & McMahon T. (2002). Modelling the impacts of climate change on Australian streamflow. *Hydrological Processes*, 16, 1235-1245.

Chuvieco E., Giglio L. & Justice C. (2008). Global characterization of fire activity: toward defining fire regimes from Earth observation data. *Global change biology*, 14, 1488-1502.

Dahm C.N., Baker M.A., Moore D.I. & Thibault J.R. (2003). Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology*, 48, 1219-1231.

Death R. (2002). Predicting invertebrate diversity from disturbance regimes in forest streams. *Oikos*, 97, 18-30.

Death R.G. (2010). Disturbance and riverine benthic communities: What has it contributed to general ecological theory? *River Research and Applications*, 26, 15-25.

Death R.G. & Zimmermann E.M. (2005). Interaction between disturbance and primary productivity in determining stream invertebrate diversity. *Oikos*, 111, 392-402.

DeBano L., Neary D. & Ffolliott P. (1998). *Fire's effects on ecosystems*. John Wiley & Sons, Inc., New York, NY.

Dewson Z.S., James A.B.W. & Death R.G. (2007). Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology*, 52, 357-369.

Doeg T.J. & Koehn J.D. (1994). Effects of draining and desilting a small weir on downstream fish and macroinvertebrates. *River Research and Applications*, 9, 263-277.

Downes B.J., Barmuta L.A., Fairweather P.G., Faith D.P., Keough M.J., Lake P.S., Mapstone B.D. & Quinn G.P. (2002). *Monitoring Ecological Impacts: Concepts and Practice in Flowing Waters*. Cambridge University Press, Cambridge.

Downes B.J., Lake P.S., Glaister A. & Bond N.R. (2006). Effects of sand sedimentation on the macroinvertebrate fauna of lowland streams: are the effects consistent? *Freshwater Biology*, 51, 144-160.

Dube O. (2009). Linking fire and climate: interactions with land use, vegetation, and soil. *Current Opinion in Environmental Sustainability*, 1, 161-169.

Dufrêne M. & Legendre P. (1997). Species assemblages and indicator species definition: the need of an asymmetrical and flexible approach. *Ecological Monographs*, 67, 345-366.

Dwire K.A. & Kauffman J.B. (2003). Fire and riparian ecosystems in landscapes of the western USA. *Forest Ecology and Management*, 178, 61-74.

Earl S.R. & Blinn D.W. (2003). Effects of wildfire ash on water chemistry and biota in South-Western USA streams. *Freshwater Biology*, 48, 1015-1030.

Engstrom R. (2010). First-order fire effects on animals: review and recommendations. *The Journal of the Association for Fire Ecology*, 6, 115.

Fairchild G., Cruz J., Faulds A., Short A. & Matta J. (2003). Microhabitat and landscape influences on aquatic beetle assemblages in a cluster of temporary and permanent ponds. *Journal of the North American Benthological Society*, 22, 224-240.

Feminella J.W. & Hawkins C.P. (1995). Interactions between stream herbivores and periphyton: A quantitative analysis of past experiments. *Journal of the North American Benthological Society*, 14, 465-509.

Fisher S.G. & Likens G.E. (1973). Energy Flow in Bear Brook, New Hampshire: An Integrative Approach to Stream Ecosystem Metabolism. *Ecological Monographs*, 43, 421-439.

Flannigan M., Krawchuk M., de Groot W., Wotton B. & Gowman L. (2009). Implications of changing climate for global wildland fire. *International Journal of Wildland Fire*, 18, 483-507.

Folke C., Carpenter S., Walker B., Scheffer M., Elmqvist T., Gunderson L. & Holling C.S. (2004). Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology Evolution and Systematics*, 35, 557-581.

Fonseca D.M. & Hart D.D. (2001). Colonization history masks habitat preferences in local distributions of stream insects. *Ecology*, 82, 2897-2910.

Foster D., Knight D. & Franklin J. (1998). Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems*, 1, 497-510.

Fuller R.L., LaFave C., Anastasi M., Molina J., Salcedo H. & Ward S. (2008). The role of canopy cover on the recovery of periphyton and macroinvertebrate communities after a month-long flood. *Hydrobiologia*, 598, 47-57.

Gama M., Goncalves A.L., Ferreira V., Graça M.A. & Canhoto C. (2007). Decomposition of Fire Exposed Eucalyptus Leaves in a Portuguese Lowland Stream. *International Review of Hydrobiology*, 92, 229.

Garcia E. & Sorolla A. (2007). La restauració del paisatge de ribera de la vall d'Horta. *VI Trobada d'Estudiosos de Sant Llorenç de Munt i l'Obac*, 223-228.

Gasith A. & Resh V.H. (1999). Streams in Mediterranean climate regions: Abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics*, 30, 51-81.

Goldammer J.G. & Seibert B. (eds.) (1990). *Fire in the Tropical Biota: Ecosystem Processes and Global Challenges*. Editorial Berlin, Spring-Verlag.

Graham R.T., Jain T.B. & Loseke M. (2009). Fuel treatments, fire suppression, and their interaction with wildfire and its impacts: the Warm Lake experience during the Cascade Complex of wildfires in central Idaho, 2007. In: *Gen. Tech. Rep. RMRS-GTR-229.* U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station Fort Collins, CO., p. 36.

Gresswell R.E. (1999). Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society*, 128, 193-221.

Grimm N., Gergel S., McDowell W., Boyer E., Dent C., Groffman P., Hart S., Harvey J., Johnston C. & Mayorga E. (2003). Merging aquatic and terrestrial perspectives of nutrient biogeochemistry. *Oecologia*, 137, 485-501.

Guasch H. & Sabater S. (1995). Seasonal variations in photosynthesis-irradiance responses by biofilms in Mediterranean streams. *Journal of Phycology*, 31, 727-735.

Guinart D. (2007). Restauració de l'ecosistema cremat al sector oriental del Parc Natural de Sant Llorenç del Munt i l'Obac. *VI Trobada d'Estudiosos de Sant Llorenç de Munt i l'Obac*, 37-44.

Gunderson L. (2000). Ecological Resilience- in Theory and Application. *Annual Reviews in Ecology and Systematics*, 31, 425-439.

Gurtz M. & Wallace J. (1984). Substrate-mediated response of stream invertebrates to disturbance. *Ecology*, 65, 1556-1569.

Haddad N., Holyoak M., Mata T., Davies K., Melbourne B. & Preston K. (2008). Species' traits predict the effects of disturbance and productivity on diversity. *Ecology letters*, 11, 348-356.

