

Long-term effects of Portuguese forest fires on morphology and aquatic habitat structure of lotic ecosystems

Pedro Jorge Gonçalves Vaz

Tese apresentada à Universidade de Évora para obtenção do Grau de Doutor em Biologia

ORIENTAÇÃO: Paulo Nuno dos Santos Lopes Pinto CO-ORIENTAÇÃO: Christopher Thomas Robinson; Francisco Manuel Cardoso de Castro Rego

ÉVORA, DEZEMBRO 2013



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Em conformidade com o Regulamento do Ciclo de Estudos conducente ao Grau de Doutor pela Universidade de Évora (Ordem de Serviço N.º1/2010), esta tese integra um conjunto de cinco trabalhos de investigação publicados em revistas internacionais indexadas (Journal Citation Reports) e com arbitragem científica. Tendo em conta que os referidos trabalhos foram realizados em colaboração com outros autores, o candidato esclarece que em todos eles liderou e participou activamente na sua concepção, recolha, análise e discussão de resultados, bem como na escrita dos artigos. Algumas das normas relativas ao padrão de formatação de cada revista foram retidas nesta tese.

Em apêndice, reproduzem-se ainda três resumos de apresentações em conferências internacionais, três artigos científicos, e um capítulo de livro, realizados em paralelo pelo candidato no contexto dos trabalhos de investigação que conduziram a esta tese.

Lisboa, 12 de Junho de 2013

Pedro Jorge Gonçalves Vaz

De todas as pessoas que me ajudaram durante estes quatro anos em que estive envolvido nesta tese de doutoramento, começo por agradecer à minha familia adoptiva, a família Dias. Sem eles esta saga não seria mesmo possível. Estar quatro anos a ouvir falar de madeira em rios deve tê-los feito odiar o tema e desejar mais do que eu próprio o fim desta tese. Susana, chegámos ao fim!

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Abstract

This thesis investigates long-term effects of forest fires on morphology and functioning of Portuguese streams via burned wood. Wildfires influenced the landscape dynamics across three regions examined, towards increases in shrublands encroaching into previously forested areas. Large wood amounts within 27 streams were low and are expected to decline in the future owing to wildfire. Likewise, wildfire was promoting wood lacking structural complexity, thus likely reducing habitat heterogeneity that improves conditions for aquatic organisms. The effect of fire providing wood with greater diameter will increase its probability for stream functions such as pool formation. However, this functionality may not persist because most of this wood was decayed and less stable in the channel. It is critical for aquatic communities if fire-derived wood falls directly into the river or if it is previously conditioned for some time on the forest floor.

Efeitos a longo prazo dos fogos florestais na morfologia e estrutura do habitat em ecossistemas lóticos de Portugal

Resumo

Esta tese avalia os efeitos a longo prazo dos fogos florestais na morfologia e funcionamento de rios portugueses através da madeira ardida. O fogo influenciou a dinâmica da paisagem em três regiões estudadas, favorecendo a invasão por matos de áreas previamente florestadas. A quantidade de pedaços de madeira em 27 rios foi baixa e prevê-se a sua diminuição futura por influência do fogo. O fogo promoveu também a presença de madeira com menor complexidade estrutural, reduzindo provavelmente a heterogeneidade de habitat que melhora as condições para os organismos aquáticos. A madeira queimada tinha maior diâmetro, aumentando a probabilidade de função no rio, como a criação de fundões. Esta funcionalidade pode não persistir porque esta madeira estava degradada e menos estável no canal. É determinante para as comunidades aquáticas se a madeira dos fogos cai directamente no rio ou se é previamente condicionada durante algum tempo no solo da floresta.

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CHAPTER 1



General introduction

1. General introduction



1.1 The Portuguese wildfire-landscape context

A changing global climate and evolving anthropogenic activities are combining to increase the probability and severity of fire in Europe and around the world (Moriondo et al. 2006, Flannigan et al. 2009, Moreira et al. 2011). In the European region, about 65,000 forest fires occur every year, burning approximately 0.5 million hectares of forests and other rural areas (European Commission 2011). Approximately 85% of the total burnt area occurs in the Euro-Mediterranean region (San-Miguel-Ayanz and Camia 2010), where Portugal deserves special mention. The average number of fires in Portugal in the last decade corresponds to over 50% of the average number of fires in the whole Euro-Mediterranean region. These fires have burnt on average 148,555 ha per year in this decade (JRC 2011, San-Miguel-Ayanz et al. 2013). Between 1975 and 2007, the total estimated burnt area corresponds to 41% of the country's area (Marques et al. 2011). In the last decade, the fire-seasons of 2003 and 2005 are especially noteworthy, constituting the two peaks of total burnt area. Wildfires are thus a challenge for forest management in Portugal, whether for terrestrial environments or inland waters.

To understand the progress of wildfire phenomenon in Portugal (and across the Euro-Mediterranean region), we also must understand landscape and human dynamics, as the three factors are intertwined and influence each other (Vaz 2009). In the Mediterranean, people have lived with fire since prehistory, using fire to clear vegetation and promote grasslands for hunting, gathering, farming, and pastoral activities (Pausas et al. 2008). It is noteworthy that in the Euro-Mediterranean region, people-ignited fires are largely predominant over natural ignitions (Ganteaume et al. 2012). Fire spread rate and intensity can be, in turn, facilitated or retarded by landscape heterogeneity, depending on the differential fire behaviour in various land cover types that are not equally fire prone. In general, Euro-Mediterranean landscapes have increased the fire hazard in the last decades, resulting from more homogeneous landscapes covered by more shrublands and abandoned agricultural lands (Moreira et al. 2011). Several studies have demonstrated that shrublands are the land cover most prone to fire, whereas cultivated areas, particularly those with irrigated crops, is the land use burning in a lower proportion than the surface area they cover in the landscape (Nunes et al. 2005, Moreira et al. 2009). These dynamics have been accompanied by abandonment of land by people (see Sluiter and Jong 2007) due to socio-economic changes, in what have been described as a "rural exodus syndrome" (Hill et al., 2008).

The human presence is also fundamental in forests of the Euro-Mediterranean region. In Portugal, forests are mostly managed private forests, contrasting with a more natural scenario found in some other regions. Forest occupies 35% of the territory, of which 26% is eucalyptus

(*Eucalyptus globulus*), 23% maritime pine (*Pinus pinaster*), and 23% cork oak (*Quercus suber*), cultivated for the production of wood for paper pulp, timber wood, and cork, respectively. Among the forest types, maritime pine stands have the highest fire proneness (Godinho-Ferreira et al. 2006, Silva et al. 2009) and its area dropped from 30 to 23% between 1995 and 2010, especially in burned areas (Garcia-Gonzalo et al. 2012), having been replaced mostly by areas of shrublands and eucalyptus. Eucalyptus forest, in turn, increased gaining area mainly from maritime pine but also from shrublands and agriculture (ICNF 2013). Cork oak forests are commonly considered less fire-prone, although 15–20% of its area also have burned since 1990 (Catry et al. 2012). Regardless of the forest or other land cover types, several studies have shown that steep slopes are more prone to fire (Carmo et al. 2011, Nunes 2012), setting a favorable scene for wildfires in valleys along forested streams and rivers that were depopulated over the past decades.

1.2 Fire disturbance on lotic ecosystems

In valley bottoms, streams reflect the landscape through which they flow. Under the current Portuguese wildfire-landscape dynamics, surprisingly little is known about what is happening in our lotic ecosystems as a consequence of fire disturbance (Pinto et al. 2009). Moreover, the effects of fire on aquatic ecosystems globally have received increasing attention only in the last two decades (Resh et al. 1988, Gresswell 1999, Robinson et al. 2005, Verkaik et al. 2013). The beginning of research on fire impacts in aquatic ecosystems is located in the western United States, following the 1988 fires in Yellowstone National Park (Minshall et al. 1989, Minshall et al. 1997, Romme et al. 2011). Since then, published studies from other parts of the world beyond North America remain limited, especially those documenting fire effects on habitat structure and the biology of lotic ecosystems. Some notable reviews addressing the topic have been published (Gresswell 1999, Minshall 2003, Rieman et al. 2003, Verkaik et al. 2013). In general, the effects of fire on aquatic ecosystems may be separated into direct and indirect effects (Minshall 2003). Direct effects last from days to weeks and include, for example, atmospheric inputs and water and soil heating, having generally short-term effects on ecological processes and biological communities. Indirect effects can be more persistent and have midand long-term ecological consequences.

Short-term effects of wildfires in the Euro-Mediterranean streams primarily occur up to and including the first rainfalls and consequent runoffs, which in Portugal begin generally in October, i.e. between one and five months post-fire. Following wildfire, an increase in temperature occurs along with inputs of ash and atmospheric deposition of particulates (e.g. from gas dissolution from smoke) (Ferreira et al. 2005, Lion and O'Connor 2008, Leach and Moore 2010, Rhoades et al. 2011). Solar radiation on the stream can begin to increase through the opening of the riparian canopy consumed by wildfire, accompanied by an initial entrance of fire exposed leaves and wood (Gama et al. 2007, Jones and Daniels 2008). Suspended sediment increases, being deposited on the stream bottom (e.g. in pools), pH may increase, water chemistry changes, and

dissolved oxygen levels likely go down (Moody and Martin 2001, Vila-Escalé et al. 2007, Hall and Lombardozzi 2008, Smith et al. 2011, Pereira et al. 2013). Stream biota, such as algae, macroinvertebrates, fishes, and some amphibians can be readily and dramatically affected during this phase (Robinson et al. 1994, Rinne 1996, Dunham et al. 2003, Earl and Blinn 2003, Pilliod 2003). On streamside slopes, soil hydrophobicity and erosion are enhanced due to low impedance of regenerating vegetation and the exposure of bare soil (Coelho et al. 2004, Moody et al. 2013). As a consequence, with the first runoffs, water enters the stream laterally and favors high peak discharges (Shakesby and Doerr 2006, Tessler et al. 2008). More sediment, nutrients, salts, organic matter, and contaminants from upland areas are then delivered into and transported through the fluvial system (Mayor et al. 2007, Ferreira et al. 2008). The following spring, post-fire bare soils along streamside slopes begin to be covered by fire-adapted shrublands (typically within 1-3 years in Portugal), reducing the time of soil erosion compared with other world regions and with consequences to streams (Varela et al. 2005). As a rule, the direct and short-term effects of wildfire are considered less detrimental to the sustained maintenance of an ecological equilibrium of lotic systems (Minshall et al. 2001a,b, Minshall 2003, Verkaik 2010).

While a substantial body of knowledge has accumulated on the direct and short-term effects of wildfire on lotic ecosystems, scant information is available on its long-term consequences for stream hydraulics, channel morphology, sediment and organic matter dynamics, habitat structure, and biological communities. Also, the immediate effects of fire on streams appear to be essentially similar across different regions, whereas long-term effects are likely more variable (Rull and Vegas-Vilarrúbia 2011). A long-term effect can range from 1-4 years in an Euro-Mediterranean context or more than 100 years in temperate forests (Bruns et al. 1992, Minshall et al. 1989, Verkaik et al. 2013). This wide range reflects the distinct post-fire recovery time and resilience ability across different regions of the world. Few studies have followed recovery trajectories from wildfire in aquatic ecosystems for multiple years, perhaps with the most notable exception being the case study on the Yellowstone National Park 1988 fires (Romme et al. 2011). Globally, the long-term effects of fire on aquatic ecosystems depend synergistically on the intensity and severity of fire, the resilience of the vegetation in the stream corridor and its slope, but also on the timing, magnitude, and frequency of subsequent rainfalls (Verkaik et al. 2013). In Portugal, wildfires are common events and the ability to recover to a prefire state is quite high in burned forests of cork oak, eucalyptus, and even mature maritime pine, the main forest types in the country. In steep riparian corridors, a rapid establishment of post-fire shrubs is common, especially in moist and nutrient-rich environments, but a quantification of long-term effects of fire on streams is yet to be done and if there is a fast recovery rate paralleling that of the upland and riparian vegetation remains a knowledge gap.

1.3 Fire-derived wood in forested streams

Downed wood pieces in forests are key links between terrestrial and aquatic ecosystems. Processes that can affect stream wood recruitment vary by region, but generally include biological processes such as insect outbreaks and disease, and abiotic processes such as fire, floods, bank erosion, wind storms, ice storms, and snow avalanches (Resh et al. 1988, Naiman et al. 2005). During fire, wood from riparian trees may be injured and then directly enter stream channels, or wood may fall onto the forest floor and remain there until it moves laterally into stream channels during floods or from eroding banks. Trees injured by fire can also become more susceptible to mortality via windthrow and disease, and thereby enter fluvial systems more readily (Benda et al., 2003). Because the main Portuguese forest types are managed stands, wood may further enter streams as intended or unintended results of management actions. In the stream, wood pieces then affect virtually every physical, chemical, and biological process, including morphological dynamics, habitat structuring, hydraulics, transport of materials, algal biomass accrual, nutrient uptake, and trophic interactions (Gregory et al. 2003, Ashkenas et al. 2004, Daniels 2006, Baillie et al. 2008, Coe et al. 2009, Merten et al. 2013). Thus, the presence of large burned wood in streams remains for years as a major and conspicuous intermediate of the long-term effects of the fire event.

Despite the fact that fire effects on stream wood input has been documented and is apparent in the stock of burned wood (Young 1994, Zelt and Wohl 2004, Arseneault et al. 2007, Jones and Daniels 2008), its role on post-fire stream functioning remains largely unexplored. In addition, the rare studies assessing the overall stock of burned stream wood have studied mainly a single large fire event and thus had little replication, hence decreasing the applicability and generalization of results to different forest situations. Across forest types, factors such as forest age, time since the last fire, methods of post-fire logging and silviculture practices often differ. In addition, studies on stream wood dynamics in the context of fire history have focused on pristine regions with mixed-forest systems or those with a single forest-management system. This contrasts with Portuguese landscapes having generally long legacies of land management or multi-use systems with production forests and agriculture. Furthermore, extending the study of the ecology of stream wood to the Euro-Mediterranean region, with streams characterized by strong seasonality and large interannual variability in rainfall (commonly intermittent or temporary streams), is a valuable research perspective (Gasith and Resh, 1999).

For aquatic invertebrates, wood plays a major role providing refuge, foraging and attachment substrate at varying stages of their life cycles (i.e. oviposition, pupation and emergence) (Hoffmann and Hering 2000, Benke and Wallace 2003, Pitt and Batzer 2011). While the nutritional value of wood is low, several stream macroinvertebrates ingest wood fragments (Spänhoff et al. 2000) and a few can digest wood (Monk 1976) or the epixylic biofilm established on its surface. Several studies have addressed the structural role of wood on macroinvertebrate communities in streams (Wallace et al. 1995, Hilderbrand et al. 1997, Lemly and Hilderbrand 2000, Warren and Kraft 2006), such as the effects of wood on flow patterns

and retention (Entrekin et al. 2009, Testa et al. 2011). For fish, wood primarily provides habitat and refuge. For example, some fish species may prefer pool habitat created by wood (Bilby and Bisson 1998; Dolloff and Warren 2003). Fish diversity and abundance is usually higher in streams with high large wood loadings (Fausch and Northcote 1992, Neumann and Wildman 2002, Wright and Flecker 2004). Nevertheless, the research topic on how wildfire structures aquatic communities through instream fire-derived wood is still unexplored.

1.4 Thesis rationale and structure

In this thesis, the role of forest fires on landscape dynamics in Portugal is initially evaluated, followed by the use of fire-derived wood to address the long-term effects of fire on stream physical structure and stream functioning. Five studies are undertaken with fire as the common underlying process, encompassing a range of spatial and temporal scales depending on the effect of fire in evaluation. Fire is assessed as a driving factor of: (1) landscape dynamics; (2) stream wood (SW) structure; (3) SW stock and distribution; (4) SW function, and (5) SW colonization by macroinvertebrates. Landscape dynamics is addressed at a coarse scale for a time-period of about 14 years. Three of the studies were conducted at a regional scale in the Tagus River Basin, across nine subbasins burned within six years prior. SW colonization by macroinvertebrates is evaluated at the local (reach) scale from over one month to one year.

For the first study regarding wildfire-landscape dynamics, the study areas are located in central and northern Portugal where the greatest number of fires occurs. The other four studies were conducted in east-central Portugal, a region particularly affected in 2003 and 2005, the two highest fire years in the existing record for Portugal (e.g. Viegas et al. 2006, San-Miguel-Ayanz et al. 2013). These fires, and the fact that they affected vast areas of maritime pine, eucalyptus, and cork oak forest types, created a unique opportunity to conduct these studies across basins but within a relatively uniform climatic region.

1.4.1 Objectives

The overall aim of this thesis is to enhance knowledge on the long-term effects of fire on lotic ecosystems mediated by fire-derived wood under Portuguese landscape and forest contexts. The following research objectives were identified:

- 1) To address the role of fire on landscape dynamics of three fire-prone regions in Portugal with different landscape patterns;
- To evaluate the structure of burned and unburned downed wood from trees of eucalyptus, maritime pine, cork oak, and riparian species, with potential implications for stream functioning;
- 3) To quantify and compare the post-fire amount and organization of stream wood among the main three forest types interacting with different stream sizes;
- 4) To determine which SW characteristics, in interaction with burned status, will influence ecological, geomorphological, and hydraulic functions;
- 5) To assess the effects of wood burn status and preconditioning on the patterns of colonization by stream macroinvertebrates.

Overall, it is hypothesized that fire can influence landscape dynamics, and the morphology and aquatic habitat structure of lotic ecosystems at long-term periods through its effect on stream wood.

1.4.2 Outline

The thesis is organized in 7 Chapters (Fig. 1). **Chapter 1** provides the motivation, scope and background information of the research topics. The next five chapters (Chapters 2-6) have been produced as a series of scientific papers for publication in international peer-reviewed journals, four of which are published and the latter is under peer review. As a result, there is some overlap between chapters. **Chapter 2** assesses the Portuguese landscape context while addressing objective 1; this study also supports selection of study areas for the remaining four studies. Selected streams flow through upland forests of maritime pine, eucalyptus, and cork oak and comprise the study sites for the research in Chapters 3 to 6. **Chapters 3 and 4** essentially set the scene for the potential of fire-derived stream wood in creating habitat structure while addressing objectives 2 and 3. **Chapters 5 and 6** examine how stream functioning may be affected by fire-derived wood, specifically addressing objectives 4 and 5. **Chapter 7** provides an integrated overview of the most important results from the previous chapters and includes recommendations for conservation and management as well as possible research directions.



7. General discussion

Fig. 1. Thesis outline. Five scientific papers are presented as chapters 2 to 6 (ellipses). Chapter 2 provides a landscape context, a broad assessement of the fire phenomenon in Portugal, and supports selection of study areas. The rectangle represents fire as the underlying disturbance process addressed across the main Portuguese forest systems. Dashed lines separate three conceptual components of this thesis.

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Wildfires as a major driver of landscape dynamics in three fire-prone areas of Portugal

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2. Wildfires as a major driver of landscape dynamics in three fire-prone areas of Portugal

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Abstract: Wildfires are a common event in Mediterranean landscapes. We assessed the implications of wildfires on the landscape dynamics of three fire-prone areas of Central and Northern Portugal during a time period of 13-15 years, starting in 1990. Using an informationtheoretical approach and probability analysis, we assessed the relative importance of fire and initial land cover on the overall landscape dynamics. We further explored the role of fire on specific land cover dynamics by building transition matrices separately for burned and unburned areas. Finally we simulated future landscapes using the transition matrices to project landscape composition, according to a Markovian process. Fire had a determinant role in the landscape changes observed in the three study areas, as it favored shrubland persistence and the conversion of other land cover types to shrublands and mixed forests. The effect of fire on land cover dynamics could be explained mainly by post-fire vegetation responses due to land abandonment, but human-driven changes were also an important influence on land cover dynamics. In the long term, the current landscape dynamics would result in an increase in landscape diversity. When compared with this projection, either a scenario without fire or a complete periodic burn of the study areas, would result in lower landscape diversity. Comparing the two opposite scenarios, the latter would reduce the proportion of agriculture, while increasing the proportion of shrublands and unmanaged mixed forests of exotic and native species, therefore leading to an increase of fire hazard and to less sustainable landscapes.

Keywords: wildfires; landscape changes; land abandonment; transition matrices; exotic species; Portugal.

2.1 Introduction

Wildfires constitute a major disturbance in Mediterranean landscapes (Rundel, 1998) and have profound consequences in landscape structure and functioning (Bajocco & Ricotta, 2008). The relationship between fire and landscape pattern and dynamics is one of strong reciprocal influence. On one hand, landscape pattern will influence fire spread, as certain land cover types are more fire-prone than others due to differences in vegetation structure, moisture content, and fuel load composition (e.g. Forman, 1995; Mermoz, Kitzberger, & Veblen, 2005; Moreira, Vaz, Catry, & Silva, 2009). On the other hand, fire occurrence will subsequently affect landscape pattern and dynamics (Lloret, Calvo, Pons, & Díaz-Delgado, 2002; Viedma, 2008) by changing vegetation structure and soil processes according to the fire adaptations of each ecosystem (Mouillot, Ratte, Joffre, Mouillot, & Rambal, 2005; Pausas, Llovet, Rodrigo, & Vallejo, 2008; Viedma, 2008). In the case of Mediterranean-type ecosystems, many authors refer a strong resilience allowing the persistence of plant communities after fire (e.g. Mitchell, Simonson, Flegg, Santos, & Hall, 2009; Naveh, 1975; Trabaud & Galtiè, 1996). But on Mediterranean landscapes, where human management is widespread, human activities may also interact with fire in different ways. Some studies have shown that post-fire regeneration patterns may be affected by the historical land use of burned areas (Baeza, Valdecantos, Alloza, & Vallejo, 2007; Pérez, Cruz, Fernández-González, & Moreno, 2003). Baeza et al. (2007) found that, in a region of southern Spain, previous land use (forest or cropland) determined the type of post-fire regenerating shrub. But at the same time, land owners' decisions as a response to the presence (or absence) of fire are likely to have also a determinant role in post-fire land cover dynamics (Viedma, Moreno, & Rieiro, 2006). In fact, wildfires may offer an opportunity for land cover change, or may be a discouraging element leading land owners to stop managing their land. In summary, landscape changes in humanized fire-prone regions may result from interactions between fire regime, natural vegetation dynamics and human management decisions.

Most empirical studies about the role of fire on vegetation dynamics were carried out in burned areas, with no comparison with nearby unburned landscapes. To our knowledge, only two studies clearly focused on the influence of fire on landscape dynamics in the Mediterranean, by comparing burned versus unburned areas. One was carried out by Lloret et al. (2002) for a region of Catalonia (Spain). These authors compared landscape composition and dynamics during a 15-year period, and found that in burned areas shrublands were more persistent and that there was a faster transition from pine forests to shrublands. Burned areas had lower landscape diversity and larger patch sizes. The other was undertaken by Viedma et al. (2006) in central Spain. These authors monitored landscape changes during 1975–1990 in areas with different fire frequencies. They have also found a decrease in the area covered by pines and an increase in shrublands, and higher landscape homogeneity, in burned areas.

Portugal is the European country presenting the largest percentage of the territory affected by wildfires (San-Miguel & Camia, 2009) and is also the European country presenting the largest percentage of private forests (FAO, 2005). Additionally, most of the country is characterized by very fragmented landscapes composed of very small land plots belonging to different land owners (DGRF, 2007). These aspects are likely to have strong implications on landscape dynamics and its link with wildfires. Different studies dealing with landscape dynamics in Portugal (Gaspar & Fidalgo, 2002; Moreira, Rego, & Ferreira, 2001; Timóteo, Bento, Rego, & Fernandes, 2004), and elsewhere in the Iberian Peninsula (Loepfe, Martinez-Vilalta, Oliveres, Piñol, & Lloret, 2010; Romero-Calcerrada & Perry, 2004) have shown that land abandonment due to socio-economic changes is contributing to increase fire hazard, namely by increasing the area covered by shrublands and forests. However, the role of wildfires on subsequent land cover dynamics has not deserved a similar attention from researchers. It is important to understand which land cover transitions are associated with wildfires and which can be expected in the absence of fire, as this knowledge can help managers directing their efforts to recently burned areas in order to promote sustainable landscapes.

In the present paper we address the role of fire on the landscape dynamics of three regions in Portugal with different landscape patterns. For that purpose we characterized landscape changes during a time period of 13–15 years beginning in 1990, both overall and separately for areas that have been affected versus not affected by wildfires during that period, with the aim of answering the following research questions: (a) what is the influence of wildfire occurrence on the probability of land cover change?; (b) which land cover transitions are fire-driven? (c) what is the expected landscape composition at the end of the XXI century, based on modeled land cover transitions and according to different scenarios of fire regime?

2.2 Methods

2.2.1 Study areas

We have collected data on landscape changes and wildfire occurrence for 13- and 15-year study periods, starting in 1990, in three Portuguese fire-prone areas: Águeda (6512 ha), in the Northern Coastal region; Mação (12,177 ha), in the Central region; and Bragança (11,533 ha), in the Northeastern region of Portugal (Fig. 1). These three areas were chosen because of their distinctive proportions in land cover and high fire incidence during the study period. Águeda and Mação were selected because they include the most representative forest types in Portugal, eucalyptus and maritime pine, respectively. Bragança lacked the fast-growing eucalyptus plantations (due to the lower temperatures of this region) and had a higher proportion of native broadleaved forests.



Fig. 1. Location of the three study areas.

2.2.2 Characterization of land cover and wildfire patterns

Our base map was a 1990 land-cover map for Portugal (reference scale 1:25,000) developed by the National Centre of Geographical Information. The legends of the base land-cover map were simplified to a seven-class legend considered adequate:

- Agriculture – all types of diverse agricultural mosaics and pastures, including annual crops, permanent crops (vineyards, orchards, olive groves). In Bragança, this class included recent agro-forestry plantations of chestnut (*Castanea sativa* Mill.).

Shrublands – plant communities dominated by shrubs at different developmental stages.

- Conifers – artificially and naturally regenerated forests of maritime pine (*Pinus pinaster* Aiton). Other species of conifers are residual in our data.

- Eucalyptus - forests of blue gum (Eucalyptus globulus Labill.).

- Broadleaves – forests with different species of oaks (*Quercus* spp.), riparian tree species and other native broadleaves, but also including exotic *Acacia* spp. patches particularly in Águeda but also in Mação. In Bragança mature closed forests of chestnut (not present in the other two regions) were included in this class.

- Mixed forests of eucalyptus and conifers (mixed E–C) – mixed forests of maritime pine and blue gum in different levels of dominance, presenting in general a developed understory.

- Other mixed forests (mixed) – mainly composed of broadleaves and conifers but also broadleaves mixed with blue gum, presenting in general a developed understory.

These land cover categories occurred in all areas with the exception of eucalyptus and mixed E–C, which did not occur in Bragança.

We used 4-band digital orthophotomaps (0.5 m resolution) from 2005 (Mação and Bragança) and Quickbird high resolution satellite orthorectified imagery (panchromatic band with a spatial resolution of 0.61 m and infrared false–color image of 2.4 m resolution) from 2003 (Águeda), to acquire the final maps of the study areas, 15 and 13 years after 1990. Therefore, we have considered a 15-year study period for Mação and Bragança and a 13-year study period for Águeda. The images were interpreted on screen (patches \geq 0.5 ha) and the resulting land cover map was confirmed by field surveys. Photointerpretation was validated by field-checking randomly distributed sampling units of 250 m radius circles (n = 15 in Mação and Bragança, n = 12 in Águeda). Both the 1990 and 2003/2005 land cover maps were integrated in a vector-based Geographic Information System (GIS). In both maps (initial and final), social areas and water bodies were excluded from the analysis.

Yearly maps of fire scars (≥5 ha) in the study areas during the period 1990–2003/2005 were assessed from cartography available in vector format from the National Forest Authority.

Maps representing the final landscape state (2003 and 2005) were intercepted with the initial maps (1990) in order to identify those areas where land cover had changed and those areas where land cover remained the same. Transition polygons smaller than 0.25 ha were not considered (each was merged with the neighboring patch with the longest shared border). Finally, this layer with transition polygons was overlaid and cross-tabulated with fire maps.

2.2.3 Fire effects on the overall landscape dynamics

To determine the relative importance of wildfires and land cover on landscape dynamics, we defined a regular grid of points which was then overlaid on each study area. The number of points was established in order to match approximately the number of polygons (homogeneous areas in terms of land cover transition and fire occurrence), considering a minimum surface of 0.25 ha. The number of sampling points was 1764 in Águeda, 2160 in Bragança and 2530 in Mação. For each point we recorded information on fire occurrence (burned – 1; unburned – 0) and on the initial and final land cover, from which we derived the change status (change – 1; no change – 0) during the study period.

Logistic regression (Hosmer & Lemeshow, 2000) was used to evaluate the influence of fire occurrence and initial land cover in 1990 (both categorical variables) on landscape changes (binary dependent variable). To assess the relative importance of these variables, we used an information-theoretical approach (ITA) (Burnham & Anderson, 2002). The ITA looks for simplicity and parsimony of several working hypothesis and is based on finding the strength of evidence of each model, for a set of candidate predictive models. The AIC (Akaike Information Criterion) adjusted for small samples (AIC_c) was used as a measure of information loss of each candidate model, with the best fitting model having the lowest AIC_c and the highest Akaike weight (w). The latter measures the probability that a given model is true, given the data and the set of competing candidate models. AIC_c differences (Δ AIC) between each model and the
model with the smaller AIC can be used to assess the relative support for the different alternative models (Burnham & Anderson, 2002; Rushton, Ormerod, & Kerby, 2004).

Our set of candidate models included four models: one separate model for each predictor variable (fire occurrence and land cover), one model with both variables and one last model with the two main factors and their interaction. The relative importance of each variable was also estimated by summing the Akaike weights across all models that contained that variable (Burnham & Anderson, 2002). Model fit and predictive performance of each model were evaluated by calculating the area under the receiver operating characteristics curve (AUC) (Pearce & Ferrier, 2000).

Since the obtained models would provide a similar change probability for all points sharing the same combination of the two categorical variables (land cover and fire occurrence) we decided to compute the average of 0's and 1's from the original data, for each combination of the two variables in order to have a measure of dispersion (standard error) and to assess statistical significance in comparisons between burned and unburned areas. These averages represented the mean probability of change for each land cover. Differences between burned and unburned areas were tested for statistical significance using the Mann–Whitney *U*-test.

2.2.4 Fire effects on land cover transitions

To characterize in detail the landscape changes during the study period, we computed transition matrices separately for each area using the surface (in hectares) occupied by each land cover. Each column represented the number of hectares of each land cover in 1990 converted to the different land covers in 2003/2005. Values were standardized as proportions of the total surface of each land cover in 1990, in order to obtain transition probabilities between different classes.

For each study area, matrices were built separately for the overall (matrix *O*), for the burned (matrix *B*) and the unburned (matrix *U*) surfaces. Therefore each matrix represented different landscape dynamics according to different fire regime scenarios. We computed a difference matrix D = U - B in order to detect, for each value d_{ij} the transitions with higher probability to occur in burned areas ($d_{ij} < 0$) and those transitions which were more likely to occur in the absence of fire ($d_{ij} > 0$).

2.2.5. Long term landscape change scenarios

In a further step, using the same set of transition matrices we performed a Markov analysis (Balzter, 2000) to simulate future landscape scenarios according to 15-year (13 in the case of Águeda) time-steps. This was computed by multiplying the overall vector of land cover proportions $o(_t)$, at year 2005 (2003 for Águeda) by the three transition matrices (*O*, *B* and *U*) in such a way that:

 $o_{(t+ns)} = o_{(t)} \cdot O^{n} (1)$ $b_{(t+ns)} = o_{(t)} \cdot B^{n} (2)$ $u_{(t+ns)} = o_{(t)} \cdot U^{n} (3)$

where $o_{(t+ns)}$, $b_{(t+ns)}$ and $u_{(t+ns)}$, represent the projected landscapes produced by the overall, the burned and the unburned transition matrices (respectively) after *n* time-steps of *s* years (*s* = 13 for Águeda; *s* = 15 for Mação and Bragança) starting at year *t* (2003 for Águeda; 2005 for Mação and Bragança). The final year of projections (*t* + *ns*) corresponded to approximately one century after 1990 (2094 for Águeda; 2095 for Mação and Bragança). We used Euclidean distances to check that the differences of land cover proportions between consecutive time-steps at the end of this period were relatively small (less than 6%, for each one of the three projections) and also to measure the differences between initial and final landscapes. These landscape projections allowed assessing the effects of wildfires on landscape dynamics and the expected landscape pattern if the modeled land cover transitions were maintained throughout time. Similarly, we assessed the trends in landscape diversity by computing the equitability index (based on the Shannon–Wiener index of diversity) for the beginning of the study period (*t*) and for the end of the projected period (*t* + *ns*), according to the three transition scenarios.

2.3 Results

2.3.1 Fire occurrence and main land cover changes

The Águeda area was mainly covered by eucalyptus (58%) and conifers (13%) in 1990 (Table 1 and Fig. 2). The main land cover changes during 1990–2003 were an important increase of mixed (969%) and mixed E–C forests (352%), and a decline of conifer (-52%), eucalyptus (-37%) and agricultural areas (-23%). Overall, during the 1990–2003 period, fire burned 33% of the area, most of which (27%) in 1991.

In Mação, agriculture and conifers were the main land cover classes in 1990 (49% and 19%, respectively). During 1990–2005 the main landscape changes were an increase of shrublands (151%) and mixed forests (76%) and a decline of conifers (-23%). During the studied time period, fire burned 32% of the area, most of which (26%) in 1991.

The Bragança area was covered mainly by agriculture (54%) and shrublands (33%) in 1990. The main changes during 1990–2005 were an increase of mixed forests (91%) and broadleaved forests (50%). Overall, during the concerned period, fire burned 15% of the study area in nine different years, particularly in 2000 (3%) and 2004 (4%).

		Initial (1990)		Final ^a	% change	Burned
Águeda	Agriculture	630		483	-23.3	91
	Shrublands	382		781	104.5	151
	Conifers	857		414	-51.7	437
	Eucalyptus	3706		2333	-37.0	1072
	Broadleaves	392		395	0.8	124
	Mixed E–C	347		1569	352.2	165
	Mixed	35		374	968.6	32
	Total		6349			2072
Mação	Agriculture	5385		4778	-11.3	518
	Shrublands	356		893	150.8	133
	Conifers	2066		1582	-23.4	1416
	Eucalyptus	657		861	31.1	133
	Broadleaves	404		350	-13.4	98
	Mixed E-C	1517		1484	-2.2	981
	Mixed	574		1011	76.1	202
	Total		10,959			3481
Bragança	Agriculture	6107		6007	-1.6	334
0,	Shrublands	3660		3350	-8.5	1165
	Conifers	652		622	-4.6	117
	Broadleaves	712		1066	49.7	45
	Mixed	95		181	90.5	18
	Total		11,226			1679

 Table 1. Overall landscape dynamics for each study area and each land cover: initial, final and burned surfaces in hectares.

^a 2003 for Águeda; 2005 for Mação and Bragança.

2.3.2 Fire effects on the overall landscape dynamics

As a result of the logistic regression analysis, we obtained two models for Águeda with a similar fit to the data (Table 2), one including fire and land cover (Akaike weight of 0.53) and the second with these main factors and also their interaction (Akaike weight of 0.47). According to Burnham and Anderson (2002), models with AIC_c differences between 0 and 2 have substantial support. Moreover, the second model presented the highest AUC (0.66). Therefore the second model ($\Delta_{AIC} = 0.3$) is also considered an alternative fit to the data. In Bragança and Mação the best model for predicting land cover changes included fire, initial land cover and the interaction between these variables. Both of these models had an Akaike weight of 1.00 and represented by far, the best model from the analyzed set, with a $\Delta_{AIC} > 45.0$ in comparison with the second best model. For all the best models, Akaike weights were similar for both fire and land cover, showing that these variables had a similar importance in explaining landscape dynamics.



Fig. 2. Maps of the three study areas including information on land covers (in 1990) and areas burned during the study periods.

Table 2. Results of AIC-based model selection for the likelihood of land cover changes in each study area. For each model, the table shows the predictor variables entering each model: Land cover (LC), wildfire (fire), the respective interaction (LC×fire), the AIC_c value, AIC_c differences (Δ_{AIC}), Akaike weights (w), and model fit (AUC-area under curve and respective *p*-value). For each area, models are ordered by increasing Δ_{AIC} .

	LC	Fire	LC × fire	AICc	Δ_{AIC}	w	AUC	р
Águeda	Х	х		2198.8	0	0.534	0.64	<0.001
	х	х	х	2199.1	0.3	0.466	0.66	<0.001
	Х			2226.4	27.6	0.000	0.61	<0.001
		х		2307.6	108.8	0.000	0.56	<0.001
Mação	х	х	х	2349.0	0	1.000	0.72	<0.001
-	Х	х		2395.2	46.2	0.000	0.71	<0.001
	х			2425.3	76.3	0.000	0.68	<0.001
		Х		2495.5	146.4	0.000	0.63	<0.001
Braganaa	×	×	×	2091 0	0	1 000	0.70	~0.001
ыауапçа	<u>^</u>	~	~	2061.9		1.000	0.70	<0.001
	Х			2158.1	76.2	0.000	0.66	<0.000
	Х	Х		2159.4	77.4	0.000	0.66	<0.001
		Х		2277.6	195.7	0.000	0.54	0.008

According to the computation of the average change status, fire increased significantly the likelihood of change for most land covers in all three study areas (Fig. 3). Change probability in Águeda was significantly higher in burned areas of agriculture (p = 0.003), conifers (p = 0.024), eucalyptus (p < 0.001) and broadleaves (p = 0.006). Change probability in Mação was significantly higher in burned areas of agriculture (p < 0.001), eucalyptus (p = 0.006). Change probability in Mação was significantly higher in burned areas of agriculture (p < 0.001), eucalyptus (p = 0.006). Change probability in Bragança was significantly higher in burned areas of agriculture (p < 0.001), broadleaves (p = 0.031) and mixed forests (p = 0.043). Shrublands presented higher change probability in unburned areas (p < 0.001).



Fig. 3. Change probabilities (mean + SE) for the different land cover classes and for

2.3.3. Fire effects on land cover transitions

The results obtained for the transition matrix in Águeda (Table 3) showed that broadleaves presented the highest persistence (96%), whereas the lowest persistence was registered for conifer forests (35%). The main transitions reflected a change towards mixed E–C, mainly from conifers (32%), eucalyptus (24%), shrublands (20%) and agriculture (17%). Other important transitions were towards eucalyptus forests, mainly from mixed E–C forests (13%), shrublands (11%) and conifers (10%) and towards shrublands, mainly from conifers (15%) and eucalyptus (10%). The analysis of the effect of fire on landscape transitions (Fig. 4) showed that land cover persistence was usually higher in the absence of fire, most noticeably for agricultural areas (d = 35%) and eucalyptus forests (d = 13%). Fire favored the transitions from agriculture to shrublands (d = -11%) and mixed E–C (d = -13%) and from conifers to mixed E–C (d = -15%). The absence of fire favored the conversion of conifers to eucalyptus (d = 13%) and the conversion of other mixed forests to broadleaves (d = 16%).

		1990						
		Agriculture	Shrublands	Conifers	Eucalyptus	Broadleaves	Mixed E-C	Mixed
Águeda (2003)	Agriculture Shrublands Conifers Eucalyptus Broadleaves Mixed E–C Mixed	0.60 0.04 0.01 0.09 0.00 0.17 0.09	0.00 0.59 0.05 0.11 0.00 0.20 0.05	0.02 0.15 0.35 0.10 0.00 0.32 0.06	0.02 0.10 0.02 0.57 0.00 0.24 0.05	0.00 0.00 0.00 0.01 0.96 0.03 0.00	0.06 0.09 0.02 0.13 0.04 0.60 0.05	0.00 0.05 0.05 0.09 0.02 0.00 0.79
Mação (2005)	Agriculture Shrublands Conifers Eucalyptus Broadleaves Mixed E–C Mixed	0.85 0.03 0.02 0.01 0.03 0.03	0.08 0.39 0.02 0.23 0.04 0.17 0.08	0.02 0.12 0.59 0.03 0.00 0.18 0.05	0.02 0.03 0.03 0.77 0.00 0.10 0.06	0.06 0.09 0.02 0.02 0.68 0.02 0.11	0.03 0.16 0.11 0.05 0.00 0.54 0.11	0.06 0.07 0.02 0.02 0.01 0.00 0.82
Bragança (2005)	Agriculture Shrublands Conifers Broadleaves Mixed	0.86 0.09 0.02 0.02 0.00	0.14 0.68 0.03 0.13 0.01	0.08 0.31 0.55 0.00 0.05		0.21 0.09 0.00 0.68 0.02		0.12 0.32 0.00 0.00 0.56

Table 3. Overall transition matrices for the three study areas. Bold values indicate transitions ≥0.10.

In Mação the land covers with higher persistence were agriculture (85%) and mixed forests (82%), whereas the lowest persistence was registered for shrublands (39%). The main transitions were from shrublands to eucalyptus (23%) and mixed E–C (17%) and from conifers to mixed E–C (18%). Other important transitions were the replacement of mixed E–C by shrublands (16%), conifers (11%), and mixed forests (11%), the transition from broadleaved to mixed forests (11%), and the transition of conifers to shrublands (12%). Fire was associated with a lower persistence of the majority of land covers with the exception of shrublands (d = -13%). Fire absence allowed the persistence of agriculture (d = 35%), eucalyptus, (d = 32%), broadleaves (d = 26%) and mixed forests (d = 17%). Fire favored the transitions to shrublands, mainly from broadleaves (d = -21%), agriculture (d = -14%), mixed (d = -12%) and mixed E–C forests (d = -12%). The transition from eucalyptus to mixed E–C was also promoted by fire (d = -28%).

In Bragança, the land covers with higher persistence were agricultural areas (86%), whereas the lowest persistence was registered for conifer forests (55%). The main transitions were from conifers to shrublands (31%), from broadleaves (21%) and shrublands (14%) to agriculture, and from shrublands to broadleaves (13%). Fire was associated with a lower persistence of the majority of land covers with the exception of shrublands (d = -17%). Fire favored the transitions to shrublands, mainly from conifers (d = -63%), agricultural areas (d = -27%), broadleaves (d = -23%) and also mixed forests (d = -79%, but small sample size). The absence of fire favored the transition of broadleaves to agriculture (d = 0.16) as well as the transition of other mixed forests to agriculture (d = 0.15).



Fig. 4. Graphical representation of the transition matrices for unburned (first bar) and burned (second bar) areas. On each bar, the different proportions represent transitions.



Fig. 5. Long term projected trends (2003–2094 for Águeda, 2005–2095 for Mação and Bragança) according to three different scenarios. The tip of each arrow represents the final land cover proportion, obtained by multiplying the overall landscape vector (the starting point of each arrow) by the unburned, the burned and the overall transition matrices.

2.3.4. Long term landscape change scenarios

Compared to the land cover composition in 2005 (Fig. 5), and according to the overall transition matrix, the projected landscape composition in Águeda would result in a landscape dominated by mixed E–C forests (+8%), eucalyptus (-50%), mixed forests (+196%) and shrublands (+24%). The absence of fire would result in a landscape dominated by mixed E–C forests (+2%), eucalyptus (-40%), broadleaves (+228%) and mixed forests (+112%). In contrast, a fire-driven landscape dynamics would create a landscape dominated by mixed E–C forests (+13%), shrublands (+71%), mixed forests (+227%) and eucalyptus (-65%). Compared to 2005, landscape diversity would be expected to increase (0.87–0.93) assuming the overall

landscape dynamics. When compared with this projection, either a scenario without fire (0.87–0.91) or a complete periodic burn of the study areas (0.87–0.90), would result in lower landscape diversity. The projected landscapes differed from the initial landscape according to the following Euclidean distances: overall 23%, burned 30% and unburned 22%.

In Mação, according to the overall transition matrix the projected landscape would be dominated by agriculture (-35%) mixed forests (+129%), eucalyptus (+111%) and mixed E–C forests (-7%). The absence of fire would create a landscape dominated by agriculture (-5%), mixed forests (+179%), eucalyptus (+55%) and mixed E–C forests (-37%). Fire-driven transitions would create a landscape dominated by mixed E–C forests (+91%), shrublands (+173%), eucalyptus (+127%) and conifers (+13%). Compared to 2005, landscape diversity would be expected to increase (0.85-0.92) assuming the overall landscape dynamics. When compared with this projection, either a scenario without fire (0.85-0.80) or a complete periodic burn of the study areas (0.85-0.89), would result in lower landscape diversity. The projected landscapes differed from the initial landscape according to the following Euclidean distances: overall 22%, burned 45% and unburned 21%.

In Bragança, according to the overall transition matrix the projected landscape would be dominated by agriculture (-1%), shrublands (-12%) and broadleaves (+41%). Compared to this current fire regime, a scenario without fire would create a landscape still dominated by agriculture (+10%), shrublands (-35%) and broadleaves (+32%). In contrast, a fire-driven transition dynamics would create a landscape dominated by shrublands (+119%), agriculture (-70%) and broadleaves (+57%). Compared to 2005, landscape diversity would be expected to increase (0.71-0.74) assuming the overall landscape dynamics. When compared with this projection, either a scenario without fire (0.71-0.73) or a complete periodic burn of the study areas (0.87-0.61), would result in lower landscape diversity. The projected landscapes differed from the initial landscape according to the following Euclidean distances: overall 5%, burned 52% and unburned 12%.

2. 4 Discussion and conclusions

2.4.1. General aspects

The three study areas presented very different initial landscape composition, with Águeda being dominated by eucalyptus forests, Mação by agricultural areas and conifers, and Bragança by agricultural areas and shrublands. There were also differences in fire occurrence during the study period, most noticeably the fact that Águeda and Mação burned mainly at the beginning, whereas Bragança burned at the end of the study period. These differences including time-since-fire (Mouillot et al., 2005; Trabaud & Galtiè, 1996) probably had consequences on land cover dynamics. However, some common land cover change patterns were found in all areas.

Given the characteristics of the three study areas, it is particularly relevant to separate transitions which are a consequence of management decisions from those related only with land abandonment, leading to natural vegetation succession. In this latter case we can include most transitions to shrublands, to mixed eucalyptus–conifer forests and to other mixed forests, because transitions to these land cover classes normally do not represent the result of land management decisions. On the contrary, transitions to agriculture and to eucalyptus are very likely related to an active strategy of land use change, given the artificial nature of this type of land occupation. Transitions to conifers and to broadleaves can be associated either to natural vegetation succession or to land management decisions.

