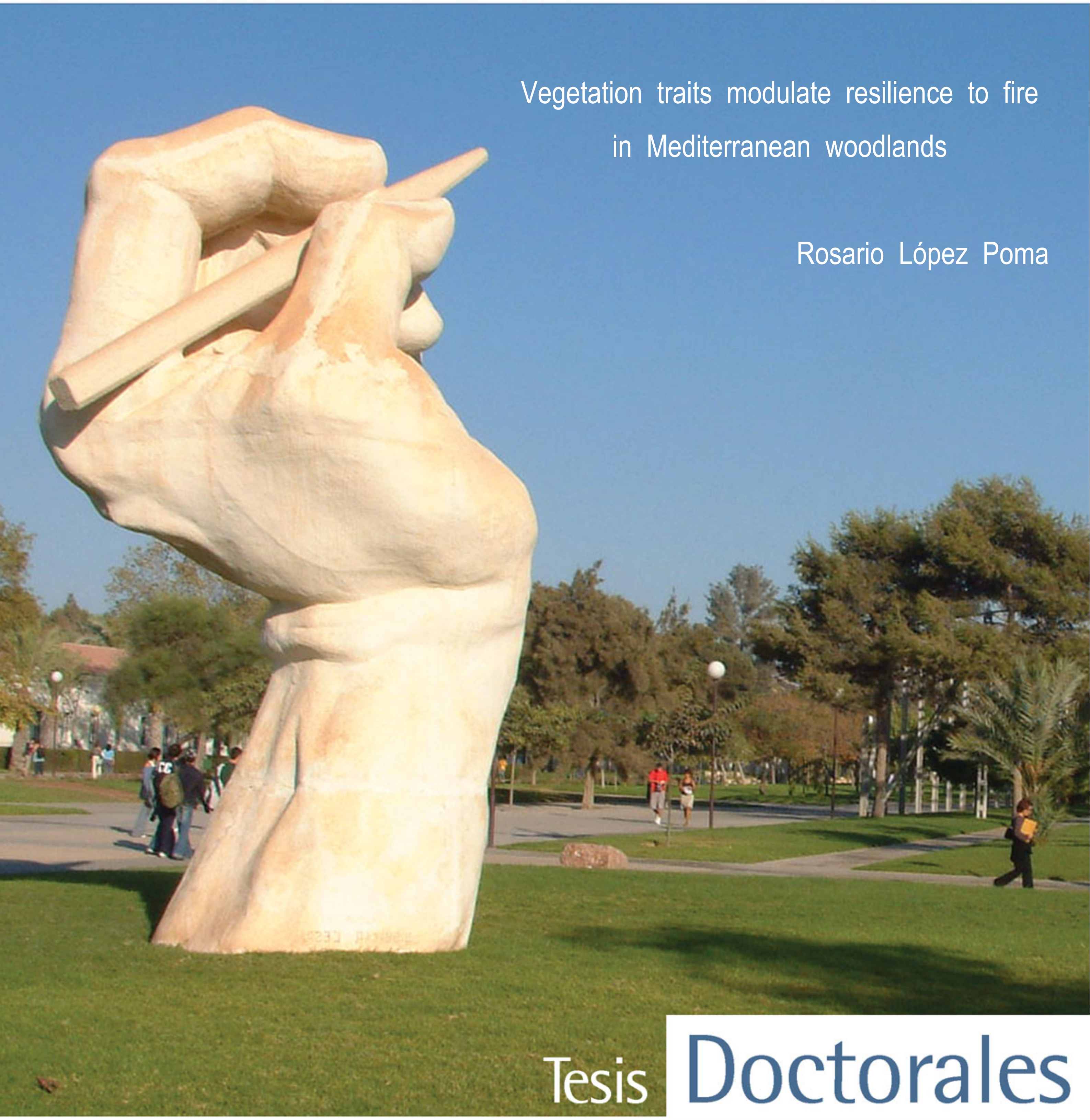


Vegetation traits modulate resilience to fire in Mediterranean woodlands

Rosario López Poma

Universitat d'Alacant
Universidad de Alicante

Departament d'Ecologia
Departamento de Ecología

Vegetation traits modulate resilience to fire in Mediterranean woodlands

Memoria presentada por Rosario López Poma para optar al grado de Doctor con Mención International por la Universidad de Alicante

Directora
Dra. Susana Bautista Aguilar

Alicante, 31 Marzo 2014

Universitat d'Alacant
Universidad de Alicante

Departament d'Ecologia
Departamento de Ecología

Susana Bautista Aguilar; Profesora titular de la Universidad de Alicante e Investigadora del Instituto Multidisciplinar para el Estudio del Medio "Ramón Margalef"

HACE CONSTAR:

Que el trabajo descrito en la presente memoria, titulado: "**Vegetation traits modulate resilience to fire in Mediterranean woodlands**" ha sido realizado bajo su dirección por Rosario López Poma en la Universidad de Alicante, y reúne todos los requisitos necesarios para su aprobación como Tesis Doctoral con Mención International.

Alicante, 31 de Marzo de 2014

Dra. Susana Bautista Aguilar

A mi madre

Table of contents

List of figures

List of tables

Chapter 1

Introduction:
Factors modulating resilience to fire in Mediterranean woodlands

1. Introduction: Factors modulating resilience to fire in Mediterranean woodlands.

1.1 Wildfires in the Mediterranean Basin

Wildfire is a common and natural disturbance in Mediterranean regions worldwide. As a consequence, many plants have acquired adaptive mechanisms to persist and regenerate after wildfires. The dominant natural ecosystems in the Mediterranean Basin and other Mediterranean regions are therefore commonly viewed as rather resilient to fire and, in general, are able to cope with the natural high fire-recurrence regimes observed in Mediterranean regions (Naveh 1975; Keeley 1986; Pausas and Verdú 2005). However, wildfire is also a primary factor driving ecosystem processes and structure (Bond and Keeley 2005; Pausas and Keeley 2009), and in turn landscape pattern (Lloret et al. 2002; Baeza et al. 2007). Wildfires promote flammable ecosystems deviating from the physiognomy that could be expected according to the climate of the region (Bond et al. 2005; Moreira et al. 2011). Thus, vast areas of Mediterranean shrublands have the potential to be forest, but frequent wildfires, together with grazing, are largely responsible for maintaining the dominance of shrubs. Wildfires in Mediterranean Basin have occurred for millennia, and therefore biodiversity of Mediterranean Basin may have been structured by fire regime (Pausas et al. 2008). However, one of the most relevant differences between the Mediterranean Basin and other Mediterranean regions in the world is the millenary impact of intense land use, including burning, woodland clearing, grazing, terracing, and cultivation, which has resulted in strongly human-modified landscapes with consequences for the Mediterranean fire regime (Moreira et al. 2001; Carrión et al. 2003; Mouillot et al. 2003; Vannière et al. 2008). On the one hand, human activities have created a heterogeneous mosaic of land uses and land cover types that are not equally fire-prone, retarding the spread of fire and resulting in relatively small areas burned by individual wildfires. On the other hand, intense land use by humans, which often included uprooting of oaks and other resprouting species (Vallejo and Alloza 1998), combined with frequent fires, has led to changes in vegetation towards ecosystems dominated by seeder species. These ecosystems are in turn more susceptible to the risk of wildfire and less resilient than those dominated by non-seeder species, resulting in longer windows of disturbance, and therefore longer post-fire periods with soils exposed to erosive agents.

In European Mediterranean countries, the number of fires and area burned have increased significantly during the last decades as compared with earlier parts of the 20th century (Pausas et al. 1999; Pausas 2004). In the Valencia region (eastern Iberian peninsula), this increasing trend has been particularly remarkable since the mid-1970s, with a conspicuous shift between regimes around 1972-1973 (Pausas and Fernández-Muñoz 2012). Thus, in 1978-1979, 154000 ha burned in two consecutive fire seasons, and in 1994 140000 ha burned over a few summer days, representing nearly 12% of the forest area (Pausas 2004). Similarly, in the Minho region (northwestern Portugal) the number of fires increased three-fold in the 1980-1996-period (Moreira et al. 2001).

According to Dube (2009), the spatial pattern of wildfires may result from the interaction of numerous factors at multiple scales. However, at the regional scale, it mainly responds to climate-fire-vegetation feedbacks. In the Mediterranean Basin the change in the fire regime over the past century was associated with two drivers: climatic changes and socioeconomic causes (Fernández-Ales et al. 1992; Moreira et al. 2001; Pausas 2004; Pausas and Fernández-Muñoz 2012). A clear increase in temperatures over the last 50 years (1950-2000) and a decrease in average summer rainfall, may imply a decrease in fuel moisture and a consequent increase in fire hazard (Piñol et al. 1998; Pausas 2004). Socioeconomic factors like the industrial development that had taken place in various European Mediterranean countries during the 1960s led to depopulation of rural areas (Fernández-Ales et al. 1992; Moreira et al. 2001; Duguy and Vallejo 2008), inducing drastic changes in traditional land-uses including the abandonment of cultivated fields and reduction of livestock grazing. This land use change together with the implementation of extensive afforestation programmes increased the accumulation and continuity (in some cases) of the amount of fuel, frequently consisting of very flammable vegetation at early successional stages (Baeza et al. 2011). Pausas and Fernández-Muñoz (2012) suggest that while wildfires prior to the 1970s period were fuel-limited fires, mainly related to land use, post-1970s fires are currently less fuel limited and more drought-driven.

Despite the fact that Mediterranean ecosystems are generally resilient to fire, various studies suggest that current fire regimes may induce important changes in community composition, and therefore affect ecosystem resilience. For instance, in communities dominated by obligate seeders, high recurrent fires result in times between fires that are too short for plant establishment, maturation and seed dormancy, leading to replacement of forest by shrub dominated landscapes, or to changes in the dominance of species (Kazanis and Arianotsou 2004; De Luís et al. 2006). At the landscape level, fires can change landscapes towards either homogenization or heterogenization, depending on the size of burned areas and the scale at which the landscapes are studied/observed/analyzed. For example, large wildfires that burn different forest types in the same fire, could drive this mosaic of forest types towards a more homogeneous shrubland-type landscape (Rodrigo et al. 2004; Viedma et al. 2006), particularly if forest resilience is low due to high fire frequency (Díaz-Delgado et al. 2002; Kazanis and Arianotsou 2004). However, fires can also fragment homogeneous areas of forests or shrublands and create mosaics of successional stages (Lloret et al. 2002).

1.2. Stability against disturbances: Resistance and resilience

The response of an ecosystem to disturbance like fire reflects its stability, which has two main facets: resistance and resilience (Pimm 1984; Grimm and Wissel 1997). Resistance is commonly defined as the ability of a system to withstand a disturbance; it is measured as the magnitude to which the target attributes or variables change due to the disturbance. Resilience has been defined in multiples ways, emphasizing different aspects of stability, but most definitions can be grouped in two main categories: engineering and ecological resilience (Holling 1996). Engineering resilience is defined as the rate at which a system returns to a single steady or cyclic state following a disturbance; the definition assumes the behaviour of a system to be like an engineering material that will show displacement (immediate response to disturbance) and recovery towards its pre-disturbance state; it focuses on stability near an equilibrium steady state and, according to this definition, resilience is measured as the speed or degree of return to the equilibrium or pre-disturbance conditions. Ecological resilience considers how much disturbance is required to move the system from one stable state to another alternative stable state, to another stability domain (Holling 1973; Walker et al. 1981). This definition emphasizes conditions far from any equilibrium. Using the ball and cup model (Holling 1973; Gunderson 2000; Fig. 1.1), resilience is a measure of how much disturbance can the system (ball) absorb so that it still remains in the same basin, before it flips over into another stable state (different basin-cup). This definition assumes that ecosystems may cross a threshold line and dramatic changes can occur in critical variables, moving the systems towards different trajectories from pre-disturbance conditions.

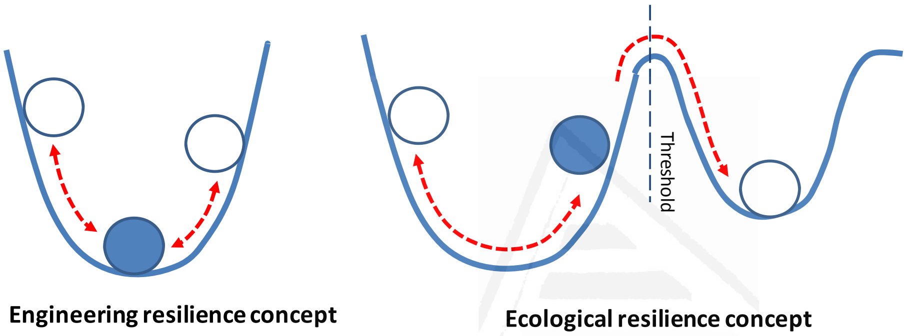


Figure 1.1: *Description of resilience concepts through the "Ball and cup" model (adapted from Holling 1996)*

The stability of plant communities against fire has been addressed from multiple perspectives as well. Vegetation resistance to fire has been defined as the degree to which properties such as vegetation cover, species composition or species richness, remain unchanged in the face of fire; it will vary depending on the sensitivity and degree of protection against fire of seeds and buds of the resident species (Keeley 1986). Vegetation resilience defines the recovery rate of vegetation variables to pre-fire values (Halpern 1988; Lavorel 1999), and may depend on pre-fire species composition, the persistence traits of the species (ability to recruit seedling or to resprout after fire), and the degree of damage produced by the fire regime (severity and frequency). Thus, the stability of vegetation communities reflects the ability of resident species to resist change, or, if altered by disturbance, their ability to readjust or recover (Halpern 1988). Westman and O'Leary (1986) measured the response of a coastal sage scrub community to fire in southern California by four components of resilience: elasticity (rate of recovery after disturbance), amplitude (threshold of disturbance beyond which recovery to the original state no longer occurred), malleability (extent of the alteration of the new stable-state from the original) and damping (extent and duration of the oscillation in an ecosystem parameter following disturbance). Similarly, for a *Quercus coccifera* garrigue in southern France, Malanson and Trabaud (1987) analysed the same four components of resilience, while other authors such as Halpern (1988) working on *Pseudotsuga* forests in Oregon, and Proença et al. (2010) working on broadleaved forest (*Quercus robur*, *Ilex aquifolium*) and pine plantations (*Pinus pinaster, Pinus sylvestris*) in Portugal, only distinguished between resistance and resilience.

Many studies have addressed resistance and resilience of soils against disturbances (e.g., Seybold et al. 1999; Orwin and Wardle 2005; Wertz et al. 2007; Chaer et al. 2009; De Vries et al. 2012). Seybold et al. (1999) specifically defined soil resistance (qualitative property) as the inherent ability of a soil to continue functioning without major changes throughout a disturbance or period of stress, staying essentially unchanged despite the presence of disturbing agents; while soil resilience (quantitative property) would be the capacity of a soil to recover its functional and structural integrity after a disturbance. For Herrick (2000), resistance can be defined in terms of soil properties; however, resilience is more often a function of soil processes, such as decomposition or mineralization.

Ecosystem resilience can be evident at different scales and can simultaneously act at all scales. For instance, fires can transform one vegetation type into another, like the change of dense pine forest into shrublands after fire (Kazanis and Arianoutsou 2004), changing in this way the structure of the landscape mosaic (Lloret et al. 2002; Loepfe et al. 2010). Similarly, resilience of different ecosystem components and processes may covary. For example, due to plant-soil feedback, resistance and resilience of above- and below-ground ecosystems are expected to be interrelated (Seybold et al. 1999; Herrick 2000; Certini 2005), although testing of this assumption is scarce. However, it is important to emphasize that different ecosystem components and processes may vary largely in their sensitivity to disturbances and in their capacity for recovery (Lavorel 1999). For example, the recovery of vegetation cover after fire can be relatively fast, while the species relative abundance may need more time to return to pre-fire values.

This dissertation primarily uses the engineering concept of stability, assuming that resistance is the ability to withstand the fire effect and resilience as the ability of an ecosystem or community to return to pre-fire conditions. Therefore, resistance is measured as the amount of immediate fire-driven change in the properties of interest, and resilience as the amount of change in these properties towards recovery of pre-fire values, measured at a given time after fire. However, the concept of ecological resilience is also present throughout the dissertation when potential for ecosystem shifts into alternative states are considered.

1.3. Factors affecting ecosystem resistance and resilience to fire

Resistance and resilience of an ecosystem to fire results from a combination of biotic and abiotic factors that are related to (1) the fire regime (fire severity and frequency); (2) post-fire climatic conditions; and (3) factors inherent to the physical and biological structure of the vegetation community and to the site conditions. These factors interact between themselves and act at different scales. Fire potentially may affect all levels of biological organizations, and therefore plays an important role in the structuring and functioning of populations, communities, and ecosystems. The magnitude of the effect of fire on vegetation and soil (resistance) depends essentially on fire severity, which actually can be considered as the reverse property of resistance (see below), together with other plants and soil characteristics that relate to their sensitivity and degree of protection; while the recovery capacity (resilience) of vegetation and soils after fire depends on fire severity, the regenerative ability of the resident species, and the post-fire conditions.

1.3.1. Fire intensity and severity

It is essential to clarify the differences between fire severity and fire intensity since these terms are sometimes used interchangeably in the literature. Fire intensity is related to the quantity of fuel consumed and the energy released in the combustion process. It can be measured by a variety of metrics, although the most extensively used metric is what is known as fireline intensity (sensu Byram 1959: the rate of heat transfer per unit length of the fireline, kWm^{-1}). However, fire intensity is too narrow to fully capture the multitude of ways that fire energy affects ecosystems (Keekey 2009). Fire severity is generally and increasingly used to describe fire effects on ecosystems; it is defined as the fire impacts on ecosystems caused by the direct transformation or loss of organic matter, both aboveground and belowground (Keeley 2009). Thus, fire severity correlates with fire intensity; it captures the effect of fire intensity and residence time on plants and soil (Pérez and Moreno 1998). To some extent, fire severity and resistance to fire can be viewed as the two sides of the same coin, yet fire severity normally refers to the loss or decomposition of organic matter (Keeley 2009), while resistance to fire applies to any ecosystem component or process.

Fire severity is a major control factor of ecosystem resilience, as it can greatly affect patterns of seedling recruitment, resprouting ability, microbial activity, and many other ecosystem processes (Bond and Van Wilgen 1996; Neary et al. 1999; Keeley et al. 2005). Fires do not burn homogenously within a given burned area (Gimeno-Garcia et al. 2004); the spatial heterogeneity of fire severity partially relates to the spatial distribution of fuel load within the affected area, and it is a major influence on ecological processes and states in post-fire vegetation and soils (Odion and Davis 2000; Crotteau et al. 2013).

During experimental or prescribed fires, fire intensity can be estimated in several ways by using devices that are installed in the area before the fire: thermocouples record temperatures continuously at a given place; thermo-sensitive paints, based on chemicals that change appearance as a function of the exposure to heat, capture the maximum peak of temperature reached during the fire; open calorimeters, made of containers filled with water that evaporates when is heated by the fire, can be used to relate water mass loss to fire intensity (Wally et al. 2006). Estimation of fire severity in controlled fires can be done, for example, by comparisons of pre- and post-fire biomass (e.g., Santana et al. 2011). However, estimating severity of wildfires is difficult, since all the measurements must be done *a posteriori*. In forest, classes of fire severity have been defined by visual estimation of the degree of crown scorched (Turner et al. 1997), and through quantification of the percentage of the tree mortality after fire (Chappell and Agee 1996). Fire severity has been also estimated by measuring the diameter of the terminal branches remaining after fire, which is used as an indicator of biomass loss (Moreno and Oechel 1989; Pérez and Moreno 1998). For determining soil fire severity, several visual indicators have been used that are based on immediate changes in the forest floor (level of consumption of organic layer) and mineral soil (changes in colour or structure), and the deposition of ash from the aboveground combustion of biomass after fire, which reflect different degrees of the level of organic matter consumed (Neary et al. 1999; Brais et al. 2000). Near-infrared (NIR) reflectance spectroscopy is used as a fast, simple and non-destructive method to estimate *a posteriori* the maximum temperatures reached on burned soils (Guerrero et al. 2007), since NIR spectra change in accordance with change in soil maximum temperatures. At a landscape scale, remote sensing images are used for discrimination of spectral variability (severity classes) produced by fire severity in large fires, normally using the Normalized Difference Vegetation Index (NDVI) (Díaz-Delgado et al. 2003).

1.3.2. Fire frequency

The impact of fire frequency on ecosystems is a function of interval-dependent processes related to the availability of time for plant establishment, maturation, seed production and longevity (in dormancy) of seeder species, as well as for the recovery of the storage of non-structural carbohydrates of resprouter species (Zedler 1995; Clarke et al. 2013). Fire-dependent obligate seeder species can face the risk of either immaturity or senescence for short and long intervals between fires, respectively (Zedler 1995). Short intervals may negatively affect density and growth rates of tree and shrub populations (e.g. *Pinus* sp) (Ne'eman et al. 1999; Eugenio et al. 2006a). Seeder shrub species (e.g., *Rosmarinus officinalis*, *Cistus albidus*) seem to achieve maximum abundance at intermediate fire frequencies (Lloret et al. 2003). Furthermore, high fire recurrence may increase the abundance of resprouter perennial grasses (e.g., the tussock grass *Ampelodesmos mauritanica*; Lloret et al. 2003), while productivity and recovery of some resprouter shrub species may decrease (Delitti et al. 2005) due to the exhaustion of stored carbohydrate resources (Paula and Ojeda 2009). Fires of short return interval cause higher exposure of the soil surface, which leads to higher runoff rates and consequently increased soil erosion (Campo et al. 2006; Wittemberg and Inbar 2009; Malkinson et al. 2011); and reduction of soil nutrient content (Eugenio et al. 2006b). In general, highly frequent fires can greatly delay the recovery of plant cover and biomass in Mediterranean ecosystems (Mouillot et al 2003; Delitti et al 2005; Malak and Pausas 2006), leading to longer windows of disturbance and therefore decreased resilience.

1.3.3. Community structure and plant traits

Vegetation traits play a decisive role in determining flammability, fire severity and post-fire recovery, which in turn affect the composition of the post-fire community leading to feedback processes between vegetation and fire. Species composition and stand age determine the fuel load and structural characteristics (compactness, surface-volume ratio, vertical and horizontal continuity, live to dead fuel ratio, and bulk density), which influence the moisture dynamics, ignition process, combustibility of fuels, and fire spread rates (Baeza et al. 2002; Schwilk 2003; Alessio et al. 2008a; Saura-Mas et al. 2010; Santana et al. 2011), and therefore the potential fire severity. At the same time, pre-fire species and functional composition (particularly regarding post-fire persistence traits) are of crucial importance for post-fire vegetation recovery (Whelan 1995; Lloret and Vilà 2003; Arnan et al. 2007; Duguy and Vallejo 2008).

Many species of Mediterranean regions can recruit abundant seedlings (seeder) or resprout from vegetative organs (resprouter) after fire; other species are capable of using both regeneration mechanisms (facultative). These species traits allow pre-fire species or individuals to persist after fire, making Mediterranean communities highly resilient to fire (Keeley 1986; López-Soria and Castell 1992; Pausas et al. 2004a; Keeley et al. 2005; 2006).

Although not all Mediterranean species survive fires in all situations. Forest and woodlands dominated by resprouter trees (e.g. *Quercus ilex, Q. cerrioides, Q. suber, Q. pyrenaica*) or shrubs (*Quercus coccifera*) (Calvo et al. 2003; Rodrigo et al. 2004; Delitti et al. 2005), or by seeder species with efficient seedling recruitment after fire (e.g., *Pinus halepensis*, *P. pinaster*) can be highly resilient to wildfires (Pausas et al. 2003; Rodrigo et al. 2004; Arnan et al. 2007). Conversely, forests dominated by seeder species that produce low seedling recruitment (e.g., *P. nigra, P. sylvestris*, and *P. pinea*) could easily shift to another community type after the fire (Rodrigo et al. 2004; Arnan et al. 2007). Mediterranean ecosystems vary largely in terms of the proportion of resprouter and seeder species. To a large extent, this variation depends on the land use history (Duguy and Vallejo 2008; López-Poma et al. *in press;* see Chapter 2), which may modulate the relative presence of species with different fire-persistence traits. Land-use history also determines the physico-chemical properties of the soil (soil fertility) in the medium term (Duguy et al. 2007). Consequently it is expected that areas with different land use histories probably differ in their response to fire, leading to differences in post-fire regeneration patterns (Duguy and Vallejo 2008; Puerta-Piñero et al. 2012). However, little is known about the influence of the agricultural legacy of the species pool in determining the demography of resprouters and obligate seeders after fire. Moreover, there is limited understanding of the global effect of the functional composition (resprouter versus seeder) of Mediterranean woodlands on community resilience to fire through the combined effect of regeneration capacity, flammability, and severity.

Apart from plant fire-persistence traits, other plant individual and community characteristics can be relevant in determining post-fire vegetation recovery. The plant size of resprouter individuals seems to be the most important factor determining the number and biomass of resprouts (Canadell et al. 1991). Stand age, which relates to fire frequency may be also crucial in post-fire regeneration, particularly for seeder species, as it affects the capacity for producing seeds as well as for seed storage and canopy banks (Kazanis and Arianotsou 2004; Eugenio et al. 2006a). Species diversity may also be relevant. For example, long standing forests with a high number of species, and thus more diverse functional traits, will ensure forest recovery after fire and high resilience after intense disturbances (Puerta-Piñero et al. 2012). However, diversity-resilience relationships have been addressed in relatively few studies (e.g., Lloret and Vilà 2003; Dimitrakopoulos et al. 2006), so no well accepted theory has been established yet.

The resilience of some soil components and functions may also depend on the structure of the plant community. The recovery of soil organic matter in the burnt areas starts with the recovery of vegetation (Certini 2005), which, in turn, will define the re-establishment of the microbiological activity of the rhizosphere (Hernández et al. 1997).

1.3.4. Climatic conditions

Weather conditions during a wildfire are important in determining fire behaviour and in turn the virulence of the fire. After the fire, climatic conditions are critical for soil stability and successful re-establishment and vegetation regrowth. Unfavourable dry conditions after the fire may hamper the recovery of species that typically regenerate well after fire, such as obligate seeders, which are particularly sensitive to the availability of water at the time of establishment (Céspedes et al. 2012). As a result, different successional dynamics are possible depending on post-fire climatic conditions (Quintana et al. 2004), which in combination with other factors such as fire severity, can greatly affect species response to fire. Slow post-fire vegetation recovery caused by a drought period immediately after the fire can lead to a very limited initial soil protection and a high soil susceptibility to crusting and erosion, particularly in fine textured soils such as those developed over marls (Mayor et al. 2007). The current climate trend in the Mediterranean towards longer summer droughts and intensification of extreme events, both drought and heavy rainfalls (Giorgi and Lionello 2008), can further increase the risk of reduced resilience and subsequent greater wildfire impact on ecosystems (Mouillot et al. 2002).

1.3.5. Site physiographic conditions

Physiographic factors inherent to site conditions like aspect, slope, and bedrock type may have considerable effects on the ecosystem resilience of burned areas (Pausas et al. 1999). Aspect seems to be an important variable regarding fire behaviour and vegetation recovery because of its relationship with wind intensity, fuel amounts and moisture, and heat and water stress. South-facing slopes in the northern hemisphere are commonly characterized by drier conditions, which normally limits post-fire vegetation recovery and ecosystem resilience as compared with north-facing slopes (Pausas et al. 1999; Mouillot et al. 2003; Malkinson et al. 2011). Low plant recovery rates on south-facing slopes may increase post-fire erosion rates as compared with north-facing slopes (Marqués and Mora 1992), which could further impact resilience. Slope angle is also an important factor for vegetation and soil resilience. On steep slopes, plant recovery may be significantly reduced (Tsitsoni 1997), which, combined with direct effect of slope angle on runoff energy could further increase post-fire damage to the ecosystem. In the Mediterranean basin, the post-fire recovery rate of vegetation varies largely with bedrock type (Pausas et al. 1999), as the bedrock type is strongly related to soil type and land use in this region. For example, post-fire vegetation recovery is commonly higher on soils developed over limestones than on soils over marls, which can be partially related to a more intense agricultural use and associated removal of resprouting shrubs.

1.4. Measures of resistance and resilience

Measurements of resistance and resilience following fire disturbance are usually made by comparing pre- and post-disturbance values of the studied variables, either functional or structural variables. Single structural variables, such as plant cover or remote-sensing based vegetation Indexes, can be used to describe resilience to fire in vegetation communities (e.g., Keeley 1986; Díaz-Delgado et al. 2002; Wittenberg et al. 2007). However, vegetation resilience after fire is commonly measured by capturing the rate of change in plant species composition. Thus, floristic dissimilarity or similarity indices (distance in species space) are commonly used to measure temporal changes in species composition and to express the relative displacement or recovery of the plant community after fire (Armour et al. 1884; Westman and O'Leary 1986; Rydgren et al. 2004; Keeley et al. 2005; Buhk et al. 2007). Ordination techniques such as Detrended Correspondence Analysis (DCA), a two dimensional ordination space that is reliable for representing ecological distances among communities, and Euclidean distances between pre- and post-fire samples in the ordination space have also been used to compare community resistance to fire and long-term recovery or resilience (Halpern 1988; Malanson and Trabaud 1987; Santana et al. 2010).

Measures of soil resistance and resilience have particularly focused on the response to disturbances of biochemical and microbiological soil properties (e.g., Seybold et al. 1999; Orwin and Wardle 2004; Wertz et al. 2007; Chaer et al. 2009; Griffiths and Philippot 2012). Several equations are used for measuring resilience and resistance, which are usually based on the engineering concept of stability and resilience. Thus, resistance is quantified by the immediate disturbance-driven change of the studied variable as compared with undisturbed or pre-disturbance conditions, and resilience is calculated by the recovery of the disturbed variable, at a particular post-disturbance time, in relation to the pre-disturbance values and the immediate change produced by the disturbance (Fig.1.2, Table 1.1).

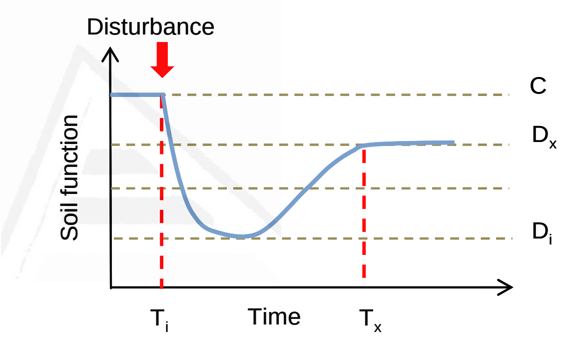


Figure 1.2: *Outline of the dynamics of a given soil function in relation to a disturbance. The letters represent critical soil function values used to estimate resistance and resilience (see Table 1) according to the engineering definition of resilience.* T_i*: moment in time at which disturbance occurs;* T_x*: moment in time for which resilience is evaluated (ideally once the variable stabilizes around a new value after recovery); C: value of the soil function for pre-disturbance conditions;* D_i*: minimum value of the soil function resulting from the direct impact of the disturbance;* D_x*: value of the soil function at time* T_x *(adapted from Seybold et al. 1999 and Orwin and Wardle 2004)*

Table 1.1: *Summary of equations for quantifying soil resistance and resilience (See Fig. 2 for descriptions of the variables used in the equations).*

Reference	Resistance	Resilience
Seybold et al. 1999	$RS = D_i \div C$	$RL = (D_x - D_i) \div (C - D_i)$
Griffiths et al. 2001	$RS = \left(C - \frac{D_i}{C}\right)$	$RL = \left(C - \frac{D_x}{C}\right)$
Orwin and Wardle 2004	$RS = 1 - \frac{2 \times \lvert C - D_i \rvert}{C + \lvert C - D_i \rvert}$	$RL = \frac{2 \times \lvert C - C_i \rvert}{\lvert C - D_i \rvert + \lvert C - D_x \rvert} - 1$
Banning and Murphy 2008	$RS = -100\left[\frac{C - D_i}{C}\right]$	$Rx = -100\left[\frac{C - D_x}{C}\right]$ $RL = -(RS - Rx)$
Chaer et al. 2009	$RL = \left[\left(\frac{D_i}{C}\right) - 100\right]$	$RS = \left[\left(\frac{D_x}{C}\right) - 100\right]$
Van Ruijven and Berendse 2010.	$RS = D_i - C$	$RS = D_x - D_i$ $RL = \frac{D_x}{C}$

1.5. Objectives and structure of the dissertation

The general objective of this dissertation is to assess the role of vegetation traits in the resilience to fire of Mediterranean woodlands, with a particular focus on (a) vegetation fire-persistence (regeneration) traits, and (b) plant community and soil functioning responses to fire. The underlying general assumptions of this work are depicted in Figure 1.3. Both plant community composition (and associated functional traits) and soil functions are involved in ecosystem resistance and resilience. Soil functions depend on plant composition (functional groups) through a variety of feedback mechanisms. Plant functional groups modulate fire severity and resistance of both vegetation and soil functions by influencing fuel properties. They also modulate ecosystem resilience through differences in their capacity for re-growth, colonization, and the re-establishment of plant-soil feedback.

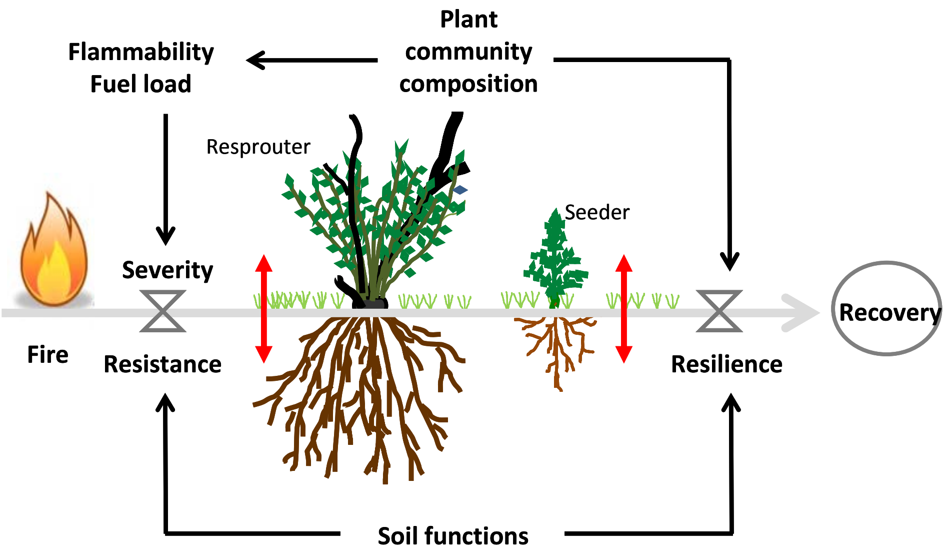


Figure 1.3: *Scheme of the main factors and processes involved in the response of Mediterranean ecosystem to fire addressed in this dissertation.*

The dissertation is structured as follows[1]:

Chapter 1: General introduction.

Chapter 2 analyzes how the successional stage after farmland abandonment in Mediterranean mountain areas, and the associated plant community composition and structure, influence fire severity and vegetation resilience.

---

[1] Chapters 2 to 5 are, respectively, enlarged versions of the following articles:

López-Poma R, Orr BJ, Bautista S. Successional stage after land abandonment modulates fire severity and post-fire recovery in a Mediterranean mountain landscape. International Journal of Wildland Fire (*in press*)

López-Poma R., Bautista S. Fire severity modulates the seeder / resprouter ratio in burned Mediterranean plant communities (*in review*)

López-Poma R., Mayor A.G., Santana V., Baeza J., Bautista S. Plant traits mediate the resistance and resilience of soil functions to fire in Mediterranean shrublands. (*in review*)

López-Poma R., Bautista S. Plant regeneration traits modulate the response to fire of soil enzyme activity in Mediterranean shrublands (*in review*)

Chapter 3 addresses the question of how fire severity influences the post-fire assembly of plant regeneration traits. The chapter analyzes the post-fire dynamics of obligate seeders and resprouters and the variation in post-fire seeder / resprouter abundance ratio as a function of the variation in fire severity and the type of pre-fire plant community.

Chapter 4 focuses on how fire-related plant functional traits modulate the response of soil functions to fire disturbance in Mediterranean shrublands. The chapter analyzes the role played by plant regeneration traits (resprouter versus seeders), life-forms (grasses versus shrubs) and flammability-related traits in the amount of change (resistance) and the recovery (resilience) after fire of soil stability, infiltration and nutrient cycling functions in repeatedly burned shrublands.

Chapter 5 evaluates the resistance and resilience of two soil enzyme activities involved in phosphorus and carbon cycling (acid phosphatase and β-glucosidase, respectively) as a function of the dominant mechanism (resprouting, seeding, or both) involved in the post-fire recovery of the vegetation patches in a Mediterranean shrubland.

Chapter 6: General discussion and conclusions.

Chapter 2

Successional stage after land abandonment modulates fire severity and post-fire recovery in a Mediterranean mountain landscape

2. Successional stage after land abandonment modulates fire severity and post-fire recovery in a Mediterranean mountain landscape

2.1. Introduction

Land-use change has played a critical role in shaping landscape pattern in the Mediterranean Europe during the 20th century (Debussche et al. 1999; MacDonald et al. 2000). Several changes in the socio-economic and political conditions during the second half of the 20th century led to a dramatic rural exodus, resulting in an abandonment of agricultural and pasture land with subsequent land cover changes (Fernández-Ales et al. 1992; Pausas et al. 1999), particularly in mountain areas (Weissteiner et al. 2011). Abandonment began in the marginal soils of cultivated terraced hillsides, which were less productive than their counterparts in the plains (García-Ruiz and Lana-Renault 2011). The progressive abandonment of former cultivated areas has led to tessellated patterns in the landscape formed by a mosaic of patches with some remaining cropped terraces and a variety of other land cover types, including grassland, shrubland, and forest, which represent key stages in the most common successional trajectories after land abandonment in the Mediterranean basin (e.g., Poyatos et al. 2003, Tzanopoulos et al. 2007; Santana et al. 2010).

Wildfires are also an important disturbance shaping Mediterranean ecosystems and landscapes (Trabaud and Galtié 1996; Lloret et al. 2002; Viedma et al. 2006) Fire severity, defined operationally as the loss or comsumption of organic matter, both aboveground and belowground (Keeley 2009), is the major factor in controlling post-fire regeneration of plant communities (Moreno and Oechel 1991a; Pausas et al. 2003). Low severity fire is usually not detrimental to species persistence, allowing species that were present before the fire to recover rapidly from the seed bank, or through resprouting from below- or above-ground plant parts (Moreno and Oechel 1991a; b; Debano et al. 1998). However, high severity fire can destroy the seed bank and kill dormant buds, decreasing or eliminating the regenerative capacity of species (Zedler 1995).