Hall S. & Lombardozzi D. (2008). Short-term effects of wildfire on montane stream ecosystems in the southern Rocky Mountains: one and two years post-burn. *Western North American Naturalist*, 68, 453-462.

Hawking J.H., Smith L.M. & Le Busque K. (2009). Identification and Ecology of Australian Freshwater Invertebrates (http://www.mdfrc.org.au/bugguide) [internet]

Hawkins C., Murphy M. & Anderson N. (1982). Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology*, 63, 1840-1856.

Herrando S. & Baltà O. (2005). Recuperació de l'avifauna de la zona cremada del Parc Natural de Sant Llorenç del Munt i l'Obac. In: Diputació de Barcelona. Oficina Tècnica de Parcs Naturals Barcelona.

Heyerdahl E., Morgan P. & Riser II J. (2008). Multi-season climate synchronized historical fires in dry forests (1650-1900), northern Rockies, USA. *Ecology*, 89, 705-716.

Hillebrand H. (2008). Grazing regulates the spatial variability of periphyton biomass. *Ecology*, 89, 165-173.

Hose G.C., Jones P. & Lim R.P. (2005). Hyporheic macroinvertebrates in riffle and pool areas of temporary streams in south eastern Australia. *Hydrobiologia*, 532, 81-90.

Houghton J., Meira Filho L.G., Callander B.A., Harris N., Kattenberg A. & Maskell K. (1996). *Climate change 1995: The science of climate change. IPCC*. Cambridge University Press, Cambridge.

Hughes A.R., Byrnes J.E., Kimbro D.L. & Stachowicz J.J. (2007). Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology letters*, 10, 849-864.

Humphries P. & Baldwin D.S. (2003). Drought and aquatic ecosystems: an introduction. *Freshwater Biology*, 48, 1141-1146.

Hurlbert S.H. (1971). The Nonconcept of Species Diversity: A Critique and Alternative Parameters. *Ecology*, 52, 577-586.

Hynes H.B.N. (1975). The stream and its valley. *Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen*, 19, 1:15.

Jeffrey S., Carter J., Moodie K. & Beswick A. (2001). Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling and Software*, 16, 309-330.

Jeffrey S.W. & Humphrey G.F. (1975). New spectrophotometric equations for determining chlorophylls a, b, c_1 and c_2 in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie der Pflanzen*, 167, 191-194.

Jones R.D., Carty D.G., Gresswell R.E., Hudson C.J. & Mahony D.L. (1991). Fishery and aquatic management program in Yellowstone National Park. Technical Report for 1992. In: *US Fish and Wildlife Service* Wyoming.

Jurskis V. (2005). Eucalypt decline in Australia, and a general concept of tree decline and dieback. *Forest Ecology and Management*, 215, 1-20.

Kobayashi S. & Kagaya T. (2009). Colonization of leaf patches at topographically different locations by insect shredders in a small mountain stream. *Limnology*, 10, 143-147.

Krawchuk M., Moritz M., Parisien M., Van Dorn J. & Hayhoe K. (2009). Global pyrogeography: the current and future distribution of wildfire. *PLoS ONE*, 4.

La Point T.W., Parker M., Brewer C.A. & Crossey M. (1983). Impact of fire on recreation stream water quality and spawning habitat. Final report. In: *U.S. Forest Service*. Department of Zoology and Physiology Laramie, Wyoming.

Lake P.S. (1995). Of floods and droughts: River and stream ecosystems of Australia. In: *River and Stream Ecosystems of the World* (eds. Cushing C, Cummins K & Minshall G). Elsewer Amsterdam.

Lake P.S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of North American Benthological Society*, 19, 573-592.

Lane P.N.J., Sheridan G.J. & Noske P.J. (2006). Changes in sediment loads and discharge from small mountain-catchments following wild-fire in south eastern Australia. *Journal of Hydrology*, 331, 495-510.

Lavorel S., Flannigan M., Lambin E. & Scholes M. (2007). Vulnerability of land systems to fire: Interactions among humans, climate, the atmosphere, and ecosystems. *Mitigation and Adaptation Strategies for Global Change*, 12, 33-53.

Lawrence D.E. & Minshall G.W. (1994). Short-and long-term changes in riparian zone vegetation and stream macroinvertebrate community structure. Technical Report NPS/ NRYELL/NRTR-93/XX. In: *Plants and their environments: proceedings of the first biennial scientific conference on the Greater Yellowstone Ecosystem* (ed. Despain DG). U.S. National Park Service, Natural Resources Publication Office Denver, pp. 171–184.

Ledger M., Harris R., Armitage P. & Milner A. (2008). Disturbance frequency influences patch dynamics in stream benthic algal communities. *Oecologia*, 155, 809-819.

Legendre P., Dallot S. & Legendre L. (1985). Succession of species within a community: chronological clustering, with applications to marine and freshwater zooplankton. *American Naturalist*, 257-288.

Legendre P. & Legendre L. (1998). *Numerical ecology*. Elsevier Science Ltd, Oxford, UK.

Lepori F. & Hjerdt N. (2006). Disturbance and aquatic biodiversity: reconciling contrasting views. *BioScience*, 56, 809-818.

Lepori F. & Malmqvist B. (2009). Deterministic control on community assembly peaks at intermediate levels of disturbance. *Oikos*, 118, 471-479.

Levine J. (1999). *Wildland fires and the environment: A global synthesis*. United Nations Environment Programme.

Lobo A. (2005). Monitorització de l'àrea incendiada al Parc Natural de Sant Llorenç de Munt i l'Obac a l'agost del 2003. In: Diputació de Barcelona. Oficina Tècnica de Parcs Naturals Barcelona.

Lotspeich F.B., Mueller E.W. & Frey P.J. (1970). Effects of large scale forest fires on water quality in interior Alaska. In: *Federal Water Pollution Control Administration*. Alaska Water Laboratory College, Alaska.

Ludlam J. & Magoulick D. (2010). Environmental conditions and biotic interactions influence ecosystem structure and function in a drying stream. *Hydrobiologia*, 644, 127-137.

Lyon J.P. & O'Connor J.P. (2008). Smoke on the water: Can riverine fish populations recover following a catastrophic fire-related sediment slug? *Austral Ecology*, 33, 794-806.

Lytle D.A. & Poff N.L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, 19, 94-100.

Lloyd N.J., Mac Nally R. & Lake P.S. (2005). Spatial autocorrelation of assemblages of benthic invertebrates and its relationship to environmental factors in two upland rivers in southeastern Australia. *Diversity and Distributions*, 11, 375.

Maamri A., Chergui H. & Pattee E. (1997). Leaf litter processing in a temporary northeastern Moroccan river. *Archiv fuer Hydrobiologie*, 140, 513-531.