2.4.2. The role of wildfires

In all three areas, both fire and initial land cover influenced the likelihood of land cover changes. Therefore, we confirmed that fire was an important driver of land cover change in all three studied areas, which is consistent with other studies (e.g. Acácio, Holmgren, Rego, Moreira, & Mohren, 2009; Baeza et al., 2007). Overall, fire decreased land cover persistence, hence increased the likelihood of land cover changes. Nevertheless the interaction between land cover and fire was very important in explaining the overall landscape dynamics, as not all land cover classes presented a similar response to fire in terms of change probability.

Shrublands were an obvious exception to the general trend because, contrarily to the remaining land cover classes, fire maintained or decreased the probability of change to other land covers. There are two potential explanations for this trend: first, fire interrupts the ecological succession preventing shrublands to become forests; and second, fire acts as a discouraging factor preventing new investments in agriculture or eucalyptus plantations, for example. Previous studies from other regions (Chuvieco, 1999; Loepfe et al., 2010; Viedma et al., 2006) provided evidence that fire promotes more homogeneous landscapes as it maintains shrublands by preventing their succession to forests, and bringing forests back to a shrubland-like physiognomic stage.

As to the remaining land covers, fire consistently increased change probability i.e. decreased land cover persistence. Fire induced changes in these land covers by transforming different land cover types into shrublands or by creating an opportunity for other tree species to participate in the ecological succession, leading to mixed forests of different kinds. Similarly to burned shrubland areas, the result of active management seems to have played a less important role than nature in burned areas of the remaining land covers. In fact, although fire could create new opportunities for land cover change by land owners, this does not seem to have been the case. Burned agricultural fields and burned eucalyptus stands showed a particularly consistent higher change probability, when compared with unburned areas of these land covers. In the case of eucalyptus we could expect a higher persistence of this land cover, given the high resilience and rapid recovery of the species after fire as shown by Gouveia, Camara, and Trigo (2010) for Southern Portugal. Instead, our results suggest that fire created

conditions for land abandonment, resulting in many cases in the conversion of eucalyptus into different kinds of mixed forests or shrub-dominating vegetation at the end of the study period. A similar reasoning is valid for burned agricultural areas, mainly converted into shrublands. This suggests that agricultural areas affected by wildfires were also more prone to abandonment, as previously found by Lloret et al. (2002). Although socio-economic variables are not the core issue within the present work, they are important drivers of land use conversion and should therefore be taken into account (Moreira et al., 2001; Van Doorn&Bakker, 2007). In agricultural lands the influence of fire on land abandonment seems to be more important than for the other land uses, therefore contributing to increase the overall trend of agriculture abandonment in Portugal (Moreira et al., 2001; Nunes et al., 2005).

2.4.3. The resulting landscape changes

The major common overall changes in the three study areas were a decrease of agriculture and conifers and an increase of mixed forests of both types and shrublands. These latter land covers can be reliably associated with land abandonment. If we consider the resulting landscape changes in the three study areas concerning these land covers, there was an increment of at least 38% of abandoned land at the end of the study period. In burned areas the increase was 42% whereas in unburned areas it was 36%, which seems to confirm that fire only contributed to enhance an already existing abandonment trend.

Agricultural abandonment, widely documented for the Mediterranean region (Mouillot et al., 2005; Poyatos, Latron, & Llorens, 2003; Pueyo & Beguería, 2007; Romero-Calcerrada & Perry, 2004), can explain the decline observed in farmland in all areas, and transition matrices confirmed the conversion of agricultural areas into a large variety of forest types and shrublands. In Bragança the rate of loss was lower than in the other areas, but this is explained by the fact that some shrubland and broadleaved areas have been converted to agriculture (including subsidized chestnut plantations for agro-forestry). In this study area, the high transition rate of broadleaves to agriculture suggests an active land use change due to economic reasons, although this has occurred essentially in unburned areas. Similarly, in Mação there was an important transition from shrublands to agricultural areas but almost exclusively in unburned areas, confirming the role of fire in discouraging the investment in new land uses.

Consequently, the abandonment factor could explain the widespread increase of shrublands. The fact that important transition rates were observed from different forest types to shrublands, suggests that wildfires or tree harvesting followed by abandonment are the main drivers of the increase of shrubland area, by converting forests into a shrubland stage (Acácio et al., 2009; Baeza et al., 2007). In particular, the transition from conifer forests to shrublands showed high rates in all areas, which could be explained by the fact that maritime pine (basically the only conifer species) does not have resprouting capacity after fire. Persistence is dependent on the seed bank in serotinous cones, which might not exist if the stand is burned before reaching

reproductive maturity (Fernandes & Rigolot, 2007). However, some differences between areas may be attributable to time-since-fire. For example, in Bragança, the effect of fire on decreased conifer persistence was much more obvious than in the other areas, probably because fire was quite recent and the potentially regenerating conifer forests did not have time enough to grow and pass the shrubland-like stage. This area also had the highest fire-driven increases in the transition from broadleaves to shrublands, probably due to the same reason. In the three study areas, conifers followed the general decreasing trend shown by previous national forest inventories, partly because of forest fires (DGF, 2001; DGRF, 2007). However, there were important transitions to conifers, particularly in Mação. Most transitions to conifers were fire-driven which can be related to the capacity of maritime pine to colonize burned areas. Maritime pine is known to act as a typical seeder, often presenting very high seedling densities in recently burned areas (Fernandes & Rigolot, 2007).

The area of eucalyptus declined in Águeda (where it was more widespread) at the beginning of the study period but increased in Mação. In this latter area, most eucalyptus forests originated from former shrublands and also from agriculture. Although *E. globulus* regenerates in Portugal from naturally dispersed seeds (Marchante, Freitas, & Marchante, 2008; Silva, Feith, & Pereira, 2007), the dispersal distance should be normally limited to a few meters around the tree trunk (Potts, 1990; Virtue & Melland, 2003). Therefore, natural seed dispersal should not be the main reason explaining the large increase observed. A more likely explanation is the result of active management due to land owner decisions to plant eucalyptus. Economic reasons may also explain the transition from conifers to eucalyptus in Águeda in the absence of fire, suggesting that this is a normal conversion process implemented by land owners, once conifer trees are harvested.

Broadleaves increased in Bragança, declined in Mação and presented a similar surface in Águeda. In Bragança they originated mainly from shrublands suggesting that secondary succession was the major driver. Transitions from agriculture in Mação could also have a similar explanation. In Águeda this forest type was mainly constituted by *Acacia dealbata*, an exotic invasive species, highly resilient to fire and other disturbances (Almeida & Freitas, 2006; Marchante et al., 2008; Yongqi & Fuwen, 2006), which may explain the high persistence of this land cover in this study area.

In Águeda and Mação transitions from conifers and eucalyptus to mixed E–C forests were more important than transitions to shrublands. With the exception of conifers in Mação, all transitions were more important in burned areas, as revealed by the transition matrices. Given the regenerative characteristics of eucalyptus already mentioned, transitions from conifers may be partly explained by a two-stage process, where conifers were replaced by eucalyptus plantations which were then colonized by pine plants, after fire. Transitions from eucalyptus to mixed eucalyptus–conifer forests can be explained by the high spreading capacity of maritime pine (Fernandes & Rigolot, 2007) leading to the colonization of mismanaged eucalyptus plantations, with fire playing a role in this transition (Fernandes & Rigolot, 2007). Previous

studies showed that mixed forests of conifers and eucalyptus present a high level of fireproneness (Moreira et al., 2009; Nunes et al., 2005), suggesting that fire is creating a feedback loop, where burning changes forest composition towards higher fire hazard.

Given the small surface of mixed forests in Águeda and Bragança, results from these areas should be interpreted with caution. The observed increase in mixed forests can be interpreted as lack of management leading to vegetation succession. The original native forests in the study regions were dominated by oaks (Vasconcellos & Franco, 1954). Oak regeneration in the understory of unmanaged conifer or eucalyptus plantations, or within shrublands and abandoned agricultural fields, is expected to result in mixed forests. This hypothesis was supported by the results of transition matrices, which showed that mixed forests originated mostly from pure conifer and pure eucalyptus forests, former agricultural land and shrublands. In Mação, broadleaves have been converted mainly to mixed forests, probably due to natural colonization by conifers given the high travelling distance of the wing-shaped maritime pine seeds.

2.4.4. Future landscapes

The projection of future landscapes using the three transition scenarios revealed important differences relatively to the initial landscape. The burned transition scenario corresponded to the most different landscape in all three areas, which is relevant about the role of wildfires in shaping Mediterranean landscapes (Arianoutsou, 2001; Mouillot et al., 2005; Trabaud & Galtiè, 1996). In terms of diversity, both burned and unburned transition scenarios would lead to more homogeneous landscapes, which is in accordance with findings from other studies (Loepfe et al., 2010; Rescia, Willaarts, Schmitz, & Aguilera, 2010; Viedma et al., 2006).

In Águeda landscape dynamics would be mainly driven by eucalyptus since this land cover was associated with the most important changes in the landscape. The decreasing trend of eucalyptus in all scenarios has to be understood in a context where the starting landscape was strongly dominated by this land cover due to the "eucalyptus rush" in the 1980s of the previous century (Silva, Sequeira, Catry, & Aguiar, 2007). As a result, the decrease of eucalyptus in a fire-free landscape would be compensated by the expansion of broadleaves (mainly *Acacia* spp.), whereas a fire-driven landscape dynamics would promote the expansion of mixed forests of both types. In Mação, landscape dynamics would be dominated mainly by the decrease of agriculture both in the overall and in the burned transition scenarios, and by the increase of mixed forests in the unburned transition scenario. In Bragança landscape dynamics would be dominated by the decrease of agriculture and the increase of shrublands in burned areas. Given the lower percentage of burned surface in Bragança, the overall and the unburned transition scenarios would result in similar landscapes (dominated by agriculture/agro-forestry).

With the exception of the two latter scenarios described for Bragança, all forecasted landscapes would present an increase of fire hazard due to the loss of agricultural areas and

due to the increase of shrublands and unmanaged mixed forests of both types. Besides the reduced economic value and the higher fire hazard of these projected landscapes, those in Águeda and Mação would also have a reduced conservation value given the permanence or expansion of exotic species like Acacia spp. and *E. globulus*. Wildfires seem to play an important role in this trend, by enhancing land abandonment which results in less valuable and less sustainable landscapes. Due to these reasons, our findings reinforce the need of a particular attention to the management of burned areas in order to prevent landscape degradation and increasingly hazardous fire regimes.

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Tree type and forest management effects on the structure of stream wood following wildfires

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3. Tree type and forest management effects on the structure of stream wood following wildfires

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Abstract: Wildfires are an increasingly common disturbance influencing wood recruitment to streams, and thereby affecting their physical and biological condition. Mediterranean countries such as Portugal, where more than 25% of the land area has burned since 1990, are ideal areas to study impacts of wildfire effects on streams. We evaluated the physical structure of 2206 downed wood pieces (DWP) across 27 first- to third-order streams in central Portugal, all of which had experienced recent wildfires. The streams flowed through monospecific upland forests of Eucalyptus, Maritime pines, or Cork oaks and were fringed by a mixture of riparian tree species. DWP structure differed between tree types and between burned and unburned pieces. Post-fire timber-production forests (Maritime pines and Eucalyptus) contributed a higher quantity of thinner, longer and straighter DWP to streams than Cork oak stands. Pieces from Maritime pines had more rootwads and branches than DWP from the other tree types. Pieces from Cork oak and riparian species generally had a bent form, were shorter and had no rootwads. Burned DWP in streams were often from riparian trees. Relative to unburned DWP, the burned DWP occurred more frequently, were larger and straighter, had branches less often, and were more decayed. With more complex branches, rootwads, and a larger diameter, inputs from burned Maritime pine forests are more likely to change stream hydraulics and habitat complexity, relative to inputs from Eucalyptus forests with their simpler structure. This study shows that, less than a decade after wildfires, structure of downed wood in and near streams is

strongly influenced by wildfire, but also still reflects intrinsic species characteristics and respective silviculture practices, even after the effects of fire have been accounted for. Under an anticipated shift in landscape cover with higher shrubland proportions and more mixing of Maritime pine and Eucalyptus forests, our results suggest that instream large wood will become scarcer and more structurally homogeneous.

Keywords: large woody debris; wildfire; eucalyptus; riparian vegetation; cork oak; Portugal.

3.1 Introduction

The amount and characteristics of wood delivered from forests to streams depends on the type of forest supplying the wood (Evans et al., 1993) and the processes that introduce it into the stream channels. Processes that can affect wood recruitment vary by region, but generally include biological processes such as insect outbreaks and disease, and abiotic processes such as fire, floods, bank erosion, wind storms, ice storms, and snow avalanches (Naiman et al., 2005; Resh et al., 1988). The volume and type of wood entering streams is a function of the synergy between dominant input processes and the susceptibility of riparian trees to those processes (Bendix and Cowell, 2010a). Ultimately, the recruitment, characteristics, transport and storage of wood can affect a stream's physical and biological condition, through direct and indirect mechanisms (Chen et al., 2008; Everett and Ruiz, 1993; Gurnell et al., 2002; Schneider and Winemiller, 2008). The current study focuses on the impacts of wildfire, an increasingly common disturbance, on the characteristics of wood recruited to streams. In addition to changing wood mass, fire changes the form of wood pieces and alters post-fire decomposition rates (Harmon, 1992). The specific effects of fire on characteristics of wood recruited to streams remain poorly understood.

A changing global climate and continued anthropogenic activities are combining to increase the probability and severity of fire in Europe and around the world (Flannigan et al., 2009; Moriondo et al., 2006). Fire is a disturbance process affecting trees in both riparian zones and adjacent slopes. Trees injured by fire are more susceptible to mortality via windthrow and disease, and thereby enter fluvial systems more readily (Benda et al., 2003; Pinto et al., 2009). Given the importance of large wood in streams (Gregory et al., 2003), fire-induced changes to the quantity and character of large wood inputs have the potential to cause shifts in stream ecosystems. The degree to which fire affects wood recruitment is dependent on a number of factors, including the type (surface or crown) and intensity of fire, the tree species resistance to fire, age and size of the trees, and the time since the previous fire (Brais et al., 2005; Harper et al., 2005). Variability in the quantity, size, decay and wood form of downed wood pieces (DWP) is influenced by the characteristics of forest fuels including flammability, combustibility and wood density (Boulanger et al., 2011; Browne, 1958; DeLuca and Aplet, 2008) and, after the fire, by elements like post-fire tree resistance and forest management (Brassard and Chen, 2008; Tinker and Knight, 2000). Therefore, the post-fire physical characteristics and quantity of DWP on forest floors (Pedlar et al., 2002) and in "burned streams" differs according to forest type.

Among the structural characteristics of DWP in streams, there is a set of core variables that can be easily measured for comparative purposes and that interact with the stream to influence the function and transport potential of a given piece of wood (Bocchiola et al., 2006; Gregory et al., 2003; Wohl et al., 2010). Wood size can influence the degree to which wood affects biological diversity and biota abundance (Lester et al., 2009), and wood size in relation to the channel width and depth is a primary control on wood stability in streams (Cadol and Wohl, 2010; Haga et al., 2002; Merten et al., 2010, 2011), which, in turn, influences channel

morphology (Andreoli et al., 2007; Comiti et al., 2008; Jackson and Sturm, 2002). Abbe and Montgomery (2003) found that wood longer than half the bankfull width tends to form key pieces in logjams. Beyond size, the shape of wood is also important (O'Connor, 1991). A rootwad, for example, raises the center of mass of a wood piece and is therefore a fundamental control on log stability (Braudrick and Grant, 2000, 2001). DWP with stout branches have a geometry that extends well beyond their bole diameter, whereas pieces without branches may be transported more readily and routed through river systems.

Others have evaluated the impact of fire on wood loading to streams (Arseneault et al., 2007; Jones and Daniels, 2008; Young, 1994; Zelt and Wohl, 2004), however, most have studied a single large fire event and thus had little replication. This lack of replication decreases the applicability and generalization of results to different forest situations, where factors such as forest age, time since the last fire, methods of post-fire logging and silviculture practices often differ. No previous studies have focused on differences in the abundance and structure of DWP in streams across multiple single-species forest stands impacted by fire. Others have examined fire susceptibility of different species and input in streams of mixed-forest systems (Arseneault et al., 2007; Jones and Daniels, 2008; Young, 1994; Zelt and Wohl 2004), but not in single-species stands where differences between forests may be more clear.

In this study, we evaluated the physical structure of wood in 27 streams in central Portugal. All streams experienced recent fires and they encompassed three different upland forest types. This is the first study to quantify species-specific differences in DWP that eventually is recruited into streams. Contrary to previous studies neglecting source trees, we hypothesized that, once burned, downed wood from separate species retain some differences in terms of their potential effect on stream ecosystem structure and function. We aimed to address the following specific questions: in areas where fire occurred less than 10 years prior, (i) To what extent does DWP still retain species-specific physical architecture of the pre-burned trees? (ii) How does the physical structure of DWP that moves into streams reflect prior production silviculture practices? and (iii) For DWP within streams, how does wood structure differ between burned and unburned pieces and what are the long-term potential implications for stream wood function and movement after wildfires?

3.2 Methods

3.2.1 Study area

This study was conducted from fall 2009 to fall 2010 in nine sub-basins of the Tagus River, which experienced wildfires between 2003 and 2007. Sub-basins are located in east-central Portugal between latitude 39°16'–39°39'N and longitude 7°30'–8°14'W. The resident population within the study area was ca. 60 thousand people, although across the selected sub-basins the human presence is scattered. Climate is Mediterranean with hot, dry summers and cool, wet winters. The mean annual precipitation from 2005 to 2010 was 512 mm (ranging from 3 mm in

July to 82 mm in November) and the mean annual temperature was 15.8 °C (range: 9° in December–January to 23 °C in July–August). The area has gentle slopes with altitudes ranging from 19 to 643 m (mean elevation ~266 m). Land cover is dominated by forests, shrublands and agriculture (Table 1). Burned areas of maritime pine (*Pinus pinaster*) are now in a shrubland-like structure, with dense growth of *Erica* spp., *Cistus* spp. and *Ulex* spp. along with young post-fire maritime pine. Less dense shrublands, mainly *Cistus* spp. and *Ulex* spp., are present in the understory of burned (but already recovered) stands of eucalyptus (*Eucalyptus globulus*). Ferns (*Pteridium aquilinum*) are common understory plants in more humid burned zones. In contrast, cork oak (*Quercus suber*) drainage areas usually have bare soil surface with some low understory grasses.

Table 1. Characteristics of the sub-basins from where sites were selected. Ec = Eucalyptus; MP = Maritime pine; CO = Cork oak.

Sub-basin	Maximum stream order	Drainage area (km²)	Mean stream gradient (%)	Percentage burned	Year 2000 forest/shrubs/ agriculture (%)	Dominant forest
Abrançalha	3	26	4.5	75	68/20/11	Ec
Alferreira	3	59	4.5	92	53/23/24	
Palhais	3	49	3.8	47	35/27/38	
Arcês	4	50	5.4	39	40/26/34	MP
Rio Frio	3	37	5.1	71	55/22/22	
Eiras	4	143	5.6	64	59/28/12	
Fouvel	3	50	5.2	66	41/32/27	CO
Salgueira	3	81	2.3	86	40/26/33	
Vale da Lama	3	36	3.1	83	82/4/15	

3.2.2 Study sites

We selected nine burned sub-basins representing three dominate forest types: eucalyptus (Ec), maritime pine (MP) and cork oak (CO), with three replicate sub-basins in each forest type. Although two of the selected sub-basins have a maximum stream order of 4 (Table 1), we restricted our assessments to stream orders 1, 2 and 3 within each sub-basin. In total, 27 burned reaches of ~500 m each were assessed, totaling ~13,460 m of stream channel (Fig. 1).

For a statistical analysis comparing wood characteristics, there would, ideally, be an equal number of DWP that were burned and not burned for each species. However, it is difficult to have a well-balanced design to study the effects of large natural disturbances (Wiens and Parker, 1995; Reich et al., 2001; Parker and Wiens, 2005), and we did not expect a priori to find equal frequencies of instream DWP originating from riparian trees compared to upland forests. To circumvent this instream bias in sample size, we added 100–200 m transects perpendicular to the stream and immediately beyond the riparian area for each study reach when possible. We considered these transects to include wood that could potentially enter the stream.

3.2.3 Tree types characterizations

In the study area, MP is grown for timber in pure (monoculture) stands. These trees have a pyramidal structure with branches forming an acute angle with the trunk. Trees reach ~5–25 m

tall and ~7–50 cm diameter at breast height (DBH) (Catry et al., 2010). MP wood is heavy and moderately hard (Carvalho, 1997). Each year, the crown increases one or two increments, each consisting of 5–7 branches. Trunks have a cylindrical straight shape and branches are relatively weak. The bark is thick and has fissures. Roots penetrate poorly in compacted soils and are easily impeded by obstacles below ground (Correia et al., 2007), making trees susceptible to falling on steep hillslopes. In Portugal, MP is the species most affected by fire (Moreira et al., 2009; Silva et al. 2009), with high flammability resulting from volatile compounds (e.g. resin), fuel accumulation, including a well-developed shrub understory, and stand structure. Although thick bark enables MP to withstand low to moderate intensity fires (Fernandes and Rigolot, 2007), trees usually die (especially younger trees) as a result of intense wildfires and fall within 1–3 years, with almost unaltered overall structure. As far as we could observe in the MP study sites, no post-fire logging was carried out and fire-killed trees were left on the ground on stream side-slopes.



Fig. 1. Digital terrain model of a typical study site, including the stream reach and a perpendicular sideslope transect.

Trees of Ec are planted as pure stands for paper pulp production. These trees have a slender and upright trunk (~6–31 m tall; 5–60 cm DBH) which, when mature, contains almost 90% of the tree biomass (Pereira, 2007). The bark is smooth and thin and is replaced over time. About 90% of the roots are very thin and highly branched at the surface. The wood is denser and harder than MP (Carvalho, 1997). Eucalyptus stands are also strongly affected by fire (Moreira et al., 2009; Silva et al., 2009), but their rapid growth allows fast recovery. The stumps coppice method of regeneration was the most common management strategy in our study area for trees that were top-killed by fire.

At the study area, CO stands (~4–14 m tall; ~10–45 cm DBH) were mainly managed according to an agro-forestry system named "montado" (dehesa in Spain). In this system trees

are relatively scattered (30–60 trees per ha), are harvested for cork each 9–12 years without felling (Bugalho et al., 2011), and grow among pastures and cereal crops (Silva et al., 2009). CO trees have branches with an irregular architecture, a short trunk of very hard wood (Carvalho, 1997) and fissured, thick cork bark with insulating properties. CO has a very deep root system (Pausas et al., 2009), anchoring trees against uprooting. When compared with MP and Ec in the study area, the CO affected by fire are generally much older trees. Although CO trees are the least prone to burning and are very resilient to fire, many trees were killed in the study area in recent fires (2003–2007). CO is the only native European tree with above-ground sprouting capability similar to Ec (Silva and Catry, 2006). Branch pruning (with slash usually left on the ground), plowing and shrub clearing were the most common management practices in our study area for the rehabilitation of trees that were burned but not killed.

Most streams in the maritime pine and eucalyptus forests had riparian buffers in place, however, gaps longer than 10 m adjacent to the stream channel where managed forests occur along stream margins were common. Where present, buffers were fairly narrow (3–15 m from each margin) and were generally equal to or less than the height of managed forest trees prior to the fire. In southern parts, riparian buffers are narrower with only semi-continuous 'riparian galleries' (Ferreira et al., 2005). There was occasional evidence of logging of riparian species (e.g., saw cuts on DWP). The riparian vegetation was dominated by ash (*Fraxinus angustifolia*), alder (*Alnus glatinosa*), black poplar (*Populus nigra*) and willow (*Salix atrocinerea, S. alba, S. salvifolia*), frequently surrounded by edges of bramble-thicket (*Rubus ulmifolius*). In most southern areas, hawthorn (*Crataegus monogyna*) is another common species (Aguiar et al., 2000). Besides indigenous species, silver wattle (*Acacia dealbata*), an exotic invasive tree and highly resilient to fire, is widespread across the surveyed riparian zones (Silva et al., 2011).

3.2.4 Fire data, land-cover and streams

The years 2003 and 2005 were the two highest fire years in the existing record for Portugal (e.g. Viegas et al., 2006), particularly in the east-central areas where this study was conducted. These fires, and the fact that they affected vast areas of MP, Ec and CO forest types, created a unique opportunity to conduct this study across basins but within a relatively uniform climatic region. Yearly maps of fire scars (≥5 ha) during the period 2003–2007 were assessed from cartography available in vector format from the National Forest Authority. Fire polygons were overlapped with land-cover maps of the region. Our base maps included the 1990 land-cover map for Portugal (reference scale 1:25 000) developed by the National Center for Geographic Information, the CORINE (Coordination of Information on the Environment) land-cover data (1:100 000) from European Environment Agency (years 2000 and 2006) and data points from National Forest Inventories from 1995 and 2005. Computations for the sub-basins and stream orders (Strahler, 1957) were made using GIS processing of a 25-m digital elevation dataset and a 1:25 000-scale hydrography network. Finally, the information on these layers was overlaid and cross-tabulated, and sites checked with field reconnaissance.

3.2.5 Data collected on DWP

Each study site included one representative 500-m reach complemented whenever possible with a 100–200 m perpendicular transect onto the adjacent hillside. Census techniques (Diez et al., 2001; Elosegi et al., 1999) and the line-intercept method (Van Wagner, 1968) were used along stream reaches and corresponding burned valleys, respectively. Thus, for pieces that lie along the slope of the valley, only those intercepting the line transects were considered and its total length was measured. We included for measurement of DWP (diameter \geq 0.05 m; length \geq 0.5 m) wood pieces that were still rooted but entirely dead, or still alive but entirely uprooted (Merten et al., 2010). However, we excluded snags (following Young et al. (2006), defined as pieces leaning or suspended over the stream at an angle greater than 30°), stumps (which would be outliers, at least in terms of diameter and length) and jams (>2 logs). Inside each stream reach, only DWP intercepting bankfull boundaries were included in the tallies, but the total length of each piece was recorded. Thus, for each DWP, for transects inside or outside of streams, a single person recorded the following:

- (i) The total estimated length (excluding rootwads) of the piece for the portion over 0.01 m in diameter;
- (ii) A single diameter measurement taken from a central point. Wood lengths were estimated to the nearest 0.2 m and diameters to the nearest 0.005 m. All estimates were verified for the first 20 pieces in each transect with a tape. Field tapes were also used for all larger pieces (lengths >6 m or diameters >15 cm), where errors were likely to be greater;
- (iii) Effects of fire on the DWP (burned status) assessed by the amount of charred bark and sapwood (following Jones and Daniels (2008), where 0 = no char, 1 = charred bark but outermost ring present in at least one part of the circumference, and 2 = charred bark and sapwood resulting in significant ring loss);
- (iv) Tree type (maritime pine, eucalyptus, cork oak, or "riparian species") was identified by assessing morphological characteristics of the DWP;
- (v) Decay classes were adapted from Jones and Daniels (2008) during the fieldwork data collection but were later simplified to sound or decayed wood;
- (vi) Class of the DWP form (straight; bent; strongly bent);
- (vii) Presence of rootwads (yes/no);
- (viii) Presence of branches (yes/no).

3.2.6 Statistical analysis

To make the design more balanced and results more interpretable, the variables burned status, form and decay were ultimately reduced from a series of categories to simple binary criteria: unburned/burned wood, straight/bent wood and sound/decayed wood. All analyses were made using the statistical software R (available online at http://www.r-project.org/). The Box–Cox family of transformations was used to find the best transformation for meeting

normality and homoscedasticity assumptions when necessary (Quinn and Keough, 2002; Sokal and Rohlf, 2009). The analysis had three components:

- (i) Comparing proportions of burned/unburned DWP according to tree type: A frequency analysis was conducted comparing patterns in counts of burned and unburned DWP across tree types in a 4 × 2 contingency table. We then explored the pattern of standardized residuals to reveal which cross classifications deviated the most and in what direction from the expected values, thus contributing the most to the lack of independence between burned status and species of DWP.
- (ii) Comparing key characteristics according to DWP tree type and DWP burned status: Contingency tables were also performed for each categorical variable (branches, rootwads, form and decay), but separating burned from unburned counts of each tree type (resulting in individual 8 × 2 contingency tables). For variables diameter and length, a two-factor unbalanced model I ANOVA (using type III sums of squares in *F*-ratios) was used to test main effects and interactions of tree type and burned status.
- (iii) Comparing key characteristics of DWP inside streams according to DWP burned status: Besides individual contingency tables for categorical variables, differences in diameter and length between burned/unburned DWP in streams were investigated by two randomization *t*tests (with 5000 randomizations).

3.3 Results

A total of 2206 DWP were tallied, with counts distributed as shown in Table 2 by tree type, location and burned status. As expected, the number of DWP was unbalanced among tree types and burned status. The number of CO pieces was lower than the others and frequency of pieces from riparian trees (Ri) was higher. Also, the number of burned DWP was more than double the unburned DWP. In MP, the number of unburned DWP was particularly low, with 6 unburned pieces and 556 burned (Table 2).

Table 2. Counts of down wood pieces (≥ 0.05 m; total length ≥ 0.5 m) by tree type, location and burned status (unknown burned status refers to inconclusive visual assessments of this variable). Values represent the number of pieces of each tree type across all sites intercepting either the 100–200 m transects perpendicular to the 500 m stream reaches (Side-slope rows) or the bankfulls (In-stream rows). Tree types included are Eucalyptus (Ec), Maritime pines (MP), Cork oaks (CO) and Riparian trees (Ri).

Burned status	Location	Numb	per of p	Grand total		
		СО	Ec	MP	Ri	
Unburned	In-stream	13	34	2	522	571
	Side-slope	3	30	4	0	37
	Total	16	64	6	522	608
Burned	In-stream	50	150	116	422	738
	Side-slope	31	175	440	0	646
	Total	81	325	556	422	1384
Unknown	In-stream	1	27	5	141	174
	Side-slope	0	40	0	0	40
	Total	1	67	5	141	214
	Grand total	98	456	567	1085	2206

3.3.1 Comparing the proportions of burned/unburned DWP according to tree type

There was a clear lack of independence between DWP tree type and burned status (Fig. 2, $\chi^2 = 548.5$, *P* < 0.001). Proportionally, only Ri had more unburned than burned pieces, which, along with the high proportion of burned pieces for MP, contributed greatly to the association of tree type and burned status. The proportion of unburned pieces was higher in Ec than in MP (having comparable sample sizes), whereas Ec and CO had equal proportions of burned/unburned pieces (but unequal samples).



Fig. 2. Mosaic plot associating tree types and burned status of the different wood pieces. Rectangles are proportional to observed frequencies and color reflects the magnitude and significance of residuals from a contingency table test. Tree types included are Eucalyptus (Ec), Maritime pines (MP), Cork oaks (CO) and Riparian trees (Ri).

3.3.2 Comparing key characteristics of DWP according to tree types and DWP burned status

Diameters and lengths

Diameters were significantly different (F = 29.1, P < 0.001) between tree types (means: CO = 0.10 m; Ri = 0.09 m; MP = 0.08 m; Ec = 0.07 m), with burned pieces being thickest (F = 8.9, P = 0.003). There was no evidence of an interaction between tree type and burned status (P > 0.05), suggesting that the effect of fire was consistent across tree types (Fig. 3a). Lengths were also different (F = 47.2, P < 0.001) between tree types (means: MP = 5.2 m; Ec = 4.3 m; Ri = 3.2 m; CO = 1.2 m). Burned pieces were significantly longer (F = 10.9, P = 0.001), except for DWP from riparian trees (Fig. 3b).



Fig. 3. (*a*) and (*b*): Bar plots of mean diameters and lengths (error bars are 95% confidence intervals) of unburned and burned wood pieces for the four tree types. /bars of unburned MP were omitted due to a very low (n = 6) sample size. (*c*) to (*f*): Mosaic plots associating *tree types* and *burned status* (0 = unburned; 1 = burned) of the different wood pieces with the *presence of branches*, *presence of rootwads*, wood form and *decay status*. Rectangles are proportional to observed frequencies and color reflects the magnitude and significance of residuals from contingency table tests. Tree types included are Eucalyptus (Ec), Maritime pines (MP), Cork oaks (CO) and Riparian trees (Ri).

Branches, rootwads, form and decay

The contingency table tests rejected the null hypothesis of no association between DWP of different tree types separated by burned status and branches ($\chi^2 = 670.7$, P < 0.001), rootwads ($\chi^2 = 191.7$, P < 0.001), form ($\chi^2 = 404.9$, P < 0.001) or decay ($\chi^2 = 186.1$, P < 0.001) in all cases (Fig. 3c–f). Branches were present more often than expected (i.e., Pearson residuals were positive) for MP but not for the other tree types. Only unburned Ri showed no difference between proportions of DWP with and without branches, although burned Ri pieces had branches less often than expected.

Regarding the presence of rootwads, the standardized residuals revealed that the percentage of burned MP pieces with rootwads was clearly higher than expected (Fig. 3d). No CO pieces had rootwads. In addition, the frequency of bent DWP was higher than expected in Ri and burned CO (Fig. 3e). For the decay status of DWP (Fig. 3f) it is worth noting that, in general, burned wood was most often decayed. Sound burned DWP of Ec, Ri and CO were rare, whereas unburned sound DWP of Ec and Ri, and burned sound MP pieces, all appear more often than expected (positive Pearson residuals).

3.3.3 Comparing key characteristics of DWP in all streams according to DWP burned status

Diameters and lengths

Regarding wood in all streams combined, burned DWP was significantly thicker (Fig 4a; t = -4.9, R = 5000, P < 0.001) but not significantly longer (t = -0.5325, R = 5000, P = 0.5945) than unburned wood (Fig. 4b).



Fig. 4. (a) and (b): Bar plots of mean diameters and lengths (error bars equal 95% confidence intervals) of unburned and burned wood pieces in the study streams. (c) to (f): Mosaic plots associating burned status of the wood pieces in stream reaches with the presence of branches, presence of rootwads, wood form and decay status. Rectangles are proportional to observed frequencies and color reflects the magnitude and significance of residuals from contingency table tests. Tree types included are Eucalyptus (Ec), Maritime pines (MP), Cork oaks (CO) and Riparian trees (Ri).

Branches, rootwads, form and decay

The presence of branches was not independent ($\chi^2 = 37.3$, P < 0.001) of burned status (Fig. 4c), with burned DWP being less likely to have branches. Conversely, the presence of rootwads (Fig 4d) was not associated with burned status ($\chi^2 = 0.3$, P = 0.594). The form of DWP was not independent ($\chi^2 = 30.6$, P < 0.001) from burned status; burned pieces were most often straight (Fig. 4e). Regarding decay interactions with burned status ($\chi^2 = 138.3$, P < 0.001), burned DWP were rarely sound and, with residuals of opposite sign in Fig. 4f, unburned sound DWP appeared more frequently than expected.

3.4 Discussion and conclusions

In this study, we demonstrated that the physical characteristics of post-fire wood delivered to streams were markedly different depending on the source tree type. Many of the wood pieces retain their species-specific characteristics even after burning. There were also structural differences between burned and unburned pieces of wood reaching streams, which were generally consistent across the studied tree types. When filtering the analysis for DWP already recruited to streams (mainly from riparian trees), it became clear that diameter, presence of branches, wood form and decay status were influenced by fire. Regarding the quantity of DWP in "burned streams" and eventual recruits from the side-slope, we discuss below which tree types contributed more DWP to standing stocks in streams and, proportionally, which tree types supplied more burned wood.

3.4.1 Differences between post-fire DWP originating from cork oak montados and timber-production forests

Overall patterns in wood size and architecture among the Mediterranean forests studied reflect intrinsic species characteristics that are inseparable from silviculture practices (Brin et al., 2008). In general, timber-production forests (MP and Ec) contributed thinner, longer and straighter DWP to streams than CO, independent of burned status. In the study sites, timber-production forests of Ec and MP were young stands when they burned (which may be an increasingly common situation on production forests in Portugal), thus it is not surprising that their downed wood had thinner pieces than Ri and the older CO forests (Benda et al., 2002). This is consistent with work from the Pacific Northwest region of North America where Rot et al. (2000) reported diameters of wood in streams of old-growth forests exceeding the diameter of trees in riparian forests. CO pieces also share with riparian DWP a bent form when compared to timber-production forests. DWP of CO, much shorter and always without rootwads, should reflect their origin as slash from branch pruning, along with the fact that the trees themselves are shorter and very difficult to uproot.

Maritime pine and eucalyptus pieces also showed well-marked structural differences from each other. Our data indicate that postfire DWP from MP have more branches and rootwads than Ec. This could be due to differences in rooting structure and branching patterns. Living Ec invest more energy in the trunk than in the branches (Pereira, 2007). The presence of rootwads in DWP of MP probably highlights the tendency for the trees to uproot easily from side-slopes in the study sites. Another pattern observed was that MP pieces were longer and thicker than Ec. Although there are differences in growth form and growth rates, this probably has more to do with post-fire management (or lack thereof) than specific characteristics of the trees. A number of burned MP wood pieces were whole trees, while most Ec pieces were slash left behind after post-fire clear-cutting along with fallen wood from young recovered trees.

3.4.2 Relations between DWP quantities and tree type post-fire recovery

Although a complete analysis of wood standing stocks is beyond the scope of this study, differences in wood frequency among study forests were conspicuous (Table 2). First, despite larger and more connected riparian buffers, and therefore a low probability of upland wood entering the streams, timber-production stands contributed more wood to streams following fire than CO stands with more limited buffers. Discounting pieces originated from riparian trees, the average number of recruited pieces of MP (2.3 pieces/100 m) and Ec (4.5 pieces/100 m) were ~2 and ~3 times higher than the frequency of CO wood (1.4 pieces/100 m) in CO sub-basins (Table 3). This likely reflects a combination of the low density of CO trees in *montado* systems, their higher fire resistance (e.g., cork insulation), post-fire resilience and salvage logging in post-fire management. Second, another contrast between tree types is linked with proportions of unburned pieces (Fig. 2). Only DWP of Ri trees had more unburned than burned pieces, which can be interpreted as a result of burned wood transport downstream since fire occurrence, while at the same time there was a sustained input of unburned wood from the riparian zone. Arseneault et al. (2007) conceptually stressed these asynchronies when "source and sink systems" recover at different rates.

Another explanation for the prevalence of unburned Ri pieces may be that riparian vegetation presents a lower fire proneness (Fernandes et al., 2010; Moreira et al., 2001) or that riparian zones experienced less severe wildfires due to their lower elevation and more hydric environment (Bendix and Cowell, 2010b; Everett et al., 2003). Unfortunately, few data are available regarding fire and riparian vegetation (Pettit and Naiman, 2007); some authors refer to riparian vegetation as being subjected to frequent fires (Kobziar and McBride, 2006) while, as stated by Dwire and Kauffman (2003), others ignore fire effects in riparian zones because of the belief that riparian areas are too wet to burn. In our data the majority of burned wood inside streams came from riparian trees but DWP from this tree type had the highest proportion of unburned pieces. Riparian areas are clearly not immune to the presence or impacts of fire but continued recruitment is a confounding factor to some degree. Furthermore, the wood from side-slope forests that did enter the stream following the fire is within the riparian zone of influence if not the riparian buffer. This suggests that species-specific differences in fire susceptibility are more important to riparian zone impacts than location in the landscape influence. More work is clearly needed to address the question of fire impacts in riparian zones.

Finally, regarding contrasts between MP and Ec, the higher proportion of unburned DWP that can be found in burned Ec stands (equal to CO, with 20%, against 1% in MP) is likely due to the rapid coppice regrowth in an Ec forest after fire – with subsequent wood recruitment – as opposed to the slower natural stand-replacement in MP stands (Calvo et al., 2008). The growth of Ec is striking and we observed recruitment of new wood from coppiced growth within the two years over which these data were collected.

3.4.3 What can streams expect from fires in the long-term?

This study showed that fire contributed toward larger DWP in streams. This included a number of potential "key" pieces (Abbe and Montgomery, 1996, 2003) with the capacity to entrap other wood and form logjams (Bocchiola et al., 2008; Nakamura and Swanson, 1993). Smaller pieces may have been consumed by fires or were the first to be transported downstream. Since decay rate (Hassan et al., 2005) and probability of displacement (Merten et al., 2010, 2011; Warren and Kraft 2008) are functions of size, large pieces have a more sustained long-term influence on habitat and physical processes than small pieces (Dolloff and Warren, 2003).

Burned pieces within the stream channel also tended to lack branches (Fig. 4c), which when present increase surface area and can promote habitat complexity that improves conditions for aquatic organisms (Sundbaum and Naslund, 1998). It is known that tree boles tend to survive fire while most branches are consumed in the blaze (Agee, 1993). We therefore suggest for future studies in fire-prone areas that each DWP be assigned to a class (trunk/branch) to address this point. A related system by Newbrey et al. (2005) implemented a branching complexity for each piece, where higher complexity corresponded to a greater number of branches and twigs. In this context our data suggest a fire-driven reduction in stream wood complexity in burned streams. In addition, fire seems to have promoted the presence of straight wood in the study reaches. Straight wood pieces are less likely to become trapped or snagged in river channels than more irregular wood pieces of a similar size (Gurnell, 2003).

Fire also appears to increase the number of decayed DWP pieces in streams (Fig. 4f). Decayed pieces may be more prone to breakage (Hassan et al., 2005) and shorter pieces are depleted more readily via downstream transport (Merten et al., 2010, 2011). Zelt and Wohl (2004), compared characteristics of wood in two adjacent burned and unburned streams a decade after wildfire and, contrary to our results, reported smaller average piece sizes in the burned stream. The authors explained this difference by age distinctions among source trees on both streams. In our study, although fire-impacted wood was larger, data also indicated that burned wood was often more decayed than unburned wood. This sets up an interesting contrast. Does the larger size of wood reduce decay to a greater degree than the impacts of burning may promote decay? If burning wood substantially increases the susceptibility of stream wood to decay, the input of wood following fires may not persist. Our study could have been strengthened if DWP from unburned streams were included for comparison to those of the burned sections, especially if we had been able to find unburned forest stands of the same age as burned stands when the fire happened. This design would prevent stand age from becoming a confounding factor when comparing attributes such as DWP dimensions (Zelt and Wohl, 2004), particularly for fast-growing species such as Ec.

Table 3. Frequency, volume and burned pieces proportion of in-stream downed wood (mean \pm SE) across 27 first- to third-order streams in central Portugal following wildfires. Stocks are reported by upland forest: Maritime pine (MP), Eucalyptus (Ec) or Cork oak trees (CO). For each forest type, 9 stream reaches of ~500 m each were surveyed. The contribution of the upland forest for the respective total stock of instream wood (pieces intercepting the bankfull) is also given. Results are presented by our size criteria (diameter \ge 0.05 m; length \ge 0.5 m) and the standard definition for large wood (diameter \ge 0.1 m; length \ge 1 m).

Side-slope forest	In-stream wood species	≥ 0.05 m; l	ength ≥ 0.5 m		≥ 0.1 m; ler	ngth ≥ 1 m	ıgth ≥ 1 m			
		Proportion of burned pieces	Frequency (# 100 m ⁻¹)	In-stream volume (m ³ /100 m)	Proportion of burned pieces	Frequency (# 100 m ⁻¹)	In-stream volume (m ³ /100 m)			
MP	MP	1.0 ± <0.1	2.3 ± 1.0	0.12 ± 0.06	1.0 ± <0.1	1.1 ± 0.5	0.11 ± 0.05			
	All species	0.7 ± 0.1	12.6 ± 2.1	0.65 ± 0.18	0.8 ± 0.1	5.0 ± 1.1	0.56 ± 0.17			
Ec	Ec	0.7 ± 0.1	4.5 ± 2.3	0.11 ± 0.05	0.7 ± 0.2	0.3 ± 0.2	0.05 ± 0.02			
	All species	0.7 ± 0.1	10.8 ± 3.5	0.38 ± 0.17	0.7 ± 0.1	2.9 ± 1.4	0.28 ± 0.15			
СО	CO	0.8 ± 0.1	1.4 ± 0.6	0.02 ± 0.01	0.9 ± 0.1	0.4 ± 0.2	0.01 ± 0.01			
	All species	0.6 ± 0.1	9.6 ± 2.9	0.22 ± 0.08	0.7 ± 0.1	2.0 ± 0.6	0.15 ± 0.05			
Total across	27 streams	0.7 ± 0.1	11.0 ± 1.6	0.42 ± 0.09	0.7 ± 0.1	3.3 ± 0.7	0.33 ± 0.08			

It is possible to predict the implications of future DWP inputs from upland Ec, MP and CO trees following fire. More MP pieces should change stream hydraulics and habitat complexity, due to the frequency of branches and rootwads. By comparison, Ec pieces are often straight pieces without rootwads, which may be transported more readily downstream (Braudrick and Grant, 2001) or stay in positions (e.g., bridges) with little contribution to stream morphology and function (Jones and Daniels, 2008). Nevertheless, the individual ease of transport of Ec pieces can be hindered by the higher quantities of DWP coming from upland Ec relative to MP. In agrosystems, Elosegi and Johnson (2003) suggested that thinner, longer wood pieces were more common than in other streams. In this sense, post-fire pieces from CO agro-systems delivered to their streams can predictably contrast with other pre-existent wood.

3.4.4 Management concerns

Less than a decade after large scale wildfires, structural characteristics of downed wood in and near streams are clearly fire-driven and directly influenced by silviculture practices. Changes in forest management will not only affect standing stocks of in-stream wood in the short term following a fire, but will change the susceptibility of wood pieces to downstream transport and decay, thus changing stocks in the long term as well. Changes in wood stocks can have dramatic effects on stream ecosystems (Gregory et al., 2003) and warrants consideration when decisions are being made regarding forest management. Reduced stocks, for example, can lead to decreased in habitat for fish, substrate for invertebrates and biofilms, leaf litter retention, transient storage, and hyporheic exchange (Gregory et al., 2003). Maintaining riparian buffers – probably less susceptible to fire than surrounding forest stands – may reduce, but will not eliminate, the impacts of fire on stream wood.

