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Fire as a disturbance in mediterranean climate streams

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Abstract Mediterranean climate ecosystems are among the most fire-prone in the world; however, little is known about the effects of fire on mediterranean streams (med-streams). Fire impacts on med-streams are associated with increased runoff and erosion from severely burned landscapes during storms, particularly the first intense rains. Increased inputs of water, solutes, nutrients, sediment, organic matter, and ash to streams after fires are usually observed for months to up to 4 years. Return to pre-fire conditions is associated with vegetation recovery. Benthic algae, invertebrates, and

fish are reduced to low levels by scouring floods after wildfire. If riparian zones are burned, benthic algae increase, and invertebrate communities become dominated by *r*-strategist species. Fishes are eradicated from reaches affected by intense wildfire and often do not re-colonize quickly because of downstream barriers. In general, med-stream communities appear to be more resilient to fire compared to streams in other ecosystems because of the rapid recovery of mediterranean upland and riparian vegetation and geomorphological conditions (1–4 years in med-streams vs 5–10 years in non-med streams). However, drought or mass sediment movements after fire can prolong fire effects. Studies of the long-term effects of fire and the consequences of fire management practices are still needed.

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Guest editors: N. Bonada & V. H. Resh / Streams in Mediterranean climate regions: lessons learned from the last decade

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Introduction

Wildfire affects ecosystems throughout the world (Lavorel et al., 2007; Bowman et al., 2009; Flannigan et al., 2009; Pausas & Keeley, 2009). With an average of 383 million hectares burned annually over the last decade (Schultz et al., 2008), wildfire is an important process determining the evolution, distribution, structure, and function of the world's biomes (Bond et al., 2005; Bond & Keeley, 2005; Cowling et al., 2005).

The effects of fire on terrestrial communities have been well-studied in the tropics (Goldammer & Seibert, 1990; van der Werf et al., 2008), mediterranean climate and desert regions (Moreno & Oechel, 1994; Pausas, 2004; Rodrigo et al., 2004; Brooks & Minnich, 2006; Wright & Clarke, 2007), and temperate climate areas in the western United States (Agee, 1998; Flannigan et al., 2009), and Australia (Bradstock et al., 2002). In contrast, studies of altered sediment and solute movement in streams subsequent to fires (Engle et al., 2008; Shakesby, 2011) and, especially, information on fire effects on the biology of aquatic systems are more limited (Minshall et al., 1989; Rinne, 1996; Gresswell, 1999; Minshall, 2003; Rieman et al., 2003). Surprisingly, studies of fire impacts on aquatic ecosystems in mediterranean regions (med-regions) are scarce despite the prominence of fire in these regions.

The focus of this paper is to review the responses of stream ecosystems to fire in med-regions. Although there have been studies of the effects of fire on sediment erosion, transport, and deposition in med-regions (reviewed in Pausas et al., 2008; Shakesby, 2011), there have been fewer studies on physical, chemical, and biological responses of streams to fire. We concentrate on recent information from streams in the northwestern Mediterranean Basin (Vila-Escalé et al., 2007; Vila-Escalé, 2009; Verkaik, 2010) and California (Simpson, 2006; Rehn, 2010; Coombs & Melack, 2012), but also include information from other med-regions when available (e.g., Britton, 1991a, b; Cowell et al., 2006).

The geographic delineation of mediterranean streams (med-streams) has been described in other parts of this special issue. In general, mediterranean ecosystems (med-ecosystems) are found on the western edges of continents between 30° and 40° north and south of the equator and are characterized by strong seasonality and large interannual variability in rainfall (Gasith & Resh, 1999). Despite their similarities, med-ecosystems vary from region to region in topography, microclimate, and recent modal fire frequency (Table 1), and there is substantial variation in fire recurrence intervals among mediterranean vegetation types (Stephens et al., 2007; Van de Water & Safford, 2011). The extent, frequency, intensity, and timing of fires are driven by climatic, meteorologic, topographic, and vegetation conditions (Leith & Whittaker, 1975; Rothermel, 1983; Woodward, 1987; Flannigan et al., 2009). With the exception of the Chilean matorral and parts of coastal California where natural fires were rare (Keeley 1982; Muñoz & Fuentes,

1989), fire has been a frequent natural feature of med-ecosystems through the late Quaternary (e.g. Carrión et al., 2003; Stephens et al., 2007), being promoted by the wet season accumulation followed by dry season desiccation of vegetation and ignition from lightning strikes. Lightning was originally the primary cause of fires in med-regions; however, mediterranean fires have been ignited largely by human activity since extensive human settlement (Komarek, 1964; Kruger & Bigalke, 1984; Fuentes et al., 1994; Vázquez & Moreno, 1998; Keeley, 2002; Pausas & Keeley, 2009). Prehistoric humans often used fire to clear vegetation and promote grasslands for hunting, gathering, farming, or pastoral activities, with fire use continuing into historic times (Pausas & Vallejo, 1999; Keeley, 2002). Low to medium intensity fires burned large areas in med-regions in prehistoric and historic times, but their frequency declined with the institution of fire suppression activities in the early to mid 1900s (Stephens et al., 2007; Van de Water & Safford, 2011). Because of rapid human population growth in med-regions and associated changes in land use and ignition sources, concerns about wildfires became prominent in the 1980s when there was a large rise in fire frequency, severity, and extent, even in central Chilean ecosystems (Burrows et al., 1995; Keeley et al., 1999; Pausas, 2004; Pausas et al., 2008; Syphard et al., 2009). As an indication of the current extent of fires in med-regions, more than 400,000 ha burned in Spain in 1994 (Terradas, 1996) and another 400,000 ha burned in California in 2007 (Keeley, 2009). Further, most climate change models predict that med-regions will experience longer and more frequent droughts, and higher temperatures leading to an increased intensity and frequency of fire (Lenihan et al., 2003; Bowman et al., 2009). Because of the destructive effects of fires on natural and human systems, large amounts of money, time, and effort have been devoted to preventing, fighting, and recovering from fires. Increased efforts have focused on fire prevention by reducing fuels through prescribed or controlled burns or mechanical vegetation removal (Shea, 1982; Brown et al., 1991; Fernandes & Botelho, 2004); however, the ecological consequences of these actions are not fully known (Fernandes & Botelho, 2003; Arkle & Pilliod, 2010). Although fire suppression activities have continued to be used to limit fire damage over the last 50 years, such efforts, while reducing fire frequency, have not affected the size of fires or the total area burned in mediterranean shrub, scrub, and wood lands (Keeley

Table 1 Area, topographic heterogeneity, interannual rainfall predictability, and estimated natural mean fire frequency for the five med-regions of the world. Fire frequency ranges are typical ranges for shrublands (based on Cowling et al., 1996, 2005)

Region	Area ($\times 10^6$ km ²)	Topographic heterogeneity	Interannual rainfall predictability	Natural mean fire frequency (years)
California	0.32	High	Low	40–60
Central Chile	0.14	Very high	Moderate	Fire-free
Mediterranean Basin	2.30	High	Low	25–50
Cape Region	0.09	Moderate	High	10–20
S.W. Australia	0.31	Low	High	10–15

et al., 1999; Moritz et al., 2004; Pausas et al., 2008). In fact, fires have burned larger areas with increased severity in some instances (e.g., Miller et al., 2009).

From information examined in preparing this review, we contend that severe fires constitute pervasive, extensive, and frequent disturbances for med-streams, which have direct natural (ash deposition, canopy opening, increased temperatures) and direct anthropogenic (introduction of contaminants such as fire retardants) effects on aquatic ecosystems. Additional, sometimes dramatic, fire effects on streams result from the increased transport of water, sediment, organic matter, nutrients, and contaminants during and following subsequent rains. Although many immediate direct effects on streams may be short-lived, lasting for days to weeks, indirect effects following rains may influence the geomorphology, chemistry, and biology of receiving water bodies for longer periods of time, paralleling the recovery of upland and riparian vegetation, and of catchment ecosystem processes. Because fire has long been a frequent and natural perturbation in most med-ecosystems and because med-streams are exposed to wide hydrologic fluctuations through the seasons and across years, we hypothesize that med-stream communities are resilient to fire and other disturbances, recovering more quickly than aquatic ecosystems in non-med regions.

Fire effects on med-ecosystems

Just after the fire

Effects on terrestrial vegetation relevant for streams

Because of the wet season accumulation of plant biomass that dries during the long dry season, vegetation

in mediterranean landscapes is among the most fire-prone in the world (Barro & Conrad, 1991; Halsey, 2008). Unlike forests, where fire frequency and severity are linked with the age and condition of upland vegetation (e.g., fuel continuity, canopy closure, accumulated dead plant material), fires in mediterranean shrublands have been more directly related to ‘fire weather’, which includes high temperatures, low humidities, and strong winds that generally override the age or condition of vegetation in promoting major wildfires (Moritz et al., 2004; Piñol et al., 2007). In some cases, fire activity also increases when wet rainy seasons precede the fire season by promoting the accumulation of fine fuels (particularly non-native forbs and grasses that dry during the summer) (Keeley, 2004; Pausas, 2004). The relative importance of climate and fuels can vary through the sequence leading from ignition through fire spread, with both acting synergistically and varying topographically, such as when ridge line fuels determine fire ignition and expansion patterns but fire weather then drives fires into lower elevation areas (Moritz et al. 2004; Pausas & Paula, 2012). Wind-driven fires in med-regions produce extensive, but highly heterogeneous impacts on vegetation, ranging from the complete combustion of organic material to areas of unburned vegetation receiving inputs of ash from nearby burned areas (Zedler & Seiger, 2000; Keeley et al., 2009a). Patchiness in the presence, intensity (energy released), and severity (loss or change in above and below ground organic matter) of fires are created by uneven topography, variable winds, spatial heterogeneity in vegetation, and isolated ignitions by wind-blown embers (DeBano et al., 1998; Keeley, 2009; Prepas et al., 2009).

One consequence of human land use and the result of more frequent ignition of wildfires, has been the conversion of mediterranean shrublands and other vegetation types, particularly in California and Australia,

into grasslands comprising invasive, non-native grasses and forbs (Brooks et al., 2004; Keeley et al., 2005). These invasive plants form continuous stands of flammable vegetation with copious seed production that have changed fire ignition and spread in these med-regions. Although the frequency and areal extent of large fires has changed little since the European colonization of southern California beginning in the late 1700s (Keeley et al., 2009b), fires have assumed a greater role in southern Europe because of vegetation re-growth following the abandonment of farmlands, orchards, and plantations (Pausas & Fernández-Muñoz, 2011). Through increased fire ignitions, changes in land use, and fire suppression and management activities, humans have fundamentally altered fire regimes in med-regions (Pausas et al., 2008).

Of particular interest for fire effects on streams is the impact of fires on riparian vegetation, which differs from upland vegetation in species composition, and stem and foliar moisture content particularly during dry seasons (Agee et al., 2002; Dwire & Kauffman, 2003; Pettit & Naiman, 2007; Rood et al., 2007). Although most studies have not differentiated fire effects on riparian versus surrounding upland vegetation in med-ecosystems, recent reviews based on temperate forest ecosystems have begun to clarify fire impacts on riparian zones, drawing conclusions that appear to be relevant to med-systems (Dwire & Kauffman, 2003; Pettit & Naiman, 2007). In both med- and other ecosystems, the effectiveness of the riparian zone, as a barrier and buffer to wildfire spread, is directly proportional to its width, foliar moistness, and humidity, with fire severity, soil disruption, and the destruction of understory fuels increasing with distance from the stream edge (Chen et al., 1999; Bêche et al., 2005; Kobziar & McBride, 2006; Pettit & Naiman, 2007; Halofsky & Hibbs, 2008). In addition, species of riparian plants tend to be less ignitable than upland plants (Ellis, 2001; Dudley et al., 2011). Nevertheless, fire weather can cause dry, windy conditions when even riparian areas will burn, although patchily because of heterogeneity in winds, fuels, and moisture levels (Moritz, 2003; Skinner, 2003). As in surrounding uplands, highly flammable invasive plants also change riparian fire regimes (Lambert et al., 2010). For example, the widespread establishment of massive stands of *Arundo donax* (giant reed), a tall rhizomatous grass occupying low-gradient riparian systems in the Mediterranean Basin, California, South Africa, and

Australia, has turned riparian vegetation from a barrier to fire spread to a pathway carrying fire through riparian zones (Dudley, 2000; Coffman et al., 2010). Invasions of riparian zones by introduced *Acacias* in South Africa also have changed the hydrologic, biogeochemical, and fire regimes of these systems (Le Maitre et al., 2011).