Mackay R. (1992). Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 617-628.

Magoulick D. & Kobza R. (2003). The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology*, 48, 1186-1198.

Magurran A.E. (2004). *Measuring Biological Diversity*. Blackwell Publishing, Oxford.

Malison R.W. & Baxter C.V. (2010a). Effects of wildfire of varying severity on benthic stream insect assemblages and emergence. *Journal of North American Benthological Society*, 29, 1324-1338.

Malison R.W. & Baxter C.V. (2010b). The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Canadian Journal of Fisheries and Aquatic Sciences*, 67, 570-579.

Marchant R., Lake P.S. & Doeg T.J. (1991). Longitudinal variation in recolonization rates of macroinvertebrates along an upland river in south-eastern Australia. *Freshwater Biology*, 25, 349-356.

Marlon J. (2009). The geography of fire: A paleo perspective. PhD thesis. In: University of Oregon, Oregon.

Mayor A., Bautista S., Llovet J. & Bellot J. (2007). Post-fire hydrological and erosional responses of a Mediterranean landscpe: Seven years of catchment-scale dynamics. *Catena*, 71, 68-75.

McClain M., Boyer E., Dent C., Gergel S., Grimm N., Groffman P., Hart S., Harvey J., Johnston C. & Mayorga E. (2003). Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. *Ecosystems*, 6, 301-312.

McCullough D., Werner R. & Neumann D. (1998). Fire and insects in Northern and Boreal Forest Ecosystems of Noth America. *Annual Review of Entomology*, 43, 107-127.

McCutchan J.J. & Lewis W.J. (2002). Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. *Limnology and Oceanography*, 47, 742-752.

Melody K.J. & Richardson J.S. (2004). Responses of invertebrates and algae of a boreal coniferous forest stream to experimental manipulation of leaf litter inputs and shading. *Hydrobiologia*, 519, 197-206.

Mellon C.D., Wipfli M.S. & Li J.L. (2008). Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, USA. *Freshwater Biology*, 53, 2331-2343.

Meyer E. (1989). The Relationship between Body Length Parameters and Dry Mass in Running Water Invertebrates. *Archiv Fur Hydrobiologie*, 117, 191-203.

Mihuc T.B. & Minshall G.W. (1995). Trophic Generalists Vs Trophic Specialists - Implications for Food-Web Dynamics in Postfire Streams. *Ecology*, 76, 2361-2372.

Mihuc T.B. & Minshall G.W. (2005). The trophic basis of reference and post-fire stream food webs 10 years after wildfire in Yellowstone National Park. *Aquatic Sciences*, 67, 541-548.

Mihuc T.B., Minshall G.W. & Robinson C.T. (1996). Response of benthic macroinvertebrate populations in Cache Creek, Yellowstone National Park to the 1988 wildfires. In: *The Ecological Implications of Fire in Greater Yellowstone: Proceedings of the Second Biennial Conference on the Greater Yellowstone Ecosystem.* (ed. Greenlee J). International Association of Wildland Fire Fairfield, Washington, U.S.A., pp. 83-94.

Miller D., Luce C. & Benda L. (2003). Time, space, and episodicity of physical disturbance in streams. *Forest Ecology and Management*, 178, 121-140.

Minshall G.F., Brock J.T., Andrews D.A. & Robinson C.T. (2001a). Water quality, substratum and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek fire. *International Journal of Wildland Fire*, 10, 185-199.

Minshall G.W. (2003). Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management*, 178, 155-161.

Minshall G.W., Andrews D.A., Brock J.T., Robinson C.T. & Lawrence D.E. (1990). Changes in wild trout habitat following forest fire. In: *Wild trout IV: proceedings of the symposium* (eds. Richardson F & Hamre RH). Trout unlimited Arlington, Virginia, pp. 174-177.

Minshall G.W., Brock J.T. & Varley J.D. (1989). Wildfires and Yellowstone's stream ecosystems. *BioScience*, 39, 707-715.

Minshall G.W., Robinson C.T. & Lawrence D.E. (1997). Postfire responses of lotic ecosystems in Yellowstone National Park, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 2509-2525.

Minshall G.W., Robinson C.T., Lawrence D.E., Andrews D.A. & Brock J.T. (2001b). Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbance by wildfire. *International Journal of Wildland Fire*, 10, 201-213.

Minshall G.W., Royer T.V. & Robinson C.T. (2001c). Response of the Cache Creek macroinvertebrates during the first 10 years following disturbance by the 1988 Yellowstone wildfires. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1077-1088.

Minshall G.W., Royer T.V. & Robinson C.T. (2004). Stream Ecosystem Responses to Fire: The First Ten Years. In: *After the Fires: The Ecology of Change in Yellowstone National Park* (ed. Wallace LL). Yale University Press New Haven.

Moreira F., Rego F.C. & Ferreira P.G. (2001). Temporal (1958-1995) pattern of change in a cultural landscape of northwestern Portugal: implications for fire occurrence. *Landscape Ecology*, 16, 557-567.

Moreno J. & Oechel W. (1994). The role of fire in Mediterranean-type ecosystems. *Ecological studies (USA)*.

Munné A., Prat N., Solà C., Bonada N. & Rieradevall M. (2003). A simple field method for assessing the ecological quality of riparian habitat in rivers and streams: QBR index. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 13, 147-163.

Munro N.T., Kovac K.J., Niejalke D. & Cunningham R.B. (2009). The effect of a single burn event on the aquatic invertebrates in artesian springs. *Austral Ecology*, 34, 837-847.

Murphy B. & Timbal B. (2008). A review of recent climate variability and climate change in southeastern Australia. *International journal of Climatology*, 28, 859-879.

Murphy J. & Riley J.P. (1962). A modified single solution method for the determination of phophate in natural waters. *Analytica Chimica Acta*, 27, 31-36.

Nakamura F., Swanson F.J. & Wondzell S.M. (2000). Disturbance regimes of stream and riparian systems - a disturbance-cascade perspective. *Hydrological Processes*, 14, 2849-2860.

Nowlin W., Vanni M. & Yang L. (2008). Comparing resource pulses in aquatic and terrestrial ecosystems. *Ecology*, 89, 647-659.

Oksanen J., Kindt R., Legendre P., O'Hara B., Stevens M.H.H. & Oksanen M.J. (2008). The vegan Package. In: *A Community Ecology Package. Version 1.15-0*, p. 190.

Ordóñez J.L., Reanta J. & Espelta J.M. (2005). Effects of tree size, crown damage, and tree location on post-fire survival and cone production of *Pinus nigra* trees. *Forest Ecology and Management*, 206, 109-117.