Different plant communities that develop along a succession trajectory are characterized by specific plant species composition and fuel characteristics such as load, particle size, moisture content, surface-volume ratio, vertical and horizontal continuity, bulk density, and the percentage of dead fuel (Van Wilgen et al. 1990; Whelan 1995; Pereira et al. 1995; Miller and Urban 2000; Baeza et al. 2002; Baeza et al. 2011; Santana et al. 2011). Total fuel loading is the potential fuel which might be consumed by fire. However at a given time under a given set of moisture, weather and topographic conditions, only a portion of the available fuel would be consumed by a fire; fine fuel particles (diameter < 5-6 mm) burn more readily than coarse ones (Saglam et al. 2008), and dead fine fuels are particularly important in the initial stages of all fires (Baeza et al. 2002). Other fuel characteristics such as flammability (ease of ignition of a plant when exposed to a heat source; Anderson, 1970) and heat content (calorific value: the energy released per unit of combustible mass; Dimitrakopoulos and Panov 2001) are also essential components of fire risk and fire hazard. Plant species vary widely in their flammability and heat content depending on different structural traits like the tissue type and the architecture and structure of the plant and its organs, including the retention of dead branches (Elvira-Martín and Hernando-Lara 1989; Núñez-Regueira et al. 1996; Dimitrakopoulos and Papaioannou 2001; Cornelissen et al. 2003; Schwilk 2003; Alessio et al. 2008b). As species are nested within plant communities, they also differ in flammability and heat content (Behm et al. 2004).

At the landscape scale, the effects of the interactions between land use change and fire may vary. For example, Viedma et al. (2006) found that fire created a more contiguous landscape due to the increase of shrublands beyond pre-fire levels. A similar tendency of homogenization was also described by Perez et al. (2003). However, Lloret et al. (2002) found that fires increased landscape heterogeneity by creating gaps in large woody homogeneous areas that were a result of land abandonment. Several other studies have pointed to differential vulnerability of land cover types to fire. Santana et al. (2010) found that different post-fire succession pathways are possible, ranging from auto-succession to changes into alternative plant communities. Duguy and Vallejo (2008) showed that the most recently abandoned areas had the lowest resilience to fire, while Giovannini et al. (2001) and Llovet et al. (2009) found that pine forests developed after abandonment were the most vulnerable cover type with respect to post-fire soil erosion.

Despite the critical importance of terraced land abandonment in the Mediterranean mountain regions (García-Ruiz and Lana-Renault 2011) and the recent changes in fire regime towards more frequent and large wildfires in the Mediterranean Basin (Pausas and Fernández-Muñoz 2012), little is known about the role played by the successional stage after abandonment of bench terrace fields in the response to fire in Mediterranean mountain landscapes. We hypothesize that the variation in vegetation structure and composition, and therefore in fuel quantity and quality, that derive from the successional stage after farmland terrace abandonment in the Mediterranean region, determine fire severity and vegetation resilience in a way that contributes to reducing the existing pre-fire structural and functional differences. Thus, with increasing time after abandonment, the more severe the fire and the less resilient the plant community against fire. To explore this hypothesis, our research is focused on the effects of the successional stage after land abandonment in bench terrace fields on post-fire vegetation recovery in a mountain terraced landscape in Southeast Spain. Specific objectives of this study were to i) compare fuel characteristics and fire severity in three common successional stages: dry grasslands, dense shrublands, and pine stands; each type resulting respectively from short (< 15 years), medium (20-25 years) and long (>40 years) time periods after abandonment of agricultural terraces in Mediterranean mountain areas, ii) analyse the effect of the pre-fire successional stage on the regenerative response of vegetation at one, four and seven years after wildfire, and iii) analyse the relative vulnerability (i.e., potential for soil degradation and/or ecosystem shift) to wildfires of the successional stages. Understanding how different stages along the succession after land abandonment result in variations in vegetation structure, and therefore in both potential fire severity and potential resilience after fire, can lead to a determination of relative vulnerability to wildfire among the mosaic of major plant communities in terraced Mediterranean landscapes.

2.2. Methods

2.2.1. Study area

The study was carried out in the Xortà Range in the Alicante province, Southeast Spain (Lat 38°43′25″- 38°41′15″N, Long 0°12′25″- 0°11′10″W). The abandoned terraces under study are located on equatorial-facing slopes that drain to the Guadalest reservoir, at an elevation range of 400 to 800 m.a.s.l. (Fig. 2.1). The climate is dry-subhumid Mediterranean, with a mean annual precipitation of 658 mm (Guadalest reservoir station, 1972-2004 period) that falls mainly in autumn and winter. The mean annual temperature is 15.6 °C. The dominant soil type is Calcaric Cambisol (Lithic Xerocrept) developed over white marls with some levels of limestone (Driessen *et al.* 2001). Surface soils (0-1 cm of mineral horizon) contain 29% clay, 56% silt, 15% sand, and a 2.4% of organic carbon (Llovet 2005).

Figure 2.1: *View of study site on the on terraced slopes.*

The study area represents a common Mediterranean mountainous landscape: a mosaic of successional stages after land abandonment on terraced slopes (Fig. 2.1). The relief is rough and steep, with slopes steeper than 20% that were cultivated in the past with bench terraces that are now mostly abandoned and partly degraded. The progressive abandonment and vegetation colonization of the terraces have created patches of different plant communities. Combining field surveys, analyses of aerial photography (from 1956, 1978, 1985 and 1993), and interviews with local farmers, we identified the following main successional stages: 1) terraces that were abandoned in 1950s-60's, currently covered by *Pinus halepensis* Mill. forest through the natural colonization from scattered individual pines remaining along the borders between farmlands and on the top of the range (hereafter pine stands); 2) terraces abandoned in 1970's, covered by shrub vegetation mainly composed of *Ulex parviflorus* Pourr., *Rosmarinus officinalis* L., *Cistus albidus* L., *Calicotome spinosa* (L.) Link, *Erica multiflora* L., and an herbaceous layer dominated by *Brachypodium retusum* (Pers.) P.Beauv. (hereafter dense shrubland); 3) recently abandoned terraces (abandoned in late 1980's and 1990's), dominated by herbaceous and subshrub species like *B. retusum*, *Brachypodium phoenicoides* L., *Psoralea bituminosa* L., *Thymus vulgaris,* and *Dorycnium pentaphyllum* Scop. (hereafter dry grassland); some crop tree individuals, e.g. *Ceratonia siliqua* L. (carob tree) and *Olea europaea* L. (olive tree), and some individuals of shrub species like *Anthyllis cytisoides* L., *C. albidus*, *U. parviflorus* are also present as scattered patches in the dry-grassland matrix; and 4) cultivated terraces with *O. europaea* (olive tree) and *Prunus dulcis* Mill. (almond tree). On the upper part of the mountain slope, rock outcrops are abundant and most land was never terraced and cultivated: scatter dwarf shrubs cover this area (Fig. 2.2). Land ownership parcels in the study area are small (commonly less than 1 ha), with different dates of abandonment, resulting in a mosaic of different, interspersed successional stages.

A 263 ha portion of the study area was burned by a severe wildfire in August 1998. The shape of the burned area was very irregular, due to rough topography and the heterogeneous spatial distribution of post-abandonment successional stages, creating an interspersed distribution of different burned and unburned plant communities (Fig. 2.2). Climatic conditions during the study period were characterized by scarce rainfall over the first two years after the fire (292 mm and 335 mm of total annual rainfall, respectively; much lower than the long-term average), followed by wet years, especially the 4th, 6th and 7th years after the fire (832 mm, 1045 mm, and 870 mm total annual rainfall, respectively).

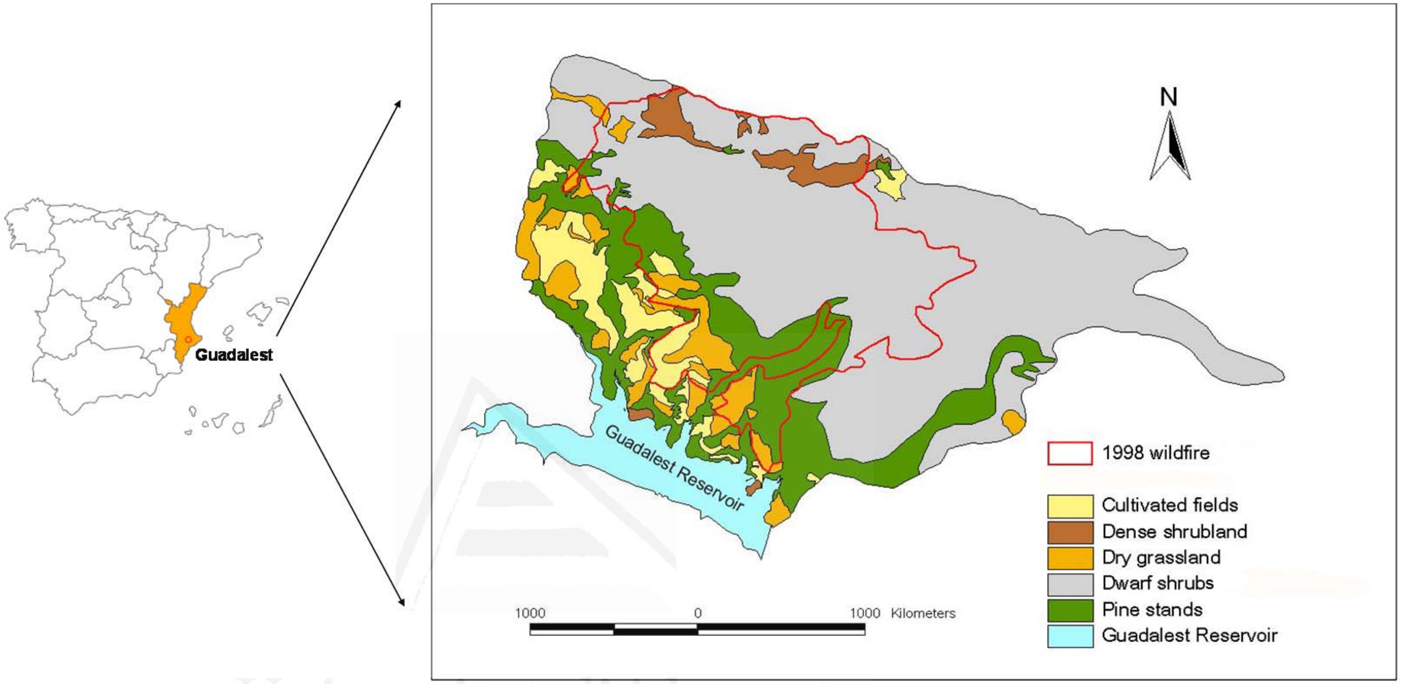


Figure 2.2: *Location of the study site. Wildfire perimeter and spatial distribution of plant communities at different successional stages after farmland terrace abandonment.*

2.2.2. Experimental design

The experiment was arranged in a two-way factorial design involving two fixed factors, a fire factor with two levels consisting of an unburned and a burned state, and a successional stage factor involving three levels associated with the predominant community types at the time of wildfire: 1) dry grassland, 2) dense shrubland, and 3) pine stands. We excluded the terraces located on the border of the burned area and the terraces with intermediate stages between the main successional stages selected for the study. We then selected five terraces per each combination of factors (fire x stage) at random among all the terraces available for each combination, resulting in 30 plots, 15 unburned and 15 burned. The burned plots were monitored one, four and seven years after fire. The experimental unit was a rectangular 3x23m plot. Plot size was chosen to fit within single terraces; due to the small size of terraces, in most cases the plots covered almost the whole terrace. Within each plot, five 1x1-m quadrats were randomly placed for vegetation sampling and monitoring. We assessed fuel characteristics by measuring total and fine-fraction of fuel load (above-ground biomass), the horizontal and vertical distribution of vegetation cover, and the flammability and heat-content classes of the species present in the unburned terraces. We used total and specific plant cover and diversity data to evaluate post-fire vegetation recovery in burned terraces.

2.2.3. Fuel load

Fuel loads were estimated for each successional stage in the unburned 3x23 m plots. This involved quantifying the total aboveground biomass and its fractions. Aboveground biomass (herbaceous and shrub layers) was collected from each of the five randomly placed 1x1-m quadrats. Biomass was sorted into two categories: (1) fractions belonging to herbaceous species and (2) fractions belonging to shrub species and tree seedlings and saplings. Following collection, samples were oven dried at 80° C for 48 h to obtain a constant weight. Adult pine trees were not cut down. Instead, their number and average diameter at breast height (DBH) were recorded at each plot. The biomass of each individual tree was calculated following regression equations, previously obtained in similar pine forests, which relate DBH (cm) and tree dry weight (g) (Lledó 1982, unpublished data):

$Bt = DBH^{1.935} * EXP(5.992)$; $r^2 = 0.976$,

$Bf = DBH^{1.430} * EXP(4.456)$; $r^2 = 0.976$,

$Bl = DBH^{1.430} * EXP(4.997)$; $r^2 = 0.974$,

where Bt is total pine dry weight, Bf is the fine wood fraction (diameter <5 mm) dry weight, and Bl is the dry weight of leaves.

For each 3x23 m plot, total biomass of pine trees, and fine fraction (leaves and fine wood) biomass were calculated by adding up the estimated dry weight of the individual pine trees in the plot. Fuel load per plot was calculated by adding up the total biomass of pine trees and the aboveground biomass of the shrub and herbaceous layers, which was estimated as the average of the values obtained from the 1x1 m quadrats. In this way, the total biomass of the fine fractions (<5mm) is the addition of aboveground biomass of shrub and herbaceous vegetation and the biomass of the leaves and fine wood of the pine trees. For each successional stage, the total litter dry mass was estimated from the dry weight (60°C, 24 h) of five samples from 0.2 x 0.2 m quadrats randomly distributed on each plot.

2.2.4. Vegetation cover, structure and flammability

The horizontal and vertical distribution of vegetation was monitored in the 1x1 m quadrats in unburned and burned terraces using the permanent quadrat method (Kent and Coker 1992). This method employs a point intercept sampling procedure; we recorded 100 points in a regular grid across the 1x1 m quadrat, made up of 100 10x10 cm cells, noting the presence of the species at different height strata (< 10, 10 - 15, 25 - 50, 50 - 100 and > 100 cm). These measurements were repeated one, four and seven years following the fire. Canopy cover of mature pine trees was estimated visually for unburned pine stands.

Floristic diversity was calculated from the specific cover data collected in the sampling quadrats at one, four and seven years after the fire. Species richness, species diversity and evenness (Begon et al. 1986) were estimated for each plot. Species richness is the total number of species encountered in the plots. Species diversity was calculated by using the Shannon index (*H*): $H = -\sum p_i \log_2 p_i$, where p_i is the specific cover fraction of the *i-th* species. Evenness (*E*) was calculated as: $E = H / \log_2 S$, where *H* is the Shannon index and *S* is the number of species.

Based on the flammability and heat content classes established for Mediterranean woody species by Elvira-Martín and Hernando-Lara (1989), Valette (1990), Dimitrakopoulos (2001), and Dimitrakopoulos and Papaioannou (2001), and for a variety of grass types by Guijarro et al. (2002), we classified the recorded species in the study area into low, medium, high, and unknown flammability and heat content classes. We then estimated the percentage of plant cover of each flammability and heat-content class as the summation of the specific plant cover of all the species grouped in the respective class that were present (see Annex, Supplementary material S2.1). These classes, which were established from the comparative assessment of a variety of pyric properties (e.g., time-to-ignition, heat content, total and mineral ash content, surface area-to-volume ratio, and particle density) of individual species, capture broad differences in species potential flammability, which is expected to be modulated by fuel bed properties such as fuel loading, size distribution, spatial arrangement and dead:live ratio (Fernandes and Cruz 2012).

2.2.5. Fire severity assessment

We used a biological indicator of biomass lost to fire for estimating fire severity, obtained by measuring the minimum diameter of the branches of the woody species (*U. parviflorus*) that remained after the fire. This species was present and abundant in all the successional stages analysed. We estimated fire severity in five 2x2m sub-plots per plot and successional stage. To assess the relationship between the fine-scale variation in fire severity and in plant cover for each successional stage, these sub-plots were established so that the 1x1-m quadrats used for vegetation assessment were included and centred on each of them. For each sub-plot, the average minimum diameter of the remaining branches of *U. parviflorus* was estimated from measurements taken at 2.5 cm from the end of the branches of all *U. parviflorus* individuals within the sub-plot (Fig. 2.3). This type of measurements correlates with maximum temperatures at the soil surface (Moreno and Oechel 1989) and with maximum consumption of biomass (Pérez and Moreno 1998; Keeley 2009).

Figure 2.3: *A posteriori estimation of fire severity, by measuring the diameter of the tip of the branches of burned remains of Ulex parviflorus individuals.*

2.2.6. Data analysis

Differences in fuel characteristics, fire severity, plant cover, and plant diversity (species richness, Shannon diversity index and evenness) between the successional stages were tested using one-way ANOVA followed by a post-hoc Tukey test. Prior to analysis, the normality and homoscedasticity of the data were tested and all data met these assumptions. A two-way repeated measures ANOVA was employed to examine post-fire changes in total plant cover and diversity over time. The relationship between vegetation characteristics (plant cover and diversity) and fire severity (minimum diameter of remaining branches) was assessed by linear regression. Data were analysed using SPSS Statistics v. 17.0 (SPSS Inc., Chicago, IL). Variation in species composition (based on cover) between successional stages and comparison between unburned and burned plots seven years after fire were identified through principal components analysis (PCA) ordination. This analysis was performed using the Vegan 1.9 package (Oksanen et al. 2007) in the R free software environment (R Development Core Team 2010).

2.3. Results

2.3.1. Fuel quantity and quality: unburned plots

In the unburned plots, total plant cover (all around 90%) did not show differences between successional stages (F=0.360, *P*=0.964). However, woody species cover differed between stages (F=5.43, *P*=0.007), with higher values in pine stands (71% ± 8) and dense shrubland (63% ± 9) than in dry grassland (38% ± 8). The distribution of vegetation cover across height strata also varied between stages (Fig. 2.4). In pine stands, understory plant cover was distributed among all height stratum, with lower cover at the 50-100 cm range (corresponding to younger *P. halepensis* and *R. officinalis* individuals); the strata > 100 cm (corresponding to canopy cover of adult pine trees) approached 72% ± 9% (mean ± standard error). In dense shrubland, plant cover was mainly concentrated at heights under 50 cm, with almost complete continuity from the soil surface. Plant cover in the dry grassland was mainly concentrated in the 10-25 cm height range (predominantly *B. retusum*, *B. phoenicoides*, *Avena sp*. and other herbaceous species).

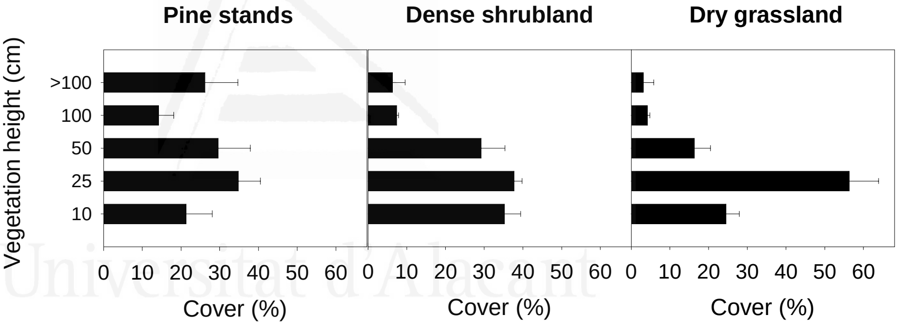


Figure 2.4: *Vertical distribution of plant cover per successional stage. Mean values and standard error.*

All three successional stages showed high cover of species considered to be highly flammable (Fig. 2.5 left). In pine stands, this corresponds to greater cover of *P. halepensis, R. officinalis* and *B. retusum*. In dry grassland and dense shrubland, the highly flammable species were *U. parviflorus*, *T.vulgaris* and *B. retusum*. After classifying species by heat content (Fig. 2.5

right), pine stands and dense shrubland exhibited the greatest cover of species of the higher heat content; this cover corresponded mainly to *U. parviflorus*, *T. vulgaris*, *P. halepensis*, and *E. multiflora*, while in dry grassland species of high heat content were practically nonexistent. In considering these results, however, it is important to take into account that there is limited information on flammability and heat content values for some species.

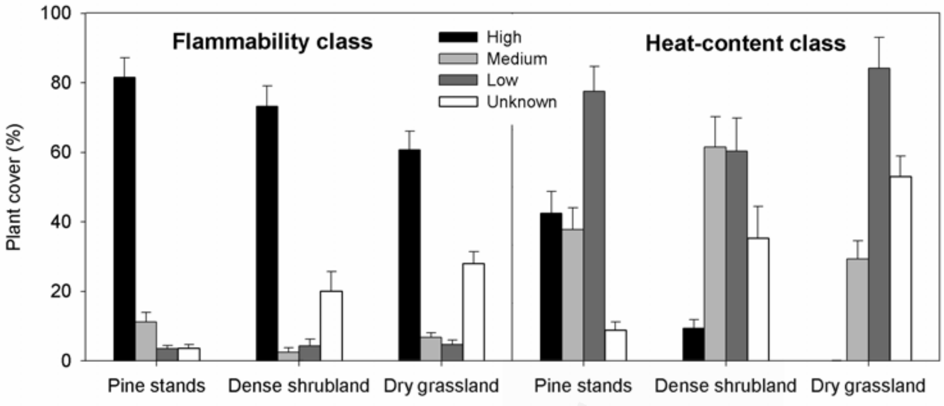


Figure 2.5: *Plant cover as a function of the flammability (left) and heat content (right) class of the species present in each successional stage. Mean values and standard error.*

The values of total biomass and total fine fraction biomass were significantly different between unburned successional stages (Table 2.1); dry grassland exhibited significantly lower values of both variables, whereas pine stands showed the highest amount of total biomass. Shrub biomass showed a similar gradient across successional stages, with more biomass in pine stands, and less in dry grassland, but these differences were marginally significant. Herbaceous biomass did not vary between successional stages. Litter dry weight was significantly different across stages (F= 134.6, *P*<0.001) (Table 2.1).

Table 2.1: *Fuel amount estimated as aboveground biomass and litter dry weight (kg m^{2}) (Mean Value ± Standard deviation, n=5) per successional stage in unburned terraces. Results of one-way ANOVA (Statistic F; significance P) for comparisons between successional stages (Significant results are depicted in bold).*

	Successional stages			
	Dry grassland	Dense shrubland	Pine stands	ANOVA results: F (*P*)
Total biomass ^{A}	0.40 ± 0.16 ^{b}	6.49 ± 4.52 ^{b}	19.61 ± 8.03 ^{a}	**14.7 (0.005)**
Fine fraction biomass ^{B}	0.40 ± 0.17 ^{c}	1.13 ± 0.42 ^{b}	2.74 ± 0.58 ^{a}	**31.6 (0.001)**
Shrub biomass ^{C}	0.26 ± 0.13 ^{a}	0.37 ± 0.23 ^{a}	0.63 ± 0.25 ^{a}	3.2 (0.051)
Herbaceous biomass	0.14 ± 0.07 ª	0.10 ± 0.03 ^{a}	0.08 ± 0.05 ^{a}	1.3 (0.287)
Litter dry weight	0.26 ± 0.22 ^{b}	0.61 ± 0.17 ^{b}	3.49 ± 1.68 ^{a}	**134.6 (0.001)**

Different letters mean significant differences (*P*<0.05) between successional stages (Tukey test).

[A] Total biomass includes biomass of adult pines.

[B] Shrub and herbaceous biomass + fine biomass (<5 mm diameter) of adult pines.

[C] Shrub biomass includes biomass of pine seedlings and saplings.

2.3.2. Fire severity and post-fire recovery

The minimum diameter of the branches of *U. parviflorus* plants remaining after the fire showed significant differences between successional stages (F=6.228, *P*=0.016). The smallest diameter values of remaining branches, and therefore the lowest severity, was recorded in dry grassland (Fig. 2.6), whereas the larger diameters were recorded in dense shrubland and pine stands without differences between them.

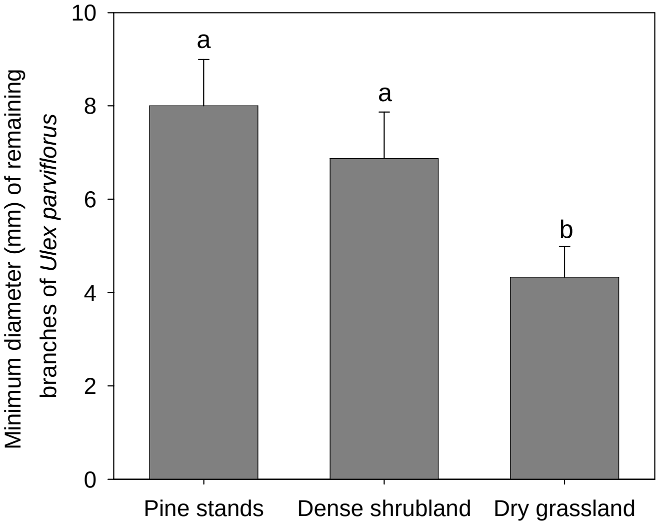


Figure 2.6: *Minimum diameter of remaining branches of Ulex parviflorus individuals as a function of successional stage. Mean values and standard error. Different letters mean significant differences between successional stages.*

One year after fire, the successional stages significantly differed in responses to fire in terms of vegetation cover (F=6.292, *P*=0.014; One-way ANOVA). Dry grassland re-established a higher percentage of vegetation cover in the first year than the other stages (Fig. 2.7), due in large part to *B. retusum*. Four years after fire, differences between successional stages in vegetation recovery disappeared, and plant cover reached the values of unburned terraces (Fig. 2.7). These high cover values were mainly due to an increase of *U. parviflorus* and *Cistus* species cover, particularly in pine stands and dense shrubland.

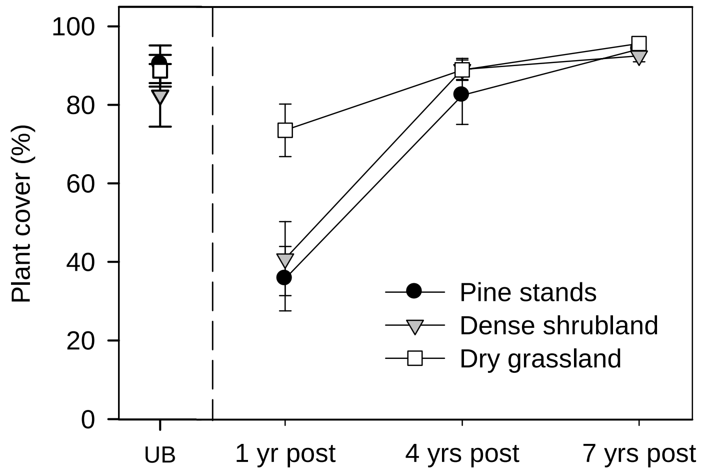


Figure 2.7: *Total plant cover for unburned (UB) and burned plots (one, four, and seven years after the wildfire) per successional stage. Mean values and standard error.*

In the unburned plots, no differences between successional stages were observed in species richness, diversity and evenness, although dry grassland showed higher number of species (Table 2.2). One year after fire, species diversity and evenness were lower in burned terraces, particularly for dense shrubland and pine stands. However, over time, species richness, diversity and evenness gradually increased. Seven years after fire, species diversity and evenness were similar in burned and unburned terraces, while species richness was higher in burned terraces for all three successional stages (Table 2.2).

Table 2.2: *Species richness, species diversity and evenness per successional stage in unburned and burned terraces1, 4 and 7 years after fire. Mean values ± Standard error (n=5).*

	Unburned	**1 year post-fire**	**4 years post-fire**	**7 years post-fire**
Species richness				
Pine stands	11.4±1.9	10.6±1.4	16.4±2.7	20.4±1.4
Dense shrubland	13.0±1.2	14.2±2.5	25.8±0.8	25.6±3.0
Dry grassland	18.0±2.2	20.6±1.5	22.2±3.3	30.0±2.1
Species diversity				
Pine stands	2.21±0.28	1.12±0.08	2.90±0.25	3.36±0.28
Dense shrubland	2.49±0.24	1.49±0.23	3.02±0.28	3.10±0.12
Dry grassland	2.88±0.36	2.61±0.36	3.37±0.32	3.80±0.32
Species evenness				
Pine stands	0.64±0.06	0.34±0.04	0.74±0.04	0.78±0.06
Dense shrubland	0.67±0.05	0.39±0.05	0.64±0.06	0.67±0.02
Dry grassland	0.69±0.07	0.59±0.07	0.76±0.05	0.77±0.06

The results of repeated measures ANOVA show that both time and successional stage significantly affected the recovery of plant cover, and a significant interaction occurred between both factors (Table 2.3), pointing to the different response to fire of each stage over the monitoring period. Species richness, diversity and evenness also showed a significant effect of both time and successional stage. However, no significant interaction between both factors was found for these variables (Table 2.3).

Table 2.3: *Summary of results of the repeated-measures ANOVA considering total plant cover, species richness, species diversity and evenness as the dependent variables, Successional stage as the between-subject factor and Time as the within-subject factor (over studying period) (Significant results are depicted in bold).*

Factors	**Total plant cover**	**Species richness**	**Species diversity**	**Species evenness**
Time	F= 61.548	F= 23.245	F= 32.460	F= 30.979
(d.f. = 2)	***P*< 0.001**	***P*< 0.001**	***P*< 0.001**	***P*< 0.001**
Succesional stage	F= 4.373	F= 6.620	F= 9.090	F= 6.169
(d.f. = 2)	***P*= 0.037**	***P*= 0.012**	***P*= 0.004**	***P*= 0.014**
Time x Succesional stage	F= 4.958	F= 2.062	F= 1.370	F= 1.930
(d.f. = 4)	***P*= 0.005**	*P*= 0.117	*P*= 0.274	*P*= 0.138

One year after the fire, a significant negative relationship was detected between the fine-scale (1-m^2 plots) variation in plant cover and the variation in fire severity for the three pre-fire successional stages (Fig. 2.8), although this relationship was marginally significant for pine stands. Four years after the fire, the fine-scale negative relationship between plant cover and severity continued, but it was weaker; and seven years after fire, it disappeared (Fig. 2.9).

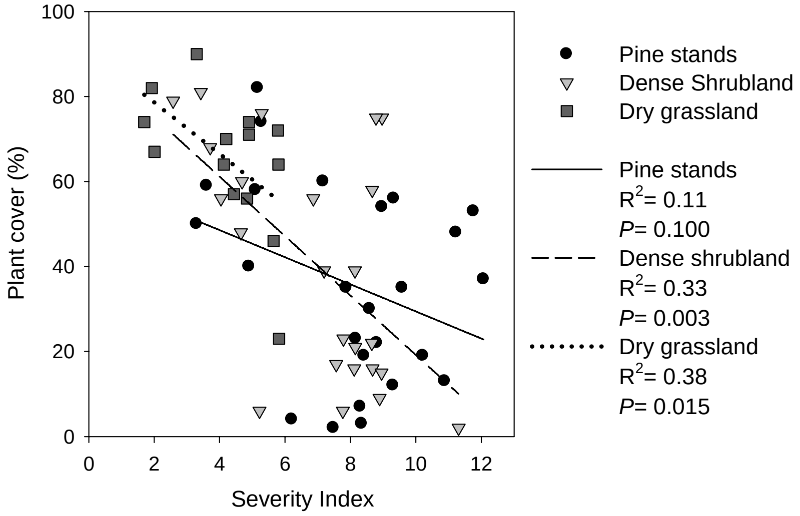


Figure 2.8: *Relationship between plant cover and fire severity index (minimum diameter of remaining branches of Ulex parviflorus individuals) per successional stage one year after the wildfire.*

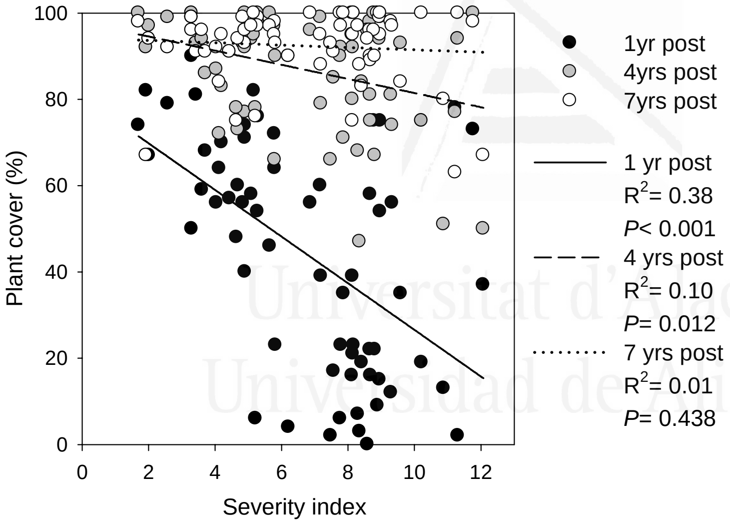


Figure 2.9: *Relationship between plant cover and fire severity index (minimum diameter of remaining branches of Ulex parviflorus individuals) one, four, and seven years after the wildfire.*

2.3.3. Fire effect on species composition

Figure 2.10 illustrates the changes in community composition between unburned and burned (seven years after fire) terraces according to the PCA ordination of the plots. For the unburned conditions, the first axis explains 37% and the second axis explains 15% of the total variance in community composition of the different plots.

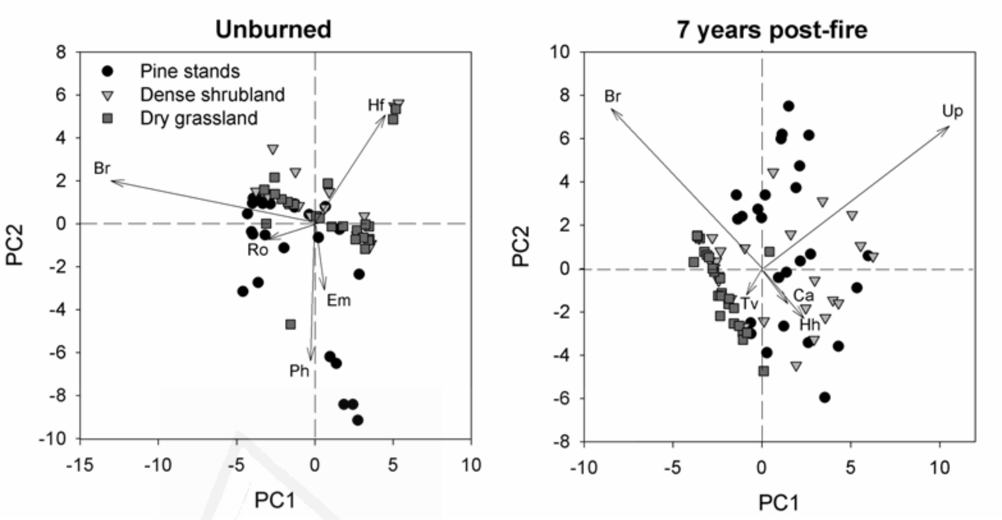


__Figure 2.10:__ PCA-based ordination of sampling plots (symbols) for each successional stage according to the specific cover values of the species present in unburned and seven-year post-fire plant communities. The lengths of arrows are proportional to the strength of association between species and ordination. Br: Brachypodium retusum; Ca: Cistus albidus; Em: Erica multiflora; Hf: Helictotrichon filifolium; Hh: Hedysarum humile; Ph: Pinus halepensis; Ro: Rosmarinus officinalis; Tv: Thymus vulgaris; Up: Ulex parviflorus.

Within successional-stage differences were mostly captured by the first axis, and were largely due to differences in the abundance of perennial grasses (e.g., *B. retusum, Helictotrichon filifolium* Lac.) and *R. officinalis.* The second axis captured the differences between successional stages, which were mostly due to the abundance of *P. halepensis*, and *E. multiflora* in terraces with pine stands, while perennial grasses were abundant in dense shrubland and dry grassland terraces. Seven years after fire, dense shrubland and pine stands showed similar species composition that differed from dry grassland (Fig. 2.10 right). The first axis of the PCA explains 36% and the second axis explains 20% of the total variance of species composition. The variation in species composition was mostly due to *U. parviflorus*, *Hedysarum humile*, and *C. albidus*, which were abundant in both pine stands and dense shrubland, but were scarce in dry grassland terraces, while *B. retusum* was particularly abundant in dry grassland.

2.4. Discussion

The different vegetation structure and composition that result from the successional stage after the abandonment of former cultivated terraces in Mediterranean landscapes lead to differences in fire severity, post-fire recovery, and resilience against wildfire. The assessment of fuel load in unburned terraces suggests that dry grassland would burn less severely than dense shrubland, which in turn would burn less severely than pine stands, as both total and fine-fraction (< 5 cm diameter) biomass showed a significant increasing trend for these successional stages. However, this approximation was not fully in agreement with the estimation of fire severity after the wildfire. The minimum diameter of remaining branches after fire, an indicator of biomass lost to fire (Moreno and Oechel 1989; Keeley 2009), showed lower values for dry grassland, but indicated similar fire severity for dense shrubland and pine stands. In dry grassland, a great portion of the fuel fine fraction was comprised mainly of herbaceous species, probably leading to higher rates of spread and shorter residence time of fire (Santana et al. 2011), which explains the low severity measured. The comparable high fire severity in pine stands and dense shrubland could be explained by (1) the dominance of *U. parviflorus* in dense shrubland, as this species accumulates dead biomass with age and thus contributes to increase fire temperature (Baeza et al. 2002; 2006; Santana et al. 2011); (2) the rather compacted layer of vegetation near the ground in dense shrubland; and (3) the high cover values of species considered to have a greater (high and medium) heat content, which were similar between dense shrubland and pine stands.