In a previous study (Silva et al., 2011), we concluded that wildfires strongly influenced the landscape dynamics of three fire-prone areas across Portugal over ~14 years. Fire-driven transitions revealed that land abandonment led to increases in shrublands (encroaching into
previously forested areas) and more mixed forests of MP with Ec over time. Under this scenario, our results suggest that large pieces of wood will slightly become less common in these streams and that stream reaches will become more homogeneous in terms of wood characteristics. At the global scale, the combination of increasing wildfire disturbance along with changing forest composition (from older, more traditional mixed uses to single-use, single-species forests managed for timber) can alter the characteristics of wood entering streams with a shift from large DWP to thinner and straighter wood. We reiterate that DWP, even after burning, still retain species-specific physical architecture of the pre-burned trees and could not be lumped together in terms of their effect on stream ecosystem structure and function or in-stream wood movement. The interaction between the unique physical traits of a species and production silviculture practices are responsible for long-term implications for stream function and structure after wildfires.

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Effects of forest type and stream size on volume and distribution of stream wood: legacies of wildfire in a Euro-Mediterranean context

4. Effects of forest type and stream size on volume and distribution of stream wood: legacies of wildfire in a Euro-Mediterranean context

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Abstract: Downed wood pieces are key links between terrestrial and aquatic ecosystems. They promote organic matter retention, create habitat, and potentially increase stream productivity. The stock of downed wood in a river system is a product of the interaction between wood supply, transport, in situ losses, and retention characteristics of the system. Fire and forest management are important disturbances that influence the amount and organization of stream wood with boom-and-bust periods of recruitment and fluvial transport processes. We examined 1st- through 3rd-order Portuguese streams flowing through 3 common silvicultural systems in southern Europe: forests of cork oak, eucalyptus, and maritime pine. Our data set included 1483 pieces of wood in 27 streams, all of which had experienced extensive wildfires within the previous 6 y. We used binned neighbor-k analysis to assess wood organization (segregated, random, or aggregated). We then used linear mixed-effects modeling to evaluate the effects of stream order, forest type, and their interaction on wood volume and organization. The best predictor of wood volume and organization was the interaction between forest type and stream order. Most wood pieces were burned and organization was low, suggesting that arrangement of wood was largely a product of input dynamics rather than transport processes at this time. Potential drivers of across-system variability included vegetation obstructions, wood length:channel width ratios, management actions, and effects of fire. Climate models predict more droughts in the Euro-Mediterranean region in the future, with implications for wood volume, transport, and function as terrestrial vegetation invades intermittent stream channels and plant communities shift from managed forests to shrublands with few trees.

Keywords: wildfire; Portugal; wood distribution; wood volume; forest management; eucalyptus; cork oak; maritime pine; disturbance; intermittent streams.

4.1 Introduction

Downed wood pieces are key links between terrestrial and aquatic ecosystems and promote organic-matter retention, create habitat, and increase productivity in streams (Naiman et al. 2002). The stock (amount and arrangement) of wood in a river system is fundamentally a product of the interaction between wood supply, transport, and retention characteristics of a river (Gurnell et al. 2002, Abbe and Montgomery 2003). These factors vary along the river continuum (Gurnell 2003) and among streamside forests. Therefore, stocks are expected to vary among streams of differing sizes within a watershed and between forest types. However, few investigators have considered source-to-sink aspects of wood in rivers (Arseneault et al. 2007) across a breadth of spatial scales, differing forest types, and stream sizes.

Fire is an important driver of wood recruitment to streams. It can kill trees or cause injuries that increase their susceptibility to windthrow and disease (Resh et al. 1988). Such trees are recruited more readily into fluvial systems (Spies et al. 1988, Benda et al. 2003). Studies on stream wood dynamics in the context of fire history have been focused on pristine regions or those with a single forest-management system, but rarely on landscapes with long legacies of land management or multiuse systems with production forests and agriculture. This landscape is common across Euro-Mediterranean countries, where ~0.5 million ha/y are burned by wildfires (Moreira et al. 2011). In Portugal, where we conducted our study, wildfires have burned >30% of the land area since 1980 (Camia et al. 2008), and varying forest management activities have affected the characteristics of stream wood (Vaz et al. 2011).

Fire and forest management are important disturbances because they can influence both the amounts and organization of stream wood with boom-and-bust periods of recruitment to and transport in stream channels. Shortly after a fire, high inputs of wood to streams are expected because of tree mortality (Harmon et al. 1986, Benda and Sias 2003). However, during the postfire period of regrowth when inputs are low (Minshall et al. 1989), existing stream wood is redistributed and in-stream transport processes may dominate wood transfer from upstream to downstream reaches. Fluvial transport is greatest when the length of stream wood is shorter than the channel width (Lienkaemper and Swanson 1987, Nakamura and Swanson 1993). Thus, one might expect a greater degree of wood organization (i.e., nonrandom distribution) in larger streams where transport capacities are greater than in smaller streams where transport capacity is low (Kraft et al. 2011). Human activities also can affect amount, size, and organization of stream wood. In the short term, tree thinning can contribute many small, discarded pieces of wood that are readily moved by the river (Gurnell 2003), but in the longterm, forest management leads to changes in tree species composition and age structure with further consequences for the amount and size distribution of stream wood. Intended or unintended effects of management actions on the quantity and arrangement of stream wood are poorly understood (Nakamura and Swanson 2003), especially when coupled with the effect of wildfire in fire-prone landscapes.

We quantified the volume and organization (random, aggregated, segregated) of wood in 27 burned streams of central Portugal. Our study encompassed a range of stream sizes and adjacent land uses, including 3 common managed forest types in southern Europe. We quantified and compared stocks of stream wood across varying channel sizes and adjacent forest types to address 2 main objectives and associated hypotheses. Our 1st objective was to assess the effects of forest type, stream size, and their interaction on volume of stream wood in Mediterranean-type ecosystems of southern Europe. We tested the hypothesis that a forest type x stream size interaction would be the primary factor accounting for volume of stream wood per unit area rather than a simple pattern of decreasing volume in a downstream direction independent of forest type. Our 2nd objective was to assess the effects of forest type. Our 2nd objective was to assess the effects of news type, stream size, and their interaction on the expectation that transport capacity increases with increasing stream size, we tested the hypothesis that the organization of wood in the river network would show increased aggregation in a downstream direction independent of forest type.

4.2 Methods

4.2.1 Study area and study design

We conducted our study in east-central Portugal from October 2009 to August 2011 in subbasins of the Tagus River that experienced extensive wildfires between 2003 and 2007 (Fig. 1). Land cover in these subbasins is dominated by forests, shrublands, and agriculture. We selected 9 subbasins (mean drainage area = 59 km², range = 26–143 km²) representing 3 dominant forest types: eucalyptus (*Eucalyptus globulus*), maritime pine (*Pinus pinaster*), and cork oak (*Quercus suber*). We used geographic information system processing of a 25-m digital elevation data set and a 1:25,000-scale hydrography network to calculate subbasins and stream orders (Strahler 1957). Within each subbasin, we selected one 1st-, 2nd-, and 3rd-order stream reach (~500 m each) representative of the general conditions in the subbasin. In total, we assessed 27 burned reaches comprising ~13,460 m of stream channel.

The local climate is Mediterranean with hot, dry summers and cool, wet winters. Mean annual precipitation is 512 mm (range: 3 mm in July to 82 mm in November), and mean annual temperature is 15.8°C (range: 9°C in December–January to 23°C in July–August). The area has gentle slopes. The structure of burned areas of maritime pine (MP) was shrubby with dense growth of *Erica* spp., *Cistus* spp., and *Ulex* spp. and young postfire maritime pine. Sparse shrubs were present in the understory of postfire recovered stands of eucalyptus (EC). In contrast, cork oak (CO) stands usually had bare soil with some low understory grasses. Additional details are provided in Vaz et al. (2011).



Fig. 1. Location of the 27 sampling sites in east-central Portugal within nine subbasins of the Tagus River. The subbasins were dominated by 3 forest types: eucalyptus (1–3), maritime pine (4–6), or cork oak (7–9). Within each subbasin, three 500-m stream reaches were assessed, one each from 1^{st} -, 2^{nd} -, and 3^{rd} -order streams.

4.2.2 Forest and stream characterization

CO stands are managed mostly by an agro-forestry system called *montado* (*dehesa* in Spain). CO trees occur irregularly at densities from 30 to 60 trees/ha and are harvested for cork every 9 to 12 y without felling. Trees grow among pastures and cereal crops (Bugalho et al. 2011). CO trees in the region had a mean age of 20 to 40 y, >90% of the stands had a basal area <10 m²/ha, and 64% had <50% crown cover (NFA 2010). Branch pruning for rehabilitation of burned CO trees is done on almost all trees. Slash from this activity produces wood 0.5 to 2 m long that eventually reaches streams where trees occur along the stream (Fig. 2A, B).

MP is grown for timber in monoculture stands with ~235 stems/ha. More than 50% of these stands were <10 y old (30% had irregular ages), >75% had a basal area <10 m²/ha, and >70% had >50% crown cover area (NFA 2010). Intense wildfires kill most MP trees (especially younger trees), and the dead trees fall within 1 to 3 y (PV, personal observation). No postfire logging was done in the MP sites, and fire-killed trees were left on the ground on stream side slopes (Fig. 2C, D).

EC is planted in monocultures with ~377 stems/ha for paper pulp production. A substantial part of these stands had irregular ages (45% was 1–15 y old) or was very young (22% was <4 y old), >90% had a basal area <10 m²/ha, and >90% had >50% crown cover (NFA 2010). Rapid growth of EC allows rapid postfire recovery. Across EC systems, the intensity of human interventions following fire is variable. When these interventions exist, managers use a stumps–

coppice method of regeneration for top-killed trees. The burned trees are cut and wood is removed to create a stump that will coppice. Slash (e.g., trunks, limbs) from this activity produces wood pieces 2 to 3 m long that can eventually reach streams (Fig. 2E, F).

Riparian zones (0–15 m in width, with a distinct riparian community) were often present along streams in MP and EC forests, and their width increased with stream size. Uncultivated riparian vegetation was dominated by ash (*Fraxinus angustifolia*), alder (*Alnus glatinosa*), black poplar (*Populus nigra*), and willow (*Salix atrocinerea*, *Salix alba*, *Salix salvifolia*), and frequently was surrounded by edges of bramble-thicket (*Rubus ulmifolius*). In most southern areas, hawthorn (*Crataegus monogyna*) also was common. In addition to the indigenous species, silver wattle (*Acacia dealbata*), an exotic invasive and fire-prone tree, was widespread across the surveyed riparian zones (Silva et al. 2011). Trees from the adjacent forest often extended near 1st-order streams, but 3rd-order streams generally had a distinct riparian community (Fig. 2C). Gaps >10 m in the riparian community were common where trees of the managed forest species occurred directly along the stream margins. CO areas followed the same pattern of increasing riparian-zone width increasing with stream size, but generally had more limited riparian zones (Fig. 2A), and potential sources of large wood (adjacent forest or riparian species) could be absent for tens of meters.

Many of the streams in all 3 forest types were intermittent with stretches that remained dry for several months in a seasonal sequence of flooding and drought events. All 1st-order streams were intermittent, and flows were more continuous with increasing stream order and from CO to EC to MP streams. We often found woody vegetation and terrestrial plants in the channels and along the edges of intermittent streams (Fig. 2D). In 1st-order streams, terrestrial vegetation invaded the channel and sometimes extended for tens of meters. For example, dense entanglements of bramble-thicket were common obstructions across 1st- and some 2nd-order streams. At the reach scale, mean channel widths were 1.34 to 12.75 m, bed slopes were 0.02 to 7.80%, and side slopes within 50 m of the stream were 0.80 to 18.27%.

We observed removal of stream wood from some streams in the study subbasins, but outside of our study reaches. Signs of recent harvest were absent from the 27 reaches and respective riparian zones (evaluated by saw cuts on wood and piles of EC logs; see Fig. 2E). In CO forest, cattle fences, which can affect stream wood stocks and transport, were present downstream of 3 of the 9 study reaches (Fig. 2B). Overall, the intensity of postfire management across the 3 systems was higher at CO than EC and negligible at MP streams. In these 3 types of managed forest in central Portugal, wood enters streams by falling directly into the channel or as intended or unintended results of management actions. Wood on the floodplain also can float laterally into channels during floods or roll down eroding banks. Other mechanisms of lateral transport of wood, such as landslides, are negligible.



Fig. 2. Photographs of 1st- to 3rd-order streams and riparian conditions in 2010 after the 2003–2007 wildfires in central Portugal. The streams flow through monospecific managed forests of cork oak (A, B), maritime pine (C, D), and eucalyptus (E, F).

4.2.3 Data collection

Each study site included a 500-m reach where we measured downed pieces of wood (diameter ≥ 0.05 m; length ≥ 0.5 m) that were dead or alive but entirely uprooted. We excluded snags (Young et al. 2006), defined as pieces leaning or suspended over the stream at an angle $>30^{\circ}$. We measured all pieces that were accessible (10–20 pieces) in 3 wood jams (ranging from >10 to <50 pieces) found in 3 different reaches. We included only downed wood extending >5% of the length of the piece within bankfull boundaries in the tallies.

One individual recorded all of the information for a piece of wood. We geo-referenced the position of each piece of wood along the reach at its center with a global positioning system (GPS) unit (0.3–1 m precision by post-processing). The GPS reading was taken for 30 to 60 s and the average recorded then converted to a distance along the thalweg. We estimated the length (m) of each piece to the nearest 20 cm for the segment of the piece that was >1 cm in diameter. We measured length with a meter tape for pieces >6 m long and estimated it for pieces <6 m (verified by measurement for the first 20 pieces/reach). We estimated the diameter of each piece to the nearest 0.5 cm at a single point considered the mean diameter by visual assessment. We measured diameter with a meter tape for pieces >15 cm diameter and estimated it for pieces <15 cm diameter (verified for the first 20 pieces/reach). We assessed the burned status of each piece following Jones and Daniels (2008) during the field-data collection but later simplified the assessment to burned (bark or sapwood charred) or unburned. We identified tree type (MP, EC, CO, or riparian species) from morphological characteristics of the piece. We recorded the orientation of each piece to flow direction as 0° (parallel), 90° (perpendicular), or intermediate. Wood decay classes used were adapted from Jones and Daniels (2008) for field-data collection. EC bark usually comes off in fires, so we adapted the method and did not assess bark integrity as an attribute of decay for this species.

We measured channel widths every 10 m (~51 widths/reach) with a laser meter (precision: 1 mm) and a target. We measured only unobstructed channel (width available to transport stream wood). We recorded the shorter of bankfull width or the distance across the stream between the innermost plant stems (diameter \geq 0.03 m) every 10 m. We derived the wood length:channel width ratio for each piece of wood (L*; length divided by nearest channel width).

We further characterized the following variables for each stream reach using GIS: 1) reach gradient (gradient = ratio of vertical drop per unit of horizontal distance), 2) mean side slope (sslope) within 50 m on each side of the stream reach, 3) sinuosity (ratio of reach length to straight-line distance between reach ends), 4) year of the wildfire (fireyear = 2003, 2005, 2007) affecting the stream reach, 5) drainage area (drainarea = side-slope drainage area [ha] of the stream reach), and 6) proportion of burned area within the drainage area (burnarea).

4.2.4 Data analysis

Binned neighbor-k analysis

We quantified stream wood distribution with binned linear neighbor-k analysis (Kraft et al. 2011). We coded the location of each piece of wood as the distance (m) of the center of the piece from an initiation point along the thalweg. Thus, the collective arrangement of wood in a reach was presented as a series of numbers with values from 0 to 500 that corresponded to wood location along the reach relative to the initiation point. Next, the pieces of wood within set distance intervals (10-m bins) from a focal piece of wood were counted; i.e., the number of pieces within 0 to 10 m of the focal piece, within 11 to 20 m, 21 to 30 m, 31 to 40 m, and so on. This process was repeated for each piece of wood in the reach until the number of wood pieces

occurring at each interval distance from each piece of wood had been counted. Hence, this analysis produces a histogram of the collective number of wood pieces at a given distance from any other piece as defined by binned distance intervals. This histogram (the number of pieces within each interval for our observed wood distribution) was compared to a histogram produced by the same process applied to 1000 random arrangements of wood (a series of random numbers between 0 and 500 equal to the number of pieces of wood in the reach and chosen with replacement) along a stream reach. The collective numbers of wood pieces occurring in each distance interval bin (0–10 m, 11–20 m, 21–30 m, etc.) for each of the 1000 randomized wood distributions were ranked, and the results from our observed data were compared to the ranked values.

We considered wood significantly aggregated at a particular distance interval if the observed number of wood pieces in that distance-interval bin was >975th ranked number of pieces of wood from the 1000 randomizations in that bin. In other words, more wood occurred in that distance interval than would be expected by chance alone. We considered wood to be significantly segregated if the observed number of wood pieces in that distance-interval bin was <25th ranked number of pieces of wood from the 1000 randomizations in that bin. That is, less wood occurred in that bin than would be expected by chance alone. The 25th and 975th rank thresholds correspond to the 0.025 proportion of a normal distribution that would collectively represent *p* = 0.05 in a 2-tailed test (Kraft and Warren 2003, Kraft et al. 2011).

This measure of distribution carries potential bias associated with wood occurring at the ends of the reach (Kraft et al. 2011). Only wood pieces near the ends of the reach (upstream or downstream) can occur at distance intervals that extend the full length of the reach. For example, many wood pieces could occur within 50 m or 100 m of another piece, but only a few pieces could occur within 450 m of another piece of wood. To correct this bias, we considered only bin distances $\leq \frac{1}{2}$ the total reach length (250 m, 25 bins). This correction does not cut the reach in half in regard to which wood is counted. All wood is included in the analysis, but the results are evaluated only over bin intervals that collectively added up to $\frac{1}{2}$ the length of the stream. This correction caused the final bin in the series to include all distance intervals >240 m (up to 500 m). Thus, these larger distances were included but were grouped into a single bin to address the low number of occurrences. Greater detail on this analysis and terms are given by Kraft and Warren (2003) and Kraft et al. (2011).

Results from the binned neighbor-*k* analysis allowed us to assess whether the arrangement of wood was consistent with a random distribution or differed from what we would expect if wood were randomly arranged in a stream for each 10-m distance interval. We also were able to evaluate the number of bin intervals within the entire reach (of the 25 total bins) that showed significant aggregation, which would reflect increased wood accumulation (at variable intervals) along a stream. Conversely, the number of bins showing significant segregation would reflect increased transport capacity or decreased wood recruitment at regular intervals along a stream. We grouped significant aggregation and significant segregation into a broader category that we

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called wood organization within a stream (see Kraft et al. 2011 for greater detail on these metrics). We used the number of bins exhibiting these measures of organization (i.e., nonrandom wood arrangement along a reach) to compare patterns of wood distribution among reaches relative to stream and riparian-forest characteristics.

Stream wood volume and organization

We derived volume (*V*) of individual wood pieces from the equation $V = \pi r^2 L$, where *r* is the radius and *L* is the length. To derive volume per area at the reach scale, we summed the volumes of individual pieces (m³) and then divided by the reach area (ha). We summed volumes by species separately by reach to assess patterns in species of stream wood (adjacent managed-forest species vs riparian species).

We evaluated the effects of forest type (foresttype), stream order (order), and order × foresttype interaction on wood volume/ha (volume) and wood organization (organization). We also tested the effects on volume and organization of the covariates— gradient, sslope, sinuosity, fireyear, drainarea, burnarea, and proportion of burned pieces (burnwood). Each variable was expressed per stream reach (n = 27). A matrix of Spearman's correlations for initial explanatory variables revealed that order was significantly correlated with gradient (r = -0.489, p < 0.01), sinuosity (r = 0.600, p < 0.01), drainarea (r = 0.629, p < 0.01), and burnwood (r = 0.566, p < 0.01). Correlation coefficients between the remaining variables used in the model (order, foresttype, sslope, fireyear, and burnarea) were all <[0.30], indicating no collinearity problems.

Groups of 3 stream reaches (orders 1, 2, and 3) were nested within a subbasin (3 subbasins per foresttype: CO, EC, MP), so we used mixed-effects models for the analysis of volume and organization, with subbasin as a random factor. Before analysis, we log(x)-transformed sslope and arcsin(x)-transformed burnarea to satisfy assumptions of normality. We treated fireyear as factorial with 3 levels (2003, 2005, 2007) and centered sslope and burnarea when building the models. We did all tests in R (R Development Core Team, Vienna, Austria).

The 2 components for modeling were tests for effects on volume and for effects on organization. We log(x)-transformed volume to satisfy assumptions of normality. After comparing the linear regression model with the linear mixed-effects model (LMM) with the random intercept for subbasin, we chose the LMM (L = 4.13, df = 1, p = 0.021) and used the nlme package in R (Pinheiro et al. 2011) to fit LMM. We modeled counts of organized 10-m bins per reach with generalized linear mixed-effects models (GLMMs). The response variable was expressed as a count, so we used a Poisson GLMM. We ran 3 models: one applied to the total number of organized bins per reach (no. segregated + no. aggregated), and 2 separate models for the number of aggregated or segregated bins/stream reach. We used the *Ime4* package (Bates et al. 2011) to fit GLMM.

For both components of the analysis, we started with a model with all 5 variables (order, foresttype, sslope, fireyear, and burnarea) and the order × foresttype interaction in the fixed part

of the model. We used backward elimination of variables (Zuur et al. 2009) to remove each main term in turn, and then applied the likelihood ratio test of nested models. We calculated variance inflation factors (VIF) for the full set of explanatory variables to detect eventual collinearity (VIF > 5). We evaluated model adequacy by plotting residuals vs fitted values and explanatory variables and model fit by the proportion of the null deviance explained. We applied post hoc tests (Tukey contrasts for multiple comparisons of means [MCM]) to final models to investigate which effects were different from each other (*multcomp* package; Hothorn et al. 2008).

4.3 Results

4.3.1 Stream wood frequencies, volumes, orientations, and decay

We measured 1483 pieces of wood (mean = 70% burned/reach), whose frequencies and volumes were distributed as shown in Table 1. Mean volume was $\geq \frac{1}{3}$ lower in CO streams than in EC or MP streams. Only 8% of the volume in CO streams came from the managed forest type species. This value was 4 and 63 lower than in MP and EC streams, respectively. Percent contribution from the managed forest type for total volumes (Fig. 3A) was lowest in 3rd-order streams and highest in 1st-order CO and EC streams. L* were distributed as shown in Fig. 3B. Stream wood decay was generally high (Table 2).

EC 1st-order streams had the greatest proportion of wood oriented at intermediate angles to the flow (Fig. 4A). More stream wood was oriented parallel to the flow in larger than in smaller streams (Fig. 4B). The number of pieces oriented perpendicular to flow was similar among stream sizes.

4.3.2 Effects on volume

Foresttype, order, and the foresttype × order interaction were the best predictors of volume. Thus, the effect of stream size on volume of wood per area was not the same for all foresttypes. During the model selection process fireyear, sslope, and burnarea were sequentially dropped. The resulting model ($R^2 = 0.545$) is shown in Table 3.

Volume did not differ among foresttypes or orders (*F*-test with *anova* command in *nlme*; *p* > 0.1), but the order × foresttype interaction was significant ($F_{4,12} = 4.261$, *p* = 0.022; Fig. 5). Fitted values for MP streams were higher than values for CO streams (MCM, *Z* = 2.752, *p* = 0.032) and did not differ from values for EC streams (*p* > 0.1). Volume tended to be higher in EC than in CO streams (*Z* = 2.55, *p* = 0.056). Comparing volume between pairs of stream orders revealed no significant differences. We did not test to see which order × foresttype combinations differed, but instead assumed that confidence intervals that did not overlap in Fig. 5 represented significantly different mean volumes. The pattern clearly differed between CO and EC or MP (Fig. 5). Unlike the pattern in MP and EC, 1st-order CO streams had significantly less volume than 2nd- or 3rd-order CO streams. Only MP streams had our hypothesized pattern of decreasing volume per unit area from 1st- to 3rd-order.

Table 1. Mean (±1 SE) proportion of burned pieces and frequency and volume of wood pieces in 2 size classes /m stream and /ha stream area in 1st- to 3rd-order streams flowing through managed eucalyptus (EC), maritime pine (MP), and cork oak (CO) forests in central Portugal following wildfires. *n* = 3 for each stream order × forest type combination.

				Diamet	er ≥ 0.05 m; leng	jth ≥0.5 m	Diame	ter ≥ 0.1 m; leng	th ≥1 m
Forest type	Channel width (m)	Stream order	Wood species	Proportion burned	Frequency (no./100 m)	Volume (m³/ha)	Proportion burned	Frequency (no./100 m)	Volume (m³/ha)
MP	2.04 ± 0.44	۲-	МР	0.9 ± 0.1	3.4 ± 2.5	8.62 ± 5.36	0.9 ± 0.1	1.9 ± 1.2	7.53 ± 4.35
			All species	0.8 ± 0.1	11.3 ± 5.1	27.44 ± 14.26	0.9 ± 0.2	5.4 ± 2.5	24.30 ± 13.23
	3.57 ± 0.92	2	MP	1.0	3.2 ± 1.7	5.38 ± 4.12	1.0	1.2 ± 1.0	4.37 ± 4.00
			All species	0.8 ± 0.1	9.9 ± 2.8	16.26 ± 7.01	0.9 ± 0.2	4.2 ± 2.4	14.12 ± 7.28
	5.33 ± 0.37	с	MP	1.0	0.2 ± 0.2	0.47 ± 0.47	1.0	0.1 ± 0.1	0.43 ± 0.43
			All species	0.5 ± <0.1	16.7 ± 2.5	10.16 ± 2.23	0.8 ± 0.1	5.3 ± 1.7	7.96 ± 2.30
	3.64 ± 0.57	1, 2, 3	MP	1.0 ± <0.1	2.3 ± 1.0	4.82 ± 2.29	1.0 ± 0.1	1.1 ± 0.5	4.11 ± 2.00
			All species	0.7 ± 0.1	12.6 ± 2.1	17.96 ± 5.28	0.8 ± 0.1	5.0 ± 1.1	15.46 ± 5.01
EC	2.22 ± 0.48	-	EC	0.8 ± 0.1	10.7 ± 5.9	14.33 ± 9.86	0.9 ± 0.1	0.7 ± 0.4	3.20 ± 1.60
			All species	0.8 ± 0.1	15.7 ± 6.2	26.09 ± 12.18	0.8 ± 0.2	3.5 ± 2.9	13.69 ± 10.11
	3.52 ± 0.62	2	EC	0.6 ± 0.2	1.4 ± 0.7	0.29 ± 0.13	Ι	0.0	0.00
			All species	0.7 ± 0.2	4.3 ± 2.4	1.86 ± 1.5	0.6	0.6 ± 0.6	1.01 ± 1.01
	7.69 ± 2.49	ю	EC	0.5 ± 0.3	1.3 ± 0.7	0.89 ± 0.74	0.5 ± 0.5	0.2 ± 0.1	0.71 ± 0.70
			All species	0.5 ± 0.1	12.4 ± 8.2	8.91 ± 6.14	0.5 ± 0.1	4.5 ± 3.5	7.59 ± 5.55
	4.48 ± 1.12	1, 2, 3	EC	0.7 ± 0.1	4.5 ± 2.3	5.17 ± 3.66	0.7 ± 0.2	0.3 ± 0.2	1.30 ± 0.70
			All species	0.7 ± 0.1	10.8 ± 3.5	12.29 ± 5.35	0.7 ± 0.1	2.9 ± 1.4	7.43 ± 3.81
CO	4.91 ± 1.26	-	CO	0.9 ± 0.1	1.9 ± 1.5	0.57 ± 0.47	1.0	0.6 ± 0.6	0.44 ± 0.44
			All species	0.8 ± 0.1	3.0 ± 1.8	0.76 ± 0.50	1.0	0.7 ± 0.6	0.52 ± 0.47
	4.83 ± 1.16	2	CO	0.9 ± 0.1	1.5 ± 1.1	0.35 ± 0.28	0.8 ± 0.2	0.5 ± 0.3	0.25 ± 0.20
			All species	0.6 ± 0.3	11.5 ± 5.3	7.83 ± 4.86	0.7 ± 0.3	2.5 ± 1.0	5.62 ± 3.52
	10.10 ± 1.64	ю	CO	0.6 ± 0.4	0.6 ± 0.5	0.02 ± 0.02	I	0.0	0.00
			All species	0.4 ± 0.2	14.5 ± 6.0	4.01 ± 2.52	0.5 ± 0.2	2.8 ± 1.1	2.64 ± 1.73
	6.61 ± 1.11	1, 2, 3	CO	0.8 ± 0.1	1.4 ± 0.6	0.32 ± 0.18	0.9 ± 0.1	0.4 ± 0.2	0.23 ± 0.15
			All species	0.6 ± 0.1	9.6 ± 2.9	4.20 ± 1.89	0.7 ± 0.1	2.0 ± 0.6	2.93 ± 1.36
MP, EC, CO	4.91 ± 0.59	1, 2, 3		0.7 ± 0.1	11.0 ± 1.6	11.48 ± 2.72	0.7 ± 0.1	3.3 ± 0.7	8.61 ± 2.30



Fig. 3. Mean (± 95% CI) % contribution of the tree species in the adjacent managed forest to the total volume of stream wood (A), and wood length:channel width ratios (L*) (B). n = 3 stream reaches surveyed (~500-m each) within each stream order × forest type combination (coded as order.forest type). Streams are 1st-, 2nd-, or 3rd-order. Forest types are cork oak (CO), eucalyptus (EC), or maritime pine (MP). The horizontal dashed line in (B) indicates a ratio of 1.

Table 2. Decay classes of wood pieces in streams with counts and percentages by forest type. Decay classes were adapted from Jones and Daniels (2008). Classes 1 and 2 were merged. Forest types were cork oak (CO), Eucalyptus (EC), and maritime pine (MP).

	Decay class					
Forest type	1 and 2	3	4			
CO	28 (7%)	177 (41%)	229 (53%)			
EC	25 (5%)	237 (49%)	225 (46%)			
MP	107 (19%)	233 (41%)	222 (40%)			
Total across forests	160 (11%)	647 (44%)	676 (46%)			



Fig. 4. Mean percentages of alignments of stream wood by stream order × forest type combinations (A) and by stream order (B). See Fig. 3 for codes. The alignment of each wood piece refers to the angle relative to flow direction: perpendicular = 90° , intermediate = other angles, parallel = 0° . Error bars are 95% confidence intervals.

Table 3. The fixed part of the optimal linear mixed-effects model predicting volume of stream wood following wildfires in central Portugal. Main effects are forest type (EC = eucalyptus, MP = maritime pine) and stream order (2, 3). SE = standard error, VIF = variance inflation factor.

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	$R^2 = 0.545$								
Variable	Estimate	SE	t	р	VIF				
Intercept	-0.328	0.407	-0.81	0.436					
EC	1.467	0.575	2.55	0.044	1.87				
MP	1.584	0.575	2.75	0.033	1.87				
2 nd order	0.868	0.377	2.30	0.040	4.00				
3 rd order	0.686	0.377	1.82	0.094	4.00				
2 nd -order EC	-2.136	0.533	-4.01	0.002	2.84				
2 nd -order MP	-1.055	0.533	-1.98	0.071	2.84				
3 rd -order EC	-1.425	0.533	-2.67	0.020	2.84				
3rd-order MP	-0.960	0.533	-1.80	0.097	2.84				

4.3.3 Effects on organization

Number of organized bins

The optimal GLMM showed that foresttype and order were the best predictors of the number of organized bins. Sslope also had a nonsignificant positive effect on organization (Table 4). The foresttype × order interaction, burnarea and fireyear were not significant and were dropped sequentially. Wood in CO streams was significantly more organized (more bin intervals that were significantly aggregated or segregated) than wood in MP streams (MCM, Z = -2.900, p =0.010). Wood tended to be more organized in CO than in EC streams (Z = -2.101, p = 0.086). Organization did not differ between MP and EC streams (p > 0.1). Organization was greater in 1st- than in 3rd-order streams (Z = -2.809, p = 0.013), but organization in 2nd-order streams did not differ from that in 1st- or 3rd-order streams (Fig. 6A).

Table 4. The fixed portion of the 3 optimal generalized mixed-effects models predicting the number of 10m bins with wood abundances suggesting an organized (nonrandom) distribution pattern. The 1st model includes the total number of organized bins as the response variable. The 2nd and 3rd models include the number of aggregated or segregated (wood absence) bins, respectively, as response variables. Main effects are forest type (EC = eucalyptus, MP = maritime pine), stream order (2, 3), and sslope (side slope for side bands of 50 m on stream reaches). VIF = variance inflation factors. Underlined values indicate the % deviance explained.

Variables	Estimate	SE	Z	Pr(> z)	VIF
Number of organized bins (18.2%)					
Intercept	2.769	0.193	14.33	<0.0001	
EC	-0.564	0.268	-2.10	0.036	2.84
MP	-0.875	0.302	-2.90	0.004	3.35
2 nd order	-0.102	0.144	-0.71	0.480	1.66
3 rd order	-0.361	0.128	-2.81	0.005	1.23
Sslope	0.550	0.322	1.71	0.088	3.48
Number of aggregated bins (39.4%)					
Intercept	0.961	0.377	2.55	0.011	
EC	1.210	0.442	2.74	0.006	3.30
MP	0.690	0.470	1.47	0.142	3.85
2 nd order	0.319	0.467	0.68	0.495	4.42
3 rd order	0.811	0.427	1.90	0.057	4.99
2 nd -order EC	-1.668	0.632	-2.64	0.008	2.50
2 nd -order MP	-0.258	0.583	-0.44	0.658	4.45
3 rd -order EC	-1.910	0.576	-3.31	<0.0001	2.59
3 rd -order MP	-0.876	0.559	-1.57	0.117	3.73
Number of segregated bins (38.6%)					
Intercept	2.857	0.256	11.18	<0.0001	
EC	-1.232	0.413	-2.98	0.003	1.84
MP	-0.721	0.388	-1.86	0.063	1.55
2 nd order	-0.281	0.210	-1.34	0.179	2.37
3 rd order	-0.879	0.254	-3.46	<0.001	2.83
2 nd -order EC	0.723	0.368	1.97	0.049	2.64
2 nd -order MP	-0.338	0.393	-0.86	0.391	1.65
3 rd -order EC	1.515	0.387	3.92	<0.0001	3.21
3 rd -order MP	-0.433	0.497	-0.87	0 384	1 52

Models for aggregation and segregation evaluated separately were similar. In both cases the sslope term was dropped and the foresttype × order interaction remained, indicating that effects of stream size differed among foresttypes (Table 4). CO streams had fewer aggregated bins than EC streams (Z = 2.737, p = 0.031), probably because of a difference in the number of bins with significant aggregation in EC 1st-order streams (Fig. 6B). CO streams had an increase of

wood aggregation from 1st- to 3rd-order streams. CO streams had more segregated bins than EC streams (Z = -2.984, p = 0.016). First-order streams had more segregated bins than did 3rd- order streams (Z = -3.464, p = 0.003).Within CO and MP foresttypes, the number of segregated bins was higher in 1st- than in 3rd-order streams.



Fig. 5. Mean (± 95% CI) fitted values for the optimal mixed-effects model predicting volumes of stream wood by stream order × forest type combination. See Fig. 3 for codes.



Fig. 6. Mean (± 95% CI) fitted values for the optimal mixed-effects models predicting the number of 10-m bins having stream wood in an organized (nonrandom) distribution pattern (A) and number of bins having aggregated or segregated distributions (B).

4.4 Discussion

4.4.1 Across-system variability

Wood volume per area and distribution patterns differed among forest types. CO streams had the least wood, but in the most organized pattern, a result reflecting either lower inputs or greater mobility of wood. Only CO streams had the expected pattern of increasing aggregation with increasing stream size, a result that suggests a higher mobility of stream wood in CO than in other stream types. The highest contrast in wood volume was between CO and MP. MP streams had more wood in a less organized pattern of distribution. Both systems shared a clear decreasing trend of segregated areas (with less wood than expected by chance) from 1st- to 3rd- order streams. EC streams were intermediate between CO and MP streams, but were more similar to MP than to CO streams in regard to volume, organization, and aggregation/segregation. EC streams differed from CO and MP streams by having the most complex patterns of volume and organization across stream sizes and the highest dispersion for their fitted values.

4.4.2 Drivers of across-systems variability

Volume and organization were not affected by side slope, burn year, or proportion of the drainage area burned. Below, we discuss 4 potential drivers of across-system variability: vegetation obstructions, L*, management actions, and fire effects.

Within-channel vegetation obstructions and L*

Within-channel living woody vegetation traps and hinders transport of stream wood. The patterns of segregation in CO and MP (decreasing from 1st- to 3rd-order streams) were consistent with our field observations. Wood segregation was more common in streams with more woody vegetation growing in the channel, particularly in channels with intermittent flow. We recommend quantifying within-channel extensions of terrestrial vegetation in future studies of wood dynamics in intermittent streams.

L* is recognized as a primary control on stream wood stability (Haga et al. 2002, Abbe and Montgomery 2003, Cadol and Wohl 2010, Merten et al. 2010, 2011) and can be considered in conjunction with organization when evaluating the probable interaction between input and transport in a stream (Kraft et al. 2011). Within CO streams, mean L* < 1 favored transport-based control (Swanson 2003) of wood distribution, an interpretation that also is suggested by increasing aggregation with increasing stream size. In contrast, in smaller streams in timber-production forests (EC,MP), especially 1st-order EC streams, L* > 1 favored organization dominated by input processes rather than transport. Wood orientation affects its exposure to hydraulic forces (Merten et al. 2010) and, thus, its propensity for transport. The high proportion of wood oriented at intermediate angles in 1st-order EC streams reinforced their input-based dynamics. The high proportion of wood oriented parallel to flow in larger streams suggested

repositioning by fluvial forces. The proportion of wood oriented perpendicular to the flow was constant across stream sizes. These pieces may not have been transported yet.

Management and effects of fire

Human activities influenced the kinds of wood input in CO and EC. In CO, branch pruning and salvage logging reduced wood input, and mostly smaller pieces of wood ($L^* < 1$) entered streams (Vaz et al. 2011). In CO streams, obstruction of flow by vegetation favored segregation of wood in some reaches, whereas management in other reaches promoted $L^* < 1$ and, thus, transport and aggregation. For instance, 1^{st} -order CO streams had the lowest volumes per stream area and the highest organization of stream wood. Thus, vegetation obstructions and management probably were the main drivers of the unexpected values for this stream size. Because of their limited riparian zones and low side slopes, 1^{st} -order CO streams also were more exposed to external disturbances (e.g., stream wood removal, forest roads, mechanical cutting) than larger CO streams.

A wider range of intensity of human activity, varying from postfire abandonment (similar to MP) to active management near streams (similar to CO) occurred in EC streams. Unlike in CO systems, where management activities were consistent, postfire management actions in EC forests varied across the region and probably yielded different effects on stream wood (see Thomas et al. 2000). Over the long term, stream clearing and clearcutting in EC stands caused depletion of stream wood and reduced wood inputs. The variability of management situations between EC systems is reflected in the lack of pattern in wood volume per stream area or organization and the greater dispersion of values across stream sizes.

Forest management affects the amount and size of wood in a river. In general, forest management, especially riparian logging, reduces total stream wood storage and increases wood mobility (Gurnell 2003, Mellina and Hinch 2009). However, this generalization was not applicable under the complex forestry scenarios we examined. We assumed that forest management in our systems would lead to straightforward reductions in wood recruitment with associated increases in wood movement and subsequent wood organization. However, wood dynamics are not that simple in our study systems, and we found important interactions between managed forest type and stream size. If hydraulic processes associated with stream size dominated wood dynamics, stream order but not forest type should have been significant in our models. However, forest management and postfire activities differed among the 3 forest types and, to some degree, among stream sizes. These differences led to different wood input rates and different wood characteristics (Vaz et al. 2011) and, thus, to variability in total wood volume and movement potential among stream sizes within a forest type. Euro-Mediterranean forestry is best understood from a total-human-ecosystem perspective (Naveh and Lieberman 1984), where single-species stands are often characterized by different silviculture practices. Thus, stream-size × forest-type interactions are key factors affecting stream wood dynamics.

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The legacy of the 2003–2007 wildfires was highlighted by our finding that 70% of stream wood per reach was burn. Burned stream wood is straighter, has fewer branches, is more decayed, and is larger than unburned wood in these systems (Vaz et al. 2011). Over time, these differences are likely to become more pronounced, except that stream wood should become smaller because of decay and breakage (Hassan et al. 2005). Decay rates of stream wood should be greater in our study systems than in systems where stream wood remains waterlogged because stream drying in summer exposes wood to aerobic conditions in this region (Suberkropp 1998). During wet periods, hydraulic forces also may break or abrade weakened burned wood into smaller transportable pieces. We expect burned stream wood volume to decrease as future inputs diminish. Smaller pieces will then be governed by greater transport, leading to increasing organization of burned wood distributions. The overall structure of stream wood is strongly influenced by wildfire, but the effect may be obscured by among-system variability in species characteristics and management (Vaz et al. 2011).

Little research has addressed effects of wildfire on the organization of wood in streams despite the important effect of fire on forest cover and, thus, wood input, mobility, and distribution (Marcus et al. 2011). Our prediction that the organization of stream wood will reflect its increased mobility over time is in line with results of previous studies. Minshall et al. (1997) reported that 2 to 53 more stream wood than usual moved in burned 1st- to 3rd-order streams after fires in Yellowstone National Park. Young (1994) found that wood was more likely to move in a watershed that burned in 1988 than in an unburned watershed. This finding was confirmed 11 y after the fires by Zelt and Wohl (2004). Additional research is needed to fully test our prediction.

4.4.3 Low quantities of stream wood

Compared to values reported in literature reviews of wood in unmanaged river corridors (Gurnell 2003) and in catchments highly modified by human activities (Elosegi and Johnson 2003), the volumes of stream wood in our study systems are extremely low. Volumes in our study streams are similar to the lowest values published by Gregory et al. (1993) for the Lymington River basin (0.6–50 m³/ha) and Richmond and Fausch (1995) for streams in a harvested forest in the Rocky Mountains, USA (12.0–147 m³/ha). Volumes reported by Hauer (1989) for streams in a mixed landuse catchment recovering from discharges from nuclear reactors in South Carolina, USA (2 m³/ha) are of the same magnitude as those in CO streams (2.93 m³/ha). Stream wood volumes in the Agüera basin in northern Spain (Diez et al. 2001) are much greater than volumes in central Portugal. Even the values reported by Diez et al. (2001) for 1st-order agricultural streams (2 m³/ha) are greater than the volumes in our 1st-order CO agro-forestry systems (0.76 m³/ha). Frequent disturbance by fire and forest management might be the cause of the exceptionally low volumes in east-central Portugal. These disturbances favor the presence of young riparian trees with small diameters (mean diameter of stream wood in our study was 9 cm; PV, unpublished data).

4.4.4 Looking ahead

Patterns in stream wood stocks still reflect the 2003–2007 wildfires and are likely to retain a strong fire signal for years to come. After the 1988 Yellowstone fires, Romme et al. (2011) noted that stream wood recruitment reached its maximum 20 y postfire in smaller streams, wood patterns varied with stream size, and depletion of wood differed from stream to stream. In our study, the volume of stream wood is still dominated by burned wood and organization is low, results suggesting that the current arrangement of wood is largely a product of input dynamics rather than transport processes. We expect a similar pattern of future postfire stream wood that varies with stream size, but with high across-system variability. Conversely, most fire-killed snags in the riparian zone of our streams were in advanced decay and are likely to fall soon (PV, personal observation), an observation suggesting that peak wood inputs associated with the 2003–2007 fires are likely to occur sooner than 20 y postfire. We expect burned stream wood to disappear soon because of rapid breakdown and decay, even though transport is limited. Overall, burnt stream wood probably is more ephemeral in Euro-Mediterranean intermittent streams than elsewhere.

Wildfires are natural in the Euro-Mediterranean region, and the ability to recover to a prefire state is quite high in burned forests of CO and EC (and even MP). However, several studies suggest a decrease in forest resilience as higher frequencies of wildfires and droughts (Acácio et al. 2009) change areas from forests to shrubland (Diaz-Delgado et al. 2002, Acácio et al. 2007). In the Mediterranean Basin, these landscape changes have been accompanied by abandonment of land by people (see Sluiter and Jong 2007). As a consequence, many previous production forests that burned are now shrubland dominated by species that naturally resprout following fire (Pausas 1999). Under this scenario of shrubland expansion, the contribution of adjacent forest types to stream wood loadings should decline (a prediction that is in line with our low values) and wood inputs should become more dependent on riparian communities.

Dynamics of stream wood in Mediterranean Basin streams will be strongly influenced by future climate conditions. Projections indicate that fires will become increasingly frequent in the coming decades because of changing global climate and anthropogenic activities (Moriondo et al. 2006, IPCC 2007, Flannigan et al. 2009). Stream flows have decreased in the last 40 y in southern Europe (Stahl et al. 2010). On the Iberian Peninsula, the decrease in stream flow is likely to accelerate in the coming decades because climate projections show a decrease in precipitation and more evapotranspiration induced by higher temperatures (Lorenzo-Lacruz et al. 2012). As stream flows decrease, upland plants will encroach on the channel (see Santos 2010), and stream energy to mobilize, export, and organize wood will decline. Plants will have greater access to water in the hyporheic zone of the stream. Reductions of water in the hyporheic zone can cause major shifts in hydrological dynamics (Huxman et al. 2005), including greater frequency of intermittent flows. Overall, shrubland encroachment probably will promote the absence of large wood over large areas of stream ecosystems. Habitats in such streams are particularly sensitive to changes in stream wood loading, and the full implications of reduced

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amounts of stream wood are unknown but potentially far-reaching for many taxa and life stages of aquatic organisms (Dolloff and Warren 2003). In small, drought-prone streams, such as those in CO forests, large wood may provide the only refuge during low flows, making stream wood particularly important to stream biota in the years to come.

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Which stream wood becomes functional following wildfires?

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5. Which stream wood becomes functional following wildfires?