Pañella P. (2009). Impacte de la gestió de la fusta cremada i del subsolat al Parc Natural de Sant Llorenç del Munt i l'Obac. In: *VII Trobada d'Estudiosos de Sant Llorenç del Munt i l'Obac*. Diputació de Barcelona Terrassa.

Pardo I., Álvarez M., Casas J., Moreno J.L., Vivas S., Bonada N., Alba-Tercedor J., Jáimez-Cuéllar P., Moyà G., Prat N., Robles S., Suárez M.L., Toro M. & Vidal-Abarca M.R. (2002). El hábitat de los ríos mediterráneos. Diseño de un índice de diversidad de hábitat. *Limnetica*, 21, 115-133.

Paricio S. (2007). Comparació d'un sòl cremat i d'un de no cremat de l'incendi de Sant Llorenç de Munt i l'Obac de l'agost del 2003. *VI Trobada d'Estudiosos de Sant Llorenç de Munt i l'Obac*, 253-259.

Pausas J. & Keeley J. (2009). A burning story: the role of fire in the history of life. *BioScience*, 59, 593-601.

Pausas J.C., Llovet J., Rodrigo A. & Vallejo R. (2008). Are wildfires a disaster in the Mediterranean basin? - A review. *International Journal of Wildland Fire*, 17, 713-723.

Pausas J.G. (2004). Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change*, 63, 337-350.

Pausas J.G. & Verdú M. (2008). Fire reduces morphospace occupation in plant communities. *Ecology*, 89, 2181-2186.

Peterson C. & Stevenson R. (1992). Resistance and resilience of lotic algal communities: importance of disturbance timing and current. *Ecology*, 73, 1445-1461.

Pettit N. & Naiman R. (2007). Fire in the riparian zone: characteristics and ecological consequences. *Ecosystems*, 10, 673-687.

Piñol J., Terradas J. & Lloret F. (1998). Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. *Climatic Change*, 38, 345-357.

Poff N.L. (1997). Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, 16, 391-409.

Power M., Parker M. & Dietrich W. (2008). Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecological Monographs*, 78, 263-282.

Prat N. & Manzano A. (2009). Resum executiu i taula resum. In: *Aigua i canvi climatic. Diagnosi dels impactes previstos a Catalunya* (ed. Catalunya Gd). Agència Catalana de l'Aigua Barcelona.

R Development Core Team. (2006). R: a language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria, www.R-project.org.

Reich P. & Downes B. (2003). Experimental evidence for physical cues involved in oviposition site selection of lotic hydrobiosid caddis flies. *Oecologia*, 136, 465-475.

Reid D.J., Quinn G.P., Lake P.S. & Reich P. (2008). Terrestrial detritus supports the food webs in lowland intermittent streams of south-eastern Australia: a stable isotope study. *Freshwater Biology*, 53, 2036-2050.

Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W., Reice S.R., Sheldon A.L., Wallace J.B. & Wissmar R.C. (1988). The Role of Disturbance in Stream Ecology. *Journal of the North American Benthological Society*, 7, 433-455.

Reznickova P., Paril P. & Zahradkova S. (2007). The Ecological Effect of Drought on the Macroinvertebrate Fauna of a Small Intermittent Stream-An Example from the Czech Republic. *International Review of Hydrobiology*, 92, 514-526.

Richards C. & Minshall G.W. (1992). Spatial and Temporal Trends in Stream Macroinvertebrate Communities - the Influence of Catchment Disturbance. *Hydrobiologia*, 241, 173-184.

Rieman B.E., Luce C.H., Gresswell R.E. & Young M.K. (2003). Editorial. Introduction to the effects of wildland fire on aquatic ecosystems in the Western USA. *Forest Ecology and Management*, 178, 1-3.

Rieradevall M., Bonada N. & Prat N. (1999). Community structure and water quality in the Mediterranean streams of a natural park (St. Llorenç del Munt, NE Spain). *Limnetica*, 17, 45-56.

Rinne J.N. (1996). Short-Term Effects of Wildfire on Fishes and Aquatic Macroinvertebrates in the Southwestern United States. *North American Journal of Fisheries Management*, 16, 653-658.

Robinson C. & Minshall G. (1986). Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *Journal of the North American Benthological Society*, 5, 237-248.

Robinson C.T., Minshall G.W. & Royer T.V. (2000). Inter-annual patterns in macroinvertebrate communities of wilderness streams in Idaho, USA. *Hydrobiologia*, 421, 187-198.

Robinson C.T., Rushforth S.R. & Minshall G.W. (1994). Diatom assemblages of streams influenced by wildfire. *Journal of Phycology,* 30, 206-216.

Robinson C.T., Uehlinger U. & Minshall G.W. (2005). Functional characteristics of wilderness streams twenty years following wildfire. *Western North American Naturalist,* 65, 1-10.

Roby K. & Azuma D. (1995). Changes in a reach of a northern California stream following wildfire. *Environmental Management*, 19, 591-600.

Roby K.B. (1989). Watershed response and recovery from the Will fire: ten years of observation. General Technical Report PSW-109. In: *U.S. Forest Service* pp. 131–136.

Rodrigo A., Retana J. & Pico X. (2004). Direct regeneration is not the only response of Mediterranean forests to large fires. *Ecology*, 85, 716-729.

Rowell A. & Moore P. (2000). Global review of forest fires. In: IUCN The World Conservation Union: Forests for Life Programme Unit, WWF International.

Russell M., Brooks A. & Williams S. (2008). Impact of the 2002-03 wildfires on the macroinvertebrate assemblages of the Snowy River catchment. In: Department of Water and Energy Sydney, p. 42.

Sabater F., Butturini A., Martí E., Muñoz I., Romaní A., Wray J. & Sabater S. (2000). Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of the North American Benthological Society*, 19, 609-620.

Sabater S., Butturini A., Muñoz I., Romaní A., Wray J. & Sabater F. (1998). Effects of removal of riparian vegetation on algae and heterotrophs in a Mediterranean stream. *Journal of Aquatic Ecosystem Stress and Recovery,* 6, 129-140.

Santos X., Bros V. & Miño À. (2009). Recolonization of a burned Mediterranean area by terrestrial gastropods. *Biodiversity and Conservation*, 18, 3153-3165.

Schoennagel T., Nelson C., Theobald D., Carnwath G. & Chapman T. (2009). Implementation of National Fire Plan treatments near the wildland–urban interface in the western United States. *Proceedings of the National Academy of Sciences*, 106, 10706-10711.

Schultz M., Heil A., Hoelzemann J., Spessa A., Thonicke K., Goldammer J., Held A., Pereira J. & van het Bolscher M. (2008). Global wildland fire emissions from 1960 to 2000. *Global Biogeochemical Cycles*, 22, 1-17.

