Which pyrodiversity for what biodiversity? A multi-scale comparative study of two Mediterranean ecosystems

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Which pyrodiversity for what biodiversity?
A multi-scale comparative study of two Mediterranean ecosystems.

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Abstract (French)

Contexte & Objectifs

Le feu est une perturbation récurrente dans les écosystèmes méditerranéens et est souvent considéré comme une composante intrinsèque pour le fonctionnement de ces écosystèmes. Cependant, le rôle des incendies de forêt sur la biodiversité reste controversé. Ainsi, bien que la perception de cette perturbation par la communauté scientifique prenne en compte les effets négatifs et positifs, le feu reste pour une grande part de l'opinion publique une catastrophe humaine et environnementale. Mes recherches ont eu pour objectif de quantifier les effets du feu sur la biodiversité végétale dans les écosystèmes à climat méditerranéen en abordant la relation feu-biodiversité à différentes échelles et en particulier en considérant les caractéristiques spatiales et temporelles des mosaïques générées par les feux au niveau du paysage. L'étude a été dupliquée dans deux biomes méditerranéens distincts (France méditerranéenne et Sud-ouest Australien) de sorte à rechercher à travers les différences les patrons de réponse communs.

Méthodologie

Généralement, les feux ont été étudiés comme des évènements singuliers dont il convenait de mesurer l'impact sur les écosystèmes. Dans cette étude, les feux ont été considérés comme une succession d'évènements formant au niveau du paysage des mosaïques en s'additionnant dans le temps et en se superposant dans l'espace. La diversité de ces mosaïques a été quantifiée et a permis de définir un nouveau paramètre, la pyrodiversité. Mes recherches proposent une méthodologie objective et adaptée à la caractérisation de la pyrodiversité à l'échelle du paysage. Les patrons de feux, compilés sur 50 ans, ont été analysés et la diversité de la végétation (habitats, espèces et traits fonctionnels) a été échantillonnée en suivant le protocole développé dans le cadre du projet Européen EBONE. En utilisant la même échelle géographique pour croiser patrons de feu et patrons de végétation, il a été possible de relier pyrodiversité et biodiversité et d'examiner cette relation simultanément au niveau de la communauté végétale (habitat) et du paysage (mosaïque d'habitats).

Résultats

Cette étude démontre qu'une pyrodiversité élevée (grande variabilité des patrons spatio-temporels des feux à l'échelle du paysage) est associée à des stades de succession de

végétation plus variés et de ce fait maximise la diversité des habitats au niveau du paysage. Les résultats acquis permettent de montrer que le feu exerce une influence significative, avec d'autres facteurs comme les conditions environnementales ou l'utilisation du sol, sur la composition des habitats ainsi que sur l'hétérogénéité spatiale de la mosaïque d'habitats au sein du paysage. Que l'on considère les effets du feu sur les espèces végétales ou les traits fonctionnels de ces taxons, mes travaux montrent également que la diversité des plantes vasculaires au niveau de l'habitat varie avec la fréquence des feux suivant l'hypothèse de perturbation intermédiaire. À l'échelle du paysage, la relation pyrodiversité-biodiversité vérifie l'hypothèse de perturbation hétérogène : les maxima de diversité alpha et beta ont été observés lorsque les mosaïques de feux étaient caractérisées par un niveau élevé de pyrodiversité. À l'échelle régionale, la pyrodiversité favorise la diversité des habitats (diversité gamma) jusqu'à un certain seuil. Les deux aires d'étude affichent des profils de pyrodiversité contrastés, du fait de leurs gestions opposées du feu, mais égalemet des flores très contrastées. Il en résulte des différences de résilience et résistance au feu au sein de leurs écosystèmes respectifs. Toutefois, les deux biomes méditerranéens et leur végétation présentent des convergences évidentes dans leurs réponses écologiques au gradient de pyrodiversité.

Conclusions

Cette étude permet de resituer le rôle du feu et sa contribution à la richesse floristique des écosystèmes méditerranéens. Même si l'on peut se poser la question de la nécessité des feux pour le fonctionnement de ces écosystèmes, les biocénoses actuelles requièrent un niveau suffisant de pyrodiversité pour maintenir la diversité de leurs habitats et de leurs flores. Les effets du feu ne peuvent donc pas être déduits directement de la réponse locale d'un écosystème à un feu, mais doivent prendre en compte la complexité spatio-temporelle des répétitions des perturbations qui génèrent des mosaïques complexes et favorables à la biodiversité au niveau du paysage.