The higher fire severity estimated for pine stands and dense shrubland corresponded to slow vegetation regeneration, particularly during the first post-fire years. Dry grassland, which burned with low severity, quickly recovered, mainly due to the resprouter strategy of *B. retusum*, whose buried undamaged rhizomes allowed a faster colonization of the space opened up after the fire (Caturla et al. 2000). Regardless the overall effect of the successional stage on fuel properties and fire severity, the fine-scale (1 m^2 plot) variation in plant recovery after fire clearly illustrated the influence of fire severity on the regenerative dynamics of the vegetation for each pre-fire stage. One year after the fire, a negative relationship between plant cover and fire severity was observed for each of the successional stages studied, although it was marginally significant for pine stands, which showed a narrower variation in severity towards the moderate to high severity range. This negative relationship decreased with time after fire, becoming unappreciable seven years after fire. The effects of high fire severity were probably associated with the destruction of meristematic tissues of belowground organs of resprouter species (Lloret and López-Soria 1993), while obligate seeder species may have been limited by the drier conditions during the first two years after the fire. The significant increase in plant cover by the fourth year after fire was mostly due to the germination and growth of obligate seeder species such as *U. parviflorus*, and *C. albidus*. It must be stressed that *P. halepensis* showed poor or no regeneration, in spite the fact that it is considered to regenerate quite well after fire (Arianotsou and Ne'eman 2000). The results suggest that the fine-scale spatial variation in fire severity left a number of low-recovery microsites that mostly consisted of bare-soil. Once the dry period following the fire was over, these microsites were later colonized by obligate seeder species that have persistent soil seed banks and grow well on open and disturbed areas (Trabaud 1995), such as *U. parviflorus*, and *C. albidus*. Conversely, pine seeds do not persist for long in the soil and post-fire recruitment of pine seedlings is commonly limited to the first one or two years after the fire (Ne'eman et al. 2004), provided that soil moisture conditions are appropriate for germination (Daskalakou and Thanos 2004). Therefore, the lack of pine regeneration in our study may have been caused by the two relatively dry years that followed the fire (Daskalakou and Thanos 2004).

Moreover, diversity and evenness greatly decreased in pine stands and dense shrubland, reflecting the differential effect of fire on the various species (Zedler et al. 1983). Higher fire severity in pine stands and shrubland terraces combined with two dry post-fire years seem to have hampered the recovery of many species in these two stages, resulting in less diverse communities at the short term and delaying the common early post-fire peak in plant diversity that has been reported in previous works (e.g., Caturla et al. 2000; Capitanio and Carcaillet 2008).

At the landscape scale, wildfires can increase heterogeneity by fragmenting continuous blocks of forests or shrublands, introducing younger successional stages in the landscape mosaic (Lloret et al. 2002). Sometimes, extensive and severe fires can induce less heterogeneity in burned landscapes (Trabaud and Galtiè 1996; Viedma et al. 2006; Van Leeuwen et al. 2010). In our results, a homogenizing effect resulted from a synergistic effect of fire severity and post-fire climatic conditions that changed pine stands into dense shrublands dominated by *U. parviflorus*. In these shrublands, the colonization of species in later successional stages may be arrested, and subsequent fires may lead the system to further degradation (Santana et al. 2010; Malkinson et al. 2011). Meanwhile, the species composition of dry grassland –dominated mainly by herbaceous species– remained different from the other community types and similar to unburned conditions. In the same way as results reported by Pérez *et al.* (2003) and Viedma *et al.* (2006), the fire-driven changes in pine stands influence the larger mosaic landscape, making this landscape more homogeneous by increasing shrubland cover.

The lower post-fire plant recovery recorded in pine stands and dense shrubland after the fire suggests an increased sensitivity to erosion process (DeBano et al. 1998; Pausas et al. 2008; Llovet et al. 2009). In many Mediterranean areas, such as our study area, hillslopes were terraced and cultivated and later were abandoned. Once denuded by fire or any other disturbance, abandoned terraced slopes can produce a great quantity of sediments (Mayor et al. 2007), particularly when the pre-fire community is dominated by obligate seeder species (Pausas et al. 1999). In a similar landscape near our study site, Giovannini et al. (2001) reported a higher increase in soil erodibility after fire in pine stands than dense shrubland, and both exhibited higher levels of erobidility than dry grassland.

Our results point to terrace-based pine stands and dense shrubland as the most vulnerable to fire in terms of post-fire soil degradation risk in abandoned agricultural landscape. However, the risk for *Pinus halepensis* stands to shift into fire-prone shrublands as a result of severe fire combined with a dry period after fire point to this type of community as the most vulnerable of the three successional stages studied. This risk could be further enhanced in stands of *P. nigra*, *P. sylvestris*, or *P. pinea*, which produce few seedlings after fire (Rodrigo et al. 2004). We have not analyzed later successional stages. In Mediterranean ecosystems, a successional replacement of pine forest to hardwood forest has been observed after long intervals without fire (Bond and Van Wilgen 1996), with the latter type showing a higher resilience against fire (Puerta-Piñero et al. 2012). Therefore, ecosystem vulnerability does not seem to monotonically increase with increasing successional stage. In contrast, the most vulnerable communities in Mediterranean abandoned farmlands appear to be in the middle stages of the succession, in the pine-forest stage. These results can help prioritize target areas in fire-prevention and management plans in Mediterranean fire-prone ecosystems.

2.5. Conclusions

Vegetation properties of the successional stage after land abandonment in a terraced Mediterranean landscape significantly affected fire severity and plant recovery. Dry grasslands burned at low severity and quickly recovered after fire due to the ability of grass species such as *B. retusum* to resprout from fire-resistant organs. Dense shrubland and pine stands burned at higher severity and re-established their cover over the medium term (4-7 years). Both successional stages resulted in similar shrubland communities after the fire, which were dominated by highly flammable obligate seeder species such as *U. parviflorus* and *Cistus* species. In this way, changes in plant composition and abundance in pine stands contributed to homogenize the landscape structure towards a more fire-prone type, and thus increasing fire hazard. The pine stands showed the largest changes in community structure after the fire and the lowest short-term post-fire plant recovery, so pine stands can be considered the most vulnerable of the three successional stages studied in the terraced Mediterranean landscape, particularly if wildfires are followed by relatively dry years.

Chapter 3

Fire severity modulates the seeder/resprouter ratio in burned Mediterranean plant communities

3. Fire severity modulates the seeder/resprouter ratio in burned Mediterranean plant communities

3.1. Introduction

The resilience of Mediterranean plant communities to fire disturbance depends on the success of species' post-fire regeneration mechanisms. Although there is a wide spectrum of intra- and inter-specific variation in post-fire regeneration mechanisms and capacities (Moreira et al. 2012; Clarke et al. 2013), species that regenerate exclusively from seeds (obligate seeders) or by vegetative regrowth (resprouters) are considered to be the two main functional groups related to post-fire persistence in Mediterranean ecosystems, with some species (facultative resprouters) being able to use both post-fire regeneration mechanisms (Keeley 1986; Bond and Van Wilgen 1996; Pausas et al. 2004a). Obligate seeders persist as hard-coated seeds in dormancy status in the soil seed bank, such as many *Legunimosae* and *Cistaceae* species (Herranz et al. 1998; Ferrandis et al. 1999; Céspedes et al. 2012), or as seed protected by cones in canopy seed banks, such as several Mediterranean pine species (e.g., *Pinus halepensis, P. pinaster)* (Tapias et al. 2001). The germination of these seeds can be triggered by heat, temperature fluctuations, charred wood, or smoke, which act as scarification agents, breaking seed dormancy (Keeley 1987; Herranz et al. 1998; Reyes and Trabaud 2009; Moreira et al. 2010; Santana et al. 2012a; Tormo et al. 2013). High temperature also triggers the opening of serotinous cones, which release their seeds after the fire (Keeley and Zedler 1998; Tapias et al. 2001). Resprouter individuals persist in situ throughout fire by resprouting from buds located in aerial, basal or below-ground structures that are more or less protected by leaves, bark, or soil (Klimešová and Klimeš 2007; Clarke et al. 2013).

Post-fire regeneration traits may covary with other functional attributes (Pausas et al. 2004a). Thus, according to Verdú (2000), Mediterranean seeder species grow faster and allocate more biomass to leaves than resprouters; they are mainly anemochorous, dry-fruited, and small-seeded species that are associated with earlier successional stages, while resprouters are mainly vertebrate-dispersed, fleshy-fruited, large-seeded species that are associated with late successional stages. Along a climate gradient, Lloret et al. (2005) found that seeder species were more common in drier and warmer areas typical of Mediterranean conditions than they were in moister and colder conditions. This was attributed to differential tolerance to summer water stress (Saura-Mas and Lloret 2007) and differential ability to colonize disturbed and open areas between obligate seeder and resprouter species. It has been suggested that seedlings of obligate seeder species are physiologically better adapted to drought and water oscillations, and to efficiently explore the upper soil layer than seedlings of resprouter species, whereas seedling roots of resprouters better facilitate both carbon storage and deep soil penetration (Paula and Pausas 2011; Vilagrosa et al. 2013). Of particular interest is the relationship between obligate-seeding regeneration trait and flammability-enhancing traits, particularly a higher dead-to-live fuel ratio and lower moisture content in above-ground biomass in seeder than in resprouter species (Saura-Mas et al. 2010).

Obligate seeder and resprouter species have very different demographic patterns in response to fire. Most obligate seeders can efficiently recruit high density of seedlings, although their initial post-fire cover is low (Bell 2001; Bond and Midgley 2001; Calvo et al. 2003) and post-fire recruitment largely depends on post-fire climatic conditions (Daskalakou and Thanos 2004). In contrast, resprouters may regenerate immediately after fire, recovering rapidly their original cover with little or no demographic changes (Keeley 1986; Bellingham and Sparrow 2000; Caturla et al. 2000; Calvo et al. 2003). Furthermore, obligate seeders and resprouters differ in their response to fire regime. Frequent fires or short intervals between fires may limit the number of seeds in the seed bank or kill seeder individuals before they reach reproductive maturity (Zedler et al. 1983; Tapias et al. 2001). Severe fires may also consume seeds stored in the seed bank and may reduce the recruitment potential of obligate seeder species (Keeley et al. 2008; Maia et al. 2012) or facultative resprouter species (Moreno and Oechel 1994). However, increasing fire severity could benefit obligate seeders (e.g., Moreno and Oechel 1991a) by increasing soil nutrient and light availability, as well as by opening abundant and large vegetation gaps with disturbed soils (Hollingsworth et al. 2013).

Short intervals between fires may also reduce the capacity of resprouters to recover (Moreno and Oechel 1991b; Delitti et al. 2005; Paula and Ojeda 2009; Enright et al. 2011). Similarly, resprouter species seem to be highly sensitive to fire severity, as severe fires may induce high mortality of these species (Lloret and López-Soria 1993). However, resprouter species that have their resprouting vegetative tissues well protected against fire by a relatively thick soil layer, such as rhizomatous *Brachypodium retusum*, can largely survive high-severity fires (De Luís et al. 2004), which suggests that fire severity filters resprouting regeneration traits so that severe fires favour below-ground resprouting (Clarke et al. 2013).

Overall, differences in seeder/resprouter abundance ratio seem to greatly modulate flammability, post-fire recovery rates and resilience of plant communities (Pausas et al. 2004a; Keeley et al. 2005; Arnan et al. 2007; López-Poma et al. *in press;* see Chapter 2). In turn, fire regime is expected to modify the post-fire seeder/resprouter ratio in the affected areas. Several studies have specifically assessed the effect of fire frequency on this ratio. For example, empirical research suggests that Mediterranean obligate seeder species are present in areas subjected to frequent fires in greater numbers than expected (Franklin et al. 2004; Pausas et al. 2004a; Lloret et al. 2005), which is generally attributed to the early-successional nature of most seeder species. Modeling exercises that analyzed the dynamics of a variety of regenerative and life-history traits' assemblages under various fire-regime scenarios found that obligate seeder species achieved maximum abundance at intermediate fire frequency, while resprouter grasses increased at the highest frequencies (Lloret et al. 2003). However, the role of fire severity in modulating post-fire seeder / resprouter ratios in Mediterranean plant communities has not been directly assessed. Assuming that some similarities may exist between the filtering potential of fire frequency and fire severity on the assembly of post-fire plant communities, we hypothesize that the post-fire seeder/resprouter abundance ratio increases with fire severity in Mediterranean communities. Since low-severity fires normally do not trigger some of the processes that favour seeder species (e.g., opening of vegetation gaps, increasing light availability and soil disturbance; damaging of resprouting tissues in competing resprouter species), we predict that the variation in the seeder/resprouter ratio with fire severity should follow a non-linear trend, with the ratio barely varying at low severity and rapidly increasing at intermediate to moderate severity. We expect the strength of the positive relationship between seeder/resprouter ratio and fire severity to vary across plant community types, as both pre-fire seeder/resprouter ratio and potential fire severity largely vary as a function of the composition and spatial structure of the plant community (Saura-Mas et al. 2010; López-Poma et al. *in press;* see Chapter 2).

To test our hypothesis, we analyzed the post-fire dynamics of obligate seeders and resprouters and the variation in post-fire seeder/resprouter abundance ratio as a function of the variation in fire severity and the type of pre-fire plant community. We studied three Mediterranean communities (dry grassland, gorse shrubland, and pine stands), which represent increasing successional stages after agricultural land abandonment (see Chapter 2), that were burned by a single wildfire event at contrasting ranges of fire severity. Understanding the role of fire severity in shaping the post-fire assembly of plant regeneration traits would help anticipating the impacts on plant communities of the ongoing and predicted changes in the Mediterranean fire regime (Pausas 2004).

3.2. Methods

3.2.1. Study area

The study was carried out in the Xortà Range, in the Alicante province of southeastern Spain (Lat 38°43′25″-38°41′15″N, Long 0°12′25″- 0°11′10″W). The study area is located on the south-facing slopes of the range that drain to the Guadalest reservoir (see Chapter 2 for detailed description of the study area).

The study area was partially affected by a wildfire that burned 263 ha in August 1998. The shape of the burned area was very irregular, due to rough topography and the heterogeneous spatial distribution of successional stages after agriculture abandonment, creating an interspersed distribution of different burned and unburned plant community types, ranging from dry grasslands developed on recently abandoned agricultural terraces to pine stands developed on terraces abandoned more than 50 years ago, and including more or less mature gorse shrublands on terraces abandoned in 1970's.

3.2.2. Field assessment

The assessment followed a factorial design with two fixed factors, a Fire factor with two levels: unburned and burned, and a Plant community factor with three levels: 1) dry grassland, 2) gorse shrubland, and 3) pine stands. Per each factor combination (Fire x Plant community), we selected five terraces at random, resulting in 30 terraces, 15 unburned and 15 burned. Plot size (3x23m) was adapted to fit within single terraces, which were particularly small in the study area. Within each plot, five permanent 1x1-m quadrats were randomly placed for vegetation sampling and monitoring. In order to understand the potentially chaning post-fire relationship between obligate seeders and resprouters with fire severity over time, the burned plots were monitored one, four and seven years after the 1998 fire.

The vegetation was monitored using the permanent quadrat method (Kent and Coker 1992). We recorded 100 points in a regular grid across the 1x1 m quadrats, made up of 100 10x10 cm cells, noting the species intercepted at each point. Based on information available (BROT database; Paula et al. 2009; www.uv.es/jgpausas/brot) and field observations, each recorded plant species was labelled as either obligate seeder or resprouter species (see Annex, Supplementary material S3.1). Facultative species were assigned to the resprouter trait group. For each quadrat, the cover of each plant regeneration trait (obligate seeder or resprouter) was calculated by adding the percent cover of all the species belonging to the group. From these values, we estimated the abundance ratio of obligate seeders and resprouters (hereafter seeder/resprouter ratio) per quadrat. For each terrace plot, we estimated obligate seeder and resprouter cover and seeder/resprouter ratio as the averages of the respective values from each sampling quadrat. The canopy of mature pine trees was estimated visually for the whole plot on each unburned plot of pine stand. We estimated species richness for each regeneration trait by pooling the species recorded per trait in the five 1x1-m sampling quadrats established per plot (i.e., total area sampled per plot was 5 m^2).

To estimate fire severity after the wildfire, we used a biological indicator: the minimum diameter of the branches of the dominant woody species (*U. parviflorus*) that remained after the fire (hereafter, Severity index). This type of measurements correlates with maximum temperatures at the soil surface (Moreno and Oechel 1989) and with maximum consumption of biomass (Pérez an Moreno 1998; Keeley 2009). The target species was present and abundant in all the plant communities assessed allowing the assessment of between- and within-community variation in fire severity. To estimate the Severity index, we used five 2x2m quadrats per plot, which were established so that the 1x1-m quadrats used for vegetation assessment were included and centred on each of them. For each 2x2-m quadrat, Severity index was estimated as the average of the minimum diameter measured at 2.5 cm from the end of the branches of each *U. parviflorus* individuals within the quadrat (Fig. 2.6, Chapter 2).

3.2.3. Data analysis

Differences in plant cover and species richness of obligate seeders and resprouters between unburned plant communities were tested using one-way ANOVA. Differences in the post-fire dynamics of these variables between plant communities were tested using repeated-measures ANOVA, with Time as within-subject factor and Plant community as between-subject factor. We tested the differences in plant cover and number of species of obligate seeders and resprouters between unburned and seven-year post-fire conditions using Two-way ANOVA with two fixed factors (Fire and Plant community). We used regression analyses to test the relationships between fire severity and plant cover of obligate seeders and resprouters one, four, and seven years after the fire, and between fire severity and final seeder/resprouter ratio seven years after the fire. Data were analysed using SPSS Statistics v. 17.0 (SPSS Inc., Chicago, IL).

3.3. Results

Plant cover of obligate seeders significantly differed between unburned plant communities (F=14.918, *P*=0.001), increasing from dry grassland to pine stands. Conversely, resprouter species cover did not vary between plant communities (F=0.044, *P*=0.957), with values ranging between 60-90 % (Fig. 3.1). After the wildfire, initial cover of resprouter species was higher than obligate seeder cover. The type of plant community had a marginally significant effect on resprouters cover along the study period (Table 3.1), with resprouters cover in dry grasslands being higher than in pine stands and gorse shrubland, which did not differ between them (Fig. 3.1). A significant interaction effect between Time and Plant community for obligate seeders cover (Table 3.1) reflects the varying effect of plant community on the recovery of obligate seeder species, which showed lower cover in pine stands and gorse shrublands than in dry grassland one year after fire, and shifted to higher cover in pine stands and lower cover in dry grassland seven years after the fire (Fig. 3.1). Seven years after the fire, there were not significant differences for either obligate seeder or resprouter cover between burned and unburned plots (Fire factor; Table 3.2). However, marginal interaction between Fire and Plant community factors for obligate seeder species indicates that this was not the case for all communities. Thus, while burned pine stands and dry grassland approached or recovered the obligate seeder cover values existing in the respective unburned terraces, obligate seeder cover in burned gorse shrubland was higher seven years after the fire than in unburned terraces (Fig. 3.1).

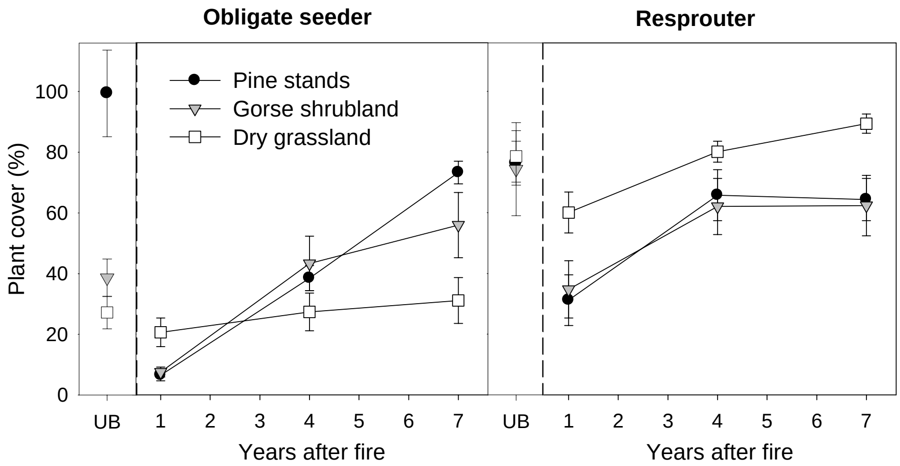


Figure 3.1: *Plant cover dynamics of obligate seeder (left), and resprouter (right) species for each plant community in unburned plots (UB), and one, four, and seven years after the wildfire in burned plots (n= 5).*

Table 3.1: *Summary of results of repeated-measures ANOVA analyses on post-fire plant cover and number of species, considering Plant cover and Number of obligate seeder and resprouter species as the dependent variables, Plant community type as the between-subject factor and Time as the within-subject factor (over studying period).*

Factors	***Plant cover***		***Number of species***	
	Obligate Seeder	***Resprouter***	***Obligate Seeder***	***Resprouter***
Time	F= 42.203	F= 59.050	F= 12.855	F= 15.413
(d.f. = 2)	***P*< 0.001**	***P*< 0.001**	***P*< 0.001**	***P*< 0.001**
Plant community	F= 2.500	F= 3.595	F= 8.774	F= 4.204
(d.f. = 2)	*P*= 0.124	*P*= 0.060	***P*= 0.004**	***P*= 0.041**
Time x Plant community	F= 7.025	F= 1.116	F= 2.277	F= 0.969
(d.f. = 4)	***P*= 0.001**	*P*=0.372	*P*= 0.091	*P*= 0.442

The number of obligate seeder and resprouter species increased with time after fire, particularly in the case of obligate seeders (Fig. 3.2). The type of plant community had a significant effect on the post-fire number of species of both obligate seeders and resprouters (Table 3.1), with a general trend towards less species in pine stands and more species in dry grasslands (Fig.

3.2). Seven years after the fire, the number of both obligate seeder and resprouter species was higher in burned plots (Table 3.2), with no significant interaction effect between Fire and Plant community, the latter having a significant effect only for obligate seeder species number, which was higher in dry grassland and lower in pine stands.

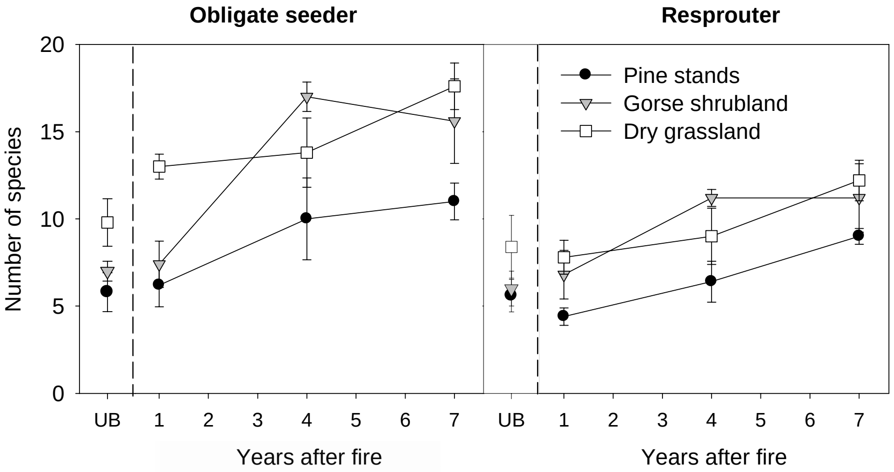


Figure 3.2: *Number of species of obligate seeders (left), and resprouters (right) for each plant community in unburned terraces (UB), and one, four, and seven years after the wildfire in burned terraces (n= 5).*

Table 3.2: *Summary of results of two-way Univariate ANOVA for two fixed factor (Fire and plant community), for obligate seeder, resprouter cover and species number (n=5 for each plant community), (comparing Unburned and 7 years after fire).*

Factors	***Plant cover***		***Number of species***	
	Obligate Seeder	***Resprouter***	***Obligate Seeder***	***Resprouter***
Fire (d.f. = 1)	F= 0.053 *P*= 0.821	F= 0.402 *P*= 0.533	F= 32.346 ***P*< 0.001**	F= 12.944 ***P*= 0.002**
Plant community (d.f. = 2)	F= 21.768 ***P*< 0.001**	F= 2.101 *P*= 0.146	F= 6.507 ***P*= 0.006**	F= 2.538 *P*= 0.102
Fire x Plant community (d.f. = 2)	F= 2.898 *P*= 0.076	F= 1.283 *P*=0.297	F= 0.668 *P*= 0.523	F= 0.207 *P*= 0.814

Obligate seeders and resprouters showed a contrasting relationship with fire severity that varied with time after fire (Fig. 3.3). One year after fire, cover of both functional groups was inversely related with fire severity (R^2=0.51, P=0.004 for obligate seeders; R^2=0.68, P<0.001 for resprouters), with plots that burned at the highest severity having very low cover of any of them. Resprouters cover showed the same type of negative relationship with fire severity four (R^2=0.41, P=0.014) and seven (R^2=0.69, P<0.001) years after the fire, while the relationship between obligate seeders cover and severity shifted to a positive one four years after fire (R^2=0.37, P=0.020), which became stronger seven years after fire (R^2=0.76, P<0.001). Seven years after fire, the seeder/resprouter abundance ratio (pooled data from all community types) showed a nonlinear increasing trend with increasing classes of Severity index values (Fig. 3.4). When analyzed separately, the three types of communities show a consistent nonlinear increase in seeder/resprouter ratio with fire severity, although it is only marginally significant for dry grassland (Fig. 3.5). Figure 3.6 shows the variation in post-fire seeder/resprouter ratio as a function of the pre-fire ratio, pointing to a nonlinear relationship between them. Dry grassland, a community with low pre-fire seeder/resprouter ratios, also resulted in a community with low seeder/resprouter ratio seven years after the fire; while shrubland, with a slightly larger pre-fire ratio than dry grassland, largely increased the proportion of obligate seeders after the fire. Pine stands, with a much larger pre-fire ratio than the other communities, showed no increase seven years after the fire.

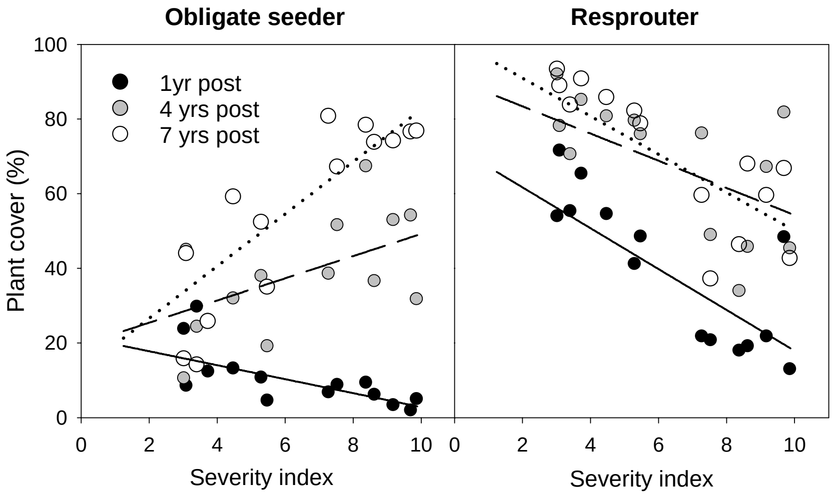


Figure 3.3: *Relationships between plant cover of obligate seeder and resprouter species and Severity index in burned terraces one, four, and seven years after the wildfire.*

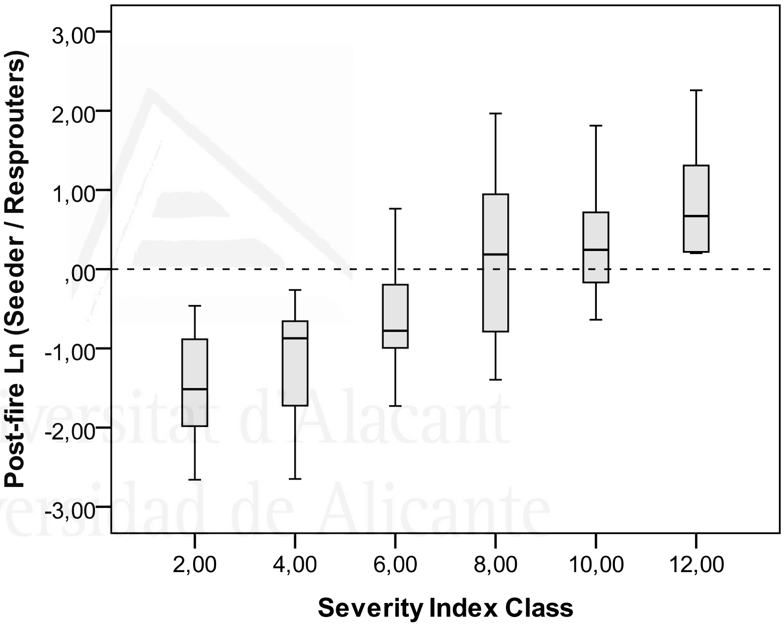


Figure 3.4: *Seeder/resprouter abundance ratio seven years after the wildfire per class of Severity index (Pooled data from the three plant communities assessed). Boxplot indicates the median (horizontal line); the first and third quartiles (box); the 1.5 interquartile range (whiskers); and outliers (points). The dashed line points to equal abundance (plant cover) of obligate seeder and resprouter species.*

3.4. Discussion

The contrasting post-fire regeneration mechanisms of obligate seeder and resprouter species and their varying control factors support the assumption that fire characteristics can play a critical role in determining the functional composition of plant communities (Pausas et al. 2004a; Hollingsworth et al. 2013). We found clear evidences that variations in fire severity modulate the seeder/resprouter abundance ratio in Mediterranean plant communities. The ratio between obligate seeder and resprouter plant cover non-linearly increased with increasing fire severity within the burned area. This relationship was consistent for three common Mediterranean plant communities - dry grasslands, gorse shrublands, and pine forests, which represent increasing successional stages after agricultural land abandonment (See Chapter 2).

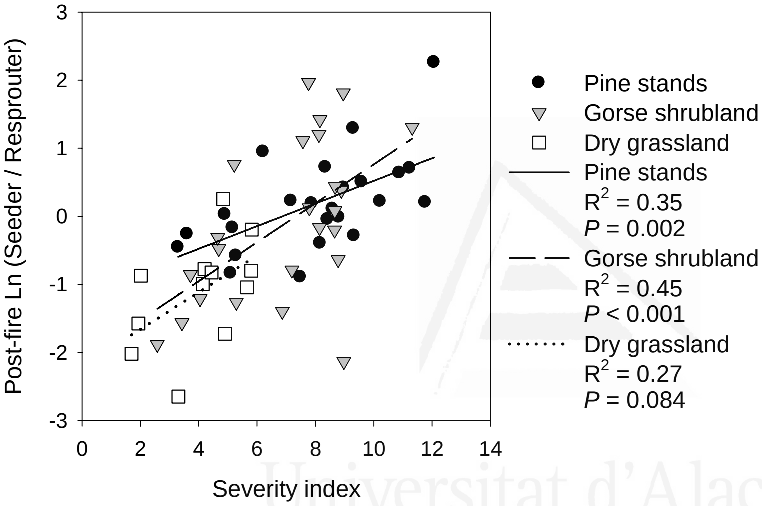


Figure 3.5: *Relationships between post-fire seeder/resprouter abundance ratio (plant cover; natural logarithm) and fire severity (Severity Index) for each plant community assessed. Legend includes results from the regression analyses performed per community type.*

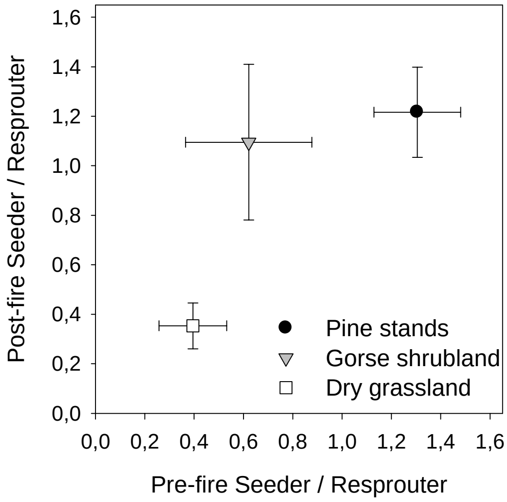


Figure 3.6: *Relationships between pre-fire and post-fire seeder/resprouter abundance ratio (plant cover) for each plant community assessed.*

Fire severity varies widely between and within burned plant communities. This spatial variability relates to the spatial variation in fuel quantity and quality, which in turn is a function of the species composition of the plant community (López-Poma et al. *in press*; see Chapter 2). The spatial variation in fire severity creates a variety of micro-environments that influence post-fire plant dynamics via effects on the mortality of seeds and buds (Odion and Davis 2000), availability of resources (Pausas et al. 2003; Certini 2005), and plant-plant interactions (Bond and Midgley 1995). We observed that the recovery dynamics of obligate seeders and resprouters responded differently to fire severity. Early after the wildfire, there was a negative relationship between plant cover and fire severity for both obligate seeder and resprouter species, yet it was stronger for resprouter species. Increasing fire severity could have damage aboveground resprouting buds as well as belowground buds located near the soil surface, reducing the overall resprouting vigour and leading to low recovery (Lloret and López-Soria 1993; Bond and Midgley 2001). Similarly, increasing fire severity could have caused higher mortality of seeds that were in the most superficial soil layers (Ferrandis et al 1999; Odion and Davis 2000). In contrast with these results, several studies have reported a positive effect of fire severity on early postfire seed germination and seedling growth (Moreno and Oechel 1991a; Pausas et al. 2003), which has been attributed to fire-related cues (heat, charred wood, smoke) that stimulate seed germination of some species (Keeley 1987; Herranz et al. 1998; Baeza and Vallejo 2006; Reyes and Trabaud 2009; Moreira et al. 2010), and to a postfire improvement in nutrient availability (Pausas et al. 2003; Certini 2005). However, it is worth noting that our site experienced two particularly dry years after the wildfire, which may have particularly affected the recruitment of obligate seeder species, as this process is largely controlled by water availability (Céspedes et al. 2012). This fact could have masked or delayed some positive effects of fire severity on obligate seeders, contributing to a shift in the balance between the various effects of fire severity towards an overall negative effect at this early stage after the wildfire.

While the negative correlation between fire severity and resprouter species cover persisted four and seven years after fire, the relationship between obligate seeder cover and fire severity shifted to a positive dependence, which was already clear four years after fire and became stronger seven years after the fire. The increase in obligate seeder cover with fire severity was probably mediated by higher nutrient and light availability in high-severity microsites (Pausas et al. 2003; Certini 2005), but also by the reduction in the interspecific competition with resprouter species, as they were particularly damaged in high-severity microsites. New, opportunistic species recruited to the burned area, as reflected from the clear increase in the number of species -particularly obligate seeder species- after the wildfire in the three communities assessed. However, the increase in obligate seeder cover was mainly due to the contribution of obligate seeder shrubs, such as *Ulex parviflorus* and *Cistus* species, that were already present in the unburned area and have long-lived persistent hard-coated seed banks in the soil (~20-30 years) (Thanos et al. 1992; Baeza et al. 2002). Dormancy breakage of these species can be triggered by the effect of fire (Baeza and Vallejo 2006; Reyes and Trabaud 2009; Céspedes et al. 2012), but also by high fluctuations in temperature and moisture (Baeza and Vallejo 2006; Baeza and Roy 2008; Santana et al. 2012a; b), which are common in bare-soil areas. It is therefore probable that a number of the remaining undamaged seeds in the soil bank germinated over time after the fire, taking advantage of persistent gaps in high-severity microsites and better moisture conditions during wet years.

Despite the general increase in resprouter species cover with time after fire, the negative relationship between cover and fire severity was consistent through time, which highlights the potential of severe fires to induce high mortality of resprouter species (Lloret and López-Soria 1993), causing persistent damage to this functional group. This suggests that the increase in resprouter cover was mostly due to the growth of the individuals that survived the impact of fire, while colonization by facultative resprouter species (considered in this study as part of the resprouter functional group) increased resprouter species richness but barely contributed to increase resprouter cover in the area.

In sum, the observed increase in the ratio of seeder/resprouter cover with increasing fire severity seems to be mediated by the mortality of resprouter individuals and the creation of bare-soil areas, which increase the availability of favourable microsites for seed germination (either from the existing seed bank or from seed sources located outside the burned area) and seedling growth. A suite of plant traits that help in dealing with water-limited and highly variable conditions covary with the obligate seeder regeneration trait (Saura-Mas and Lloret 2007; 2009; Vilagrosa et al. 2013), which contributes to improve obligate seeders performance in areas that burn at high severity and result in postfire vegetation gaps prone to drought. The results suggest that the positive effects of improved postfire microhabitat for obligate seeder species outweigh the negative effects on seedbank consumption in severely burned sites, even in the case of particularly dry years early after the fire.

This study provides evidence that fire severity filters on plant regeneration traits, and thus on the functional composition in Mediterranean shrublands, so that higher severity favors obligate-seeder functional group. This is consistent with recent findings in boreal forests (Bernhardt et al. 2011; Hollingsworth et al. 2013). Several recent studies that focused on the impact of fire frequency on plant communities also pointed out the role of fire as a strong community assembling process (Pausas et al. 2004a; Lloret et al. 2005; Pausas and Verdú 2008, Malkinson et al. 2011). Overall, these findings suggest that changes in the functional composition of plant communities in response to changes in fire characteristics can be predicted by considering the mediating role of regeneration traits. The final fire outcome in terms of community composition will depend on the interaction between fire severity and pre-fire functional composition. Thus, in our study area, gorse shrublands and pine stands burned at a similar average and range of fire severity (López-Poma et al. *in press;* see Chapter 2). However, after the fire, the seeder/resprouter ratio clearly increased in gorse shrubland, while it barely changed in pine stands, probably because it was already very high in pre-fire conditions. Changes in the abundance ratio of seeders and resprouters could in turn lead to changes in the flammability of the plant communities (Baeza et al. 2006; Saura-Mas et al. 2010), contributing to the level of fire hazard in the new communities and the characteristics of future fires.

3.5. Conclusions

Obligate seeder and resprouter regeneration traits differentially respond to fire severity, resulting in changes in the abundance ratio of seeder/reprouter species that are mediated by variations in fire severity. Our results showed a positive non-linear relationship between the relative abundance of obligate seeder species and fire severity, so that seeder/resprouter abundance ratio barely varied at low severity and rapidly increased with increasing severity. This relationship was consistent for three common Mediterranean plant communities - dry grasslands, gorse shrublands, and pine forests. This response to increasing fire severity might have important consequences on community assembly in Mediterranean ecosystems and needs to be considered in any model aiming to predict vegetation dynamics in fire-prone ecosystems.

Chapter 4

Plant traits mediate the resistance and resilience of soil functions to fire in Mediterranean shrublands

4. Plant traits mediate the resistance and resilience of soil functions to fire in Mediterranean shrublands

4.1. Introduction

Plant-soil interactions are major drivers of key soil functions, e.g., water infiltration or nutrient cycling, which in turn can affect plant performance through a variety of feedback mechanisms (Ehrenfeld et al. 2005). The effect of plant functional traits on soil functioning has been documented for a large variety of ecosystems and soil functions. Thus, plant species and functional groups control nutrient cycling and net soil carbon storage through differences in carbon inputs to the soil, litter quality, interaction with microbes in the rhizosphere, and simple morphological and chemical root traits, among other properties and processes (Hobbie 1992; De Deyn et al. 2009; Aulen et al. 2012). A large number of studies on Mediterranean ecosystems have reported differences driven by plant traits and functional groups in soil processes and functions such as soil respiration, water infiltration, soil erosion, carbon storage, and nutrient cycling (e.g., Maestre and Cortina 2003; García et al. 2005; Mataix-Solera et al. 2007; Mayor et al. 2009; Pérez-Bejarano et al. 2010). However, little is known about the role played by plant traits and functional groups in the stability of soil functions against disturbances.