Immediate direct effects on streams

Immediate direct effects of fire on streams before the first rain events encompass high temperatures, the movement of particles down steep slopes under dry conditions (dry ravel erosion), and inputs of ash and atmospheric deposition (e.g., from smoke). The effects of ash inputs on stream communities depend on stream flow, being diluted and carried downstream by substantial flows but deposited in pools when flows are very low or nonexistent. Ash inputs may change stream pH and be metabolized by microbes, resulting in low dissolved oxygen levels; however, such immediate direct effects have not been observed in med-streams. Davis et al. (1989), working in southern California watersheds, recorded substantive dry ravel inputs to stream channels in the first month after fire and mobilization of these inputs after 4–5 months. Nutrient levels and sediment transport were not affected by a fire during the dry season directly after the fire, but increased during storms in the ensuing wet season (Coombs, 2006; Coombs & Melack, 2012).

Although many riparian trees were killed or damaged by fires in southern California, most trunks (snags) remained standing immediately after fires, contributing to bank stability (Davis et al., 1989; Bendix & Cowell, 2010b). In South Africa, Britton (1990) reported an increase in riparian leaf fall after a prescribed burn, but no change in stream benthic organic matter levels were reported. In Portugal, Gama et al. (2007) found that breakdown rates, fungal biomass, and fungal community structure were not different, but that fungal sporulation and microbial respiration were lower, for *Eucalyptus* leaves when exposed to fire as compared to when unexposed to fire.

There are limited data on the immediate responses of the stream biota in med- and nearby regions to fire before rains occur. From a study completed in flowing intermittent streams in the Grampians National Park (southern Australia), Cowell et al. (2006) reported that algal richness, total density, and the density of major algal groups did not differ between two unburned

streams and two streams subjected to an intense bushfire 5 months before sampling. As part of the same study, Cowell et al. (2006) performed a manipulative experiment in two other intermittent streams where they exposed dry rocks to vegetation burning, to smoke and heat, or to ash. These experimental rocks were returned to the dry streambed and sampled 1 week after flow recommenced. The responses of algal assemblages to these treatments varied between the two streams with direct burning reducing algal density in both streams and radiant heat additionally reducing algal density in one of the streams. In general, however, Cowell et al. (2006) concluded that fire effects on algal assemblages in intermittent streams were either minor or short-lived.

Working in perennial streams near Santa Barbara (California), Simpson (2006) reported considerable variation in stream algal biomass levels in basins burned a month earlier, overlapping values obtained from nearby streams in unburned basins; however, macroalgae (vs. diatoms) constituted a higher proportion of the community at sites in burned compared to those in unburned watersheds (see also Fig. 1, methods in the Supplementary Material). These findings suggest that these dry season algal responses were mediated through the opening of the riparian canopy, which increased light, because nutrient levels did not change.

Cooper (e.g., Fig. 2, methods in the Supplementary Material) found that the assemblage structure, total density, and functional feeding group and trait representation of pool epibenthic and water column invertebrates in six burned and seven unburned southern California streams were similar 1 month before and 1 month after the 2009 Jesusita fire. Four months post-fire, however, there were increased densities of small, eurythermal, non-insect, collector-gatherer, and bi/multivoltine taxa in the one stream draining a burned basin where riparian vegetation was destroyed and which did not dry compared to streams draining basins which did not burn or where their basins burned but riparian vegetation remained intact (Fig. 2). In the same streams, Cooper observed little immediate effect of fire on tadpole (*Pseudacris regilla* and *cadaverina*) and rainbow trout (*Oncorhynchus mykiss*) densities with the exception of a fish kill in a stream which was directly hit by aerially applied fire retardant during fire-fighting activities (Cooper, 2009). In summary, most studies and reports before ensuing rains occur

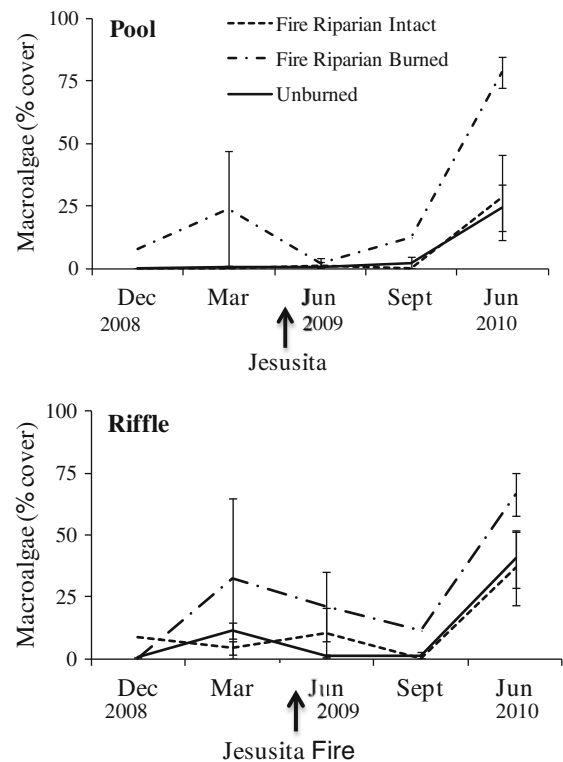


Fig. 1 Average percent cover (± 1 SE) of hard substrata (rocks, cobbles, boulders, bedrock) in pools (top) and riffles (bottom) by colonial algae (primarily *Cladophora*) before and after the Jesusita Fire, Santa Barbara, CA, USA (study area and methods in Supplementary Materials). The arrow indicates the time of the fire. The solid line represents stream sites in unburned basins ($n = 6-7$), the dashed line sites in burned basins where riparian vegetation remained intact ($n = 2-3$), and the dash-dot line burned basins where the riparian vegetation was burned ($n = 1-2$)

indicate that these direct, immediate effects are muted and short-lived, agreeing with general conclusions derived by Minshall (2003). Possible exceptions to this pattern are biotic responses to the introduction of contaminants such as fire retardants.

Short-term fire effects during and after subsequent rains

Catchment vegetation responses

With the exception of the matorral of central Chile (Muñoz & Fuentes, 1989), which did not have an evolutionary history with fire, plants in mediterranean shrublands appear to be well-adapted to and recover quickly from fire, including shrubs that quickly re-

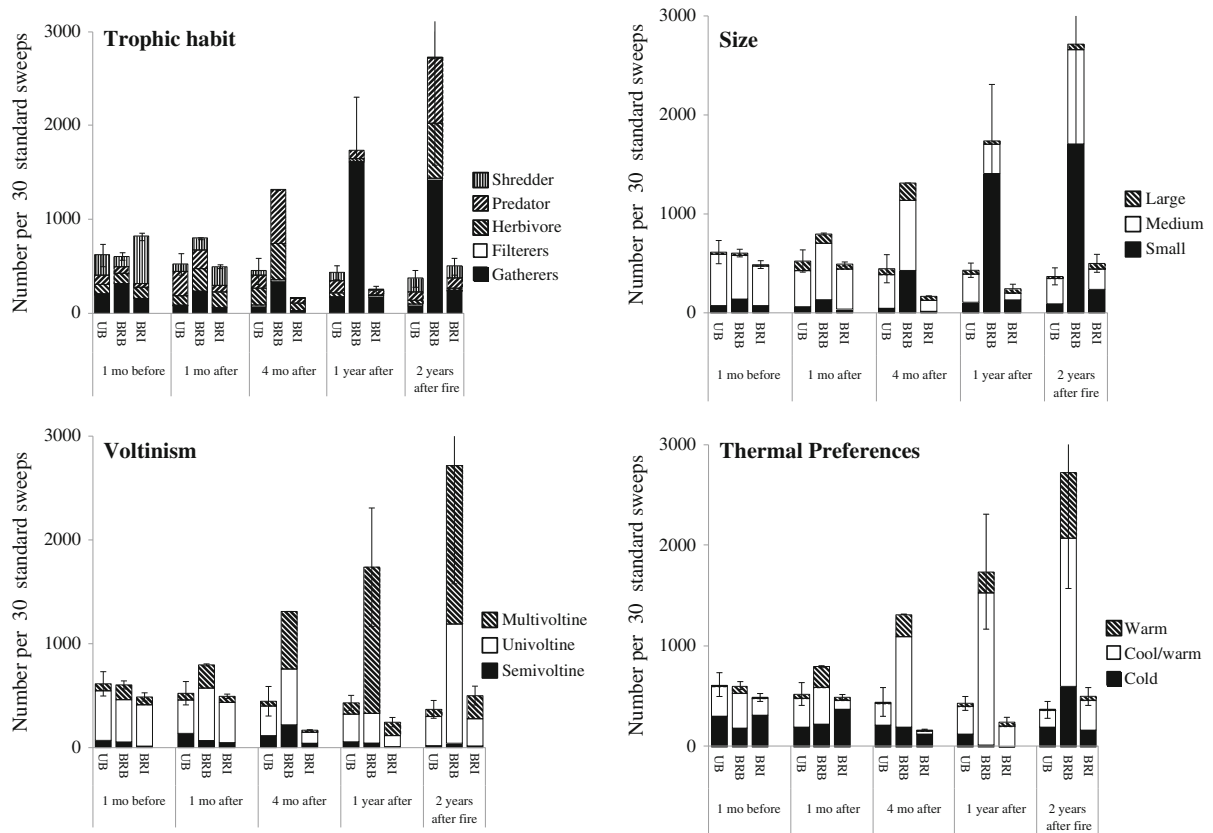


Fig. 2 Average abundance (no./30 standard sweeps \pm 1 SE) of benthic macroinvertebrates categorized by trophic, life history, morphological, and thermal traits in pools at stream sites in unburned basins (UB; $n = 6-8$), burned basins with riparian vegetation intact (BRI; $n = 2-3$), and burned basins where the

riparian vegetation burned (BRB; $n = 1-3$) at 1 month (mo) before and 1 and 4 months, and 1 and 2 years, after the Jesusita Fire, Santa Barbara, CA, USA (the study area and methods are described in the Supplementary Materials)

sprout even in the absence of substantial precipitation, and perennial and annual species whose seed germination is stimulated by smoke, heat, or charred wood (Le Houérou, 1987; Barro & Conrad, 1991; Wisheu et al., 2000; Keeley et al., 2012). Other vegetation types are found in med-regions where climatic or edaphic conditions favor their establishment, such as coniferous or hardwood forests, which are often found at higher elevations, or grasslands. Plants from these formations also show fire adaptations. For example, oaks (*Quercus*) and some conifers (*Pseudotsuga macrocarpa*, *Pinus pinea*) have thick bark, which allows trees to tolerate canopy removal while resisting damage to boles (Fernandes et al., 2008; Pausas et al., 2008; Lombardo et al., 2009), and perennial grasses re-grow from subapical meristems or rhizomes after fire (Reiner, 2007). Because freezing temperatures are rare and the growing season is year-

round, many med-plants can recover from fire at any time that soil moisture is adequate.