Ces recherches mettent également en évidence que biomes méditerranéens n'ont pas une réponse homogène, mais répondent en fonction de leurs spectres fonctionnels (diversité de formes de vie) et de leur position au sein du gradient de pyrodiversité. Dans un contexte où le changement climatique et les pressions humaines ont une influence croissante sur l'environnement, cette étude offre une perspective innovante sur l'importance du feu en milieu méditerranéen tout en proposant une base de connaissances nécessaire à l'amélioration des stratégies actuelles de gestion du feu en milieu méditerranéen.

Abstract (English)

Aim and Background

Fire is an integral component of Mediterranean type ecosystems and other fire-prone systems worldwide but the perception of fire as an ecological disaster remains a widely-held view among human societies. Understanding whether and to what extent fire is beneficial or detrimental to biodiversity is a current research priority for conservation management in fire-prone systems.

My research has attempted to quantify the multi-scale effects of fire on various facets of vegetation diversity, including landscape diversity, taxonomic diversity and functional diversity from a landscape ecology perspective. We used two contrasted Mediterranean study cases i.e., south-eastern France and south-western Australia in order to distinguish from their differences common ecological patterns.

Methods

Fires and their effects on vegetation are normally studied as single and localized events. Here, we considered landscape-scale fire mosaics resulting from the compilation of fire events that occurred among time and space in a given landscape. The diversity of those fire mosaics has been quantified and permitted to define a new parameter i.e., pyrodiversity. This research proposes a conceptual and practical methodology for the objective characterization of pyrodiversity based on the comparison of two Mediterranean environments: south-west of Western Australia and southern France. Fire patterns were analyzed retrospectively over a 50-year period while vegetation, habitats and species diversity were quantified at the landscape scale using a monitoring protocol developed within the EBONE EU-project. Using the same geographical scale for fire and vegetation patterns permitted to cross the information on biodiversity and pyrodiversity. The relationship between pyrodiversity and biodiversity was examined at the community level (i.e., habitat) and landscape level (mosaic of habitats) with considering successively habitat diversity, taxonomic diversity and functional diversity.

Results

This study provides evidence that high pyrodiversity (i.e., spatio-temporal diversity of fire patterns) is associated to various successional trajectories of vegetation and thereby maximizes the diversity of habitats at landscape scale. The results indicate that fire significantly contributes with environmental factors and land management to determine the

composition of habitats across a landscape and spatial heterogeneity of landscape mosaics. Whether considering the effects of a single fire event on plant species or on plant functional traits, I found that plant diversity varies with fire frequency according to the intermediate disturbance hypothesis at the habitat level. At the landscape level, the pyrodiversity-biodiversity relationship verified the heterogeneous disturbance hypothesis i.e., maxima of alpha and beta diversity are associated to fire mosaics of high spatiotemporal heterogeneity. At the regional scale, pyrodiversity enhances habitat diversity (gamma diversity) within the landscape until a certain threshold. The two studies areas display contrasting profiles of pyrodiversity due to their different fire management strategies but also exhibit taxonomically unrelated floras. Hence, the two Mediterranean biomes were characterized by different ecosystem resilience and resistance to fire. Despite these differences, the two Mediterranean biomes show convergence trends in their ecological response to the gradient of pyrodiversity.

Conclusion

This study tackled the Pyrodiversity-Biodiversity paradigm and demonstrated that Mediterranean-type ecosystems need pyrodiversity to maintain the variety of habitats and species at both habitat and landscape levels. Fire effects on vegetation cannot be interpreted directly from a local perspective with considering a single fire event. Therefore, it is necessary to consider the spatio-temporal complexity associated to recurrent fires that originate heterogeneous and favorable conditions to maximize biodiversity at the landscape level.

Moreover, this research highlights that ecological responses to fire are different from one Mediterranean biome to another because of different life forms spectra but also because they occupy different positions within the gradient of pyrodiversity. In the context of climate change and intensification of human pressures on the environment in Mediterranean-type ecosystems this research offers an innovative ecological perspective in replacing the contribution of fire to biodiversity found in Mediterranean-type ecosystems while providing a sound basis of knowledge to strengthen and improve current fire management for conservation issues in Mediterranean areas.

Table of Contents

List of Figures

List of Tables

Glossary

The glossary that follows lists alphabetically the most common terms used in this study.