Serra-Cobo J. (2005). Estudi dels quiròpters del Parc Natural de Sant Llorenç del Munt i l’Obac com a base per a la seva gestió. In: Diputació de Barcelona. Oficina Tècnica de Parcs Naturals Barcelona.

Seymour B. & Collett N. (2009). Effects of fire retardant application on heathland surface-dwelling ant species (Order Hymenoptera; Family Formicidae) in Victoria, Australia. *Forest Ecology and Management*, 257, 1261–1270.

Shakesby R., Wallbrink P., Doerr S., English P., Chafer C., Humphreys G., Blake W. & Tomkins K. (2007). Distinctiveness of wildfire effects on soil erosion in south-east Australian eucalypt forests assessed in a global context. *Forest Ecology and Management*, 238, 347-364.

Shakesby R.A. & Doerr S.H. (2006). Wildfire as a hydrological and geomorphological agent. *Earth-Science Reviews*, 74, 269-307.

Smith J. & Lyon L. (2000). *Wildland fire in ecosystems: Effects of fire on fauna*. US Dept. of Agriculture, Forest Service, Rocky Mountain Research Station.

Smith R. (2007). Key Issues Identified from Operational Reviews of Major Fires in Victoria 2006/07. In: Department of Sustainability and Environment Melbourne, p. 95.

Smock L.A. (1980). Relationships between Body Size and Biomass of Aquatic Insects. *Freshwater Biology*, 10, 375-383.

Sostoa A., Caiola N., Vinyoles D. & Casals F. (2006). Diagnosi de les poblacions de peixos del Parc Natural de Sant Llorenç del Munt i l’Obac. In: Diputació de Barcelona. Oficina Tècnica de Parcs Naturals Barcelona.

Spencer C.N.G., K.O.; Hauer, F. R. (2003). Wildfire effects on stream food webs and nutrient dynamics in Glacier National Park, USA. *Forest Ecology and Management*, 178, 141-153.

Stanley E.H., Buschman D.L., Boulton A.J., Grimm N.B. & Fisher S.G. (1994). Invertebrate Resistance and Resilience to Intermittency in a Desert Stream. *American Midland Naturalist*, 131, 288-300.

Stefan D.C. (1977). Effects of a forest fire upon the benthic community of a mountain stream in northeast Idaho. Master's thesis. In: University of Montana Missoula.

Stone M.K. & Wallace J.B. (1998). Long-term recovery of a mountain stream from clearcut logging: the effects of forest succession on benthic invertebrate community structure. *Freshwater Biology*, 39, 151-169.

Tachet H., Richoux P., Bournard M. & Usseglio-Polatera P. (2000). *Invertébrés d'eau douce: systématique, biologie, écologie*. CNRS Éditions, Paris.

Tague C., Seaby L. & Hope A. (2009). Modeling the eco-hydrologic response of a Mediterranean type ecosystem to the combined impacts of projected climate change and altered fire frequencies. *Climatic Change*, 93, 137-155.

Terradas J. (ed.) (1996). *Ecologia del foc*. Edicions Proa, S.A., Barcelona.

Tily C. (2008). Annual Fire Report 2007. In: *Payette National Forest*. U.S. Department of Agriculture, Forest Service, Payette National Forest McCall, ID, p. 32.

Touloumis K. & Stamou G.P. (2009). A metapopulation approach of the dynamics of arthropods from Mediterranean-type ecosystems. *Ecological Modelling*, 220, 1105-1112.

Townsend S.A. & Douglas M.M. (2004). The effect of a wildfire on stream water quality and catchment water in a tropical savanna excluded from fire for 10 years (Kakadu National Park, North Australia). *Water Research*, 38, 3051-3058.

Trabaud L. & Prodon R. (eds.) (1993). *Fire in Mediterranean ecosystems*. Office for Official Publications of the European Communities, Brussels.

Turner M., Romme W. & Tinker D. (2003). Surprises and lessons from the 1988 Yellowstone fires. *Frontiers in Ecology and the Environment*, 1, 351-358.

Turner M., Smithwick E., Metzger K., Tinker D. & Romme W. (2007). Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *Proceedings of the National Academy of Sciences*, 104, 4782-4789.

van der Werf G., Randerson J., Giglio L., Gobron N. & Dolman A. (2008). Climate controls on the variability of fires in the tropics and subtropics. *Global Biogeochemical Cycles*, 22, 1-13.

Velasco J., Millán A., Vidal-Abarca M., Suarez M., Guerrero C. & Ortega M. (2003). Macrophytic, epipelic and epilithic primary production in a semiarid Mediterranean stream. *Freshwater Biology*, 48, 1408-1420.

Victoria E. (2003). The impact of Bushfires Following a Flash Flood Event in the Catchment of the Ovens River. In: EPA Victoria, www.epa.vic.gov.au/water/rivers/docs/ovens_catchment_report.pdf.

Victoria E. (2004). River health: a snapshot of the effects of the 2003 bushfires. In. EPA Victoria, http://www.epa.vic.gov.au/Water/Threats/docs/bushfire.pdf.

Vieira N.K.M., Clements W.H., Guevara L.S. & Jacobs B.F. (2004). Resistance and resilence of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology*, 49, 1243-1259.

Vila-Escalé M. (2009). Efectes d'un incendi forestal en una riera mediterrania (Sant Llorenç del Munt, 2003). PhD thesis dissertation. In: *Departament d'Ecologia*. Universitat de Barcelona. Barcelona, p. 214.

Vila-Escalé M., Vegas-Vilarrubia T. & Prat N. (2007). Release of polycyclic aromatic compounds into a Mediterranean creek (Catalonia, NE Spain) after a forest fire. *Water Research*, 41, 2171-2179.

Vinson M. & Hawkins C. (1998). Biodiversity of stream insects: variation at local, basin, and regional Scales 1. *Annual Review of Entomology*, 43, 271-293.

Wagener S., Oswood M. & Schimel J. (1998). Rivers and soils: parallels in carbon and nutrient processing. *BioScience*, 48, 104-108.

Wellnitz T. & Ward J. (1998). Does light intensity modify the effect mayfly grazers have on periphyton? *Freshwater Biology*, 39, 135-149.

Wells F., Metzeling L. & Newall P. (2002). Macroinvertebrate regionalisation for use in the management of aquatic ecosystems in Victoria, Australia. *Environmental Monitoring and Assessment*, 74, 271-294.

Westerling A., Hidalgo H., Cayan D. & Swetnam T. (2006). Warming and Earlier Spring Increase Western US Forest Wildfire Activity. *Science*, 313, 940-943.