The stability of soil processes and functions to withstand fire disturbance depends on their capacity to remain unchanged throughout the fire (resistance) and to recover after the disturbance (resilience) (Grimm and Wissel 1997; Seybold et al. 1999). Several studies on Mediterranean shrublands provide indirect evidences that suggest plant traits modulate both soil resistance and resilience. For example, plant traits such as flammability, density of above-ground biomass, and accumulation of fine dead fuel affect biomass consumption, heat released, and soil temperatures during the fire (Elvira-Martín and Hernando-Lara 1989; Dimitrakopoulos 2001; Santana et al. 2011), which in turn modulate immediate and direct fire impacts on soil properties and processes such as water repellency and infiltration, microbial activity, decomposition of organic matter, and nutrient mineralization

(Romanyà et al. 2001; Fioretto et al. 2005; Tessler et al. 2008; Bodí et al. 2013.). At the same time, the degree of plant consumption and soil heating combined with the regeneration traits of the plant species (i.e., seeding or resprouting) affect the post-fire recovery of vegetation communities (Lloret and López-Soria 1993; Paula and Pausas 2008; Maia et al. 2012; López-Poma and Bautista, *in review*; see Chapter 3), which in turn could be expected to influence soil recovery rates through plant-soil interactions. However, direct testing of the effect of plant functional groups and traits on soil resistance and resilience to fire is lacking.

Fire-prone shrublands are spreading in the Mediterranean Basin over the last decades as the result of secondary succession in increasing areas of abandoned fields and burned pine woodlands (Díaz-Delgado et al. 2002; Baeza et al. 2007; Riera et al. 2007). This increasing trend in the abundance of fire-prone shrublands, particularly in the western Mediterranean basin, is expected to continue under the current global change context, which has been associated with a shift in the fire regime to larger and more frequent wildfires, as described in Chapter 1 (Pausas 2004; Moreira et al. 2011; Pausas and Fernández-Muñoz 2012). Furthermore, increasing frequency and/or severity of wildfires may trigger significant shifts in plant community composition in Mediterranean woodlands (Lloret at al. 2003; Santana et al. 2010; López-Poma et al. *in press;* see Chapter 2) and other fire-prone ecosystems (Hollingsworth et al. 2013) towards either favouring or filtering particular plant traits. Understanding how plant functional traits modulate the response of soil functions to fire disturbance is necessary to predict the overall impact of increased fire frequency in fire-prone woodlands and shrublands. In this study, we conducted experimental burnings in three Mediterranean fire-prone shrublands in eastern Spain and evaluated the role played by vegetation patches and fire-related plant traits in the resistance and resilience of three main soil functions, namely soil stability, water infiltration, and nutrient cycling. Specifically we used eleven soil indicators to assess the fire-induced changes and further recovery of soil functions in bare areas (no or very scarce vegetation cover) and in soils under (i) a resprouter grass, (ii) a resprouter shrub, and (iii) three obligate seeder shrub species with contrasting fire-related traits.

4.2. Materials and methods

4.2.1. Study area

The study was carried out at three sites in the Valencia region, eastern Spain: Onil, Pardines and Ayora (Fig. 4.1). The experimental sites share a similar land use and fire history; they all are located on former agricultural terraces that were abandoned on the 1950s-1960s, colonized by shrublands after the abandonment and later burned twice by wildfires (Table 1). Soils at the three sites are Regosols (FAO, 1988) developed over marls. The sites varied, however, in some key environmental conditions such as slope angle, which ranged from nearly flat in Pardines to very steep in Onil, and mean annual rainfall (Table 4.1), which provided a representative range of conditions for Mediterranean fire-prone shrublands. At the onset of the experiment, the vegetation was an open Mediterranean shrubland that developed on each site after the last wildfire occurred a decade earlier. The vegetation cover, around 70%, was dominated by obligate seeder shrubs such as *Ulex parviflorus* Pourr., *Cistus albidus* L., and *Rosmarinus officinalis* L., which summed to approximately 40% of the total vegetation cover. Resprouting shrubs such as *Quercus coccifera* L. and *Juniperus oxycedrus* L. were less abundant (around 20% of total vegetation cover). The herbaceous layer was dominated by the resprouting perennial grass *Brachypodium retusum* (Pers.) Beauv.

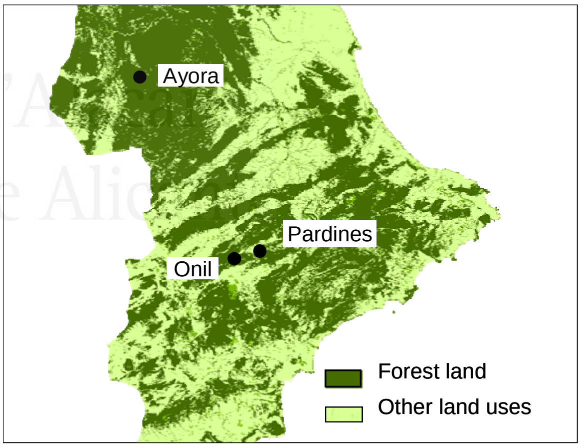


Figure 4.1*: Location of the three study sites in the Valencia region, East Spain.*

4.2.2. Experimental design and field sampling

On each study site, we established an area of ~600 m^2 to be burned by an experimental fire. The areas to be burned were previously delimited by a 4-m-wide fire break in which the vegetation was eliminated through mechanical brushing. At each experimental area, prior to the fires, we randomly selected five 0.5 x 0.5 m monitoring quadrats for each of the following microsite types: Bare soil (BS), and plant patches of *B. retusum* (BR), *Q. coccifera* (QC), *U. parviflorus* (UP), *R. officinalis* (RO), and *C. albidus* (CA), totalling up to 30 quadrats/site. At the Ayora site there were not enough *Q. coccifera* patches and this type of microsite was excluded from the assessment at that site. The species selected have contrasting fire-related plant traits that might affect fire behaviour and the response of the vegetation to fire, including contrasting (a) post-fire regeneration strategy: resprouter (BC, QC) vs. obligate seeder (UP, RO, and CA) (hereafter seeder); (b) life form: grass (BR) vs. shrubs (QC, UP, RO, and CA); and (c) fuel structural traits such as specific fuel load and structure (e.g., proportion of live and dead material or fine and coarse fractions). For example, UP has higher canopy bulk density and fine dead fuel than the other seeder species (CA and RO), while RO has higher live fine fuel than CA and UP (Santana et al. 2010).

In June 2006, all three experimental sites were burned. Fires were ignited as headfires from a line along the entire upwind flank of the burning area. Weather conditions during the fire were similar in the three sites (Table 4.1). We measured the soil temperature at the 1-cm depth under the different vegetation patches using insulated chrome-alumel thermocouples (K-type) placed in the centre of the sampling quadrats. Between two and four quadrats per microsite and site were instrumented with thermocouples, except for *Q. coccifera* and bare-soil microsites which were not monitored for temperature due to the limited number of sensors available (see Santana et al. 2010 for further details).

Table 4.1: *Characteristics of the study sites, including fire history and weather conditions during the experimental fires.*

	Onil	**Pardines**	**Ayora**
Geographic coordinates	38º39'05''N 0º39'47''W	38º40'19''N 0º34'20''W	39º07'04''N 0º57'57''W
Slope angle (º)	35	4	23
Aspect	NW	N	N
Total annual rainfall (mm)	508	547	430
Mean annual temperature (°C)	14	14	13
Elevation (m)	926	806	1031
Previous fire events	1986, 1994	1986, 1994	1979, 1996
Conditions during the experimental fires:			
Air temperature (ºC)	21	25	24
Air relative humidity (%)	42	53	57
Wind speed (m s^{-1})	4,9	1,6	3,7

The functional condition of the surface soil for each microsite type was assessed two weeks before the experimental fire (UB), and two months (B2) and nine months (B9) after the fire. We estimated the stability, infiltration, and nutrient cycling indices defined by the Landscape Functional Analysis method (LFA; Tongway and Hindley 2004). These indices represent the potential of the surface soil for resisting soil erosion, infiltrating water and cycling nutrients, respectively, and have been successfully tested for Mediterranean drylands (e.g., Maestre and Puche 2009; Mayor and Bautista 2012). They are estimated from different combinations of the following soil surface indicators: soil cover, patch basal cover, litter (cover, origin, and decomposition degree), cryptogams cover, crust brokenness, erosion (type and severity), deposited materials, micro-topography, surface compaction, crust stability, and soil texture (see Annex, Supplementary materials, S4.1 and S4.2, for further details on the method). For each sampling quadrat, we estimated the overall response of soil functioning to fire using a simple multifunctional index (hereafter MFI) calculated as the average value of the three LFA indices.

4.2.3. Resistance and resilience indices

The response of soil functions to fire disturbance was determined by two properties: resistance (the amount of change caused by fire) and resilience (the recovery capacity after fire). Among the diverse approaches to measure these properties (e.g., Seybold et al. 1999; Griffiths et al. 2001; Van Ruijven and Berendse 2010), we used the indices developed by Orwin and Wardle (2004), which perform properly for a large variety of scenarios in belowground systems. We adapted these resistance (RS) and resilience (RL) indices to our sampling times and response variable as follows:

Resistance $$RS = 1 - \frac{2 \times \left| UB - B2 \right|}{UB + \left| UB - B2 \right|}$$

Resilience $$RL = \frac{2 \times \left| UB - B2 \right|}{\left| UB - B2 \right| + \left| UB - B9 \right|} - 1$$

where *UB, B2* and *B9* are the values of the soil response variable (multifunctional index, MFI) before the fire, two months, and nine months after the fire, respectively. The index of resistance is standardised by the pre-fire soil condition, reflecting the relative amount of change caused by the fire. Similarly, the index of resilience is standardised by the amount of change initially caused by the fire, as this determines the state from which it has to recover. The index of resistance is bounded by -1 and 1, with a value of +1 indicating that the fire had no effect on MFI (maximum resistance), and lower values indicating less resistance, where a value of 0 indicating a 100% decrease in MFI as compared with the pre-fire condition (minimum resistance). However, if fire had a positive effect on soil functioning and the value of MFI for *B2* is higher than 2*UB*, the index will give a negative value. We avoided this case by assigning a value of *RS* = +1 to all the cases for which MFI values were equal or higher for *B2* than for *UB*. The index of resilience is also bounded by 1 and -1. Likewise for RS index, we assigned a value of *RS* = +1 to all the cases for which MFI values were equal or higher for *B9* than for *UB*. A RS value of +1 indicates full recovery (maximum resilience), and lower values indicate a slower recovery rate. A value of 0 indicates no recovery, and negative values occur when an initial decrease in MFI caused by the fire disturbance is further decreased with time after fire. Resilience was not calculated for the sampling quadrats where resistance was maximal, which only occurred in some bare soil areas.

4.2.4. Data analysis

For each site, differences between microsites in stability, infiltration and nutrient cycling indices, and resistance and resilience indices were evaluated by the non-parametric Kruskal-Wallis H test. Differences between specific pairs of microsites and functional groups (e.g., bare soil vs. plant patches; resprouter vs. seeder patches) were analysed using the non-parametric Mann-Whitney U test. Relationships between resistance and resilience of soil functions and maximum temperatures reached by the soil surface were analyzed by linear regression. All data analyses were performed using SPSS Statistics v. 17.0 (SPSS Inc., Chicago, IL).

4.3. Results

The dynamics of the three soil functional indices at thethree study sites from pre-fire conditions to nine months after the experimental fires are depicted in Figure 4.2. Pre-fire values of the three functional indices were similar between the sites, yet Pardines showed slightly lower values, particularly for the infiltration and nutrient-cycling indices. The microsites in Pardines also showed the least contrasting pre-fire values between bare soils and plant patches. Fire decreased all soil functional indices in all sites. In general, fire impact varied between microsites, being higher for plant patches than for bare soil, but also varying between plant patches. The degree of recovery to pre-fire values also varied between microsites, from almost no change between two months and nine months after the fire (e.g., UP microsites) to a total recovery of the soil function indices in few cases (e.g., most QC microsites). These dynamics were rather consistent between the three study sites and the three soil functional indices (Fig. 4.2).

For pre-fire condition in all sites, MFI was significantly lower in bare soils than in plant patches and significantly lower in patches of resprouter grasses (BR) than in patches of resprouter shrubs (QC), but it did not vary among the three seeder shrub species (UP, CA, RO) assessed (Table 4.2, Fig. 4.3). For the three sites, MFI resistance significantly varied between microsites (Fig. 4.2). MFI resistance was higher for bare soil than for vegetation patches; it was higher for patches of resprouter species (BR and QC) than for patches of seeder species (RO, CA, and UP); and it showed significant variation within seeder patches, with a trend of higher resistance for RO and lower resistance for CA and UP (Table 2, Fig. 4.3). For MFI resilience, general differences between microsites and between bare soil and vegetation patches were not as clear as for MFI resistance, being significant for Pardines, marginally significant for Onil, and non-significant for Ayora site (Fig. 4.3). Differences between resprouter and seeder patches, with higher MFI resilience for resprouters, were highly significant for the three sites, while between-species differences within resprouter and seeder groups were not significant (Table 4.2). MFI resistance showed a significant (F= 5.212, *P*= 0.028) negative dependence on the maximum temperature recorded in the soil surface (Fig. 4.4), while MFI resilience was not related to maximum temperature (F= 0.054, *P*= 0.817).

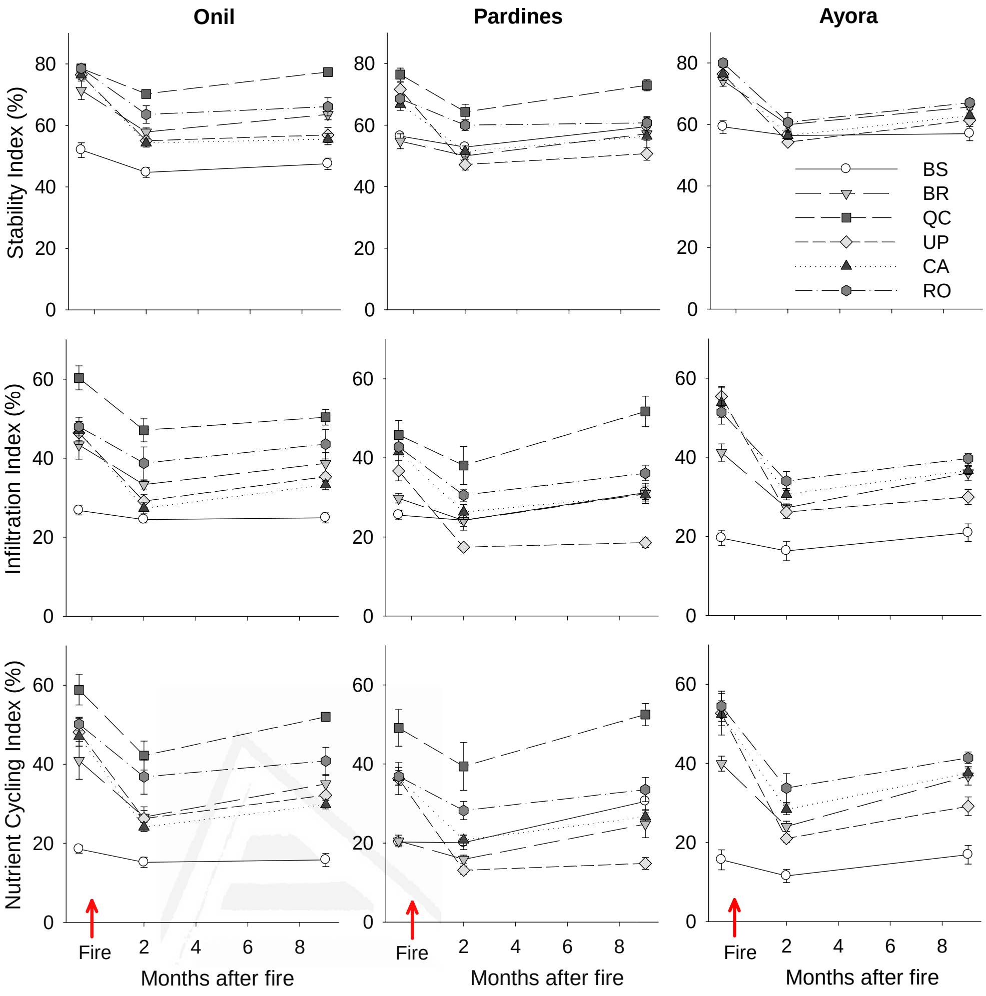


__Figure 4.2:__ Variation in soil functional indices (Stability, Infiltration, and Nutrient cycling) for pre-fire conditions, two months after fire, and nine months after fire as a function of the microsite type for each study site. BS: Bare soil; BR: Brachypodium retusum; QC: Quercus coccifera; UP: Ulex parviflorus; CA: Cistus albidus; RO: Rosmarinus officinalis. Mean values (n=5) and standard error. QC was not available in Ayora site.

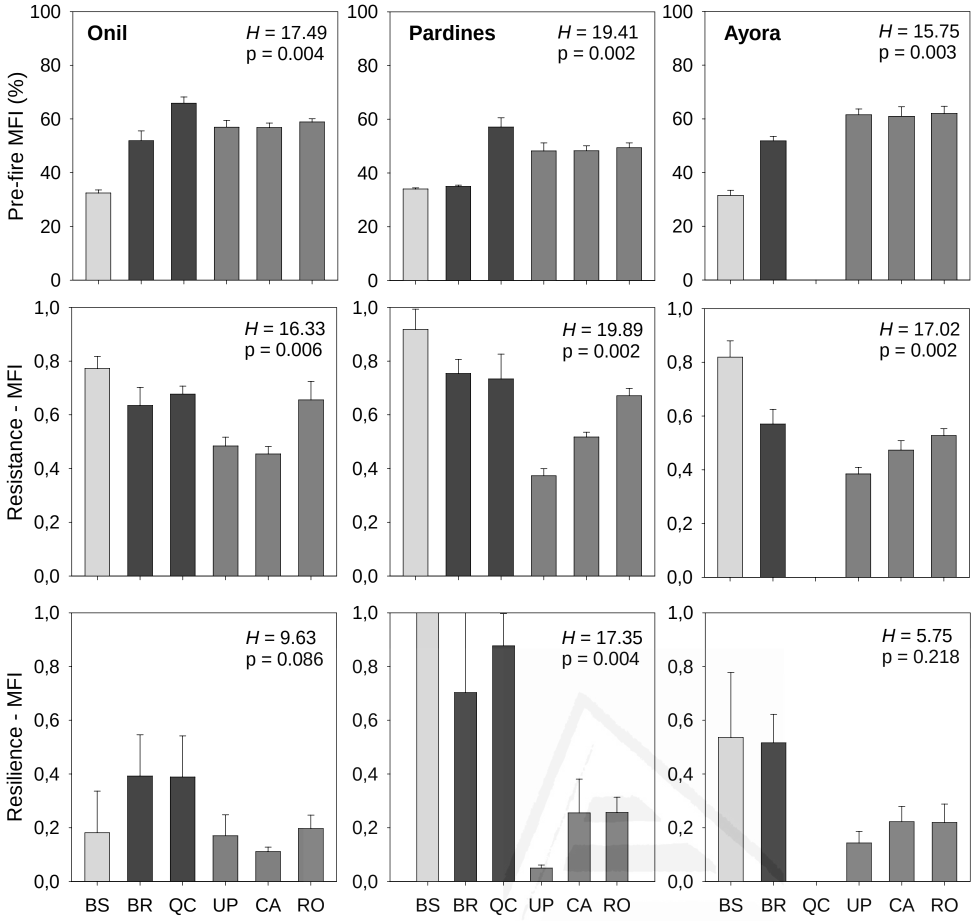


Figure 4.3: *Soil multifunctional index, MFI, for pre-fire conditions (up), MFI resistance (middle) and MFI resilience (bottom) for each microsite type and study site. Light-grey bars: Bare-soil microsites; Black bars: resprouter-species microsites; dark-grey bars: seeder species microsites. BS: Bare soil; BR: Brachypodium retusum; QC: Quercus coccifera; UP: Ulex parviflorus; CA: Cistus albidus; RO: Rosmarinus officinalis. Mean values (n=5) and standard error. QC was not available in Ayora site.*

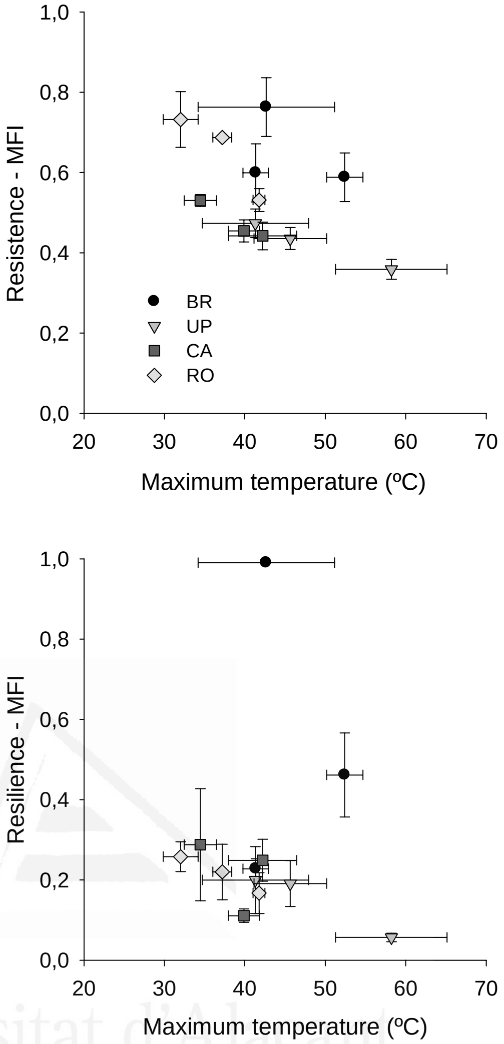


Figure 4.4: Relationships between Resistance (up) and Resilience (bottom) of soil multifunction (multifunctional index, MFI) and maximum soil (1-cm depth) temperature reached during the experimental burnings. Different symbols represent microsite types; white circles: B. retusum; Light-grey triangles: U. parviflorus; grey squares: C. albidus; Dark-grey diamonds: R. officinalis. Mean values (n=5 for MFI resistance and resilience; 2<n<4 for soil temperature) and standard error. No temperature data available for BS and QC.

Table 4.2: *Differences between specific pairs of microsites and functional groups (bare soil vs. plant patch; resprouter vs. seeder patches), and within resprouter and seeder groups, analysed with the non-parametric tests Kruskal Wallis H and Mann-Whitney U. P values in parenthesis*.

		Onil	**Pardines**	**Ayora**
Bare soil vs Plant patch (d.f. = 1)	Pre-fire MFI	*U* < 0.1 (0.001)	*U* = 4.0 (0.001)	*U* < 0.1 (0.001)
	Resistance- MFI	*U* = 14.5 (0.007)	*U* = 9.0 (0.004)	*U* = 2.0 (0.001)
	Resilience - MFI	*U* = 28.5 (0.082)	*U* = 7.5 (0.028)	*U* =33.0 (0.587)
Resprouters vs Seeders (d.f. = 1)	Pre-fire MFI	*U* = 57.5 (0.875)	*U* = 57.0 (0.846)	*U* = 9.0 (0.011)
	Resistance- MFI	*U* = 26.5 (0.028)	*U* = 20.0 (0.010)	*U* = 21.0 (0.168)
	Resilience - MFI	*U* = 21.0 (0.011)	*U* = 9.0 (0.001)	*U* = 9.0 (0.011)
Resprouter species (d.f. = 1)	Pre-fire MFI	*U* < 0.1 (0.024)	*U* < 0.1 (0.017)	-
	Resistance- MFI	*U* = 6.0 (0.655)	*U* = 7.0 (0.881)	-
	Resilience - MFI	*U* = 7.0 (0.881)	*U* = 7.0 (0.864)	-
Seeder species (d.f. = 2)	Pre-fire MFI	*H* = 0.34 (0.844)	*H* = 0.31 (0.858)	*H* = 0.33 (0.848)
	Resistance- MFI	*H* = 6.78 (0.034)	*H* = 12.37 (0.002)	*H* = 6.82 (0.033)
	Resilience - MFI	*H* = 1.86 (0.394)	*H* = 3.79 (0.151)	*H* = 0.98 (0.612)

4.4. Discussion

Our field study in three fire-prone Mediterranean shrublands showed that plant fire-related traits largely and consistently determine the resistance and resilience of soil functions (as captured by a combination of stability, infiltration, and nutrient cycling functional indices) against fire. Before the fire, the overall variation in soil functioning between plant patches was rather small, with slightly higher values for the resprouting shrub *Q. coccifera*, and lower values for grass patches, which is in agreement with previous research in unburned Mediterranean shrublands (e.g., Maestre and Puche 2009; Mayor and Bautista 2012). However, after the fire, the soil functional indices showed the influence of additional plant traits. Resilience of soil functions mostly depended on regeneration traits, while resistance seemed to be mostly driven by plant structural traits that could modulate soil heating. Thus, the rather consistent trend in soil resistance between seeder shrub patches, with *U. parviflorus* showing the lowest resistance values and *R. officinalis* showing the highest values, could be associated with differences in the flammability of the plant canopies, which is supported by the positive relationship found between soil function resistance and maximum soil temperature reached during the fire. Indeed, previous research in the study sites found that the load of fine dead fuel accumulated by plants was the critical trait determining fuel consumption and soil temperatures during the experimental fires, and that *U. parviflorus* patches showed the highest accumulation and *R. officinalis* patches the lowest (Santana et al. 2011). The density of fine dead fuel was also high in herbaceous patches of *B. retusum*, but the total fuel load was low due to the small size of this grass (<15-cm height) (Santana et al. 2011). In this way, a suite of flammability-related traits appeared to control soil heating, which in turn controlled the amount of change in soil functions caused by fire. Soil temperature was not assessed for *Q. coccifera* patches and thus we do not know if heat released was similar to that in patches of the seeder shrub species. Biomass density of *Q. coccifera* canopies is typically very high (Velázquez-Martía et al. 2010), which could have led to high local fire severity. However, relative water content of leaves of resprouter species such as *Q.*

coccifera are typically higher than that of seeder species (Vilagrosa et al. 2013), which would explain lower biomass consumption and associated soil heating.

The variation in soil function resistance between plant functional groups and species did not fully match the variation in soil resilience, which was low and similar for all patches of seeder species and higher in *Q. coccifera* and *B. retusum* patches. Higher resilience in soil functioning for patches of resprouter species can be explained by the faster post-fire recovery rate of these species as compared with that of seeders, which has been observed in many previous studies in Mediterranean ecosystems (e.g., Keeley 1986; Pausas et al. 1999; López-Poma and Bautista, *in review;* see Chapter 3). The fast recovery of aboveground biomass in resprouter plant patches reduces the time that the soil surface is exposed to erosion and compaction agents, and increases surface rugosity and rainfall interception, which enhances water infiltration under the plant patch. Furthermore, since resprouter individuals normally survive the fire, the root systems in resprouter plant patches maintain their role in nutrient cycling, providing inputs of organic matter and secreting soil enzymes, after the fire (Lambers et al. 2009).

For unburned conditions, soil functioning in bare soil interpatches was lower than in plant patches. Conversely, the resistance of soil functions to fire was higher in bare soils. These results can be attributed to both the baseline, pre-fire poorer functioning of bare soils, which can only be minimally further reduced, and the characteristic lower fuel load of these microsites, which reduces potential fire impact, as compared with plant patches. Similarly, working in a Mediterranean shrubland in E Spain, González-Pelayo et al (2006) found that high and moderate-severity fires homogenized the water retention capacity of the surface soil by having a higher impact in vegetation patches than in bare interpatches. In burned grasslands of the Chihuahuan desert, Ravi et al. (2009) found fire-induced water repellency and higher soil erodibility in soils underneath vegetation patches, but not in adjacent bare soil interpatches. Gimeno-García et al. (2011) reported a similar negligible fire effect on water repellency of bare soils in a Mediterranean shrubland, while fire either increased or decreased soil water repellency in the vegetation patches as a function of the plant species.

The observed role played by plant functional and structural traits in modulating the response of soil functions to fire anticipates the impact of possible shifts in the composition and structure of plant communities driven by increasing fire frequency. In general, recent studies in fire-prone Mediterranean shrublands have observed that short fire intervals (e.g., up to 3 fires in 15 years) may increase the proportion of short-lived herbs, resprouter grasses, and subshrub species (Delitti et al. 2005; Grigulis et al. 2005;Vila-Cabrera et al. 2008; Santana et al. 2012b). According to our results, this kind of change would adversely impact soil functioning, as it is generally poorer in herbaceous patches than in shrub patches. This would be also the case if plant cover recovery is decreased or delayed by repeated fires (Mouillot et al. 2003; Malak and Pausas 2006; Wittemberg and Inbar 2009; González-Pelayo et al. 2010), or if there is an increase in the ratio between seeder and resprouter species due to either high fire frequency (Lloret et al. 2003; 2005) or severity (Hollingsworth et al. 2013), since long post-fire windows of scarce plant cover could greatly jeopardise the recovery of soil functions (Mayor et al. 2007, Wittemberg and Inbar 2009). The observed post-fire differences in soil functions among the various patch types may be reduced over the long term, once all species reach maturity and adult size. Nevertheless, differences in the resilience of soil functions are particularly relevant the first months after the fire, when degradation risk is at its peak.

Although the soil functional indices used in this work have captured consistent and clear differences in soil functioning among a variety of plant and bare-soil microsites, major fire impacts on soils, involving the transformation of organic matter and nutrients are not expected when soil temperatures do not exceed 100°C (Giovannini 1994; De Bano 2000; Gimeno-García et al. 2000), as occurred during our experimental fires and is not uncommon for Mediterranean shrublands (e.g., Fioretto et al. 2005). Thus, most likely, the main fire impact on soil processes and functions in our study were mediated by fire effects on plant material followed by plant-soil interactions.

The LFA methodology used in this work has proven to be a cost-effective method for a rapid and integrative assessment of the overall soil functioning in burned areas. Although originally designed for the assessment of dryland ecosystems (Tongway and Hindley 2004), LFA has great potential for the assessment of all kind of ecosystems and conditions where soil surface properties can be good indicators of soil functioning, as it is the case in drylands with patchy vegetation (e.g., Cerdà 1998; García et al. 2005; Mayor et al. 2009) and also in recently burned areas (Gimeno-Garcia et al. 2011; Bodí et al. 2013).

4.5. Conclusions

Plant structural and functional traits modulate the response of soil functions to fire disturbance in terms of resistance (the amount of change caused by fire) and resilience (the recovery capacity after fire). Our results point to different control traits for the resistance and resilience of soil functions, being soil resistance more influenced by plant structural traits related to the potential fuel consumption, and soil resilience highly determined by the post-fire regeneration strategy of the plant species (resprouter vs. seeder). Overall, soil functions were more resistant in patches of resprouter species and in patches of seeder species with lower contents of fine dead fuel, while soil functions were more resilient in patches of resprouter plants. The consistency of these results across the three study sites, despite some variation in environmental conditions, highlights the robustness of the observed role for plant traits in modulating fire impact on soil functioning. According to these results, changes towards an increasing presence of resprouter grasses, seeder species, and bare soil caused by frequent fires in Mediterranean shrublands would decrease soil functioning and increase the vulnerability of the ecosystem to post-fire degradation.

Chapter 5

Plant regeneration traits modulate the response to fire of soil enzyme activity in Mediterranean shrublands

5. Plant regeneration traits modulate the response to fire of soil enzyme activity in Mediterranean shrublands

5.1. Introduction

In Mediterranean ecosystems, wildfires are major disturbances that can produce short and long lasting impacts on a variety of soil properties and processes, and greatly alter soil functioning (Neary et al. 1999; Hernández et al. 1997; Certini 2005; Knicker 2007; Shakesby 2011). Soil enzymes are important in soil functioning because of their role in decomposition of organic inputs and nutrient cycling; they are critical to carbon (e.g., β-glucosidase and β-galactosidase), phosphorus (phosphatases), nitrogen (urease) and sulphur (sulphatase) cycles (Karaca et al. 2011). Soil enzymes are considered good indicators of fire impacts on soil quality as they are involved in key soil processes, rapidly response to natural and anthropogenic disturbances, and can be easily measured (Ajwa et al. 1999; Zornoza et al. 2007; Boerner et al. 2008; Karaca et al. 2011). However, knowledge on the factors and underlying mechanisms that control the resistance (magnitude of the decline) and resilience (post-fire recovery) of soil enzyme activities in response to fire remains very limited (Guénon and Gros 2013).

Soil enzymes are highly sensitive to fire (Saá et al. 1993; Boerner et al. 2008), which can cause denaturation of proteins, decomposition of metabolites, temporary soil sterilization, changes in the soil microbial community, increased phosphorus and nitrogen mineralization, and reduced water availability, among other relevant changes in the environment and conditions of the enzyme pool (DeBano et al. 1998; Hernández et al. 1997; Wan et al. 2001; Guénon et al. 2011; Goberna et al. 2012). Both fire severity and frequency have proven to control fire impact on soil enzyme activities, yet with varying effects depending on the enzyme type. For example, Saá et al. (1993) found a drastic reduction in acid phosphatase and an intense mineralization of organic P in soils affected by severe wildfires, while the activity of this enzyme hardly changed in soils that had been subjected to low-severity controlled fires. Boerner and Brinkmanm (2003) found that repeated prescribed fires decreased acid phosphatase and β-glucosidase activities, but increased phenol oxidase activity, which was attributed to a reduction in organic matter quality and increased dominance of recalcitrant organic matter forms. The persistence of these fire effects on the soil enzyme pool over time, which relates to the resilience of the soil enzyme activity, has been reported to last from several months (e.g., Hernández et al. 1997) up to four years (Staddon et al. 1998).

The specific response of soil enzymes to fire may largely depend on fire-induced changes in the plant community (Hart et al. 2005). The amount and type of vegetation determine the quantity and quality of litter, nutrient demands, root detritus and exudates, soil surface temperature, evapotranspiration rates, and soil water availability, all of which can greatly affect soil enzyme activity (Ajwa et al. 1999; Neary et al. 1999; Papa et al. 2007; Fioretto et al. 2009). However, little research has focused on the role of vegetation type (i.e., species and/or functional composition) as a controling factor of fire effects on soil biochemical functions (Bárcenas-Moreno et al. 2014). In Mediterranean ecosystems –and other crown-fire ecosystems worldwide– the post-fire regeneration response of plant species defines two main plant functional groups: (1) obligate seeders (hereafter seeders), which are species that regenerate exclusively from seeds, and (2) obligate and facultative resprouters (hereafter resprouters), which are species that can regenerate by vegetative regrowth (Keeley 1986; Pausas et al. 2004a). Seeder and resprouter species may differ in nutrient demands; biomass allocation to either above or belowground growth; leaf nutrient content; and litter decomposition rates (Pate et al. 1990; Verdú 2000; Knox and Clarke 2005; Schwilk and Ackerley 2005; Saura-Mas and Lloret, 2009). Furthermore, resprouters are often long-lived species that survive fire impact by resprouting from protected regenerative organs, generally from root systems that may continue to be active through repeated fires. In contrast, seeder species have a shorter life cycle and recruit new individuals after fire (e.g., Keeley 1986; Pausas et al. 1999). Consequently, it can be hypothesized that seeder and resprouter species develop contrasting plant-soil systems, which differ in their abilities to withstand and recover from fire disturbance. In line with this hypothesis, using indicators of overall soil functioning, López-Poma et al. (*in* *review*; see Chapter 4) have recently reported that both resistance and resilience of soil functioning were higher in patches of resprouter species than in patches of seeder species, with patches of seeder species that typically accumulate high content of fine dead fuel showing the highest decrease in soil functioning.

In this study we evaluated the role of fire-related plant functional groups in modulating fire impact on soil enzyme activity in a Mediterranean fire-prone shrubland. Our objectives were to investigate (1) the effect of seeder and resprouter species on the resistance to fire, post-fire recovery dynamics, and resilience of soil enzyme activity, and (2) the potential role of soil organic C and plant cover dynamics as control factors of the soil enzymatic response to fire. Using experimental burnings, we specifically assessed fire impacts and post-fire recovery dynamics of soil enzyme activity, plant cover, and soil organic C in (1) resprouter shrub patches; (2) seeder shrub patches; (3) patches of mixed resprouter and seeder species; and (4) interpatches (i.e., areas between shrub patches with bare soil or scarce vegetation, typically grasses and chamaephytes). For this study, we chose two extracellular enzymes involved in P and C cycling: Phosphomonoesterase (hereafter acid phosphatase) and β-glucosidase. Acid phosphatase is produced by plant roots and has been pointed out as particularly good indicator of fire effects as compared with other soil enzymes (Staddon et al. 1998). It catalyzes the hydrolysis of a variety of organic and inorganic phosphomonoesters, and is therefore important in soil P mineralization and plant nutrition, particularly in P-limited soils. Its activity is inhibited by high levels of inorganic P. The most predominant glycosidase in soil is β-glucosidase, which is produced by fungi and bacteria. It is the third enzyme in a chain of three which break down labile cellulose and other labile C forms and its activity is stimulated by complex organic substrate to be degraded (Tabatabai 1994). These characteristics suggest that these two enzymes represent a range in production and regulation mechanisms and therefore in potential soil enzymatic response to fire disturbance.

5.2. Materials and methods

5.2.1. Study area

The study was conducted in a *Rosmarinus-Erica* Mediterranean shrubland of eastern Spain, in the province of Valencia. The study site (39°07'N 0°57'W; 20% NE facing slope; 980 m.a.s.l.) has a dry-Mediterranean climate, with a mean annual precipitation of 430 mm, and mean annual temperature of 13°C. Soils are Humic Leptosols (FAO, 1998) (Lithic Xerocrept, Soil Taxonomy) developed over white marls and limestone (See Table 5.1 for a description of main soil properties). Vegetation was a dense shrubland that developed after a wildfire on a *Pinus halepensis* forest in 1979. The dominant shrub species were the seeder species *Rosmarinus officinalis* L. (27% plant cover), and the resprouter species *Erica multiflora* (26% plant cover). Other seeder shrub species, such as *Ulex parviflorus* Pourr., and resprouter shrub species, such as *Quercus coccifera* L. and *Juniperus, oxycedrus* L. were also abundant in the study site. The herbaceous layer was dominated by the resprouting perennial grass *Brachypodium retusum* (Pers.) Beauv.