Alpha, Beta and Gamma diversity: Whittaker (1965) distinguished three forms of diversity: α-diversity is the diversity within individual communities, β-diversity represents the relative extent of differentiation of communities along environmental gradients and γ-diversity was encompassing the diversity of vegetation patterns among the landscape. In the following, I refer respectively to alpha and gamma diversity as 'inventory diversity' and to beta diversity as 'differentiation diversity' according to the terminology of Jurasinski et al. (2009).

Biodiversity: 'Biodiversity' is the variety and variability among living organisms and the ecological complexes in which they occur. In common usage 'biodiversity' is often taken to be the variety of vertebrate animals and vascular plants but in reality it encompasses the ecosystem or community diversity, species diversity and genetic diversity. In the present contribution, as the focus is on vascular plants, biodiversity refers to plant diversity.

Diversity indices: Diversity indices provide important information about rarity and commonness of species in a community. Diversity indices such as the Shannon's index or the Simpson's index account for both abundance and evenness of the species presents whereas pecies richness (i.e., the number of species present) is based on presence/absence data.

Ecological niche: An ecological niche is the range of environmental conditions in which a population is currently found (realized niche) or may persist in the absence of competition between species (potential niche).

Fire mosaic: Wildland fires create a mixture of totally burned, partially burned, and unburned patches called a fire mosaic. The varying degrees of burn are a result of many factors including wind shifts, daily temperature changes, moisture levels, and varying chemical composition of the vegetation. The fire mosaic results in diverse regrowth rates that create the landscape mosaic or mosaic of habitats.

Fire regime: Fire regimes are the patterns of wildland fires that include factors such as frequency, extent, intensity, type, and season. Fire frequency is the number of fire events in a given area over a specific time. Fire intensity is the energy release per unit length of flame front.

Fire return interval: Fire return interval or fire cycle refers to the number of years between two successive fire events at a specific site or an area of a specified size.

Fuel Load: Fuel or fuel load describes the amount of available and potentially combustible material (vegetation); it is usually expressed as tons/acre.

Functional diversity: Functional diversity can be considered as the variety of responses expressed by species in the ecosystem to environmental change. High functional diversity indicates a high degree of niche differentiation, and thus low resource competition. Plant communities with high functional diversity have usually an efficient use of resources, which further enhances ecosystem functioning. Here we consider functional diversity as the variety of plant species groups with similar regenerative and adaptative traits (see definition of Life form and Plant functional trait).

Habitat: In Ecology, a Habitat is the physical environment in which an organism lives, and which provides for all (or almost all) of its needs. This concept was extended in this study to describe any landscape element composing an area of land that can be consistently defined spatially in the field in order to define the principal environments in which particular organisms live. In this way, habitats are not strictly linked to a single species and can either be urban areas, tall evergreen shrublands or herbaceous crops.

Landscape: I refer to the term 'landscape' when considering the mosaic of vegetation types, landforms and land uses (i.e., mosaic of habitats). As a general rule, I use the term 'landscape scale' or 'landscape level' to refer to the 1km scale, at which I choose to characterize landscape patterns. Regional landscape scale encompasses the different landscape mosaics present in a region.

Landscape metrics: Landscape metrics are indices (algorithms) developed for categorical map patterns that quantify specific spatial characteristics (e.g., area, shape, diversity) of patches, classes of patches, or entire landscape mosaics.

Life form: The idea of 'life form' has been proposed by Danish botanist J. E. Warming to describe the ecological significance of a group of plants with similar adaptive structures different plant forms in any ecosystem. The concept of life forms is based on the structures of aboveground and underground vegetative organs of plants and is connected with the rhythm of their development and their longevity. Danish biogeographer C. Raunkiaer elaborated a classification based on the position of growing points in relation to the surface of the soil under unfavorable conditions (in winter or during drought). I used in this study the life form classification developed in the EBONE project (Table 6.1).

Plant functional trait: Plant functional traits (PFTs) encompass the physiological attributes that condition how a species responds to a disturbance or change in environment (functional response traits) as well as the plant characteristics that determine how that species affects ecosystem properties (functional effect traits). Note: Only the functional response traits will be considered in this study.

Plant regenerative trait: In this study, I use the term 'plant regenerative trait' to describe the post-fire regenerative strategies exhibited by plant forms. Two main regenerative PFTs are observed within Mediterranean-type ecosystems: (i) the ability to resprout after fire from epicormics or underground organs (resprouter species) and (ii) the capacity to have their seed recruitment stimulated by fire (seeder species).

Prescribed burning: Prescribed burning refers to the planned use of fire to achieve specific land management objectives (e.g., mitigation of wildfires risk), where fire is applied under specific environmental conditions (i.e., mild weather conditions) to a predetermined area.