Westerling A.L. & Swetnam T.W. (2003). Interannual to decadal drought and wildfire in the western United States. *Eos*, 84, 545-554.

Western Regional Climate Center W. (2008). Idaho climate summaries. Western Regional Climate Center. http://www.wrcc.dri.edu/summary/climsmid.html

Whelan R.J. (1995). *The Ecology of fire*. Cambridge University Press, Cambridge.

Williams A., Karoly D. & Tapper N. (2001). The sensitivity of Australian fire danger to climate change. *Climatic change*, 49, 171-191.

Williams D.D. (2006). *The biology of temporary waters*. Oxford University Press, USA, Oxford New York.

Wooton J.T. & Power M.E. (1993). Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Sciences*, 90, 1384-1387.

Wootton J. (1998). Effects of disturbance on species diversity: a multitrophic perspective. *The American Naturalist*, 152, 803-825.

Yang L., Bastow J., Spence K. & Wright A. (2008). What can we learn from resource pulses. *Ecology*, 89, 621-634.

Zimmermann E. & Death R. (2002). Effect of substrate stability and canopy cover on stream invertebrate communities. *New Zealand Journal of Marine and Freshwater Research*, 36, 537-545.

Appendix 1. List of all the recorded taxons and mean abundance per square meter for closed and open canopies (February 2006 – February 2007) separated by habitats: stone, sediment, and leaf litter.

STONE HABITAT			**Closed canopy**											**Open canopy**								
Order	Family	taxon	**feb06**	**mar**	**apr**	**may**	**july**	**sep**	**oct**	**nov**	**dec**	**jan**	**feb07**	**feb06**	**mar**	**apr**	**may**	**oct**	**nov**	**dec**	**jan**	**feb07**
OTHERS	Glossiphoniidae	*Helobdella stagnalis*						7					2									
	Oligochaeta	Oligochaeta	108	2803	4373	852	116	266	272	110	1212	318	900	193	2111	8056	4642	7	42	1036	1219	2923
	Ostracoda	Ostracoda	167	1379	1068	372	1564	1850	799	112	2520	294	899	24	184	10659	1608	138	76	300	1413	4074
	Hydracarina	Hydracarina		12	276	99	58	90		3	821		41		17	815	258	77	10	65	17	26
ODONATA	Coenagrionidae	*Pyrrhosoma nymphula*						32	13									3				
	Corduliidae	*Somatochlora pro parte*									192		13							15	5	69
	Lestidae	*Chalcolestes viridis*					15									6						
	Libellulidae	*Crocothemis erythraea*									5											
		Libellula sp.							7	3						6						
PLECOPTERA	Leuctridae	*Pachyleuctra* sp.																		31		
	Nemouridae	*Nemoura* sp.	14	16						63	575	70	28	13	31	24		40	222	483	62	20
	Perlodidae	*Isoperla* sp.	7			10					34		6		4	9						
EPHEMEROPTERA	Baetidae	*Acentrella* sp.											317			31		3				202
		Baetis sp.	18	14		61				128	700	779	23	104	28		61		175	4840	829	51
		Pseudocentroptilum sp.					428	830	120	40		3	17					6			9	50
	Caenidae	*Caenis* sp.		7			80	348	299	89	1453	3	129				4		7		6	37
	Ephemerellidae	*Ephemerella* sp.	7	37	154	430				3		5	5		55	326	34					
	Heptageniidae	*Heptagenia* sp.																	3			
	Leptophlebiidae	*Habroleptoides* sp.	6		5				231	187	3091	75		4					11			
		Habrophlebia sp.		40	7	12						220	450								28	103
		Paraleptophlebia sp.	4											4								
HETEROPTERA	Hydrometridae	*Hydrometra* sp.			3	51											57					
	Notonectidae	*Notonecta* sp.				3		4	3													
	Pleidae	*Plea* sp.							3													
TRICHOPTERA	Hydropsychidae	*Hydropsyche* sp.															22		4	4	8	
	Hydroptilidae	*Allotrichia* sp.			2								2									
		Hydroptila sp.			5	3						32	7			125	40			24	35	15
	Limnephilidae	*Limnephilus* sp.																	8			
		Mesophylax sp.				2						3	9							35	8	42

STONE HABITAT			**Closed canopy**											**Open canopy**								
Order	Family	taxon	**feb06**	**mar**	**apr**	**may**	**july**	**sep**	**oct**	**nov**	**dec**	**jan**	**feb07**	**feb06**	**mar**	**apr**	**may**	**oct**	**nov**	**dec**	**jan**	**feb07**
	Philopotamidae	*Wormaldia* sp.														6						
	Polycentropodidae	*Plectrocnemia* sp.									102											
	Psychomyiidae	*Tinodes* sp.					9															
COLEOPTERA	Dryopidae	*Dryops* sp.								3			7									7
	Dytiscidae	*Agabus* sp.	4		18		3		3	21	169	29	6		3	23	7	112	34	84	36	73
		Deronectes sp.		23		6			3	7	68		9		3	91	7	4		6		28
		Dytiscus sp.		7																		
		Hydroporus sp.	3	51	81	22	3	19		3	34			14	3	102	12		17	55	13	45
		Meladema sp.			5													16				2
		Stictonectes sp.	14	35	7	53	15	142	26	7	1427	6	26		4	5			10	43	22	192
	Elmidae	*Oulimnius* sp.	6	21	3		22		3		72		2									
	Haliplidae	*Haliplus* sp.	13	10	126			49	16	14	140		6	20	70	25			26	22	123	30
	Hydraenidae	*Hydraena* sp.					39															
		Limnebius sp.				10	9								4			4				
	Hydrochidae	*Hydrochus* sp.					3															
	Hydrophilidae	*Coelostoma* sp.					3										7					
		Laccobius sp.			5	6	3									3	3			4	3	3
DIPTERA	Anthomyidae	Anthomyidae			7										3	12				10	6	
	Ceratopogonidae	Ceratopogoninae		7			15			7		5	9		7		117	10				
		Dasyheleinae									34											
		Forcipomyiinae					31										4					
	Chaoboridae	Chaoborus sp.						65														
	Chironomidae	Chironominae	28	208	230	61	305	303	132		1261	17	148		40	531	415	9	7	176	91	369
		Orthocladiinae	1746	1155	3491	2022	15	3	389	866	1266	1018	929	3909	4625	4533	1253	2513	3313	3716	3850	3244
		Tanypodinae	4	35	220	120	280	201	29	24	381	71	101		3	182	292	13	7	45	173	538
	Culicidae	Culicinae					74	8														
	Dixidae	*Dixa* sp.																			3	
		Dixella sp.				11								4		6						
	Dolichopodidae	Dolichopodidae														9						
	Empididae	Clinocerinae			3							2	2		29	61	3			36		
		Hemerodromiinae																		14	8	9