Table 5.1: *Soil characteristics of the experimental site (Mean ±SE, n=12).*

Variable	**Mean ±SE**
Organic C (%)[1]	6.25±0.35
Total nitrogen (%)[1]	0.35±0.02
C/N ratio	17.82±0.27
Available P (ppm)[1]	26.42±2.74
pH	7.13±0.03
EC (mS/cm)	0.35±0.01
Sand (%)	59.70±0.89
Silt (%)	27.05±0.76
Clay (%)	12.82±0.57

[1] Organic C was measured using the titration (Walkley & Black Method) method; total Nitrogen was measured by the Kjeldahl method; and available P by the Olsen method (In: Carter M. R. (Ed.). 1993. Soil sampling and methods of analysis. CRC Press.).

In general, the climatic conditions during the study period were drier than the long term (1950-2009: Ayora weather station - 39°01'N 1°03'W) average (Fig. 5.1), except for few months with extreme rainfall events, such as September 2009 and March 2011, when monthly precipitation exceeded average values by a large amount.

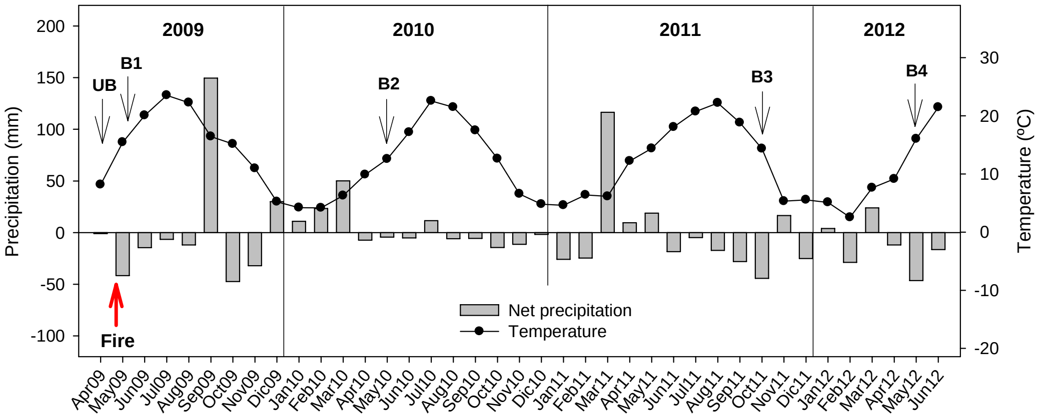


Figure 5.1: *Net monthly precipitation: difference between monthly rainfall over the study period (May 2009- May 2012) and the respective monthly long-term (1950-2009) average; and mean monthly temperature over study period. Data from Ayora Weather Station (Confederación Hidrográfica del Jucar Network).The arrows point to the experimental burning and sampling times: Two weeks before the fire (UB), and two weeks (B1), 12 (B2), 30 (B3) and 36 months (B4) after the fire.*

5.2.2. Experimental design, sampling, and laboratory procedures

For the experimental treatments, we selected four types of shrubland microsites: (1) patches dominated (i.e., where plant cover of the target functional group was higher than 90% of total patch cover) by seeder shrubs (SS), patches dominated by resprouter shrubs (RR), mix patches co-dominated (between 40 and 60% cover each) by seeder and resprouter shrubs (SR), and shrub interpatches (IP), which represented areas between shrubs, typically covered by scattered grasses and chamaephytes.

On May 2009, an experimental burn (Fig. 5.2) was conducted over a homogeneous ~500 m^2 area. The fire completely burned the shrub cover and litter. Maximum temperature measured by thermocouples installed at the soil surface was 492 ± 32°C (mean ± SE, n=35). Prior to the burning, we marked all individual shrub patches that fit into any of the selected patch microsite types, and all interpatch areas equal or larger than 1m^2; then we randomly selected 12 circular (1m-diameter) plots for each microsite type (SS, RR, RS, and IP), totalling 48 sampling plots in the study site. For each plot, we measured soil acid phosphatase and β-glucosidase activities, soil organic C, and plant cover dynamics over a three-year period.

Figure 5.2: *From left to right and top to bottom, images of the experimental site before, during, inmediatelly after, and two years after the experimental fire.*

The soil variables were assessed two weeks before fire (UB), and two weeks, 12, 30, and 36 months after the fire (B1, B2, B3, and B4 respectively) (Fig. 5.2). In order to make pre- and post-fire enzyme activities comparable and to control for the influence of seasonal variability, soil sampling always took place in spring or autumn, when the maximum enzyme activities can be expected in response to optimum conditions of temperature and water-availability and to the peaks in plant growth (spring) and litterfall (autumn) in

Mediterranean ecosystems (Sardans and Peñuelas 2005; Sardans et al. 2008). At each sampling time, we took one soil core (0-5 cm depth; 5 cm diameter) from each circular sampling plot. The soil cores for the various sampling times were taken ~ 15cm apart from each other, at a similar distance (~30 cm) from the centre of the circular plot, and on the south-facing side of the plot. The soil samples were air-dried and sieved, and the <2mm diameter fraction was stored in plastic boxes until analysis. Soil organic C was determined by potassium dichromate-sulphuric acid oxidation (Mebius 1960). Soil acid phosphatase and β-glucosidase activities were determined colorimetrically as the amount of ρ-nitrophenol (PNP) produced after incubation of 0.5 g of soil (37°C, 1 h) with ρ-nitrophenyl-phosphate and ρ-nitrophenyl-β-D-glucopyranoside, respectively (Tabatabai and Bremner 1969; Tabatabai 1994).

On each sampling plot, total plant cover and total cover of seeder and resprouter species were independently estimated by the grid-point intercept method, using a 0.25 m^2 quadrate frame with 100 grid points. Plant cover was assessed two weeks before the fire and 9, 12, 18 and 36 months after the fire.

5.2.3. Resilience and resistance calculations

The soil enzymatic response to fire disturbance was quantified using resistance and resilience indices developed by Banning and Murphy (2008). Resistance (RS) is defined as the magnitude (%) of change in a given soil function caused by fire (measured immediately after fire), while resilience is captured by two indices: The Recovery index (Rx), which defines the difference (%) between burned and unburned conditions at a given time after the fire regardless the initial fire impact (RS values), and the Resilience index (RL), which is expressed relative to the initial resistance. The indices were applied to our data as follows:

Resistance: $RS = -100\left[\frac{UB - B1}{UB}\right]$

Resilience: $Rx = -100\left[\frac{UB - Bx}{UB}\right]$ and $RL = -(RS - Rx)$

where UB represents pre-fire values for the target variable, B1 represents the values recorded immediately after fire (two weeks after fire), and Bx corresponds to average values for the last two sampling periods (B3 and B4; i.e., 30 and 36 months after fire).

An RS value of zero indicates maximum resistance, with no difference between recently burned soils (B1) and unburned soils (UB), while an RS value of -100 indicates a complete depletion of soil enzyme activity in burned soils (B1). Positive values of the RS index may occur when soil enzyme activity in burned soils (B1) is higher than in unburned soils (UB). Rx values are interpreted similarly to RS values, with values of zero indicating complete recovery at a given time x. For the RL index, a value of zero indicates no resilience. Negative RL values indicate further decline in enzyme activity beyond the initial fire impact. Positive values indicate resilience.

5.2.4. Data analysis

We used a repeated measures ANOVA to test the effect of Fire (unburned versus two weeks after fire) and Microsite type (SS, RR, SR, and IP) on soil enzyme activities (acid phosphatase and β-glucosidase) and organic C. The effect of Microsite type on the post-fire dynamics of soil enzyme activities (acid phosphatase and β-glucosidase), organic C, and plant cover over the monitoring period (two weeks, 9, 12, and 36 months after fire) was tested using repeated measures ANOVA, with Time as the within-subject factor and Microsite type as the between-subject factor. The effect of Microsite type on pre-fire soil enzyme activity and on the resistance, recovery and resilience of these activities (i.e., RS, Rx, and RL indices) were analysed using one-way ANOVA, followed by Tukey test in the case of a significant microsite effect. Relationships between acid phosphatase and β-glucosidase activities and soil organic C, and between these soil biochemical properties and plant cover were analyzed using Pearson correlation. Prior to analysis, the normality and homoscedasticity of the various sets of data were tested and all data met these assumptions. Statistical analyses were performed with SPSS Statistics v. 17.0 (SPSS Inc., Chicago, IL).

5.3. Results

5.3.1. Microsite effect on soil and plant dynamics in response to fire

Pre-fire activities of acid phosphatase and β-glucosidase significantly varied among the microsite types, with acid phosphatase showing the gradient IP< SS< RR≤ SR (F= 20.895, *P*< 0.001; one way ANOVA) and β-glucosidase showing the gradient IP<SS≤ RR≤SR (F= 12.804, *P*< 0.001; one way ANOVA). The highest values for both enzyme activities were recorded in the patches with presence of resprouter species (RR and SR) (Fig. 5.3).

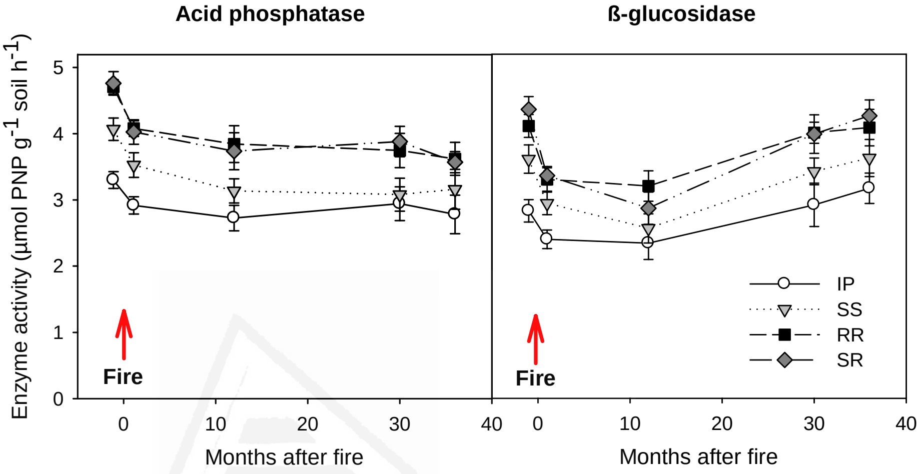


Figure 5.3*: Pre-fire values and post-fire dynamics of soil acid phosphatase and β-glucosidase activities in interpatch areas (IP), seeder shrub patches (SS), resprouter shrub patches (RR) and mixed patches of resprouter and seeder species (SR).*

Enzyme activity decreased after fire (Fig. 5.3). Repeated measures ANOVA on pre-fire and immediately (two weeks) after fire data showed significant effect of both Fire and Microsite on acid phosphatase and β-glucosidase, with no interaction between these factors (Table 5.2). All over the post-fire period assessed, the activity of both enzymes varied among microsite types in a consistent way, with shrub patches including resprouter species, with or without seeder species, showing the highest values (Table 5.3, Fig. 5.3). The post-fire temporal dynamics of enzyme activity varied between acid phosphatase and β-glucosidase. In both cases, there was an initial decrease in enzyme activity that lasted at least one year. However, while β-glucosidase increased its activity afterwards, acid phosphatase showed a decreasing trend till the end of study period (Fig. 5.3).

Table 5.2: *Results from repeated measures ANOVA (F and P values) on soil acid phosphatase, β-glucosidase, and organic C data, with Fire (two weeks before and after the fire) as within-subject factor, and Microsite (IP, SS, RR, and SR) as between-subject factor (Significant results are depicted in bold).*

	Acid phosphatase	β-glucosidase	Organic C
Within subject			
Fire	**F= 47.573**	**F= 49.954**	F= 2.353
	***P*< 0.001**	***P*< 0.001**	*P*= 0.132
Fire x Microsite	F= 0.919	F= 1.562	F= 0.233
	P= 0.440	*P*= 0.212	*P*= 0.873
Between subject			
Microsite	**F= 22.098**	**F= 15.624**	**F= 3.180**
	***P*< 0.001**	***P*< 0.001**	***P*= 0.033**

Microsite type significantly affected soil organic C, with microsites including resprouter species showing the highest values (Fig. 5.4). We did not find any effect of Fire (Table 5.2) and Time after fire (Table 5.3), nor interaction effects between Microsite and Fire or Microsite and Time after fire on this variable.

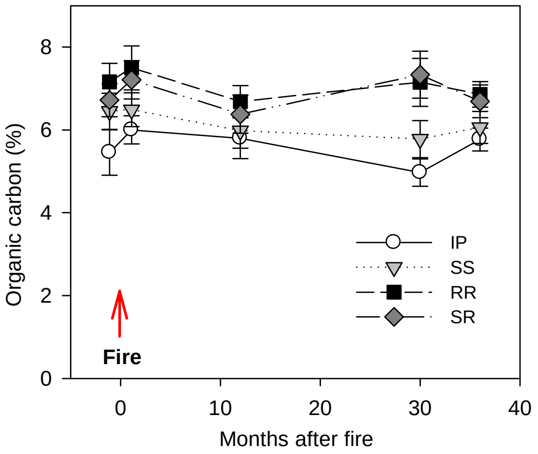


Figure 5.4: *Pre-fire values and post-fire dynamics of soil organic C (%) per microsite type: interpatch areas (IP), seeder shrub patches (SS), resprouter shrub patches (RR) and mixed patches of resprouter and seeder species (SR).*

Table 5.3: *Results from repeated measures ANOVA on soil acid phosphatase, β-glucosidase, organic C, and plant cover data, with Time (two weeks, 12, 30, and 36 months after fire) as within-subject factor and Microsite (IP, SS, RR, and SR) as between-subject factor (Significant results are depicted in bold).*

	Acid phosphatase	β-glucosidase	Organic C	Plant cover
Within subject				
Time	F= 2.051	**F= 19.025**	F= 1.964	**F= 117.272**
	P= 0.110	***P*< 0.001**	*P*= 0.123	***P*< 0.001**
Time x Microsite	F= 0.278	F= 0.362	F= 0.690	**F= 10.646**
	P= 0.980	*P*= 0.951	*P*= 0.717	***P*< 0.001**
Between subject				
Microsite	**F= 11.333**	**F= 12.858**	**F= 6.167**	**F= 29.901**
	***P*< 0.001**	***P*< 0.001**	***P*= 0.001**	***P*< 0.001**

Two weeks after the fire acid phosphatase and β-glucosidase were positively correlated between them and with soil organic C. However, at the end of the study period (36 months after the fire), acid phosphatase and β-glucosidase were no longer correlated; the correlation of acid phosphatase and organic C were still significant but weaker, and the correlation between β-glucosidase and organic C was not significant. At this last sampling time, both enzyme activities and organic C were positively correlated with plant cover (Table 5.4).

Table 5.4: *Pearson correlation coefficients (r) and significance (P) for pair-wise relationships between soil acid phosphatase, β-glucosidase, organic C, and total plant cover, early (two weeks) after fire and 36 months after fire (Significant results are depicted in bold).*

	2 weeks post-fire (n= 48)	36 months post-fire (n= 48)
Acid phosphatase – β-glucosidase	**r= 0.438**	r= 0.196
	***P*= 0.002**	*P*= 0.183
Acid phosphatase - Organic C	**r= 0.502**	**r= 0.306**
	***P*< 0.001**	***P*= 0.034**
β-glucosidase - Organic C	**r= 0.302**	r= 0.279
	***P*= 0.037**	*P*= 0.055
Acid phosphatase - Plant cover		**r= 0.293**
		***P*= 0.043**
β-glucosidase - Plant cover		**r= 0.383**
		***P*= 0.007**
Organic C - Plant cover		**r= 0.467**
		***P*= 0.001**

Repeated measures ANOVA showed a significant effect of Time and Microsite, and significant interaction (Time x Microsite) on post-fire plant cover (Table 5.3). Throughout the study period, plant cover followed the gradient IP<SS<SR<RR (Fig. 5.5, Fig. 5.6). The interaction between Microsite and Time pointed to the different recovery rates of plant cover for the various types of microsites, with the microsites that included resprouter species showing fastest recovery.

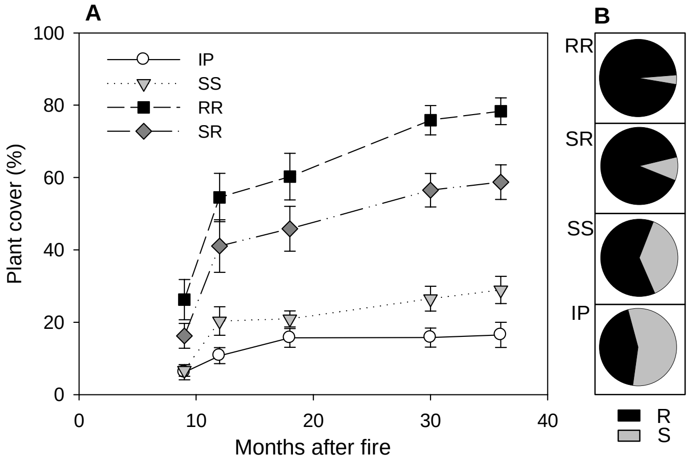


Figure 5.5: *A) Post-fire plant cover dynamics per microsite type: interpatch areas (IP), seeder shrub patches (SS), resprouter shrub patches (RR) and mixed patches of resprouter and seeder species (SR). B) Cover ratio of seeder (S) and resprouter (R) species per microsite type 36 months after the fire.*

Figure 5.6: *From left to right and top to bottom, images of the microsite types: interpatch areas (IP), seeder shrub patches (SS), resprouter shrub patches (RR) and mixed patches of resprouter and seeder species (SR) 30 months after fire.*

5.3.2. Resistance and resilience of soil enzyme activity

Fire decreased the activity of both enzymes, but acid phosphatase appeared to be slightly more resistant (less percentage of change immediately after fire) than β-glucosidase (Fig. 5.7). Neither acid phosphatase nor β-glucosidase showed significant differences in resistance between microsites, although there was an apparent higher resistance in interpatch areas (IP) (Table 5.5, Fig. 5.7).

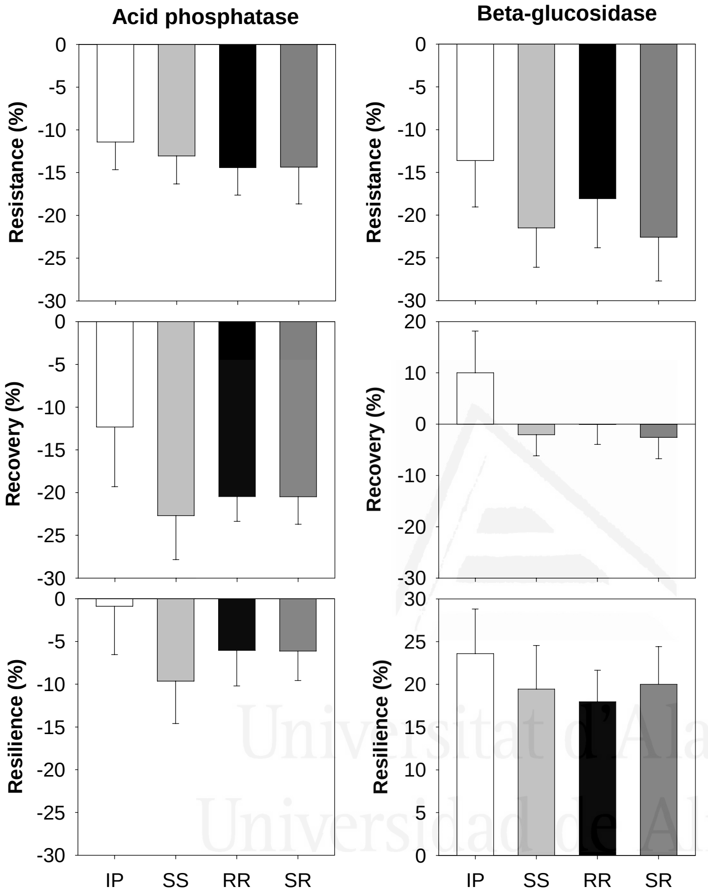


Figure 5.7: *Resistance (RS), recovery (Rx) and resilience (RL) of acid phosphatase and β-glucosidase activities per microsite type: interpatch areas (IP), seeder shrub patches (SS), resprouter shrub patches (RR) and mixed patches of resprouter and seeder species (SR). RS= 0 means complete resistance, while increasing negative values indicate lower resistance. Rx values are interpreted similarly to RS values. RL= 0 means no resilience; positive values indicate resilience, and negative values indicate further degradation of enzyme activity beyond the initial fire impact.*

Table 5.5: *Microsite effect on Resistance, Recovery and Resilience indices for soil acid phosphatase and β-glucosidase activities (One-way ANOVA; F and P values).*

	Resistance (RS)	Recovery (Rx)	Resilience (RL)
Acid phosphatase	F= 0.156 *P*= 0.925	F= 0.871 *P*= 0.464	F= 0.604 *P*= 0.616
β -glucosidase	F= 0.569 *P*= 0.638	F= 1.149 *P*= 0.341	F= 0.155 *P*= 0.926

Three years after the fire, and for all microsite types, the difference in acid phosphatase activity between pre-fire and burned conditions was even higher than the difference created immediately after fire. Thus, this enzyme showed very negative recovery values and negative resilience values (Fig. 5.7). Conversely, β-glucosidase activity recovered well in all microsites, reaching the unburned values and even exceeding pre-fire values in the case of interpatches. There were no significant differences in resilience between microsites (Fig. 5.7, Table 5.5), although interpatch areas (IP) seemed to be slightly more resilient than shrub patches for both enzymes assessed, and seeder species (SS) patches seemed to be the least resilient microsite type. For β-glucosidase activity, SS shrub patches seemed to be less resistant but more resilient.

5.4. Discussion

5.4.1. Post-fire regeneration traits and soil enzyme activity

There is abundant evidence that plant species can have major impacts on soil biochemical properties (e.g., Knops et al. 2002; Rutigliano et al. 2004; García et al. 2005) and their responses to disturbances (e.g., Hart et al. 2005; Sardans and Peñuelas 2010; 2013; Bárcenas-Moreno et al. 2014). We expected that plant functional groups that relate to the post-fire regeneration traits of plant species (i.e., seeder and resprouter species; Keeley 1986; Pausas et al. 2004a) develop group-specific plant-soil systems that differ in their functioning and their abilities to withstand and recover from fire disturbance. We found that post-fire regeneration functional groups modulate soil enzyme activity in

Mediterranean fire-prone shrublands. For two key soil enzymes involved in P and C cycling (i.e., acid phosphatase and β-glucosidase, respectively) soil enzyme activity was higher under shrub patches dominated or co-dominated by resprouter species than under patches dominated by seeder species. Soils in interpatch areas showed the lowest enzyme activity. These differences among microsite types were consistent between pre-fire and post-fire conditions, yet they slightly vanished over the post-fire period.

Vegetation patches that vary in their proportion of resprouter and seeder species may largely vary in the quantity and quality of root exudates and litter inputs (Saura-Mas and Lloret 2009), which in turn may have a significant influence on soil enzyme activity (Garcia et al. 2005; Zang et al. 2013). However, several previous works that compared soil enzyme activities for a variety of Mediterranean plant species in unburned conditions did not show consistent differences between seeder and resprouter species (Rutigliano et al. 2004, Garcia et al. 2005; Papa et al. 2007). Probably the most contrasting differences in soil biochemical and microbiological properties between seeder and resprouter species appear once the plant community has experienced one or repeated fires. Most resprouter individuals survive the fire and keep their root systems alive and active, recovering their above-ground biomass on the same spot. Conversely, seeders are killed by fire, their root systems decompose and the new individuals establish from seeds in different, more or less distant spots than pre-fire ones (Keeley 1986). Therefore, in case of fire, the so-called microbiological hotspots (i.e., enhanced microbial activity under plant patches; Goberna et al. 2007) are more durable if linked to resprouter species than to seeder species. As a result, differences between the soil systems of these two functional groups would accumulate through repeated fires. Our study site was burned by a wildfire in 1979, and then burned again by our experimental fire in 2009. Despite the likely inter-specific differences within both the resprouter (*E. multiflora*, *Q. coccifera*, and *J. oxycedrus*) and the seeder (*R. officinalis*, *U. Parviflorus,* and *C. albidus*) groups of species that were assessed in this study, we found a clear pattern of enhanced soil enzyme activity in resprouter and mixed (resprouter and seeder combined) shrub patches as compared with seeder shrub patches.

5.4.2. Soil enzyme response to fire

Fire reduced the activity of both acid phosphatase and β-glucosidase in all microsite types. This decline in soil enzyme activity immediately after the fire may be attributed to enzyme denaturation, temporary soil sterilization, P mineralization, and changes in soil microbial community, among other direct thermal effects of fire (DeBano et al. 1998; Certini 2005; Guénon et al. 2011; Goberna et al. 2012). The high correlation found between acid phosphatase and β-glucosidase activities two weeks after fire suggests that both enzymes responded to these fire-driven changes similarly, yet the decline in soil enzyme activity was slightly higher for β-glucosidase than for acid phosphatase. In both cases, enzyme resistance did not show significant differences between microsite types. However, there was an apparent tendency towards higher resistance in interpatch soils as compared with soils under shrub patches. This can be attributed to lower fuel load and therefore lower fire severity in interpatch soils, combined with lower pre-fire enzyme activity in this microsites, which can therefore only slightly be further reduced (López-Poma et al. *in review*; see Chapter 4).

One year after the fire, there was no sign of recovery for any of the two enzyme activities. Similar and longer periods of persistent fire impacts on enzyme activity have been previously reported for Mediterranean ecosystems (Hernández et al. 1997; Guénon et al. 2011). However, after the first post-fire year, the two target enzymes showed diverging trends: while β-glucosidase activity shifted towards a positive recovery trend, acid phosphatase showed no recovery throughout the study period and even further decreased with time after fire. Contrasting resilience between these two enzymes was also reported by Guénon et al. (2011). Comparing unburned and burned (four years after fire) cork oak forests, these authors found that acid phosphatase activity was still significantly lower in burned than in unburned forests, while β-glucosidase activity showed the opposite pattern.

Persistent low activity of acid phosphatase could result from high availability of inorganic P, which inhibits this enzyme activity (Sinsabaugh 1994; Allison and Vitousek 2005). Initially, the pyro-mineralization of organic P during the fire (Serrasolsas and Khanna 1995; Certini 2005) could have satisfied P demands by plants and microorganisms. In addition, immediately after the experimental burning, there was an increase in the activity of alkaline phosphatase (Goberna et al. 2012). This enzyme is involved in the degradation of phospholipids and nucleic acids and contributes to further increase the availability of inorganic P. However, many studies have reported that this initial burst of P mineralization and availability is rather ephemeral (but see Creech et al. 2012). Furthermore, in neutral or alkaline soils, as the soil in the study site, inorganic P binds to Ca-minerals or precipitates as discrete Ca-phosphates (Certini 2005), quickly declining its bioavailability. An alternative explanation to the persistent low activity of acid phosphatase relates to the particularly dry conditions that prevailed over most of the study period. Acid phosphatase is mostly produced by plants and its activity is rather sensitive to water scarcity (Sardans et al. 2006). Drought-stressed plants reduce post-fire recovery, nutrient demand, and the production of acid phosphatase by roots, which can exacerbate the initial fire-driven decline in acid phosphatase (Fontúrbel et al. 2012; Hinojosa et al. 2012). The contrasting response of β-glucosidase may be attributed to the availability of complex substrates to be degraded, as a consequence of both fire and drought impacts, which induce the synthesis and activity of β-glucosidase (Allison and Vitousek 2005; Geisseler and Horwath 2009). Furthermore, β-glucosidase is mostly produced by fungi, which seems to be remarkably resistant to drought (Yuste et al. 2011).

Conversely to soil enzyme activity, total soil organic C (SOC) showed only small differences between microsite types; it was not affected by fire and barely changed throughout the study period. Furthermore, the positive correlations found between SOC and both β-glucosidase and acid phosphatase activities immediately after fire largely vanished three years after fire. Overall, these results do not support a relevant role of total SOC as control factor of enzyme activity, which probably is more dependent on labile SOC forms (Wang et al. 2013). However, some degree of covariation between total SOC and enzyme activity can always be expected, as they both reflect and indicate soil quality. Furthermore, organic matter is the primary source of enzyme substrates and it contributes to the physical stabilization of enzymes (Sinsabaugh 1994; Dick and Tabatabai 1992; Karaca et al. 2011).

5.4.3. Post-fire regeneration traits and soil enzyme resilience

López-Poma et al. (*in review*; see Chapter 4), found that soil functions were more resilient to fire in patches of resprouter plants. In agreement with these results, we expected higher resilience of soil enzyme activity under resprouter and mixed shrub patches than under seeder shrub patches. Resprouter and mixed shrub patches quickly increased plant cover after fire, benefiting from the ability of resprouter individuals to rapidly mobilize underground reserves and reactivate nutrient and water uptake soon after fire (Canadell et al. 1991; Whelan 1995). Conversely, plant cover on seeder patches was still very low (~20%) three years after fire, only slightly higher than plant cover on interpatch areas. This contrasting plant response probably affected nutrient demand and rhizosphere activity and, therefore, it could be expected to control soil enzyme resilience. In fact, three years after fire, β-glucosidase and acid phosphatase were positively correlated to plant cover. However, we found only minor, non-significant differences in soil enzyme resilience between shrub patch types, which suggest that other factors could have counterbalanced or masked the role played by plant recovery. The lack of differences in the resilience of β-glucosidase between the various types of shrub patches could have resulted from the counterbalancing effect of higher rhizosphere activity under resprouter shrubs on the one hand, and higher availability of decaying organic matter under seeder shrubs, most of which are killed by fire, on the other hand. The apparent higher resilience of interpatch areas as compared with shrub patches could be explained by a lower initial fire impact on these microsites. The recovery of acid phosphatase was probably hindered by the effect of a persistent drought that followed the fire, which seems to have magnified the initial fire impact and masked any potential effect of microsite type (Hinojosa el al. 2012). However, despite the general post-fire decline in acid phosphatase activity across microsite types, there was a tendency towards lower resilience in seeder shrub patches, which is in agreement with our expectations and previous work by López-Poma et al. (*in review*; see Chapter 4).

5.5. Conclusions

Plant functional groups that relate to post-fire regeneration traits (i.e., obligate seeder and resprouter species) modulate the activity of soil extracellular enzymes acid phosphatase and β-glucosidase in Mediterranean fire-prone shrublands. The activity of both enzymes is enhanced under shrub patches dominated or co-dominated by resprouter species as compared with soils under seeder shrub patches and interpatch soils. Fire similarly reduced the activity of both acid phosphatase and β-glucosidase in the short term. However, these enzymes showed contrasting differences in resilience. β-glucosidase, a substrate-dependent enzyme that is involved in the degradation of cellulose and is mostly produced by microorganisms, particularly fungi, proved to be very resilient to fire. Conversely, acid phosphatase, which is mostly produced by plants, did not show any sign of recovery over the first three pre-fire years, probably due to the combined effect of fire and post-fire drought. How the resulting alteration in P cycling processes can affect vegetation recovery in P-limited soils would deserve further research. Overall, the results suggest that the positive influence of resprouter shrubs on soil enzyme activity is very resistant to fire. However, contrasting responses to fire and drought disturbances between the various enzyme types could greatly alter nutrient cycling dynamics. Our results provide insights on how plant functional traits and groups modulate soil biochemical and microbiological response to fire and contribute to define general patterns and control factors of ecosystem resistance and resilience to wildfires.

Chapter 6

General discussion and conclusions

6. General discussion and conclusions

6.1. Fire severity and resilience of Mediterranean plant communities

Disturbances like fire can shape patterns of secondary succession by affecting processes of community assembly. Fire regime (frequency and/or severity) affects plant recovery patterns and may act as environmental filter that selects species with regeneration traits adapted to that particular fire regime, with consequent impacts on species abundance in the post-fire community (Moreno and Oecheel 1991a; Pausas et al. 2003; Lloret et al. 2003; Hollingsworth et al. 2013). This doctoral research work (Chapters 2 and 3) provides evidence that the post-fire biological structure of Mediterranean plant communities is largely shaped by fire severity. In turn, fire severity depends on plant traits that relate to the potential flammability of the community, such as tissue moisture content and chemical composition, fuel area-to-volume ratio, plant height, canopy density, and retention of dead branches (Dimitrakopoulos and Panov 2001; Baeza et al. 2002; Schwilk 2003; Baeza et al. 2011; Santana et al. 2011).

In a common Mediterranean landscape, with a mosaic of plant communities that represent different successional stages after agricultural land abandonment, fire severity controlled the recovery rate (*engineering resilience - sensu* Holling 1996) of vegetation abundance, and filtered species composition, promoting shifts to alternative communities (*ecological resilience – sensu* Holling 1996). It is worth noting that engineering and ecological resilience do not always follow the same pattern. For example, pine forest areas were moderately resilient regarding the post-fire recovery of total plant cover. However, this type of community shifted to a new domain (gorse shrubland) with low probability of re-establishing the biological structure of the previous state, therefore proving to be low resilient in ecological terms (Holling 1973). It is known that severe fires on young pine stands may result in local extinction of pines, since they may have not produced a significant canopy seedbank before the fire (Pausas et al. 2004b). Furthermore, pine forest resilience also depends on the dominant pine species. Thus, species that produce few seedlings after fire (e.g. *P. nigra*, *P. sylvestris*, and *P. pinea*) favour post-fire ecosystem shifts to other community types (Rodrigo et al. 2004). In our case, low ecological resilience of mature pine forest seems to have resulted from the combination of high fire severity and post-fire drought, which acted together as a selective filter that favoured the spreading of seeder shrubs (although delaying their recovery at the earliest post-fire stage), and hindered the germination of pine seeds, which do not maintain viable seeds for long after dispersal. Out of several combinations of factors that could hinder community self-succession after fire and promote ecosystem shifts, our results point to factors of particular relevance in a context of climate change, according to which more severe and frequent wildfires and droughts are expected in the Mediterranean region (Schröter et al. 2005).

The filtering role of fire severity was evident at the microsite scale. The spatial variation in fire severity within plant communities was highly correlated with variations in plant recovery, but this relationship was modulated by fire-related plant functional groups. Microsites burned at high severity filtered out sensitive resprouters, and created degraded bare-soil gaps. These microsites were later colonized by seeders that maintain persistent viable seeds in the soil seed bank, such as *Ulex parviflorus* and *Cistus albidus*. As a result of this contrasting response of seeders and resprouters to fire severity, there was an exponential increase in the seeder/resprouter abundance ratio with increasing fire severity within the burned area (Chapter 3).

Overall, our results show that both ecosystem resilience and resistance are strongly influenced by the plant post-fire regeneration traits of the dominant plant species. On the one hand, these traits act as response traits (*sensu* Lavorel and Garnier 2002). First, they affect the way species resist fire impacts. For example by maintaining viable seeds in the soil seed bank (e.g., *Ulex parviflorus, Cistus albidus,* and *Rosmarinus officinalis*), and by keeping protected living tissues in belowground structures (e.g., *Brachypodium retusum, Quercus coccifera, Erica multiflora* and *Juniperus oxycedrus*). Second, post-fire regeneration traits modulate the recovery of the plant community after fire (Keeley 1986; Pausas et al. 2004a; Bond and Midgley 2001; Lloret et al. 2005) (Fig. 6.1). On the other hand, plant post-fire regeneration traits *per se* seem to have a significant influence on ecosystem functions (effect traits). Conversely to the hypothesis formulated by Lavorel and Garnier (2002), according to which regeneration and demographic traits associated with response to disturbance would be of little relevance to mature-ecosystem processes, we found that post-fire regeneration traits largely affect soil functions (Chapter 4 and 5) and propensity to disturbance (Chapter 2). Thus, different species from the same post-fire regeneration functional group may share similar structural traits determining flammability and fire severity. For example, seeder species tend to have lower total fuel load but higher dead-to-live fuel ratio, and lower moisture content than resprouter species of comparable life forms (Saura-Mas et al. 2010). However, the results presented in Chapter 4 also highlight the importance of species-specific structural traits in determining fire effects (See also Section 6.2 below).

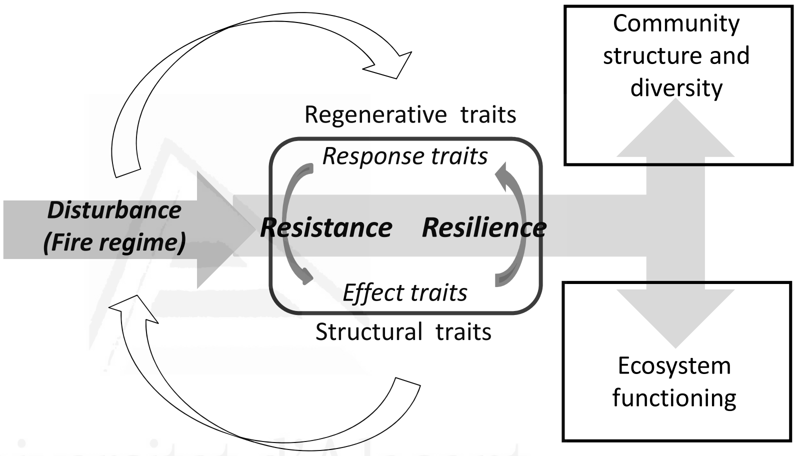


Figure 6.1: *Plant structural traits and post-fire regeneration traits interact to determine ecosystem resistance and resilience to fire, which in turn influence community structure and diversity, and therefore ecosystem functions. Adapted from Lavorel and Garnier (2002).*

Many traits, either regeneration or structural features, have been showed experimentally to correlate with the response of plants and communities to fire (Pausas et al. 2004a; Brasdshaw et al. 2011). Table 6.1 compiles reported results in that regard. Some plant traits have been described as adaptations to surviving fire (Keeley et al. 2011); the main two fire-persistence traits (resprouter and seeder), have been used in predictive modelling along fire-regime gradients (Pausas 1999; Vesk and Westoby 2004; Hollingsworth et al. 2013), highlighting the importance of the patterns and processes that underlie the expression of these plant traits on ecosystem response to fire**.** Plant regeneration traits should not be randomly distributed along the geographical gradient, plant trait distribution should follow a predictable trend along the combined fire and climatic gradient (Lloret et al. 2005) or productivity gradient (Pausas and Bradstock 2007). Further research on the functional linkages and trade-offs among traits, would help to determine the filtering potential of target environmental factors, to capture the complexities of community assembly, predict the impact of fire regime, and identify ecosystem vulnerability to disturbances.