Pyrodiversity: Pyrodiversity describes the spectrum of fire regimes within any given landscape and refers to the variability in recurrence, intensity, seasonality and dimensions of fire patterns across that landscape (Martin and Sapsis 1991, Faivre et al. 2011). Pyrodiversity in all fire-prone systems is determined to a large extent by climatic conditions and terrain characteristics but also increasingly by human influences.

Resilience: Here, resilience is defined as the ability of a system to absorb and recover a disturbance event (e.g., fire) with no fundamental change of its structure (i.e., ecosystem processes, species composition).

Resistance: Resistance or inertia refers to the capacity of a system to continue to function without change when stressed by disturbance

Wildfire: A wildfire is a fire of natural origin (e.g., lightning) or caused by humans but that is not meeting land management objectives.

Statement of Candidate Contribution

The present thesis has been completed during the course of my enrolment at the University Paul Cézanne of Aix-Marseille to obtain the degree of Doctor of Philosophy. This manuscript has not previously been accepted for any other degree in this or any other institution. This thesis is my own work, except where otherwise acknowledged. It is a condition of use of this dissertation that anyone who consults, must recognize that the copyright rests with the author and that no quotation from the dissertation and no information derived from it may be published unless the source is properly acknowledged.

This thesis is presented as a series of manuscripts (Chapters 3-6) that have either been published (Chapter 3) or in the submission process (Chapter 4-6) to peer-reviewed journals. I was the main contributor for each of these core chapters, and was in charge of data collection, statistical analyses, and manuscript preparation. These manuscripts also have co-authors, namely my supervisors Drs Philip Roche, Matthias Boer, Pauline Grierson and Lachlan McCaw, who provided statistical and technical advice for analyses in each chapter, as well as editorial advice to improve the clarity and content of the writing.

Signed ______________________ Date ______________________

Nicolas Faivre

Signed ______________________ Date ______________________

Philip Roche – coordinating supervisor

Note:

The core chapters of this thesis were prepared for the publication requirements of specific journals and thereby may present minor inconsistencies in formatting and notation. As each paper is a "stand-alone" paper, there is also some unavoidable repetition in the text among chapters (e.g. the study area sections of the chapters).

Prologue

In many parts of the world, fire is primarily perceived as a threat to human life and property and as an ecological disaster causing irreversible damages to Nature and its biodiversity. Population experience of catastrophic wildfires over the last decades in many parts of the world (e.g., 2003 in Europe, 2009 in Australia) has served to reinforce this belief. Globally, wildfires annually burn an area equivalent to about half of the Australia continent (ca. 600 billions hectares) and can have major impacts in terms of deforestation, climate change and biodiversity. However, contentions that fire is a threat to nature fail to make distinctions about different types of fires and disregard the fact that nowadays 90% of worldwide wildfires are caused by human activities.

Fire is a paradox- it is both a disturbance that can cause extensive ecological damages, but it is also nature’s way to ensure the regeneration and the persistence of biological systems. Fire is an old phenomenon that has largely contributed to shape the evolution of the vegetation of many biomes including Mediterranean areas. We thus need to recognize that fire is one of the main factors that helps in maintaining this precious treasure we call “Biodiversity”.

1. General Introduction

Motivation

Is fire an ecological disaster in Mediterranean ecosystems or conversely, does fire maintain their specific biodiversity? The purpose of this thesis is to tackle the controversy lying between fire and biodiversity from a multi-scale perspective. My research seeks to quantify the effects of fire on multiple facets of vegetation diversity, including landscape diversity, taxonomic diversity and functional diversity. This research focuses on Mediterranean-type environments because they are among the most heavily disturbed by fire and among the most biodiverse regions on Earth. In this introductory chapter, I provide an overview of the current state of biodiversity in Mediterranean type ecosystems and introduce the role of fire as an ecological process. I also review the current state of knowledge and existing theories on fire-biodiversity relationships before identifying the knowledge gaps this study will be addressing.

Biodiversity in Mediterranean environments… and why does it matter?

Mediterranean-type ecosystems (hereafter named MTEs) lie between 30-45 degrees latitude north and 30-40 latitude south along the western edges of all continents (Fig. 1.1). The five Mediterranean-climate regions comprise about 3% of the Earth's land area but account for 16% of the world's flora (i.e., 48,250 vascular plant species; Cowling *et al.* 1996). In particular, the Cape Region of South Africa and the southwest of Australia show remarkable levels of species richness and endemism considering their relatively small size. Nearly 80% of the plant species (ca. 3,000 species) of southwestern Australia can be found nowhere else in the world. All five Mediterranean biomes contain biodiversity hotspot areas, defined as region gathering at least 1,500 endemic species of vascular plants (> 0.5% of the world's total), and having lost at least 70% of its original habitat size (Myers 1988, 1990).