Vegetation recovery from fires in med-regions, then, is relatively rapid, often with ground cover well-established within the first year following burning, and comprises both re-sprouting shrubs and germinating herbaceous species, including species found primarily after fires (Halsey, 2008). Even where managers have seeded burned slopes with exotic grasses, much of the vegetation recovery which stabilizes soils is composed of native species (Borchert & Odion, 1995). The short-term recovery of riparian vegetation, compared to upland vegetation, is less dependent on native seed banks and primarily depends on the re-generation of woody species that survived the fire or the germination of annuals on surrounding higher terraces (California—Davis et al., 1989; Bêche et al., 2005; Australia—Radford et al., 2008). Post-fire flooding, however, can

substantially disrupt the re-vegetation of channel banks and cause secondary mortality of fire-damaged trees with tree recovery coming from re-sprouting or the germination of seeds produced after the fire (Davis et al., 1989).

Effects on riparian vegetation

Floods often have large effects on riparian vegetation by undermining and uprooting trees that were killed or damaged by fire (Bendix & Cowell, 2010a, b). Working in southern California watersheds, Bendix & Cowell (2010b) reported that 94% of riparian trees (alders and willows) were killed by a wildfire, with the fall of dead trees (snags) being associated with subsequent undermining floods. Estimates of snag fall have ranged from 17 to 43% over 2 to 3 years (Davis et al., 1989; Bendix & Cowell, 2010b). After an autumnal prescribed burn in the South African fynbos, Britton (1990) reported that summer leaf litter fall and total benthic organic matter (BOM) concentrations were about half the pre-fire levels, but that fine BOM concentrations were higher after than those before the fire, which she attributed to higher nitrate concentrations that may have accelerated leaf decomposition rates. Britton (1990) reported that the riparian canopy had recovered by 6 months after this prescribed burn, but Rehn (2010) reported a median decline in canopy cover from 60–75% to 12% from before to ca. 5 months after fall wildfires in southern California.

Stream physicochemical conditions

Most studies have shown that fire effects on stream ecosystems are associated with rainstorms which deliver water, sediment, nutrients, and organic matter to stream channels (Prosser & Williams, 1998). Substantial research has been done on runoff and erosion, landslides, debris flows, and sediment transport that can have large effects on stream geomorphology and substrata characteristics (Shakesby & Doerr, 2006; Shakesby, 2011). Fire alters hydrology by reducing infiltration, evapotranspiration, and interception. Fire reduces infiltration rates by decreasing soil porosity and by promoting the formation of a hydrophobic layer (DeBano, 2000; DeBano et al., 1998). When fire consumes the vegetative canopy, as is common during fires in med-ecosystems, evapotranspiration and interception are reduced. Inbar et al. (1998) reported that

overland flow in a burned area increased up to 500 times that of an equivalent unburned area on Mt. Carmel (Israel), although the first post-fire year runoff coefficient was still relatively low (2%). Scott (1993) also reported increases in overland flow in the first year after wild fires in South Africa, with a 300% increase in peak flows in catchments covered by pine and eucalyptus forests but only a maximum increase of 17% in a catchment covered by fynbos. Doerr et al. (2003), combining field and laboratory experiments, found that catchment hydrologic responses to fire were large with wet antecedent conditions but that discharge responses were muted under dry conditions when enhanced overland flow during storms was balanced by increased storage in subsoils.

These changes in the routing and volumes of water flowing from burned landscapes have large effects on stream hydrology. Lavabre et al. (1993), for example, found that stream discharge increased 30% during the first year after a fire in southern France. In southern California, fires have been observed to increase streamflow by up to 20–30%, reduce time to peak discharge by 2–2.5 h, and increase peak discharges by up to 300 fold compared to similar unburned watersheds (Sinclair & Hamilton, 1995; Riggan et al., 1994; Keller et al., 1997; Loaiciga et al., 2001; Coombs, 2006).

The magnitude of sediment erosion, transport, and deposition after fire in med-catchments will depend on vegetation, soil type, topography, fire severity and extent, and, especially, on the intensity, frequency, and timing of ensuing precipitation (Scott & Van Wyk, 1990; Scott et al., 1998; DeBano, 2000). Erosion can occur as dry ravel or be induced by rain splash and transport, rilling, and mass movements (Florsheim et al., 1991; Gabet, 2003; Gabet & Dunne, 2003). Rice (1974) suggested that most stream sediment export occurs in the first year after a fire by transporting sediment that has accumulated in channels since the last large flood rather than sediment generated from hillslope erosion. Davis et al. (1989), however, calculated that 90% of the sediment entering a stream during the first storms after a southern California fire came directly from hillslope erosion, including rilling and slope failures. Soil losses are prominent during intense storms in the first year after fire, but quantities can be variable depending on soil and vegetation types and topographies (Rubio, 1987; Cerdà & Doerr, 2005; Pausas et al., 2008; Shakesby, 2011). In California (Santa Barbara), suspended sediment exported from a

burned catchment during the first post-fire year was ten times higher than that in a nearby unburned catchment (Coombs, 2006). In France, relationships between erosion and rainfall depended on scale, with small plots being sensitive to short-duration rainfall and catchments being responsive to long-duration rainfall patterns (Lavabre & Martin, 1997). Catchment erosion and sediment export usually decrease within 2 to 3 years after wildfire (Cerdà & Doerr 2005; Mayor et al., 2007).

The most obvious effects, then, of fire on stream geomorphology and substrata in many med-streams revolve around increased erosion and sediment inputs, transport, and deposition during and after storms. In many cases, stream pools fill in with fine sediments (sand, gravel), decreasing pool depths, and reducing pool-riffle differences (Davis et al., 1989; Gamradt & Kats, 1997; Rehn, 2010). Davis et al. (1989) reported that gravel filled in stream pools and buried bedforms during the first storms after an intense fire in southern California, but that storms a month later moved fine substrata out of their study reach, nearly returning it to its pre-fire configuration. In most cases, however, alterations to stream geomorphology and substrata size distributions engendered by intense fire persist after the first rainy season into the subsequent dry season (Rehn, 2010). On the other hand, where fire intensity is low or moderate and ensuing precipitation is low, fire effects on stream geomorphology or substrata conditions may be limited (Spina & Tormey, 2000).

In studies of a first order stream in Catalonia (Gallifa stream), Vila-Escalé (2009) found that runoff transported large quantities of ash and mud into and along the stream during the first rains 12 days after the fire, filling pools with mud and ash (see picture 1 in Supplementary Material). As a consequence, the values of many physicochemical variables at this time showed the greatest differences between pre-fire and other post-fire samples (Fig. 3; Vila-Escalé et al., 2007; Vila-Escalé, 2009). These conditions caused a large fish kill in a nearby stream, where brown-ocher deposits of ferric salts were observed resulting from the oxidation of ferrous iron dissolved in anoxic waters earlier and in upstream pools (see pictures 1 and 2 in Supplementary Material). The following heavy rains (62 mm in 24 h, 120 mm over the next 30 days) caused flooding (see picture 3 in Supplementary Material) and removed most of the ash and mud from the river channel. Flow re-established

45 days after the fire, and anoxic conditions disappeared. Although the concentrations of salts and nutrients decreased, they remained higher than those before the fire, eventually returning to pre-fire levels about 1 year after the fire (Fig. 3; Vila-Escalé et al., 2007; Vila-Escalé, 2009).

Compared to wildfires, prescribed burns may have short or muted effects on stream ecosystems because of reduced fire severity and rapid post-fire recovery of vegetation (Britton, 1991b). In the fynbos of South Africa, small increases in the concentrations of chloride, bicarbonate, polyphenols, and potassium, and larger increases in nitrate occurred during the first winter after a prescribed burn, while ammonium, calcium, and magnesium concentrations remained unchanged (Britton, 1991b). In contrast, prescribed fires within the San Dimas Experimental Forest (southern California), which receives high atmospheric nitrogen deposition, led to large fluxes of ammonium during the first few storms and of nitrate in the first post-fire year (Riggan et al. 1994). After a wildfire in central coastal California watersheds, which receive low atmospheric N deposition, ammonium export was 32 times greater in burned than unburned watersheds during the first few post-fire storms, and the annual post-fire export of other nutrients (NO_3 , DON, PO_4) ranged from ca. 2 to 5.5 times greater in burned than unburned watersheds (Coombs, 2006; Coombs & Melack, 2012).

Polycyclic aromatic hydrocarbons (PAHs) are released and mobilized by wildfire (Olivella et al. 2006, Vila-Escalé et al. 2007). Vila-Escalé et al. (2007) observed the highest dissolved and particulate values for 16 PAHs 12 days after a fire, but PAHs in sediments peaked after 95 days. PAH concentrations followed precipitation patterns but, in general, were low and did not represent a toxicologic hazard. Olivella et al. (2006) reported that mean PAH concentrations in a Catalonian stream peaked about a month after a fire but declined to the lowest recorded values during subsequent heavy rains. Stein & Brown (2009) reported elevated concentrations of zinc and PAHs in stormwater runoff after fires in southern California.

Effects on the freshwater biota

Increased inputs of water, sediment, and ash associated with the first floods after a fire usually have major effects on the biological communities of med-streams.

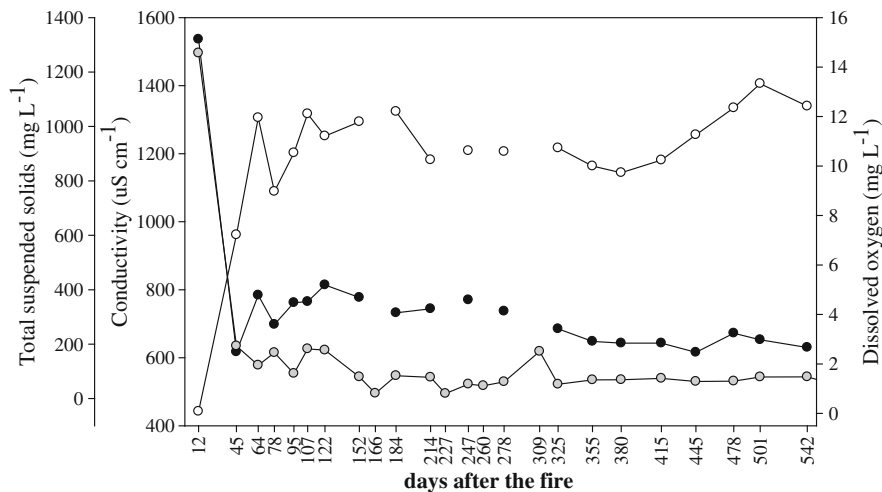


Fig. 3 Conductivity ($\mu\text{S cm}^{-1}$, black), total suspended solids (mg l^{-1} , grey), and dissolved oxygen concentrations (mg l^{-1} , white) after the fire (expressed in days after the fire) occurring in the Gallifa creek basin (Catalonia). Twelve days after the fire, dissolved oxygen concentrations dropped to 0.08 mg l^{-1} , conductivity doubled, and suspended solids increased by an

order of magnitude. The following heavy rains re-established flow 45 days after the fire, and anoxic conditions disappeared. Although the concentrations of salts and nutrients decreased, they remained higher than those before the fire, eventually returning to pre-fire levels about 1 year after the fire (data from Vila-Escalé, 2009)

As indicated in Fig. 5b, short-term fire effects after the first scouring floods reduced algal cover and biomass, most invertebrates and fishes, and some amphibians. Recovery rates of these groups depended on whether the riparian zone burned, post-fire precipitation patterns, and the response variable considered (Figs. 1, 2, 5b; Vila-Escalé, 2009; Rehn, 2010).