STONE HABITAT			**Closed canopy**											**Open canopy**								
Order	Family	taxon	**feb06**	**mar**	**apr**	**may**	**july**	**sep**	**oct**	**nov**	**dec**	**jan**	**feb07**	**feb06**	**mar**	**apr**	**may**	**oct**	**nov**	**dec**	**jan**	**feb07**
	Ephydridae	Ephydridae				2			7													
	Limoniidae	Hexatomini										3	5		6	249	7		3	49		7
		Limoniini										8				17					9	
		Pediciini																	8			
	Psychodidae	Psychodidae			5		60					3	2				4			5		
	Sciomyzidae	Sciomyzidae								3												
	Simuliidae	Simuliidae	559	106	80	218			10	170	2842	1160	475	415	1247	993	4	491	278	3764	411	23
	Stratiomyidae	Stratiomyidae					88			10		11	2							5		
	Tabanidae	Tabanidae						6		7												
	Tipulidae	Tipulidae							6			2					10			6	12	
MOLLUSCA	Ancylidae	*Ancylus fluviatilis*	25	12	8	8	177	87	29	74	1589	14	185		40	25	850	14	341	49	499	484
	Lymnaeidae	*Galba* sp.		104	202	310	12			3	246		7			78	464	13		36	42	126
		Radix sp.	28				511	761	114		481	8	19							6	6	
	Physidae	*Physella* sp.		7		42	266	71	23	14	212	2	18									
	Planorbidae	*Gyraulus* sp.				32	1182	1008	179	51	558		6					3	4			
	Sphaeriidae	*Pisidium* sp.						4	9		68											

SEDIMENT HABITAT			**closed canopy**											**open canopy**								
Order	Family	taxon	**feb06**	**mar**	**apr**	**may**	**july**	**sep**	**oct**	**nov**	**dec**	**jan**	**feb07**	**feb06**	**mar**	**apr**	**may**	**oct**	**nov**	**dec**	**jan**	**feb07**
OTHERS	Glossiphoniidae	*Helobdella stagnalis*						68		102												
	Oligochaeta	Oligochaeta	102	10962	10556	4534	11165	2808	1624	271	643	880	338	3282	7410	8628	21891			271	305	643
	Ostracoda	Ostracoda	914	1658	2199	1895	6462	1793	3620	372	135	846	102	1387	1996	4195	5447	68	135	135		406
	Hydracarina	Hydracarina	34			102	169	68	34					102		34	34					
ODONATA	Coenagrionidae	*Pyrrhosoma nymphula*					34	34														
	Corduliidae	*Somatochlora pro parte*									34			34		34						
	Libellulidae	*Libellula* sp.																	135			
PLECOPTERA	Nemouridae	*Nemoura* sp.												135	34					34		
EPHEMEROPTERA	Baetidae	*Baetis* sp.		34		34					237			34	34					68		
		Pseudocentroptilum sp.					372	474	102	68		34						34			102	68
	Caenidae	*Caenis* sp.					169	271	1184	102	135	338	68						34	34	102	
	Ephemerellidae	*Ephemerella* sp.		34																		

SEDIMENT HABITAT			**closed canopy**											**open canopy**								
Order	Family	taxon	**feb06**	**mar**	**apr**	**may**	**july**	**sep**	**oct**	**nov**	**dec**	**jan**	**feb07**	**feb06**	**mar**	**apr**	**may**	**oct**	**nov**	**dec**	**jan**	**feb07**
	Leptophlebiidae	*Habroleptoides* sp.							474	169	271			34						34	34	
		Habrophlebia sp.										102					34					34
HETEROPTERA	Corixidae	*Arctocorisa* sp.															34					
TRICHOPTERA	Hydroptilidae	*Hydroptila* sp.													34					34		
	Limnephilidae	*Limnephilus* sp.																	34			
		Mesophylax sp.		34								34		271						135	102	305
COLEOPTERA	Dytiscidae	*Agabus* sp.														34		34				
		Deronectes sp.		102												68						
		Hydroporus sp.	34	68										68	68				34			
		Stictonectes sp.	34	135	643	237	102	203	68	102	135	68		34	135	338	34		237	305	305	68
	Elmidae	*Oulimnius* sp.					34															
	Haliplidae	*Haliplus* sp.	102	34	34			34						68	34	68			135	135	68	34
	Hydrophilidae	*Laccobius* sp.																	34			
DIPTERA	Ceratopogonidae	Ceratopogoninae				34	1150										34		34			
		Dasyheleinae												34								
	Chironomidae	Chironominae	271	338	5616	1861	12688	643	406	34	271	880	237		880	7680	10049	135	68	440	711	1015
		Orthocladiinae	1117	2165	237	338	102		102	68	338	135	169	3113	3823	203	744	2402	135	305	34	474
		Tanypodinae	34	102	2030	2030	1387	406	169	68	68	271	102		68	1049	1962	135	1421	271	135	541
	Culicidae	Culicinae					305															
	Ephydridae	Ephydridae	34				305															
	Limoniidae	Hexatomini												34	34							
	Rhagionidae	Rhagionidae		34						34												
	Simuliidae	Simuliidae		169														34	34	203		
	Tipulidae	Tipulidae																		34		
MOLLUSCA	Ancylidae	*Ancylus fluviatilis*					34	34		68		102	68			34	135			34	68	
	Lymnaeidae	*Galba* sp.	34	34	203	135	102			34	34					102	440	34		237	68	34
		Radix sp.	34		68	68	3823	575	102	34	34		68									
	Physidae	*Physella* sp.					305	102														
	Planorbidae	*Gyraulus* sp.				135	846	440	271	34	135		169									
	Sphaeriidae	*Pisidium* sp.		34																		