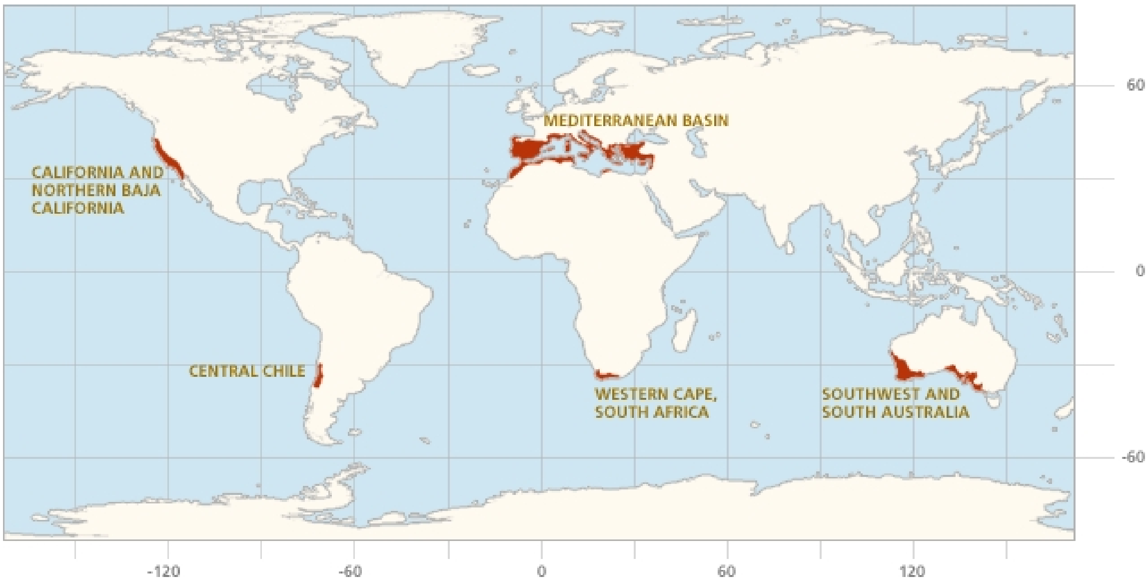


Fig. 1.1 The five Mediterranean-climate regions of the world

There is considerable concern about the conservation of biodiversity in MTEs around the world, not only because species and habitats within these hotspots are rare, threatened of extinction, or show evolutionary uniqueness, but also of the recognition that biodiversity has an economic value (Costanza *et al.* 1997). Biodiversity directly benefits our well-being by contributing to the quality of life, supports local economies by providing food and ensures the regulation of natural processes (Díaz *et al.* 2005). The significance of such ecosystem services for human well-being has been highlighted, amongst others, by the recent publication of the Millennium Ecosystem Assessment (MEA, 2005).

Biodiversity is also of significant importance for the regulation of ecosystem-level biogeochemical functions (i.e., capture, storing and transfer of carbon, water and nutrients). However human pressures may impact biological systems at a rate faster than research can supply ecological insight, especially regarding the extent to which biodiversity can be reduced without significantly and irreversibly altering ecosystem functioning. Over recent decades, many studies have highlighted the importance of biological diversity for enhancing ecosystem productivity and the fluxes of matter and energy such as nutrient cycling, carbon storage or hydrologic cycles (Tilman *et al.* 1996, Hooper *et al.* 1997). For example, in a recent comprehensive review, Hooper et al. (2005) listed several effects of biodiversity on ecosystem properties. First, the influence of biological diversity can be null if the changes in abundance or richness of species are not significant enough to alter process rates or pool sizes. Alternatively, an increase of species or functional richness may be associated with the likelihood of key species dominance and lead to competitive success (i.e., the selection probability effect; Tilman *et al.* 2001), thereby enhancing ecosystem productivity. In other respects, species or functional diversity may also increase ecosystem pools and process rates through facilitation and complementary processes (Bruno *et al.* 2003). A conceptual framework proposed by Hooper et al. (2005) is reproduced in Figure 1.2 to describe the linkage between biodiversity, ecosystem functioning and services, and human activities within the scope of global changes and abiotic controls.