In a stream in northeastern Spain, changes in the richness and composition of diatom assemblages occurred after wildfire and floods. Three to four months after the fire, a large increase in macroalgae and eutrophic diatoms (*Navicula veneta*, *Nitzschia palea*, *Mayamea atomus* var. *permitis*, and *Amphora montana*) was observed (Farrés-Corell, 2005; Gomà et al., unpublished data). Although algal species richness recovered to pre-fire values in less than a year, species composition remained different (Vila-Escalé, 2009). In California, scouring floods after fires reduced algal biomass in burned basins, and the pace of recovery depended on whether the riparian zone burned (Fig. 1). By a year after this fire, the percent cover of filamentous macroalgae was greater in both the pools and riffles of streams with burned riparian zones than in unburned streams or burned streams with intact riparian canopies (Fig. 1). Simpson (2006) observed that algal biomass increased in a basin that was largely burned (85%), 1 year after a southern

California fire, but recorded little algal response in basins that only partially (<18% of basin) burned.

Invertebrate responses to wildfire and subsequent rains are also rapid, but some taxa show slow recovery rates (e.g., Gastropoda and some Odonata). Twelve days after a wildfire in northeastern Spain, only one individual of the semi-aquatic hemipteran, *Hydrometra* sp., was collected from a burned stream, at a time when stream waters were anoxic, ferrous iron concentration was high, and fish kills were observed in a nearby stream in a burned catchment (Vila-Escalé 2009; see picture 3 in Supplementary Material). Forty-five days after the fire, after heavy rains and high discharge, only adult Gyrinidae and Hydraenidae beetles, nematodes, and stratiomyid fly and *Rheocricotopus* (Chironomidae) larvae were found in this stream (Vila-Escalé, 2009; Rieradevall et al., unpublished data). In the following months, macroinvertebrate communities were dominated (ca. 70% of individuals) by Simuliidae, Baetidae, and especially Chironomidae, whereas macroinvertebrates with longer life cycles, like molluscs and odonates, were absent (Vila-Escalé, 2009). By 309 days after the fire, the number of macroinvertebrate families found in the stream in the burned catchment (29) reached pre-fire levels, and 1 year after the fire, the number of orders was the same (12), and the number of families slightly

exceeded (38 vs. 34) those found in a nearby, unburned stream (Fig. 4; Prat & Rieradevall, 2006; Vila-Escalé, 2009).

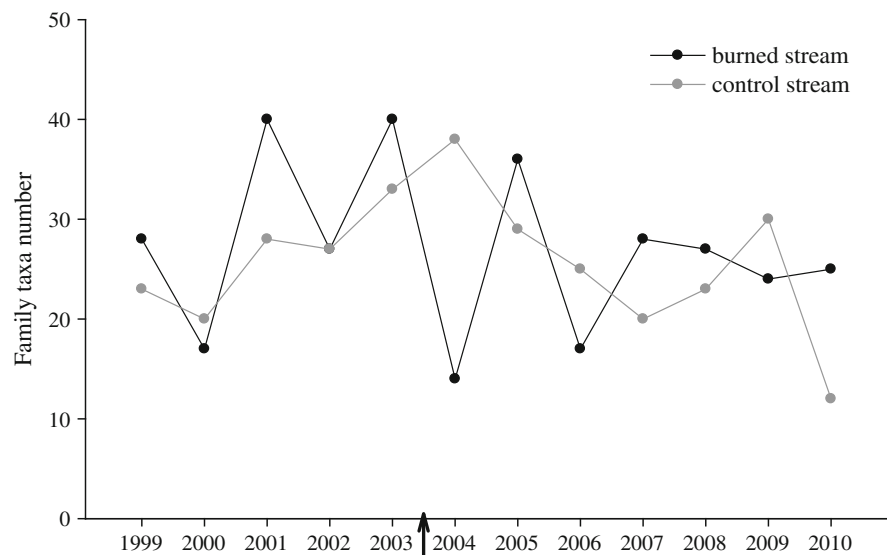
Studies in the same area of northeastern Spain, 10 months after the fire, revealed few significant differences in invertebrate community structure between streams in six burned and three unburned catchments (Verkaik, 2010). In the first couple of months after the fire, streams in burned versus unburned basins had higher densities of macroinvertebrates with active or passive aerial dispersal stages, such as the Limoniidae, Stratiomyidae, and Tabanidae among the Diptera and *Agabus* sp., *Gyrinus* sp., *Hydraena* sp., and *Laccobius* sp. among the Coleoptera, suggesting that they had arrived from nearby, unburned tributaries (Vila-Escalé et al., 2007; Vila-Escalé, 2009). Among functional feeding groups, collectors and predators dominated 1 year after the fire, but all functional feeding groups were found at similar proportions in the burned and unburned streams by 100 days after the fire (Vila-Escalé, 2009).

One year after the Jesusita wildfire in southern California, after a winter with rainfall that was above average, Baetidae dominated pools in burned streams while unburned streams contained higher proportions of the caddisfly *Lepidostoma* (Cooper et al., unpublished data; methods in the Supplementary Material). The relative representation of different odonate genera also shifted from *Argia* and *Octogomphus* in unburned streams to *Archilestes* in burned streams. Total

invertebrate densities and densities of collector–gatherers, weak fliers, small taxa, cool/warm and warm eurytherms, and bi or multivoltine taxa were significantly higher in streams draining burned basins where riparian vegetation was destroyed than in streams in unburned basins or in burned basins where riparian vegetation remained intact (Fig. 2). In addition, collector–filterers were more abundant in streams in burned catchments with intact riparian zones than in unburned basins, and shredders and non-insects were more abundant in streams draining unburned basins than in burned basins where riparian vegetation was intact. Shredders were nearly absent in streams in burned basins where the riparian vegetation burned. In contrast, stream invertebrate communities may show little response to prescribed burns (Britton, 1991a).

As previously mentioned, stream fish communities are strongly affected by intense wildfire. In Sant Llorenç Natural Park, Spain, high densities of both native (e.g., 8070 fish ha⁻¹ of *Barbus meridionalis* and *Squalis cephalus* in the Ripoll basin) and introduced fish species were completely extirpated by a wildfire (i.e., no fishes were collected after the fire, Sostoa et al., 2006). At present, it is not clear if fire impacts on fish in this area were mediated through fire effects on sediment inputs and transport or through the introduction of fire retardants during fire-fighting activities (Sostoa et al., 2006). Where they were present, native rainbow trout (*Oncorhynchus mykiss*) populations in

Fig. 4 Numbers of macroinvertebrate families recorded in springs from 1999 to 2010 in a stream in an unburned catchment (Mura in grey) and in a stream in a burned catchment (Gallifa in black) both in Catalonia. The arrow indicates the timing of the wildfire (data from Prat et al., 2012)



Santa Barbara area (California) streams persisted through the remaining dry season after the Jesusita fire, but then completely disappeared during the ensuing wet season, presumably because of the direct effects of flood flows and suspended sediment on trout or because sediment deposition filled in pool habitats.

Regarding amphibians, in northeastern Spain, the common species *Alytes obstetricans* and *Bufo bufo* were not recorded from streams in burned basins 1 year after a fire (Guinart, 2007), but other species, such as *Salamandra salamandra*, *Hyla meridionalis*, and *Rana perezzi*, were detected (Villero & Campeny, 2005). In a stream in the Santa Monica Mountains of southern California, pools and runs became filled with sediment after a wildfire, reducing the preferred oviposition habitat of California newts (*Taricha torosa*) and hence, newt egg mass numbers (to a third of pre-fire levels, Gamradt & Kats, 1997). Terrestrial earthworm availability increased in stream pools in a burned catchment, resulting in more earthworms and fewer newt eggs and larvae being found in adult newt stomachs (Kerby & Kats, 1998).

Based on the findings of the studies conducted in northeastern Spain and California examined here, the major short-term responses of aquatic communities to fires were similar, and differences in recovery trajectories were probably related to the magnitude, frequency, and timing of storms. In northeastern Spain, the first storms occurred shortly after a fire and caused large changes in physical, chemical, and biological conditions in streams; however, frequent, subsequent storms diluted and transported initial sediment, nutrient, major ion, and PAH inputs, returning to pre-fire conditions within a year (Fig. 6; see also picture 4 in Supplementary Material). Concordantly, initial large differences in stream algal and invertebrate communities in burned versus unburned basins were ameliorated over time, becoming similar within a year. In southern California, the lag time between fires and the first storms of the ensuing rainy season ranged from 1 to 6 months (Fig. 6). In the years of the California study, fine sediment filled pools and affected macroinvertebrate, amphibian, and fish assemblages in the dry season after the first rainy season after the fire. As a consequence, stream algal and invertebrate communities had recovered to pre-fire configurations within a year after a fire in Spain, but were different in burned and unburned streams 1 year after fires in California (Figs. 1, 2, 6).

Mid and long term effects

Catchment vegetation responses and stream physico-chemical conditions

Despite the rapid recovery of many fire-adapted upland plants in chaparral, the total leaf area of upland plants may not reach pre-fire levels for up to 15 years (McMichael et al., 2004). Upland vegetation may not produce a continuous canopy until 10–20 years after a fire, but soil erosion may be limited, depending on landscape slopes and rain intensity, owing to soil stabilization by snag roots (B. Bookhagen, personal communication). Even where all vegetation is burned, soil erosion may occur for only a short time because of the rapid establishment of post-fire herbaceous species and shrubs that are then replaced by large shrubs. Because of lower intensities and severities of fire in riparian zones, and because of the rapid growth of riparian vegetation in moist, nutrient-rich environments, riparian zone canopies can reach pre-fire levels in 3–6 years depending on post-fire patterns in rainfall, flooding, and bank erosion (Davis et al., 1989; Bêche et al., 2005; Kobziar & McBride, 2006; Rehn, 2010).

The time required for sediment levels, discharge, and water chemistry in streams draining burned catchments to become similar to those in streams in unburned catchments or to pre-fire conditions appears to vary from one to several years. However, few studies have followed recovery trajectories for multiple years. Erosion rates declined to half of their immediate post-fire levels ($30 \text{ g m}^{-2} \text{ h}^{-1}$) in the summer after a fire in an eastern Spanish basin, reaching values of $<10 \text{ g m}^{-2} \text{ h}^{-1}$ after 2 years (Cerdà & Doerr, 2005). Similarly, the model developed by Candela et al. (2005) indicated that watershed erosion and runoff would decline after the first post-fire year (Scott & Van Wyk, 1990; Scott et al., 1998; DeBano, 2000). Overland flow decreased by an order of magnitude in the second wet season after a fire in a montane basin in eastern Spain; however, runoff and sediment yield were still two orders of magnitude higher than pre-fire levels 5 years after this fire and were related to frequent and intense rainfall events (Mayor et al., 2007). The relatively long recovery rates of runoff and sediment yields in this basin have been attributed to dry conditions after the fire which slowed vegetation recovery, with the percent cover of bare soil remaining above 50% for up to 4 years after the

fire (Mayor et al., 2007). In contrast, sediment export from the San Onofre catchment near Santa Barbara (California) was similar to neighboring unburned catchments after 2 years, although low rainfall contributed to this response (Coombs, 2006; Coombs & Melack, 2012). Although Rehn (2010) reported that large amounts of sediment were observed in some burned streams for up to 2 years after fires in southern California, most of this sediment had disappeared by the fourth spring after the fires. In contrast to ammonium, which returned to pre-fire concentrations within 1 year, nitrate and phosphate concentrations returned to those in similar nearby unburned catchments after 4 years (Coombs 2006; Coombs & Melack, 2012). Stream nitrate concentrations and export from the San Dimas Experimental Forest, located in southern California, remained high compared to those in unburned catchments for 7–10 years after fire (Meixner et al., 2006).