LEAF LITTER HABITAT			**closed canopy**											**open canopy**								
Order	Family	taxon	**feb06**	**mar**	**apr**	**may**	**july**	**sep**	**oct**	**nov**	**dec**	**jan**	**feb07**	**feb06**	**mar**	**apr**	**may**	**oct**	**nov**	**dec**	**jan**	**feb07**
OTHERS	Glossiphoniidae	*Helobdella stagnalis*						18	24	44		6	3			97						
	Oligochaeta	Oligochaeta	447	2716	1475	1108	1887	814	482	1822	76	2354	173	2407	1675	2275	2584	3	262	811	367	946
	Ostracoda	Ostrcacoda	1784	626	1570	820	1587	664	438	323	267	238	150	1187	1196	2927	517	388	129	38	173	705
	Hydracarina	Hydracarina	18	3	3	12	62	138	109		21	3		35	26	29	6	38		18		3
ODONATA	Aeshnidae	*Anax* sp.						6														
		Boyeria irene			6		3															
	Coenagrionidae	*Ischnura* sp.								9									3			
		Nehalennia sp.										6										
		Pyrrhosoma nymphula						29	47		3	3	3									
	Corduliidae	*Somatochlora pro parte*	3		6		3				32		9	9	3	3				68		3
	Lestidae	*Sympecma* sp.			26																	
	Libellulidae	*Diplacodes lefebvrii*										3										
		Libellula sp.	12		3				3	53	3								47	6	21	
		Orthetrum sp.									6											
		Sympetrum sp.	3		21	3				3	3	6			3	3			41			
PLECOPTERA	Nemouridae	*Nemoura* sp.		3						3	6	3							3	26		
EPHEMEROPTERA	Baetidae	*Acentrella* sp.							12									94				3
		Baetis sp.	6	3		21					35	3		3			9					
		Pseudocentroptilum sp.	79	29	62	9	285	223	147	197	56	123	97	3	3	9	3	73	215	32	273	179
	Caenidae	*Caenis* sp.	6		6	3	29	168	56	26	312	79	150	3	3					3	15	21
	Ephemerellidae	*Ephemerella* sp.	3	9		3								3	3							
	Leptophlebiidae	*Habroleptoides* sp.	29						18	21	285				9				21			
		Habrophlebia sp.		9	338	15						62	59			26	9				18	118
		Paraleptophlebia sp.	38											3								
HETEROPTERA	Corixidae	*Arctocorisa* sp.				3																
	Gerridae	*Gerris* sp.				3			3													
	Hydrometridae	*Hydrometra* sp.				9		3							3	3	3					
	Mesoveliidae	*Mesovelia* sp.		3	3		3								3					12		
	Nepidae	*Nepa* sp.				3									3							
	Notonectidae	*Notonecta* sp.			9	3	3	21	9						3	3	6				3	
	Pleidae	*Plea* sp.								9												

LEAF LITTER HABITAT			**closed canopy**											**open canopy**								
Order	Family	taxon	**feb06**	**mar**	**apr**	**may**	**july**	**sep**	**oct**	**nov**	**dec**	**jan**	**feb07**	**feb06**	**mar**	**apr**	**may**	**oct**	**nov**	**dec**	**jan**	**feb07**
	Veliidae	*Microvelia* sp.					3		3					3	3				3			
TRICHOPTERA	Hydroptilidae	*Hydroptila* sp.									3	3	3								3	
	Limnephilidae	*Limnephilus* sp.																				12
		Mesophylax sp.	15			3				3					3					24	53	65
COLEOPTERA	Dryopidae	*Dryops* sp.			3								3			3			3		3	
	Dytiscidae	*Agabus* sp.	18	15	3	6					6				3	9		26	6	24	6	
		Deronectes sp.	3		6						3			12	9	6				18		9
		Dytiscus sp.			6																	
		Hydroglyphus sp.													9							
		Hydroporus sp.		3							6			3	3		3		3	41	9	
		Laccophilus sp.			3																	
		Meladema sp.					3				3											
		Stictonectes sp.	153	35	212	176		35	35	76	147	65	21	56	88	65	15	3	126	53	138	59
		Suphrodytes sp.										3										
		Yola sp.													6							
	Elmidae	*Oulimnius* sp.			3				3		3											
	Gyrinidae	*Gyrinus* sp.								3		9							3	6		
	Haliplidae	*Haliplus* sp.	59	88	6		6	15	15	29	6	9	6	35	12	32		3	91	50	6	9
	Hydraenidae	*Hydraena* sp.		3																		
		Limnebius sp.		29										3	9							
	Hydrochidae	*Hydrochus* sp.																	3			
	Hydrophilidae	*Helochares* sp.		3																		
		Laccobius sp.		6		3			9							24	3		6			
	Scirtidae	*Cyphon* sp.		3					6													
		Hydrocyphon sp.		6	6										3							
DIPTERA	Anthomyidae	Anthomyidae							3								9				3	
	Athericidae	Athericidae						9														
	Ceratopogonidae	Ceratopogoninae		6	3		3		3	3		3		12	12			6	3			
		Forcipomyiinae					3															
	Chaoboridae	*Chaoborus* sp.						9														
	Chironomidae	Chironominae	444	194	1772	926	1082	62	47	526	141	558	159	312	362	849	362	15	126	76	168	85

LEAF LITTER HABITAT			**closed canopy**											**open canopy**								
Order	Family	taxon	**feb06**	**mar**	**apr**	**may**	**july**	**sep**	**oct**	**nov**	**dec**	**jan**	**feb07**	**feb06**	**mar**	**apr**	**may**	**oct**	**nov**	**dec**	**jan**	**feb07**
		Orthocladiinae	467	241	262	73		6	26	100	197	288	121	2066	135	191	450	426	635	990	179	118
		Tanypodinae	144	76	1132	394	309	179	129	159	21	115	68	50	91	250	194	3	15	68	103	76
	Culicidae	Culicinae					118	18	35													
	Dixidae	*Dixa* sp.									3										6	3
		Dixella sp.			12												3		3			
	Empididae	Clinocerinae		3					3					3		6						
		Hemerodromiinae		3										3								
	Ephydridae	Ephydridae											6				3					
	Limoniidae	Limoniini										3										
	Psychodidae	Psychodidae		3			3				3					15						
	Simuliidae	Simuliidae	6								6	6	3						3			
	Stratiomyidae	Stratiomyidae		3			6		3	3					3	6						
	Tabanidae	Tabanidae						32		6	6											
	Tipulidae	Tipulidae		3							3	6				12	6					
MOLLUSCA	Ancylidae	*Ancylus fluviatilis*				24	38	21	12	18	24	21	26		3	18	65		12	24	35	53
	Lymnaeidae	*Galba* sp.	21	47	382	350	3		9	3	21		6	15	32	259	217	18	94	82	335	91
		Radix sp.	6				779	300	200	29	29	26	18		32		24	9		35	15	24
	Physidae	*Physella* sp.				141	461	41	18	59	88	50	18									
	Planorbidae	*Gyraulus* sp.	12	6	53	520	1455	844	244	144	68	59	29						6			
	Sphaeriidae	*Pisidium* sp.			15		3	3		12	9	3	15									
	Valvatidae	*Valvata* sp.							3													

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Pepi