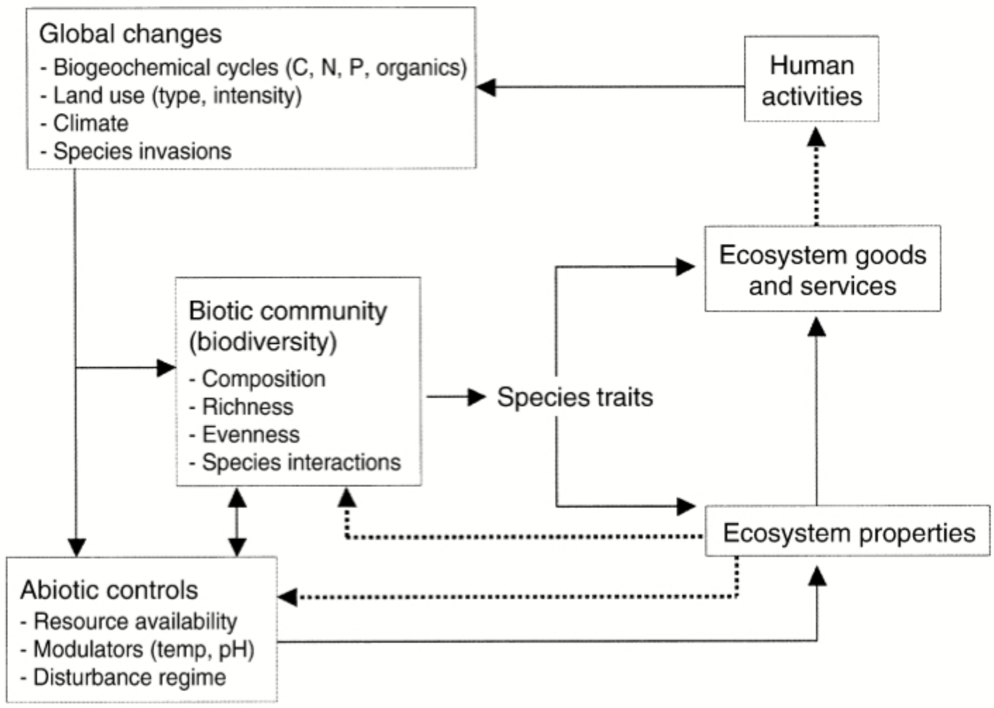


Fig. 1.2 Feedback mechanisms between human activities, biodiversity and abiotic controls.
Various aspects of biodiversity can modify the range and proportion of species traits. A gain or loss of key species traits represented in the biotic community may further alter ecosystem properties and ecosystem services. Changes in ecosystem properties can feed back to further alter the biotic community either directly or via further alterations in abiotic controls (dotted lines). Feedbacks from altered goods and services can lead to modification of human activities that will furher impact biodiversity through global changes. This diagram can be found in Hooper *et al.* (2005).

Threats to Biodiversity in a changing world

All Mediterranean regions are characterized by an increasing human pressure due to their favorable climate conditions and coastal localization. Human activities impact biodiversity directly through population density and growth of urban areas (Schwartz *et al.* 2006) or through land use change such as the conversion of natural habitats to agricultural systems (Hobbs *et al.* 1998) and indirectly, by modifying the regime of natural disturbances as suggested by Montenegro et al. (2004). The threats differ from one Mediterranean region to another depending on the overriding human activity. For example, the population density of California-Baja California is the highest of the five Mediterranean regions and is positively correlated with the number of threatened plants (Underwood *et al.* 2009). In southwestern Australia, intensive agro-pastoral activity has transformed a substantial part of native bush to arable land for wheat cultivation. As a result, only 2-3% of the native habitats exhibiting rare and endangered taxa remain from the original area (Underwood *et al.* 2009). In the time span between the European settlements in the early 1800s and the 1990s, about 54 of the circa 7465 native vascular plant species of Western Australia may have gone extinct (Greuter 1994). Nowadays, human activities are threatening about 17% of all Mediterranean-climate vascular plant species (Vogiatzakis *et al.* 2006), through habitat fragmentation (e.g., urban settlement among the Mediterranean Basin coastline), diseases (e.g., *Phytophthora* dieback in southwestern Australia) and invasive weeds (e.g., European poisonous weed *Fumaria officinalis* in South Africa).