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Abstract: Large wood is a critical element in stream ecosystems, but only a subset of wood pieces actually provide hydraulic, geomorphic, and ecological functions. We test the current paradigm that larger pieces provide more function, and examine the role wildfires may play in affecting functionality of recruited wood. We conducted a cross-basin analysis in nine central Portugal watersheds, obtaining a variety of measurements on 1483 wood pieces (diameter ≥ 0.05 m; length \geq 0.5 m) in 27 streams burned within six years prior. We examined nonlinear relationships and indirect effects on function using Generalized Additive Modeling and Structural Equation Modeling. Variables with direct effects on function were piece diameter, rootwads, anchoring, position (bridging, ramping, loose), longitudinal distance along the stream continuum, and the ratio of piece length to channel width. The effect of length ratio on function was nonlinear. Relatively long pieces were more likely to be functional until they were ~3 times the channel width, at which point longer pieces became less likely to be functional. Post-fire wood likely lacked complexity and longer pieces were more likely to be bridging; both conditions may have prohibited them from interacting with the wetted area. Wildfires had indirect effects on function. Burned pieces were more likely to be large in diameter (thus more likely functional) but not anchored (thus less likely functional); these antagonistic effects may be the reason burned status had no direct effect on function. Our results challenge the well-established idea that the function of wood in streams is simply a matter of wood size, along with indicators of longevity (e.g. stability and decay status). Relatively long pieces may in fact provide less function to the

stream, at least until they break or are transported further downstream. Practitioners installing wood to streams should consider pieces with wide diameter and rootwads, approximately 3 times the channel width, and anchored but not bridging the channel.

Keywords: emulating natural processes; Euro-Mediterranean; fire; function; large wood; stream restoration.

5.1 Introduction

Large wood is widely recognized as an important structural element in stream ecosystems, but only a subset of wood pieces actually influence stream hydraulics, channel morphology, sediment and organic matter retention, flow routing and storage, habitat heterogeneity, and biological communities (Gregory et al., 2003 and references therein). We refer to such pieces as functional; that is, performing some observable function in the stream. Major knowledge gaps remain regarding the recruitment of functional large wood, including the influence of disturbance history such as riparian fires (Nakamura and Swanson, 2003). In this study, we evaluated which wood pieces have a high probability of becoming functional in streams following wildfire.

Broadly, the fact that fire affects stream wood input has been well documented and is apparent in the stock of burned wood in streams following a fire (Zelt and Wohl, 2004). In addition to the direct effects on tree mortality and associated wood recruitment, fire may also promote wood recruitment indirectly by increasing the susceptibility of riparian trees to windthrow and disease (Benda et al., 2003). Wood affects stream features, redirects flow, and traps other wood moving through the system only if it remains stable and is of sufficient size and shape (Abbe et al., 2003). Quantification of functional wood is rare and the effects of wildfire on stream wood function (rather than overall stock) remain largely unexplored.

Over the past several decades, various studies have identified functional roles of stream wood (SW), but only a few characterized the functional wood itself. Most studies have focused on the relationship between SW quantity and channel structure (Thompson, 1995; Manga and Kirchner, 2000; Chen et al., 2008). However, the characteristics of individual pieces can also affect SW function in small streams (Rosenfeld and Huato, 2003). Studies on SW function have separately focused on particular categories: geomorphological, ecological, and hydraulic function. However, it is difficult to isolate such functions, since a single piece of wood can cover all three categories. Cordova et al. (2007), for example, documented up to five functions for one piece of SW. Rather than splitting SW functions into specific sub-categories in the current study, we consider any piece of wood having at least one function recognized in the literature and directly observed in the field to be functional (Montgomery et al., 2003).

Determining stream wood function requires knowledge of both the quantity and "quality" of individual pieces. SW quality depends on critical functional factors such as its physical structure (Vaz et al., 2011), its local position relative to the stream channel, its interaction with other wood, its distance along the stream, and its location throughout the river network (Martin and Benda, 2001; Jones et al., 2011). Among the structural characteristics of SW, there is a set of core variables that interact with the stream to influence wood function (Gregory et al., 2003; Bocchiola et al., 2006; Wohl et al., 2010). Major structural factors that may influence SW function are piece diameter, presence of rootwads and branches, decay state, form, and piece species. Elements of the SW relationship with a stream channel include wood length/channel width ratio, how it rests within the channel (position), degree of anchoring, and horizontal

orientation (Braudrick and Grant, 2000; Chen et al., 2008; Cordova et al., 2007; Baillie et al., 2008; Magilligan et al., 2008; Jones et al., 2011). In an earlier study, we documented that burned wood recruited to streams following a fire generally was thicker, had less structural complexity, and was more decayed than wood that was not burned (Vaz et al., 2011). This suggested that SW burned status, while affecting size, geometry, and overall stability, will also likely influence the effect of SW on stream physical processes. In the current study, we incorporated SW burned status with a large suite of potential functional factors and evaluated how they interact to influence stream function.

A few studies have examined relationships between observable functions of a particular category and SW characteristics. For example, probability of pool habitat formation increases with SW diameter and presence of rootwads (Braudrick and Grant, 2000, 2001; Magilligan et al., 2008), and Beechie and Sibley (1997) identified a minimum-diameter threshold below which SW is unlikely to initiate pool formation. In addition, decayed SW contributes more to bank stability, sediment retention, debris jams, and riffle and pool formation (Jones et al., 2011). Abbe and Montgomery (2003) found that wood longer than half the bankfull width could initiate logjams. Only one study (Rosenfeld and Huato, 2003), specifically evaluated the probability of individual SW pieces becoming functional, although the dataset did not capture functions beyond the creation of primary pools.

In this study, we propose an initial framework for using SW critical factors (regarding physical structure and relation to the stream channel) to assess its functionality in streams following wildfire. We conducted a cross-basin analysis in nine central Portugal watersheds, obtaining a variety of measurements on 1483 individual SW pieces in 27 streams burned within six years prior. Large SW amounts within these streams are remarkably low (3.3 pieces per 100 m), and so functional wood acquires additional importance (Vaz et al., 2011, 2013). This work encompassed a range of stream sizes and upland land-uses, including three common fire-prone forest types in southern Europe. We addressed the following objectives and associated hypotheses:

- (1) Determine SW critical functional predictors and quantify their influence on the probability of stream function following wildfires. Hypothesis: As we had a broad criteria capturing observable SW functions, we expect that major SW critical factors (such as diameter, presence of rootwads or branches, decay state, degree of anchoring, and piece length/channel width ratio) will significantly influence the probability of a given piece being functional following wildfires.
- (2) Determine how SW critical functional predictors and burned status interact to influence stream function. Hypothesis: As burned status influences SW size positively and complexity negatively (Vaz et al., 2011), we expect no clear direct relationship between SW burned status and function. Instead, we hypothesize that burned status will likely affect stream function indirectly through relationships with SW critical functional predictors.

This knowledge is essential for assisting resource managers in maximizing the effectiveness of riparian management (e.g. selective harvest, thinning) and stream wood installation to mimic natural processes and restore ecological functions.

5.2 Materials and methods

5.2.1 Study area and site selection

We conducted this study in east-central Portugal (39°16' to 39°39'N, 7°30' to 8°14'W) from October 2009 to August 2011 in nine sub-basins of the Tagus River, which experienced extensive wildfires between 2003 and 2007. The area has gentle relief with altitudes ranging from 19 to 643 m (mean ~266 m). The land cover is dominated by forests, shrublands, and agriculture. The local climate is Mediterranean with hot, dry summers and cool, wet winters. Mean annual precipitation is 512 mm (range: 3 mm in July to 82 mm in November) and mean annual temperature is 15.8 °C (range: 9 °C in December–January to 23 °C in July–August). The selected burned sub-basins (mean drainage area 59 km²; range: 26–143 km²) represented three dominant forests in Portugal – eucalyptus (*Eucalyptus globulus*), maritime pine (*Pinus pinaster*), and cork oak (*Quercus suber*). Within each sub-basin, three homogeneous reaches (~500 m each) having a burned sideband of at least 100 m were selected, one each from stream order 1–3 (Strahler, 1957). We selected reaches distributed as evenly as possible from stream sources to mouths across the 27 streams. In total, 27 burned reaches were assessed, totaling ~13,460 m of stream channel. Many of the streams were intermittent, with stretches remaining dry for several months, in a seasonal sequence of flooding and drought events.

Riparian zones (with a distinct riparian community) along streams in maritime pine and eucalyptus forests were often present (0–15 m in width) but cork oak sub-basins generally had more limited riparian zones. The uncultivated riparian vegetation was dominated by ash (*Fraxinus angustifolia*), alder (*Alnus glatinosa*), black poplar (*Populus nigra*), and willow (*Salix atrocinerea*, *S. alba*, *S. salvifolia*), frequently surrounded by edges of bramble-thicket (*Rubus ulmifolius*). In most southern areas, hawthorn (*Crataegus monogyna*) was also common. In addition to the indigenous species, silver wattle (*Acacia dealbata*), an exotic invasive and fire-prone tree, was widespread across the surveyed riparian zones (Silva et al., 2011). Further details about the study area are provided in Vaz et al. (2011).

5.2.2 Data collection

Each study site included one representative 500 m reach where we measured dead downed wood pieces (diameter ≥ 0.05 m; length ≥ 0.5 m) and those that were still alive but entirely uprooted. We excluded snags, following Young et al. (2006), defined as pieces leaning or suspended over the stream at an angle greater than 30°. In wood jams (>2 pieces), we measured pieces that were accessible and whose functions were not influenced by the

functions of other pieces. Three larger wood jams (>10 and <50 pieces) were present in 3 reaches. Only downed SW extending within bankfull boundaries were included in the tallies.

We measured channel widths every 10 m (~51 widths per reach) using a laser meter (precision: 1 mm) and a target. Exposed rooted vegetation was observed to retain SW in our stream reaches. Consequently, we measured only the unobstructed channel width, i.e. the portion of the channel width available to transport wood unimpeded, every 10 m for each study reach. We defined channel obstructing vegetation as rooted stems at least 3 cm diameter within the bankfull channel, and measured the widest unobstructed channel width in regards to potential wood transport. When no obstructing vegetation was present, we recorded the distance across the stream between bankfull channel margins. At the reach scale, mean channel widths ranged from 1.34 to 12.75 m and bed slopes ranged from 0.02 to 7.80%.

We recorded the following SW characteristics:

- (i) Burned status of the SW piece was assessed following Jones and Daniels (2008), using three classes (unburned: no char; moderately: charred bark but outermost ring present in at least one part of the circumference; heavily: charred bark and sapwood resulting in significant ring loss);
- (ii) Source tree (maritime pine, eucalyptus, cork oak, or "riparian species") was identified by assessing morphological characteristics of the wood piece;
- (iii) Length in meters was determined to the nearest 0.2 m for the segments of the pieces that were >1 cm in diameter. We measured length using a meter tape for pieces >6 m long, and estimated length for pieces <6 m (verified for the first 20 pieces per reach);</p>
- (iv) Diameter was determined to the nearest 0.5 cm by a single measurement taken from a point considered the mean diameter by visual assessment. For pieces >15 cm diameter, we measured using a meter tape; for pieces <15 cm, we estimated (verified for the first 20 pieces per reach);
- (v) Decay of the SW piece was assessed using the four classes proposed by Jones and Daniels
 (2008) (evaluating bark, branches, and overall structural integrity);
- (vi) Class of the SW piece form (straight; bent; strongly bent);
- (vii) Presence of rootwads (yes/no);
- (viii) Presence of branches (yes/no).

We recorded the following metrics, quantifying SW relationships with the stream channel:

- (i) Horizontal orientation of each SW piece, starting upstream, parallel to the thalweg direction, and rotating clockwise (0°, 30°, 60°, 90°, 120°, 150°);
- (ii) Position of the SW on the stream (bridge: log spans channel, touching both banks and resting on the floodplain; loose: resting entirely on the streambed; ramp: resting on one bank only). Due to sample size, 54 wood pieces forming collapsed bridges were reclassified as ramps;
- (iii) Anchoring (number of ends or sides attached or buried in either the bank or the stream: 0–4);

- (iv) Wood length/channel width ratio per wood piece was derived from its length divided by the nearest channel width;
- (v) Percent distance of the wood piece along the stream. The center of each piece was georeferenced with a GPS unit (whenever possible, with a 0.3–1 m precision by postprocessing). The GPS reading was taken for 30–60 s and the average recorded then converted to a distance along the stream thalweg and then to percentage (0% = stream source; 100% = stream mouth).

The function of each piece of SW was assessed with respect to its role in deflecting flow (e.g. creating pools or riffles, forming steps), retaining bedload or sediment (sediment wedge >2 cm deep and >40 cm wide), armoring banks (e.g. protect bank from erosion, maintaining bank stability), creating debris jams (braced other wood or serving as a key piece in wood jams), retaining organic matter (twigs, leaves, fine organic matter; observable volume > $\sim 10^{-3}$ m³), or serving as a substrate to aquatic vegetation, periphyton, and/or epixylic biofilms (submersed wood with a conspicuous biofilm layer) or to conspicuous ovipositions (e.g. of amphibians). This variable was ultimately reduced to simple binary criteria: with/without function.

5.2.3 Data analysis

Critical predictors to the stream wood function

Relationships between the presence of observable functions of stream wood (function) and explanatory variables was explored using Generalized Additive Models (GAM; Wood, 2006; Zuur et al., 2009), thereby accounting for potential non-linearities in function responses. Because function was binary (wood piece with or without function), we used binomial GAM with a logit link. A matrix of Spearman's correlations for initial explanatory variables revealed that burned status was significantly correlated with decay (r = 0.404, p < 0.001) and was excluded from GAM analysis, since a frequency analysis revealed no (direct) association of burned status alone and function. Correlations between the remaining variables used in the model were all <[0.30], indicating that there were no collinearity problems. Prior to statistical analysis, diameter was log-transformed to approach normality and to reduce the influence of a few large values. For the analysis, decay, presence of rootwads, presence of branches, and horizontal orientation were treated as factors. Since collected data were nested within 27 stream reaches, we compared GAM and Mixed-GAM (with stream reach as a random factor), and chose the first as it had the lowest value for Akaike Information Criterion ($\Delta AIC = 5258$). All calculations were carried out using R (R Development Core Team, 2009). The mgcv package (Wood, 2006) was used to fit GAM, using penalized regression splines with the optimal amount of smoothing estimated by unbiased risk estimator (UBRE). We defined the basis dimension (k = 5) to allow some complexity in the functions, while avoiding over-fitting the data.

The modeling procedure involved the fitting of the full model, with the six SW characteristics and the five relationships with the stream channel defined above, followed by backward elimination of non-significant (p > 0.05) variables (Zuur et al., 2009). Model fit was evaluated by the proportion of the null deviance explained.

SW burned status and critical predictors to the stream wood function

We used structural equation modeling (SEM; Arbuckle, 2010) to separately examine the linkages between significant factors in GAM plus SW burned status related to *function*. Additionally, SEM allowed us to highlight indirect effects not revealed by GAM. Using the software IBM SPSS Amos[™], a path diagram was constructed first based on theory using the exogenous variables for each wood piece. Error terms were added as needed, and regression weights were examined to iteratively add (based on modification indices) or remove (based on p-values) linkages from the model. Once a good model fit was achieved, based on both the minimum discrepancy (Browne, 1984) and the root mean square error of approximation, *function* was added as a categorical endogenous variable with linkages from all other variables. Bayesian estimation was then used on the retained paths to fit the model, and linkages to function were iteratively removed based on the posterior distributions of the regression weights. Linkages were removed if their 80% credible interval did not include zero (considered supportive of a model derived from maximum likelihood procedures). For the SEM analysis, SW position was reduced to simple binary criteria: bridge/non-bridge.

5.3 Results

5.3.1 Critical predictors to the stream wood function

Overall, 53.1% of the 1483 pieces of stream wood were deemed to have a function in our surveys, and 51.8% of the burned wood subset was functional (Table 1). Evaluation of the significance of variables resulted in the sequential dropping of branch presence, horizontal orientation, decay, form, and source tree. The resulting model is shown in Table 2 and Fig. 1. The significant SW characteristics were diameter and presence of rootwads. The probability of function increased on pieces of greater diameter and the same trend was found for pieces with rootwads.

Table	1.	Counts	of	stream	wood	pieces	(diamete	er ≥ 0.05 n	n; total	leng	th ≥ 0.5 m)	with/w	ithout func	tions
detect	ed	during	the	fieldwo	ork by	burned	status	(unknown	refers	to in	conclusive	visual	assessme	nt of
burned	l st	atus). V	'alu	es repre	esent p	ieces in	iterceptii	ng the ban	kfull.					

Stream wood function	Number of stream wood pieces by burned status					
	Unburned	Moderately burned	Heavily burned	Unknown		
Function not detected	272	238	118	66	694	
With functions detected	303	214	168	104	789	
Total	575	452	286	170	1483	



Fig. 1. Generalized additive model fits and 95% pointwise confidence bands from the optimal model, illustrating the different relationships between probability of function of stream wood pieces and each explanatory variable: diameter (a), wood length/channel width ratio (b), distance long the stream in percentage (c), presence of rootwads (d), position (e), and number of anchoring sides. Estimated degrees of freedom are given parenthetically in the y-axis label.

Table 2. Model obtained for explaining presence of stream wood function by piece characteristics and its relationship with the stream channel (binomial GAM with a logit link). Variables included are presence of rootwads, position on the stream (bridge, loose, ramp), degree of anchoring (anchor = 0-4), piece diameter, distance along the stream, and wood length/channel width ratio (Iratio). Deviance explained = 19.7%, UBRE score = 0.13, edf = effective degrees of freedom.

Parametric coefficients	es	stimate	z-value	Pr(> <i>z</i>)
(intercept)	-3.	21±0.35	-9.23	<0.0001
factor(rootwads)yes	0.	58±0.26	2.27	0.023
factor(position)loose	2.	75±0.25	11.01	<0.0001
factor(position)ramp	1.	77±0.21	8.47	<0.0001
factor(anchor)1	0.	85±0.30	2.84	0.004
factor(anchor)2	1.	83±0.30	6.15	<0.0001
factor(anchor)3	2.	79±0.34	8.09	<0.0001
factor(anchor)4	5.	09±1.08	4.71	<0.0001
Smooth terms	edf	Chi.so	9	<i>p</i> -value
s(diameter)	1.40	29.20)	<0.0001
s(<i>Iratio</i>)	2.52	12.88	3	0.006
s(distance)	3.83	24.48	3	<0.0001

Regarding SW relationship with the stream channel, the significant variables were anchoring, position, distance along the stream, and length/channel width ratio. Wood pieces with more anchoring sides in either the bank or the stream had a higher probability of having a function. Concerning position, wood resting entirely on the streambed (loose) had a higher probability of having an observable function, followed by pieces resting on one bank only (ramp), and finally, pieces spanning the channel, touching both banks and resting on the floodplain (bridges) had the lowest probability of performing a function. As for distance, pieces at both beginning and ending of streams tended to have a similar lower probability of function; this probability was higher in the second half of streams, reaching a peak at ~3/4 of the stream length. Finally, wood longer than ~3 times the channel width tended to have a decreasing relationship with probability of function.

5.3.2 SW burned status and critical predictors to the SW function

A variety of linkages were present among variables (Fig. 2), and the factors that affected function directly were the same as those identified by the GAM. In addition to the direct effects, several indirect effects (those connecting predictor variables) were identified where the variable's effect on function was mediated by another variable. We highlight that SW burned status indirectly affected function positively through an effect on diameter. Moreover, burned status had a negative effect on anchoring, which, in turn, affected function positively. All linkages retained in the model had coefficients with a 90% credible interval, except length ratio, for which we used our cutoff of 80%. The final structural equation model had a posterior predictive p = 0.42 – indicating a good fit (Lee, 2007) – and was advantageous in identifying both unique and synergistic contributions of function predictor variables.



Fig. 2. Final structural equation model using Bayesian estimation to determine variables affecting function of instream wood pieces. Variables included are presence of rootwads, position on the stream (bridge/non bridge), degree of anchoring (anchor = 0-4), piece diameter, distance along the stream, and wood length/channel width ratio (Iratio). Gray: variables concerning wood relationship with the stream channel; black: SW characteristics. Arrows represent causal pathways from predictor to response variables. The sign associated with each arrow indicates whether the relationship is positive or negative for the unstandardized partial regression coefficient for that direct effect.

5.4 Discussion

The success of management initiatives to offset the long-term effects of wildfire on stream ecosystems will depend on understanding which wood fallen from burned riparian trees will tend to be functional in the river system and which will not. This study determined that – as hypothesized – burned status had the potential to influence wood function indirectly. Specifically, burned wood affected diameter positively and degree of anchoring negatively, with both relating positively to the probability of function. Overall, functionality of stream wood in this study was influenced directly by four factors concerning the relationship with the stream channel and two factors concerning SW structural characteristics. By specifically quantifying functional wood and how critical predictors influenced the probability of function, our results allow more robust recommendations for improving riparian management techniques, particularly in fire-prone landscapes.

5.4.1 What wood structure favors function within streams?

Our study clearly demonstrated that stream wood functions were more likely for pieces thicker in diameter or with an attached rootwad. We suggest that these characteristics are relevant for a broad spectrum of SW functions, including their well-established role on the probability of pool formation and as primary controls on the stability of SW (Beechie and Sibley, 1997; Braudrick and Grant, 2000, 2001; Martin and Benda, 2001; Baillie et al., 2008; Magilligan et al., 2008). Piece diameter and the presence of rootwads (raising the center of mass of a piece) strongly influence the depth of flow required to entrain and transport logs (e.g. Bilby and Ward, 1989; Braudrick and Grant, 2000, 2001; Abbe et al., 2003), therefore likely influencing the prevalence of acquired functions. Owing to frequent forest disturbances by fire and management in this region, favoring the presence of young riparian trees with small diameters (Kreutzweiser et al., 2005), we found our results for SW diameter especially noteworthy. Although we were not able to measure bankfull depths, they greatly exceeded the average SW diameter (9 cm; P. Vaz, unpublished data), with consequences for transport and function. When considering eventual management initiatives, the inclusion of large wood, less common across these systems, acquires additional importance for stream function.

Our dataset has been used elsewhere to examine in detail stream wood physical structure in terms of burned status (Vaz et al., 2011). Among other structural differences, we concluded that, relative to unburned SW, burned wood was thicker in diameter and was more decayed. Here, we reiterate the trend for diameter and suggest that the effect of fire providing wood with greater diameter will also increase its probability for stream functions. On the other hand, among the potential SW critical factors, we found it striking that decay state had no significant effect on the probability of function given its importance in other systems. For example, Jones et al. (2011) found that less-decayed wood contributed less geomorphic functions in 21 streams in Alberta, Canada. A peculiarity of the SW across our 27 streams in central Portugal is that 90% was decayed (classes 3 and 4 adapted from Jones and Daniels, 2008) and that decay was positively associated to burned status (Vaz et al., 2011, 2013). Interestingly, if burning wood substantially increases the susceptibility of SW to decay, the functionality of wood amplified by greater diameters following fires may not persist.

5.4.2 How and where is wood more functional within streams?

This study contributed specifically to a better understanding on how and where wood should be located within a stream to be functional. Although prior works have recognized possible influences on functionality (Abbe et al., 2003; Montgomery et al., 2003; Cordova et al., 2007; Baillie et al., 2008; Magilligan et al., 2008; Jones et al., 2011), few specific guidelines exist as functionality has rarely been quantified. Also, we have shown that burned wood led to a reduction in anchoring, which corresponds to our expectations given that burnt pieces are straighter and less likely to have branches (Vaz et al., 2011). Another possibility is that less anchoring of burned wood reflected their recent arrival to the river system (<6 years). In general,

the degree of anchoring favoring functionality agrees with previous research stating that more stable wood has more influence on channel morphology (Jackson and Sturm, 2002; Andreoli et al., 2007; Comiti et al., 2008), since partial burial may be the single most important determinant of stability (Merten et al., 2010). Overall, the negative effect of fire on anchoring causes an indirect negative effect of fire on function, the opposite of the indirect effect mediated by diameter. On balance, the lack of a direct effect of fire on SW function is not surprising, given these opposing effects.

Concerning how SW rests within the channel, our finding that wood forming bridges tended to be less functional is in line with previous research from Jones and Daniels (2008). However, that study found the same trend for wood loose on the streambed, which is in marked contrast with our results where these pieces were the most functional. The discrepancy may be because Jones and Daniels (2008) focused on morphological functions, while we considered a wider range of functions. In fact, we estimate that ~50% of functional wood resting entirely on the streambed (loose) was performing biological/ecological functions only (P. Vaz, unpublished data). Moreover, loose wood in deep portions of the stream, where it is more likely to remain saturated, is more resistant to decay and thus prolonged the functionality in the system (Abbe et al., 2003).

Our analysis also expanded the current understanding of the role of the length ratio in determining function. The length ratio has been widely recognized as critical to transport processes (Haga et al., 2002; Merten et al., 2010, 2011) and – for pieces not oriented parallel to the flow - is related to channel blockage, which in turn is related to hydrodynamic drag (Hygelund and Manga, 2003). Pieces experiencing more drag, should they resist mobilization, are more likely to produce hydraulic functions such as flow deflection. However, a caveat exists regarding length ratio, as its relation to function tends to be greatly simplified, stating that longer pieces are invariably more stable and thus functional (Gurnell et al., 2002, Baillie et al., 2008). The possibility of diminishing function with greater lengths has only been recognized by Jones et al. (2011) who noted that - from a geomorphic perspective - functional wood averaged 2 times and non-functional wood averaged 6 times the channel width. Our GAM analysis showed that length ratio only increased the probability of function until a piece was 3 times the channel width, at which point further increases in length ratio led to decreased probability of function. Our SEM analysis gave a probable explanation. The model showed that length ratio, in fact, had a positive relationship with function, but only after the indirect effects of anchoring and bridging were accounted for. When considering a range of pieces including those much longer than the channel width, anchoring and bridging likely have synergistic contributions on function.

Finally, our results suggest a key zone along the river system located at about 3/4 of the stream's length where wood was most likely to be functional. In general, this demonstrated that functionality varies throughout the river network, but the reason for the peak in the second half of the streams is unclear and this trend opposes previous research focused on morphological functions (Baillie et al., 2008). However, our functions were not just morphological and, on the

other hand, we did not perceive any particularity of the reaches representing the peak for function besides distance. At the end, extrapolating our results for distance must be considered cautiously. We speculate that more SW could be involved in various functional categories (not captured by morphological studies) with an increase on stream channel size (Chen et al., 2008), but only discriminating those functions and relating them to distance along the stream could shed light on our finding of more functional wood around 3/4 length of the stream. More work is still required to address how function changes with distance along the river.

5.5 Management implications and conclusions

Recognition of the value of wood to stream geomorphology, to stream biota, and to stream ecosystem function has lead to regular use of wood in stream management. Projects incorporating SW into restoration and riparian management are increasingly interested in functional predictors such as those assessed here (Abbe et al., 2003). Particularly, restoration projects are including the addition of potentially mobile wood that is expected to develop function more naturally with less reliance on bolts, cables, and rebar. To date these restorations rely largely on subjective decisions and lack a strong basis in research (Reich et al., 2003). Currently, there is a growing consensus that the use of wood in river restoration should be founded on emulating natural processes (Bisson et al., 2003), and the poor performance of some restoration projects is partially due to an insufficient understanding of what wood structure is optimal for the fluvial processes, and how and where wood can be placed to be more functional within streams.

Across fire-prone Euro-Mediterranean forestry systems, there are a wide range of post-fire human interventions in the riparian zone and associated streams. The type of forest management, from post-fire abandonment to active management near streams, has important consequences for SW function. In Portugal, to comply with national legislation, owners of land parcels in the beds and banks of inland waters are required to clean and clear the waterways. In contrast, the European water framework directive (WFD) requires "good conditions" that are "not far from natural conditions" for streams throughout Europe. Clearly, stream wood plays an important role to meet the intent of this policy, and authorities seek for good management practices following wildfires to meet WFD.

Our study provide useful information in developing guidelines for stream and riparian management operations. Interestingly, our suggestion that wood much longer than stream width is also less functional align well with security and navigability concerns, as this wood could also be the first to be removed after fire when decisions must be made which weigh safety versus ecosystem function. Nevertheless, we acknowledge that SW function is dynamic in space and time, and relatively long pieces may break or be transported downstream and become functional. Also, post-fire very long pieces may be less functional because they lack complexity. If complex, pieces long enough to create bridges may have branches protruding downward from the trunk and thus be functional (e.g. with the branches themselves trapping smaller pieces).

Our results challenge the well-established idea that the function of wood in streams is simply a matter of its stability, size, and decay state. As we demonstrated, SW further above the channel (e.g. bridging the channel) may be stable (well anchored) but may be unlikely functional. We also clarify the "size paradigm" by identifying a maximum-length ratio threshold above which SW is unlikely to be functional. Moreover, decay state was not a significant predictor of function, despite its relationship with burned status. Wood function was a result of synergistic contributions from several predictors, and although burned status itself was not a significant predictor, fire affected function indirectly by affecting both stability (via anchoring) and size (via diameter). Overall, our findings provide a way in which to refine the paradigm of wood functionality in streams with direct implications to stream management.

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Effects of burn status and conditioning on colonization of wood by stream macroinvertebrates

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6. Effects of burn status and conditioning on colonization of wood by stream macroinvertebrates



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Abstract: The combination of changing climate and anthropogenic activities is increasing the probability of wildfire around the world. When fires occur in riparian zones, associated tree mortality can add wood directly to streams or wood may fall to the forest floor and remain there for some time before being transported into stream channels. Wood provides critical structure for aquatic macroinvertebrates, so our objectives were to assess the effects of wood burn status, conditioning, and their interaction on macroinvertebrate community composition, taxon and functional diversity, and trait affinities. We conducted a field experiment with pieces of freshly cut wood (length = 10 cm, diameter \approx 7.5 cm) for which we first manipulated burn status (burned, unburned) and second, conditioning by placing burned and unburned wood directly into streams (no conditioning) or leaving pieces in streams (water conditioning) or on the forest floor (soil conditioning) for a year before submergence. We used distance-based redundancy analysis to assess community structure by wood treatments and linear mixed-effects modeling to assess effects of wood treatments on taxon and functional diversity and trait affinity. Changes in wood quality resulting from fire may not alter macroinvertebrate community structure. Taxonomic and functional patterns of stream invertebrate colonization did not differ between burned and unburned wood, even after a year of incubation in the stream or on the forest floor. Conditioning status affected taxonomic composition, taxon and functional diversity, and trait affinities of wood invertebrate communities. The terrestrial legacy of soil conditioning was clearly important in structuring macroinvertebrate assemblages. Our results suggest that macroinvertebrate communities may be more sensitive to fire effects on the dynamics of wood input than to effects of fires on the wood itself.

Keywords: wildfire; wood debris; wood condition; invertebrates; Portugal; traits; community structure.

6.1 Introduction

Changing climate and anthropogenic activities are synergistically increasing the probability of fire around the world (Moriondo et al. 2006, Flannigan et al. 2009, Moreira et al. 2011). As a consequence, the effects of fire disturbance on aquatic ecosystems have received increasing attention (Resh et al. 1988, Gresswell 1999, Romme et al. 2011, Verkaik et al. 2013). Forest wildfires promote recruitment of wood to aquatic ecosystems in many regions (Zelt and Wohl 2004, Arseneault et al. 2007, Jones and Daniels 2008, Vaz et al. 2011, 2013a, b).Wood from riparian trees may be injured by fire and then directly enter stream channels, or wood may fall to the forest floor and remain there until it moves laterally into stream channels during floods or from eroding banks. The mechanism by which wood enters the channel (i.e., directly or after some time on the forest floor) may affect the condition or quality of fire-derived wood for stream biota, such as benthic macroinvertebrates (Cummins and Klug 1979, Mihuc and Minshall 1995), but no investigators have examined the interplay between wood burn status and conditioning in structuring the composition and function of epidendric macroinvertebrate assemblages.

Wood can be characterized by its structural and chemical properties. Structure reflects bark type (e.g., looseness), holes, protrusions, grooves, small depressions, crevices, cracks, and availability of interstitial spaces (O'Connor 1991, Mathooko and Otieno 2002). Chemically, wood has high C:N and C:P (relative to leaves) and large quantities of cellulose, lignocellulose, and lignin (Gulis et al. 2004). Bark can contain defensive compounds, such as polyphenols and terpenes (Sakai 2001, Gonçalves et al. 2007). The physical and chemical properties of wood are thermally degraded during fires >300°C. Bark is primarily affected and becomes loosely attached, softened, or removed. Charred wood results from incomplete combustion via surface oxidation in the form of smoldering (nonflaming) that depolymerizes cellulose. Char (black C) is chemically heterogeneous and biologically inert. Degradation of lignin occurs at ~225 to 450°C, and at ~450°C, production of volatile compounds is complete. Water and extractants (namely lipids and terpenoid hydrocarbons) are lost from burned wood, but volatilization of repellent compounds (Schniewind 1989, Gama et al. 2007, Hyde et al. 2011) may make burned wood more attractive than unburned wood to colonizing organisms.

Soil conditioning and water conditioning differ in terms of fungal and bacterial colonization, but both precondition wood and facilitate colonization by organisms (Wong et al. 1998). In terrestrial environments, soil-conditioned wood decomposes relatively rapidly and decomposition is enhanced by fungi and to a lesser extent by bacteria. Brown- and white-rot fungi are 2 major kinds of decay fungi. Brown-rot fungi degrade cellulose and hemicellulose, whereas white-rot fungi degrade lignin and cellulose. Soft-rot fungi affect the outer surface of wood, especially in fissures under wet conditions (Bucher et al. 2004, FPL 2010). In water, microbial colonization of wood is a slow phenomenon that affects the surface of the wood (Harmon et al. 1986). Some fungi that colonize wood prior to submergence in water may survive and continue to produce fruiting bodies (Anderson et al. 1978). Within 2 wk, epixylic biofilms develop and coat the submersed wood, forming organic layers of fungi, bacteria, algae,

extracellular polysaccharides, and trapped seston (Golladay and Sinsabaugh 1991, Couch and Meyer 1992). Most fungi in freshwaters carry out soft-rot on wood surfaces (Zare-Maivan and Shearer 1988), and basidiomycetes, which degrade lignin, are rare and usually absent.

Colonization of wood by stream macroinvertebrates is primarily a surface phenomenon, resulting from food and substrate affinities. Despite the recalcitrant (Spänhoff and Gessner 2004) and refractory nature of wood, several taxa ingest wood fragments (Pereira et al. 1982), and a few can digest (assimilate) wood (Monk 1976). As biofilms continue to develop over time, the wood is mechanically softened and its nutrient content and palatability increases (Anderson et al. 1978, Phillips and Kilambi 1994). Colonizing microorganisms and associated fine detritus also provide food for numerous aquatic invertebrates (Anderson 1982, Winterbourn 1982, Anderson et al. 1984, Tank et al. 2010). Lock et al. (1984) refers to biofilms accrued during conditioning as transducers of energy and matter that act as intermediates of polymer metabolism (e.g., cellulose) and are readily assimilated by stream invertebrates (Golladay and Sinsabaugh 1991, Hax and Golladay 1993, Eggert and Wallace 2007). Temporal modifications of wood structure and quality result in macroinvertebrate–wood interactions accompanied by shifts in community and biotic trait composition (Johnson et al. 2003).

Several investigators have examined the effects of wildfire on stream macroinvertebrates (Minshall et al. 1997, Minshall 2003, Vieira et al. 2004, Robinson et al. 2005, Malison and Baxter 2010, Oliver et al. 2012), but none addressed the role of fire-derived wood in stream function. Knowledge regarding interactions between macroinvertebrates and allochthonous inputs is based mainly on leaf-litter studies (Wallace et al. 1997, Gessner et al. 1999, Graça 2001, Gulis et al. 2006, Casas et al. 2011), but leaf and wood decomposition differ greatly (e.g., Hax and Golladay 1993). Others have addressed the structural effects of wood, e.g., effects on flow patterns and retention (Entrekin et al. 2009, Testa et al. 2011) on macroinvertebrate communities in streams (Wallace et al. 1995, Hilderbrand et al. 1997, Lemly and Hilderbrand 2000, Warren and Kraft 2006). Last, some researchers have specifically examined the colonization of submerged wood by macroinvertebrates (Magoulick 1998, Collier and Halliday 2000, Collier and Smith 2003, Kaller and Kelso 2007, Lyon et al. 2009, Ballinger et al. 2010), but results have been inconsistent making generalizations difficult (Kaller and Kelso 2006).

We conducted a field experiment in which we manipulated the burn status (burned, unburned) and types of conditioning (water, soil, none) of small, uniform-sized pieces of freshly cut wood. Our objectives were to assess the effects of wood burn status, conditioning, and their interaction on macroinvertebrate community composition, taxon and functional diversity, and trait affinities (after Tachet et al. 2010). We hypothesized that: 1) colonization patterns would differ between burned and unburned wood because of physical, chemical, and nutritional degradation of burned wood; 2) colonization patterns would differ between conditioned (water, soil) and unconditioned wood; and 3) colonization would differ between water- and soil-conditioning. We expected conditioned wood to have the greatest taxonomic and functional

diversity, and a higher prevalence of shredders (see Cummins and Klug 1979), and we expected more scrapers on wood that was conditioned in water (Hall et al. 2001).

6.2 Methods

6.2.1 Site description

We worked in 3 unregulated 3rd-order streams (Strahler 1957) with 3 different upland forest types in each of 3 separate subbasins of the Tagus River in east-central Portugal: Fouvel, Alferreira, and Rio Frio. Geology at the streams was mainly characterized by siliceous rocks with low mineralization (INAG 2008). The area has gentle relief, and land cover is dominated by forests, shrublands, and agriculture. The local climate is Mediterranean with hot, dry summers and cool, wet winters. Mean annual precipitation is 512 mm (Fig. 1), and mean annual temperature is 15.8°C (range: 9°C in December–January to 23°C in July–August).



Fig. 1. Local daily precipitation for the duration of the experiment (17 April 2010–26 May 2011). The rain gauge is 53, 29, and 12 km from Fouvel, Alferreira, and Rio Frio stream reaches, respectively.

The Fouvel subbasin (drainage area = 50 km2) is dominated by cork oak (Quercus suber) managed by an agroforestry system called montado (dehesa in Spain). The Alferreira subbasin (59 km2) has pure stands of eucalyptus (Eucalyptus globulus) planted for paper pulp production. The Rio Frio subbasin (37 km2) has pure stands of maritime pine (Pinus pinaster) grown for timber. The subbasins experienced extensive wildfires (66, 92, and 71% burned area) between 2003 and 2007. After these fires, the amount of large wood in 3rd-order streams across the region was remarkably low: 2.8, 2.9, and 5.3 pieces/100 m in subbasins dominated by cork oak, eucalyptus, and maritime pine, respectively. About 70% of this wood, including pieces of the dominant managed tree species (Vaz et al. 2011, 2013a), was burned.

The streams generally have neutral-basic waters and are intermittent with stretches that remain dry for several months in a seasonal sequence of floods and droughts. The natural discharge regime is primarily precipitation-dominated with highest discharge occurring during autumn and winter. Discharge responds rapidly to precipitation events, which can result in major changes in flow over relatively short periods of time (Raven et al. 2009). Channel gradients at the study reaches were gentle (~1–2%). The Fouvel reach (lat 39°35'45.65"N, long 7°36'23.98"W, 151 m asl) had a treeless, sparsely vegetated riparian zone. This site was dominated by cobble and pebble substrates, interspersed with some boulders in the main channel and bedrock outcrops in one margin. The Alferreira (lat 39°28'3.81"N, long 7°51'17.46"W, 127 m asl) and Rio Frio (lat 39°29'55.37"N, long 8°3'35.60"W, 100 m asl) reaches had similar riparian vegetation, dominated by ash (Fraxinus angustifolia), alder (Alnus glutinosa), and black poplar (Populus nigra). The Rio Frio site also had silver wattle (Acacia dealbata) trees. The Alferreira reach was dominated by pebble and gravel substrates and Rio Frio mainly by gravel. Both reaches had some boulders in the main channel. During the study, maximum wetted widths were 7.22, 7.01, and 5.98 m, at Fouvel, Alferreira, and Rio Frio reaches, respectively, with corresponding minimum water depths of 28, 40, and 30 cm.

6.2.2 Wood burning and preconditioning

We used the dominant wood species in each subbasin as the species examined in the stream reach. We obtained freshly cut wood pieces with bark (length = 10 cm, diameter \approx 7.5 cm, volume \approx 442 cm3) of cork oak (mean mass = 212 g), maritime pine (344 g), and eucalyptus (398 g) (Fig. 2A). For each species, a replicate comprised 10 wood pieces (1 set). We used 54 sets of wood for the entire experiment: 18 sets each of cork oak, eucalyptus, and maritime pine.

We randomly selected 9 sets of each species (27 sets) and burned them at the Reaction to Fire Testing Laboratory, National Laboratory for Civil Engineering, in Lisbon, with a Single Burning Item EN 13823 (Fig. 2B). Pieces were burned for 20 min at 750°C (burner heat release = 25 kW/h, gas flow to burner = 539 mg/s). Mass lost measured immediately after burning was 26% for cork oak, 48% for maritime pine, and 54% for eucalyptus.

We randomly assigned 3 burned and 3 unburned sets of each species to 3 conditioning treatments: soil, water, and none. Soil-conditioned sets were left undisturbed on bare soil (slope = 5%) with some low grasses (Fig. 2C, D) from 23 July 2010 to 15 April 2011 at the Institute of Agronomy campus (lat $38^{\circ}42'42.00''N$, long $9^{\circ}11'20.13''W$, 93 m asl). Soil was clay to clay loam with medium and wide cracks when dry (vertisol; IUSS 2006). Sets were arranged randomly in a 1 × 1-m regular grid (distance among sets ≤ 80 cm). During conditioning, local mean daily temperature 5 cm above ground was $16.8^{\circ}C$ ($11.4-23.3^{\circ}C$), mean daily air humidity was 71.4% (56.8-81.8%), and mean daily solar insulation was 7.2 h (2.9-12.4 h). Water-conditioned sets were submerged in plastic mesh bags (described below) in the stream reaches for 1 y between spring 2010 and spring 2011. Unconditioned sets were freshly cut in spring 2011 and underwent no further conditioning other than burning (described above).



Fig. 2. Photographs of the experimental setting showing freshly cut wood pieces (length = 10 cm; diameter \approx 7.5 cm) from cork oak (A), burning process at the Reaction to Fire Testing Laboratory using a Single Burning Item (B), soil conditioning of unburned wood (C) soil conditioning of burned wood (D), mesh bags (mesh = 1.5×1.5 cm) with wood (E), and mesh bags with wood secured in the stream with a nylon cable (F).

6.2.3 Field and laboratory procedures

During the colonization step, we piled the pieces of each set irregularly in plastic mesh bags (mesh = 1.5×1.5 cm) (Fig. 2E). The bags prevented wood pieces from being swept away, but had large enough mesh to allow access of most invertebrates. On 17 April 2010, we placed the first sets in the water to be colonized for ~1 y (water conditioning). At each reach, we secured 3 burned and 3 unburned sets to a nylon cable in an alternating arrangement with bags spaced ~80 cm apart (Fig. 2F). The bags were submerged in a line, and each bag was anchored to the stream bed with a boulder. On 29 April 2011, we added the sets that had undergone soil

conditioning or no conditioning, mounted <1.5 m from the first sets on nylon cables. Thus, at each ~11-m reach, another 12 bags were added and submerged, tethered in a random arrangement and spaced as above for a total of 18 sets/reach. Twelve sets assigned to water conditioning (6 at the cork oak reach, 3 each at the eucalyptus and maritime pine reaches) were destroyed and lost during winter floods.

On 26 May 2011, we collected the bags in buckets filled with stream water (1 bag/bucket). We separated all macroinvertebrates in each bag from the 10 wood pieces with a soft brush and a water spray bottle. Thus, all invertebrates on the 10 wood pieces combined constituted 1 sample. Visual assessment of the wood provided evidence that burning decreased the coating of epixylic biofilm and that decay of wood sets that had undergone soil conditioning or water conditioning was greater than decay of unconditioned wood. We filtered the water in each bucket through a 500-µm mesh sieve to collect any remaining macroinvertebrates in the sample. We also used a kick-net (500-µm mesh net, aperture = 30 cm) to collect a sample from the substrate at the previous location of each bag. We used this sample to characterize the reach in a different way to allow us to detect, for example, taxa was not captured by the wood/mesh bags. Immediately after collection, we preserved macroinvertebrates, detached smaller pieces of wood, and loose bark with 70% ethanol in 1-L plastic flasks. We also characterized the location of each bag and recorded 3 stream microhabitat features: depth (cm), bed substrate (gravel, pebbles, cobbles), and flow type (imperceptible, unbroken waves, broken waves, rippled). We defined bed substrates and flow types as in the River Habitat Survey Manual (EA 2003).

Upon returning to the laboratory, we cleaned and filtered (500-µm mesh sieve) samples and hand-picked all macroinvertebrates for identification with the aid of a microscope at 10× magnification. We identified macroinvertebrates to lowest-feasible taxonomic level (mostly family or genus) with available keys (e.g., Tachet et al. 2010, Oscoz et al. 2011) and counted them. We used absolute abundances/sample in all analyses.

6.2.4 Macroinvertebrate traits

We assigned ecological trait composition of each sample according to the traits database published by Tachet et al. (2010), which uses a fuzzy-coding procedure to describe the link between a taxon and categories within 21 traits (Usseglio-Polatera 1991, Chevenet et al. 1994, Usseglio-Polatera et al. 2000). In the database, each taxon is assigned a score that describes its affinity to each category of a given trait. Scores range from 0 (no affinity) to 3 or 5 (high affinity). The range of taxon-trait scores (0–3 or 0–5) depends on the available information in the literature and on the number of categories describing the trait. We used only the 5 traits that potentially influence wood colonization via food (food, feeding habits) or substrate affinities (maximal potential size, substrate preference, locomotion and substrate relation). We considered all categories describing each trait. After applying the scores to our data, we transformed the range of each taxon-trait category link by rescaling it between 0 and 1.