Table 6.1: *Plant traits that may have functional relevance in the response of plant individuals and communities to fire impact.*

	Functional role	**References**
Structural traits		
Growth form or life form (grasses, herbaceous, shrubs, trees)	Determines the fuel structure and ecosystem flammability.	Pausas and Bradstock 2007
Accumulation of dead biomass	Modulates local fire temperatures and heat release	Baeza et al. 2002, Schwilk 2003
Dead-to live fuel ratio	Mediates fuel combustibility and flammability	Saura-Mas et al. 2010
Canopy architecture	Determines the fuel flammability and continuity, and canopy density.	Goubitz et al. 2004; Ruiz-González and Álvarez-González 2011.

Surface to volume ratio	Determines fuel flammability. Smaller twigs and smaller leaves commonly have higher surface: volume ratio, and therefore be more flammable	Pereire et al. 1995; Cornelisse et al. 2003.
Chemical components of plant tissues (volatile oils, waxes and resins)	Contribute to enhance flammability and heat-content.	Dimitrakopoulus and Panov 2001; Nuñez-Regueiro et al. 2005; Alessio et al. 2008a
Water content of branches, twigs and leaves	Determines fuel flammability, High leaf and twig dry matter content are expected to increase flammable.	Saura-Mas et al. 2010
Regeneration traits		
Serotiny	Protects seeds from fire damage in serotinous cones, and to confer plant tolerance to fire	Moya et al. 2013
Seed dormancy	Leads to production soil seed-bank, allowing seed to avoid unfavourable conditions and recover later.	Ferrandis et al. 1996; Valbuena et al. 2000
Timing of seed release and dispersal mode	Modulates seed ability to disperse and colonize.	Keeley and Fotheringham 2000; Bastida and Talavera 2002.
Bark thickness in trees	Modulates protection of stem buds.	Pausas 1997; Bellingham and Sparrow 2000;
Resprouting ability	Modulates resprouting from dormant buds once foliage is removed	Bellingham and Sparrow 2000; Bond and Midgley 2001;
Root stored reserves	Modulates resprouting; plants require a substantial pre-fire allocation of resources.	Bond and Midgley 2001; Moreira et al. 2012
Root lateral spreading (Root system morphology)	Allows plants to explore the surface soil horizons, and favours wide-spread of clonal growth	Guerrero-Campo et al. 2006
Root depth (root system morphology)	Modulates uptaking capacity.	Guerrero-Campo et al. 2006

6.2. Plant-traits and soil functioning relationships

Plant and soil interactions and feedbacks drive important ecosystem processes such as biomass production, water availability, and nutrient cycling (Wardle et al. 2004). Plant effects on these processes are mediated by multiple plant traits (Eviner and Chapin 2003). For example, litter chemistry, litter mass, biomass, quality of root exudates and labile C inputs, and rate and pattern of root growth modulate the structure and activity of the soil microbial community (Fioretto et al. 2000; Eviner 2004; Hart et al. 2005; Bárcenas-Moreno et al. 2014). Different plant species create their own microenvironment, leading to small-scale variations in soil organic carbon, nitrogen and phosphorus content, pH, and soil microbial diversity (Garcia et al. 2005; Pérez-Bejarano et al. 2010). However, groups of species share particular combinations of traits (functional group) that influence ecosystems function in a specific ways. For example, litter decomposition rates and pattern vary between resprouter and seeder species, which attributed to differences in leaf chemistry between these two functional groups (Saura-Mas et al. 2012).

Understanding how plant functional traits modulate the response of soil functions to fire disturbance is critical to predict the overall impact of increased fire frequency in fire-prone woodlands and shrublands and would help to identify the plant-soil interactions and feedbacks behind the ecosystem response to fire. Plant-soil interactions and feedbacks may shape the magnitude and ecological impact of disturbances. For example, species-specific and group-specific structural traits such as accumulation of fine dead fuel determine fuel consumption, and soil maximum temperature and residence time during the fire (Santana et al. 2011), and thus largely influence fire impact on soils and plants, and further post-fire recovery (Chapter 4). In turn, soil characteristics may also have an influence on fire behaviour by filtering plant traits. For example, plants with high accumulation of polyphenolic compounds, which enhance flammability, are common in acidic and infertile soils (Northup et al. 1998; Orians and Milewski 2007).

We found significant plant effects of plant traits and functional groups on overall soil functioning (Chapter 4) and particularly on soil enzyme activity (Chapter 5). Growth-form traits combined with post-fire regeneration traits modulate soil functions. Thus soils under the resprouter grass *B. retusum* was less functional than under the resprouter shrubs *Q. coccifera*, while soil functions under the three different seeder shrub species (*Ulex parviflorus*, *Cistus albidus,* and *Rosmarinus officinalis*) did not vary between species. Despite the findings supporting that species within the same post-fire regeneration functional group may share structural traits related to flammability (Saura-Mas et al 2010), our results revealed that species-specific structural traits appeared to control fire severity and the amount of change in soil functions (*resistance*). Thus, soil function resistance was higher under *R. officinalis* patches than under patches of other shrub seeders (*U. parviflorus* and *C. albidus*), which can be attributed to differences in the amount of fine dead fuel and leaf chemistry. Conversely, post-fire regeneration functional group, regardless the species, was the most important factor controlling resilience of soil functions to fire, being resprouters the group enhancing soil function resilience (Chapter 4).

Narrowing the focus of our research on plant traits as control factor of soil functions and stability against fire, we assessed the response of two key soil enzyme activities: β-glucosidase and acid phosphatase (Chapter 5). In agreement with our previous results (Chapter 4), both enzymes showed higher activities in soils under patches dominated or co-dominated by resprouter species. However, the enzymes largely differed in their post-fire recovery pattern. β-glucosidase proved to be very resilient at medium term, and even increased activity as compared with pre-fire values, while acid phosphatase did not show any sing of recovery during the entire study period (three years after fire). To what extent, this sustained low activity of acid phosphatase can compromise plant recovery and to what extent it is counterbalanced by alkaline phosphatase, also involved in soil P cycling, deserve further research. Conversely to our results from Chapter 4, post-fire regeneration functional groups did not show any relevant effect on the resilience of soil enzyme activity. This can be attributed to the masking effect of drought in the case of acid phosphatase, and the positive effect of increased availability of C sources under dead seeder shrubs due to the decomposition of root biomass.

6.3. Future research

- Seeder/resprouter ratio appears to increase with increasing fire severity; several previous works have proven similar outcome from increasing fire frequency. Further research should investigate the combined effect of fire recurrence and severity in the abundance ratio of these two main functional groups.
- Relationships and trade-offs between different plant traits, particularly between post-fire regeneration traits and traits closely related to soil functions (e.g., root architecture, production of root exudates) deserve further research. This will provide additional insights about the modulating role of plant persistence traits on soil biogeochemical cycling.
- Assessment of the recovery of a large variety of soil enzyme activities, and their control factors, as a function of post-fire regeneration functional groups.
- Longer-term post-fire monitoring of soil acid phosphatase activity and further research on the role of droughts as control factor of its activity and on the consequences for plant recovery in P-limited soils.

GENERAL CONCLUSIONS

The successional stage after agricultural land abandonment in a terraced Mediterranean landscape modulates fire severity and post-fire plant recovery. Dry grasslands burned at low severity and quickly recovered after fire, while dense shrubland and pine stands burned at higher severity and re-established their cover at a lower rate.

Seven years after fire, dense gorse shrubland and pine forest resulted in similar post-fire shrubland communities, dominated by highly flammable seeder species such as *U. parviflorus* and *Cistus* species, which contributed to homogenize the landscape structure towards a more fire-prone type, and thus to increase fire hazard.

Pine stands showed the largest changes in community structure after the fire and the lowest short-term post-fire plant recovery, so pine forest can be considered the most vulnerable of the three successional stages studied, particularly if wildfires are followed by relatively dry years.

Fire severity filters plant regeneration traits, and drive the functional composition in Mediterranean shrublands, so that higher severity favours obligate-seeder functional group.

In three common Mediterranean plant communities - dry grasslands, gorse shrublands, and pine stands, the seeder/resprouter abundance ratio barely varied at low severity and rapidly increased with increasing severity, leading to a positive non-linear relationship between the relative abundance of seeder species and fire severity.

Plant structural and functional traits modulate the response of soil functions to fire disturbance in terms of resistance (the amount of change caused by fire) and resilience (the recovery capacity after fire). Soil resistance seems to be more influenced by plant structural traits related to the potential fuel consumption, while soil resilience is highly determined by the post-fire regeneration strategy of the plant species (resprouter vs. seeder).

Soil functions were more resistant and resilient in patches of resprouter species, while soil functions in patches of seeder species with high content of fine dead fuel were the least resistant.

Plant functional groups that relate to post-fire regeneration traits (i.e., obligate seeder and resprouter species) modulate the activity of soil extracellular enzymes acid phosphatase and β-glucosidase in Mediterranean fire-prone shrublands. The activity of both enzymes is enhanced under shrub patches dominated or co-dominated by resprouter species as compared with soils under seeder shrub patches and interpatch soils.

Fire reduced the activity of both acid phosphatase and β-glucosidase in the short term. However, these enzymes showed contrasting differences in resilience. β-glucosidase, a substrate-dependent enzyme that is involved in the degradation of cellulose and is mostly produced by microorganisms, particularly fungi, proved to be very resilient to fire. Conversely, acid phosphatase, which is mostly produced by plants, did not show any sign of recovery over the first three post-fire years, probably due to the combined effect of fire and post-fire drought.

Overall, the results suggest that the positive influence of resprouter shrubs on soil enzyme activity is very resistant to fire. However, contrasting responses to fire and drought disturbances between the various enzyme types could greatly alter nutrient cycling dynamics.

References

References

Ajwa H.A., Dell C.J., Rice C.W. 1999. Changes in enzyme activities and microbial biomass of tallgrass prairie soil as related to burning and nitrogen fertilization. Soil Biology and Biochemistry 31(5), 769-777.

Alessio G.A., Peñuelas J., De Lillis M., Llusià J. 2008b. Implications of foliar terpene content and hydration on leaf flammability of *Quercus ilex* and *Pinus halepensis*. Plant Biology 10, 123-128.

Alessio G., Peñuelas J., Llusià J., Ogaya R., Estiarte M., De Lillis M. 2008a. Influence of water and terpenes on flammability in some dominant Mediterranean species. International Journal of Wildland Fire 17, 274-286.

Allison S.D., Vitousek P.M. 2005. Responses of extracellular enzymes to simple and complex nutrient inputs. Soil Biology and Biochemistry 37(5), 937-944.

Anderson H.E. 1970. Forest fuel ignitability. Fire Technology 6, 312-319.

Arianoutsou M., Ne'eman G. 2000. Postfire regeneration of natural *Pinus halepensis* forests in the east Mediterranean Basin. In 'Ecology, Biogeography and Management of *Pinus halepensis* and *P. brutia* Forest Ecosystems in the Mediterranean Basin'. Eds G Neeman, L Trabaud, Backhuys Publishers: Leiden, the Netherlands, pp. 269-290.

Armour C.D., Bunting S.C., Neuenschwander L.F. 1984. Fire intensity effects on the understory in Ponderosa Pine Forests. Journal of range management 37(l), 44-49.

Arnan X., Rodrigo A., Retana J. 2007. Post-fire regeneration of Mediterranean plant communities at a regional scale is dependent on vegetation type and dryness. Journal of Vegetation Science 18, 111-122.

Aulen M., Shipley B., Bradley R. 2012. Prediction of in situ root decomposition rates in an interspecific context from chemical and morphological traits. Annals of botany 109(1), 287-297.

Baeza M.J., Santana V.M., Pausas J.G., Vallejo R. 2011. Successional trends in standing dead biomass in Mediterranean basin species. Journal of Vegetation Science 22(3), 467-474.

Baeza M.J., Roy J. 2008. Germination of an obligate seeder (*Ulex parviflorus*) and consequences for wildfire management. Forest Ecology and Management 256, 685-693.

Baeza M.J., Valdecantos A., Alloza J.A., Vallejo R. 2007. Human disturbance and environmental factors as drivers of long-term post-fire regeneration patterns in Mediterranean forests. Journal of Vegetation Science 18(2), 243-252.

Baeza M.J., Vallejo R. 2006. Ecological mechanisms involved in dormancy breakage in *Ulex parviflorus* seeds. Plant Ecology. doi: 10.1007/s11258-005-9016-0

Baeza M.J., Raventós J., Escarré A., Vallejo R. 2006. Fire risk and vegetation structural dynamics in Mediterranean shrubland. Plant Ecology 187, 189-201

Baeza M.J., De Luis M., Raventós J., Escarré A. 2002. Factors influencing fire behaviour in shrubland of different stand ages and the implications for using prescribed burning to reduce wildfire risk. Journal of Environmental Management 65, 199-208.

Banning N.C., Murphy D.V. 2008. Effect of heat-induced disturbance on microbial biomass and activity in forest soil and the relationship between disturbance effects and microbial community structure. Applied Soil Ecology 40(1), 109-119.

Bárcenas-Moreno G., García-Orenes F., Mataix-Beneyto J., Bååth E. 2014. Plant species influence on soil microbial short-term response after fire simulation. Plant and Soil 374(1-2), 701-713.

Bastida F., Talavera S. 2002. Temporal and spatial patterns of seed dispersal in two *Cistus* species (Cistaceae). Annals of Botany 89(4), 427-434.

Begon M., Harper J.L., Townsend C.R. 1986. Ecology: Individuals, Populations, and Communities. Sinauer Associates, Sunderland, MA, USA.

Behm A.L., Duryea M.L., Long A.J., Zipperer W.C. 2004. Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland–urban interface. International Journal of Wildland Fire 13, 355-365.

Bell D.T. 2001. Ecological Response Syndromes in the Flora of Southwestern Western Australia: Fire resprouters versus reseeders. The Botanical review 67(4), 417-440.

Bellingham P.J., Sparrow A.D. 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89(2), 409-416.

Bernhardt E.L., Hollingsworth T.N., Chapin III F.S. 2011. Fire severity mediates climate driven shifts in understory composition of black spruce stands in interior Alaska. Journal of Vegetation Science 22, 32–44.

Bodí M.B., Muñoz-Santa I., Armero C., Doerr S.H., Mataix-Solera J., Cerdà A. 2013. Spatial and temporal variations of water repellency and probability of its occurrence in calcareous Mediterranean rangeland soils affected by fires. Catena 108, 14-25.

Boerner R.E.J., Giai C., Huang J., Miesel J.R. 2008. Initial effects of fire and mechanical thinning on soil enzyme activity and nitrogen transformations in eight North American forest ecosystems. Soil Biology and Biochemistry 40, 3076-3085.

Boerner R.E.J., Brinkman J.A., 2003. Fire frequency and soil enzyme activity in southern Ohio oak–hickory forests. Applied Soil Ecology 23(2), 137-146.

Bond W.J., Keeley J.E. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution 20(7), 387-394.

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

Bond W.J., Midgley J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16(1), 45-51.

Bond W.J., Van Wilgen B.W. 1996. Fire and Plants (Population and Community Biology Series 14).

Bond W.J., Midgley J.J. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. Oikos 73, 79-85.

Bradshaw S.D., Dixon K.W., Hopper S.D., Lambers H., Turner S.R. 2011. Little evidence for fire-adapted plant traits in Mediterranean climate regions. Trends in plant science 16(2), 69-76.

Brais S., David P., Ouimet R. 2000. Impacts of wild fire severity and salvage harvesting on the nutrient balance of jack pine and black spruce boreal stands. Forest Ecology and Management 137, 231-243.

Buhk C., Meyn A., Jentsch A. 2007. The challenge of plant regeneration after fire in the Mediterranean Basin: scientific gaps in our knowledge on plant strategies and evolution of traits. Plant Ecology 192, 1-19.

Byram G.M. 1959. Combustion of forest fuels. In KP Davis (ed.), Forest Fire: Control and Use. McGraw-Hill, New York, pp. 61-89.

Calvo L., Santalla S., Marcos E., Valbuena L., Tárrega R., Luis E. 2003. Regeneration after wildfire in communities dominated by *Pinus pinaster*, an obligate seeder, and in others dominated by *Quercus pyrenaica*, a typical resprouter. Forest Ecology and Management 184(1), 209-223.

Campo J., Andreu V., Gimeno-García E., González O., Rubio J.L. 2006. Occurrence of soil erosion after repeated experimental fires in a Mediterranean Environment. Geomorphology 82, 376-87.

Canadell J., Lloret F., López-Soria L. 1991. Resprouting vigour of two mediterranean shrub species after experimental fire treatments. Vegetatio 95, 119-126.

Capitanio R., Carcaillet C. 2008. Post-fire Mediterranean vegetation dynamics and diversity: a discussion of succession models. Forest Ecology and Management 255, 431-439.

Carrión J.S., Sánchez-Gómez P., Mota J.F., Yll R., Chaín C. 2003. Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, southern Spain. The Holocene 13(6), 839-849.

Caturla R.N., Raventós J., Guàrdia R., Vallejo R. 2000. Early post-fire regeneration dynamics of *Brachypodium retusum* Pers. (Beauv.) in old fields of the Valencia region (eastern Spain). Acta Oecologica 21(1), 1-12.

Cerdà A. 1998. Soil aggregate stability under different Mediterranean vegetation types. Catena 32, 73-86.

Certini G. 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1-10.

Céspedes B., Torres I., Luna B., Pérez B., Moreno J.M. 2012. Soil seed bank, fire season, and temporal patterns of germination in a seeder-dominated Mediterranean shrubland. Plant Ecology 213(3), 383-393.

Chaer G., Fernandes M., Myrold D., Bottomley P. 2009. Comparative resistance and resilience of soil microbial communities and enzyme activities in adjacent native forest and agricultural soils. Microbial ecology 58(2), 414-424.

Chappell C.B., Agee J.K. 1996. Fire severity and tree seedling establishment in *Abies magnifica* forests, southern cascades, Oregon. Ecological Applications 6 (2), 628-640.

Clarke P.J., Lawes M.J., Midgley J.J., Lamont B.B., Ojeda F., Burrows G.E., Knox K.J.E. 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytologist 197(1), 19-35.

Cornelissen J.H.C., Lavorel S., Garnier E., Díaz S., Buchmann N., Gurvich D.E., Reich P.B., ter Steege H., Morgan H.D., van der Heijden M.G.A., Pausas J.G., Poorter H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51, 335-380.

Creech M.N., Kirkman L.K., Morris L.A. 2012. Alteration and recovery of Slash Pile burn sites in the restoration of a fire-maintained ecosystem. Restoration Ecology 20 (4), 505-516.

Crotteau J.S., Varner III M., Ritchie M.W. 2013. Post-fire regeneration across a fire severity gradient in the southern Cascades. Forest Ecology and Management 287, 103-112.

Daskalakou E.N., Thanos C.A. 2004. Post-fire regeneration of Aleppo pine-the temporal pattern of seedling recruitment. Plant Ecology 171, 81-89.

De Deyn G.B., Quirk H., Yi Z., Oakley S., Ostle N.J., Bardgett R.D. 2009. Vegetation composition promotes carbon and nitrogen storage in model grassland communities of contrasting soil fertility. Journal of Ecology 97(5), 864-875.

De Luís M., Raventós J., González-Hidalgo J.C. 2006. Post-fire vegetation succession in Mediterranean gorse shrublands. Acta Oecologica 30(1), 54-61.

De Luís M., Raventós J., Cortina J., González-Hidalgo J.C., Sánchez J.R. 2004. Fire and torrential rainfall: effects on the perennial grass *Brachypodium retusum*. Plant Ecology 173, 225-232.

De Vries F.T., Liiri M.E., Bjørnlund L., Setälä H.M., Christensen S., Bardgett R.D. 2012. Legacy effects of drought on plant growth and the soil food web. Oecologia 170(3), 821-833.

DeBano L.F. 2000. The role of fire and soil heating on water repellency in wildland environments: a review. Journal of Hydrology 231, 195-206.

Debano L.F., Neary D., Ffolliott P. 1998. 'Fire's effects on ecosystems.' John Wiley & Sons Inc.: New York.

Debussche M., Lepart J., Dervieux A. 1999. Mediterranean landscape changes: evidence from old postcards. Global Ecology and Biogeography 8, 3-15.

Delitti W., Ferran A., Trabaud L. Vallejo R. 2005. Effects of fire recurrence in *Quercus coccifera* L. shrublands of the Valencia Region (Spain): I. plant composition and productivity. Plant Ecology 177, 57-70.

Díaz-Delgado R., Lloret F., Pons X. 2003. Influence of fire severity on plant regeneration by means of remote sensing imagery. International Journal of Remote Sensing 24 (8), 1751-1763.

Díaz-Delgado R., Lloret F., Pons X., Terradas J. 2002. Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. Ecology 83(8), 2293-2303.

Dick W.A., Tabatabai M.A. 1992. Significance and potential uses of soil enzymes. In: Metting Jr., F.B. (Ed.). Soil Microbial Ecology. Marcel Dekker, New York, NY, USA, pp. 95-127.

Dimitrakopoulos A.P. 2001. A statistical classification of Mediterranean species based on their flammability components. International Journal of Wildland Fire 10, 113-118.

Dimitrakopoulos A.P., Panov P.I. 2001. Pyric properties of some dominant Mediterranean vegetation species. International Journal of Wildland Fire 10(1), 23-27.

Dimitrakopoulos A.P., Papaioannou K.K. 2001. Flammability assessment of Mediterranean forest fuels. Fire Technology 37, 143-152.

Dimitrakopoulos P.G., Siamantziouras A.D., Galanidis A., Mprezetou I., Troumbis A.Y. 2006. The interactive effects of fire and diversity on short-term responses of ecosystem processes in experimental Mediterranean grasslands. Environmental Management 37 (6), 826-839.

Driessen P., Deckers J., Spaargaren O., Nachtergaele F. 2001. 'Lecture notes on the major soils of the world.' (Food and Agriculture Organization of the United Nations: Rome).

Dube O.P. 2009. Linking fire and climate: interactions with land use, vegetation, and soil. Current Opinion in Environmental Sustainability 1(2), 161-169.

Duguy B., Vallejo R. 2008. Land-use and fire history effects on post-fire vegetation dynamics in eastern Spain. Journal of Vegetation Science 19(1), 97-108.

Duguy B., Rovira P., Vallejo R. 2007. Land-use history and fire effects on soil fertility in eastern Spain. European journal of soil science 58(1), 83-91.

Ehrenfeld J.G., Ravit B., Elgersma K. 2005. Feedback in the plant-soil system. Annual Review of Environmental Resources 30, 75-115.

Elvira-Martín L.M., Hernando-Lara C. 1989. Inflamabilidad y energía de las especies de sotobosque. Instituto Nacional de Investigaciones Agrarias (Ministerio de Agricultura, Pesca y Alimentación: Madrid). Colección Monografías INIA, no 68.

Enright N.J., Fontaine J.B., Westcott V.C., Lade J.C., Miller B.P. 2011. Fire interval effects on persistence of resprouter species in Mediterranean-type shrublands. Plant Ecology 212(12), 2071-2083.

Eugenio M., Lloret F., Alcañiz J.M. 2006b. Regional patterns of fire recurrence effects on calcareous soils of Mediterranean *Pinus halepensis* communities. Forest Ecology and Management 221(1), 313-318.

Eugenio M., Verkaik I., Lloret F., Espelta J.M. 2006a. Recruitment and growth decline in *Pinus halepensis* populations after recurrent wildfires in Catalonia (NE Iberian Peninsula). Forest Ecology and Management 231, 47-54.

Eviner V.T. 2004. Plant traits that influence ecosystem processes vary independently among species. Ecology 85(8), 2215-2229.

Eviner V.T., Chapin III F.S. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. Annual Review of Ecology, Evolution, and Systematics 34, 455-485.

Fernandes P.M., Cruz M.G. 2012. Plant flammability experiments offer limited insight into vegetation–fire dynamics interactions. New Phytologist 194(3), 606-609.

Fernández-Ales R., Martin A., Ortega F., Ales E.E. 1992. Recent changes in landscape structure and function in a Mediterranean region in SW Spain (1950-1984). Landscape Ecology 7, 3-18.

Ferrandis P., Herranz J.M., Martínez-Sánchez J.J. 1999. Effect of fire on hard-coated *Cistaceae* seed banks and its influence on techniques for quantifying seed banks. Plant Ecology 144(1), 103-114.

Ferrandis P., Herranz J.M., Martínez-Sánchez J.J. 1996. The role of seed bank in the early stages of plant recovery after fire in a *Pinus pinaster* forest in SE Spain. International Journal of Wildland Fire 6 (1), 31–35.

Fioretto A., Papa S., Pellegrino A., Ferrigno A. 2009. Microbial activities in soils of a Mediterranean ecosystem in different successional stages. Soil Biology and Biochemistry 41(10), 2061-2068.

Fioretto A., Papa S., Pellegrino A. 2005. Effects of fire on soil respiration, ATP content and enzyme activities in Mediterranean maquis. Applied Vegetation Science 8, 13-20.

Fioretto A., Papa S., Curcio E., Sorrentino G., Fuggi A. 2000. Enzyme dynamics on decomposing leaf litter of *Cistus incanus* and *Myrtus communis* in a Mediterranean ecosystem. Soil Biology and Biochemistry 32(13), 1847-1855.

Fontúrbel M.T., Barreiro A., Vega J.A., Martín A., Jiménez E., Carballas T., Fernández C., Díaz-Raviña M. 2012. Effects of an experimental fire and post-fire stabilization treatments on soil microbial communities. Geoderma 191, 51-60.

Franklin J., Coulter C.L., Rey S.J. 2004. Change over 70 years in a southern California chaparral community related to fire history. Journal of Vegetation Science 15(5), 701-710.

García C., Roldan A., Hernández T. 2005. Ability of different plant species to promote microbiological processes in semiarid soil. Geoderma 124, 193-202.

García-Ruiz J.M., Lana-Renault N. 2011. Hydrological and erosive consequences of farmland abandonment in Europe, with special reference to the Mediterranean region - A review. Agriculture Ecosystems and Environment 140, 317-338.

Geisseler D., Horwath W.R., 2009. Relationship between carbon and nitrogen availability and extracellular enzyme activities in soil. Pedobiologia 53(1), 87-98.

Gimeno-García E., Pascual J.A., Llovet J. 2011. Water repellency and moisture content spatial variations under *Rosmarinus officinalis* and *Quercus coccifera* in a Mediterranean burned soil. Catena 85, 48-57.

Gimeno-García E., Andreu V., Rubio J.L. 2004. Spatial patterns of soil temperatures during experimental fires. Geoderma 118, 17-38.

Gimeno-García E., Andreu V., Rubio J.L. 2000. Changes in organic matter, nitrogen, phosphorus and cations as a result of fire and water erosion in a Mediterranean landscape. European Journal of Soil Science 51, 201-210.

Giorgi F., Lionello P. 2008. Climate change projections for the Mediterranean region. Global and Planetary Change 63(2-3), 90-104.

Giovannini G., Vallejo R., Luchesi S., Bautista S., Ciompi S., Llovet J. 2001. Effects of land use and eventual fire on soil erodibility in dry Mediterranean conditions. Forest Ecology and Management 147, 15-23.

Giovannini G. 1994. The effect of fire on soil quality. In: Sala M., Rubio J.L. (Eds.), Soil Erosion and Degradation as a Consequence of Forest Fires. Geoforma Ediciones, Logroño, pp. 15-29.

Goberna M., García C., Insam H., Hernández M.T., Verdú M. 2012. Burning fire-prone Mediterranean shrublands: immediate changes in soil microbial community structure and ecosystem functions. Microbial ecology 64(1), 242-255.

Goberna M., Pascual J.A., García C., Sánchez J. 2007. Do plant clumps constitute microbial hotspots in semiarid Mediterranean patchy landscapes?. Soil Biology and Biochemistry 39(5), 1047-1054.

González-Pelayo O., Andreu V., Gimeno-García E., Campo J., Rubio J.L. 2010. Rainfall influence on plot-scale runoff and soil loss from repeated burning in a Mediterranean-shrub ecosystem, Valencia, Spain. Geomorphology 118(3), 444-452.

González-Pelayo O., Andreu V., Campo J., Gimeno-García E., Rubio J.L. 2006. Hydrological properties of a Mediterranean soil burned with different fire intensities. Catena 68 (2–3), 186-193.

Goubitz S., Nathan R., Roitemberg R., Shmida A., Ne'eman G. 2004. Canopy seed bank structure in relation to: fire, tree size and density. Plant Ecology 173(2), 191-201.

Griffiths B.S., Philippot L. 2012. Insights into the resistance and resilience of the soil microbial community. Federation of European Microbiological Societies (FEMS) microbiology Reviews, 1-18.

Griffiths B.S., Bonkowski M., Roy J., Ritz K. 2001. Functional stability, substrate utilisation and biological indicators of soils following environmental impacts. Applied Soil Ecology 16(1), 49-61.

Grigulis K., Lavorel S., Davies I.D., Dossantos A., Lloret F., Vilà M. 2005. Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, *Ampelodesmos mauritanica* in Catalan shrublands. Global Change Biology 11, 1042-1053.

Grimm V., Wissel C. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109(3), 323-334.

Guénon R., Gros R. 2013. Frequent-wildfires with shortened time-since-fire affect soil microbial functional stability to drying and rewetting events. Soil Biology and Biochemistry 57, 663-674.

Guénon R., Vennetier M., Dupuy N., Roussos S., Pailler A., Gros R. 2011. Trends in recovery of Mediterranean soil chemical properties and microbial activities after infrequent and frequent wildfires. Land Degradation and Development 24(2), 115-128.

Guerrero C., Mataix-Solera J., Arcenegui V., Mataix-Beneyto J., Gómez I. 2007. Near-infrared spectroscopy to estimate the maximum temperatures reached on burned soils. Soil Science Society of America Journal 71(3), 1029-1037.

Guerrero-Campo J., Palacio S., Pérez-Rontome C., Montserrat-Martí G. 2006. Effect of root system morphology on root-sprouting and shoot-rooting abilities in 123 plant species from eroded lands in north-east Spain. Annals of Botany 98(2), 439-447.

Guijarro M., Hernando C., Diez C., Martínez E., Madrigal J., Lampin-Cabaret C., Blanc L., Colin P.Y., Pérez-Gorostiaga P., Vega J.A., Fonturbel M.T. 2002. Flammability of some fuel beds common in the South-European ecosystems. Forest Fire Research and Wildland Fire Safety, Viegas (ed.), Millpress, Rotterdam.

Gunderson L.H. 2000. Ecological Resilience-In Theory and Application. Annual Review of Ecology and Systematics 3, 425-439.

Halpern C.B. 1988. Early Successional Pathways and the Resistance and Resilience of Forest Communities. Ecology 69 (6), 1703-1715.

Hart S.C., DeLuca T.H., Newman G.S., MacKenzie M.D., Boyle S.I. 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. Forest Ecology and Management 220(1), 166-184.

Hernández T., Garcia C., Reinhardt I. 1997. Short-term effect of wildfire on the chemical, biochemical and microbiological properties of Mediterranean pine forest soils. Biology and Fertility of Soils 25(2), 109-116.

Herranz J.M., Ferrandis P., Martínez-Sánchez J.J. 1998. Influence of heat on seed germination of seven Mediterranean *Leguminosae* species. Plant Ecology 136(1), 95-103.

Herrick J.E. 2000 Soil quality: an indicator of sustainable land management? Applied Soil Ecology 15, 75-83.

Hinojosa M.B., Parra A., Ramírez D. A., Carreira J.A., García-Ruiz R., Moreno J.M. 2012. Effects of drought on soil phosphorus availability and fluxes in a burned Mediterranean shrubland. Geoderma 191, 61-69.

Hobbie S.E. 1992. Effects of plant species on nutrient cycling. Trends in ecology and evolution 7(10), 336-339.

Holling C.S. 1996. Engineering resilience versus ecological resilience. In P. C. Schulze (ed.), Engineering within ecological constraints. National Academy Press, Washington D.C., USA, pp. 31-43.

Holling C.S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematic 4, 1-23.

Hollingsworth T.N., Johnstone J.F., Bernhardt E.L., Chapin III F.S. 2013. Fire Severity Filters Regeneration Traits to Shape Community Assembly in Alaska’s Boreal Forest. PloS one 8(2), e56033.

Karaca A., Cetin S.C., Turgay O.C., Kizilkaya R. 2011. Soil enzymes as indication of soil quality. In Soil Enzymology. Springer Berlin Heidelberg, pp. 119-148.

Kazanis D., Arianoutsou M. 2004. Factors determining low Mediterranean ecosystems resilience to fire: the case of *Pinus halepensis* forests. In Proceedings of the 10th MEDECOS Conference (Vol. 25).

Keeley J.E., Pausas J.G., Rundel P.W., Bond W. J., Bradstock R.A. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in plant science 16(8), 406-411.

Keeley J.E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18, 116-126.

Keeley J.E., Brennan T., Pfaff, A.H. 2008. Fire severity and ecosytem responses following crown fires in California shrublands. Ecological Applications 18(6), 1530-1546.

Keeley J.E., Fotheringham C.J., Baer-Keeley M. 2006. Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. Ecological Monographs 76(2), 235-255.

Keeley J.E., Fotheringham C.J., Baer-Keeley M. 2005. Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. Ecological Applications 15(5), 1515-1534.

Keeley J.E., Fotheringham C.J. 2000. Role of fire in regeneration from seed. Seeds: The ecology of regeneration in plant communities 2, 311-330.

Keeley J.E., Zedler P.H. 1998. Evolution of life histories in *Pinus*. In Richardson DM, ed. Ecology and Biogeography of *Pinus*. Cambridge, pp. 219-250.

Keeley J.E. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68(2), 434- 443.

Keeley J.E. 1986. Resilience of Mediterranean shrub communities to fires. In: Dell B., Hopkins A.J.B. & Lamont B.B. (eds.) Resilience in Mediterranean-type ecosystems. Junk, Dordrecht, The Netherlands, pp. 95-112.

Kent M., Coker P. 1992. 'Vegetation description and analysis: a practical approach.' Belhaven Press, London.

Klimešová J., Klimeš L. 2007. Bud banks and their role in vegetative regeneration - A literature review and proposal for simple classification and assessment. Perspectives in Plant Ecology, Evolution and Systematics 8(3), 115-129.

Knicker H. 2007. How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. Biogeochemistry 85, 91-118.

Knops J.M.H., Bradley K.L., Wedin D.A. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. Ecology Letters 5, 454–466.

Knox K.J.E., Clarke P.J. 2005. Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. Functional Ecology 19(4), 690-698.

Lambers H., Mougel C., Jaillard B., Hinsinger P. 2009. Plant-microbe-soil interactions in the rhizosphere: an evolutionary perspective. Plant and Soil 321(1-2), 83-115.

Lavorel S., Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16(5), 545-556.

Lavorel S. 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. Diversity and Distributions 5, 3-13.

Lledó M.J. 1982 unpublished data (University of Alicante: Alicante, Spain).

Lloret F., Estevan H., Vayreda J., Terradas J. 2005. Fire regenerative syndromes of forest woody species across fire and climatic gradients. Oecologia 146(3), 461-468.

Lloret F., Vilà M. 2003. Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands. Journal of Vegetation Science 14, 387-398.

Lloret F., Pausas J.G., Vilá M. 2003. Responses of Mediterranean plant species to different fire frequencies in Garraf Natural Park (Catalonia, Spain): field observations and modelling predictions. Plant Ecology 167, 223-235.

Lloret F., Calvo E., Pons X., Díaz-Delgado R. 2002. Wildfires and landscape patterns in the Eastern Iberian Peninsula. Landscape Ecology 17, 745-759.

Lloret F., López-Soria L. 1993. Resprouting of *Erica multiflora* after experimental fire treatments. Journal of Vegetation Science 4(3), 367-374.

Llovet J., Ruiz-Valera M., Josa R., Vallejo R. 2009. Soil responses to fire in Mediterranean forest landscapes in relation to the previous stage of land abandonment. International Journal of Wildland Fire 18, 222-232.

Llovet J. 2005. 'Degradación del suelo posterior al fuego en condiciones mediterráneas. Identificación de factores de riesgo.' Ph.D. Thesis. (University of Alicante: Alicante, Spain).

Loepfe L., Martinez-Vilalta J., Oliveres J., Piñol J., Lloret F. 2010. Feedbacks between fuel reduction and landscape homogenisation determine fire regimes in three Mediterranean areas. Forest Ecology and Management 259, 2366-2374.

López-Poma R., Bautista S. Fire severity modulates the seeder/resprouter ratio in burned Mediterranean plant communities. (*in review*).

López-Poma R., Orr J., Bautista S. Successional stage after land abandonment modulates fire severity and post-fire recovery in a Mediterranean mountain landscape. (*in press*).

López-Poma R., Mayor A.G., Santana V., Baeza J., Bautista S. Plant traits mediate the resistance and resilience of soil functions to fire in Mediterranean shrublands. (*in review*)

López-Soria L., Castell C. 1992. Comparative genet survival after fire in woody Mediterranean species. Oecologia 91, 493-499.

MacDonald D., Crabtree J.R., Wiesinger G., Dax T., Stamou N., Fleury P., Gutierrez Lazpita J., Gibon A. 2000. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. Journal of Environmental Management 59, 47-69.

Maestre F.T., Puche M.D. 2009. Indices based on surface indicators predict soil functioning in Mediterranean semi-arid steppes. Applied Soil Ecology 41(3), 342-350.

Maestre F.T., Cortina J. 2003. Small-scale spatial variation in soil CO_2 efflux in a Mediterranean semiarid steppe. Applied Soil Ecology 23(3), 199-209.

Maia P., Pausas J., Arcenegui V., Guerrero C., Pérez-Bejarano A., Mataix-Solera J., Varela M.E.T., Fernandes I., Pedrosa E.T., Keizer J.J. 2012. Wildfire effects on the soil seed bank of a maritime pine stand – the importance of fire severity. Geoderma 191, 80-88

Malak D.A., Pausas J.G. 2006. Fire regime and post-fire Normalized Difference Vegetation Index changes in the eastern Iberian peninsula (Mediterranean basin). International Journal of Wildland Fire 15(3), 407-413.

Malanson G.P., Trabaud L. 1987. Ordination analysis of components of resilience of *Quercus coccifera* garrigue. Ecology 68, 463-472.

Malkinson D., Wittenberg L., Beeri O., Barzilai R. 2011. Effects of repeated fires on the structure, composition, and dynamics of Mediterranean maquis: Short-and long-term perspectives. Ecosystems 14(3), 478-488.

Marqués M.A., Mora E. 1992. The influence of aspect on runoff and soil loss in a Mediterranean burnt forest (Spain). Catena 19, 333-344.