Besides the direct anthropogenic impact on Mediterranean vegetation, climate change is another threat that may cause considerable modifications in plant communities in MTEs (Underwood *et al.* 2009, Vogiatzakis *et al.* 2006, Sala *et al.* 2000). According to the Millennium Ecosystem Assessment (2005), global warming is about to become the overriding threat to biodiversity. Predictions of global mean surface temperature increase (i.e., 2.0-6.4 °C above pre-industrial levels by 2100) raise the probability of recurrent catastrophic events such as large high-intensity wildfires (Pausas 2004). Hence, species at risk may not survive as their niche is already constrained to patchy habitats or specific environmental conditions. The effects of a single fire event may lead locally to temporary species extinction within the landscape however the potential of permanent loss of species at a global scale lies in the alteration of landscape fire regimes (Reilly *et al.* 2006, Turner *et al.* 1994).

In addition to climate change, direct human activities may also cause significant changes in the fire regimes in these areas. Fire is the main ecological disturbance in MTEs and is managed differently in each area (e.g., near total suppression of wildfires in the Mediterranean Basin versus widespread use of prescribed fire in southwestern Australia). The consequences of climate change and land use change combined with inadequate fire management may originate cascading and irreversible ecological effects resulting in a global loss of biodiversity (Syphard *et al.* 2007). For instance, in the Mediterranean Basin region land abandonment since the 1950s has contributed to increasing fuel loads and spatial continuity of flammable vegetation types (Moreira *et al.* 2001). Strong suppression of wildfires causes further thickening of fuels. In the meantime, urban development has increased the number of ignitions. Consequently the wildfire hazard in many areas in the Mediterranean Region is very high; the extreme fire events observed in the last decade in several Mediterranean countries are evidence of the fire-proneness of these environments. Fire danger resulting from changes in land use are exacerbated by longer drought periods that are thought to result from global climate change (Mouillot *et al.* 2002). Consequences for plant communities translate to a progressive homogenization of the mosaic of habitats (Lloret *et al.* 2002), usually accompanied by a reduction of species niche and by the extinction of endemic taxa. In the light of rapid global change and increasing human influence, there is a pressing need to understand how biodiversity is constrained by biotic and abiotic factors and whether a modification of these factors is detrimental to biodiversity and ecosystem functioning.

Relationship between Fire and Biodiversity

The role of Fire in Mediterranean-type ecosystems

Fire is a major disturbance factor in Mediterranean-type ecosystems (Naveh 1975, Di Castri *et al.* 1981). Mediterranean forests and shrublands are prone to recurrent fires due to the prevailing climate with its marked bi-seasonality (i.e., prolonged summer droughts followed by winter periods with high rainfall) and often high flammability of plants. However, most fires occurring within MTEs in modern times are anthropogenic (e.g., 95-99% in the Mediterranean Basin; Ganteaume *et al.* 2009). Negligence (37%) related to forestry or agricultural activities and arson (20%) are the main identified causes of fire ignition in southern France (Ganteaume *et al.* 2009).

The incidence and spread of fires across the landscape is conditioned by multiple biotic and abiotic factors. Among them, climate and local weather conditions are believed to be the major determinants of the timing and severity of burns (Schoennagel *et al.* 2004). Topography and aspect also partially influence the spatial distribution of fire patterns. Fires are predicted to be most probable on south facing slopes and burnt areas are more likely to be distributed across ridges and upper slopes than bottom valleys in case of frequent fires (Mouillot *et al.* 2003). Combined with climatic and terrain parameters, edaphic conditions (e.g., litter and substrate composition, soil moisture) also play a key role in determining the spatial arrangement of fuel patterns (i.e., vegetation biomass) and thereby the likelihood of a fire event (Diaz-Delgado *et al.* 2004). Besides the influence of those abiotic constraints, vegetation itself exerts a strong influence on fire spread. In the Mediterranean Basin, studies have demonstrated that fires were more likely to occur in the middle and early stages of vegetation succession, usually corresponding to grasslands, shrublands or heathlands (Mouillot *et al.* 2003). These vegetation types usually feature continuous fuel patterns that favor fire spread. In addition, the Mediterranean flora shows adaptation and even predisposition to particular fire regimes. Although these adaptative traits cannot be interpreted as evolutionary responses exclusive to fire (Keeley *et al.* in press), they confer plant species the capacity to resist to and even promote a fire event as illustrated by the high proportion of pyrophytic species within the Mediterranean biomes. Some plants contain highly flammable oils (e.g., *Juniperus* spp., *Eucalyptus* spp.), terpenes or resins (e.g., *Pinus* spp., *Xanthorrhoea* spp.) that may assist fire propagation by accelerating burning speed, increasing heat output, and releasing large quantities of embers (Ormeño *et al.* 2009). Similarly, vegetative resprouting and serotiny are adaptative responses that can be found in non-fire prone systems but that are widespread over MTEs and originate in the persistence of many plant species among these areas (Keeley *et al.* in press).