6.2.5 Functional diversity and taxon diversity

We quantified functional diversity, i.e. the overall difference in terms of traits among taxa within a wood set with the Rao index of diversity (Botta-Dukát 2005, Lepš et al. 2006, De Bello et al. 2009, Lavorel et al. 2008). The Rao index represents the probability of picking 2 individuals in a community that differ in their ecological function. If the proportion of the ith taxon in a community is pi and the dissimilarity of taxon i and j is dij, the Rao index has the form

Functional diversity =
$$\sum_{i=1}^{t} \sum_{j=1}^{t} d_{ij} p_i p_j$$
, (Eq. 1)

where t is the number of taxa in the community and dij varies from 0 (2 taxa having the same traits) to 1 (2 taxa having different traits). To convey taxon diversity, we used the Simpson index of diversity expressed as 1 minus Simpson index of dominance

$$D = 1 - \sum_{i=1}^{t} p_i^2 .$$
 (Eq. 2)

6.2.6 Data analysis

Community by wood treatments

We analyzed community composition in relation to explanatory variables by distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999, McArdle and Anderson 2001), based on Bray–Curtis dissimilarities (Bray and Curtis 1957) on untransformed abundances, with the capscale algorithm in the R package vegan (version 2.0-5; Dixon 2003, Oksanen et al. 2012). We used wood burn status (burned, unburned), conditioning (water, soil, none), the burn status × conditioning interaction, and habitat variables (water depth, streambed substrate, flow type) as predictors. We assessed final models with a forward variable selection procedure. We entered predictors one at a time, recorded their pseudo-F and significance values, and chose the most significant predictor. Then we entered all other independent variables and chose the next most significant (F-test with anova command in vegan; p-values generated by permutation using p < 0.05 criteria). The procedure stopped when no significant term could be added. As a measure of overall db-RDA fit, we used the pseudo-F ratio obtained by permutation tests (permutest command in vegan). Colonization conditions varied according to the site, so we first ran a db-RDA model applied to the entire data set (sites combined) but with permutations stratified within sites, and then ran a separate model per site. The procedure can accommodate an unbalanced design, but p-values close to the 0.05 must be interpreted with special caution (Borcard et al. 2011).

We quantified the contributions of each taxon to the average Bray–Curtis dissimilarity between treatments (% contribution) with a similarity percentages analysis (SIMPER; simper command in vegan; Clarke 1993). Taxon composition could differ among sites, so we ran SIMPER between treatments only within sites.

Taxon diversity, functional diversity, and trait affinity by wood treatments

We acrsin \sqrt{x} -transformed taxon diversity, functional diversity, and trait affinity data to satisfy assumptions of normality before analysis. Groups of 3 conditioning treatments and 2 burn status treatments were nested within each site (one site/forest type: cork oak, eucalyptus, maritime pine), so we used a linear mixed-effects models (LMM) with site as a random factor (random intercept) for the analysis of response variables. We fitted a separate LMM to taxon diversity, functional diversity, and to each trait category with the above set of explanatory variables, and used the *nlme* package in R (version 3.1-104, R Project for Statistical Computing, Vienna, Austria; Pinheiro et al. 2012) to fit each model. In all cases, we started with a model with all 5 variables (burn status, conditioning, bed substrate, flow type, and depth) and the burn status × conditioning interaction in the fixed part of the model. We used backward elimination (Zuur et al. 2009) to remove each main term in turn, and then at each step, we applied the likelihood ratio test of nested models. We evaluated model adequacy by plotting residuals vs fitted values and explanatory variables.

6.3 Results

We identified 77 macroinvertebrate taxa in the wood sets. Chironomidae was the most represented taxon (62%), followed by *Habrophlebia* (13%), *Choroterpes* (3%), *Ephemerella* (3%), *Baetis* (3%), and Elmidae (3%). Other taxa were less represented (\leq 1%). Taxon composition differed among sites. For example, *Choroterpes* and *Ephemerella* were absent from eucalyptus and cork oak sites, respectively. Trichoptera and Plecoptera were rarely present in cork oak site samples, and Gastropoda did not occur at the eucalyptus site. Wood bags captured all taxa present in the kick-net samples at all sites (Appendix S1).

6.3.1 Community by wood treatments

Wood burn status was not selected for any of the 4 final db-RDA models (forward-selection, $\alpha \le 0.05$; Table 1). Thus, wood burn status was not considered a significant predictor of community composition, whether we evaluated sites in combination or separately. In contrast, wood conditioning was a significant predictor of community composition in all cases, even though the water-conditioning treatment was absent at the cork oak site. The burn status × conditioning interaction also was not a significant predictor, indicating that the effect of conditioning probably was comparable for burned and unburned wood.

Community composition differed between conditioned (soil, water) and unconditioned wood sets when all sites were considered (Fig. 3A) and at each site separately (Fig. 3B–D). Community composition differed significantly between unconditioned and soil-conditioned wood at each site. However, differences between communities on water- and soil-conditioned wood depended on site (no differences when sites were combined, partial overlap at the eucalyptus site, different at the maritime pine site).

Table 1. Final distance-based redundancy analysis models for macroinvertebrates on wood treated with no, soil, or water conditioning at all sites combined (analysis stratified by site) and separately for each 3 sites. At the cork oak site, data were available only for no and soil conditioning. Numbers in parentheses are pseudo-*F* values, *p*-values were generated by 999 permutations and p = 0.01 in the 4 models.

Variable	df	MS	F	р
Sites combined (3.58)				
Conditioning	2	1.10	5.89	0.01
Stream bed substrate	3	0.67	2.40	0.01
Water depth	1	0.23	2.49	0.01
Residuals	33	3.09		
Cork oak site (5.71)				
Water depth	1	0.47	7.82	0.01
Conditioning	1	0.21	3.60	0.02
Residuals	9	0.53		
Eucalyptus site (5.20)				
Conditioning	2	1.03	6.36	0.01
Water depth	1	0.23	2.88	0.02
Residuals	11	0.89		
Maritime pine site (4.21)				
Conditioning	2	0.54	4.21	0.01
Residuals	12	0.77		

The taxon that contributed most to all significant dissimilarities between conditioning treatments within sites was Chironomidae, followed by *Habrophlebia* (except at the cork oak site) (Tables 2, 3, 4). Chironomidae was more abundant in unconditioned wood in all pairwise comparisons involving this wood treatment. Other taxa that contributed >5% of the dissimilarity between at least 1 pair of conditioning treatments within sites were *Choroterpes, Baetis, Ephemerella*, Elmidae, Thaumaleidae, Psychodidae, and Psychomyiidae (Appendix S2).

Table 2. Output of similarity percentages analysis at the cork oak site showing taxa responsible for 90% of the overall average dissimilarity between the macroinvertebrate communities on wood with no or soil conditioning. Bold highlights the conditioning treatment in which the taxon was more abundant. Ctr% = % contribution to the overall dissimilarity between conditioning treatments. No data were available for water conditioning at the cork oak site.

Taxon	Average a	bundance	Overall dissimilarity (%)	Ctr%
Comparison	soil	none	47.6	
Chironomidae	117.5	<u>256.5</u>		56.3
Elmidae	<u>21.7</u>	10.7		7.2
Choroterpes	<u>27.2</u>	20.0		5.9
Thaumaleidae	0.5	<u>12.2</u>		5.2
Psychodidae	0.5	<u>12.0</u>		5.2
Naididae	0.8	<u>5.2</u>		2.1
Cloeon	0.5	<u>4.3</u>		1.8
Centroptilum	<u>4.8</u>	3.7		1.5
Dixidae	1.3	<u>2.7</u>		1.4
Procloeon	1.5	<u>3.7</u>		1.3
Dytiscidae	2.3	<u>3.5</u>		1.1

Table 3. Output of similarity percentages analysis at the eucalyptus site showing taxa responsible for 90% of the overall average dissimilarity between the macroinvertebrate communities on wood with no, water, or soil conditioning. Bold highlights the conditioning treatment in which the taxon was more abundant. Ctr% = % contribution to the overall dissimilarity between conditioning treatments. No differences were detected between communities on wood with soil and water conditioning.

Taxon	Average a	abundance	Overall dissimilarity (%)	Ctr%
Comparison	water	none	61.2	
Chironomidae	85.3	<u>386.5</u>		68.4
Habrophlebia	<u>61.0</u>	54.0		7.6
Ephemerella	0.3	<u>33.2</u>		7.3
Psychomyiidae	<u>21.3</u>	0.5		5.0
Comparison	soil	none	60.7	
Chironomidae	88.8	<u>386.5</u>		71.3
Habrophlebia	29.0	<u>54.0</u>		9.0
Ephemerella	21.3	<u>33.2</u>		6.2
Baetis	7.0	<u>17.3</u>		3.3

6.3.2 Taxon diversity, functional diversity, and trait affinity by wood treatments

Wood burn status was not a significant predictor of taxon or functional diversity, nor, in general, of trait affinity (Table 5). Wood conditioning was a significant predictor of taxon diversity, functional diversity, and of trait affinity for 23 categories among the traits assessed. The burn status × preconditioning interaction was always dropped during the model-selection processes, indicating that the effect of conditioning was independent of burn status. Fitted values for taxon diversity and functional diversity were lower for unconditioned wood than for soil- or water-conditioned wood and did not differ between soil- and water-conditioned wood (Fig. 4).

Pairwise comparisons of fitted trait affinity between wood conditioning treatments generally revealed that unconditioned wood differed significantly from the other 2 treatments (Fig. 5). In 20 of the 23 categories, the confidence intervals of mean trait affinity on unconditioned wood did not overlap with the trait affinity on wood with soil or water conditioning (Fig. 5), i.e., trait affinities differed significantly. Macroinvertebrates colonizing wood were characterized as follows based on food or substrate affinities.

Food

Fewer shredders and more filter-feeders, predators, and parasites occurred on unconditioned than on conditioned wood. Macroinvertebrates tended to feed less on living microphytes, and more on microorganisms, detritus <1 mm, dead animals \geq 1mm, living microinvertebrates, and living macroinvertebrates on unconditioned than on conditioned wood.

Table 4. Output of similarity percentages analysis at the maritime pine site showing taxa responsible for 90% of the overall average dissimilarity between the macroinvertebrate communities on wood with no, water, or soil conditioning. Bold highlights the conditioning treatment in which the taxon was more abundant. Ctr% = % contribution to the overall dissimilarity between conditioning treatments.

Taxon	Average a	bundance	Overall dissimilarity (%)	Ctr%
Comparison	water	none	38.2	
Chironomidae	95.0	<u>119.0</u>		37.0
Habrophlebia	<u>41.3</u>	38.8		11.9
Baetis	<u>22.0</u>	5.7		10.8
Simuliidae	<u>6.7</u>	0.7		4.0
Lumbricidae	<u>5.3</u>	0.0		4.1
Physa	0.0	<u>5.0</u>		3.3
Choroterpes	0.0	<u>4.5</u>		3.1
Polycentropodidae	<u>5.3</u>	3.5		2.8
Elmidae	0.3	<u>4.5</u>		2.8
Hydropsychidae	<u>3.0</u>	0.0		1.8
Beraeidae	0.0	<u>2.5</u>		1.8
Dixidae	1.0	2.0		1.6
Rhyacophila	2.3	0.0		1.4
Leuctridae	2.0	0.0		1.3
Ephemerella	2.3	1.3		1.3
Comparison	soil	none	45.2	
Chironomidae	44.5	<u>119.0</u>		49.6
Habrophlebia	<u>55.5</u>	38.8		18.5
Choroterpes	<u>10.5</u>	4.5		5.2
Baetis	5.5	<u>5.7</u>		3.6
Elmidae	<u>7.7</u>	4.5		3.0
Physa	1.7	<u>5.0</u>		2.8
Polycentropodidae	<u>5.0</u>	3.5		1.8
Beraeidae	0.7	2.5		1.5
Dixidae	0.5	2.0		1.5
Centroptilum	<u>1.3</u>	0.3		1.2
Ephemerella	2.2	1.3		12
Comparison	Water	soil	46.5	
Chironomidae	<u>95.0</u>	44.5		33.7
Habrophlebia	41.3	55.5		12.7
Baetis	22.0	5.5		10.3
Choroterpes	0.0	10.5		6.3
Elmidae	0.3	7.7		4.6
Lumbricidae	5.3	0.0		3.9
Simuliidae	6.7	0.3		3.8
Polvcentropodidae	5.3	5.0		2.7
Hvdropsvchidae	3.0	0.0		1.8
Rhvacophila	2.3	0.0		1.3
Ephemerella	2.3	22		1.3
Leuctridae	2.0	0.0		12
Dvtiscidae	0.0	1.7		11
Centroptilum	0.0	13		1.1
Lumbriculidae	1.0	12		1.0
Physa	0.0	17		0.9
Hvdraena	17	0.0		1.0
Philopotamidae	13	0.0		0.8

Table 5. Significance levels for fixed terms in optimal linear mixed-effects models predicting taxon or functional diversity and trait affinity by wood burn status (burn) and conditioning (cond) type. Only those trait categories where the effect of wood conditioning was significant are shown. Sub = streambed substrate. Blank cells were terms dropped during the model selection process. *** = <0.001, ** = <0.01, * = <0.05.

	Response			Model predicto	rs			R^2
		Cond	Burn	Burn×Cond	Sub	Flow	Depth	
Diversity	Taxon diversity	***					**	0.44
	Functional diversity	***			*			0.41
Trait	Trait category							
Maximal potential size	2-4 cm	***	*					0.45
	1-2 cm	***						0.41
Substrate preference	mud	***						0.50
	twigs/roots	*						0.17
	microphytes	***						0.44
	sand	***			**			0.61
	flags/boulders/cobbles/pebbles	**			**			0.46
Locomotion and	permanently attached	***					**	0.43
substrate relation	temporarily attached	***					*	0.41
	interstitial	***			**			0.51
	burrower	***			***			0.62
	crawler	***					*	0.51
	full water swimmer	**				**	*	0.13
Food	living macroinvertebrates	***						0.34
	living microinvertebrates	***			**			0.54
	dead animal >= 1mm	**					**	0.35
	living microphytes	*						0.13
	detritus < 1 mm	*			**			0.53
	microorganisms	**			*			0.36
Feeding habits	parasite	***	*		**			0.61
0	predator	***			*			0.49
	filter-feeder	***			*			0.47
	shredder	*			*			0.40

Substrate affinities

Only 2 of the 7 maximal potential size categories of macroinvertebrates (1-2 and 2-4 cm; Tachet et al. 2010) tended to be more prevalent on unconditioned than on conditioned wood. Unconditioned wood was colonized by macroinvertebrates with less affinity to twigs/roots as preferred substrate and more affinity to mud. microphytes, sand. or flags/boulders/cobbles/pebbles. Macroinvertebrates colonizing water-conditioned wood had higher affinity for permanent or temporary attachment to substrates than for other locomotion/substrate categories, whereas unconditioned tended wood to have macroinvertebrates with more interstitial or burrower habits than preconditioned wood. Macroinvertebrates having higher crawler affinity were most prevalent on soil-conditioned wood followed by unconditioned and water-conditioned wood. Full water swimmers were more prevalent on unconditioned wood than on soil-conditioned wood, whereas macroinvertebrates on water-conditioned wood had an intermediate affinity for this trait category.



Fig. 3. Distance-based redundancy analysis (db-RDA) ordination plots for macroinvertebrates on burned (burn.) and unburned (unburn.) wood at all sites combined (A), and cork oak (B), eucalyptus (C), and maritime pine (D) sites. Percentages next to axis titles are % variance explained by axis. Ellipses indicate where 95% of sampling units with the same conditioning (none, soil, water) are expected to occur. Water-conditioning data were absent for the cork oak site and sample size was reduced at eucalyptus and maritime pine sites.



Fig. 4. Mean (± 95% CI) fitted values for the optimal mixed-effects models predicting taxon or functional diversity by type of wood conditioning.



Fig. 5. Mean fitted values (vertical ticks) and \pm 95% confidence intervals (horizontal bars) for the optimal mixed-models predicting trait affinity by wood conditioning treatment. One model was run for each category within traits. Only those trait categories where the effect of wood conditioning was significant are shown.
6.4 Discussion

6.4.1 Burned stream wood and macroinvertebrates

The data did not support our 1st hypothesis that patterns of stream macroinvertebrate colonization would differ in response to wood burning. Central to our expectation was the nutritional depletion of burned wood, in line with the observed decreased coat of biofilm. We were not able to measure biofilm growth (e.g., chlorophyll a), but the nutritional depletion of other burned allochthonous inputs is recognized in the literature. For example, Mihuc and Minshall (1995) found that only 1 macroinvertebrate taxon was able to grow when fed burned organic matter. In addition, Gama et al. (2007) reported a reduction in nutritional quality of fireexposed leaves relative to normal eucalyptus leaves in a central Portugal stream. However, the diversity and macroinvertebrate abundance were similar between treatments (Gama et al. 2007). Our study followed the same trend, in which alteration of stream wood quality by fire did not appear to be a determinant of macrtoinvertebrate colonization. The degree of xylophagy differs among regions (Benke and Wallace 2003) and our results suggest colonization by predominantly nonxylophages (sensu Hoffmann and Hering 2000). Like Gama et al. (2007), we suggest that invertebrates colonizing wood may use it more as substratum than as food. Our results showed that fire-induced changes in quality of allochthonous inputs per se may not alter the structure of macroinvertebrate communities. In his review regarding responses of macroinvertebrates to fire. Minshall (2003) noted that most results support the conclusion that fire is not detrimental to sustained maintenance of diverse and productive aquatic ecosystems. Our results align well with Minshall's statement that "there is no fire crisis" (Minshall 2003, p. 159).

6.4.2 Taxon responses

Our 2nd hypothesis that preconditioning would lead to changes in macroinvertebrate community assembly was clearly supported, independent of wood burn status. The number of individuals was consistently higher and was composed of a higher proportion of chironomids on unconditioned than on conditioned wood (Appendix S1). Chironomids are frequently among the first colonizers of submerged wood (McLachlan 1970, Nilsen and Larimore 1973, Spänhoff et al. 2000). As expected, greater taxon and functional diversity was found on conditioned than on unconditioned wood. This difference might be the result of the more advanced state of decay, higher prevalence of microorganisms, or greater microhabitat diversity on the surface of conditioned than of unconditioned wood. We suggest that the decrease in the relative dominance of chironomids (Cummins and Klug 1979) and to coexistence of more taxa (O'Connor 1991) might have been a consequence of greater resource availability on conditioned than on unconditioned wood. Collier and Halliday (2000) documented dominant species with varying preferences for wood at different stages of decay, and their findings suggested invertebrate community succession with increasing wood decay. In our study,

chironomids were the major pioneer taxon on unconditioned wood, whereas more diverse but less dense communities were attained on water- and soil-conditioned wood.

Wood that entered the stream after some time on the forest floor was colonized by macroinvertebrates differently than wood that entered the channel directly. This terrestrial legacy had already been hypothesized (see Anderson et al. 1984), but it has never been tested explicitly in a multiple-factor experimental setting. Some authors have addressed the effect of the stage of decay of stream wood on macroinvertebrates but the decay process (e.g., terrestrial, aquatic, or both) has rarely been controlled. In general, authors of observational studies and single-factor experiments have reported relationships between wood decay and diversity, richness, or density (Benke and Wallace 2003). For instance, invertebrate richness may increase with decay (Braccia and Batzer 2001, Ballinger et al. 2010), and density may vary (Collier and Halliday 2000) or be unrelated to decay (Braccia and Batzer 2001). Based on some of these studies and on their own findings, Kaller and Kelso (2006) stressed the difficulty of making generalizations about the effect of decay on macroinvertebrates. We think that part of the difficulty arises from limited tracking of crucial features in the decay of sampled wood, such as decay time, age, size, species, and waterlogging period. We controlled these variables and were able to measure the effects of wood conditioning on the structure of stream invertebrate communities.

The invertebrate community on wood after 1 y of submergence (water-conditioning) differed from the community on unconditioned wood colonized over 1 mo. A time series analysis is beyond the scope of our study, but we suggest that this result indicates a possible shift in community composition over the 1-y period. For instance, the community on water-conditioned wood probably had more chironomids a month after initial submergence. On the other hand, macroinvertebrate communities did not differ markedly between water- and soil-conditioned wood even though the duration of in-stream colonization varied between the 2 conditioning treatments (1 y vs 1 mo). Communities on water- and soil-conditioned wood had had similar diversities (taxon and functional) at the eucalyptus and maritime pine sites, and community composition differed significantly only at the maritime pine site. If invertebrate communities do undergo succession during water-conditioning (Collier and Halliday 2000), we suggest that the first stage of that succession can be influenced by soil conditioning, although the progress of succession would be site-specific. Our ability to draw inferences regarding water conditioning would have been stronger had we been able to include data from the cork oak site. More work is necessary to shed light on these possibilities.

6.4.3 Trait responses

We quantified trait affinities to examine the influence of wood treatments on macroinvertebrate communities. Taxonomic-based metrics are often poor tools for identifying the mechanisms underlying patterns, whereas modeling trait responses allowed us to better understand how the functional role of communities was constrained (Wooster et al. 2012).

Shredders usually select the most conditioned material (Cummins and Klug 1979), and as expected, taxa with higher shredding affinity were associated with conditioned wood. However, our prediction of higher prevalence of scrapers on water- than on soil-conditioned wood was not supported. We based our prediction on the expectation that periphyton growth would be greater on water- than on soil-conditioned wood (Oliver et al. 2012), but the conditioning period might have been too short for us to detect a response (Golladay and Webster 1988, Hall et al. 2001).

Less specialized feeders with a large breadth of food requirements (Oliver et al. 2012) prevailed on unconditioned wood. For example, the higher proportion of predators on unconditioned than on conditioned wood might be explained by the greater abundance of macroinvertebrates (potential prey) on unconditioned wood (Malison and Baxter 2010). Also, filter-feeders do not depend on biofilm accrual because their food is produced elsewhere in the system and is delivered by drift (Benke and Wallace 2003). Thick biofilms may inhibit filterfeeders from making firm attachments to the underlying substrate. Conversely, taxa with shredder and living microphytes affinities were correlated within wood sets (mean rs > 0.8) and were more common on conditioned than unconditioned wood, a result consistent with previous work on the relationship between microphyte abundance and the number of shredders on stream wood (Spänhoff et al. 2006). Macroinvertebrates preferring wood substrates (twigs/roots) prevailed on the conditioned wood, whereas taxa preferring some other substrates prevailed on the unconditioned wood. This result lends support to the notion that use of unconditioned wood was opportunistic. Overall, food and substrate affinities were similar between water- and soil-conditioned wood, except for 'locomotion and substrate relation'. Most individuals did not use the wood for permanent attachment, although the affinity for attachment was higher on water-conditioned wood than on soil-conditioned or unconditioned wood. Interstitial, borrower, and full water swimmer affinities were high on unconditioned wood, a pattern that further suggests opportunistic use of this wood (e.g., refuge or perching habitat).

In our study, wood conditioning, whether in the stream or on the forest floor, was important to macroinvertebrate taxa and trait responses. In contrast, Pitt and Batzer (2011) found that conditioning had minimal influence on how wood was used by macroinvertebrates in streams in the southeastern USA. Kaller and Kelso (2006) suggested that stream invertebrates readily used all incoming wood regardless of its condition, and they invoked opportunistic colonization as the primary mechanism explaining similar assemblages on wood with various conditioning. In disentangling this contradiction between our results and those reported by others, we first note that our systems differ markedly from those where most other related work has been conducted. Some studies were conducted in sand- or silt-dominated streams and in the absence of stable rocky materials, so wood may have been the only stable habitat available. Such circumstances would decrease the importance of conditioning. However, in all of our study streams, macroinvertebrates had other stable substrates were readily available, so reliance on wood per se may have been less pronounced, and preconditioning would acquire greater importance as biofilms become a more important direct food source.

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6.4.4 Concluding remarks

We worked in 3 common southern European fire-prone forest types where tree mortality associated with fire contributes riparian and upland wood to stream ecosystems (Vaz et al. 2011, 2013a, b) every year. We responded to a need and to an opportunity and conducted a first study of the effect of fire-derived wood on the structure of stream macroinvertebrate communities. In contrast to our expectations, taxonomic or functional patterns of stream macroinvertebrate colonization did not differ substantially between burned and unburned wood, even after a year of incubation in the stream or on the forest floor. This finding is an important contribution to our understanding of how wildfire structures aquatic communities and it can be used to guide postfire stream and riparian management operations that take ecosystem function into account. In conclusion, when fire affects riparian trees, the path by which fallen wood enters the stream has a greater influence on colonization by epidendric macroinvertebrates than whether the wood has been burned. Ultimately, biotic rather than abiotic conditioning influences invertebrate communities on wood following fire, and this fact has implications for the response of the entire stream food web.

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Appendix S1. Total absolute abundances (bottom row) and taxa list with percentage of collected specimens by kick-net and wood bags, assigned to the 3 types of preconditioning: no conditioning (none), soil conditioning, or water conditioning, within sites of cork oak, eucalyptus, and maritime pine.

Group	Family	Genus/Species	Cork	oak		Euca	lyptus			Marit	ime piı	ne	
				Woo	ł	-	Wood	t			Wood	t	
			Kick-net	None	Soil	Kick-net	None	Soil	Water	Kick-net	None	Soil	Water
Turbellaria	Dugesiidae	Dugesia									0.1		
Nematoda					0.1		<0.1						
Bivalvia	Sphaeriidae			<0.1		0.3				0.2			
Gastropoda	Bithyniidae	Bithynia									0.2		
	Hydrobiidae	Bythinella										0.1	
	Hydrobiidae [*]												0.3
	Physidae	Physa [†]		0.2	0.3						2.6	1.1	
	Planorbidae	Ancylus	0.4	0.1	0.1					0.5		0.1	0.3
	Planorbidae	Planorbis		0.8	0.3							0.2	
Hirudinea	Glossiphoniidae	Glossiphonia									0.2		
Oligochaeta	Branchiobdellidae	Branchiobdella			0.1								
	Lumbricidae				0.2								2.7
	Lumbriculidae ^T			0.1		5.5			1.2		0.3	0.8	0.5
	Naididae	Chaetogaster										0.1	
	Naididae	Stylaria lacustris					0.1					0.3	
	Naididae '			1.5	0.4				0.5	18.2	0.3		0.2
	lubificidae			0.2			<0.1		0.7				
Hydrachnidia	Ohmenneliden			-0.4			-0.4	0.2					0.3
Coleoptera	Chrysomelidae			<0.1	0.0		<0.1						
	Curculionidae	During		0.1	0.2						0.0		
	Dryopidae	Dryops		1.0	1.2		-0.1	0.1		0.0	0.2		
	Elmidaat		10.6	1.0	1.2	16	<0.1	0.1	17	0.2	0.3	1.1 5.2	0.2
	Curinidae		10.0	0.2	0.4	1.0	0.9	0.7	1.7	2.1	2.3	0.1	0.2
	Byrinidae	Hydroonat		0.5	0.4		0.1	0.2	1.2			0.1	0.8
	Hydrochidae	Hydrochus									0.1		0.0
	Hydrophilidae	Tiyaroonas			02						0.3		0.5
Dintera	Ceratopogonidae			01	0.2			02		09	0.2	0.3	0.3
Diptoru	Chironomidae [†]		54 1	72.1	61 9	68 6	75 9	49.4	44 8	54.2	61.0	30.2	47.7
	Culicidae		•		0.1	00.0	. 0.0			•	0110	00.2	
	Dixidae [†]			0.7	0.7			0.1			1.0	0.3	0.5
	Dolichopodidae			0.3	0.1		0.1						
	Empididae											0.1	0.2
	Limoniidae			0.5	0.3	0.6	0.1	0.1		2.1			0.7
	Psychodidae [†]			3.4	0.3								
	Simuliidae										0.3	0.2	3.4
	Stratiomyiidae					0.3							
	Syrphidae [†]						<0.1						
	Thaumaleidae [†]			3.4	0.3								
	Tipulidae			0.6	0.1						0.1		0.2

(continued on next page)

Appendix S1 (continuation)

Group	Family	Genus/Species	Cork	oak		Eucal	yptus			Maritin	me pine	Э	
				Wood			Wood				Wood		
			Kick-net	None	Soil	Kick-net	None	Soil	Water	Kick-net	None	Soil	Water
Ephemeroptera	Baetidae	Baetis [†]		0.2	0.3	1.6	3.4	3.9		0.2	2.9	3.7	11.1
	Baetidae	Centroptilum [†]	8.5	1.0	2.5		0.1	1.5	0.3		0.2	0.9	
	Baetidae	Cloeon [†]		1.2	0.3								
	Baetidae	Procloeon [†]	17.0	1.0	0.8		0.1			0.5		0.8	
	Caenidae	Caenis	4.9	0.3	1.4	3.6	0.4	0.9		2.1	0.3	0.8	
	Ephemerellidae	Ephemerella [†]				0.3	6.5	11.9	0.2	0.5	0.7	1.5	1.2
	Ephemerellidae	Torleya						1.3	1.2				
	Leptophlebiidae	Choroterpes [†]	2.5	5.6	14.3						2.3	7.1	
	Leptophlebiidae	Habrophlebia [†]		0.1	0.4	12.6	10.6	16.1	32.0	15.5	19.9	37.6	20.8
	Leptophlebiidae	Paraleptophlebia						3.3					
	Leptophlebiidae	Thraulus		0.2		0.6	0.1	4.7	3.0	0.5		0.7	
Heteroptera	Corixidae		0.4									0.1	
	Gerridae			<0.1	0.2								
	Hydrometridae	Hydrometra		0.5	0.4								
	Mesoveliidae	Mesovelia		<0.1									
	Naucoridae	Naucoris		0.2	0.1						0.2	0.2	
	Nepidae	Nepa									0.1	0.1	
	Veliidae				0.1		<0.1						
Megaloptera	Sialidae	Sialis			0.1				0.2				
Odonata	Aeshnidae			0.1	0.1		0.1	0.4			0.7	0.8	0.7
	Calopterygidae	Agrion virgo										0.1	
	Gomphidae						0.1						0.2
	Lestidae		1.8	0.3	0.6				0.2				
	Libellulidae								0.2				
	***			0.3									
Plecoptera	Chloroperlidae						<0.1						0.2
	Leuctridae [†]					1.6	<0.1						1.0
	Perlidae						0.2						
	Perlodidae						0.1	0.5				0.1	
Trichoptera	Beraeidae [†]			<0.1						1.6	1.3	0.5	
	Glossosomatidae						0.1						
	Hydropsychidae [†]							0.2					1.5
	Hydroptilidae										0.1		
	Leptoceridae							0.2	0.2			0.2	
	Limnephilidae						0.3	0.4			0.3	0.2	0.2
	Philopotamidae [†]							0.1	0.2				0.7
	Phryganeidae					0.6							
	Polycentropodidae [†]					0.6	0.4	1.8	0.7		1.8	3.4	2.7
	Psychomyiidae [†]					0.6	0.1	1.9	11.2	0.2	0.1	0.1	
	Rhyacophilidae	Rhyacophila [†]				0.6	0.1		0.3				1.2
Total absolute a	bundance		283	2134	1139	309	3055	107 <u>9</u>	572	439	<u>117</u> 0	885	<u>597</u>

* and **: other genera within Hydrobiidae and Naididae (unidentified); ***: other family within Odonata (unidentified). †: taxa that contributed the most to all significant dissimilarities between wood preconditionings within sites based on SIMPER analysis.

Appendix S2. Values of taxon-trait links (trait affinity) assigned according to the trait database from Tachet et al. (2010) and re-scaled between 0 and 1. The table shows only the 26 taxa that contributed the most to all significant dissimilarities between wood preconditionings within sites, and the 23 trait categories where the effect of wood preconditioning was significant.

	Maximal potential size	Γ	ocomotic	on and :	substrate	e relatior	-	Fc	po					Fee	ding hab	its		Subst	rrate (pre	eferendi	(m		
Taxa	1-2 cm	<mark>.2-4</mark> cm	full water swimmer	crawler	burrower	interstitial	temporarily attached	pemanently attached	smsinsgroorganisms	mm t > sutitieb	sətydqoraim gnivil	mm↑ =< lsmins bsəb	sətərdətrəvnioroim privil	living macroinvertebrates	spredder	filter-feeder	predator	parasite	fiags/boulders/cobbles/pebbles	pues	microphytes	stoot/sgiwt	pnu
Dytiscidae	0.14	0.09	0.42	0.42	0.00	0.01	0.00	0.00	0.00	0.00	00.00	0.00	0.33 (.59	0.50 C	.00	02 0.	00	01 0.(06 0.	00	00.00	28
Elmidae	0.00	0.00	0.00	0.65	0.07	0.10	0.00	00.00	00.00	0.21	0.70	0.00	0.00	00.0	0.30 C	.00 00.	00 00	00	26 0.2	28 0.	00	0. 0.	00
Hydraena	0.00	0.00	0.43	0.43	0.00	0.00	0.00	0.00	0.00	0.25	0.75	0.00	0.00	00.0).25 C	.00 00.	00 00	00	38 0.	13 0.	13 0.	0.0	8
Chironomidae	0.24	0.08	0.21	0.34	0.18	0.13	0.13	0.00	0.02	0.28	0.23	0.02	0.19 (.14	0.13 C	.13 0.	22 0.	00 0.	18 0.(0 60	03 0.	0.0	08
Dixidae	0.00	0.00	0.23	0.15	0.00	0.00	0.15	0.00	00.00	0.27	0.40	0.00	0.33 (00.0	0.17 0	.50 0.	33 0.	00	33 0.(0 00	00 0.	14 0.	29
Psychodidae	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.18	0.18	0.18	0.00	00.0	0.50 C	.00	00 00	00	17 0.(080	00 00	13 0.	17
Simuliidae	0.00	0.00	0.00	0.29	0.00	0.14	0.57	0.00	0.00	0.63	0.25	0.00	0.13 (00.0	0.00 C	.75 0.	00 00	00	36 0.(05 0.	00	0.0	60
Thaumaleidae	1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.25	0.50	0.00	0.00	00.0).25 C	.00 00.	00 00	0.0	71 0.(0 00	00	.0 0.	14
Baetis	0.25	0.00	0.38	0.50	0.00	0.13	0.00	0.00	0.00	0.18	0.45	0.09	0.00	00.0	0.00 C	.00 00.	00 00	00	25 0.1	13 0.	00 00.	19 0.	00
Centroptilum	0.00	0.00	09.0	0.20	0.20	0.00	0.00	0.00	00.0	0.40	0.60	0.00	0.00	00.0	0.00 C	.00 00.	00 00	0.0	08	17 0.	00	<u> 0.</u>	17
Cloeon	0.00	0.00	0.75	0.25	0.00	0.00	0.00	0.00	00.0	0.33	0.33	0.00	0.11 (00.0	0.14 0	.00	00 00	0.0	0.0 0.0	0.00	00	0.0	18
Procloeon	0.00	0.00	0.75	0.25	0.00	0.00	0.00	0.00	00.0	0.33	0.67	0.00	0.00	00.0	0.00	.00	00 00	0.0	00 0.(0.00	00	00	00
Ephemerella	0.00	0.00	0.17	0.83	0.00	0.00	0.00	0.00	0.00	0.08	0.33	0.00	0.08	00.0	J.33 C	.00 00.	17 0.1	00	16 0.1	11 0.	00 0.	21 0.	1
Choroterpes	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.43	0.43	0.00	0.00	00.0	J.33 C	.00 00.	00 00	00	18 0.0	0.0	00 0.	18 0.	60
Habrophlebia	0.00	0.00	0.25	0.75	0.00	0.00	0.00	0.00	00.0	0.14	0.43	0.00	0.00	00.0	0.75 C	.00	00 00	0.0	00 0.(0.0	00 0.	20 0.	30
Physa	0.75	0.00	0.00	0.67	0.00	0.00	0.00	0.00	00.00	0.00	0.45	0.09	0.00	60.0	0.25 0	.00 00.	00 00	00	21 0.(07 0.	0.0	00	07
Lumbricidae	0.00	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.20	09.0	0.20	0.00	0.00	00.0	0.00	.00	00 00	00	13 0.	13 0.	00	0.0	60
Lumbriculidae	0.00	0.25	00.00	0.00	0.00	1.00	0.00	0.00	0.20	0.60	0.20	0.00	0.00	00.0	0.00 C	.00 00.	00 00	00	14 0.2	25 0.	04 0.	0.0	07
Naididae	0.33	0.14	0.45	0.00	0.20	0.25	0.07	0.02	0.06	0.38	0.42	0.00	0.08	90.0	0.00 0	.00	0 60	00	13 0.1	13 0.	0 60	0.0	7
Leuctridae	0.25	0.00	0.00	0.63	0.25	0.13	0.00	0.00	0.00	0.14	0.29	0.14	0.00	00.0	0.60 C	.00	00 00	0.0	19 0.`	14 0.	00 0.	19 0.	10
Beraeidae	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	00.0	0.13	0.38	0.25	0.00	00.0	0.91 C	.00	00 00	00	19 0.(0.00	00 0.	19 0.	29
Hydropsychidae	0.33	0.08	0.00	0.40	0.00	0.00	09.0	0.00	00.0	0.30	0.22	0.00	0.26 (60.0	0.00	.75 0.	25 0.	00	51 0.1	18 0.	00 0.	14 0.	00
Philopotamidae	0.30	0.00	0.00	0.40	0.00	0.00	09.0	0.00	00.0	0.43	0.48	0.00	0.00	0.05	0.00	.57 0.	06 0.	00	59 0.(05 0.	00	0.	1
Polycentropodid	ae 0.53	0.16	0.20	0.20	0.00	0.00	09.0	0.00	00.0	0.04	0.14	0.00	0.32 (.42	0.07 0	.23 0.	70 0.	00	31 0.0	05 0.	05 0.	10 0.	10
Psychomyiidae	0.11	0.00	0.00	0.36	0.00	0.00	0.54	0.11	00.0	0.26	0.44	0.00	0.12 (0.03	0.00	.28 0.	04 0.	00	51 0.(07 0.	00	24 0.	02
Rhyacophila	0.50	0.33	0.33	0.50	0.00	0.00	0.17	0.00	0.00	0.11	0.11	0.00	0.11 (.56	0.00	.00	00 00	0.	45 0.(0 0.	00 00.	18 0.	60





CHAPTER 7



General Discussion

7. General Discussion

7.1 Synthesis



This research lends support for its unifying hypothesis that fire has the potential to influence the long-term structure and function of Portuguese forested lotic ecosystems, besides driving landscape dynamics. Stream wood was confirmed to warrant consideration in terms of its implications for interpreting long-term fire consequences to streams (Nakamura and Swanson 2003). Via the research results on stream wood dynamics, this research showed that lotic ecosystems still reflect wildfires that occurred less than a decade prior and are likely to retain a strong fire signal for years to come. This fact became clear in Chapters 3 and 4, where more attention was given to lotic habitat structure, assessing primarily physical variables. This component of the thesis (Chapters 3, 4) documented fire-induced characteristics of stream wood in terms of its physical structure, quantity, and distribution in the stream network, further setting the scene for potential shifts in channel form with consequences for stream function. In the next component of the thesis (Chapters 5 and 6), wood-ecosystem functioning relationships (sensu Lyons et al. 2005, Wallace 2007) were evaluated, with Chapter 5 focusing on geomorphological, hydraulic, and ecological functions combined, while Chapter 6 further focused on the role of wood for stream macroinvertebrates. As one might have expected (see Elosegi and Sabater 2013), by dealing with variables also influenced by biological activities, the response of stream functioning to burned wood was complex and less straightforward. Overall, the effect of fire on stream wood functioning combined was indirect and burnt wood was likely innocuous relative to unburned wood for the patterns of macroinvertebrate colonization.

7.1.1 Portuguese wildfire-landscape dynamics

The set of studies forming this research was started by investigating wildfire-landscape dynamics in central and northern Portugal during a time period of about 14 years (**Chapter 2**). A unique perspective of this study was to specifically quantify the probability of land cover change in relation to wildfire occurrence and to identify which land cover transitions were likely fire-driven. Wildfires strongly influenced the landscape dynamics across the three fire-prone areas examined. Fire-driven transitions revealed that land abandonment led to increases in shrublands (encroaching into previously forested areas) and more mixed forests over time, such as mixed forests of maritime pine and eucalyptus. Especially in central Portugal, forecasted landscapes would present an increase in fire hazard. Under the landscape-scale scenario of shrubland expansion, large downed wood pieces from upland trees will likely become less abundant (see Rego et al. 2013) in central Portugal streams in the future. The eventual reduction in stocks of large wood can lead to important consequences for stream ecosystems, such as decreased habitat for fish, substrate for invertebrates and biofilms, leaf litter retention, transient storage, and hyporheic exchange (Gregory et al. 2003, Sawyer and Cardenas 2012).

7.1.2 Post-fire lotic habitat structure

Moving to a finer scale, the following studies were conducted in east-central Portugal in 27 streams evenly distributed by nine burned sub-basins of the Tagus River dominated by forests of cork oak, eucalyptus, and maritime pine. The first of these studies (Chapter 3) shed light on the specific effects of fire on physical characteristics of wood recruited to streams, with potential implications for lotic ecosystem structure and function. The overall structure of stream wood was strongly influenced by wildfire. Specifically, burned stream wood was straighter, had fewer branches, was more decayed, and was thicker in diameter than unburned wood. This suggested that stream wood burned status, while affecting size, geometry, and overall stability, will also likely influence the effect of wood on a stream's physical and biological condition, through direct and indirect mechanisms (Everett and Ruiz 1993, Gurnell et al. 2002, Chen et al. 2008, Schneider and Winemiller 2008). For example, alterations in size and shape can influence the degree to which wood affects biological diversity and biota abundance, and wood stability, in turn, influences channel morphology (Jackson and Sturm 2002, Andreoli et al. 2007, Comiti et al. 2008, Lester et al. 2009). Large wood pieces have a more sustained long-term influence on habitat and physical processes than small pieces (Dolloff and Warren, 2003). Likewise, by promoting wood lacking structural complexity (no branches, straighter), wildfire is likely reducing habitat complexity that improves conditions for aquatic organisms (Sundbaum and Näslund 1998). Furthermore, this was the first study to quantify species-specific differences in stream wood, clearly demonstrating that, even after burning, wood from separate species retain some differences in terms of their potential effect on stream ecosystem structure and function. Interestingly, some of these differences had to do with forest management practices.

Chapter 4 completed the second component of this research, i.e. the setting of the scene for post-fire lotic habitat structure in east-central Portugal. In general, this study showed that the three forested lotic ecosystems were probably far from recovery from the 2003-2007 wildfires, whose legacy was highlighted by the current 70% of burned wood per stream reach six years post-fire. Decay was high for 90% of the wood pieces examined. The low spatial organization of these pieces in the streams suggested that the present arrangement was largely a product of input dynamics; i.e. fire-derived wood was likely still entering the system at a rate higher than transport processes (and a consequent non-random distribution; Kraft and Warren 2003, Kraft et al. 2011). Also, the stock of wood in these 27 streams was notably low compared to values reported in the worldwide literature. Wood volume per area and distribution patterns differed among forest types, especially between cork oak and the other two forest types, having the least wood but in the most organized pattern. It was tested as well, and not supported by data, that the organization of wood in the river network would show increased aggregation from first to third order streams independent of forest type. Instead, the best predictor of wood volume and organization was the interaction between forest type and stream order. To explain these partly unexpected patterns, there are important specificities of these forest types common across the southern Euro-Mediterranean that were discussed as hypothetic explanatory variables, including within-channel vegetation obstructions, management actions, and fire effects.

7.1.3 Post-fire stream functioning

Stream wood amounts within these streams were thus remarkably low and the three former studies (Chapters 2, 3, 4) point out to a future fire-driven scenario where large wood will become even less abundant. Under these circumstances, individual pieces acquire additional importance for small streams (Rosenfeld and Huato, 2003), providing habitat for biota and the physical framework for ecosystem processes (Elosegi et al. 2010). Beyond the low abundances, only a subset of that wood will substantially influence geomorphological, hydraulic, and ecological functions. Understanding which stream wood would tend to become functional following wildfires was hence the goal for the next study (Chapter 5). As hypothesized upon the results of the second study (Chapter 3), i.e. burned status influencing stream wood size positively and complexity negatively, this study determined that fire affected stream function indirectly through relationships with wood characteristics. Burned pieces were more likely to be large in diameter (thus more likely functional) but not anchored (thus less likely functional); these antagonistic effects may be one reason burned status had no direct effect on function. On the one hand, the effect of fire providing wood with greater diameter will increase its probability for stream functions such as pool formation (e.g. Magilligan et al. 2008). On the other hand, this functionality may not persist because most of this wood was decayed and less stable in the channel. Besides examining the role wildfires may play in affecting functionality of recruited wood, this study used relatively novel modeling approaches and powerful tools for incorporating wood burned status with a large suite of potential functional factors and evaluated how they interact to determine nonlinear relationships and indirect effects on function.

Further reducing the scale extent (three 11-m stream reaches), the final step of this research focused on the topic on how wildfire structures aquatic communities through fire-derived wood (**Chapter 6**). The aims were to assess the effects of wood burn status and preconditioning on the patterns of colonization by stream macroinvertebrates. Contrary to expectations, the results demonstrated that taxonomic or functional patterns of colonization were not substantially different between burned and unburned wood, even after a year of incubation in the stream or on the forest floor. However, this study suggested that when fire occurs and affects riparian trees, the path of fallen wood to the stream has a disproportionate influence on epidendric macroinvertebrate colonization relative to the actual act of being burnt. When wood directly enters stream channels, it may attract more opportunistic taxa (chironomids acting as the major pioneer taxon), which consistently explains the taxonomic and functional patterns observed. Conversely, water- and soil-conditioned wood may have less dense colonizing communities, with greater taxa and functional diversities. Moreover, the type of wood conditioning did not differ markedly between them in terms of macroinvertebrate assemblages. Functionally, conditioned wood had taxa with higher shredding affinity, possibly feeding on living microphytes.

In terms of substrate affinities, macroinvertebrates preferring wood substrates (twigs/roots) also prevailed on conditioned wood. In general, water- and soil-conditioning drove food and substrate affinities similarly, except that taxa preferring to be temporarily or permanently attached to a substrate selected wood incubated in the stream for one year.