Effects on riparian vegetation

Fire effects on riparian vegetation will depend on fire severity and the plant species present. Rehn (2010) reported that the riparian canopy had recovered to 40–50% cover by the sixth spring after fires compared to pre-fire canopy covers of 60–75%. Pulses of woody debris inputs will depend on the susceptibilities of different tree species to fire and subsequent floods, but major inputs have been reported to occur mainly during the first 2 years (Davis et al., 1989; Bendix & Cowell 2010b). Vaz et al. (2011) reported that the rapidity and magnitude of woody inputs from pine and *Eucalyptus* plantations to streams were greater than those from oak woodlands, and that the characteristics (e.g., size) of woody debris differed among different tree species and burn status (i.e., burned vs. unburned debris). Although riparian zones were patchy and narrow (3–15 m where present), riparian tree species contributed substantial amounts of burned and unburned woody debris to these streams.

Effects on the freshwater biota

The recovery of algal and invertebrate communities after fire is rapid in med-streams, concordant with the re-establishment of pre-fire geomorphological, substrata, and chemical conditions. However, as depicted in Fig. 5b, whether or not the riparian canopy burned

appears to have a large effect on algal and invertebrate communities, presumably as mediated through effects on temperature, shading, cover, and leaf litter inputs. Although some amphibian species in streams in burned basins recovered, fish appeared to be decimated by the indirect effects of fire, and barriers inhibited their re-colonization.

The detailed study of the Gallifa stream in northeastern Spain showed that diatom taxa like *Navicula tripunctata*, *Sellaphora seminulum*, and *Amphora pediculus*, which were not present in the pre-fire community, were abundant 2 years after a fire (Vila-Escalé, 2009). Two years after the 2004 Gaviota fire in California, there were no consistent differences in algal biomass or taxonomic composition in streams draining burned versus unburned basins (Simpson, 2006).

In the ongoing study of fire effects on Gallifa stream in northeastern Spain, macroinvertebrate family richness of the stream in a burned catchment fell compared to a stream in an unburned catchment in the spring after the fire, but richness values in both burned and unburned basins fluctuated over the next 7 years and were not consistently different (Fig. 4). Vila-Escalé (2009) reported that the fire eliminated some Mollusca and Odonata. Among these groups, limpets (Ancyliidae) appeared in the burned stream sooner than other mollusc groups but at lower densities than in pre-fire years. Likewise, Lymnaeidae, which were abundant in pre-fire samples, did not reach substantial densities until 5 years after the fire, and the Planorbidae and Libellulidae (Odonata) were not collected from the burned stream until 2008 (5 years after the fire, Vila-Escalé, 2009). In a study in the same area (northeastern Spain), macroinvertebrate communities in burned catchments were not consistently or substantially different from those in unburned catchments after the second post-fire year (Verkaik, 2010). After the second post-fire year, macroinvertebrate community structure was associated with hydrologic conditions, as measured by accumulated precipitation over the previous 3 months, as observed in other studies on streams in med-regions (Bêche & Resh, 2007; Munné & Prat, 2011). Although many community parameters, such as richness, recovered to pre-fire levels in a year or two, a few individual taxa, primarily species with limited dispersal powers, were still less abundant in streams in burned versus unburned basins after 5 years.

Based on indicator species analysis of invertebrate data from southern California streams, Rehn (2010)

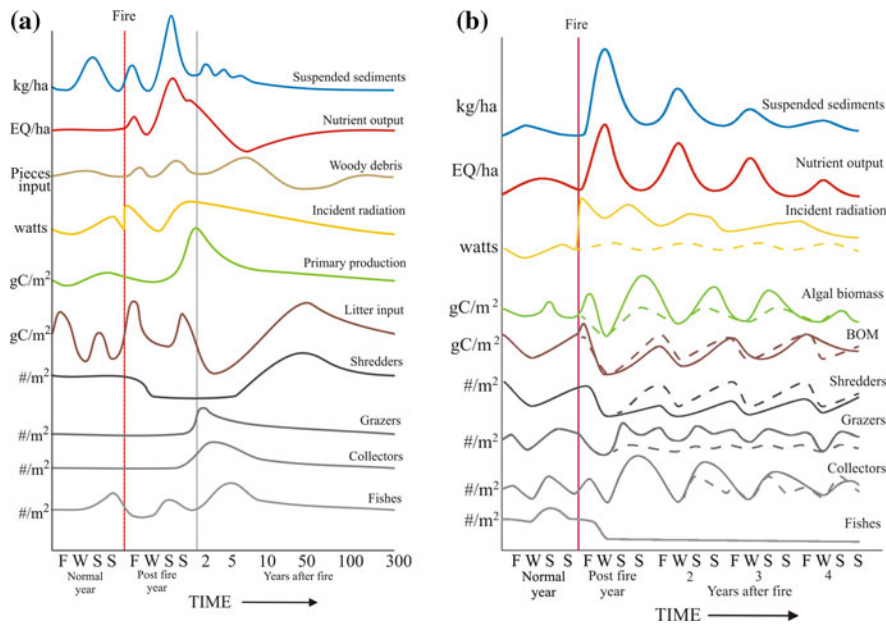


Fig. 5 a Hypothetical changes in physical, chemical, and biological characteristics of a temperate stream before and following wildfire. The letters *F*, *W*, *S*, and *S* indicate fall, winter, spring, and summer, respectively (Adapted from Minshall et al., 1989 and Gresswell, 1999). **b** Schematic diagram of changes in physical, chemical, and biological variables before and for up to 4 years after wildfires in streams in southern California and Catalonia. In post-fire years, the *solid*

lines represent streams in burned basins where riparian vegetation burned, whereas the *dashed line* represents streams in burned basins where riparian vegetation remained intact. If only a *solid line* is shown, it indicates that the response variable for streams in basins with burned and unburned riparian vegetation were similar. The letters *F*, *W*, *S*, and *S* indicate fall, winter, spring, and summer, respectively

reported that *Baetis*, Simuliidae, and the beetle *Agabus* in undisturbed streams, and Simuliidae, Muscidae, and Ostracoda in degraded streams, were associated with sites in burned basins in the first springs after fires. Furthermore, a diversity of Trichoptera, Plecoptera, Diptera, and non-insect taxa in both undisturbed and degraded streams, as well as Coleoptera and other Ephemeroptera taxa in undisturbed streams, was indicative of times before fires occurred or after streams had recovered (recovery based on similarities of IBI and O/E metrics (see biomonitoring section later) in burned and unburned streams). Sustained differences in riparian canopy cover and, presumably, stream light, temperature, and benthic detritus levels, over 6 years following fires could perhaps account for some of the shifts in indicator species from pre-fire to recovered times. For example, two caddis larvae, *Gumaga* and *Neophylax*, indicative of recovered but not pre-fire times in reference streams are primarily grazers in southern California streams. In contrast, several Elmidae beetle genera, two snail families (Planorbidae, Hydrobiidae), and the water penny (*Eubrianax*, Psephenidae) were

indicative of pre-fire but not recovered times in reference streams, suggesting that they had not recovered from fire-associated disturbances after 6 years.

Although invertebrate community structure in the pools of California streams was similar in unburned basins and basins with burned upland but intact riparian zones 2 years after fires, pool community structure was still different in basins with burned upland and riparian zones (Fig. 2). Large deposits of fine sediment in pools present in the first year after the fire had been largely washed out of these burned streams by the second year, concordant with the recovery of invertebrate communities in streams where the riparian zone remained intact. Continued differences in invertebrate communities in streams with burned riparian zones after 2 years were related to continued reduced canopy cover and increased temperature and light levels (Fig. 2). Verkaik (2010), working in Catalonia, reported that the values of most physical–chemical variables were not different between closed and open canopy reaches of a stream in a burned basin, but that aquatic vegetation was

higher and leaf litter cover was lower in the open reach. The reach without a riparian canopy had higher macroinvertebrate densities than the closed canopy reach, probably reflecting increases in algal abundance in the open canopy reach. The open canopy reach also dried during the summer probably as a consequence of higher evaporation. After flow was restored, invertebrate re-colonization occurred quickly, and invertebrate communities followed similar trends in both open and closed canopy reaches (Verkaik, 2010).

Densities of fishes in streams in burned basins in the Sant Llorenç del Munt Natural Park (Spain) have remained low following fire. Although *Barbus meridionalis* and *Squalis cephalus* were observed in some streams 2 years after the fire, their densities and biomasses remained low compared to pre-fire values ($<8,000$ ind ha^{-1} and $<14,000$ kg ha^{-1}) (Sostoa et al., 2006). Eight years after the fire, some tributaries of the Ripoll stream in this Natural Park still lacked fish, while streams in unburned basins continued to host high densities of native fish species (Sostoa et al., 2006). In many of the streams in burned basins still lacking fish, fishes have been unable to re-colonize because of various natural and human-made barriers (e.g., dams, road crossings, dry reaches). Similarly, in California, trout have not been able to re-colonize streams in burned basins where they were present before fires because of numerous, usually human-made, barriers to trout migration. Historical evidence, however, indicates that, although trout populations are severely reduced by intense wildfires in southern California, re-colonization eventually occurs (>3 years post-fire) in stream reaches without barriers to fish access (Alagona et al., 2012).

In Spain, all amphibian species had re-colonized streams in burned catchments by 3 years after the fire (Campeny, 2007).

Comparisons of fire effects on mediterranean and non-mediterranean fluvial ecosystems

Differences in fire effects on response variables and their recovery times

Although information on the effects of fire on med-streams is scarce compared to information on fire effects on streams in other regions (see review in Gresswell, 1999), comparisons of fire impacts on

streams in temperate or cold ecosystems to those in med-ecosystems reveal some similarities and dissimilarities (Fig. 5a, b). The immediate effects of fire on streams appear to be similar across different regions, but subsequent stream responses to fire depend on the timing, intensity, and frequency of subsequent storms (Gresswell, 1999; Vieira et al., 2004; this review). Fires occur primarily in the summer or autumn in most ecosystems, but floods occur in autumn and winter in med-ecosystems, often closely following fires, whereas floods occur with snow melt in the spring in most temperate or polar ecosystems. The timing and magnitude of sediment and nutrient inputs following fire, then, will depend critically on the seasonal timing and intensity of runoff (Shakesby et al., 2007; Coombs & Melack, 2012). The limited data collected to date indicate that another important difference in stream responses to fire in med- and non-med ecosystems, is the high resilience of med-streams to fire, with most variables returning to pre-fire values within a few years, whereas recovery usually takes much longer in temperate streams (Figs. 5a, b) (Minshall et al., 1989; Verkaik, 2010; Rehn, 2010). Finally, med-streams differ from those in many other ecosystems by exhibiting large fluctuations in most physical, chemical, and biological variables resulting from large seasonal (dry vs. wet season) and interannual (wet vs. dry years) variation in precipitation and runoff (Gasith & Resh, 1999). Large variation in stream physical–chemical conditions can be ameliorated by processes in the riparian zone (Fig. 5b), which itself is affected by climatic fluctuations and fire (Pettit & Naiman, 2007). As for fire-prone med-ecosystems containing many resilient terrestrial plant species because of species sorting during community assemblage through successive fire cycles (Lloret & Zedler, 2009), the biota of med-streams may be “pre-adapted” to, and shows rapid recovery from wildfires because of their adaptation to large seasonal and interannual variation in stream flows (frequent droughts and floods). In essence, then, selection pressures from frequent hydrologic disturbances (floods, drying) have produced a stream flora and fauna, which are also resilient to less frequent natural disturbances (i.e., fires).