Mataix-Solera J., Arcenegui V., Guerrero C., Mayoral A.M., Morales J., González J., García-Orenes F., Gómez I. 2007. Water repellency under different plant species in a calcareous forest soil in a semiarid Mediterranean environment. Hydrological Processes 21 (17), 2300-2309.

Mayor A.G., Bautista S. 2012. Multi-scale evaluation of soil functional indicators for the assessment of water and soil retention in Mediterranean semiarid landscapes. Ecological Indicators 20, 332-336.

Mayor A.G., Bautista S., Bellot J. 2009. Factors and interactions controlling infiltration, runoff, and soil loss at the microscale in a patchy Mediterranean semiarid landscape. Earth Surface Processes and Landforms 34(12), 1702-1711.

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

Mebius L.J. 1960. A rapid method for the determination of organic carbon in soil. Analytica Chimica Acta 22, 120-124.

Miller C., Urban D.L. 2000. Connectivity of forest fuels and surface fire regimes. Landscape Ecology 15, 145-154.

Moreira B., Tormo J., Pausas J.G. 2012. To resprout or not to resprout: factors driving intraspecific variability in resprouting. Oikos 121(10), 1577-1584.

Moreira B., Tormo J., Estrelles E., Pausas J.G. 2010. Disentangling the role of heat and smoke as germination cues in Mediterranean Basin flora. Annals of Botany 105, 627-635.

Moreira F., Viedma O., Arianoutsou M., Curt T., Koutsias N., Rigolot E., Bilgili E. 2011. Landscape-wildfire interactions in southern Europe: implications for landscape management. Journal of Environmental Management 92(10), 2389-2402.

Moreira F., Rego F.C., Ferreira P.G. 2001. Temporal (1958-1995) pattern of change in a cultural landscape of northwestern Portugal: implications for fire occurrence. Landscape Ecology 16(6), 557-567.

Moreno J.M., Oechel W.C. 1994. Fire intensity as a determinant factor of post-fire plant recovery in southern California chaparral. In: Fire in the Environment: The Ecological, Atmospheric, and Climatic Importance of Vegetation. Wiley, New York. pp. 26-45.

Moreno J.M., Oechel W.C. 1991a. Fire intensity effects on germination of shrubs and herbs in Southern California Chaparral. Ecology 72, 1993-2004.

Moreno J.M., Oechel W.C. 1991b. Fire intensity and herbivory effects on postfire resprouting of *Adenostoma-fasciculatum* in Southern California chaparral. Oecologia 85, 429-433.

Moreno J.M., Oechel W.C. 1989 A simple method for estimating fire intensity after a burn in California chaparral. Acta Oecológica 10(1), 57-68.

Mouillot F., Ratte J.P., Joffre R., Moreno J.M., Rambal S. 2003. Some determinants of the spatio-temporal fire cycle in a Mediterranean landscape (Corsica, France). Landscape Ecology 18(7), 665-674.

Mouillot F., Rambal S., Joffre R. 2002. Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. Global Change Biology 8(5), 423-437.

Moya D., De las Heras J., Salvatore R., Valero E., Leone V. 2013. Fire intensity and serotiny: response of germination and enzymatic activity in seeds of *Pinus halepensis* Mill. from southern Italy. Annals of forest science 70(1), 49-59.

Naveh Z. 1975. The evolutionary significance of fire in the Mediterranean region. Vegetatio 29(3), 199-208.

Ne’eman G., Goubitz S., Nathan R. 2004. Reproductive traits of *Pinus halepensis* in the light of fire - a critical review. Plant Ecology 171, 69-79.

Ne'eman G., Fotheringham C.J., Keeley J.E. 1999. Patch to landscape patterns in post fire recruitment of a serotinous conifer. Plant ecology 145(2), 235-242.

Neary D.G., Klopatek C.C., DeBano L.F., Ffolliott P.F. 1999. Fire effects on below-ground sustainability: a review and synthesis. Forest Ecology and Management 122, 51-71.

Northup R.R., Dahlgren R.A., McColl, J.G. 1998. Polyphenols as regulators of plant-litter-soil interactions in northern California's pygmy forest: a positive feedback? Biogeochemistry 42(1-2), 189-220.

Nuñez-Regueira L., Rodriguez-Anon J.A., Proupin J., Mourino B., Artiaga-Díaz R. 2005. Energetic study of residual forest biomass using calorimetry and thermal analysis. Journal of Thermal analysis and calorimetry 80, 457-464.

Núñez-Regueira L., Proupín Castiñeiras J., Rodríguez Añon J.A. 1996. Calorific values and flammability of forest species in Galicia. Bioresource Technology 57, 283-289.

Odion D.C., Davies F.W. 2000. Fire, soil heating and the formation of vegetation patterns in chaparral. Ecological Monographs 70, 149-69.

Oksanen J., Kindt R., Legendre P., O’Hara B., Henry M., Stevens H. 2007. Vegan: Community Ecology Package. R package version 1.8-7. http://cran.r-project.org, http://cc.oulu. fi/fi/~jarioksa/. Accessed 12 September 2007.

Orians G.H., Milewski A.V. 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. Biological Reviews 82(3), 393-423.

Orwin K.H., Wardle D.A. 2005. Plant species composition effects on belowground properties and the resistance and resilience of the soil microflora to a drying disturbance. Plant and Soil 278, 205-221.

Orwin K.H., Wardle D.A. 2004. New indices for quantifying the resistance and resilience of soil biota to exogenous disturbances. Soil Biology and Biochemistry 36, 1907-1912.

Papa S., Pellegrino A., Ferrigno A., Fioretto A. 2007. Microbial activity of soils with different plant cover in Mediterranean area. Studi Tridentini di Science Naturali, Acta Biologica 83, 227-231.

Pate J.S., Froend R.H., Bowen B.J., Hansen A., Kuo J. 1990. Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of SW Australia. Annals of Botany 65(6), 585-601.

Paula S., Pausas J.G. 2011. Root traits explain different foraging strategies between resprouting life histories. Oecologia 165(2), 321-331.

Paula S., Ojeda F. 2009. Belowground starch consumption after recurrent severe disturbance in three resprouter species of the genus *Erica*. Botany 87(3), 253-259.

Paula S., Arianoutsou M., Kazanis D., Tavsanoglu Ç., Lloret F., Buhk C., Pausas J.G. 2009. Fire-related traits for plant species of the Mediterranean Basin: Ecological Archives E090-094. Ecology 90(5), 1420-1420.

Paula S., Pausas J.G. 2008. Burning seeds: germinative response to heat treatments in relation to resprouting ability. Journal of Ecology 96(3), 543-552.

Pausas J.G., Fernández-Muñoz S. 2012. Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. Climatic Change 110, 215-226.

Pausas J.G., Keeley J.E. 2009. A burning story: the role of fire in the history of life. BioScience 59(7), 593-601.

Pausas J.G., Verdú M. 2008. Fire reduces morphospace occupation in plant communities. Ecology 89(8), 2181-2186.

Pausas J.G., Llovet J., Rodrigo A., Vallejo R. 2008. Are wildfires a disaster in the Mediterranean basin?–A review. International Journal of Wildland Fire 17(6), 713-723.

Pausas J.G., Bradstock R.A. 2007. Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-east Australia. Global Ecology and Biogeography 16(3), 330-340.

Pausas J.G., Verdú M. 2005. Plant persistence traits in fire-prone ecosystems of the Mediterranean basin: a phylogenetic approach. Oikos 109(1), 196-202.

Pausas J.G. 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). Climatic change 63(3), 337-350.

Pausas J.G., Bradstock R.A., Keith D.A., Keeley J.E. 2004a. Plant functional traits in relation to fire in crown-fire ecosystems. Ecology 85, 1085-1100.

Pausas J.G., Bladé C., Valdecantos A., Seva J.P., Fuentes D., Alloza J.A., Vilagrosa A., Bautista S., Cortina J., Vallejo R. 2004b. Pines and oaks in the restoration of Mediterranean landscapes: New perspectives for an old practice – A review. Plant Ecology 171, 209-220.

Pausas J.G., Ouadah N., Ferran A., Gimeno T., Vallejo R. 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, eastern Iberian Peninsula. Plant Ecology 169, 205-213.

Pausas J.G. 1999. Mediterranean vegetation dynamics: modelling problems and functional types. Plant Ecology 140(1), 27-39.

Pausas J.G., Carbó E.N., Caturla R., Gil J.M., Vallejo R. 1999. Post-fire regeneration patterns in the eastern Iberian Peninsula. Acta Oecologica 20(5), 499-508.

Pausas J.G. 1997. Resprouting of *Quercus suber* in NE Spain after fire. Journal of Vegetation Science 8(5), 703-706.

Pereira J.M., Sequeira N.M., Carreiras J.M. 1995. Structural properties and dimensional relations of some Mediterranean shrub fuels. International Journal of Wildland Fire 5(1), 35-42.

Pérez B., Cruz A., Fernández-Gonzalez F., Moreno J.M. 2003. Effects of recent land-use history on the postfire vegetation of uplands in Central Spain. Forest Ecology and Management 182, 273-283.

Pérez B., Moreno J.M. 1998. Methods for quantifying fire severity in shrubland-fires. Plant Ecology 139, 91-101.

Pérez-Bejarano A., Mataix-Solera J., Zornoza R., Guerrero C., Arcenegui V., Mataix-Beneyto J., Cano-Amat S. 2010. Influence of plant species on physical, chemical and biological soil properties in a Mediterranean forest soil. European Journal of Forest Research 129, 15-24.

Pimm S.L. 1984. The complexity and stability of ecosystems. Nature 307, 321-326.

Piñol J., Terradas J., Lloret F. 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. Climatic change 38(3), 345-357.

Poyatos R., Latron J., Llorens P. 2003. Land use and land cover change after agricultural abandonment. The case of a Mediterranean mountain area (Catalan Pre-Pyrenees). Mountain Research and Development 23(4), 362-368.

Proença V., Pereira H.M, Vicente L. 2010. Resistance to wildfire and early regeneration in natural broadleaved forest and pine plantation. Acta Oecologica 36, 626-633.

Puerta-Piñero C., Espelta J.M., Sánchez-Humanes B., Rodrigo A., Coll L., Brotons L. 2012. History matters: Previous land use changes determine post-fire vegetation recovery in forested Mediterranean landscapes. Forest Ecology and Management 279, 121-127.

Quintana J.R., Cruz A., Fernández-González F., Moreno J.M. 2004. Time of germination and establishment success after fire of three obligate seeders in a Mediterranean shrubland of central Spain. Journal of Biogeography 31, 241-249.

R Development Core Team (2010) 'R: a Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna, Austria) Available at www.R-project.org [Verified 15 December 2011]

Ravi S., D'Odorico P., Wang L., White C.S., Okin G.S., Macko S.A., Collins S.L. 2009. Post-fire resource redistribution in desert grasslands: a possible negative feedback on land degradation. Ecosystems 12(3), 434-444.

Reyes O., Trabaud L. 2009. Germination behaviour of 14 Mediterranean species in relation to fire factors: smoke and heat. Plant Ecology 202(1), 113-121.

Riera P., Peñuelas J., Farreras V., Estiarte M. 2007. Valuation of climate-change effects on Mediterranean shrublands. Ecological applications 17(1), 91-100.

Rodrigo A., Retana J., Picó F.X. 2004. Direct regeneration is not the only response of Mediterranean forests to large fires. Ecology 85(3), 716-729.

Romanyà J., Casals P., Vallejo R. 2001. Short-term effects of fire on soil nitrogen availability in Mediterranean grasslands and shrublands growing in old fields. Forest Ecology and Management 147, 39-53.

Ruiz-González A.D., Álvarez-González J.G. 2011. Canopy bulk density and canopy base height equations for assessing crown fire hazard in *Pinus radiata* plantations. Canadian Journal of Forest Research 41(4), 839-850.

Rutigliano F.A., D'ascoli R., Virzo De Santo A. 2004. Soil microbial metabolism and nutrient status in a Mediterranean area as affected by plant cover. Soil Biology and Biochemistry 36(11), 1719-1729.

Rydgren K., Okland R.H., Hestmark G. 2004. Disturbance Severity and Community Resilience in a Boreal Forest. Ecology 85 (7), 1906-1915.

Saá A., Trasar-Cepeda M.C., Gil-Sotres F., Carballas T. 1993. Changes in soil phosphorus and acid phosphatase activity immediately following forest fires. Soil Biology and Biochemistry 25(9), 1223-1230.

Saglam B., Kucuk O., Bilgili E., Dinc Durmaz B., Baysal I. 2008. Estimating fuel biomass of some shrub species (Maquis) in Turkey. Turkish Journal of Agriculture and Forestry 32(4), 349-356.

Santana V.M., Baeza M.J., Blanes M.C. 2012a. Clarifying the role of fire heat and daily temperature fluctuations as germination cues for Mediterranean Basin obligate seeders. Annals of Botany 111(1), 127-134.

Santana V.M., Baeza M.J., Maestre F.T. 2012b. Seedling establishment along post-fire succession in Mediterranean shrublands dominated by obligate seeders. Acta Oecologica 39, 51-60.

Santana V.M., Baeza M.J., Vallejo R. 2011. Fuel structural traits modulating soil temperatures in different species patches of Mediterranean Basin shrublands. International Journal of Wildland Fire 22, 1-10.

Santana V.M., Marrs R.H., Baeza M.J., Vallejo R. 2010. Old-field secondary succession in SE Spain: can fire divert it? Plant Ecology 211, 337-349.

Sardans J., Peñuelas J. 2013. Plant-soil interactions in Mediterranean forest and shrublands: impacts of climatic change. Plant and Soil 365, 1-33.

Sardans J., Peñuelas J. 2010. Soil enzyme activity in a Mediterranean forest after six years of drought. Soil Science Society of America Journal 74(3), 838-851.

Sardans J., Peñuelas J., Estiarte M. 2008. Changes in soil enzymes related to C and N cycle and in soil C and N content under prolonged warming and drought in a Mediterranean shrubland. Applied soil ecology 39, 223–235.

Sardans J., Peñuelas J., Estiarte M. 2006. Warming and drought alter soil phosphatase activity and soil P availability in a Mediterranean shrubland. Plant Soil 289, 227–238.

Sardans J., Peñuelas J. 2005. Drought decreases soil enzyme activity in a Mediterranean *Quercus ilex* L. forest. Soil Biology and Biochemistry 37(3), 455-461.

Saura-Mas S., Estiarte M., Peñuelas J., Lloret F. 2012. Effects of climate change on leaf litter decomposition across post-fire plant regenerative groups. Environmental and Experimental Botany 77, 274-282.

Saura-Mas S., Paula S., Pausas J.G., Lloret F. 2010. Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. International Journal of Wildland Fire 19(6), 783-794.

Saura-Mas S., Lloret F. 2009. Linking post-fire regenerative strategy and leaf nutrient content in Mediterranean woody plants. Perspectives in Plant Ecology, Evolution and Systematics 11(3), 219-229.

Saura-Mas S., Lloret F. 2007. Leaf and shoot water content and leaf dry matter content of Mediterranean woody species with different post-fire regenerative strategies. Annals of Botany 99(3), 545-554.

Schwilk D.W., Ackerly D.D. 2005. Is there a cost to resprouting? Seedling growth rate and drought tolerance in sprouting and nonsprouting *Ceanothu*s (Rhamnaceae). American Journal of Botany 92(3), 404-410.

Schwilk D.W. 2003. Flammability is a niche construction trait: canopy architecture affects fire intensity. American Naturalist 162(6), 725-733.

Schröter D., Cramer W., Leemans R., Prentice I.C., Araújo M.B., Arnell N.W., Bondeau A., Bugmann H., Carter T.R., Gracia C.A., De La Vega-Leinert A.C., Erhard M., Ewert F., Glendining M., House J.I., Kankaanpää S., Klein R.J.T., Lavorel S., Lindner M., Metzger M.J., Meyer J., Mitchell T.D., Reginster I., Rounsevell M., Sabaté S., Sitch S., Smith B., Smith J., Smith P., Sykes M.T., Thonicke K., Thuiller W., Tuck G., Zaehle S., Zierl B. 2005. Ecosystem service supply and vulnerability to global change in Europe. Science 310, 1333-1337.

Serrasolsas I., Khanna P.K. 1995. Changes in heated and autoclaved forest soils of S.E. Australia. II. Phosphorus and phosphatase activity. Biogeochemistry 29, 25-41.

Seybold C.A., Herrick J.E., Brejda J.J. 1999. Soil resilience: A fundamental component of soil quality. Soil Science 164, 224-234.

Shakesby R.A. 2011. Post-wildfire soil erosion in the Mediterranean: Review and future research directions. Earth-Science Review 105, 71-100.

Sinsabaugh R.S. 1994. Enzymic analysis of microbial pattern and process. Biology and Fertility of Soils 17(1), 69-74.

Staddon W.J., Duchesne L.C., Trevors J.T. 1998. Acid phosphatase, alkaline phosphatase and arylsulfatase activities in soils from a jack pine (*Pinus banksiana* Lamb.) ecosystem after clear-cutting, prescribed burning, and scarification. Biology and Fertility of Soils 27(1), 1-4.

Tabatabai M.A. 1994. Soil enzymes. In: Weaver R.W., Angle J.S., Bottomley P.S. (Eds.) Methods of Soil Analysis: Microbiological and Biochemical Properties. Part 2. SSSA Book Ser. 5. SSSA, Madison, WI, pp. 775-833.

Tabatabai M.A., Bremner J.M. 1969. Use of p-nitrophenol phosphate in assay of soil phosphatase activity. Soil Biology and Biochemistry 1(4), 301-307.

Tapias R., Gil L., Fuentes-Utrilla P., Pardos J.A. 2001. Canopy seed banks in Mediterranean pines of south-eastern Spain: a comparison between *Pinus halepensis* Mill*., P. pinaster* Ait*., P. nigra* Arn. and *P. pinea* L. Journal of Ecology 89(4), 629-638.

Tessler N., Wittenberg L., Malkinson D., Greenbaum N. 2008. Fire effects and short-term changes in soil water repellency - Mt. Carmel, Israel. Catena 74, 185-191.

Thanos C.A., Georghiou K., Kadis C., Pantazi C. 1992. Cistaceae: a plant family with hard seeds. Israel Journal of Botany 41, 251-263.

Tongway D.J., Hindley N.L. 2004. Landscape function analysis: procedures for monitoring and assessing landscapes. With special reference to Minesites and Rangelands. Published by CSIRO Sustainable Ecosystems.

Tormo J., Moreira B., Pausas J.G. 2013. Field evidence of smoke-stimulated seedling emergence and establishment in Mediterranean Basin flora. Journal of Vegetation Science. doi: 10.1111/jvs.12120.

Trabaud L., Galtié J. 1996. Effects of fire frequency on plant communities and landscape pattern in the Massif des Aspres (southern France). Landscape Ecology 11, 215-224.

Trabaud L. 1995. Modalités de germination des cistes et des pins méditerranéens et colonisation des sites perturbées. Revue d'Ecologie (la Terre et la Vie) 50, 3-14.

Tsitsoni T. 1997. Conditions determining natural regeneration after wildfires in the *Pinus halepensis* (Miller, 1768) forests of Kassandra Peninsula (North Greece). Forest Ecology and Management 92(1), 199-208.

Turner M.G., Romme W.H., Gardner R.H., Hargrove W.W. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecological Monographs 67(4), 411-433.

Tzanopoulos J., Mitchley J., Pantis J.D. 2007. Vegetation dynamics in abandoned crop fields on a Mediterranean island: development of succession model and estimation of disturbance thresholds. Agriculture, Ecosystems and Environment 120(2), 370-376.

Valbuena L., Nuñez R., Calvo L. 2000. The seed bank in *Pinus* stand regeneration in NW Spain after wildfire. Web Ecology 2, 22-31.

Valette J.C. 1990. Inflammabilite des especes forestières mediterranneenes: Consequences sur la combustibilite des formations forestières. Revue Forestière Francaise 42, 76-92.

Vallejo R. J.A. Alloza. 1998. The restoration of burned lands: the case of Eastern Spain. En: Large forest fires. Moreno, J.M. (ed.). Backhuys Publ., Lei den, The Netherl ands. pp: 91-108.

Van Leeuwen W.J.D., Casady G.M., Neary D.G., Bautista S., Alloza J.A., Carmel Y., Wittenberg L., Malkinson D., Orr, B.J. 2010. Monitoring post-wildfire vegetation response with remotely sensed time-series data in Spain, USA and Israel. International Journal of Wildland Fire 19(1), 75-93.

Van Ruijven J., Berendse F. 2010. Diversity enhances community recovery, but not resistance, after drought. Journal of Ecology 98(1), 81-86.

Van Wilgen B.W., Higgins K., Bellstedt D. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. Journal of Ecology 78, 210-222.

Vannière B., Colombaroli D., Chapron E., Leroux A., Tinner W., Magny M. 2008. Climate versus human-driven fire regimes in Mediterranean landscapes: the Holocene record of Lago dell'Accesa (Tuscany, Italy). Quaternary Science Reviews 27, 1181-1196.

Velázquez-Martí B., Fernández-González E., Estornell J., Ruiz L.A. 2010. Dendrometric and dasometric analysis of the bushy biomass in Mediterranean forests. Forest Ecology and Management 259(5), 875-882.

Verdú M. 2000. Ecological and evolutionary differences between Mediterranean seeders and resprouters. Journal of Vegetation Science 11(2), 265-268.

Vesk P.A., Westoby M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. Journal of Ecology 92(2), 310-320.

Viedma O., Moren, J.M., Rieiro I. 2006. Interactions between land use/land cover change, forest fires and landscape structure in Sierra de Gredos (Central Spain). Environmental Conservation 33(3), 212-222.

Vilà-Cabrera A., Saura-Mas S., Lloret F. 2008. Effects of fire frequency on species composition in a Mediterranean shrubland. Ecoscience 15(4), 519-528.

Vilagrosa A., Hernández E.I., Luis V.C., Cochard H., Pausas J.G. 2013. Physiological differences explain the co-existence of different regeneration strategies in Mediterranean ecosystems. New Phytologist. doi: 10.1111/nph.12584.

Walker B.H., Ludwig D., Holling C.S., Peterman R.M. 1981. Stability of semi-arid savanna grazing systems. The Journal of Ecology 69, 473-498.

Wally A.L., Menges E.S., Weekley C.W. 2006. Comparison of three devices for estimating fire temperatures in ecological studies. Applied Vegetation Science 9(1), 97-108.

Wan S.Q., Hui D.F., Luo Y.Q. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecological Applications 11, 1349-1365.

Wang Q., Xiao F., He, T., Wang S. 2013. Responses of labile soil organic carbon and enzyme activity in mineral soils to forest conversion in the subtropics. Annals of forest science 70(6), 579-587.

Wardle D.A., Bardgett R.D., Klironomos J.N., Setälä H., Van Der Putten W.H., Wall D.H. 2004. Ecological linkages between aboveground and belowground biota. Science 304(5677), 1629-1633.

Weissteiner C.J., Boschetti M., Böttcher K., Carrara P., Bordogna G., Brivio P.A. 2011. Spatial explicit assessment of rural land abandonment in the Mediterranean area. Global and Planetary Change 79(1), 20-36.

Wertz S., Degrange V., Prosser J.I., Poly F., Commeaux C., Guillaumaud N., Le Roux X. 2007. Decline of soil microbial diversity does not influence the resistance and resilience of key soil microbial functional groups following a model disturbance. Environmental Microbiology 9(9), 2211-2219.

Westman W.E., O'Leary J.E. 1986. Measures of resilience: the response of coastal sage scrub to fire. Vegetatio 65, 179-189.

Whelan R.J. 1995. The Ecology of Fire. Cambridge University Press, New York.

Wittenberg L., Inbar M. 2009. The Role of Fire Disturbance on Runoff and Erosion Processes-a Long-Term Approach, Mt. Carmel Case Study, Israel. Geographical Research 47(1), 46-56.

Wittenberg L., Malkinson D., Beeri O., Halutzy A., Tesler N. 2007. Spatial and temporal patterns of vegetation recovery following sequences of forest fires in a Mediterranean landscape, Mt. Carmel Israel. Catena 71(1), 76–83.

Yuste J.C., Penuelas J., Estiarte M., García-Mas J., Mattana S., Ogaya R., Sardans J. 2011. Drought resistant fungi control soil organic matter decomposition and its response to temperature. Global Change Biology 17(3) 1475-1486.

Zang L., Song, L., Shao H., M., Liu, M., Brestic M., Xu G. 2013. Spatio-temporal variation of rhizosphere soil microbial abundance and enzyme activities under different vegetation types in the coastal zone, Shandong, China. Plant biosystems. DOI:http://dx.doi.org/10.1080/11263504.2013.770804.

Zedler P.H. 1995. Fire frequency in southern California shrublands: biological effects and management options. In 'Brushfires in California wildlands: ecology and resource management'. Eds J.E. Keeley, TA Scott. International Association of Wildland Fire: Fairfield, Washington, USA, pp 101-112.

Zedler P.H., Gautier C.R., McMaster G.S. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64(4), 809-818.

Zornoza R., Guerrero C., Mataix-Solera J., Arcenegui V., García-Orenes F., Mataix-Beneyto J. 2007. Assessing the effects of air-drying and rewetting pre-treatment on soil microbial biomass, basal respiration, metabolic quotient and soluble carbon under Mediterranean conditions. European Journal of Soil Biology 43(2), 120-129.

Annexes

Supplementary materials

Supplementary materials

S2.1. *List of species present in unburned plots and flammability and heat content classes.*

Species	**Flammability class**	**Heat-content class**
Anthyllis cytisoides L.	HI	LO
Argyrolobium zanonii (Turra) P.W.Ball	LO	UN
Atractylis humilis L.	UN	UN
Avena sp.	UN	UN
Brachypodium phoenicoides (L.) Roemer & Schultes	HI	UN
Brachypodium retusum (Pers.) Beauv.	HI	LO
Calicotome spinosa (L.) Link	ME	LO
Catananche caerulea L.	UN	UN
Cistus albidus L.	ME	ME
Cistus salviifolius L.	ME	ME
Convolvulus althaeoides L.	UN	UN
Coris monspeliensis L.	UN	UN
Dactylis glomerata L.	HI	UN
Daphne gnidium L.	LO	UN
Dorycnium pentaphyllum Scop.	UN	UN
Erica multiflora L.	ME	HI
Eryngium campestre L.	UN	UN
Euphorbia serrata L.	UN	UN
Foeniculum vulgare Miller	UN	UN
Fumana thymifolia (L.) Spach ex Webb	UN	ME
Hedysarum humile	UN	UN
Helianthemum apenninum (L.) Mill.	UN	UN
Helianthemum cinereum (Cav.) Pers	UN	UN
Helictotrichon filifolium (Lag.) Henrard	HI	UN
Hyparrhenia hirta (L.) Stapf	HI	UN
Inula viscosa (L.) Ait.	UN	UN
Linum strictum L.	UN	UN
Olea europaea L.	LO	ME
Ononis minutissima L.	UN	UN
Pallenis spinosa (L.) Cass.	UN	UN
Phagnalon rupestre (L.) DC.	UN	UN
Phagnalon saxatile (L.) Cass.	UN	UN
Phlomis lychnitis L.	ME	ME

Pinus halepensis Miller	HI	HI
Plantago albicans L.	UN	UN
Plantago sempervirens Crantz	UN	UN
Polygala rupestris Pourret	UN	UN
Prunus dulcis (Mill.) D. A. Webb	UN	UN
Psoralea bituminosa L.	LO	UN
Rosmarinus officinalis L.	HI	HI
Rubia peregrina L.	LO	LO
Rubus ulmifolius Schott	ME	ME
Sanguisorba minor Scop.	UN	UN
Santolina chamaecyparissus L.	UN	UN
Sedum sediforme (Jacq.) Pau	UN	UN
Smilax aspera L.	UN	UN
Stipa parviflora Desf.	HI	ME
Teucrium polium L. *ssp. capitatum* (L.) Arcangeli	UN	UN
Teucrium pseudochamaepitys L.	UN	UN
Thymus vulgaris L.	HI	ME
Ulex parviflorus Pourr.	HI	HI

Flammability and Heat-content classes: HI = High; ME = Medium; LO= Low; UN= Unknown.

S3.1. *List of species and regenerative traits*

Species	**Strategy**	**Growth form**
Anagallis arvensis L.	S	TH
Andryala integrifolia L.	S	TH
Anthyllis cytisoides L.	RS	TS
Anthyllis tetraphylla L.	S	TH
Aphyllanthes monspeliensis L.	RS	HE
Argyrolobium zanonii (Turra) P.W.Ball	RS	CH
Atractylis cancellata L.	S	TH
Atractylis humilis L.	R	HE
Avena sp.	S	TH
Blackstonia perfoliata (L.) Hudson	S	TH
Brachypodium phoenicoides (L.) Roemer & Schultes	R	PG
Brachypodium retusum (Pers.) Beauv.	R	PG
Calicotome spinosa (L.) Link	RS	TS
Catananche caerulea L.	RS	HE
Centaurea aspera L.	R	HE
Cistus albidus L.	S	TS
Cistus salviifolius L.	S	TS
Clematis flammula L.	R	LI
Convolvulus althaeoides L.	S	HE
Coris monspeliensis L.	R	CH
Coronilla scorpioides (L.) Koch	S	TH
Cuscuta epithymum (L.) L.	S	TH
Dactylis glomerata L.	RS	PG
Daphne gnidium L.	RS	SS
Dorycnium hirsutum (L) Ser.	RS	CH
Dorycnium pentaphyllum Scop.	RS	CH
Echinops ritro L.	S	HE
Erica multiflora L.	RS	SS
Eryngium campestre L.	S	HE
Euphorbia serrata L.	R	GE
Filago pyramidata L.	S	TH
Foeniculum vulgare Miller	RS	HE
Fumana ericoides (Cav.) Gand	S	CH
Fumana thymifolia (L.) Spach ex Webb	S	CH
Fumaria officinalis L.	S	TH
Hedysarum humile	R	HE

Helianthemum apenninum (L.) Mill.	S	CH
Helianthemum cinereum (Cav.) Pers	S	CH
Helianthemum syriacum (Jacq.) DC.	S	CH
Helichrysum stoechas (L.) Moench	S	CH
Helictotrichon filifolium (Lag.) Henrard	R	PG
Hippocrepis comosa L.	RS	CH
Hyparrhenia hirta (L.) Stapf	R	PG
Hypericum perforatum L.	S	HE
Inula viscosa (L.) Ait.	S	CH
Leontodon taraxacoides (Vill.) MÚrat	*S*	TH
Linum narbonense L.	RS	HE
Linum strictum L.	S	TH
Lithodora fruticosa (L.) Griseb.	S	CH
Medicago orbicularis (L.) Bartal.	S	TH
Medicago polymorpha L.	S	TH
Mercurialis tomentosa L.	S	HE
Olea europaea L.	R	TR
Onobrychis sp.	S	TH
Ononis minutissima L.	S	CH
Pallenis spinosa (L.) Cass.	S	HE
Phagnalon rupestre (L.) DC.	S	CH
Phagnalon saxatile (L.) Cass.	S	CH
Phlomis lychnitis L.	S	CH
Pinus halepensis Miller	S	TR
Plantago albicans L.	RS	CH
Plantago lanceolada L.	S	HE
Plantago sempervirens Crantz	R	CH
Polygala rupestris Pourret	RS	CH
Prunus dulcis (Mill.) D. A. Webb	S	TR
Psoralea bituminosa L.	RS	CH
Reichardia tingitana (L.) Roth	S	TH
Reseda alba L.	S	TH
Rosmarinus officinalis L.	S	TS
Rubia peregrina L.	R	LI
Rubus ulmifolius Schott	R	LI
Sanguisorba minor Scop.	S	HE
Santolina chamaecyparissus L.	R	CH
Scabiosa sp.	R	HE
Scolymus hispanicus	S	HE
Scorpiurus muricatus L.	S	TH
Scorzonera graminifolia L.	R	HE

Sedum album L.	S	CH
Sedum sediforme (Jacq.) Pau	S	CH
Sideritis angustifolia Lag.	RS	CH
Silene vulgaris (Moench) Garcke	S	HE
Smilax aspera L.	RS	LI
Sonchus asper (L.) Hill	S	TH
Sonchus tenerrimus L.	S	HE
Staehelina dubia L.	S	CH
Stipa parviflora Desf.	R	PG
Teucrium polium L. *ssp. capitatum* (L.) Arcangeli	R	CH
Teucrium pseudochamaepitys L.	RS	CH
Thymus vulgaris L.	RS	CH
Trifolium angustifolium L.	S	TH
Trifolium campestre Schreb.	S	TH
Trifolium stellatum L.	S	TH
Ulex parviflorus Pourr.	S	TS

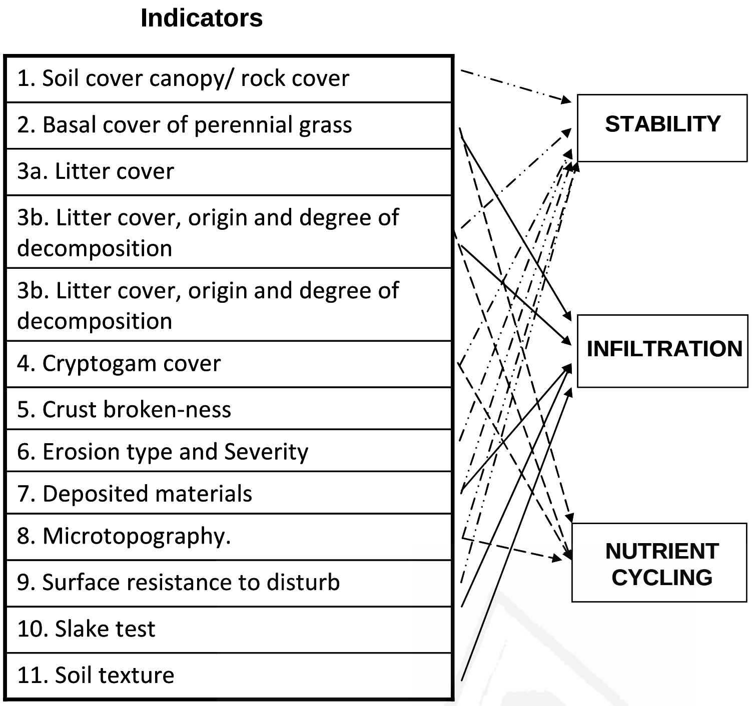
Regenerative traits: R = Resprouter; S = Seeder.
Growth forms: TR = Tree; TS = Tall shrub; SS = Small shrub; CH = Chamaephyte; PG = Perennial grass; HE Hemicryptophyte; LI = Liana.

S.4.1. *Interpretation of soil surface indicators of Soil surface Assessment from Landscape functional Analysis (LFA) (adapted from Tongway and Hindley, 2004).*

Indicators	Objective
Soil cover (Score range: 1-5)	Projected percentage cover of perennial vegetation to a height of 0.5 m, plus rocks > 2 cm and woody material > 1 cm in diameter or other long-lived, immoveable objects. This indicator assesses the degree to which physical surface cover and projected plant cover ameliorate the effect of raindrops impacting on the soil surface.
Perennial cover (Score range: 1-4)	Basal cover of perennial grass and/or canopy cover of trees and shrubs. This indicator assumes a positive relationship between perennial cover and belowground biomass, and assesses the contribution of the belowground biomass of perennial vegetation to nutrient cycling and infiltration processes.
Litter cover (Score range: 1-30)	This indicator considers amount (cover and depth), origin (local or transported) and degree of decomposition and incorporation (nill; slight; moderate; extensive) of plant litter, assessing the availability of surface organic matter for decomposition and nutrient cycling.
Cryptogam cover (Score range: 0-4)	Cover of cryptogams (algae; fungi; lichens; mosses) visible on the soil surface. This indicator assesses surface stability, resistance to erosion and nutrient availability.
Crust broken-ness (Score range: 0-4)	A crust is defined as a physical surface layer that overlies sub-crust material. This indicator assesses to what extent the surface crust is broken, leaving loosely attached soil material available for erosion.

Erosion type and severity (Score range: 1-4)	Erosion in this context refers to accelerated erosion caused by the interaction of management and climatic events. This indicator considers the nature (sheet erosion; rill erosion; pedestals and terracettes) and severity (insignificant; slight; moderate; severe) of current soil loss.
Deposited materials (Score range: 1-4)	This indicator considers the nature and amount of alluvium transported to and deposited on the query zone, understanding that the higher the amount of deposited material the lower the stability.
Microtopography (Score range: 1-5)	This indicator evaluates the surface roughness for its capacity to capture and retain mobile resources such as water, seeds, topsoil and organic matter.
Surface resistance to disturbance (Score range: 1-5)	This indicator assesses the ease with which the soil can be mechanically disturbed to yield material suitable for erosion by wind or water.
Slake test (Score range: 0-4)	This indicator assesses the stability of natural soil fragments when rapidly wetted.
Soil texture (Score range: 0-5)	This indicator classifies the texture of the surface soil, and relates this to permeability.

S.4.2. *The combination of the soil surface indicators to determine the Soil functional indices of stability, infiltration and nutrient cycling (From Tongway and Hindley, 2004).*



Resumen:
Los atributos de la vegetación modulan la resiliencia al fuego en el monte mediterráneo

Resumen: Los atributos de la vegetación modulan la resiliencia al fuego en el monte mediterráneo

1. Incendios forestales en la cuenca mediterránea

Los incendios forestales son un fenómeno común en regiones mediterráneas. Muchas especies de plantas mediterráneas presentan mecanismos adaptativos que les permite persistir y regenerarse después de un incendio, lo que permite a los ecosistemas naturales de la cuenca mediterránea y de otras regiones mediterráneas ser altamente resilientes después de un incendio, siendo en general capaces de resistir regímenes de incendio de alta recurrencia (Naveh 1975; Keeley 1986; Pausas y Verdu 2005). Asimismo, el fuego es también un factor determinante en los procesos y la estructura de estos ecosistemas (Bond y Keeley 2005; Pausas y Keeley 2009), y por ende en la configuración de los paisajes forestales (Lloret et al. 2002; Baeza et al. 2007). Los incendios promueven ecosistemas más inflamables, diferentes de la fisonomía esperada según las condiciones climáticas de la región (Bond y Midgley 1995; Bond et al. 2005; Keeley et al. 2011; Moreira et al. 2011; Pausas et al. 2012). Así, extensas áreas de matorral mediterráneo que son bosques potenciales, mantienen la dominancia de arbustos debido a la frecuencia de incendios. En la cuenca mediterránea, los incendios forestales han ido ocurriendo durante milenios, por lo que la biodiversidad de estas zonas podría haber sido estructurada por el régimen de incendios (Pausas et al. 2008). Sin embargo, una de las diferencias más relevantes entre la cuenca mediterránea y otras regiones mediterráneas es el impacto de un uso del suelo intenso durante milenios; prácticas como las quemas, aclareos de bosques, pastoreo, aterrazado y uso agrícola, han llevado a una intensa modificación del paisaje que, a su vez, tiene importantes consecuencias en el régimen de incendios (Moreira et al. 2001; Mouillot et al. 2003; Carrión et al. 2003; Vannière et al. 2008). Así, por una parte, el paisaje resultante de la actividad humana, mosaico heterogéneo de diferentes tipos de uso del suelo y cubierta vegetal que no son igualmente susceptibles al fuego, puede modificar la expansión del fuego, produciendo pequeñas áreas quemadas por fuegos individuales. Por otra parte, el intenso uso del suelo, que por lo común ha llevado a la eliminación de especies rebrotadoras para habilitar suelos para la actividad agrícola, combinado con incendios frecuentes, ha conducido a cambios en la vegetación hacia ecosistemas dominados por especies germinadoras (Vallejo y Alloza 1998), Estos ecosistemas son, a su vez, más propensos de sufrir incendios y menos resilientes que ecosistemas dominados por especies rebrotadoras. Además, la baja resiliencia de estos ecosistemas puede prolongar el periodo de impacto de las perturbaciones, con largos periodos post-incendio con suelos expuestos a agentes erosivos.