7.2 Applications

7.2.1 Management and conservation implications

Knowledge produced throughout this research provides useful information in developing guidelines for stream and riparian management operations. Nevertheless, the success of any practice will be limited by the Portuguese socio-cultural framework, legislation, and historical context. Dealing with large wood in streams may be somewhat controversial. For scientists and practitioners, wood can be currently recognized in a positive way but others can perceive riverscapes with wood to be less aesthetic, more dangerous, and needing more improvement than riverscapes without wood (Piegay et al. 2005, Gregory 2006, Wyzga et al. 2009). Throughout history, many Portuguese streams have been deprived of their natural wood loadings when people lived more near small rivers. But people no longer live in some rural areas nearby streams and so it is not feasible to comply with National legislation (e.g. Article 21 of Law 54/2005 of November 15 and number 5 of Article 33 of Law 58/2005 of 29 December) stating that owners of land including beds and banks of inland waters are required to clean and clear the waterways. As a curiosity, even an old profession called guarda-rios (rivers-keeper) no longer exists to ensure this. Furthermore, in terms of international policy, the European water framework directive (WFD) requires "good conditions" that are "not far from natural conditions" for streams throughout Europe. Clearly, stream wood plays an important role to meet the intent of this policy, and authorities seek for good management practices to meet WFD, namely following wildfires.

Overall, it is not advisable for an indiscriminate removal of wood from streams as a primary management option following wildfires. In central Portugal, in-stream large wood is not abundant and provides important functions for the morphology and aquatic habitat structure of these lotic ecosystems. Currently removing burned wood from these streams means removing most of this valuable resource, not a small part of the total wood. In addition, although shortly after wildfire, high inputs of wood to streams may have occurred because of tree mortality (Harmon et al. 1986, Benda and Sias 2003), during the current postfire period of regrowth the inputs are low (Minshall et al. 1989) and so removed wood may not be readily replaced. Alternatively, it is replaced by smaller pieces (e.g. from recovering trees); i.e. by less functional wood at least from a geomorphological perspective (Chapter 5). Removing burnt stream wood can also be a counterproductive measure as that wood is in general decayed wood that would naturally persist less in the system than sound pieces (Chapter 4). Removal of detached wood pieces should be especially avoided in small intermittent or temporary streams, such as those in

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some cork oak forests, where large wood is less abundant and may provide the only refuge during low flows, making stream wood particularly important to stream biota (Robson et al. 2012). On the other hand, as mentioned in Chapter 5, the suggestion that wood much longer than stream width is also less functional aligns well with security and navigability concerns, as this wood could also be the first to be removed after fire when decisions must be made that weigh safety versus ecosystem function.

A second major recommendation is that practitioners should consider leaving some sparsely dispersed fire-derived wood fallen from riparian trees on the stream bank or on the floodplain. The wood on the forest floor may remain there until it moves laterally into the stream channel during floods. This research clearly demonstrated that wood entering the stream after some time on the forest floor was colonized by macroinvertebrates differently than wood directly entering the channel, favoring aquatic communities with greater diversities (Chapter 6). In addition, large fire-derived wood (burned, unburned) lying near the stream usually deteriorates rapidly (Chapter 3), which may also contribute more to bank stability and sediment retention (Jones and Daniels 2008, Jones et al. 2011). However, a word of caution should be given because despite sparsely discarded wood pieces along the river banks are advisable, large piles of wood can be a different case. Within the years over which data were collected, it was observed several times the deposition of these large burnt wood piles into the stream, especially in cork oak agro-systems (e.g. slash from branch pruning for rehabilitation of burned trees). Especially when combined with within-channel vegetation obstructions, these wood jams soon become hydraulic problems. Under these circumstances, when channel form dictates an extreme spate risk, the removal of longer stream wood pieces may be considered.

An important finding of this research was that downed stream wood, even after burning, still retain species-specific physical architecture of the living trees and tree species could not be lumped together in terms of their effect on stream ecosystem structure and function or in-stream wood movement (Chapter 3). Furthermore, function of wood in streams is not simply a matter of wood size, along with indicators of longevity such as stability and decay status (Chapter 5). These conclusions are important points when considering restoration projects including the addition of natural and potentially mobile wood that is expected to develop function more naturally. Overall, practitioners installing wood to streams should consider pieces with wide diameter and rootwads, approximately 3 times the channel width, and anchored but not bridging the channel. It is acceptable to use wood previously conditioned on the forest floor (Chapter 6). Regarding tree species-specific differences, the operations aiming at increasing stream hydraulics and habitat complexity should avoid inputs from eucalyptus which have the simplest structure relative to most riparian species, cork oak, and maritime pine.

7.2.2 Research directions

Besides having contributed important findings to the body of research on the long-term consequences of wildfire for lotic ecosystems, this is the first work assessing large stream wood in an Euro-Mediterranean context. Many knowledge gaps still exist and several hypotheses shall be tested. Presently, three separate projects are ongoing to further address some topics raised during this work. Other gaps were likewise identified throughout this work pointing out to possible future research directions.

An ongoing project has been conducted since 2010 in three first- to third-order streams within one of the sub-basins already assessed for this research. Twice a year, once in the fall and another in spring, new burned/unburned wood pieces in the three stream reaches are being sampled and tagged, and all previously marked pieces are being resampled. Every fieldwork campaign includes monitoring changes in each wood piece measurements, location, position in the channel, complexity, decay, functions carried, among others. Thus, the spatio-temporal dimension was brought to the investigation of post-fire wood dynamics, which was not specifically addressed in this research so far. It will be possible to quantify inputs of burned wood over time as well, thus addressing the recovery rate of the system to fire. Furthermore, since these streams are characterized by strong seasonality and large intra- and inter-annual flow variations, this sample design will likely capture the wood-mediated long-term response of stream functioning to that variability (Gurtz and Wallace 1984).

A second ongoing project has been taking place since spring 2012 in a site located at Cedar River in Waverly, Iowa, USA. The project is being conducted in co-authorship with a working group from Wartburg College who is monthly analyzing macroinvertebrate colonization patterns on wood blocks and concrete bricks. Among other objectives, that work aims to test the hypothesis raised by the fifth study (Chapter 6) suggesting a possible shift in macroinvertebrate community composition over time on stream wood. This study will thus bridge the gap of a time series analysis which was beyond the scope of the fifth study.

Another co-authored study is about to be launched in August 2013 in tributaries to Lake Superior in northern Minnesota, USA, involving pairwise comparisons of burned and unburned streams. Part of the work consists in sampling stream wood applying the same methodology of the second study (Chapter 3). As discussed in Chapter 3, the second study could have been strengthened if wood from unburned streams were included for comparison to those of the burned sections, especially if the upland forest had not included fast-growing species such as eucalyptus. This design would prevent stand age from becoming a confounding factor when comparing attributes such as wood dimension. These prerequisites are satisfied in northern Minnesota. Lastly, a second goal of this coming work is to compare the distribution of wood in burned and unburned streams following the methods of the thirth study (Chapter 4). The hypothesis that the organization of wood in the river would increase within unburned streams will be tested.

In addition to this underway work, many gaps still exist and include the following:

- Stream wood of smaller dimensions should be considered in future studies. Considering the trend towards fire-driven landscapes with increasing shrublands (Chapter 2), a forecasted decrease in stream flow (Stahl et al. 2010, Lorenzo-Lacruz et al. 2012), and a consequent ongoing encroachment of upland plants into the channel (e.g. Santos M. 2010), stream wood of small dimensions (diameter < 0.5 cm; e.g. Elosegi et al. 1999) released by shrubs should not to be overlooked in future research in Portugal.
- The use of burned wood by fish should be studied. Because wood primarily provides habitat and refuge for fish, it is possible that fire-driven decreases in stream wood complexity (Chapter 3, 5) will affect habitat structure for fish.
- Stream wood should be tested for differences in nutrients and epixylic biofilms after conditioning in Portuguese streams. This should strengthen a study similar to the fifth study of this research (Chapter 6).
- There is no published information on decay rates of Portuguese's timbers in lotic environments. Throughout this research, it is suggested that decay rates for intermitent and temporary streams in central Portugal should be high.
- Wood should be specifically investigated as a refuge during low flows and floods. There is limited information on the role of wood in providing refuge sites in extreme hydrological events such as droughts and floods, and its potential to improve ecosystem resilience (Evans et al. 1993, Baillie 2011, Steward et al, 2012).
- A systematic historical record of wildfires in Portuguese rivers remains to be done. Tracking ancient fires could be done using charcoal morphology assessed from the sedimentary sequence (e.g. fine sediments from sand bars or retained by debris dams; Enache et al. 2006).

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Appendices



Appendices

Three abstracts for presentations at international conferences, three peer-reviewed publications and one book chapter were all written in co-authorship in the context of the research leading to this thesis.

<u>Vaz P.G.</u>, Pinto P., Rego F.C., Robinson C.T. 2010. Impact of Coarse Woody Debris Input in Contrasting Burned Forests on Stream Physical Attributes: A Mediterranean Perspective of the Long-Term Role of Fire. Oral Presentation. 2010 Summer Meeting. Joint Meeting with ASLO & NABS. Aquatic Sciences: Global Changes from the Center to the Edge. June 6-11, 2010 – Santa Fe, New Mexico, USA

Abstract

This study assessed long-term effects of wildfires on aquatic ecosystems in the Mediterranean Basin, Portugal. Among Mediterranean countries, Portugal is prominently targeted by wildfires. Since 1990, more than 25% of the country burned and in 2003 and 2005 the burnt area was maximal and created the need and opportunity for this ongoing study. In Central Portugal, 9 sub-basins burnt between 2003 and 2007, dominated by eucalyptus (euc), maritime pine (mpn) and cork oak (cok) were selected and 27 reaches of first to third order streams were sampled for coarse (>0.05 m diameter) woody debris (CWD). Line Intersect Sampling and Census techniques were used along burned valleys and corresponding streams, respectively. First results indicate differences on potential debris delivery to streams according to tree species, whether in relation to log lengths (mpn>euc>cok), diameters (cok>mpn>euc) and number (euc>mpn>cok). Output and retention of CWD to the stream channel are filtered by valley characteristics (shape and flow path ways), evidences of wildfire severity, post-fire vegetation recovery and retention features (e. g. fences and roads).

<u>Vaz P. G.</u>, Pinto P, Robinson C T, Rego F C. 2012. Factors Influencing Physical Functions of Instream Wood Following Wildfires in Central Portugal. Oral Presentation. XVI Congress of the Iberian Association of Limnology. July 2-6, 2012 – Guimarães, Portugal

Abstract

Wildfires are an increasingly common disturbance influencing wood recruitment to streams, and thereby affecting their physical and biological condition. We examined 27 1st- through 3rd-order Portuguese streams from forests of cork oak (CO), eucalyptus (Ec), and maritime pine (MP), which experienced extensive recent wildfires. Many of the streams were intermittent, with stretches remaining dry for several months.

We evaluated the physical structure of 1483 wood pieces intercepting stream bankfulls (1), and modeled the effects of wood characteristics (burned status, diameter, presence of rootwads) and its instream emplacement (position, location along the stream, wood length/channel width ratio, number of anchoring ends) on the probability of performing a physical function (e.g. creating pools and/or riffles).

Probability of function increases on wood of greater diameter, and decreases on pieces longer than ~3 times the channel width. Probability of function was higher in the second half of streams, reaching a peak at ~3/4 of their lengths. Wood pieces with more anchoring ends in either the bank or the stream have a higher probability of having a function, and the same trend can be found for pieces with rootwads. Concerning position, loose on the streambed have a higher probability of having a physical function, followed by pieces ramping on one bank only, and, finally, pieces spanning the channel (bridges) have the lowest probability of performing a function. A Bayesian structural equation model revealed that wood fire status indirectly positively affected function through an effect on diameter.

Climate models predict more droughts in the Euro-Mediterranean region in the future, where pools formed by instream wood may provide a major refuge for biota during low flows.

<u>Vaz P.G</u>, Pinto P., Robinson C.T., Rego F.C. 2012. Structure, standing stocks, and function of instream wood following wildfires in central Portugal. Oral Presentation. International Conference TEMPRIV - Ecohydrology and Ecological Quality in Temporary Rivers. September 12-14, 2012 – University of Évora, Évora, Portugal

Abstract

Wildfires are an increasingly common disturbance influencing wood recruitment to streams, and thereby affecting their physical and biological condition. We examined 27 1st- through 3rd-order Portuguese streams from forests of cork oak (CO), eucalyptus (Ec), and maritime pine (MP), which experienced extensive recent wildfires. Many of the streams were intermittent, with stretches remaining dry for several months.

First, we evaluated the physical structure of 2206 wood pieces surveyed within streams and across 100-200m transects perpendicular to the streams. Second, we quantified instream wood amounts and organization (segregated, random, aggregated). Third, we modeled the effects of wood characteristics and its instream emplacement on the probability of performing a function (e.g. creating pools and/or riffles).

Burned wood was larger and straighter, had branches less often, and were more decayed. Inputs from burned MP forests are more likely to change stream hydraulics, relative to inputs from Ec.

The best predictor of wood amount and organization was the interaction between forest and stream order. Wood organization was low, suggesting that it was largely a product of input dynamics rather than transport processes at this time.

Probability of function increases on wood of greater diameter, and decreases on pieces longer than \sim 3 times the channel width. Probability of function was higher in the second half of streams, reaching a peak at \sim 3/4 of their lengths.

Climate models predict more droughts in the Euro-Mediterranean region in the future, where pools formed by instream wood may provide a major refuge for biota during low flows.

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Relative importance of breakage and decay as processes depleting large wood from streams

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ABSTRACT

Large wood pieces affect virtually every physical, chemical, and biological process in fluvial systems, including hydraulics, transport of materials, algal biomass accrual, nutrient uptake, and trophic interactions. The processes that deplete wood are thus of broad importance to stream ecosystems. We assessed the relative contributions for breakage-induced mobilization (where pieces are more prone to transport as a result of breakage into shorter parts) and gradual biochemical decay to wood depletion rates in a field study on 12 northern Minnesota, USA, streams. Wood pieces>0.05 m in diameter for a portion>1 m in length were individually tagged (n = 651), measured, and remeasured a year later. Pieces showed significant reductions in density and branching complexity (i.e., branches and twigs) and 22% of pieces broke (i.e., lost 10% or more of length). Processes related to breakage and decay were examined using Bayesian structural equation modeling and multiple regression. Breakage was more likely for pieces that were thin in diameter, long, deeply submerged, braced, buried, and traveled long distances. Pieces lost more density if they were initially dense, traveled a long distance, were not deeply submerged, lacked bark, were thin in diameter, were steeply pitched, were long, and were not buried. Pieces lost more branching complexity if they were complex with little gap between them and the streambed. Actual mass losses related to breakage and decay were 7.3% and 1.9% (respectively), both less than the 36% observed for total fluvial export. In contrast to the associations of breakage and decay with structural properties of the wood pieces and their position, hydraulic and geomorphic variables (stream power, slope, velocity, width) had little effect.

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1. Introduction

Wood pieces affect virtually every physical, chemical, and biological process in fluvial systems, including algal biomass accrual (Coe et al., 2009), nitrogen uptake (Ashkenas et al., 2004), trophic interactions (Gregory et al., 2003), sediment storage (Daniels, 2006; Baillie et al., 2008), and fluvial transport of materials. Wood can have a dramatic effect on hydrodynamic channel roughness (Arcement and Schneider, 1989), and can also represent a large flux of organic carbon to oceans (West et al., 2011). The processes that deplete wood from streams are thus of interest. These processes include fluvial transport, biological decay, and physical breakdown along with burial in the streambed (Hyatt and Naiman, 2001) and removal by humans. In their literature review regarding wood in streams, Hassan et al. (2005) noted that a major knowledge gap existed regarding the relative importance of

different processes that deplete wood. In particular, quantification of wood breakage is rare, and no studies have quantified its effect as a process for wood depletion.

Among the mechanisms contributing to wood breakdown, gradual loss of wood mass through biochemical decay in situ has received more attention than depletion by physical processes (Gurnell et al., 2002); most studies have focused on decay of small wood veneers or twigs (Zare-Maivan and Shearer, 1988; Eggert and Wallace, 2007; McTammany et al., 2008). Although existing protocols for estimation of wood decay rates have the benefit of standardization, small pieces of wood may not be subject to the same depletion processes as larger pieces. Wood decays primarily on the surface, and the high ratio of surface area to volume for veneers and twigs can cause them to decay more rapidly than large pieces (Spänhoff and Meyer, 2004), making them inappropriate for estimating longer-term depletion of large wood. In addition, pieces of large wood, defined here as pieces>0.05 m in diameter for a portion > 1 m in length, are highly variable in physical structure (sensu Vaz et al., 2011) and in positional attributes (e.g., orientation or elevation). These idiosyncrasies - not present

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in standardized veneers – may play an important role in wood depletion, for gradual decay in situ and for susceptibility to fluvial transport (Cadol and Wohl, 2010).

Large wood depletion in streams is fundamentally a product of the interaction between downstream transport, burial, and decay (Gurnell et al., 2002). At a broad scale, these processes are affected by climatic differences. In cases where wood is constantly submersed at relatively low temperatures, it can remain sound for hundreds of years, such as in boreal forests (Arseneault et al., 2007). Conversely, in tropical regions decay rates typically are higher owing to higher rates of biological activity and consistently warm conditions. Stormflow also tends to be flashier in the tropics than in temperate zones, which may also lead to higher wood depletion via fluvial transport (Cadol and Wohl, 2010). In Mediterranean regions, streams may become intermittent in summer and expose wood to aerobic conditions, resulting in a faster decay rate (Vaz et al., 2013).

Fluvial transport of wood pieces has received recent attention thanks to its potential role in depleting wood from streams (Hyatt and Naiman, 2001; Wohl and Goode, 2008; West et al., 2011). Longer pieces clearly tend to be transported less readily (Bilby, 1984; Lienkaemper and Swanson, 1987; Jacobson et al., 1999; Gurnell et al., 2002; Daniels, 2006), but other attributes can also play a role. For example, one study found that burial, elevation relative to water level (i.e., submerged depth), length relative to wetted width, bracing, rootwads, and draft relative to wetted depth all had significant effects on mobilization of wood pieces (Merten et al., 2010). Although some of these variables are structural properties (Vaz et al., 2011) of a wood piece, others are flow-dependent and thus characterize conditions during a specific discharge.

The primary goal of this study was to assess, from a single data set, the relative importance of the main processes depleting large wood in streams. We directly compare depletion rates of large instream wood pieces by fluvial transport to rates from breakage-induced transport and rates from decay. Our data set has been used elsewhere to examine fluvial transport in terms of wood mobilization (Merten et al., 2010) and entrapment (Merten et al., 2011) in detail; herein we use new analyses to focus primarily on breakage and decay. We hypothesized that breakage would lead to more wood depletion than decay because breakage reduces the length of wood pieces and makes them more susceptible to mobilization and further transport. Comiti et al. (2006) found indirect evidence to support our hypothesis, noting that wood standing stocks showed a more rapid decrease in piece length than diameter in the downstream direction. A second goal of this study was to examine the factors that contribute to breakage or the loss of piece diameter, density, and branching complexity (i.e., attached branches and twigs). Our data set included 651 wood pieces from 12 streams, and our analyses used multiple regressions and Bayesian structural equation models.

2. Study area

The study area included 12 tributaries to Lake Superior in northern Minnesota, USA; stream orders included one second-order stream, five third-order streams, four fourth-order streams, and two fifth-order streams. The watersheds were dominated by second- and third-growth aspen (*Populus tremuloides*) forest, and the streams encompassed a wide range of geomorphic characteristics. At the reach scale, mean bankfull widths ranged from 3.4 to 24.4 m and bed slopes ranged from 0.001 to 0.034 m/m (Merten et al., 2011). Peak discharge during a fall stormflow event ranged from 2.1 m³/s at the Little West Knife River to 104.0 m³/s at the Brule River. A study reach (mean = 460 m length) was established in each stream to quantify wood characteristics. Channel beds were dominated by cobble and gravel, bedforms were generally riffle/pool although cascades were present in the steeper reaches, and standing stocks of large wood averaged 0.20 pieces per meter of stream length (Merten and Decker-Fritz, 2010). Streams in this area tend to be

nutrient-poor and flashy (Detenbeck et al., 2003), and indeed a stormflow event in fall 2007 redistributed much of the wood throughout the study area (Merten et al., 2010, 2011). Flow regimes include high snowmelt flows every spring, but stormflows in summer or fall are also common from relatively young forests and thin soils (Detenbeck et al., 2003).

Wood pieces in this study averaged 3.8 m in length and bankfull stream widths ranged from 3.3 to 24.4 m; thus the study considered a range of conditions in terms of length ratios (i.e., piece length relative to channel width). Only 8% of the pieces were in spanning logjams, meaning that the most transport occurred as uncongested flow (Braudrick et al., 1997) where pieces were moving with relatively little interaction with other pieces. Although decay rates of instream wood have not been previously studied in this boreal area of northern Minnesota, decay rates of aspen stakes on the forest floor are intermediate between those in tropical and temperate regions (Gonzales et al., 2008).

3. Methods

3.1. Data collection

We initially measured 1225 pieces of wood among the study streams in summer 2007, including all pieces that were > 0.05 m in diameter for a portion > 1 m in length. Pieces were only measured if they lay entirely within the bankfull channel or had a portion > 0.05 m in diameter extending into the bankfull channel width. We included pieces that were entirely dead but still rooted, or yet-alive but entirely uprooted. Pieces were tagged near each end and the center with three numbered tree tags.

Each wood piece was first characterized by its length, defined as the portion >0.01 m in diameter. Tree calipers were then used to measure diameters at both ends and the middle; mean diameter was calculated as the sum of end diameters plus twice the middle diameter, all divided by four. Thus for tapered pieces, mean diameters (and, by extension, volumes and weights) were determined more accurately than midpoint diameters alone. A core sample was extracted from each wood piece using an increment borer; the sample volume and weight were then measured to calculate sample density. Weight for each wood piece was calculated by $F_W = g \rho_{log} V_{log}$ where g is gravity, ρ_{log} is the density of the sample piece, and V_{log} is the total volume of the piece. Branching complexity was measured by assessing branches and twigs according to Newbrey et al. (2005).

Pitch was determined by visually categorizing the position of each piece relative to the stream bed as 0, $\pi/6$, $\pi/4$, $\pi/3$, or $\pi/2$ rad. For a sample (n=374) of all tagged wood pieces (n=1225), pitch was also measured using a clinometer. These clinometer measurements were used directly in the data analysis where available, and for the remainder of the pieces a corrected visual estimate was used by (i) determining the relationship between visual estimates and clinometer measurements ($r^2 = 0.73$) for cases where both were measured and then (ii) using this relationship to estimate the pitch for pieces based strictly on a visual estimate. Orientation was assessed as the angle of the wood piece in relation to the stream flow using categories of 0, $\pi/6$, $\pi/3$, and $\pi/2$ rad. The midpoint elevation of each piece was measured relative to the water level during the fall stormflow event (using surveyed benchmarks; Merten et al., 2010). This elevation thus represented the submerged depth for each piece and is related to hydraulic forces and wetting regardless of stream location. Gap was measured as the vertical distance between the bottom of the piece (at its midpoint) and the channel, and lateral distance was measured from the midpoint of each piece to the nearest bank. Stream power and velocity during the fall stormflow event were estimated at the location of each piece using surveyed cross-sections and HEC-RAS 4.0 hydraulic simulation models (http://www.hec.usace.army.mil/ software/hec-ras/), as described in Merten et al. (2010).
In summer 2008, all marked pieces of wood that remained in the study reaches were re-measured to assess changes, including new cores to measure density changes. In addition, wood decay rates were examined using 388 standardized veneers $(1 \times 25 \times 100 \text{ mm})$ crafted from local aspen (Populus tremuloides), the dominant tree species in the watersheds studied. Veneers were individually weighed and fastened to plastic mesh gutter guard using cable ties and identified by the colors of the cable ties. Between 25 June and 1 July 2008, mesh units were affixed to stream beds using long nails or rebar; and individual veneers were retrieved after 30, 60, 90, and 120 days. Samples were stored frozen until processing when veneers were lightly wiped to remove inorganic sediments, dried in an oven at 60 °C for 3 days, and reweighed. The exponential decay rate for veneers ($k = d^{-1}$; Eggert and Wallace, 2003) was determined for each stream by plotting days in the stream versus the natural log of the percent mass remaining; one of the 12 streams was too remote for veneer sampling and was excluded. Based on mean values for each stream, percent mass loss for veneers was regressed against percent breakage for large wood pieces, where breakage was defined as a reduction in length \geq 10% (a value large enough to be detectable amid measurement error).

3.2. Large wood characterization

We tested the length, diameter, density, and branching complexity of wood pieces for evidence of breakdown, using two-tailed paired *t*-tests for all pieces of wood that were recovered in 2008. Values were log-transformed as needed, and lengths that apparently increased over time (from measurement error) were held constant at the 2007 values.

A multiple logistic regression (Hosmer and Lemeshow, 2000) was completed with breakage as the response variable. Standard multiple regressions (i.e., not logistic) were completed for change in density and change in branching complexity. Predictor variables in all cases included the following initial conditions from each piece in 2007: length, diameter, density, branching complexity, presence of bark, and submerged depth (Erdmann and Merten, 2010). The final model was chosen using the stepAIC function in the statistical software R (version 2.10.1, available online at http://www.r-project.org/) to determine the model with the fewest significant predictors (Akaike Information Criterion; Burnham and Anderson, 2002), and the variance inflation factor was examined to cull any collinear variables.

3.3. Mass losses and structural equation modeling

We used wood pieces that were remeasured in 2008 to calculate mass losses during the one-year study period. Losses from breakage were calculated from these pieces as the percentage reduction in summed piece lengths from 2007 to 2008; actual values from 2008 were used for pieces that lost > 10% of their initial length (i.e., those that broke) and lengths were held constant for other pieces (i.e., those that did not break). Mass losses from biochemical decay were determined by combining the mean percent change in piece density with the mean percent change in diameter (if significantly different from zero).

We used structural equation modeling to separately examine the linkages between factors related to breakage and to highlight indirect effects not revealed by multiple regression. First, a path diagram was constructed based on theory using the following exogenous variables for each wood piece: diameter, change in diameter, length, density, change in density, branching complexity, change in branching complexity, bark presence, submerged depth, and distance traveled. Using the software AmosTM, error terms were added as needed, and regression weights were examined to iteratively add (based on modification indices) or remove (based on *p*-values) linkages from the model. Once a good model fit was achieved based on both the minimum discrepancy (Browne, 1984) and the root mean square

error of approximation, breakage was added as a categorical endogenous variable with linkages from all other variables. Bayesian estimation was then used to fit the model, and linkages to breakage were iteratively removed based on the posterior distributions of the regression weights. Specifically, linkages were removed if their 90% credible interval included zero.

We next completed separate analyses using structural equation modeling for the subset of pieces that moved (i.e., distance traveled was ≥ 10 m, considering measurement error) and the subset that did not move. Modeling methods were the same as described above, except that the models were simplified to omit variables that were more than two steps removed from breakage (e.g., variables that linked to another variable that linked to another that linked to breakage).

4. Results and interpretation

Wood pieces were idiosyncratic with much variation among individual pieces, but distributions for most parameters were unimodal among streams (Fig. 1). Mean values for diameter, length, density, branching complexity, submerged depth, and pitch were 0.15 m, 4.26 m, 0.78 g/cm³, 15.7, 1.00 m, and 0.21 rad (Fig. 2). These values represent the averages for the 651 pieces that were remeasured in 2008 after measurement in 2007. Regarding orientation, 22% were parallel to the flow, 21% were $\pi/6$ rad to the flow, 43% were $\pi/3$ rad to the flow, and 15% were perpendicular ($\pi/2$ rad) to the flow. Twenty-two percent of the 651 pieces that were recovered had been broken.

4.1. Veneer decay

Veneers averaged a 9.4% loss during the 120 days they were deployed (Table 1). Although 110 of the veneers were lost (during stormflows), an average of 25 veneers were recovered from each of the streams. There was no relationship between mass loss for veneers and breakage for large wood pieces (p > 0.1).

4.2. Statistical analyses for large wood

Wood pieces showed significant changes from 2007 to 2008 for most variables, including reductions in length (p<0.001; with 2007 mean of 4.25 m and 2008 mean of 3.99 m), density (p<0.001; with means of 0.79 and 0.69 g/cm³), and branching complexity (p<0.001; with means of 17.73 and 13.62). The exception was diameter (p=0.47), with means of 15.4 cm in 2007 and 15.5 cm in 2008. Of the 176 pieces that bore rootwads in 2007 (and were recovered in 2008), 14% had lost them.

Multiple regressions were significant for all variables considered (Table 2). Pieces were more likely to break (p<0.05) if they were thin in diameter, long, with greater gap, deeply submerged. There was also some evidence (i.e., inclusion based on AIC but p>0.05) that pieces broke more when they were braced, traveled a long distance, and located farther from the center of the channel. Pieces lost more density (Fig. 3) if they were dense, traveled a long distance, not deeply submerged, lacked bark, thin in diameter, in faster velocity, more steeply pitched, not buried, higher complexity, and with high length ratio. Pieces lost more branching complexity if they were short, more complex, had bark, and had less gap above the substrate (e.g., embedded pieces). There was also some evidence that pieces lost more complexity when buried, thick in diameter, in slower velocity, and more steeply pitched. Variance inflation factors were <2 for all variables.

4.3. Empirical modeling and structural equation modeling

Loss of mass through breakage was 7.3% over the one-year study. Mean loss by change in density of wood pieces was 1.9%, and there E.C. Merten et al. / Geomorphology 190 (2013) 40-47



Fig. 1. Distributions of (A) diameters (cm), (B) lengths (m), (C) densities (g/cm³), and (D) submerged depths (m) for wood pieces in 2007.

was no significant change in mean diameters (p = 0.47), thus we did not include diameter changes in calculations of mass loss.

The final structural equation model (SEM) including the full data set of all pieces had a posterior predictive p of 0.11 – indicating a marginal fit (Lee, 2007) - and confirmed the multiple logistic regression for breakage. A variety of linkages was present among variables (Fig. 4), but those that affected breakage directly were generally the same as those identified by multiple regression (Table 2). Exceptions were gap and lateral that were only present in the regression model; in the SEM, these variables were replaced with burial. In addition to the direct effects, a variety of indirect effects existed where a variable's effect on breakage was mediated by another variable. Most prominent was distance traveled, which appeared to affect breakage by integrating effects from many other variables. Pieces that moved long distances tended to be initially deeply submerged, in areas with high power but low velocity, had low pitch, were dense, not buried, had more gap above the substrate, were not braced, had low length ratio, and were thin in diameter. In addition, most variables present in regressions for change in density and complexity were also linked in the SEM, or effectively replaced with other variables



Fig. 2. Relationship of (A) initial density and (B) distance traveled with change in density for large wood pieces over one year.

(e.g., bark, length, and pitch in the SEM all had indirect effects on change in complexity via their linkages to initial complexity).

The SEM for the subset of pieces that did *not* move was simpler (Fig. 5), as the variable for distance traveled was omitted and fewer variables were retained in the final model. The posterior predictive p for the model of pieces that did not move was 0.28, indicating an acceptable fit. These pieces were more likely to break if they were thin in diameter, long, with greater gap, and deeply submerged — the same as the variables that were strongly supported by multiple logistic regression.

The SEM for the subset of pieces that *did* move suggested that these pieces were more likely to break if they were thin in diameter, lost less complexity, and were initially braced. However, the posterior predictive p for the model was 0.00, indicating an unacceptable fit and unreliable model.

5. Discussion

This study determined that breakage led to more wood depletion than did gradual decay of large wood. Breakage in the 12 streams

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Exponential decay coefficients for aspen veneers over 120 days; k is d^{-1} and intercepts are ln(% remaining); rates of breakage for large wood pieces are shown for comparison.

Stream	k	Intercept	r^2	% Mass lost	% Breakage
Beaver	-0.0003	4.627	0.20	3.5	17.4
East Beaver	-0.0002	4.603	0.41	2.4	15.0
French	-0.0004	4.620	0.48	4.7	17.4
Lt. East Knife	0	4.615	0	0	35.3
Lt. West Knife	-0.0016	4.596	0.56	17.5	27.0
Knife	-0.0004	4.621	0.49	4.7	14.5
Poplar	-0.0005	4.608	0.82	5.8	50.0
Sucker	-0.0014	4.631	0.53	15.5	23.1
Talmadge	-0.0013	4.643	0.86	14.4	25.0
Upper Knife	-0.0015	4.626	0.82	16.5	22.3
West Split Rock	-0.0017	4.638	0.94	18.5	26.5
AVERAGE				9.4	

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Table 2

Statistics for multiple regressions of changes in wood pieces; underlined values give the percent deviance explained; note that breakage used a logistic model.

	Coefficient	S.E.	р	VIF
Breakage 7.1%			< 0.001	
Intercept	-1.0537	0.2874	< 0.001	
Diameter	-0.0795	0.0175	< 0.001	1.292
Length	0.0990	0.0321	0.002	1.385
Gap	0.0039	0.0015	0.012	1.190
Submerged depth	0.2496	0.1062	0.019	1.122
Braced	0.3111	0.1934	0.108	1.037
Distance traveled	0.0004	0.0002	0.108	1.041
Lateral	-0.0096	0.0070	0.167	1.046
Change in density 48.0%			< 0.001	
Intercept	0.4549	0.0410	< 0.001	
Density	-0.7096	0.0309	< 0.001	1.195
Distance traveled	-0.0001	< 0.0001	< 0.001	1.105
Submerged depth	0.0395	0.0096	< 0.001	1.126
Bark	0.0752	0.0210	< 0.001	1.201
Diameter	0.0035	0.0011	0.001	1.057
Velocity	-0.0420	0.0159	0.009	1.121
Pitch	-0.0022	0.0009	0.011	1.085
Burial	0.0476	0.0201	0.018	1.084
Complexity	-0.0005	0.0002	0.028	1.190
Length ratio	-0.0253	0.0120	0.036	1.147
Change in complexity 10.5%			< 0.001	
Intercept	-8.1974	4.1108	0.047	
Length	2.2698	0.4364	< 0.001	1.511
Bark	9.7867	2.9626	0.001	1.233
Complexity	-0.1051	0.0330	0.002	1.335
Gap	0.0629	0.0228	0.006	1.370
Burial	5.4510	2.7871	0.051	1.071
Diameter	-0.3145	0.1614	0.052	1.189
Velocity	3.3947	2.1238	0.110	1.025
Pitch	-0.2016	0.1277	0.115	1.184

induced mass losses of 7.3% during the study period whereas decay caused 1.9% mass loss. Breakage leads to wood depletion by creating shorter parts that are more susceptible to fluvial export (Bilby, 1984; Lienkaemper and Swanson, 1987; Jacobson et al., 1999; Merten et al., 2010, 2011); the magnitude of breakage-induced depletion is thus heavily dependent on transport probabilities. Although this study focused on breakage and decay, it bears noting that mobilization of wood pieces through processes other than breakage or decay led to far greater depletion (36% of pieces). Under the range of conditions studied, fluvial transport appears to dominate wood depletion processes, with breakage and decay making smaller contributions.

A particular strength of the data set used is that it includes 651 natural, recovered wood pieces in 12 streams with a wide range of geomorphic conditions. Streams ranged from 0.001 to 0.034 m/m in slope, from 3.4 to 24.4 m in bankfull width, and from 2.1 to 104.0 m³/s in peak discharge (Merten et al., 2011). Further, the results from multiple regressions were corroborated by Bayesian structural equation modeling, with the latter having the advantage of revealing indirect effects. However, the data were limited to a single year, so it is unclear whether the results are representative in terms of climate and flow regime. It is also important to note that our estimates of breakage and decay were conservative - pieces that broke or decayed were likely exported from the study reaches more readily (owing to reduced length or density) and thus unavailable for remeasuring. Another issue is the interplay between breakage and decay, namely that pieces that decay may be more likely to break and pieces that break may be more likely to decay (as new surfaces are exposed to decomposing organisms). Finally, our definition of breakage is conservative, that is, pieces that lost <10% of their length were not considered to have been broken.

Our results agree with the findings of Comiti et al. (2006) that breakage can be more important to wood depletion than decomposition processes from loss of piece diameter. In that study, longitudinal distributions showed that wood piece lengths decreased more rapidly



Fig. 3. Rose diagrams in radians for (A) pitch and (B) orientation of large wood pieces in 2007. Pieces that were oriented parallel to flow align with the arrow.

in the downstream direction (presumably thanks to breakage) than did piece diameters. The same phenomenon could help account for the inverse relationship between watershed area and wood abundance in streams (Comiti et al., 2006); in downstream areas, the combination of shorter pieces (from breakage) and wider channels leads to greater rates of export (Merten et al., 2011).

5.1. Factors affecting breakage

Breakage of large wood pieces is a function of leverage forces and structural integrity. The identification of predictor variables with direct effects on breakage revealed several related mechanisms. Pieces were more likely to break if they were long and thin; such pieces can be acted upon with greater hydraulic leverage and have the least structural integrity (Tanaka and Yagisawa, 2009). Pieces that were braced or buried may also be more prone to breakage by providing a fulcrum against which hydraulic forces can act. The position in the stream appears to play an important role in the breakage of wood pieces, as predicted by Meleason et al. (2007). For example, breakage was more common among pieces that were deeply submerged, presumably owing to greater exposure to hydrodynamic forces, bedload, and ice flows. Pieces that traveled a greater distance were also more likely to break, possibly from the "molar action" of the channel as pieces bump and jostle their way downstream (Sykes, 1937, as cited by Jacobson et al., 1999). An alternate causal sequence is that pieces that broke were mobilized more readily and traveled a longer distance on average; both explanations likely hold some truth. Based on the models for subsets of pieces, it remains unclear what factors determine whether pieces will break once they have been set into motion, as this process may be highly stochastic.

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Fig. 4. Final structural equation model using Bayesian estimation to determine variables affecting breakage in the full data set of all wood pieces. Error terms are not shown. Arrows indicate a direct effect of one variable on another; variables linked directly to breakage have a direct effect whereas others have indirect effects (i.e., they affect other variables which themselves affect breakage) or no effects on breakage.

Unlike structural properties of wood pieces and their position, hydraulic and geomorphic variables had no measurable effect on breakage. This implies that – under the range of conditions studied – among-stream conditions are less important than among-piece conditions, which in turn implies that management for wood should focus on the pieces themselves (via direct additions or riparian management) more so than channel characteristics. The same was true for the structural equation model regarding loss in density or complexity, although the multiple regressions suggested a minor role for velocity.

Whereas we expected a significant decrease in piece diameters (Bilby et al., 1999), our diameter data may have been strongly affected by breakage. That is, mean diameter for the remaining part of a broken piece may increase or decrease if the lost part was smaller or larger.

5.2. Changes in branching complexity

Branching complexity may be an undervalued indicator variable for wood in streams. Factors contributing toward loss of complexity include initial complexity (i.e., having more branches to lose) and gap. Pieces with a larger gap between themselves and the streambed are more elevated above the bedload, which may bash off finer branches. Finer twigs contribute substantially to the surface area available to macroinvertebrates and biofilms and are processed more rapidly than large wood by invertebrate xylophages (Anderson et al., 1984). The rapid processing appears to be caused by higher ratios of surface area to volume (Golladay and Webster, 1988; Webster et al., 1999) and implies that branching complexity may be a good indicator of piece age for relatively new pieces. Stout branches (though not quantified here) could play a mechanical role in transport processes akin to that of rootwads (Braudrick et al., 1997) and preserve complexity by elevating wood pieces off the stream bed.



Fig. 5. Final structural equation model using Bayesian estimation to determine variables affecting breakage in wood pieces that *did not move*. Error terms are not shown. The model for pieces that did move was not significant and is not shown.

5.3. Changes in density

Density may be a proxy for structural integrity of large wood. Density loss was greater for pieces that were suspended above the channel, likely owing to greater biological activity above the water level (Dahlström and Nilsson, 2006). Biological activity (or lack thereof) may also explain the reduced density loss from pieces that were partially buried. Our field observations concur with others that decay classes based on observable categories (e.g., texture, shape, color) may have little bearing on density (Spänhoff et al., 2001) or age (Hyatt and Naiman, 2001; MacVicar et al., 2009), particularly in streams where bark or twigs can be rapidly removed by bedload and ice flows. Density appears to affect both processes examined in this study; pieces that lost density lost more mass directly through gradual decay and were also more prone to breakage.

5.4. Decay and fluvial transport

Whereas breakage of large wood is a function of physical forces, smaller veneers and twigs are more readily affected by biological processes (Zare-Maivan and Shearer, 1988; Eggert and Wallace, 2007). In the current study, mass loss from large wood pieces was 1.9% over one year; whereas mass loss from veneers was 9.4% over 120 days, likely because veneers exposed a greater surface area to biochemical decay relative to their volume. Although wood decay rates vary among tree species, nutrient limitation can also be important (Diez et al., 2002) and could explain the variation among veneer decay rates in this study. Nutrient levels in the current study appeared to be sufficient for biological processes, as the mean k-value observed for veneers was between values observed in other situations by Eggert and Wallace (2003) and Spänhoff and Meyer (2004). Although there was no relationship between veneer decay rates and large wood breakage in this study, the relationship would have been strong ($r^2 = 0.90$) had values from the Little East Knife River and the Poplar River been excluded. Breakage rates at the Little East Knife River were exceptionally high, and pieces there tended to be more slender than at other streams (8.8 versus 15.5 cm) and thus unusually prone to breakage. Breakage rates at the Poplar River were estimated with fewer pieces (n = 10)than other streams, and high breakage rates there may have been

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from chance. Further study would be useful in investigating the contribution of biological decay toward breakage.

Factors affecting the actual distance traveled by pieces were generally consistent with previous studies. That is, pieces with greater length ratio (Bilby, 1984; Lienkaemper and Swanson, 1987; Jacobson et al., 1999) and diameter (Haga et al., 2002) were more resistant to transport. Pieces suspended above the stream were also less prone to transport (Merten et al., 2010) compared to those that were deeply submerged and experienced greater hydraulic drag and buoyancy (Braudrick and Grant, 2000). Pieces that were braced or buried were less likely to be mobilized at all (Merten et al., 2010), and pieces that traveled long distances tended to lose more density.

5.5. Recommendations for future studies

Hassan et al. (2005) noted that the relative importance of different depletion processes was a knowledge gap regarding instream wood; our results suggest that further research should not undervalue the contribution of breakage. The standardized variables proposed for wood studies by Wohl et al. (2010) are useful for such breakage studies, and we particularly endorse density measurements for their utility in calculation of forces and mass (Merten et al., 2010, 2011) and as quantitative indicators of decay state (Spänhoff et al., 2001). Branching complexity also merits further attention, potentially using the protocol of Newbrey et al. (2005), which is both standardized and comprehensive. Future research should measure nutrients directly and examine the importance of water chemistry in accelerating decay and thus breakage of large wood, particularly in situations where tree species have notably different form, density, and branching complexity (e.g., Vaz et al., 2011). Study of breakage and decay for more than one year would also allow better judgment of temporal variability, and studies in different climactic regions would test the robustness of our results under different decay rates (Cadol and Wohl, 2010; Vaz et al., 2013).

6. Conclusions

Instream wood depletion is affected by breakage, fluvial transport, and decay; all three processes are interrelated. The present study is the first to assess the relative contribution of these three components from one data set. Through its effects on transport probabilities, breakage emerges as an important catalyst that can influence wood stocks in streams, with resultant implications for the many physical and ecological processes controlled by wood.

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Review

Landscape – wildfire interactions in southern Europe: Implications for landscape management

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ABSTRACT

Every year approximately half a million hectares of land are burned by wildfires in southern Europe, causing large ecological and socio-economic impacts. Climate and land use changes in the last decades have increased fire risk and danger. In this paper we review the available scientific knowledge on the relationships between landscape and wildfires in the Mediterranean region, with a focus on its application for defining landscape management guidelines and policies that could be adopted in order to promote landscapes with lower fire hazard. The main findings are that (1) socio-economic drivers have favoured land cover changes contributing to increasing fire hazard in the last decades, (2) large wildfires are becoming more frequent, (3) increased fire frequency is promoting homogeneous land-scapes covered by fire-prone shrublands; (4) landscape planning to reduce fuel loads may be successful only if fire weather conditions are not extreme. The challenges to address these problems and the policy and landscape management responses that should be adopted are discussed, along with major knowledge gaps.

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1. Introduction

Every year about 45000 forest fires occur in southern Europe, burning approximately 0.5 million hectares of forests and other rural lands (Camia et al., 2008). Despite the resources invested in fire prevention and suppression, the number of fires in recent decades has continued to increase remarkably (JRC, 2005). There is growing concern about the ecological and socio-economic impacts of wildfires, particularly under a climate change context that implies an increase in the frequency and severity of wildfires in European countries in the future (e.g. Arianoutsou, 2007; Mouillot et al., 2002; Pausas, 2004; Piñol et al., 1998).

At landscape level, ignition and spread of wildfires result from a complex interaction among ignition sources, weather, topography and land cover (e.g. Mermoz et al., 2005; Rothermel, 1983). From a management perspective, land cover (related to vegetation structure and fuel loads) is the only landscape variable influencing fire behaviour that can be manipulated. Wildfires start from a local epicentre (ignition point) and spread across landscapes as a function of the abundance and arrangement of disturbance-susceptible

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patches (Forman, 1997; Turner et al., 1989). Fire spread rate can be facilitated or retarded by landscape heterogeneity (Turner and Dale, 1990). Thus, the spatial pattern of fire ignition and spread across landscapes are affected by fire proneness, i.e. the differential fire behaviour in various land cover types that are not equally fire prone (e.g. Bajocco and Ricotta, 2008; Moreira et al., 2009; Moreno et al., in press).

Understanding this link between landscape pattern and fire spread would facilitate the definition of landscape-level management rules so that Mediterranean landscapes become less fire prone. A straightforward application of this knowledge lies in the definition of landscape-scale fuel breaks, whose main objective is to reduce fuel loads or change the spatial arrangement of fuels (i.e. the landscape structure), so that when a wildfire ignites in a well managed landscape, it spreads more slowly, burns with less intensity and severity, and is less costly to suppress (e.g. Duguy et al., 2007). However, the management implications of understanding the landscape-fire relationships are not restricted to fuel break design, as they also enable the definition of land use management rules and the design and implementation of policies leading to specific landscape goals (in terms of overall fuel patterns), ranging from forest and agricultural and rural development, to urban development policies.