The importance of watershed vegetation recovery

Med-ecosystems constitute one of the most fire-prone biomes in the world (Halsey, 2008). Although fire-

adapted ecosystems (e.g., savannas, lodgepole or long-leaf pine forests) occur in other parts of the world, med-ecosystems have predictable annual cycles of drought and times of high fire risk. Variability in the structure of fires also differs between mediterranean shrublands and temperate forests, with increasing fire intensity producing surface, intermittent, or crown fires in forests but with many ignitions in shrublands resulting in intense fires consuming all vegetation (Halsey, 2008; Prepas et al., 2009). In general, vegetation condition, including the accumulation of debris and understory plants, plays a larger role in temperate forests than in mediterranean shrublands, where fire weather can be of over-riding importance. Fuel structure, including size classes, volume, and continuity can influence the threshold for flammability under different moisture conditions, but ultimately ignition and fire spread are driven by weather conditions (Pausas & Paula, 2012). Because med-ecosystems have year-round growing seasons and fire-adapted plants, vegetation often quickly covers soils, and pre-fire canopy levels are often reached in 10–20 years (McMichael et al., 2004). In comparison, the recovery of temperate forests can take hundreds of years (Minshall et al., 1989).

The rapid recovery of vegetation may suggest that erosion would be lower in mediterranean than in temperate watersheds, but this is not necessarily the case because erosion also depends on watershed slopes and the timing of storms after fire. With the exception of Australia, which has a higher proportion of gentle slopes than other med-regions (Table 1; Fig. 6), med-ecosystems often occur in steep terrain with many implications for the magnitude and routing of water, solutes, and sediment across landscapes after fire. Mediterranean watersheds contain some of the most erodible soils in the world which, combined with the high frequency and intensity of fires and the steepness of the terrain, often produce mass sediment movement, such as landslides and debris flows, as well as dry ravel, sheet, and rill erosion (Barro & Conrad, 1991). In comparing North American ecosystems, Swanson (1981) reported that chaparral was the ecosystem most susceptible to fire and erosion, calculating that over 70% of the long-term sediment yield from chaparral watersheds was induced by fire, far greater than fire-induced sediment yields from all other ecosystems. Erosion induced by wildfires in the Mediterranean Basin also has had large effects on land

and stream geomorphology, being exacerbated by human land uses (Shakesby, 2011). Fire recurrence intervals also have a large effect on sediment erosion, transport, and deposition. For example, in and near urban areas of southern California, fire recurrence intervals of less than 12 years can eliminate important shrub species, promote flammable grasslands, and penetrate riparian zones, inducing higher erosion rates (Jacobsen et al., 2004).

In general, the recovery of stream geomorphology and substrata conditions appears to be faster in med- than temperate forest ecosystems, paralleling the more rapid recovery of mediterranean vegetation after fire (Shakesby et al., 2007). Water flows in med-ecosystems appear to respond more quickly and with higher intensities than flows in ecosystems dominated by snow melt (Fig. 6). Concordantly, the probability of landslides at similar rainfall intensity appears to be higher in mediterranean landscapes than in areas with a montane climate (Guzzetti et al., 2008). The mass movement of sediment and larger elements into streams in steep terrain, via landslides or debris flows, may affect stream geomorphology and act as sediment sources for long time periods in both med and other systems (Koetsier et al., 2007). Although most studies in med-regions have been done on low order streams, results from other systems indicate that some of the effects of fire on stream hydrology, hydrochemistry, and geomorphology will be attenuated as stream size increases or as watershed slopes decline (Minshall et al., 1997; Spencer et al., 2003).

Fire effects on riparian zones

A particularly important consideration is whether or not fire affects riparian vegetation, which can be largely or partially spared from burning owing to moist conditions, cool temperatures, low concentrations of flammable substances in plants, and high foliar moisture levels (Ellis, 2001; Agee et al., 2002; Dwire & Kauffman, 2003; Pettit & Naiman, 2007; Rood et al., 2007). Because of the protection of riparian zones from management activities (i.e., fuel reductions), Van de Water & North (2011) contended that riparian zones may become more fire-prone than upland areas in montane, coniferous forest ecosystems in the Sierra Nevada of California, a contention corroborated by higher fuel loads in riparian than upland areas currently, but not in the past. However,

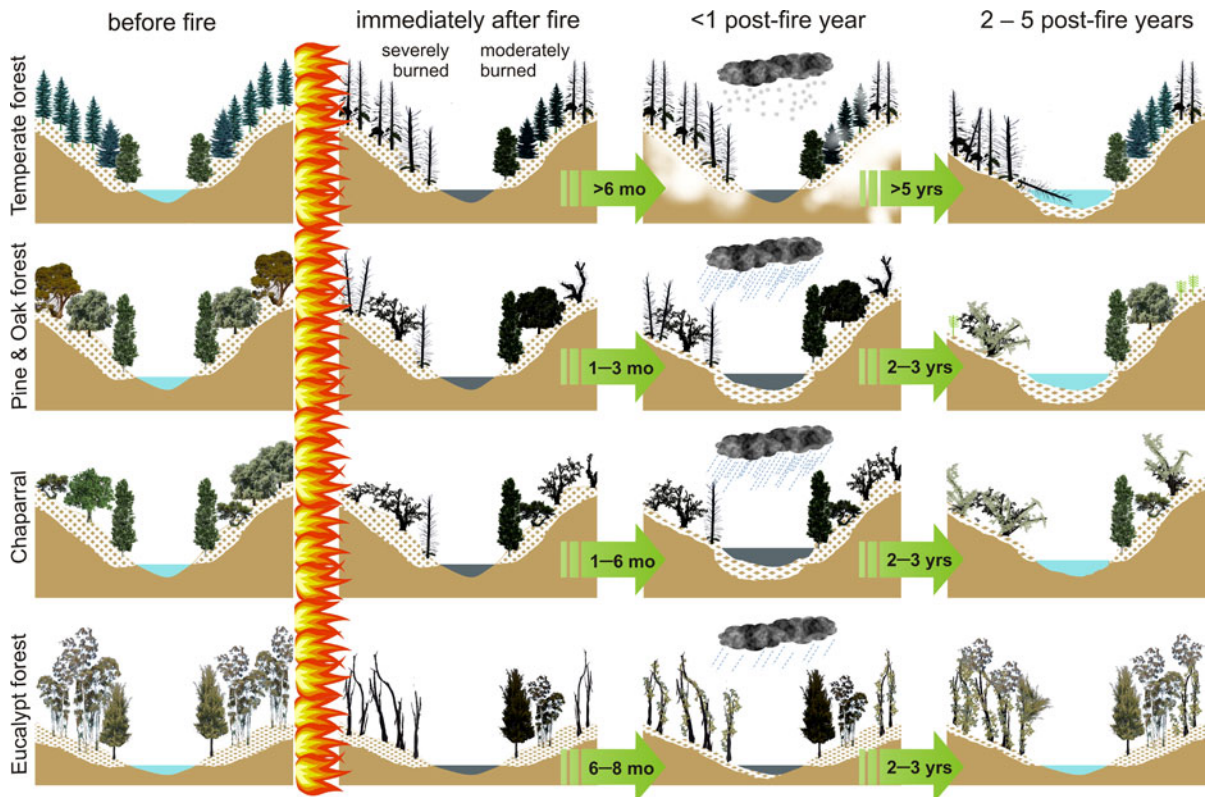


Fig. 6 Schematic diagram of hypothetical changes in drainage basins after wildfires in four different vegetation types: coniferous forest (representing a temperate stream) and *Pinus* and *Quercus* mixed forest, chaparral, and *Eucalyptus* forests (representing med-streams). The catchment and riparian vegetation has been simplified to explain the main hypothetical changes after wildfires. The left bank of each diagram represents a severely burned catchment where riparian vegetation burned, whereas the right bank represents a moderately burned catchment with the riparian vegetation remaining intact. The stippled areas represent the distribution of loose soils after wildfires, and here were related to the severely burned bank. Landslides occur in all forests, depending on the steepness of the

terrain, but the timing of landslides and debris flows may differ among regions depending in the timing and intensity of post-fire precipitation. Hypothetically, we predict that landslides will first be observed after fire in catchments in the pine and oak forests, followed by chaparral in California and Eucalypt forests in Australia, and lastly by temperate forests. Similarly, we predict that catchment vegetation will recover most quickly in Australia, followed by shrublands in California and the pine and oak forests in the Mediterranean Basin, and lastly in temperate forests. Removal of dead trees is a common practice, and occurs largely in the chaparral and pine/oak basins which are depicted here. In general, burned basins in med-regions appear to recover more quickly than those in temperate regions

Van de Water & North (2010) found no significant difference in fire recurrence intervals between riparian and upland zones for the majority of their sites and significantly longer fire recurrence intervals for riparian than upland areas for about a quarter of their sites. The latter observation is consistent with a view of riparian zone resistance to fire. Although fire loads are often higher in riparian than upland areas owing to higher productivity, the effects of increased moisture and decreased temperature appear to override fuel considerations, because sometimes only riparian vegetation survives through intense fires in med-regions.

The effects of fire on riparian vegetation have many repercussions for allochthonous inputs, shading, stream temperatures, in-stream cover, bank erosion, and the interception of sediment, nutrients, and contaminants from upland areas (Pettit & Naiman, 2007; Koetsier et al., 2010). Coombs (2006) and Coombs & Melack (2012) found that discharge, nutrient and suspended sediment concentrations, and sediment deposition were higher after fires in streams draining burned than unburned basins in southern California, regardless of whether riparian vegetation burned or not. However, levels of light, temperature, and benthic organic matter

depend greatly on riparian burning. These results indicate that fire effects on runoff, sediment, and nutrients are related to basin-wide fire impacts on vegetation and soils, but that temperature, light, and particulate organic matter levels depend on fire impacts on riparian zones. Although many studies do not report the impacts of fire on riparian versus upland areas, it does appear that riparian zones burned in most cases, resulting in increases in temperature and light levels (Minshall et al., 1997; Gresswell, 1999; Koetsier et al., 2010; Sestrich et al., 2011). Temperature and light levels after fire depend on the recovery of the riparian canopy, which may take decades in temperate forests (Gresswell, 1999).

In med-ecosystems, fires of moderate to low severity often do not kill riparian trees, even while they consume much of the above-ground biomass, and riparian areas recover to pre-fire conditions much more rapidly than surrounding uplands (Davis et al., 1989; Bêche et al., 2005; Halofsky & Hibbs, 2009). The rapid recovery of riparian vegetation after fire in most ecosystems can be attributed to the pre-adaptation of fast-growing, relatively short-lived riparian plants to rapid re-establishment and growth following frequent natural physical disturbances (e.g., floods) (Rood et al., 2007), and even burned riparian vegetation recovers quickly by re-sprouting in med-streams. Although data on riparian vegetation recovery after fires are very limited for med-ecosystems, observations suggest that riparian vegetation recovery times are about half those for upland vegetation, concordant with general conclusions derived by Pettit & Naiman (2007).

Differences in short-term fire effects

As stated previously, fires may directly affect stream ecosystems in med- and non-med ecosystems through excessive heating and inputs of ash or atmospheric deposition, but the immediate or short-term (before rains) effects of fire on the biota of both med- and non-med streams appear to be either minor or short-lived (Minshall, 2003; Hall & Lombardozzi, 2008). In Montana streams, Spencer et al. (2003) reported immediate increases in concentrations of phosphate, resulting from the leaching of ash inputs, and ammonium and nitrate, from gas dissolution from smoke; however, such effects were not observed after fire in the rivers of Sant Llorenç del Munt Natural Park in Catalonia (Vila-Escalé, 2009). Some exceptions have

been reported to this pattern of minor or short-lived stream responses during and immediately after fire. For example, Roby & Azuma (1995) reported that benthic macroinvertebrate density and richness were approximately 60% lower in a burned stream than in an unburned stream in northern California forested catchments, a few weeks after a fire, results they speculated were partly due to lethal temperatures associated with the fire. Although elevated temperatures or immediate changes in stream chemistry may cause local fish kills during fires, the introduction of chemicals, such as fire retardants, during fire fighting activities can have longer-lasting effects on stream communities, by causing high fish or crustacean mortality (Blahm & Snyder, 1974; Norris et al., 1991; Gaikowski et al., 1996; Gresswell, 1999).