En los países europeos de la región mediterránea, el número de incendios y el área quemada ha incrementado significativamente durante las últimas décadas (Pausas et al. 1999; Pausas 2004). En la región de Valencia (Este de la península Ibérica) esta tendencia ha sido particularmente marcada desde los mediados de los 70s, con notables cambios entre regímenes de incendios entre 1972 y 1973 (Pausas y Fernández-Muñoz 2012). Así, en el periodo de 1978 -1979 se quemaron 154000 hectáreas, y en 1994 se quemó casi el 12% de área forestal de la región en pocos días (140000 hectáreas) (Pausas 2004). Algo parecido ocurrió en la región de Minho (Noroeste de Portugal) donde los incendios se triplicaron en el periodo de 1980-1996 (Moreira et al. 2001).

Según Dube (2009), el régimen de incendios podría ser el resultado de la interacción entre numerosos factores a múltiples escalas. Sin embargo, a escala regional el régimen de incendios responde a la retroalimentación entre clima, incendio y vegetación. En la cuenca mediterránea, los cambios en el régimen de incendios han estado asociado principalmente a dos factores: los cambios climáticos y las causas socio-económicas (Fernández-Ales et al. 1992; Moreira et al. 2001; Pausas 2004; Pausas y Fernández-Muñoz 2012). La disminución de las precipitaciones de verano y el incremento claro de las temperaturas en los últimos 50 años (1950-2000) implicarían una reducción de la humedad del combustible vegetal, con el consecuente incremento del riego de ocurrencia de incendios (Piñol et al. 1998; Pausas 2004). Por otro lado, los cambios socio-económicos en los países mediterráneos europeos, como el desarrollo industrial durante los años 70, han derivado en la despoblación de áreas rurales (Fernández-Ales et al. 1992; Moreira et al. 2001; Duguy y Vallejo 2008), induciendo a drásticos cambios en los usos tradicionales del suelo, como el abandono de áreas cultivadas y la reducción de pastoreo del ganado. Estos cambios en los usos del suelo, junto con la implementación de programas de forestación extensiva incrementaron, en algunos casos, la acumulación y continuidad del combustible vegetal. En muchos casos, el combustible vegetal está compuesto por especies de alta inflamabilidad (Baeza et al. 2011). Pausas y Fernández-Muñoz (2012) sugieren que mientras los incendios antes de los años 70 fueron incendios restringidos por la disponibilidad de combustible y estuvieron principalmente relacionados con los cambios de usos del suelo (abandono de cultivos y plantaciones forestales), después de los años 70 los incendios no están restringidos por la disponibilidad de combustible y están determinados principalmente por episodios de sequía.

A pesar de que los ecosistemas mediterráneos se consideran resilientes al fuego, varios estudios sugieren que los regímenes actuales de incendio pueden inducir cambios importantes en la composición de especies y, por lo tanto, afectar a la resiliencia de estos ecosistemas. Por ejemplo, en comunidades dominadas por especies germinadoras obligadas, la alta recurrencia de incendios, con intervalos demasiado cortos de tiempo para el reclutamiento de plántulas, la maduración y la formación de bancos de semillas persistentes, llevaría al reemplazo o cambio de la dominancia de especies; en el caso de paisajes dominados por bosques podrían cambiar a otros dominados por matorrales (Kazanis y Arianotsou 2004; De Luís et al. 2006). A nivel de paisaje, los incendios pueden cambiar los paisajes por otros más homogéneos o heterogéneos dependiendo del tamaño del área quemada. Así, incendios grandes que queman diferentes tipos de cobertura de bosque al mismo tiempo, podrían llevar un paisaje heterogéneo y en mosaico a un paisaje dominado por matorral homogéneo (Rodrigo et al. 2004; Viedma et al. 2006), particularmente si las especies forestales son poco resilientes a la alta frecuencia de incendios (Díaz-Delgado et al. 2002; Kazanis y Arianotsou 2004). Sin embargo, los incendios pueden también fragmentar áreas forestales o áreas homogéneas de matorral, y crear un mosaico de diferentes estadios sucesionales (Lloret et al. 2002).

2. Estabilidad de los ecosistemas frente a una perturbación: resistencia y resiliencia

La respuesta de un ecosistema a una perturbación refleja su estabilidad, que se define por dos componentes: resistencia y resiliencia (Pimm 1984; Grimm y Wissel 1997). La resistencia se define como la capacidad de un sistema para resistir la presión de una perturbación y mantener intacta su estructura y funciones. La resistencia se mide como la magnitud de cambio o alteración de las variables o atributos del ecosistema afectados por la perturbación. Por su parte, la resiliencia puede ser definida desde dos perspectivas: ecológica e ingenieril. La resiliencia ingenieril se define como la velocidad a la cual un sistema retorna a su estado estable original después de la perturbación; esta definición asume que un ecosistema se comporta como un material, que muestra un desplazamiento como respuesta inmediata a la presión de la perturbación, pero luego recupera su estado pre-perturbación. Esta definición considera la estabilidad como un estado próximo a un estado de equilibrio y se cuantifica como la velocidad de retorno al equilibrio o a las condiciones pre-perturbación. Por otra parte, la resiliencia ecológica considera la cantidad de perturbación que se requiere para mover un sistema de un estado estable a otro estado estable alternativo (o dominio de estabilidad) (Walker et al. 1969; Holling 1973). Esta definición asume que los ecosistemas podrían cruzar un umbral: si se producen alteraciones críticas en las variables afectadas, el ecosistema podría verse desplazado hacia una trayectoria diferente a las condiciones previas a la perturbación.

La estabilidad de las comunidades vegetales frente al fuego ha sido analizada desde múltiples perspectivas. La resistencia de la vegetación al fuego puede ser definida como el nivel al cual las propiedades de la vegetación (cobertura vegetal, composición y riqueza de especies) pueden mantenerse inalteradas después de un incendio, lo que dependerá de la sensibilidad y el grado de protección de las semillas y las yemas de las especies presentes (Keeley 1986). Por otra parte, la resiliencia de la vegetación se define como la tasa de recuperación de los valores previos al incendio (Halpern 1988; Lavorel 1999), lo que dependerá de la composición de especies previas al incendio, de los mecanismos de persistencia de estas especies (capacidad de germinación y rebrote) y del nivel del daño ocasionado por el régimen de incendios (severidad y frecuencia). Así, la estabilidad refleja la capacidad de las especies vegetales de resistir el impacto del fuego o mantenerse inalteradas y, en el caso de sistemas afectados, la capacidad de recuperación (Halpern 1988).

La resiliencia de un ecosistema puede ser evidente a diferentes escalas y actuar simultáneamente en todas las escalas. Por ejemplo, los incendios pueden trasformar un tipo de vegetación en otro diferente, como es el caso de pinares transformados en matorrales después del fuego (Kazanis y Arianoutsou 2004), lo que a su vez modifica la configuración del paisaje (Lloret et al. 2002; Loepfe et al. 2010). Asimismo la resiliencia de diferentes componentes y procesos de un ecosistema pueden estar correlacionadas. Por ejemplo, debido a la estrecha relación planta-suelo, es de esperar que la resistencia y resiliencia de los componentes del suelo y la vegetación estén correlacionadas (Seybold et al. 1999; Herrick 2000; Certini 2005), pero son muy escasos los trabajos sobre este tema. Sin embargo, es importante enfatizar que los componentes y procesos de un ecosistema pueden variar ampliamente en su sensibilidad a una perturbación y su capacidad de recuperación (Lavorel 1999). Un ejemplo de ello es la recuperación de cobertura vegetal, que puede ser relativamente rápida, mientras que la abundancia relativa de las especies requiere más tiempo para alcanzar valores previos al incendio.

En este trabajo de tesis se usa, principalmente, la definición ingenieril de estabilidad, asumiendo la resistencia como la capacidad de resistir el impacto del fuego y la resiliencia como la capacidad de un ecosistema o comunidad para recuperar las condiciones previas al incendio. Por lo tanto, la resistencia se cuantifica como la magnitud de los cambios producidos por el fuego en las propiedades del sistema y la resiliencia se cuantifica como la cuantía de la recuperación de los valores del pre-incendio, medidos en un periodo de tiempo dado. No obstante la resiliencia ecológica también está presente en este trabajo cuando se considera la ocurrencia potencial de cambios del ecosistema hacia estados alternativos.

3. Factores que afectan la resistencia y resiliencia de los ecosistemas frente al fuego

La resistencia y resiliencia de un ecosistema frente al fuego es el resultado de la combinación de factores bióticos y abióticos, a su vez relacionados con el régimen de incendios (severidad y frecuencia), condiciones climáticas post-incendio, factores inherentes a las comunidades (estructura física y biológica) y factores relacionados con las condiciones de las áreas afectadas. Estos factores interactúan entre ellos y operan a diferentes escalas. Un incendio puede afectar potencialmente todos los niveles de organización biológica del ecosistema, por lo tanto tiene un papel importante en la estructuración y funcionamiento de las poblaciones y comunidades afectadas. La magnitud de los efectos del fuego en la vegetación y el suelo (resistencia) depende fundamentalmente de la severidad del fuego, la que podría ser considerada con una propiedad inversa a la resistencia (como se explica mas adelante), las características de la vegetación y del suelo relacionadas con su sensibilidad y nivel de protección. Por otra parte, la capacidad de recuperación de la vegetación y el suelo después del fuego (resiliencia) dependerá de la severidad del incendio, la capacidad de regeneración de las especie presentes y de las condiciones climáticas post-incendio.

3.1. Intensidad y severidad del incendio

Si bien intensidad y severidad del incendio en muchos casos son dos términos intercambiables en la literatura, no hacen referencia a lo mismo. La intensidad del fuego está relacionada con la cantidad de combustible consumido y energía liberada durante el proceso de combustión, pero esta valoración de un incendio es insuficiente para estimar los efectos que la energía liberada por el fuego produce en los ecosistemas (Keekey 2009). Por su parte, la severidad del incendio se usa generalmente para describir los efectos del fuego en los ecosistemas y se define como el impacto del fuego en el ecosistema producido por la transformación o pérdida de materia orgánica subterránea y aérea (Keeley 2009). Así, la severidad del incendio está correlacionada con la intensidad del incendio y captura los efectos en la vegetación y el suelo de la intensidad y del tiempo de residencia de altas temperaturas ocurridas durante el incendio (Pérez y Moreno 1998). Por consiguiente, hasta cierto punto, la severidad de un incendio y la resistencia del sistema al impacto de esta perturbación pueden considerarse como las dos caras de una misma moneda; aunque la severidad del incendio normalmente hace referencia a la pérdida o transformación de la materia orgánica (Keeley 2009), mientras la resistencia frente a un incendio implica a cualquier componente o proceso del ecosistema.

La severidad del incendio es uno de los principales factores que controla la resiliencia de los ecosistemas, pudiendo afectar gravemente los patrones de reclutamiento de plántulas germinadas, la capacidad de rebrote, la actividad microbiana de suelo y muchos otros procesos importantes del ecosistema (Bond y van Wilgen 1996; Neary et al. 1999; Keeley et al. 2005). Un incendio en la misma área por lo general no quema de forma homogénea, la distribución espacial del combustible vegetal puede derivar en un mosaico generado por las diferentes severidades con que se quema la vegetación. La heterogeneidad espacial de la severidad tiene una influencia importante en los procesos ecológicos y en la recuperación de la vegetación y del suelo tras el incendio.

3.2. Recurrencia de incendios

El efecto de la recurrencia de incendios en los ecosistemas es una función intervalo-dependiente, relacionada con la disponibilidad de tiempo suficiente que permita el re-establecimiento de especies germinadoras y la producción de semillas y también la recuperación de las reservas de carbohidratos en el caso de las especies rebrotadoras (Zedler 1995; Clarke et al. 2013). Las especies germinadoras obligadas que dependen del fuego pueden enfrentarse al riego de inmadurez o senescencia debido a intervalos cortos o largos entre incendios respectivamente (Zedler 1995). Los intervalos cortos pueden afectar negativamente la densidad y tasas de crecimiento de las poblaciones de árboles y arbustos (por ejemplo, *Pinus sp*) (Ne'eman et al. 1999; Eugenio et al. 2006a). Algunas especie arbustivas (por ejemplo, *Rosmarinus officinalis* y *Cistus albidus*) parecen alcanzar su máxima abundancia a una frecuencia intermedia de incendios (Lloret et al. 2003). Sin embargo, la alta recurrencia de incendios puede incrementar la abundancia de gramíneas perennes rebrotadoras (por ejemplo, la gramínea tipo macolla *Ampelodesmos mauritanica*; Lloret et al. 2003), mientras que la productividad y la capacidad de regeneración de algunas rebrotadoras arbustivas puede disminuir (Delitti et al. 2005) debido al agotamiento de carbohidratos de reserva almacenados (Paula y Ojeda 2009). Incendios con intervalos de retorno cortos, que no permiten la recuperación de la vegetación, pueden ocasionar la exposición prolongada de la superficie del suelo, lo que podría llevar a altas tasas de escorrentía y como consecuencia mayor erosión (Campo et al. 2006; Wittemberg y Inbar 2009; Malkinson et al. 2011) y a la perdida de nutrientes del suelo (Eugenio et al. 2006b). En general la alta recurrencia de incendios puede retardar la recuperación de la cubierta y la biomasa vegetal en ecosistemas mediterráneos (Mouillot et al 2003; Delitti et al 2005; Abdel Malaak y Pausas 2006), dando lugar a una ventana de perturbación de larga duración de tiempo, que podría reducir la resiliencia del sistema.

3.3. Estructura de la comunidad vegetal y atributos funcionales de la plantas

La vegetación juega un papel importante en la determinación de la inflamabilidad del combustible, la severidad del fuego y la regeneración post-incendio de la vegetación, lo que a su vez afecta la composición de especies de la nueva comunidad tras el fuego, llevando así a la retroalimentación entre vegetación e incendio. La composición de especies y la edad de la comunidad determinarán la cantidad y las características estructurales de combustible (compactación, relación superficie/volumen, continuidad vertical y horizontal, relación combustible vivo/muerto, densidad), lo que influye en la dinámica de humedad, proceso de ignición y combustibilidad del combustible y la propagación del fuego (Baeza et al. 2002; Schwilk 2003; Alessio et al. 2008; Saura-Mas et al. 2010; Santana et al. 2011) y, por tanto, determinará la severidad potencial del fuego. Al mismo tiempo, la composición funcional y específica pre-incendio (particularmente la relacionada con los atributos que permiten a las especies persistir después de un incendio) es de crucial importancia para la recuperación de la vegetación después de un incendio (Whelan 1995; Lloret y Vilà 2003; Arnan et al. 2007; Duguy y Vallejo 2008).

Muchas especies de la región mediterránea pueden reclutar abundantes plántulas (germinadoras) o rebrotar de órganos vegetativos (rebrotadoras) después del fuego, mientras que otras especies son capaces de usar ambos mecanismos de regeneración (facultativas). Estos atributos permiten a las especies o individuos persistir después de un incendio, haciendo que las comunidades mediterráneas sean altamente resilientes frente al fuego (Keeley 1986; López-Soria y Castell 1992; Pausas et al. 2004a; Keeley et al 2005; 2006). De todos modos, no todas las especies mediterráneas pueden sobrevivir al fuego en todas las situaciones. Comunidades dominadas por arboles rebrotadores (por ejemplo, *Quercus ilex*, *Q. cerrioides*, *Q. suber*, *Q. pyrenaica*) o arbustos rebrotadores (*Quercus coccifera*) (Calvo et al. 2003; Rodrigo et al. 2004; Delitti et al. 2005), o por especies germinadoras con un reclutamiento eficiente de plántulas después del incendio (por ejemplo, *Pinus halepensis*, *P. pinaster*) pueden ser altamente resilientes frente al fuego (Pausas et al. 2003; Rodrigo et al. 2004; Arnan et al. 2007). Por el contrario, comunidades dominadas por especies germinadoras que producen un reclutamiento reducido de plántulas (por ejemplo, *P. nigra*, *P. sylvestris*, *P. pinea*) puede fácilmente cambiar hacia otro tipo de comunidad después del incendio (Rodrigo et al. 2004; Arnan et al. 2007).

En los ecosistemas mediterráneos, hay una gran variación en la proporción de especies germinadoras y rebrotadoras. En gran medida esta variación depende de la historia de usos del suelo (Duguy y Vallejo, 2008; López-Poma et al. *en prensa,* véase Capítulo 2 de esta memoria), lo que podría modular la presencia relativa de especies con diferentes atributos de persistencia después del fuego. La historia de usos del suelo también determinará las propiedades físico-químicas del suelo (fertilidad del suelo) a medio plazo (Duguy et al. 2007). En consecuencia, es de esperar que áreas con diferente historia de uso del suelo difieran en su respuesta al impacto del fuego, derivando en diferentes patrones de regeneración (Duguy y Vallejo 2008; Puerta-Piñero et al. 2012). Sin embargo, poco se conoce sobre la influencia del legado de especies de la actividad agrícola que determinan la demografía de rebrotadoras y germinadoras obligadas después del incendio. Además, aún se conoce poco sobre el efecto global de la composición funcional (rebrotadoras versus germinadoras) de matorrales mediterráneos en la resiliencia post-incendio, a través del efecto combinado de la capacidad de regeneración, inflamabilidad y severidad del fuego.

Aparte de los atributos de persistencia de las especies después del incendio, otras características individuales de las plantas o de la comunidad pueden ser relevantes en la determinación de la recuperación de la vegetación. El tamaño de los individuos rebrotadores parece ser uno de los factores más importantes en la determinación de del número y biomasa de los rebrotes (Canadell et al. 1991). La edad de la comunidad, relacionada con la frecuencia de incendios, puede ser crucial en la regeneración de la vegetación tras un incendio, particularmente para especies germinadoras, tanto por sus efectos en la capacidad de producción de semillas como en el almacenamiento de semillas en los bancos del suelo y la copa (Kazanis y Arianotsou 2004; Eugenio et al. 2006a). La diversidad de especies puede ser también relevante; por ejemplo, comunidades de bosque con un gran número de especies son más diversos en atributos funcionales, lo que aseguraría su recuperación después de un incendio y una alta resiliencia después de una perturbación de alta intensidad (Puerta-Piñero et al. 2012). Sin embargo, la relación diversidad – resiliencia ha sido poco estudiada (Lloret y Vilà 2003; Dimitrakopoulos et al. 2006), por lo que aún no se tienen establecida una teoría reconocida.

La resiliencia de algunos componentes y funciones del suelo dependen de la estructura de la comunidad vegetal. La recuperación de la materia orgánica en áreas quemadas se inicia con el re-establecimiento de vegetación (Certini 2005) y la tasa de recuperación de la vegetación definirá la recuperación de la actividad de rizosfera (Hernández et al. 1997).

3.4. Condiciones climáticas

Durante el incendio, las condiciones climáticas son importantes porque determinan el comportamiento del fuego y a su vez la virulencia de incendio. Después del incendio, las condiciones climáticas son decisivas para la estabilidad del suelo y para el re-establecimiento y desarrollo de la vegetación. Condiciones desfavorables de sequía después del incendio pueden dificultar la regeneración de las especies, afectando particularmente a las germinadoras que son más sensibles a la disponibilidad de agua en los primeros estadios de establecimiento de las plántulas que en estadios tardíos (Céspedes et al. 2012). Así, dependiendo de las condiciones climáticas post-incendio, podrían ocurrir diferentes trayectorias en la dinámica sucesional (Quintana et al. 2004). Además, condiciones climáticas post-incendio desfavorables, en combinación con otros factores como la severidad del fuego, pueden afectar considerablemente la respuesta de las especies al impacto del incendio. Por ejemplo, periodos de sequía después del fuego pueden ocasionar una recuperación lenta de la vegetación, lo que implicaría una pobre protección inicial del suelo y una alta susceptibilidad al encostramiento físico y erosión, particularmente en suelos de textura fina como los suelos desarrollados sobre margas (Mayor et al. 2007). La tendencia actual del clima en regiones mediterráneas hacia largos periodos de sequía estival y la intensificación de eventos extremos, tanto de sequía y precipitaciones intensas (Giorgi y Lionello 2008), pueden incrementar aún más el riesgo de la reducción de la resiliencia del ecosistema y por consiguiente mayor impacto de los incendio forestal en los ecosistemas (Mouillot et al. 2002).

3.5. Condiciones fisiográficas de las zonas quemadas

Los factores inherentes a las condiciones de las áreas quemadas como la pendiente, su orientación, tipo de sustrato litológico, pueden afectar considerablemente en la resiliencia de los ecosistemas (Pausas et al. 1999). La orientación de la pendiente parece ser una variable importante relacionada con el comportamiento del fuego y la recuperación de la vegetación debido a la influencia en la intensidad del viento, cantidad y humedad del combustible. La orientación solana en el hemisferio norte es comúnmente caracterizada por condiciones de sequía que normalmente limitan la recuperación de la vegetación y por ende la resiliencia del ecosistema, comparado con la orientación norte (Pausas et al. 1999; Mouillot et al. 2003; Malkinson et al. 2011). La baja tasa de recuperación en la orientación solana puede favorecer el incremento de la tasa de erosión comparado con la orientación norte (Marqués y Mora 1992), lo que c puede afectar la resiliencia del sistema. La inclinación de la pendiente es también un factor importante para la resiliencia, en pendientes muy pronunciadas, la recuperación de la vegetación puede ser significativamente reducida (Tsitsoni 1997), lo que, combinado con el efecto directo en la energía de la escorrentía, puede incrementar el daño en el ecosistema después del incendio. En la cuenca mediterránea, las tasas de recuperación post-incendio varían considerablemente con el tipo de sustrato litológico (Pausas et al. 1999), ya que el tipo de sustrato está estrechamente relacionado con el tipo de suelo y el tipo de usos del suelo en esta región. Así, por ejemplo, la regeneración post-incendio es comúnmente más alta en suelos desarrollados sobre calizas que en suelos sobre marga, lo que puede estar relacionado con el intenso uso agrícola, y la eliminación consiguiente de arbustos rebrotadores, en suelos desarrollados sobre margas.

4. Objetivos y estructura de la tesis

El objetivo general de esta tesis es la valoración de papel de los atributos de la vegetación en la resiliencia después de un incendio en el monte mediterráneo, particularmente centrado en los atributos de persistencia de las especies después del fuego (regeneración), y en la respuesta al fuego de la comunidad vegetal y de las funciones del suelo. Los supuestos generales subyacentes a la tesis están representados en la Figura 1.3 (véase Capítulo 1). Tanto la composición de la comunidad vegetal (asociado a los atributos funcionales) como las funciones del suelo están involucrados en la resistencia y resiliencia de los ecosistemas. Las funciones del suelo dependen de la composición de especies (grupos funcionales) a través de una variedad de mecanismos de retroalimentación. Los grupos funcionales de plantas modulan la severidad del fuego y la resistencia de la vegetación y de las funciones del suelo al impacto del fuego mediante su influencia en las propiedades del combustible. Asimismo, los grupos funcionales de plantas modulan la resiliencia de los ecosistemas a través de diferencias en su capacidad de rebrote, colonización y del re-establecimiento de la retroalimentación planta - suelo.

La tesis esta estructurada en seis capítulos: introducción general (capítulo 1), cuatro capítulos que son versiones de artículos científicos que están en prensa o en revisión en revistas científicas (capítulos del 2 al 5) y un capítulo final de discusión y conclusiones generales (capítulo 6).

El capítulo 2 analiza cómo los estadios sucesionales después del abandono del uso agrícola (herbazal seco, matorral y pinar), así como sus características inherentes de composición y estructura de la comunidad, influyen en la severidad del incendio y en la resiliencia de la vegetación. La recuperación de la vegetación se midió uno, cuatro y siete años después del incendio. Los estadios sucesionales se diferenciaron en biomasa aérea, cantidad de hojarasca, distribución vertical y continuidad horizontal de la cobertura vegetación, y la inflamabilidad. La menor severidad del incendio se registró en el herbazal seco, mientras que el matorral y el pinar no mostraron diferencias en severidad. Un año después del incendio, el recubrimiento vegetal mostró una relación inversa con la severidad del incendio. Esta relación negativa se fue atenuando con el paso del tiempo después del incendio. Siete años después del incendio, el pinar y el matorral resultaron en comunidades arbustivas similares dominados por especies altamente inflamables como *U. parviflorus* y especies del género *Cistus*, lo que contribuyó a la homogenización del paisaje. Los pinares mostraron una alta vulnerabilidad a los incendios, debido a que estas comunidades sufrieron los mayores cambios en la composición de especies como resultado del fuego y una menor recuperación de la cobertura vegetal comparado con otros estadios sucesionales.

El capítulo 3 examina cómo la severidad del incendio influye en los atributos de regeneración post-incendio de las especies. Se analizó la dinámica post-incendio de las especies germinadoras y rebrotadoras, así como la variación del ratio germinadoras/rebrotadoras, en función de la variación de la severidad del fuego y del tipo de comunidad vegetal pre-incendio en tres comunidades mediterráneas (herbazal, aulagar y pinar) que representan diferentes estadios de sucesión después del abandono de cultivos. Los resultados mostraron que el ratio de cobertura de germinadoras/rebrotadoras se incrementó de forma no lineal con el incremento de la severidad del incendio, de forma consistente en las tres comunidades vegetales. El aumento en la tasa de cobertura germinadoras/rebrotadoras con la severidad del fuego parece estar relacionado con la mortalidad de individuos de especies rebrotadoras y la creación de espacios de suelo desnudo, lo que aumentó la disponibilidad de micrositios favorables para la germinación de las semillas (ya sea del banco de semillas existente en el suelo o semillas procedentes de zona adyacentes no quemadas) y el crecimiento de las plántulas.

El capítulo 4 examina el papel que desempeñan los atributos de las plantas relacionados con el fuego, en la magnitud de cambio (resistencia) y la recuperación (resiliencia) de las funciones del suelo después de un incendio en matorrales mediterráneos. El estudio se centró en cinco tipos diferentes de manchas de vegetación, dominadas cada una por una especie en particular (*Brachypodium retusum*, *Quercus coccifera*, *Ulex parviflorus*, *Cistus albidus*, *Rosmarinus officinalis*) y zonas de *interpach* (suelo desnudo), en tres comunidades de matorral a las que se aplicó una quema experimental. Las funciones del suelo que se evaluaron fueron la estabilidad del suelo, la infiltración de agua, y las funciones relacionadas con los ciclos de nutrientes, según la metodología del análisis funcional del paisaje (Landscape function análisis - LFA). El impacto de los incendios se evaluó utilizando índices de resistencia y resiliencia. Los resultados mostraron que la variación en la resistencia y la resiliencia de las funciones del suelo depende en gran medida de la variación de los atributos estructurales y funcionales de las especies relacionados con el fuego. La resistencia pareció estar más relacionada con atributos estructurales de las plantas, como la acumulación de combustible muerto; mientras que la resiliencia aparentemente estuvo más relacionada con atributos funcionales, como es la capacidad de rebrote de las especies estudiadas.

El capítulo 5 evalúa el papel de los grupos funcionales relacionados con lo mecanismos de regeneración de las especies después de un incendio (rebrotador, germinador), en la resistencia y resiliencia de dos enzimas involucradas en el ciclo del fósforo y carbono del suelo (fosfatasa ácida y β-glucosidasa, respectivamente) después de un incendio. Después de un fuego experimental, se monitorizó la dinámica de recuperación post-incendio de las enzimas, el carbono orgánico del suelo y la cobertura vegetal, en cuatro tipos de micrositios: manchas de arbustos rebrotadores, manchas de arbustos germinadores, manchas mixtas de rebrotadoras y germinadoras, y una matriz de suelo con herbáceas y caméfitas dispersas (*Interpatch*). Los resultados mostraron que los grupos funcionales relacionados con los atributos de regeneración post-incendio (rebrotador, germinador) modulan la actividad de ambas enzimas (fosfatasa acida y β-glucosidasa), con mayor actividad en manchas de vegetación dominados o co-dominados por rebrotadoras que en suelos debajo de especies germinadoras. El fuego afectó negativamente ambas enzimas de forma similar, aunque la dinámica posterior de las dos enzimas fue diferente. La β-glucosidasa mostró ser muy resiliente después del incendio, mientras que la fosfatasa ácida no mostró señales de recuperación. Los resultados mostraron también una influencia positiva de las especies rebrotadoras en la recuperación de las enzimas.

CONCLUSIONES GENERALES

El estadio de sucesión después del abandono de cultivos en un paisaje mediterráneo modula la severidad del fuego y la recuperación de las plantas después de los incendios. Los herbazales secos se quemaron con baja severidad y se recuperaron rápidamente después del incendio, mientras matorrales y pinares, que se quemaron con mayor severidad, mostraron una menor tasa de recuperación de su cobertura vegetal.

Siete años después del incendio, tanto los aulagares como los pinares estudiados dieron lugar a comunidades de especies arbustivas similares, dominadas por especies germinadoras altamente inflamables como *U. parviflorus* y especies del género *Cistus*. Esto contribuyó a homogeneizar la estructura del paisaje hacia un tipo de vegetación más propenso a los incendios, aumentando el riesgo de nuevos incendios en el futuro.

Los pinares mostraron los mayores cambios en la estructura de la comunidad después del incendio y la recuperación de la cobertura vegetal fue más baja a corto plazo, por lo que pueden ser considerados como el más vulnerable de los tres estadios de sucesión estudiados, sobre todo si después de los incendios se suceden años relativamente secos.

La severidad del fuego ejerció un efecto filtro en los atributos de regeneración de las especies y, por lo tanto, sobre la composición funcional en matorrales mediterráneos, de manera que la mayor severidad favoreció al grupo funcional de germinadoras obligadas.

En tres comunidades vegetales mediterráneas comunes – herbazales secos, aulagares y pinares – la relación de abundancia germinadoras/rebrotadoras apenas varió a baja severidad del fuego pero aumentó rápidamente con el aumento de la severidad, lo que llevó a una relación no lineal positiva entre la abundancia relativa de especies germinadoras y la severidad de los incendios.

Los atributos estructurales y funcionales de las especies modulan la respuesta de las funciones del suelo a la perturbación por el fuego, en términos de resistencia (la cantidad de cambio causado por el fuego) y de resiliencia (capacidad de recuperación después de un incendio). La resistencia del suelo pareció estar más influenciada por los rasgos estructurales de las plantas relacionadas con el consumo potencial de combustible, mientras que la capacidad de recuperación del suelo estuvo altamente determinada por la estrategia de regeneración post-incendio de las especies vegetales (rebrotadoras vs germinadoras).

Las funciones de los suelos fueron más resistentes y resilientes en manchas de vegetación de especies rebrotadoras, mientras que las funciones del suelo en manchas de vegetación de especies germinadoras con alto contenido de combustible fino muerto fueron menos resistentes.

En matorrales mediterráneos, los grupos funcionales relacionados con los atributos de regeneración post-incendio (germinadoras obligadas y rebrotadoras) modulan la actividad de la fosfatasa ácida y β-glucosidasa. En manchas de arbustos dominados o co-dominados por especies rebrotadoras, se registro una alta actividad de ambas enzimas en comparación con la actividad enzimática del suelo bajo manchas de arbustos germinadores y en la matriz de suelo entre las manchas de arbustos.

El fuego redujo la actividad enzimatica tanto de la fosfatasa ácida como de la β-glucosidasa en el corto plazo. Sin embargo, estas enzimas mostraron diferencias en la capacidad de recuperación. La β-glucosidasa, una enzima dependiente de la disponibilidad del sustrato, que está implicada en la degradación de la celulosa y es producida principalmente por microorganismos, demostró ser muy resiliente después del fuego. Por el contrario, la fosfatasa ácida, que se produce principalmente por las plantas, no mostró ningún signo de recuperación en los primeros tres años después del incendio, probablemente debido al efecto combinado de fuego y la sequía post-incendio.

En general, los resultados sugieren que la influencia positiva de los arbustos rebrotadores sobre la actividad enzimática del suelo es muy resistente al fuego. Sin embargo, el contraste entre las respuestas de los diversos tipos de enzimas al fuego y a la sequía podría alterar en gran medida la dinámica de los ciclos de nutrientes.

Agradecimientos

En primer lugar quiero expresar mi más profundo y sincero agradecimiento a Susana, directora de esta tesis, por haber confiado en mi persona, por la dirección de este trabajo, porque sin su valiosa ayuda no habría sido posible la realización de esta tesis; pero sobre todo quiero agradecerle por la motivación y el apoyo recibido a lo largo de estos años, que algunas veces han ido más allá del ámbito profesional.

Mi especial reconocimiento también para Barron Orr (Universidad de Arizona), por la corrección del ingles de los capítulos de esta tesis, y por su disposición a ayudarme siempre que lo he necesitado. Gracias a Dan Malkinson (Universidad de Haifa) y Ángeles por su importante contribución en diferentes capítulos de la tesis y por mucho más…

También quiero dar las gracias a Jorge Mataix Solera, Cesar Guerrero, y colaboradores de la Universidad Miguel Hernández, por su valiosa ayuda en la puesta a punto de diversas técnicas de análisis de suelos, y por resolver siempre mis dudas.

Igualmente quiero agradecer a Jacob Keizer de la Universidad de Aveiro, por facilitar mi visita a Aveiro, por permitirme muestrear en sus parcelas experimentales, y por la cálida acogida. Gracias a Oscar por su gran ayuda en la organización de la logística de campo y todo lo demás, gracias también a Ana y Mohamed por facilitarme las cosas en mi corta estancia en Aveiro.

Gracias a la gente del CEAM, en especial a Ramón Vallejo, quien siendo el vinculo entre el instituto Agronómico de Zaragoza y la Universidad de Alicante, propicio que yo llegara a Alicante. Gracias a Joan (y Maribel), Jaime y Alejandro, que siempre han mostrado la mejor predisposición para ayudarme a resolver mis problemas y darme consejos, gracias porque estos años siempre he podido contar con vuestra amistad. A José Antonio Alloza y David Corell porque siempre me han facilitado la información que he requerido (mapas y datos climáticos), a Teresa Gimeno con quien he compartí algunas campañas de campo, y muchos momentos entrañables fuera del trabajo.

Un especial reconocimiento al personal del departamento de Ecología, Andreu Bonet que siempre ha resuelto mis dudas, Jordi Cortina porque me permitió sumergirme en el mundo de las costras biológicas del suelo y el esparto mientras trabaje con su equipo. A Fina que ha resuelto muchos de mis problemas de papeles. A Fran Barrero y José que me han facilitado el trabajo en el laboratorio.

Gracias a los que con paciencia han soportado conmigo las intensas jornadas de campo: Cholo ha sido mi guía en Guadalest, con Víctor he pasado muchas horas al sol muestreando en Onil, Pardines y Ayora, Diana ha sido mi compañera de campo en Ayora, y Fran algunas veces también ha sido parte del equipo Ayora.

No puedo olvidar a mi equipo las super nenas Ángeles, Diana, Luna, Azucena, Anna, Lorena, y la otra parte del equipo Fran y Cholo; y al nuevo fichaje el pequeño Didac, gracias por ser más que compañeros, incluso más que amigos; gracias por los buenos momentos compartidos dentro y fuera del trabajo, por aguantarme y por escucharme en los buenos y malos momentos.

Un recuerdo especial para quienes han compartido conmigo estos años, Federico mi primer compañero de despacho, Juan Peña que no esta entre nosotros pero a quien nunca olvidaremos. Noelia con quien he compartido incontables horas muestreando costras biológicas del suelo y espartos en el campo, y otras tantas en el laboratorio. Son muchos más los que han pasado por el departamento, a quienes recordare siempre con mucho cariño, Jamal, Román, Marian, Raquel, Estrella, Juanjo, Carolina, Isabel, Amina, Eva, Anahi, Alma, Haroun, Silvana, Dinorah, Thanos; y no puedo olvidar a los que siguen aquí: Beatriz Terrones, Beatriz Amat, Esteban y Hassan, y tampoco a los brasileños Vania, Alessandra, Leandro, Alexandre, Beth, Mariana y Talita.

A Karen, David, Marina, Alberto, Adela, Esther, JuanAn, María, Firas, gracias por vuestra amistad, y por hacerme parte de vuestras vidas, hacéis que las cosas sean más llevaderas cada día; gracias también a la nueva generación Iván, Héctor, Jimena y Alex porque ahora son ellos los que animan nuestras reuniones. A quienes veo poco pero me gustaría ver con más frecuencia, Dani, Mila, Adrián, la pequeña Pili y Antonio Egido por acogerme con tanta

familiaridad desde el primer día que los conocí, a todos gracias por ser unas personas maravillosas conmigo.

Un especial agradecimiento a mi familia, a mi madre Rufi a quien le debo tantas cosas, ella es mi fuerza para seguir siempre adelante cuando mi ánimo decae. A mis hermanos Angélica, Ana, Miriam, Carlos y Susan porque sé que siempre puedo contar con ellos a pesar de la distancia; gracias por vuestro permanente e incondicional apoyo y cariño. A mis sobrinos Pamela, Adriana, Kenji y Sebastian por las alegrías que nos dan desde que nacieron. Gracias por estar ahí.

Si pienso en familia no puedo olvidar a la familia que he encontrado en Monóvar, Antonio y María y todos los demás incluido los pequeños Samuel y Laura, gracias porque siempre hacéis que me sienta bien.

Por último, a Antonio, quiero agradecerle todo; su infinita paciencia, su apoyo y su buen humor hacen que las cosas sean más fáciles; porque a su lado todo tiene sentido.