In this paper, we review the available scientific literature on the relationships between fires and landscape patterns and provide a critical evaluation of the scientific findings with relevant implications for landscape management. We concentrate on the geographic region covered by European Mediterranean countries where fire hazard is highest and scientific research still has important knowledge gaps. We have organised the structure of this review as a series of sections, each starting with a sentence that constitutes a key message for landscape and policy managers, and then reviewing and summarising the available scientific support. The basic structure of the approach used is shown in Fig. 1. The concluding section



Fig. 1. Schematic overview of the approach used in the current study to address wildfire-landscape relationships in the Mediterranean region. Solid lines indicate the main drivers of fire spatial spread and intensity patterns across the landscape, whereas dashed lines show how management can influence these patterns. The key sentences addressed in the text are shown in italics. Land use/Land Cover (LULC) changes have promoted changes in land cover patterns, which influence spatial patterns of fire occurrence and fire intensity in the landscape. Both topography and weather/climate, also influence fire patterns and intensity. The landscape patterns resulting from fire cause further changes in land cover patterns. In this context, landscape management aims to promote land cover management and land use policies in order to change both the current trends in LULC and land cover patterns, so that decreased fire hazard is attained at the landscape level. The final purpose is changing fire patterns towards smaller or less severe fires.

addresses overall recommendations for landscape managers, knowledge gaps, and future trends under climate change.

2. Key concepts

Across the text we will use the definitions of Hardy (2005) for fire risk (the chance that a fire might start) and fire hazard (a fuel complex, defined by volume, type, condition, arrangement, and location that determines the degree of ease of ignition and the resistance to control). Fire hazard expresses the potential fire behaviour for a fuel type, regardless of the fuel type's weatherinfluenced fuel moisture content (Hardy, 2005). Fire danger is commonly defined by the factors affecting the ignition, propagation, difficulty of control, and fire effects on the ecosystem (Helms, 1988). Fire weather is defined as the weather conditions which influence fire ignition, behaviour and suppression. Definition of large fire (LF), in terms of burned area, varies across the globe (Viegas, 1998) and it can be defined as the upper tail of the fire size frequency distributions (Gill and Allan, 2008). In Europe, fires above 100 ha (e.g. Bermudez et al., 2009), 500 ha (Moreno et al., 1998) or 1000 ha (Piñol et al., 1998; Viegas, 1998) are generally considered as LF. Along the paper we also use the terms fire intensity and fire severity according to Keeley (2009). Thus, fire intensity refers to the energy release during a fire, expressed as, e.g. temperature or fireline intensity. Fire severity relates to the loss or decomposition of organic matter above or below ground. It is, thus, a measure of the impact of the fire on soil and vegetation. Typical indicators of fire severity include plant mortality, the degree of tree canopy damage by a fire, or the amount of surface litter consumed.

3. Mediterranean landscapes have increased fire hazard in the last decades: the role of land use/land cover

Land use/land cover (LULC) changes are related to fire hazard through changes in vegetation structure and fuel load composition which, along with topography and weather, are the main drivers of fire intensity and rate of spread (Fernandes, 2009; Fernandes and Botelho, 2003; Moreira et al., 2009; Rothermel, 1983). Thus, changes in LULC are directly linked to changes in landscape fuel patterns and fire hazard (Moreira et al., 2009; Moreno et al., in press). Increased fire hazard is expected where LULC changes have promoted an increase in plant biomass (fuel load), such as those resulting from the abandonment of agricultural lands (e.g. vegetation succession in abandoned farms, pastures or woodlands) or from afforestation activities (Table 1). Conversely, other LULC changes will decrease fire hazard when associated with the removal of biomass (e.g. land clearing or forest harvesting) (Rego, 1992).

3.1. Land cover influences fire patterns

Studies of fire patterns in landscapes confirm the differences in fire hazard associated with different LULC. Several studies have demonstrated that shrublands are the land cover most prone to fire, i.e. with a higher proportion of area burned than expected given the availability of this land cover in the landscape, in different places of the Mediterranean basin: Spain (Diaz-Delgado et al., 2004; Gonzalez et al., 2006; Gonzalez and Pukkala, 2007; Lloret et al., 2002; Sebastian-Lopez et al., 2008), France (Mouillot et al., 2003, 2005), Portugal (Moreira et al., 2001, 2009; Nunes et al., 2005), Italy (Bajocco and Ricotta, 2008), and Greece (Koutsias et al., 2009). This can be explained by several factors, namely the lower priority given to fire fighting in shrublands (on the assumption that they are the least valuable land cover), the number of human-caused ignitions (e.g. burning for rangeland management purposes, such as creating pastures) and the higher rate of fire spread in this LULC

Table 1

Drivers of landscape change in European Mediterranean areas, their resulting landscape patterns, and implications for fire hazard. \uparrow = increase in area/fire hazard; \downarrow = decrease in area/fire hazard. Larger arrows in bold indicate the predominant trend for drivers with both increase and decrease in fire hazard.

Drivers	Landscape patterns	Fire hazard
Decrease of farming activities	Forests ↑ Shrublands ↑ Agricultural areas ↓	↑
Decrease of pastoral activities	Forests ↑ Shrublands ↑ Grasslands and pastures ↓	↑
Population ageing and decline/ Emigration	Forests ↑ Shrublands ↑ Agricultural areas ↓	↑
Afforestation/reforestation	Forests ↑	↑
Decreased exploitation of timber and wood resources	Forests ↑ Shrublands ↑	1
Increase of urban, tourist and industrial developments	Forests ↓ Shrublands ↓ Urbanized areas ↑	\downarrow ↑
Increase of farming activities	Forests ↓ Shrublands ↓ Agricultural areas ↑	Ļ
Increase of pastoral activities	Forests \downarrow Shrublands \downarrow Grasslands and pastures \uparrow	\downarrow ↑
Population increase/Immigration	Forests↓ Shrublands↓ Agricultural areas↑ Urbanized areas↑	↓↑

(Duguy et al., 2007; Fernandes, 2009; Moreira et al., 2009). Additionally, as a consequence of shallower soils that prevent dense forest to establish (Garcia-Fayos et al., 1995) and abandonment of hard-to-mechanize terrace cultivation (Tatoni et al., 1994), shrublands are a common land cover type in steeper slopes where the rate of fire spread is higher. On the contrary, cultivated areas (particularly those with irrigated crops) are the LULC less fire prone, burning in a lower proportion than the surface they cover in the landscape (Nunes et al., 2005; Moreira et al., 2009; Moreno et al., in press). The main reasons for the low fire-proneness of agricultural areas include their low combustibility, and their geographic association with human presence enabling quicker fire detection and easier fire fighting. Forests are usually more fire prone than agricultural areas, but less susceptible than shrublands. Within a forest context, studies in Portugal suggest that mature forests of broadleaved deciduous and mixed forests generally have a low fire hazard compared to pure pine forests, eucalypt plantations, or mixed pine and eucalyptus stands (Fernandes, 2009; Moreira et al., 2009). However, forest structure may be more important than forest composition in defining hazard (Fernandes, 2009). In fact, differences between forest types may be explained by different fuel structures, e.g. the degree of canopy closure that limits the development of a grassy or shrubby fuel bed and maintains vegetation with high moisture content (Gracia et al., 2002; Pausas et al., 2008; Vazquez et al., 2002; Zavala et al., 2000). There is some evidence that mature evergreen oak forests can even become 'self-protective' against wildfires, to the point of fire self-extinction (Fernandes et al., 2010).

In addition to landscape composition, landscape configuration also has strong implications for fire hazard. For example, the spatial patterns formed after the abandonment of rural areas have created landscapes of high combustibility through increasing significantly the availability and contiguity of fuel loads (e.g. Mazzoleni et al., 2004; Sluiter and de Jong, 2007; Saglam et al., 2008). Some studies have confirmed that fire hazard was greater in the more contiguous and homogeneous landscape portions (Lloret et al., 2002; Vega-García and Chuvieco, 2006). Other studies applied fire resistance rules to LULC types at the scale of fire events (Viedma et al., 2009) or at both stand and landscape scales (Gonzalez et al., 2005, 2008) and showed that landscape resistance to fire was negatively influenced by the spatial contiguity of LULC, and positively influenced by the diversity resulting from fuel contrast at fire edges. Simulation models also showed that fire spread and behaviour were greatly influenced by the spatial distribution of fuels (Duguy et al., 2007).

3.2. Landscape changes have been increasing fire hazard in the last decades

Studies of LULC changes in the Mediterranean Europe typically have a time span of 30–50 years, since the 1950's (coinciding with the first available aerial photographs) to the beginning of the XXI century, although there are exceptions, e.g. Preiss et al. (1997; ca. 15 years) and Mouillot et al. (2005; more than 200 years). The usual extension of a study area is 3000–5000 ha, but is also highly variable, e.g. 40 ha in Baudry and Tatoni (1993) to the whole of Italy (Falcucci et al., 2007). Aerial photographs, satellite images and land use or land cover maps have been the most common sources of data used.

A large number of studies have provided evidence of increased fire hazard in Mediterranean rural areas, mainly due to the increased cover of forests and shrublands in areas with former lower fuel loads and fire hazard (e.g. agricultural or pastoral land) (Table 1). For example, Van Doorn and Bakker (2007), in a region of southern Portugal, registered a 75% decline in the area of agricultural fields during the period 1985–2000, and an increase in matorral (shrubland) and forest plantations. Falcucci et al. (2007), for the whole of Italy, measured a 74% increase in forest cover during the period 1960–2000, and a 20% decrease in agricultural areas.

Several other studies have shown similar patterns of change across different countries: Portugal (Moreira et al., 2001; Moreira and Russo, 2007), Spain (Lloret et al., 2002; Pérez et al., 2003; Romero-Calcerrada and Perry, 2004; Viedma et al., 2006; Vega-García and Chuvieco, 2006; Duguy et al., 2007; Hill et al., 2008; Olarieta et al., 2008), France (Debussche et al., 1999; Taillefumier and Piégay, 2003; Mouillot et al., 2005), Italy (Peroni et al., 2000), Greece (Papanastasis et al., 2004) and Israel (Carmel and Kadmon, 1999), among others.

Agricultural land abandonment, including the decline of pastoral activities, is the major driver of landscape changes and increased fire hazard (Table 1), mainly in mountainous areas (Acosta et al., 2005; Aranzabal et al., 2008; Falcucci et al., 2007; MacDonald et al., 2000; Papanastasis et al., 2004). This abandonment is caused by the low economic profitability of these areas and is often associated with ageing, emigration and rural population declines. Marginal agricultural land, often located in steeper slopes, is the first to be abandoned (e.g. Peroni et al., 2000; Sluiter and de Jong, 2007; Van Doorn and Bakker, 2007). Vegetation succession then leads to scrub encroachment and forest development (e.g. Arianoutsou, 2001; Carmel and Kadmon, 1999; Scozzafava and De Sanctis, 2006). Even if farming activities do not disappear completely, the abandonment of traditional practices of exploitation of timber and wood resources (Debussche et al., 1999; Moreira et al., 2001) contribute to increasing fire hazard. Reforestations and afforestations, which have been promoted in the Mediterranean region in the last decades, both under the scope of forest policies (e.g. Pausas et al., 2004a), or, more recently, as a policy-driven management alternative in abandoned agricultural land (e.g.

MacDonald et al., 2000; Pausas et al., 2004a), have achieved certain environmental goals (i.e. to increase carbon sink capacity or to stop desertification processes), but have also increased fire hazard when creating large areas with homogeneous even-aged stands of flammable species (cf. \S 3.1).

In contrast to the general trend, only a small proportion of the studies, mainly located in coastal areas, provided evidence of decreased fire hazard coupled with the loss of forest and shrubland cover. For example, Serra et al. (2008) described increased agricultural activities and urbanization in a coastal region of southern Spain. Similar patterns were described for coastal areas in Turkey (Alphan and Yilmaz, 2005), Lebanon (Jomaa et al., 2008) and Italy (Corona et al., 2007; Falcucci et al., 2007). These changes have been driven by developments in urbanization, tourism and industry, increases in population and intensification of agricultural practices (e.g. Serra et al., 2008; Tanrivermis, 2003; Van Eetvelde and Antrop, 2004), including livestock grazing (e.g. Lyrintzis, 1996).

Depending on the social context in specific regions, some drivers may have a dual effect on fire hazard (Table 1). For example, LULC changes reflected in a hypothetically lowered fire hazard, because of biomass removal, may in fact increase fire risk. These include a more intensive use of pastures associated with an increasing use of fire for pasture renewal (Arianoutsou, 1998; Bajocco and Ricotta, 2008; Martinez et al., 2009; Mouillot et al., 2003), or an increased wildland-urban interface due to urban sprawl (e.g. Arianoutsou, 2001; Curt and Delcros, 2010; Martinez et al., 2009; Romero-Calcerrada et al., 2010; Wittenberg and Malkinson, 2009; Vasconcelos et al., 2001; Vazquez et al., 2002). In fact, population density and distance to roads are the major drivers of ignition risk and recent fire research studies identified the rural-urban interface as the most fire prone areas in Mediterranean countries (Badia-Perpinya and Pallares-Barbera, 2006; Catry et al., 2009; Curt and Delcros, 2010; Moreira et al., 2009).

In summary, most observed landscape changes can be described by what Hill et al. (2008) called the "rural exodus syndrome", the widespread increase in vegetation biomass over wide areas of southern Europe and the "strong urbanization tendencies and concentration of population along the coasts and in major cities, contrasting with decreasing population in the hinterlands". This seems to be the main trend across all the European Mediterranean countries, causing increased fire hazard except near the coast and in specific locations where tourism, intensification of agriculture and urban development prevail (Hill et al., 2008; Mazzoleni et al., 2004). This overall trend in southern Europe strongly contrasts with that observed in Mediterranean North African countries, where deforestation as a result of grazing, clearing for agriculture, woodcutting for heating and charcoal production (Mazzoleni et al., 2004), coupled with increasing population, contribute to decreasing fire hazard.

4. Large fires are becoming more common in the Mediterranean region: the role of weather, landscape patterns and fire suppression policies

4.1. Large fires are becoming more frequent

Large fires (LF) are relatively new in the recent history of the Mediterranean Basin (Lloret and Marí, 2001). Recent exceptional fire seasons (e.g. 1978/79 and 1994 in Spain, 1998, 2000 and 2007 in Greece, 2005 in Portugal, 2003 throughout Europe) helped to highlight the importance of LF in the Euro-Mediterranean (e.g. Oliveras et al., 2009; Piñol et al., 1998; Pausas, 2004; Xanthopoulos, 2007a). LFs represent a small fraction of the total number of fires, but are responsible for a large percentage of the total land area burned in the Mediterranean basin (e.g. Bermudez et al., 2009;

Diaz-Delgado et al., 2004). They tend to occur under specific, relatively uncommon synoptic meteorological conditions (like high temperatures, prolonged drought and strong winds), have different behaviour (e.g. higher intensities), have different patterns and spread mechanisms, a lower range of suppression options, and, depending on their rate of recurrence as well as landscape-scale variation in severity, more adverse ecological effects (Bermudez et al., 2009; Diaz-Delgado and Pons, 2001; Gill and Allan, 2008; Pausas et al., 2008; Romme et al., 1998).

Although some studies reported an increase of LF occurrence in Spain during the last decades (Diaz-Delgado et al., 2004; Moreno et al., 1998), others found no evidence of increasing or decreasing trends over time in Portugal (Bermudez et al., 2009), in France (Amouric, 1992) or at the European scale during a period of ca. 20 years (San-Miguel and Camia, 2009), suggesting that regional trends could be quite variable. For example, Bermudez et al. (2009) analysed the occurrence of LF in Portugal during a period of 21 years and found a cyclical pattern of occurrence of extreme fire sizes, with a return period of 3-5 years, and argued that this might result from post-fire recovery response of vegetation (i. e. rates of fuel accumulation), more than meteorological or anthropogenic factors. On the contrary, Pausas and Fernandez-Muñoz (in press) showed a large increase in LF occurrence in the 1973-2006 period in Valencia region (Spain), in relation to the 1873-1972 period.

In summary, although the number of fires and total burned area has increased in southern Europe, a clear trend of increasing occurrence of LF is not always the rule, as there is wide geographic variability. However, existing evidence does suggest an increase in LF frequency in several regions, either monotonically or in a cyclic pattern.

4.2. Fire weather is more important than landscape pattern in determining fire spread

There is still a debate on whether landscape pattern or meteorological conditions are the fundamental controller of fire spread, or whether temperature alone can explain recent and forecasted trends in fire occurrence in the Mediterranean basin (Piñol et al., 2005). While in some areas, such as in the boreal forest, it appears that landscape plays a less important role in determining what is burned by fires (Podur and Martell, 2009), in the Mediterranean region, selectivity by fire towards certain LULC types show that the landscape plays a more critical role in fire spread (e.g. Bajocco and Ricotta, 2008; Moreira et al., 2001, 2009; Moreno et al., in press).

Overall, inter annual variability in burned areas is closely linked with annual climate indices of drought, temperature or a combination of both. This has been shown from recent global remote sensing studies (Van der Werf et al., 2003) and used in global fire models (Thonicke et al., 2001). In the Mediterranean, these indices remain valid at the landscape (Mouillot et al., 2003) and regional levels (Pausas, 2004; Pereira et al., 2005; Vazquez and Moreno, 1993; Viegas and Viegas, 1994) with as simple indices as summer rainfall explaining a significant proportion of annual variability in total area burned. For example, in Cantabria (north Spain), most fires occur in conjunction with "Suradas", a weather event which combines high winds and low humidity, resulting in high-risk situations (Carracedo et al., 2006). Extreme fire weather may further promote the occurrence of fire brands and spot fires, leading to indirect climate-related extreme fire events in terms of area burned. In the Mediterranean region, people-ignited fires are largely predominant over natural ignitions, but Vazquez and Moreno (1998) showed that the number of lightning fires is also increasing, and this cause was associated to some of the largest

recorded fires (Moreno et al., 1998; Vazquez and Moreno, 1998). Thus, LF occurrence can be favoured by an increase in naturally caused ignitions, eventually even being influenced by solar activity (Gomes and Radovanovic, 2008).

In spite of the trend for the total area burned being correlated with climate, there is scarce evidence that average (or maximum) fire size increases with harsher fire weather conditions (e.g. Piñol et al. (1998) in Spain and Good et al. (2008) in Italy and Greece). Some studies do not even show a relationship between climate and fire occurrence (Fule et al., 2008; Wittenberg and Malkinson, 2009), confirming that other processes are also involved in fire ignition and spread.

Currently, the relative contribution of weather versus landscape pattern on fire spread in Mediterranean landscapes may be related to thresholds in fire weather that allow (or not) the landscape pattern to arise as a driver enhancing or, in particular, inhibiting fire spread. Under moderate fire spread conditions, fires tend to be smaller, and fuel spatial patterns would exert a stronger control on fire spread. Thus a higher selectivity towards flammable fuels would be expected. Extreme fire weather could produce large wildfires whose spread is not determined by landscape structure (Salvador et al., 2005; Moritz et al., 2010). In the past the situation may have been different. In a recent study, Pausas and Fernandez-Muñoz (in press) suggested that fire regime changes in the western Mediterranean were different before the 1970s, where fires were mostly fuel-limited, from the present, where they are mostly drought-driven.

4.3. Fire suppression policies increase large fire occurrence?

Fire suppression policies can also lead to fuel accumulation and LF outbreaks (e.g. Oliveras and Piñol, 2006). Piñol et al. (2005) used a model of vegetation dynamics and fire spread, calibrated with real data from 2 areas in the Iberian Peninsula, to evaluate the effect of different fire fighting capacities on LF occurrence. Interestingly, their simulations showed that higher fire-fighting capacities, or a lower number of ignitions, resulted in the same total annual area burned but with a higher proportion of LF. In fact, the reinforced funds on fire suppression policies observed in Mediterranean countries (especially after disastrous fire seasons), if not combined with fuel management, seem to be effective at reducing small fires, but not large ones (Diaz-Delgado et al., 2004; Duguy et al., 2007; Gonzalez and Pukkala, 2007; Xanthopoulos, 2007b, 2008a). Events in Greece since the dramatic fire season of 2000 are a good example for this. As warned by some (e.g. Xanthopoulos, 1998, 2007c), a strong fire suppression policy implemented in the 2001–2006 period, that temporarily appeared to be successful, did not solve the country's fire problem. In 2007 Greece experienced its worst fire season ever, with fires exceeding 20000-30000 ha mainly as a result of fuel accumulation.

5. Higher fire frequency in specific topographic locations and previously burned areas is creating homogeneous landscapes covered by shrublands

Contrary to what could be expected from the fuel-age paradigm, which states that fuel reduction as a consequence of wildfires would reduce the risk of future fires (Zedler and Seiger, 2000), there is evidence that areas previously burned are characterized by a higher probability to burn when compared to areas that were never burned. So, it seems that previous fires determine conditions that favour a new fire in a relatively short time period. The repeated burning phenomenon might be interpreted as a result of several spatial legacies influencing fire occurrence, nested within each other, and resulting in a strong spatial dependence of fire on previously burned areas. The mechanisms that might contribute to and the consequences of repeated burning are summarised below.

5.1. Fire hazard is higher in specific topographic locations

Topography (altitude, exposure, slope) can affect fire frequency and rate of spread. The causes behind these topographic effects can be grouped into fire ignition patterns, fire behaviour (in particular rate of spread), and fuel biomass. Disentangling these processes is not easy, as they are interrelated and dependent on the spatial scale (i.e. grain and extent). In fact, topography interacts with local wind direction, microclimates and, in turn, vegetation type, fuel loads and moisture content. Several studies have shown topographic influences on vegetation composition and structure (Fontaine et al., 2007; Rescia et al., 1994), transpiration and desiccation conditions (Rana et al., 2005; Van der Trol et al., 2007), vegetation dynamics (Carmel and Flather, 2004; Mouillot et al., 2005), fire severity (Broncano and Retana, 2004), and post-fire vegetation regeneration (Peñuelas et al., 2007; Baeza et al., 2007). Furthermore, some of the observed topographic effects on fire occurrence can be explained by human activities (e.g. Carmo et al., 2011; Catry et al., 2009; De la Cueva et al., 2006; Martinez et al., 2009; Romero-Calcerrada et al., 2010; Salvador et al., 2005). As an example, in some regions higher probabilities of ignitions have been estimated at higher altitudes, because of a higher likelihood of lighting and human use of fire for the management of pastures for livestock (Catry et al., 2009; Kilinc and Beringer, 2007; Price and Rind, 1994; Vazquez and Moreno, 1998). In other locations, high ignition risk is associated with flat and lower elevated areas because of the proximity to roads, human settlements and urban interfaces (Vasconcelos et al., 2001).

As a result, several studies have provided evidence of significant spatial pattern of fire recurrence associated with certain topographic positions across the Mediterranean region. For example, Mouillot et al. (2003) found that south facing slopes and ridge crests burned more frequently than other positions in Corsica (France). Similar patterns were observed by Vazquez and Moreno (2001) in Spain, and Trabaud and Galtié (1996) in the French Pyrenees. Fire spread simulation models, such as FARSITE (Finney, 1998), and FIRETEC, recently applied for Mediterranean landscapes in Italy (Arca et al., 2007), middle East (Carmel et al., 2009), Spain (Duguy et al., 2007) and France (Pimont et al., 2009) have highlighted the intrinsic preference for fire spread towards certain topo-climates as high altitudes and uphill directions where local winds, usually blowing towards the ridge top in the daytime, enhanced the topographical effect (Boboulos and Purvis, 2009).

5.2. Fire frequency is creating homogeneous areas covered by shrublands

Some pine forests have a low resilience to increased fire frequency. For example, *Pinus halepensis* and *Pinus pinaster* forests in eastern and Central Spain show very low resilience when burned frequently, turning into shrublands in the medium to long term after fire (e.g. Baeza et al., 2007; Pausas et al., 2008). The same was shown by Arianoutsou et al. (2002) for *P. halepensis* forests in central Greece. The reason behind this shift is related to the characteristics of the reproductive biology of these pines (Arianoutsou, 1998). *P. halepensis* individuals reach their full reproductive capacity when 15–20 years old by having a canopy seed bank in their serotinous cones. Hence, when a fire occurs over a previously burned pine stand with a return interval shorter than this time window, pines will not regenerate and the structure of vegetation communities is changed to one dominated by grasses and shrubs (Eugenio et al., 2006; Kazanis and Arianoutsou, 2004; Kazanis et al.,

2007, 2009; Lloret et al., 2003) (Fig. 2). A similar pattern should be expected for *Pinus brutia* forests.

Other fire-sensitive pine species as Pinus nigra and Pinus sylvestris which are not serotinous, do not have any specific adaptation to cope with fire and their recovery is mainly dependent upon the seed dispersal from unburned patches (Arianoutsou et al., 2010; Buhk et al., 2007; Eugenio and Lloret, 2004; Eugenio et al., 2006; Retana et al., 2002; Rodrigo et al., 2004, 2007). In the case of some deciduous oak communities, the recovery process after fire is very low, and more than 50-60 years are needed to reach the prefire conditions (Calvo et al., 2002a,b; Jacquet and Prodon, 2009). During the initial stages (0-20 years) homogeneous shrubland communities dominate spatially and influence negatively the growth of Quercus pyrenaica (Alvarez et al., 2009; Calvo et al., 2002a,b). Hence, short fire intervals could favour the expansion of shrublands communities or the persistence of resprouting oak forests with a shrubland-type physiognomy (Fig. 2). Even for some evergreen oaks (as Quercus suber and Quercus ilex) that show vigourous resprouting after fire and a quick recovery (Debussche et al., 2001; Espelta et al., 2003), high fire frequencies may decrease such ability (Diaz-Delgado et al., 2002; Trabaud and Galtié, 1996). Finally, in burned old croplands post-fire succession is mostly limited to obligate-seeders, a process that has resulted in the spread of Mediterranean gorse shrublands (Ulex parviflorus) in some areas, increasing the risk and severity of fires (Baeza et al., 2007) (Fig. 2).

5.3. Fire frequency is higher in previously burned areas

Several authors have documented high fire recurrence in previous burned areas across several Mediterranean countries. For example, in central Corsica (France), some areas were burned up to 7 times from 1957 to 1997 (Mouillot et al., 2003). In Catalonia (Spain), ca. 12% of the total areas burned during 1975–1998 burned twice during this period (Diaz-Delgado et al., 2004). In an area of Central Spain, the forests that burned twice in the years 1970–1990 accounted for about the 7% of the total forest area burned (Vazquez and Moreno, 2001). In Italy, 60% of the forest fires in the period 2005–2009 occurred in areas that had been burned in the past ten years (CFS, 2005, 2006, 2007, 2008, 2009).

As was mentioned in the previous section, one first explanation for the increased fire recurrence is the low resilience of some forest types, which prevents auto-succession and favours the establishment of more fire-prone fuel types (Acácio et al., 2009; Lloret et al.,



Fig. 2. Summary of processes leading to the replacement of forests and agricultural land by shrublands and grasslands in Mediterranean landscapes with high fire frequency. For further explanations, see text.

2002, 2003; Pérez and Moreno, 1998) (Fig. 3). Another explanation is that surface fuel loads recover very quickly after fire, often exceeding pre-fire amounts. For example, in non-salvaged burned forests, hazardous fuel production is a function of the decay and fall of fire-killed snags driving accumulation of both coarse and fine woody debris (Keyser et al., 2009). In other burned areas, highly flammable tussock grasses (some of which are alien) can replace locally dominating woody species, resulting in increasing frequencies of very large and intense fires (Grigulis et al., 2005; Vilà et al., 2001). Several studies have confirmed that the recovery rate of scrub cover after fire was quite rapid, often exceeding the pre-fire biomass amount (Hernandez-Clemente et al., 2009; Roder et al., 2008; Viedma et al., 1997). Simulation models such as FATELAND and BROLLA have shown an increase in shrublands as a response to increased fire frequency, creating a state of successional stagnation which may enhance the positive shrub-fire feedback (Pausas, 1999; Pausas and Lloret, 2007) (Fig. 3).

Thirdly, fire disturbance creates more connected and homogeneous vegetation patches (fuel continuity) that favours fire spread and future fires (Chuvieco, 1999; Lloret et al., 2002; Loepfe et al., 2010; van Leeuwen et al., 2010; Viedma et al., 2006). Shrublands form large patches of fuel of the same age because the post-fire fuel build-up is rapid (Baeza and Vallejo, 2008). Furthermore, spatial patterning of fire severity and associated fire-induced vegetation mortality can increase the amount and continuity of dead fuels contributing to reburning (Collins et al., 2007). However, it is also recognized that variations in fire severity can enhance landscape heterogeneity, creating patches with different successional stages (Lloret et al., 2002; Pérez et al., 2003; Trabaud and Galtié, 1996) and unburned patches within fire scar perimeters (Koutsias and Karteris, 1998) that can alter the probability of reburning. In general, the effects of fire on landscape may vary from region to region because of differences in local fire history, regeneration patterns among main land covers and topographic constraints (Viedma, 2008). Finally, people's perception of the low value of burned areas reinforces these positive feedbacks leading to increased fire frequencies (Blasi et al., 2004; Vazquez and Moreno, 2001). There is a social perception that burned areas are less valuable which, in the absence of proper conservation strategies, makes them more prone to land abandonment or misuse (e.g. grazing, pastoral burning) with the effects already discussed. This might potentially lead frequently burned areas to a spiral towards deforestation (Arianoutsou, 1985) that will, in turn, create shrub-dominated landscapes with higher fire risk (Espelta et al., 2008) (Fig. 3).



Fig. 3. Possible (feedback) mechanisms through which increasing fire recurrence may occur in Mediterranean landscapes. For further explanations, see text.

6. Landscape fuel breaks are not always effective tools to reduce fire hazard under extreme weather conditions

6.1. Fuel management strategies

Fuel management can be implemented using three main strategies, respectively isolation by fuel breaks, area-wide fuel modification and fuel type conversion (Rigolot et al., 2009). The isolation by fuel break strategy has been the most used, and involves compartmentalising large areas of fire prone fuel types with a network of strips where fuel has been manipulated with the objective of helping fire fighters to (i) break up the continuity of hazardous fuels across a landscape; (ii) reduce the intensity of wildfires, providing broad zones within which fire-fighters can conduct suppression operations more safely and efficiently; (iii) provide strips to facilitate subsequent area-wide fuel treatments; and (iv) provide various non-fire-related benefits (e.g. habitat diversity, landscape scenery) (Agee et al., 2000; Cumming, 2001; Rigolot, 2002; Weatherspoon and Skinner, 1996). This strategy has been implemented in southern Europe in the last decades, mainly in France, Portugal, and Spain, and to a lesser extent in Italy and Greece and Turkey (Bilgili, 1998; Xanthopoulos et al., 2006).

Area-wide fuel modifications are an extensive application of fuel treatments at the forest stand level that include reduction of fuel load, increased fuel compactness and disruption of vertical and horizontal fuel continuity (Chandler et al., 1983). Although it is much less strategically planned than fuel break networks, it may complement it by working inside the landscape units isolated by the fuel break network. The patchy pattern of fuel treatments creates a landscape mosaic that increase its resistance to fire spread by the limitation of ladder fuels (Vélez, 1990, 2000).

Fuel type conversion involves replacing highly flammable vegetation by low growing, less hazardous species (Rigolot et al., 2009). Real fuel type conversion towards fire resistant vegetation is mostly limited to wildland—urban interfaces where landowners can choose less flammable ornamental (preferably native) species. In wildland areas, natural succession can be used where site conditions enable it to promote a mixture of species and to favour mature stages (Vélez, 1990). This naturally slow process can be somewhat speeded up with some selective thinning favouring broadleaved species.

6.2. Assessing fuel break effectiveness

Duché and Rigolot (2000) distinguish three main objectives for fuel breaks: (i) to decrease fire ignition events, (ii) to decrease total burned area and (iii) to decrease fire effects on people, human resources and ecosystems. Thus, fuel break design and evaluation of effectiveness will differ depending on the objectives. Clearly, the effectiveness of fuel management in general and of landscape fuel breaks in particular can not be solely assessed by fire size reduction and effective fire suppression, but it should also take into account the benefits for fire suppression actions and the reduction of the environmental and the socio-economical impact of wildfires.

Several approaches have been used for assessing the effectiveness of fuel control techniques for fire hazard reduction (e.g. Fernandes and Botelho, 2003) or for decreasing wildfire intensity and severity (Rigolot, 2002). The expert appraisement approach uses the experience of highly skilled fire professionals to provide standards for fuel break building and maintenance based on the best knowledge and practices (Rigolot and Morvan, 2003). Experimental fires can be used to test the probability of fuel break crossing, depending on fire intensity (Davidson, 1988) or to assess fuel-break dimensions (Wilson, 1988). The experimental approach is risky and it is almost impossible to test the highest part of fire intensity scale (Davis, 1965). Computer simulations using fire behaviour or fire growth models have been successfully used for assessing the effectiveness of silvicultural and fuel treatment scenarios (Duguy et al., 2007). Finally, analysing in the field situations where fuel breaks have been hit by wildfires strongly contributes to an efficient fuel-break design (Lambert et al., 1999; Rigolot and Alexandrian, 2006).

Field studies devoted to assessing the effectiveness of fuel breaks in controlling fire size have been carried out in south eastern France during 1993–2003 (Lambert et al., 1999; Perchat and Rigolot, 2005; Rigolot and Alexandrian, 2006). On the whole, 28 fuel breaks have been analysed including a large variety of situations (topographic situation, width, vegetation types, weather conditions, alignment of fuel break with fire front). The difficulties met by suppression forces to arrive and fight the fire in the fuel break network, as well as the ability of homogeneous fuel break segments in containing fire were assessed. In all these studies, the key factors of fuel breaks success were the quality of fuel break design and maintenance, early fire detection and good knowledge of the fuel break network by firefighters. Factors of failure were late arrival of suppression forces and fuel break discontinuities due to legal restrictions on fuel management or weak points due to topographic or fuel control difficulties. Under extreme fire weather conditions (e.g. the 2003 fire season), fuel breaks perpendicular to fire propagation could never contain the fire front and were crossed over by surface fires in the absence of ground suppression forces and by heavy fire spotting. On the contrary, flank fuel breaks could systematically limit the lateral extension of wildfires, even under extreme fire conditions. But in general, fuel break design and maintenance standards (RCC, 2002) were effective for moderate to severe fire weather conditions, providing suppression forces were present on the spot.

The case studies approach is constrained by the low number of fires versus fuel break situations encountered and limited data available to analyse them. The simulation approach enables to broaden the range of possible situations and to test innovative fuel break designs. Analyses from simulation models, (e.g. the physically-based fire propagation model FIRETEC) assessed the impact of fuel break vegetation structure on fire behaviour (Dupuy, 2009). Using the same model, Pimont et al. (2006, 2009) explored the effect of tree layer cover in the likelihood of crowning fire and fire rate of spread. At landscape management scale, and using the spatially explicit fire growth model FARSITE, Duguy et al. (2007) showed that different fuel scenarios may be successful in relation to fire size control: the fragmentation of a fire prone matrix with patches in different successional stages, the introduction of narrow corridors between wooded patches and the promotion of convoluted perimeters were effective in reducing fire size. In some northern Mediterranean regions, the local administration is using FARSITE as a tool for predicting consequences of fuel management options on fire growth (Duguy et al., 2007).

7. Concluding remarks: landscape management and policy implications

The main implications of the findings from scientific research for policy and landscape management are summarised in Table 2. We have identified four main challenges to address, that need specific landscape management and policy guidelines.

7.1. Reverse the detrimental implications of land cover changes and manage LULC to reduce fire hazard

Population decline, agricultural and pastoral land abandonment (and the subsequent natural regeneration of forests), and policies promoting forest cover, particularly in former agricultural land, are

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Table 2

Summary of main findings on landscape-wildfire interactions in Mediterranean Europe (and respective sections of the paper), challenges to address and proposed policy and landscape management responses.

Main findings	Challenges to address	Policy/Landscape management responses
Land cover changes are	Reversing the detrimental implications	$\sqrt{1}$ Implement policies to reverse population decline in mountain areas;
increasing fire hazard	of land cover changes Managing land use and land cover to	\checkmark Promote agricultural and pastoral activities, particularly in mountain regions;
(Section 3)	reduce fire hazard	Promote farming practices in areas surrounding villages, and enforce existing laws on fuel management around buildings and villages;
		Stop afforestation policies in high fire hazard areas;
		$\sqrt{\text{Reduce fuel accumulation through prescribed/pastoral burning;}}$
		\surd Explore potential for biofuels as a tool to remove fuels from the landscape;
		\checkmark Forest planning should give preference to deciduous broadleaved and mixed forests, rather than pine plantations;
Large fires are becoming more frequent (Section 4)	Being prepared for large fires and aim at reduced damage, rather	\checkmark Invest more in prevention (fuel management) rather than suppression policies;
	than reduced area burned	Focus on reducing fire intensity and potential damage, rather than trying to control fire size, specially under extreme fire weather conditions;
		$\sqrt{\text{Reduce vulnerability of values at risk (landscape planning at the rural-urban interface, fuel management around buildings and villages);}$
		Educate citizens on fire-response planning (defence and evacuation);
Frequent fires are creating homogeneous landscapes	Increase landscape heterogeneity and decrease the probability of repeated burning	In landscape planning take into account that specific topographic locations (e.g. steeper slopes, ridge crests, south exposures) may have greater fire hazard;
covered with shrublands which are more fire prone		\surd Promote landscape heterogeneity, by planning land covers with alternate higher and low fire hazard;
(Section 5)		\surd In forested areas, plan forest management to spatially alternate stands with different ages/fuel types
		Implement policies for the wise use of fire in pastoral burnings;
		Increase fire prevention measures in forests that have no post-fire regeneration ability (e.g. in immature <i>Pinus halepensis</i> and <i>P. pinaster</i> forests, and in vulnerable <i>P. nigra</i> and <i>P. sylvestris</i> forests);
		\checkmark Increase fire prevention in growing oak forests, that take longer to recover;
Fuel management may be successful only if fire weather conditions are not extreme (Section 6)	Combine landscape compartmentalization with	Under normal fire weather conditions, promote fuel management to extend fire suppression options and effectiveness;
	self-protection options	Under extreme fire weather, focus on reducing fire intensity and damage through self-protection;
		\checkmark Plan fuel isolation options at the landscape level, combined with area-wide fuel modifications;
		Use the whole range of fuel management techniques, including silviculture, agricultural and pastoral management, and the use of fire, as a tool;

driving the "rural exodus syndrome" (Hill et al., 2008) and causing a widespread increase in vegetation biomass over large areas of the Mediterranean Europe, mainly in mountain areas, and a subsequent increase in fire hazard. This trend can only be counteracted effectively through the creation of policies enabling the improvement of the socio-economic conditions of people living in rural areas, promoting new immigration to these regions, and implementing rural development policies that foster activities contributing to reducing fire hazard, such as agriculture and livestock grazing. These policies are mainly related to agricultural, rural development and economic issues, rather than forest management. For example, the European Agriculture Fund for Rural Development (EAFRD) (EC 1698/2005 of 20 September 2005) could contribute to achieve these objectives in disadvantaged rural areas by: a) improving the competitiveness of agriculture and forestry activities; (b) improving the quality of life by the diversification of economic activity, and c) supporting land management strategies.

In relation to land management strategies, there is conclusive evidence that agricultural areas are the least fire-prone LULC, whereas shrublands are particularly fire prone. This general pattern highlights the relationships between agricultural abandonment and fire hazard in the Mediterranean, as the land-cover types more avoided by fire (agricultural crops) are progressively replaced, in many cases, by the most fire-prone land cover type (shrublands). So, there is a need to define policies to maintain farming activities in areas where landscape planning identified as priority sites for fuel reduction, such as areas surrounding villages or pastoral activities in landscape fuel breaks. In fact, one of the most serious consequences of the abandonment of traditional practices is that villages in mountain areas, traditionally surrounded by a belt of farmland that acted as a landscape fuel break, nowadays have forests and shrublands in the vicinity of houses and other infrastructures, which greatly increase fire hazard. Agro-environmental activities should continue to play a prominent role in supporting the sustainable development of rural areas and in responding to society's increasing demand for environmental services. In general, there is a need for reinforcement of the existing laws and regulations on fuel management around buildings and villages, either through farming or other types of fuel reduction techniques.

Prescribed fire or controlled pastoral fire, or energy policies supporting the environmentally compatible use of renewable bioenergy potential from agriculture and forestry (agricultural waste, crop mix for biomass production, complementary fellings and residues from silvicultural activities and/or fuel management) may also contribute to reducing fire hazard, while providing job opportunities to rural populations. Appropriate use of fire by rural communities coupled with the development of prescribed burning undertaken by fire professionals may be used in integrated fire

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management (Silva et al., 2010). In the Mediterranean countries, traditional use of fire is associated with rangeland management and other rural activities like burning agro-forestry remains and game management. When not used under legal regulation and good practices, traditional use of fire may be a significant cause of wildfires (Xanthopoulos et al., 2006). On the other hand, in some regions good practices in traditional burning should be maintained and this activity needs to be recognized, consolidated and regulated as part of a community based fire management approach (Silva et al., 2010). Under this new framework, traditional burning may fully contribute to fuel management at the landscape level (Rego et al., 2010b). Recent studies have shown the possible renewal of active rangeland management in south eastern France, with the clear objective of wildfire mitigation (Etienne et al., 1996). Beylier et al. (2006) showed the successful contribution of sheep grazing to fuel control on both a fuel break network and neighbouring areas in the Luberon Natural Park (France). Thavaud (2009) provided practical guidelines for reactivating rangeland management in various ecosystems of the Mediterranean area. They combine new establishments of livestock farmers in fire prone areas, together with consolidation of existing animal farming.

In areas where there are no possibilities of promoting agricultural or pastoral activities, one other alternative to manage shrublands is to carry out afforestations with less fire prone tree species. In terms of forest planning, preference should be given to deciduous broadleaved and mixed forests, usually less fire prone than pine stands or plantations of exotic species. Afforestation policies promoting large scale monocultural stands in former agricultural areas is highly detrimental in terms of fire hazard at the landscape level. Thus, priority should be given to the creation of mosaics of smaller (less than 30 ha) non-contiguous forest patches.

7.2. Being prepared for large fires and aim at reducing damage rather than reducing area burned

Large fires are becoming more frequent, at least in some regions. Available evidence indicates that we do not have the technical capabilities to avoid large fires and that they will spread irrespective of LULC planning under extreme fire weather. Even if we tried to increase our technical suppression capacity more, we would simply increase the level at which fuel accumulation creates fire danger conditions that surpass the new suppression capacity. The implication of this is that under certain climatic and fuel load conditions, wildfires will always occur. Strange as it may be to policy makers, fire suppression policies can lead to fuel accumulation and large fire outbreaks. Thus, current fire policies in Mediterranean countries, directed towards reducing the number of ignitions, or having effective fire fighting abilities, will not decrease the number of large wildfires. Stakeholders and managers have to realise that fire-fighters can extinguish most of the fires, but when there is one beyond the extinction capacity, or when the firefighting system collapses because of the large number of concurrent ignitions, a large area will be burned because of the high fuel load resulting from successful fire suppression in previous years. Currently, the unbalanced fire management in Europe, with too much resources being allocated to pre-suppression and suppression actions compared to poor fuel management measures (e.g. Fernandes, 2008), is increasingly questioned. A major shift in the way fire management is seen requires a cross-sectoral approach integrating agricultural, forest and urban policies. Simultaneously, the "learning to live with fire" objective is increasingly shared (Birot and Rigolot, 2009), recognising that fire cannot be excluded from the Mediterranean environment (Rego et al., 2010a). Under this objective, fuel management is not only devoted to limiting wildfire spread, but also to lowering fire impacts on human resources and assets. This new forest management and planning vision also supposes increasing preparedness and response capacity to fire events, especially at the wildland—urban interface (Lampin-Maillet et al., 2010). In the latter, forest and urban planning should be tuned together and citizens living in fire risk areas should also become part of the solution, by building and preparing their homes for the arrival of fire, as well as being well-informed for fire-response planning (defence and evacuation). The contrasting damages caused by two neighbouring simultaneous fires in poorly versus well planned wildland—urban interface settlements near Athens are the best possible argument for planners and convincing proof for people (Xanthopoulos, 2008b).

The success of policies and management has to be evaluated firstly by the amount of damage caused, rather than by the number of hectares burned. Reducing fire damage will be attained by reducing fuel loads and the vulnerability of the values at risk. This means better planning of locations of houses and villages, promoting policies to avoid the increase of the rural–wildland interface, greater awareness of citizens, and the enforcement of existing laws and regulations on fuel management around buildings and villages (Silva et al., 2010).

7.3. Increase landscape heterogeneity and decrease the probability of repeated burning

The fact that Mediterranean fire-prone landscapes are increasingly covered by homogeneous shrublands that promote further wildfires creates a dangerous feedback mechanism that has to be stopped. In general, fire propagation may be favoured in landscapes that are homogeneous and hindered at places of greater heterogeneity, and where discontinuities occur. This knowledge can be used in landscape planning, by promoting a diversity of LULC. At the landscape management level, the interspersion of land uses with different fuel loads will counterbalance this trend promoting landscape heterogeneity. In forested regions, this could also be achieved through the spatial planning of stands with different ages to increase fuel load heterogeneity. Furthermore, controlling human behaviour through a better regulation of the use of fire for pastoral burning, particularly by avoiding burning recovering forest patches, could be a first policy measure. In terms of fire prevention in forested areas, top priority should be given to protecting forests that have limited post-fire regeneration ability, namely (a) immature P. brutia, P. halepensis and P. pinaster forests, (b) P. nigra and P. sylvestris forests, and (c) other forest types with scarce distribution and high conservation value, and for which there is evidence of lack of any active post-fire response mechanisms, such as the Abies forests of Mediterranean mountains (Arianoutsou et al., 2010). Finally, Mediterranean oak forests, that take longer to recover, will not be able to reach maturity unless fire frequency in these ecosystems is highly reduced.

7.4. Combine landscape compartmentalization with self-protection options

Under moderate to severe fire weather conditions, fuel management should be focused on increasing the fire suppression options and effectiveness by limiting fire ignition and fire spread in strategic locations. This is what we call compartmentalization, the division of the landscape into blocks that should set a maximum fire size. However, under exceptional weather conditions, the differences of combustibility among land covers will decrease, and fire may propagate throughout a whole landscape regardless of land cover and fuel management. Increasing indirect fire-fighting capability through improved use of backfire and burn-out operations may help achieve better results in controlling maximum fire size taking advantage of compartmentalization (Miralles et al., 2010). However, that can never be assured. Thus, under extreme fire weather conditions, prevention strategy should move to self-protection options by limiting fire intensity and damages on both ecosystems and human assets, and assuming that fire fighting will not always be possible under these circumstances.