Many short-term fire impacts on streams only or primarily become evident during and after subsequent rains (Gresswell, 1999; Minshall, 2003; Prepas et al., 2009). Fire in both mediterranean and non-mediterranean catchments alters soil characteristics and induces increased dry ravel erosion in steep terrain during dry periods and increases surface erosion during rains. Because of decreased water and nutrient uptake by vegetation and increased overland flow, inputs of water, solutes, nutrients, contaminants, and organic matter increase in streams during subsequent rain events, particularly, the first intense rains after the fire, producing changes in channel morphology, water chemistry, and in-stream habitat (Gresswell, 1999; Shakesby & Doerr, 2006; Vila-Escalé et al., 2007; Engle et al., 2008; Shakesby, 2011; Coombs & Melack, 2012). Because both fires and rainstorms vary in their frequency, timing, intensity, and extent, fire impacts on streams will depend on the characteristics of a fire and on subsequent meteorologic events (Vieira et al., 2004). Depending on the timing, frequency, and magnitude of subsequent floods, materials introduced to streams in burned basins are diluted and transported downstream and the re-establishment of pre-fire flow, geomorphological, substrata, and water chemistry conditions is often rapid, usually within weeks to a few years (Minshall et al., 2001a; Benda et al., 2003; Earl & Blinn, 2003; Miller et al., 2003; Minshall, 2003; Coombs, 2006; Mast & Clow, 2008; Vila-Escalé, 2009; Nyman et al., 2011; Ryan et al., 2011). Fire effects on streams may differ between med- and temperate ecosystems because autumn and winter floods often occur within 1–6 months after fire in med-ecosystems, but 9 or 10 months after fire

during spring, snow melt in many temperate streams. Further, erosion is often severe in steep terrain during intense rain storms after fires in med-regions, but is often less severe during less intense snow melt times in temperate streams (Figs. 5a, 6). These considerations, however, may not apply in arid or semi-arid areas additionally experiencing summer monsoonal rains, such as parts of the southwestern U.S., where floods can quickly follow fires (Vieira et al., 2004, 2011). Vegetation recovery and the magnitude of runoff and erosion in drainage basins are also greatly affected by high interannual variability in rainfall in med-ecosystems, with vegetation and stream recovery after fire depending on storm intensities and precipitation amounts.

Differences in mid and long term effects of fire

In temperate streams, the destruction of terrestrial vegetation and increased runoff and erosion may introduce more woody debris and leaf litter into streams after fires and subsequent storms, but there can be a lag before large dead woody debris enters streams (Robinson et al., 2005; Arkle et al., 2010). Coarse particulate organic matter inputs often increase immediately after fire, as dead leaves and damaged twigs and branches fall into streams, but decline in subsequent years if riparian vegetation has been reduced, then recover as the terrestrial vegetation recovers (Molles, 1982; Minshall et al., 1997; Koetsier et al., 2010; Fig. 5a).

For med-streams, Davis et al. (1989) and Bendix & Cowell (2010b) observed that dead trees fall into streams for up to 3 years after fire, with many snags still standing after that time, suggesting that woody debris inputs would continue into the future, whereas Vaz et al. (2011) observed substantial amounts of woody debris in streams for up to a decade after fires. Britton (1990) found that leaf fall increased immediately after a fire and that benthic fine particulate organic matter was higher in the post-fire than pre-fire year. In temperate forests, inputs of woody debris into streams following fire can occur for decades to centuries, and higher concentrations of BOM or loose FPOM have been observed in burned than in unburned streams 5 and 20 years after fires (Minshall et al., 1997; Gresswell, 1999; Robinson et al., 2005). Conversely, Koetsier et al. (2010) observed higher benthic organic matter levels and slower leaf decomposition

rates in a stream in an unburned basin than in a stream in a basin burned 10 years before, which also was subjected to a debris flow.

During the first storms after a severe fire, transported sediment and debris scours and moves organisms and benthic substrata, resulting in reductions in algae (Robinson et al., 1994; Vila-Escalé, 2009), macroinvertebrates (Rinne, 1996; Minshall, 2003; Vieira et al., 2004, Vila-Escalé, 2009), and fishes (Gresswell, 1999; Sostoa et al., 2006) in both med- and non-med ecosystems, and their rates of recovery will depend on habitat and resource conditions. Although Minshall et al. (1989) postulated that algal levels in streams would increase after fire owing to higher light and nutrient levels (Fig. 5a), most studies have reported either little change or reductions in algal biomass in streams within or below burned basins (Minshall et al., 1995, 1997, 2001a, b; Earl & Blinn, 2003; Bêche et al., 2005; Malison & Baxter, 2010a). In contrast, greater increases in algal biomass, particularly of filamentous forms, were observed in Californian streams draining burned basins where riparian vegetation burned where riparian vegetation burned than in burned or unburned basins where riparian vegetation remained intact (Fig. 1). These contradictory results may represent differences in the relative importance of scouring events, increased turbidity, and sediment deposition, which may reduce algal biomass, compared to increased nutrient and light levels, which should increase algal biomass, as well as variation in the time elapsed after fires in different studies. In med and non-med forested streams, however, shifts in diatom communities from large to small adnate species were consistently observed after fires (Robinson et al., 1994; Minshall et al., 1995; Earl & Blinn, 2003; Vila-Escalé, 2009).

The qualitative responses of macroinvertebrate communities to fire appear to be similar in med- and non-med streams, but the rapidity of recovery may differ. Vila-Escalé (2009), Rehn (2010), and Verkaik (2010) concluded that most benthic invertebrate metrics returned to pre-fire values within 1–3 years in med-streams (Fig. 5b), but that individual taxa may still have been affected by fire impacts. In other med-ecosystems, Britton (1991a) found few effects of a prescribed burn on invertebrate communities, and Cooper et al. (Fig. 2) observed that invertebrate community responses to fire depended on whether or not riparian vegetation burned. In temperate forest

streams, the responses of invertebrate abundance, biomass, richness, and diversity to fire have ranged from no effects to substantial increases or decreases (Minshall et al., 1995, 1997, 2001b; Gresswell, 1999; Hall & Lombardozzi, 2008; Mellon et al., 2008; Malison & Baxter, 2010a). This diversity in responses was attributed to variation in the extent and intensity of fires in different basins, the magnitude of runoff events, the time since disturbances, and the size (order) of streams (Gresswell, 1999; Minshall et al., 2001c; Malison & Baxter, 2010a). For example, Malison & Baxter (2010a) reported significantly higher secondary production in streams exposed to intense burns where the riparian vegetation was destroyed compared to unburned streams and burned streams where only the riparian understory, but not the canopy, burned 5 years after fires. Changes to invertebrate communities were often observed in temperate streams for 5–10 years after fires (Fig. 5a), but recovery times varied depending on the system and the response variables considered, ranging from years to decades (Gresswell, 1999; Minshall 2003; Vieira et al., 2004; Malison & Baxter, 2010a; Arkle et al., 2010). Interannual variation in invertebrate variables in both med- and non-med streams also appeared to be greater in streams in burned versus unburned basins, perhaps because fire exacerbated the effects of hydrologic and geomorphological variability on invertebrate communities (Minshall et al., 2001c; Minshall, 2003; Arkle et al., 2010; Verkaik, 2010). Further, in both med- and other ecosystems, the effects of prescribed burns on invertebrate communities appear to be much less than the effects of wildfires (Britton, 1991a; Gresswell, 1999; Bêche et al., 2005; Arkle & Pilliod, 2010).

Despite the variation in the responses of invertebrate diversity, abundance, and biomass to fire, there appears to be commonality in the responses of community composition to fire. In the first months after a fire and subsequent rains, Vila-Escalé (2009) observed stream colonization by vagile Coleoptera and Diptera; however, from about 2 months to a year after the fire, the stream community was dominated by Simuliidae, Baetidae, and Chironomidae, taxa which dominate in most streams affected by fires (Fig. 2; Minshall et al., 1997, 2001c; Vieira et al., 2004; Koetsier et al., 2010; Malison & Baxter, 2010a; Rehn, 2010). In general, increases in r-strategists species, that is those characterized by high dispersal rates, small size, fast development, and generalist collector–

gatherer food habits, usually dominate invertebrate communities after fires for periods ranging from months to a few years in med-streams and up to 10 years in temperate forest streams (Figs. 2, 5a, b; Malison & Baxter, 2010a). In some cases, the high abundance of these taxa in intensely burned streams results in increased rates of insect emergence and export to riparian zones, resulting in increased densities of riparian predators (e.g., spiders, bats; Malison & Baxter, 2010b). In contrast, shredders generally are reduced to low levels after fire because of their vulnerability to scouring floods and because of depressed post-fire leaf litter inputs and retention, and then recover slowly, paralleling the recovery of riparian vegetation (Figs. 2, 5a, b; Molles, 1982; Koetsier et al., 2010; Vieira et al., 2011). Changes in the availability of different food resources (e.g., initial loss of riparian leaf detritus and/or increases in algae) may be apparent primarily in low order or severely burned streams, and may be reflected in the representation of different invertebrate functional feeding groups and in the diets of individual taxa (Minshall et al., 1989; Mihuc & Minshall, 1995, 2005; Spencer et al., 2003).

Although some studies in temperate forest streams have reported no fish responses to fire, other studies in med- and temperate forest streams have recorded the local extirpation or reduction of fish populations owing to the immediate effects of fire, contaminants introduced with fire-fighting activities, and particularly, subsequent scouring floods and debris slides (Rinne, 1996; Gresswell, 1999; Burton, 2005; Sostoa et al., 2006; Sestrich et al., 2011). Fish populations driven locally extinct by fires often quickly recovered in temperate forest but not many med-streams (Gresswell, 1999; Dunham et al., 2003; Burton, 2005; Reeves et al., 2006; Sostoa et al., 2006; Sestrich et al., 2011). These differences can primarily be attributed to the presence of many human-made barriers that block fish migrations in heavily populated med-regions and their relative scarcity in temperate forests on public lands. This hypothesis is corroborated by historical evidence of the eventual recovery of trout populations in med-streams affected by fire (Alagona et al., 2012). Studies of the responses of amphibians to fire are few, but indicate large species-specific differences in effects, ranging from declines to increases in population size after fire (Pilliod et al., 2003; Bury, 2004; Hossack et al., 2006). In one study in Spanish streams,

post-fire amphibian communities became similar to pre-fire communities within 3 years (Campeny, 2007). Several studies also indicate that the availabilities of different types of food, and hence, the diets of fish and amphibians are affected by fire (Kerby & Kats, 1998; Koetsier et al., 2007; Rosenberger et al., 2011).

Given the above, sometimes contradictory results of studies, are there differences in the responses of mediterranean and temperate streams to fire? The above review indicates that the general responses of stream ecosystems to fire in med- and non-med regions are similar; however, it also suggests that the resilience of stream communities in both regions is different. The generally rapid recovery of algal, invertebrate, and amphibian communities from fire in med-streams may reflect a species pool adapted to the large seasonal and interannual variation in hydrologic conditions typical of med-streams and to the rapid recovery of terrestrial vegetation in mediterranean catchments. Many of the invertebrate species found in med-streams are vagile, widely distributed, rapidly growing species that quickly re-colonize after disturbances. Múrria et al. (2010), for example, found that an insect, *Hydropsyche siltalai*, which is commonly found in temporary streams of Catalonia, but which lacks a desiccation-resistant stage, has a low genetic diversity, indicating that this species has one, widely-distributed, panmictic population that is widely dispersive.