The implementation of a fuel break network requires a fire management plan at the landscape level. Landscape fragmentation is ensured by primary and secondary fuel break networks, the former being strategically located (e.g. ridge top fuel breaks) for increasing the efficiency of fire suppression actions, and the latter for guaranteeing the safe accessibility to the former. Following European standards, strategic fuel break width should be not less than 100 m (RCC, 2002; Portuguese Republic, 2009, for France and Portugal respectively).

Both in fuel breaks and area-wide treatments, there is a wide range of possibilities to maintain or promote lower fuel loads, including silvicultural techniques, agricultural and grazing management, or even the use of fire. These treatments will increase the opportunities for safe and successful fire suppression options and reduce the fire severity on the ecosystem or valuable assets (e.g. Rigolot et al., 2009). Several surface fuel management techniques are available including mechanical clearing (increasing fuel compactness), phytocides (limiting plant growth), prescribed burning and controlled grazing (reducing fuel load) (Etienne et al., 1994; Valette et al., 1993; Xanthopoulos et al., 2006). Trees have a role to play for reducing inside stand wind speed and for limiting under storey vegetation growth, and should be maintained, ensuring the appropriate disruption in the vertical and horizontal fuel continuity. Agricultural cultivations and other land uses can be included in fuel break networks as far as they provide a low flammability cover type during the fire season.

The spatial distribution of fuel treatments should better follow a strategic than a random pattern (Fernandes, 2010; Loureiro et al., 2006), and modelling approaches that have been used for optimizing prescribed burning planning can be used at the landscape scale (e.g. Loureiro et al., 2002).

8. Knowledge gaps

Several controversial and relevant research topics in the fire—landscape relationships are still not known or totally clarified. We came across the following ones, while carrying out this review:

8.1. The role of humans in fire danger

On one hand, land abandonment increases fire hazard, due to fuel accumulation. But at the same time, given that humans account for most of the fire ignitions in the Mediterranean region (see for example Catry et al., 2009; Moreno et al., 1998), it could be hypothesised that a decline in population, and particularly farming activities, would reduce the number of fire ignitions. For instance, Koutsias et al. (2010) claim that demographic shifts from rural to urban areas may favour fuel conditions that lead to large fires, once a fire has been ignited. However, the same population reduction also reduces the probability of (human-caused) fire ignition, simply because less people are around to trigger a fire for whatever reason. Moreover, there is some anecdotal evidence that certain LULC types with low fire hazard can turned into very hazardous ones under improper management. For example, permanent crops such as olive groves and vineyards, which will act as fuel breaks under correct maintenance (periodical removal of grasses and weeds), can facilitate fire spread when not properly managed. On the other end, the increase in the extent of the wildland-urban interface might increase fire danger in areas surrounding villages and settlements. These topics should be clarified.

8.2. Will climate change increase fire intensity?

Climate change predictions point out an increase in fire risk, fire intensity, the length of fire seasons, the number of days in each season with extreme fire danger, and area burned per year (e.g. Moriondo et al., 2006; Pausas, 2004). But the detrimental effects of climate change on increased fire occurrence are not always obvious. In the Eastern Iberian Peninsula, Pausas (2004) found a positive correlation between summer rainfall and area burned two years later, suggesting that this rainfall increases fuel loads for the subsequent fire seasons. In this perspective, climate change could decrease fire hazard by constraining vegetation growth and biomass (fuel accumulation). This author concluded that more research is needed on the potential impact of lower but drier fuel loads on future fire regimes.

8.3. Is fire size limited by weather or landscape pattern?

There is still a debate on whether landscape pattern or meteorological conditions is the fundamental control of fire spread in Mediterranean landscapes. A better understanding of these processes has strong implications for landscape planning, and to the expected role LULC management has in reducing fire extent of fire damages.

8.4. Does fire suppression policies increase large fire occurrence?

Further research is needed on the impact of fire suppression policies on resulting fire sizes. If scientific research shows beyond doubt that fire suppression policies, if not accompanied by fuel management, lead to fuel accumulation and are responsible for large fire outbreaks, a major shift on resource allocation from suppression to prevention should be made.

8.5. The role of invasive exotic species in fire hazard

Scientific evidence also suggests that controlling the spread of invasive species in burned areas could decrease future fire hazard. Exotic invasive species are becoming a major problem in Europe (Lambdon et al., 2008) and in specific regions (e.g. Portugal) they are one of the main concerns of forest managers in burned areas. Their role on fire regime and post-fire ecosystem responses need to be further evaluated.

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Land use and topography influences on wildfire occurrence in northern Portugal

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ABSTRACT

Understanding the spatial patterns of wildfire ignition and spread has important implications for landscape planning for reducing fire hazard. In this paper we characterise the patterns of wildfire occurrence in 3 regions of northern Portugal, using selection ratio functions to evaluate the fire proneness of different land cover and topographic categories. For attaining this objective we characterised 1382 wildfires larger than 5 ha, which occurred in the years 1990–1991, according to land cover (10 categories), slope (5 categories) and aspect (5 categories) within which they occurred. For each fire, the use of the different land cover and topographic categories was compared with availability in a surrounding buffer. For land cover, fire proneness was much higher in shrublands, whereas agricultural areas and agro-forestry systems where less likely to burn. In terms of slope, steep slopes were more prone to fire. Differences in land cover in the different slope categories contributed to this result, although there was an overall slope effect on the fire proneness of all land cover types. In terms of aspect, only flat areas were less fire prone. Finally, there were regional variations in land cover susceptibility to fire, but these did not occur for slope or aspect. In terms of landscape planning these results suggest that the more effective fuel breaks should be implemented in areas with agricultural crops in flat slopes.

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1. Introduction

Disturbances play a fundamental role in shaping the structure and dynamics of the landscape (Turner and Dale, 1990). On one hand, the spatial propagation of the disturbances is a function of the abundance and arrangement of disturbance-susceptible habitats (Turner et al., 1989). On the other hand, landscape patterns are determined by the frequency, intensity and extension of the disturbance (Pickett and White, 1985; Krumel et al., 1987). Considering that fire is one of the main disturbances affecting Mediterranean landscapes, understanding how landscape structure affects the spatial spread of wildfires is a key issue for understanding their ecological implications and the role they play in landscape dynamics (Moreira et al., 2009). Furthermore, this knowledge has profound implications for sustainable landscape planning (e.g. Hann and Bunnell, 2001; Leitão and Ahern, 2002).

The start of a fire and its spread are the result of a complex interaction between ignition sources, weather conditions, vegetation and topography (Mermoz et al., 2005). This work analyses the relation between wildfires and these two last factors. Vegetation plays a key role as fuel structure, load and moisture content

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depend on vegetation type (Turner and Dale, 1991; Bajocco and Ricotta, 2008; Moreira et al., 2001, 2009). Topography directly affects fire behaviour by promoting the radiant energy transfer from the fire line in the direction of the higher slopes (Rothermel, 1983). Indirectly, topography also affects fire by creating different microclimates which influence the moisture content of fuels, the air temperature, as well as the biogeographic distribution of plant species (Heyerdahl et al., 2001; Mermoz et al., 2005). Topography and land cover are often linked, e.g. agricultural areas may be preferentially located on lowlands, and forests in slopes, which may hinder the understanding of the ultimate drivers of fire spread.

In Portugal, a set of socio-economic and environmental conditions leads to a landscape very prone to fire. The climate is characterised by dry summers, and large fires occur when the Azores anticyclone spreads through central Europe linked to another high pressure centre over the Mediterranean, which at the surface leads to an abnormal advection of hot dry air masses crossing the peninsula centre coming from Northern Africa (Pereira et al., 2005, 2006). The natural vegetation is typically evergreen, resistant to drought and pyrophytic (Nunes et al., 2005). Additionally, in the last decades socioeconomic and demographic evolution in rural areas led to agricultural land abandonment and subsequent shrubland encroachment, as well as the afforestation of former agriculture fields. In both cases a higher accumulation of fuels is generated which leads to a higher risk of fire (Silva, 1990; Rego, 1992; Moreira et al., 2001, 2009). Because of these factors, wildfire

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Fig. 1. Map of the study area with the three ecological regions. The location of main cities is also shown.

occurrence in Portugal has risen in the last few decades (Moreira et al., 2001; Pereira et al., 2006). The mean annual area burned in Portugal in the period 1980–2004 slightly exceeds 1% of the total area of the country, which is, by far, the highest fire incidence in Europe (Nunes et al., 2005). Most of these fires (over 95%) are ignited by people (Catry et al., 2009).

In contexts such as the one of Portugal, the analysis and understanding of fire ignition and spread patterns is important to inform landscape planning and management practices designed to reduce fire risk and hazard at the landscape scale, in particular, the location and characteristics of fuelbreaks. That is the aim of this study, which, by characterising selection patterns of wildfires occurring in northern Portugal during 1990 and 1991, addresses the following specific questions: (a) which land cover types and topographic features (slope and aspect) are more fire prone in this region?; (b) are there regional variations in fire patterns with respect to land use and topography?; (c) are the relationships between fire occurrence and topography related to land use?

2. Materials and methods

2.1. Study area

The study area occupies a total surface of 557 km^2 in northern Portugal, and is confined by the latitudes $40^\circ 38'$ to $42^\circ 09'$ N and longitudes $6^\circ 11'$ to $8^\circ 53'$ W. It is divided in three ecological regions – Noroeste (NW) Cismontano, Alto Portugal and Nordeste (NE) Transmontano – based on climatic, geologic and topographic features (Albuquerque, 1985) (Fig. 1). The resident population is ca. 3.2 millions people. The Douro river drainage basin occupies around 70% of the region. It is a mountainous area, with the altitude ranging from sea level to 1548 m in Serra do Gerês, with an average value of ca 500 m.

In bioclimatic terms, most of the territory is Mesomediterranean and Supramediterranean (Rivas-Martínez, 1987; Rivas-Martínez et al., 2002). The average annual precipitation varies between ca. 400 mm in the eastern part, below altitudes of 400 m, and over 2800 mm in the north-western ridges. The average annual temperature varies between 7.5 °C and 16 °C; the average maximum is around 22-32 °C; the average minimum is around 0-8 °C (APA, 1974). In phytogeographic terms, the region is divided by the Eurosiberian region, Galicia-Portuguese sector, in the west half, with characteristic species being *Quercus robur, Acer pseudoplatanus, Pyrus cordata* and *Ilex aquifolium*. The eastern part is occupied by the Mediterranean region, Carpetano-Ibérico-Leonesa Province with *Castanea sativa, Quercus faginea subsp. Faginea, Quercus pyrenaica, Quercus suber*, and *Quercus ilex* as characteristic species (Costa et al., 1998).

The study area has a high frequency of wildfires in Portugal (Pereira et al., 2006). This region also shows a strong climate transition where the Atlantic influence meets the Mediterranean, leading to strong spatial gradient of temperature and precipitation. This produces a heterogeneous landscape suitable for testing the existence of regional variations in fire selection patterns.

2.2. Land cover map

The base map was a 1990 land cover map for Portugal (scale 1:25,000) developed by the Instituto Geográfico Portugals (IGP, 1990). As that map is incomplete for a few parts of Portugal (ca 5%), the gaps were filled with CORINE land cover data (scale 1:100,000) (IGP, 1988), based on 1986 Landsat imagery (Moreira et al., 2009). The legends of both maps were simplified to a common ten-class legend considered adequate for the purposes of this study:

- 1. Non combustible areas (5.3% of study area): urban areas, dunes and water bodies; these were not included in the analysis.
- Annual crops (25.4% of study area): mainly composed of dry crops, irrigated crops, and diverse agriculture mosaics dominated by annual crops and natural pastures.
- 3. Permanent crops (8.4% of study area): mainly composed of olive groves, vineyards and orchards.

- 4. Agro-forestry systems (5.2% of study area): composed of a mixture of annual crops and trees, mainly holm oak (*Quercus ilex*), cork oak (*Quercus suber*), olive tree (*Olea europaea*) and other unspecified broadleaved trees.
- 5. Shrublands (28.5% of study area): mainly low shrublands but also tall shrublands, degraded or transitional forest, shallow cut or recently burned forests and sclerophyllous vegetation.
- 6. Conifer forests (10.1% of study area): mainly composed of maritime pine (*Pinus pinaster*) plantations.
- 7. Eucalyptus forests (1.9% of study area): mainly *Eucalyptus globulus* plantations.
- 8. Broadleaved forests (6.0% of study area): mainly cork oak and holm oak, but also mixed cork and holm oak, other oaks (*Quercus robur* and *Q. pyrenaica*) and unspecified broadleaves.
- 9. Mixed conifer and eucalyptus forests (4.8% of study area): composed almost totally of mixed maritime pine and eucalyptus, with pines dominant (\sim 70%) over eucalyptus.
- 10. Mixed forests of broadleaved trees and conifers (or eucalyptus) (4.4% of study): mostly mixed broadleaved/conifers but also a few mixed broadleaved/eucalyptus forests. The main species combinations are maritime pine+cork oak, maritime pine+other oaks, stone pine+other unspecified broadleaved and stone pine+cork oak.

We assumed that major land cover changes during the two year period considered for analyses (1990 and 1991) were due to wildfires, so the 1991 land cover map was updated by assigning previously burned areas to the shrubland category, the most likely vegetation physiognomy in burned patches. The implication of this assumption is that the value for the selection ratios for shrublands in 1991 may have been lowered if fires did not occur in previously burned areas that we have categorized as shrublands.

2.3. Slope and aspect maps

Slope and aspect maps were obtained from a Digital Terrain Model with a spatial resolution of 90 m (DTM 90) available in internet (NASA, 2004), using simple operations of spatial analysis over the elevation matrix. Each map was classified in five classes; in the slope map we used the categories 0-5%, 5-10%, 10-15%, 15-25%, >25% and in the aspect map we used the categories Flat terrain, north (315–45°), east (45–135°), south (135–225°) and west (225–315°).

2.4. Fire data

The location and size of burned areas during the period 1990–1991 were estimated by semi-automated processing of Landsat 5 Thematic Mapper satellite images, with a minimum-mapping unit of 5 ha (Pereira and Santos, 2003; Moreira et al., 2009). A total of 1382 burned patches larger than 5 ha were considered for analysis. As we were interested in regional variations in fire occurrence patterns, each fire was classified into one of the 3 ecological regions.

2.5. Fire proneness of different land cover and topographic categories

The methodology used to describe fire occurrence patterns was based on the computation of selection ratios, a methodology originally proposed for the study of resource selection by animals (Manly et al., 1993) and transposed to application in fire research by Moreira et al. (2001, 2009). The selection ratio (w_i) for a given land cover or topographic class *i* is an index of selection estimated as $w_i = o_i/\pi_i$ (Manly et al., 1993), where o_i is the proportion of burned patch belonging to class *i* (estimated from the area consumed by fire) and π_i is the proportion of available area belonging to class *i*

(estimated from the area in a surrounding buffer). If a given class is used in proportion to its availability, then w = 1. If w > 1 the class is used more than expected by chance. If w < 1, the class is used less than expected by chance. For determining availability (π_i) we created circular buffers centred on the patch centroid coordinates and with an area equal to the maximum fire size in the respective ecological region. We assumed a circular buffer because, in the absence of fuel, climate and topography effects, the shape of a burned area would be a circle (Ventura and Vasconcelos, 2006), so this would be the best shape for testing against the null hypothesis of no land cover or topographic effects on fire selection patterns. For further details see Moreira et al. (2009). We used selection ratios to characterize the different classes of the three variables under study (land cover, slope and aspect) by individual fires. A few outliers (n = 19)were detected through box-plot inspection of the selection ratios for each variable, corresponding to atypical situations where the values were too high. In the subsequent analyses these fires were excluded. Values for each land cover and topographic category were then averaged across fires and the respective confidence intervals (95%) were estimated. Differences between selection ratios for different classes were considered statistically significant when there was no overlap between the respective confidence intervals. Similarly, when the confidence interval did not include $w_i = 1$, the class was considered significantly more or less used than expected by chance. In order to identify regional differences in fire occurrence patterns, the average ratios and confidence intervals for each class were compared across regions.

2.6. Exploring relationships between topographical variables and land cover: could differences in selection ratios for topography be explained by land cover?

We used two different methods to explore the potential interdependence among land cover and topographic features. First, we assessed the land cover composition for each slope and aspect category in the whole study area. Based on the average selection rations estimated for each of the land covers we then estimated a weighted fire proneness index for each topographic category. This index weighted the relative abundance of each land cover in each topographic category by its selection ratio, obtaining a single value that indicated the fire proneness of the slope and aspect class, as assessed from land cover composition. We then assessed whether the obtained index, derived from land cover, was correlated with the selection ratio directly estimated for each topographic category, using the Spearman rank correlation (Sokal and Rohlf, 1995). The second method simply compared the frequency of burned land cover categories across topographic categories, using a G-test of independence (Sokal and Rohlf, 1995) to test the null hypothesis that the proportion of burned area, for a given land cover class, was independent of aspect or slope. The tendency for specific topographic categories to systematically have higher or lower proportion of burned land cover across land cover classes was tested using the Friedman's test (Siegel and Castellan, 1988).

3. Results

3.1. Fire occurrence patterns

During the study period 1382 fires burned ca 55,739 ha in northern Portugal. Of this total number, 891 fires occurred in 1990 and 491 in 1991. The average size of burned patches was ca. 40 ha and the biggest fire burned 1351 ha. Most fires occurred in NW Cismontano, although they were smaller than in the Alto Portugal and NE Transmontano (Table 1).

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Summary statistics of fires per ecological region, during the period 1990–1991.

Region	Number of fires	Total burned area (ha)	Average fire size (ha)	Median fire size (ha)
NW Cismontano	590	21363	36.2	16.8
Alto Portugal	513	22288	43.4	18.7
NE Transmontano	279	12087	43.3	20.0

3.2. Fire selection patterns

Shrublands were the only land cover type that burned more than expected if fires occurred randomly in the landscape (Fig. 2), with the selection ratio (w_i = 2.5) indicating that this land cover burned in a average proportion 2.5 times more than the available proportion. Annual and permanent crops were the less fire prone. For the remaining land covers, there seemed to be a gradient of increasing susceptibility to fire from agro-forestry systems (less susceptible) to mixed forests of conifers (or eucalyptus) and broadleaves.

In relation to slope, fire proneness progressively increased from smaller slopes (<5%, $w_i \approx 0.5$) to the steeper ones (>25%, $w_i \approx 1.3$) (Fig. 2). Aspect classes largely burned in proportion to their abundance on the landscape, although the selection ratios were slightly less than one for south-facing slopes. Flat areas were much less likely to burn (Fig. 2).

The numerical values for all estimated selection ratios (pooled and divided by region) can be seen in Appendices 1 and 2.

3.3. Regional variations in fire selection patterns

Selection ratios varied among regions for land cover but not for topography (Fig. 3). In fact, for both slope and aspect, the error bars for each class overlapped across regions. However, for land cover, significant differences emerged. Although shrublands were the only class for which the proportion burned was higher than the proportion available, the average selection ratio of this land cover in the NW Cismontano almost doubled the values of Alto Portugal and NE Transmontano. Selection ratios were lower inland (that is, along the gradient NW Cismontano to NE Transmontano) for mixed conifer and eucalyptus forests and eucalyptus forests. In contrast, other land covers increased their selection ratios inland, namely broadleaved forests, mixed forests of broadleaved and conifers or eucalyptus, annual crops and agro-forestry systems. For the remaining land covers, namely conifer forests and permanent crops, a trend across regions was not so evident.

3.4. Exploring relationships between topographical variables and land cover

There was a strong positive correlation between the weighted fire proneness index estimated from land cover and the average selection ratio directly estimated (shown in Fig. 2) for the five slope categories ($r_s = 1.0, n = 5, P < 0.01$). For aspect, there was also a positive correlation between observed selection ratios and estimated fire proneness index but it was not significant ($r_s = 0.308, n = 5, P = 0.302$).

The proportion of burned area was not independent of slope for any land cover category (*G*-tests, *P*<0.01). In fact, the proportion of area burned increased with slope for most land covers (Fig. 4), and this pattern was consistent across cover types (Friedman test, $\chi^2 = 26.9$, d.f. = 4, *P*<0.001). The same result was observed for aspect, were only for eucalyptus the proportion of burned area was independent of the aspect category (*G*-test, *G*=22.9, d.f. = 4, *P*=0.236). For most land covers, the proportion of burned area was smaller in flat areas and higher in slopes directed to East or North (Fig. 5) (Friedman test, χ^2 = 19.7, d.f. = 4, *P*=0.01).



Fig. 2. Average selection ratios (*w*) with 95% confidence intervals for land cover, slope and aspect in the study area. Abbreviations for land cover: ac - annual crops; pc - permanent crops; agf - agro-forestry systems; shr - shrublands; con - conifer forests; euc - eucalyptus forests; brl - broadleaved forests; mx - mixed conifer and eucalyptus forests; mxb - mixed forests of broadleaved and conifer, or broadleaved and eucalyptus.



Fig. 3. Average selection ratios (w) with 95% confidence intervals for land cover (top row), slope (middle row) and aspect (bottom row) in each of the three ecological regions.

4. Discussion

4.1. Overall fire selection patterns

The analysis of fire selection patterns confirmed the selective character of fire regarding land cover, and results were in line with previous studies (e.g. Nunes et al., 2005; Moreira et al., 2009). Shrublands were the more fire prone land cover, and agricultural areas (annual and permanent crops), together with agro-forestry systems, were the less susceptible land covers. For croplands, this pattern may be explained by their low combustibility, due to the usually low fuel load and high moisture content (mainly in irrigated crops). In addition, most of these agricultural areas are closer to urban areas, thus fire detection is quicker and fire fighting easier (Moreira et al., 2009). Shrublands, in contrast, are given the lowest priority for fire fighting (they are the less valuable land cover), and probably have also a larger number of ignitions (e.g. burning to creating pastures for livestock) and a higher rate of fire spread. Finally, they were the most common land cover type in steeper slopes where the rate of fire spread is even higher (Rothermel, 1983). All these factors probably contribute to the high fire susceptibility of this land cover.

To the best of our knowledge this study applied for the first time the selection ratio approach to topographic variables. Despite the lack of independence between topography and land cover, which hinders the interpretation of the patterns found, the selection ratios for slope revealed a strong selectivity pattern, with increasing fire proneness in steeped slopes. This can be explained by the fact that fires spread most rapidly uphill on steep slopes, where the higher incident radiation promotes the fuel ignition (Rothermel, 1983). Mermoz et al. (2005) also found that fires were more likely to burn on steep slopes. An alternative explanation is that the land covers most likely to burn are more common on steep slopes (see Section 4.3). Selection patterns for aspect showed a weak selectivity, with only flat areas being clearly avoided by fire. In southern slopes, however, there was a trend towards lower fire proneness. Previously, Nunes (2004) found that fire likelihood varied with aspect, namely in the NW Cismontano and NE Transmon-



Fig. 4. Proportion of the area of a given land cover type burned, for each slope category. Abbreviations for land cover type: ac – annual crops; pc – permanent crops; agf – agro-forestry systems; shr – shrublands; con – conifer forests; euc – eucalyptus forests; brl – broadleaved forests; mx – mixed conifer and eucalyptus forests; mxb – mixed forests of broadleaved and conifer, or broadleaved and eucalyptus.



Fig. 5. Proportion of the area of a given land cover type burned, for each aspect category. Abbreviations for land cover type: ac – annual crops; pc – permanent crops; agf – agro-forestry systems; shr – shrublands; con – conifer forests; euc – eucalyptus forests; brl – broadleaved forests; mx – mixed conifer and eucalyptus forests; mxb – mixed forests of broadleaved and conifer, or broadleaved and eucalyptus.

tano regions, where northerly slopes were more prone to fire than southerly ones. So, the patterns found in northern Portugal contrast with other studies that showed that dryer and warmer aspects (xeric), southern aspects in our case, are usually more prone to fire (Mermoz et al., 2005; Heyerdahl et al., 2001; González et al., 2005). Again, one alternative explanatory hypothesis was that land covers more susceptible to fire are less frequent in southern slopes (see Section 4.3). For flat areas, the clear avoidance by fire may also be explained by the null slope in these areas.

4.2. Regional variations in fire selection patterns

Regional variations in selection patterns were obvious in the case of land cover. Moreira et al. (2009) addressed, at the country level, the role of different drivers shaping the geographical variation in selection patterns for land cover, including ignition patterns, climate, agro-forestry management, forest species composition, fire fighting strategy, and the regional availability of land cover categories. Within northern Portugal, the higher selectivity for croplands as we move from the seaside (NW Cismontano) to the interior (NE Transmontano) should be related to mainly climate (getting drier and hotter as we go inland) and crop management (more irrigated crops in NW Cismontano versus dry crops in NE Transmontano). For forests, changes in climate are also accompanied by changes in species composition: broadleaved forests showed higher susceptibility from the coast, where deciduous species (e.g. Quercus robur and Q. pyrenaica) are more common, towards the inland, where evergreen species (Q. rotundifolia and Q. suber) are predominant. The latter are probably more prone to fire as they present lower moisture content compared with the

broadleaved deciduous species (Moreira et al., 2009). For shrublands, according to Moreira et al. (2009) the higher precipitation in the NW Cismontano increases the productivity and may generate higher fuel loads in shrublands. Additionaly, traditional shrubland burning for rangeland management is more common in western regions (Moreira et al., 2009).

The absence of regional variations in the selection patterns for slope and aspect suggests that they are ruled by drivers, which are similar across the three regions. At least for slope this should be expected, as the physical rules ruling their effects on fire behaviour are not expected to change geographically.

4.3. Relationships between land cover and topography in explaining fire selection patterns

We found that the observed fire selection patterns for the different slope categories could be explained by land cover, i.e., land cover types more prone to fire were more common on steeper slopes. For example, the proportion of area occupied with the fire-preferred shrublands and conifer forests increased with slope, whereas the proportion of the fire-avoided annual and permanent crops, more common on lowland flat areas, decreased with slope. But on the other hand, we also found a slope effect irrespective of land cover, in which susceptibility to fire increases with slope for most land cover types. This suggests a double mechanism by which fire spreads preferably in steeper slopes because of both the physical effect of incident radiation (Rothermel, 1983) and the occurrence of more fire-prone land covers. For aspect, a significant trend for more fire-prone land covers to occur in aspects with higher selection indices was not found. So, with the exception of the low preference for flat areas, which can be explained by the slope effect, it is difficult to find an explanation for the trend towards the lower selection index in southern slopes, which are expected to be drier and hence more fire prone. One possibility was that slopes differed in their occurrence in different aspects, i.e., steeper slopes occurring on southern aspects. But that was not the case, as the proportion of slopes over 15% was not higher in south aspects (37%), compared to other orientations (41–45%). Finally, one hypothesis that should be addressed in future studies is that other driver of fire spread, the predominant wind direction, may explain the observed pattern. The dominant winds in the region, during summer months, come from the north to northwestern quadrants (Ribeiro et al., 1987), but local variations can cause a large variability in this pattern.

5. Conclusions

This research showed that there were regional variations in the fire proneness of different land cover types in northern Portugal. In contrast, there were no variations in fire susceptibility of different slope or aspect categories. We confirmed the importance of slope in determining fire selectivity, not only because of more fire-prone land covers being associated to steeper slopes, but also because of the physical effect of slope on fire behaviour, which increased fire proneness in steeper slopes for all land covers. These results have obvious implications for landscape planning, in particular for landscape prognosis (sensu Leitão and Ahern, 2002). One of the landscape-level applications of these results is in the definition of landscape-scale fuel breaks. These can be implemented with several objectives including (a) effectively breaking up the continuity of hazardous fuels across a landscape, with the objective of reducing the occurrence of large wildfires, (b) reducing the intensity of wildfires, providing broad zones within which fire fighters can conduct suppression operations more safely and efficiently, (c) providing strips to facilitate subsequent area-wide fuel treatments, and (d) providing various non fire-related benefits (e.g. habitat diversity, landscape scenery) (e.g. Weatherspoon and Skinner, 1996; Agee et al., 2000; Cumming, 2001). Thus, when comparing alternatives for the location of fuel breaks, suitable land covers on suitable topographic categories could be used as a basis for deciding on the best location. Of course, these land covers could also be promoted in the wider landscape (block treatments) to reduce fire hazard at landscape level. In terms of landscape planning for reducing fire hazard, these results suggest that priority areas to be used as, or promoted in, landscape-scale fuel breaks should include agricultural areas (particularly if they have irrigated crops) in flat slopes. Agricultural policies should be designed and implemented with reducing fire hazard objectives in mind.

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Appendix 1.

	Mean	Std
Land cover		
ac	0.23	0.854
рс	0.16	0.923
agf	0.34	1.484
shr	2.52	2.566
con	0.57	1.766
euc	0.39	1.188
brl	0.59	1.921
mx	0.46	1.232
mxb	0.72	2.448
Slope		
<5%	0.55	0.969
5-10%	0.70	0.786
10-15%	0.92	0.811
15-25%	1.19	0.885
>25%	1.27	1.503
Aspect		
Flat	0.55	2.528
North	1.04	1.275
East	1.03	1.169
South	0.85	0.969
West	0.95	1.041

Mean and standard deviation of selection ratios for land cover, slope and aspect categories in northern Portugal. Abbreviations for land cover: ac – annual crops; pc – permanent crops; agf – agro-forestry systems; shr – shrublands; con–conifer forests; euc – eucalyptus forests; brl – broadleaved forests; mx – mixed conifer and eucalyptus forests; mxb – mixed forests of broadleaved and conifer, or broadleaved and eucalyptus.

Appendix 2.

	Noroeste cismontano		o Alto Portugal		Nordeste transmontano	
	Mean	Std	Mean	Std	Mean	Std
Land cov	er					
ac	0.08	0.431	0.33	1.163	0.37	0.808
pc	0.06	0.711	0.27	1.463	0.18	0.335
agf	0.26	1.601	0.35	1.290	0.50	1.551
shr	3.36	3.189	1.78	1.491	2.10	2.100
con	0.45	1.217	0.73	2.219	0.52	1.816
euc	0.42	1.270	0.27	0.775	0.14	0.582
brl	0.34	1.651	0.54	1.581	1.19	2.701
mx	0.51	1.302	0.08	0.399	-	-
mxb	0.39	1.459	0.88	2.635	1.21	3.624

	Noroeste cismontano		Alto Portugal		Nordeste transmontano	
	Mean	Std	Mean	Std	Mean	Std
Slope						
<5%	0.60	1.1183	0.49	0.874	0.53	0.772
5-10%	0.72	0.8573	0.68	0.766	0.72	0.654
10-15%	0.97	0.7646	0.87	0.734	0.93	1.014
15-25%	1.22	0.8548	1.15	0.905	1.16	0.910
>25%	1.35	1.7008	1.21	1.302	1.20	1.381
Aspect						
Flat	0.54	2.555	0.59	2.763	0.51	2.088
North	1.01	1.240	1.07	1.389	1.08	1.123
East	1.01	1.209	1.03	1.113	1.06	1.189
South	0.86	0.938	0.81	0.988	0.90	0.999
West	0.99	1.008	0.92	1.110	0.92	0.978

Mean and standard deviation of selection ratios for land cover, slope and aspect categories for the three studied regions. Abbreviations for land cover: ac – annual crops; pc – permanent crops; agf – agro-forestry systems; shr – shrublands; con – conifer forests; euc – eucalyptus forests; brl – broadleaved forests; mx – mixed conifer and eucalyptus forests; mxb – mixed forests of broadleaved and conifer, or broadleaved and eucalyptus.

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Wildfire impacts on aquatic ecosystems

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Abstract: Wildfires are relatively common in many biomes, often being an important vector in forest structuring. Large areas of forest are burned each year, at times causing severe social and economic impacts. Generally, the impacts of wildfires on terrestrial ecosystems are well known, but less information is available concerning the impacts on aquatic ecosystems. The vulnerability of trees as well as forest succession after wildfire can influence response and recovery of aquatic ecosystems to wildfire. Terrestrial inputs into aquatic systems following wildfire can add nutrients and fine sediments with both positive and negative impacts on aquatic communities. Long-term effects can occur when large woody debris are deposited in rivers, causing morphological modifications of rivers with various effects on aquatic communities. The recovery of adjacent landscapes. Mediterranean rivers, typically experiencing major fluctuations in water availability and temperature, tend to show faster recovery rates than rivers from other biomes that have less environmental variation in flow and temperature.

Keywords: wildfires, forest, basin management, lotic ecosystems, habitat morphology, aquatic communities, Mediterranean rivers

1. Introduction

Wildfires, common in forests of many biomes, can result from natural causes, like lightning storms during summer in continental regions, and human causes such as the use of fire to clean fields for agricultural practices (Guyette et al., 2002). Wildfires, whose occurrence and frequency depend on forest type and climatic factors, are responsible each year for the destruction of large forested areas. Although the severe effects, mainly to the human populations, wildfires are often important in the natural successional dynamics of forests and forest ecology in general. Probably no other environmental disturbance is associated with such a dialectic contradiction between destruction and creation. A dialectic already assumed by humans by associating, at the same time, fire as propriety of the Gods as means of punishment (Silva & Rego, 2007). Rivers or streams flowing through burned areas can be influenced by wildfire even during wet periods. Following wildfire, the dynamics of water retention and runoff in terrestrial ecosystems is severely altered. Burned landscapes are unable to retain rainfall water in the upper

layers of the forest, increasing the energy of erosional processes. Complete burning of vegetation produces large amounts of fine inorganic particles that once deposited on soils forms a hydrophobic surficial layer that reduces water infiltration (Scott et al., 1992). Thus, the hydrological regime of streams in those basins is often altered (Emmerich & Cox, 1984). Due to less water retention on the landscape, flood events tend to be more intense, occurring quickly and generally for a shorter period of time (Rodrigues & Brandão, 2003). The runoff from rainfall will transport fine sediments, large woody debris, nutrients and pyrogenic components to rivers, thereby influencing aquatic communities. These different inputs can have positive or negative effects on aquatic ecosystems. Consequently, it is quite complex to study the impacts of wildfires on aquatic ecosystems, often requiring an holistic approach, analyzing at the same time the instream communities, river habitat and morphology, landscape features of the drainage basin as well as the frequency and severity of wildfire. All these factors will influence the spatial and temporal scales of wildfire impacts on aquatic ecosystems. In the intermountain west, USA, large wildfires cause impacts on aquatic ecosystems that can take 5-10 years or longer to recover (Minshall et al., 2001), whereas human-controlled fires often show less impact.

In Mediterranean regions, wildfires are common and mainly occur during summer. High temperatures and low air humidity, many times associated with poor forest management, create excellent conditions for wildfires (Wondzell, 2001). These specific characteristics allow Mediterranean regions to have higher wildfire frequencies than other biomes (Chandler et al., 1983). Information concerning the impacts of wildfires on aquatic communities is scarce for Mediterranean regions (Lavabre, 1983; Vila-Escalé, 2007), although recovery rates of forests are expected to be faster and with less impact on aquatic communities than those from continental regions.

2. Frequency and ocurrence of wildfires in Portugal

Historically, wildfires have been an important ecological factor for forest establishment in Mediterranean regions. Several Mediterranean species have evolved strategies to survive wildfire, including fire resistance, seed dormancy that ends following wildfire, and pines that have cones, requirering fire to open and shed seeds (e.g. Fernandes & Rigolo, 2007).

In Portugal, having Mediterranean climatic conditions, wildfires usually occur each year, with highest frequencies during summer from July to September and mainly in central Portugal where large forest areas are found (Damasceno & Silva, 2007). Burned areas during the last decades (Fig. 1) show accentuated fluctuations in area burnt between consecutive years. There has been a general increase in burned area as well as a tendency of increasing occurrences to approximately every five years (Rodrigues & Brandão, 2003). Therefore, depending of local variables, overstory vegetation seems to have cyclic return periods and, after each growing period, an optimal of biomass fire fuel-load is attained (Wondzell, 2001). Therefore, forest vulnerability to fire is also cyclic and, during the more vulnerable periods, human

activities seem responsible for most wildfires. Although a linear positive correlation was observed between fire occurrence and surrounding population density (Silva & Catry, 2006), only 30% of the fires were considered human-caused from 2001 to 2006 (Damasceno & Silva, 2007). Other major driving forces of fire occurrence increase include land abandonment and the subsequent shrub encroachment, as well as afforestation of former agricultural land, both leading to increased fuel accumulation (Viedma et al., 2006). Hence, among reasons associated with fire causes in Portugal, many are related with territorial management and planning, important socio-cultural components and forestry strategies.



Figure 1. Areas burned (ha) in Portugal by wildfires from 1968 to 2003. Bars: raw data; solid line: transformed data by time averaging for three year periods (adapted from Rodrigues & Brandão, 2003).

3. Behavior of forests to wildfire

Each forest type has specific fire-proneness (e. g. flammability, combustibility) vulnerabilities and post-fire resilience, depending on its structure and species composition. Low density forests composed of large trees are less vulnerable as a result of the discontinuity of combustible matter from the forest floor to the tree canopy (Fernandes et al., 2006). In contrast, more dense forests composed of small trees, shrubs and with much organic matter on the forest understorey are more vulnerable to fire. Due to the continuity of combustible material in these forests, fire intensities also tend to be high. Godinho Ferreira et al. (2006) also describe a tendency of increasing wildfire probability on the bigger forest patches of the forest types that are more likely to burn in Portugal (*Pinus pinaster* forest and *Eucalyptus* sp.), while the contrary happens with other forest stands (e. g. *Quercus pyrenaica*).

Maritime pines and eucalyptus have the highest vulnerability to fire, whereas cork and holm oaks have the lowest vulnerability (see Table 1, adapted from Fernandes, 2007). Following fire, different vegetation survival and recovery rates are observed in the different forest types. While eucalyptus, being vulnerable, has high recovery rates (just after the fire small branches and leaves start growing), cork oaks, being less vulnerable, need several years to recover (Fig. 2). Maritime pines often survive fire, but without a certain amount of needles frequently die later. On another hand, post-fire logging is also a non neglectable activity in Portugal (e. g. Viegas, 1999), intending to salvage some economic value before the decay of burned trees, and also to reduce fuel-load, to prevent bark beetle pests, and to improve the landscape value of the area (e. g., McIver & Ottmar, 2007).

As a result of the relationship between natural vulnerability, recovery, and forestry post-fire management strategies, some trees survive well, while others stay in poor physiological conditions and probably die several years later (Silva et al., 2007). Standing trees, killed by wildfire, start to decompose on the next few years by the joint effects of microorganisms and moisture, then falling as large woody debris. This large woody debris, if not retained, can move further down slope, enter rivers, and be incorporated in river morphology and function for the long-term.

 Table 1. Index of vulnerability to fire for different tree species (adapted from Fernandes, 2007).

Tree species	Index of Vulnerability to fire
Maritime pine	20
Eucalyptus	12
Stone pine	9
Other conifer species	8
Other broadleaved species	7
Cork oak	2
Holm oak	1



Figure 2. Different recovery rates of tree species three years after a wildfire in the south of Portugal. At the top, the higher recovery rate of eucalyptus, at the bottom, low recovery rate of cork oaks (photo P. Pinto 2006).

4. Materials exported to aquatic ecosystems after wildfire

4.1. Chemical components

Depending on temperature, large amounts of organic matter are completely or partially mineralized, providing large amounts of nutrients (phosphorous and nitrogen) and inorganic carbon that stay in the soil. During rainfall after wildfire, surface runoff occurs and these chemical compounds are exported to rivers, increasing nutrients, dissolved inorganic carbon and turbidity (Overby & Perry, 1996; Minshall et al., 2001). Under certain conditions, the partial combustion of organic matter in the presence of chlorine can produce polycyclic aromatic compounds; pyrogenic toxicants are also exported to rivers (Barber et al., 2003; Vila-Escalé, 2007).

4.2. Fine and coarse particulate organic matter

Many partially burned leaves will fall to the forest floor or stay weakly attached to tree branches. These leaves can arrive quickly to rivers, providing an extra input of coarse particulate organic matter. This input has different characteristics than the natural one: different composition because most or all volatile components were

consumed by the fire, and the input period (during summer) is before the normal one in autumn.

4.3. Large woody debris

Rivers reflect the landscape through which they flow. As such, natural rivers follow a temporal succession that follows that of the surrounding landscape after wildfire. For instance, Minshall et al. (1989, 1997) suggested that streams in the intermountain west of North America show immediate, mid-term, and more long-term affects of wildfire as the forest slowly recovers over 100 plus years. Other biomes show rapid recovery of the terrestrial landscape and rivers show a more short-term impact from wildfire, e.g., eucalyptus forests in Australia have a recovery period of less than 10 years and streams seem to recover in 5 years or so. One reason for the differences in recovery is the output of large woody debris into rivers following wildfire. Trees killed by wildfire can eventually reach rivers if the landscape characteristics dictate downhill movement. In the northwest USA, this may take decades as the half life of a standing dead tree is 15 years.

5. Impacts on aquatic communities

Impacts on aquatic communities can have two principal origins: physical and chemical alterations that act directly on aquatic communities, and on habitat modifications that change the conditions for the establishment of aquatic communities. Both can have negative and positive impacts on aquatic communities.

Periphyton is directly influenced by the increase in nutrients that usually occurs following wildfire. Nutrients, mainly nitrogen and phosphorus, are well known as important factors for increasing periphyton biomass. Jointly with nutrients, an increase in inorganic matter inputs, sediments in more lentic habitats, can cover biofilm layers. A benthic biofilm layer covered by inorganic fine sediments is not optimal for periphyton, and a decrease in biomass is expected. Due to these opposite effects, it is difficult to predict the influence of wildfire on periphyton, and a global relationship seems unclear and dependent on season (Minshall et al., 2001).

Macroinvertebrates can be influenced by several factors. In a direct way after wildfire, water quality tends to decrease due to the input of chemical components and organic and inorganic particles. In this sense, it is expected to negatively influence the more sensitive taxa, affecting diversity, richness and composition. In another way, the increase in particulate organic matter as well an eventual decrease in periphyton biomass has important effects on food webs and trophic structure (Spencer et al., 2003), with an expected increase in collectors and a decrease in herbivores. An indirect influence results from habitat modifications that also can have positive and negative impacts depending on the specific taxa. Generally, the destruction of some habitats is related to an increase in more generalist taxa, whereas the creation of new habitats, mainly as a result of large woody debris deposition, can increase the abundance of more specific taxa. At a coarser temporal scale, wildfires induce modifications of the hydrological regime with more intense floods for shorter periods of time. It is expected that the higher level of perturbation

will result in less stable communities. In this way, it is expected to have communities composed of early colonizers and dispersers. These impacts depend on ecological river conditions. Rivers with less variability in the hydrologic regime over the year tend to have impacts that extend for more years, up to 10 years, being much longer than those in regions with higher variability in the year. For the latter, the natural communities, being adapted to a more changing environment, tend to have shorter recovery times and, consequently, wildfire impacts are found for periods of time shorter than two years (Fig. 3).

Macrophytes can experience three different types of impacts from wildfires. The more direct one, concerning helophyte communities and riparian vegetation, is the possibility of being burned. However, this direct impact is dependent on valley form. In very flat valleys, the riparian vegetation is more exposed and can be easily burned. In contrast, in a "V" shape valley, macrophytes and riparian vegetation are difficult to burn. Under this situation, the fire burns only the top of the trees because the generated air currents tend to push the fire up. The second impact is related to the higher concentrations of nutrients with well-known effects on aquatic vegetation, both helophytes and hygrophytes. A third impact is more indirect because it can result from habitat modifications such as formation of pools and debris dams, creating new habitats to be colonized by macrophytes (Blank et al., 2003).



Figure 3. Coefficient of similarity obtained for macroinvertebrate communities at five sites in the south of Portugal (F3, F4, F5, F7 and F9), between pairs of dates with 2001 being before the wildfire and 2006 and 2007 after the wildfire occurred in 2003. The bars show quite similar macroinvertebrate communities before and three years after the wildfire.

Impacts to fishes are less visible because they can move along rivers, and less information is available on this topic. More long-term effects are expected as a result of the accumulation of large woody debris creating new habitats. These new habitats can be quite important as refugia for many fishes. In another way, the possible formation of debris dams can form pools and barriers that reduce longitudinal connectivity with negative impacts on migratory fishes. Lastly, wildfire can have positive and negative impacts on fishes. Due to the scarce information on this topic, it is difficult to generalize the main result of these impacts.

6. Impacts on the morphology of aquatic habitats

Hydrological regime alterations resulting from wildfire (Lavabre et a., 1993) are an important source of habitat modification, both in quantity and quality (Rinne & Neary, 1996; Howell, 2001). Large woody debris is a major structural component of many natural rivers. This large woody debris is incorporated into channels, increasing habitat heterogeneity and providing structural support (Robinson et al., 2005). Large woody debris can directly influence river morphology by being retained and causing shifts in channels. It also is a primary habitat and food resource for some aquatic organisms and refuge to others like fishes. Wildfires increase the amount of large woody debris in rivers as trees breakdown and are transported down-valley by gravity. This input may be retained in the river or transported downstream. The effects of large woody debris inputs and their transport differ by forest type and stream size, although surprisingly little information exists on this topic.

The input of large woody debris may ultimately influence the food webs of impacted rivers by altering habitat conditions and retaining fine organic particles that aquatic organisms can use as food or habitat. Incorporation of large woody debris in rivers following wildfire can alter energy flow and nutrient cycling, that is ecosystem structure and function (Mihuc, 2004). These functional changes will manifest themselves in changes in aquatic communities, changing biological traits of these communities.

7. Final remarks

Effects of wildfires on aquatic ecosystems are complex conducting simultaneously to positive and negative impacts on the different components of the ecosystems. To predict spatial and temporal magnitude of these impacts is complex because they depend from region, fire severity, forest recovery and river hydrology. Concerning Mediterranean regions, where the scarcity of water during the dry season is a key factor to the vulnerability of the aquatic ecosystems, to balance positive and negative impacts after wildfires is very important in order to implement management practices both on rivers and on burned involving drainage areas. Construction of reservoirs is a common strategy to save water to be used during the dry season. A reservoir implanted in a river affected by wildfires cuts the longitudinal gradient and sediments and organic matter, originated by wildfires, can be retained, influencing water quality and life time of the reservoir. For these
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reasons the study of wildfire impacts on reservoirs must be a future goal on wildfire impacts research.

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