Our review highlights the importance of interactions between fire and other disturbances (e.g., droughts and floods) in determining the structure and function of med-stream ecosystems. The values of most physical, chemical, and biological variables in med-streams draining burned basins are not affected by fire during immediate dry periods; however, these variables are significantly affected by the intensity, frequency, and timing of subsequent floods. As a consequence, any prediction of the effects of fire on stream systems must consider the frequency, timing, extent, intensity, severity, and patchiness of fires and the magnitude, timing, and frequency of subsequent rain and hydrologic events (Fig. 6). The recovery of nutrient and sediment dynamics to pre-fire conditions will depend on the recovery of terrestrial vegetation, which is faster in med-climate areas but depends on the characteristics of subsequent rain events. Similarly, the recovery of stream light, temperature, and particulate organic matter levels to pre-fire conditions will depend on the recovery of the riparian vegetation, which is usually more rapid than the recovery of

upland vegetation and dependent on flood and drought disturbances. In general, then, climatic and hydrologic fluctuations are master drivers of stream community structure and ecosystem processes in med-regions, representing more frequent disturbances that interact with less frequent fires to determine ecosystem dynamics (Gasith & Resh, 1999).

Implications for watershed management

Because fire can be costly to human life and economic activities, large amounts of money have been spent on preventing, fighting, and recovering from fires in med-regions. At present, however, we know very little about how these management activities affect fire-prone natural ecosystems. To prevent or limit the extent of fires, managers often use prescribed burns or directly remove upland or riparian vegetation to reduce fuel loads (McIver & Weatherspoon, 2010; Stone et al., 2010). Although limited data indicate that prescribed fires have only transient effects on stream physical, chemical, and biological characteristics (Britton, 1991a, b; Bêche et al., 2005), longer term effects of prescribed burns on med-streams have been noted (Meixner et al., 2006). The effects of vegetation removal by controlled burns or mechanical means on stream ecosystems will likely depend on the timing, extent, intensity, and frequency of these activities. Observations in California indicate that fires that are too frequent, on the order of less than 12 years, may shift native shrubland to exotic grasslands that, in turn, are even more ignitable (Odion & Davis, 2000; Jacobsen et al., 2004; Syphard et al., 2006). Many med-ecosystems are adapted to fire, and fire often stimulates the germination or re-sprouting of mediterranean plants, although regeneration does not always occur (Rodrigo et al., 2004). Furthermore, it is unlikely that prescribed burns simulate natural wildfires because prescribed fires often are less intense, occur in a different season, and have different spatial configurations than wildfires (Arkle & Pilliod, 2010). In addition, the development of fire roads, trails, and containment lines before and during fires and the construction and maintenance of buildings, denude native vegetation in restricted areas, acting as points for erosion and the colonization of exotic plant species (Backer et al., 2004; Keeley, 2006). All of these activities have unknown repercussions for streams.

Some of the most dramatic effects of fire fighting activities have occurred when fire retardants have entered streams, causing fish kills (National Marine Fisheries Service, 2008; Cooper, 2009), which has led to recent revisions to the U.S. Forest Service's policies on fire retardant application.

Debris or check dams have been constructed on many drainage streams in med-regions to trap sediment and debris that would normally be transported downstream, perhaps clogging bridges and covering banks or floodplain developments (Karr et al., 2004). Debris dams convert upstream stream reaches to more open, lentic, or marshy areas and act as barriers to fish migration, all with local and downstream implications for the biota. Although debris basins are often "cleaned" after fires but before ensuing storms, calculations indicate that debris dams are often inadequate to handle sediment loads generated by large, infrequent storms after fires (Abramson et al., 2009).

After fires, management agencies often remove dead trees and other vegetation from upland, riparian, and stream areas (Beschta et al., 2004; Karr et al., 2004; Reeves et al., 2006). Dead vegetation, however, can still stabilize soils through their root systems, at least until the roots decompose, and dead woody vegetation along and in streams provides cover, habitat, and shading for riparian and stream organisms. Nevertheless, the removal of woody debris along and in streams after fires is widely practiced, and its effects have been largely unmeasured. After the 2003 fires in northeastern Spain, a multidisciplinary project was initiated to speed the natural regeneration of the burned area and to foster the socioeconomic recovery of the region. Fire mitigation measures used in this project included the construction of sediment traps, reforestation of riparian areas, removal of dead trees, and installation of nesting boxes (Guinart, 2007). Although management efforts resulted in the establishment of 4000 native trees (Guinart, 2007) and the increased occupation of nesting boxes by bats (60%) (Serra-Cobo et al., 2010), studies conducted up to 6 years after the fire indicated no significant differences in vegetation regeneration between areas subjected to restoration efforts and burned areas that were unmanaged (Pañella, 2011). Further, it appeared that the construction of railroads to transport dead trees that were logged or removed after the fire generated more soil erosion than the fire itself. A similar result was obtained in a study on terrestrial gastropods in the

same area, where fire had large impacts on snail communities, but where no differences were found in snail community structure between managed and unmanaged burned areas 4 years after fire (Bros et al., 2011). In the same way, because the responses of invertebrate communities to fire in some southern California streams appeared to be related to fire effects on riparian vegetation, there have been recommendations to eschew the removal of riparian or in-stream vegetation, a recommendation that has been largely ignored (Karr et al., 2004; Rehn, 2010). In some burned basins, jute mats, grass seeds, straw, and hydromulch have been applied aerially or manually to stabilize soils and prevent erosion; however, the effects of these practices on streams are unknown.

Building or rebuilding activities in mediterranean shrublands should be tightly controlled (e.g., through zoning) to prevent erosion and the introduction of exotic species and to reduce the frequency of fire. Humans start over 80% of the wildfires in California and the Mediterranean Basin, and there are direct relationships between the locations and frequency of fire and human development in med-ecosystems (Syphard et al., 2007; Pausas et al., 2008).

Biological communities in med-streams are often monitored to assess the health of natural ecosystems, sometimes in the context of evaluating fire legacy effects on stream communities. In California, several wildfires swept through a subset of long-term stream monitoring sites in San Diego and San Bernardino Counties in October of 2003 and 2007. Rehn (2010) used data from this monitoring effort to compare a macroinvertebrate Index of Biotic Integrity (IBI) (Ode et al., 2005) and the ratios of observed invertebrate richness values to expected values (O/E values), the latter calculated from relationships between richness and environmental factors for undisturbed streams, for reference (undisturbed) sites and test (degraded) sites in burned and unburned basins annually over 2–6 years. Although IBI and O/E values declined in the first spring after the 2003 fires in reference streams in burned basins, they also declined in reference streams in unburned basins. Analyses comparing IBI and O/E values, and post-fire minus pre-fire differences in IBI and O/E values, between sites draining burned and unburned basins revealed no effects of fire on test site communities and only a few, sporadic effects of fire on reference site communities up to the fourth spring after fires. Although fire effects on invertebrate

communities were inconsistent and inconclusive, owing to high variation in responses across streams, Rehn (2010) found that primarily riparian canopy cover was related to IBI and O/E scores across sites, suggesting that some of this variation in invertebrate responses could be attributed to variable fire effects on riparian vegetation. Based on these results, Rehn (2010) recommended that streams should not be used in biomonitoring efforts if their basins have been burned within the last 3 years.

In northeastern Spain, the Specific Pollution Sensitivity index (IPS) for diatoms and the Iberian Biomonitoring Working Party (IBMWP) (ACA, 2006) index for macroinvertebrates showed their lowest values during the first months after the fire in a burned stream, over a study period encompassing five pre-fire and two post-fire years. Diatom species richness peaked 3–4 months after the fire; similar diatom IPS values were found in the burned and a reference (unburned) stream after 7 months; and diatom IPS values in the stream in the burned catchment reached pre-fire values 9 months after the fire, then remained at high levels, equivalent to an interpretation of “good” conditions, for up to two post-fire years (Vila-Escalé, 2009). These results suggest that indices of biological integrity for Spanish streams can be used in biomonitoring efforts without the confounding influences of fire impacts if samples are taken ≥ 2 years after a fire.

Future research

The study of fire effects on med-streams has received surprisingly little attention despite the prominence of fires in med-ecosystems. Because stream responses to fire will depend on the frequency, intensity, timing, and extent of fires and subsequent rain events, we need much more data across a wide range of fire, meteorologic, and hydrologic conditions before we can begin to ascertain the magnitude, longevity, and mechanisms for med-stream responses to fire. Although med-ecosystems show resilient responses to wildfire, the intensity, frequency, and effects of wildfire will likely change with land use and climate changes (Pausas et al., 2008; Tague et al., 2009; Pausas & Paula, 2012). Most climate models predict that med-regions will have more severe and prolonged droughts, higher temperatures and evapotranspiration rates, and, when they occur, more intense rainstorms. As a consequence, the frequency

and intensity of wildfires, as well as large flood and prolonged drying events, are projected to increase. Ecological models also predict that suppression or prescribed fire policies will not change the total area burned, and large fires will not be eliminated (Piñol et al., 2007). As a consequence, stream ecosystems could be pushed into a different disturbance state in the future with many implications for the stream biota.

Because wildfire is such a ubiquitous and frequent feature of med-ecosystems, comprehensive monitoring efforts that sample many streams will eventually capture stream responses to wildfire (Prat & Riera-devall, 2006; Rehn, 2010). Also, because fires affect many geologic, geomorphological, hydrologic, vegetation, and chemical processes and parameters, with repercussions for stream communities, future studies of fire will be necessarily multi-disciplinary, so that information and insights from some disciplines can inform other disciplines. Based on our review, we have identified key specific topics that could be addressed by future research on stream ecosystems:

- Because fires are often patchy, it is important to examine the implications of the spatial configuration of fires for stream ecosystems (e.g., distribution of burned vegetation and fire intensity in both upland and riparian zones) (Beeson et al., 2001; Tague et al., 2009). Integration of studies of the spatial distribution of fire effects on erosion, vegetation, and nutrient cycling obtained through remote sensing, geographic information system methods, and ground measurements, with physical, chemical, and biological monitoring in receiving waters, will enable the magnitude and mechanisms for fire effects on streams to be ascertained.
- Within streams, the limited data collected to date have concentrated on state variables, such as the richness, biomass, density, or species composition of key groups. There are almost no data on how fires affect trophic webs or ecosystem processes in and along med streams, including particulate organic matter inputs and break down, microbial activity, nutrient spiraling, emergent insect export to the riparian zone, and primary and secondary production. Such gaps in our knowledge could be addressed through appropriate stable isotope, tracer, leaf decomposition, exchange rate, and production studies (e.g., as in Mihuc & Minshall, 2005; Koetsier et al., 2010; Malison & Baxter, 2010b).

- Previous research appears to indicate that fire effects on riparian zones are critical in determining fire effects on stream ecosystems. As a consequence, we recommend new studies on how chemical and soil processes, and vegetation characteristics, in the riparian zone respond to and recover from fires (Pettit & Naiman, 2007).
- To provide a longer term perspective on how fires affect stream geomorphology and, hence, stream communities, we recommend coupling studies of the effects of landslides, debris flows, and large structural elements associated with fires on stream geomorphology with studies on the responses of the stream biota to the physical template.
- As outlined above, we know very little about the impacts of management activities designed to prevent, fight, or recover from fires on med-stream ecosystems (Bisson et al., 2003; Beschta et al., 2004; Stone et al., 2010). Through cooperation between management and research agencies, studies could be framed and monitored as part of an experimental design. Such studies are needed to evaluate the effectiveness of management actions and their environmental impacts, guiding management and policy decisions.
- Finally, the effects of climate change on the hydrology and ecology of med-streams may be dramatic in the future. Little is known about possible climate change effects (Prat & Manzano, 2009), and our capacity to predict stream responses is limited. Increases in temperature and changes in precipitation regime will likely increase the frequency and intensity of fires in med-regions, perhaps exceeding the capacity of streams and their resident species to recover from fire.

Because wildfires are a pervasive feature of med-ecosystems and are projected to increase with climate change, it is critical that much more research is conducted to ascertain the effects of fire and fire management practices on med-streams.

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