There now is scientific consensus that fire has played an important role in the ecology and evolution of Mediterranean ecosystems at multiple scales and that these areas owe their floristic distribution and ecological properties to a large extent to fire (Bond *et al.* 2005, Di Castri *et al.* 1981). At the species level, many plants can be weakened or even destroyed by fire but many others rely on fire for their reproduction (e.g., dormant seed stimulation by heat or smoke, seed dispersal), the recycling of nutrients, and the removal of dead or senescent vegetation. The flora of MTEs is not adapted to fire *per se* but has selected specific adaptative traits to persist after recurrent fires (e.g., Mallee vegetation in southwestern Australia composed of species with underground root systems/lignotubers, leaf adaptations or insulated bark). At the habitat level, fire contributes to reinitialize vegetation succession stages and to promote the co-occurrence of multiple vegetation types. Ecosystem responses to fire are not uniform among the five MTEs, but they follow the succession model with different rates of recovery (Trabaud *et al.* 1980, Hanes 1971). We therefore observe among these areas a progressive return, with relatively contrasted stages, to the pre-fire structure and composition rather than a substitution of the previous plant community by another. Finally, at the landscape level, fire modifies the spatial arrangement of the mosaic of habitats either by creating new habitats of varying species composition, size, age structure or by increasing landscape homogeneity in the case of extensive fires (Moreira *et al.* 2007).

Until recently, conservation management sought to preserve natural resources by excluding any type of perturbation (human intervention or natural disturbances) that could affect the ecosystem's equilibrium. With the failure of the classical equilibrium paradigm in ecology and recognition of dynamic equilibrium as well as non-equilibrium systems (Wu *et al.* 1995, Turner *et al.* 1993), new management perspectives that integrate the historical variability of perturbations have emerged. Furthermore, fire-related forest management (e.g., site restoration with tree plantation) usually considers fires as isolated events in the landscape with omitting the effects of overlapping fires over time and space in the same region (Gill *et al.* 2002). Hence, in order to maintain the range of habitats and to preserve plant diversity within fire-prone systems, natural disturbances have to be considered from a landscape ecology perspective (i.e., consideration of disturbances at multiple spatial scales) to permit the implementation of operational and effective ecosystem-based management at landscape level.

Natural disturbance ecology and biodiversity conservation

According to White and Pickett (1985), disturbances are relatively discrete events in time that disrupt the ecosystem, community, or population structure and bring about a change in resources, substrate availability, or physical environment. The field of landscape ecology integrates natural disturbances as a main research topic and seeks to emphasize how disturbance regimes determine the distribution of plants and communities across the landscape. Disturbances operate on a wide variety of spatial and temporal scales (i.e., disturbances may affect an individual tree at a given time or a large forested area for a long period). Disturbances also impact various levels of biological organization, from the individual to ecosystem-wide. Fires can alter stand structure by killing the overstorey species, shift the patterns of plants species by modifying the biochemical processes (e.g., increase of nutrients and light availability) and therefore generate new habitats within the landscape mosaic. White and Jentsch (2001) pointed out that, in disturbance ecology, the effects of disturbance on ecosystem in dynamic equilibrium or non-equilibrium should be characterized at the patch scale as well as that at the landscape scale. Consequently, the dynamic equilibrium of ecosystems is a scale-dependent concept where disturbances greatly influence the relationship between pattern and process (Turner 2010, Turner 1989). In other words, landscape equilibrium over time relies on a suite of multidirectional post-disturbance pathways, which further contribute to shape biological diversity from the patch to the landscape level (Łaska 2001).

Applying these concepts of natural disturbances ecology to biodiversity conservation requires new research priorities as listed by Driscoll et al. (2010) with respect to the fires:
(i) characterizing fire regimes at both spatial and temporal scales and to determine how diversity is influenced by the spatial arrangement and temporal sequences of fires; (ii) developing a mechanistic understanding of responses to fire regimes using functional types as a filter of biological complexity; and (iii) determining how fire interacts with other landscape-scale processes such as land use or environmental gradients in shaping the landscape mosaic and its biodiversity.

The Pyrodiversity-Biodiversity paradigm

According to Martin and Sapsis (1991), pyrodiversity describes the wide spectrum of regimes in which fires occur and encapsulates both their spatial and temporal variability. While the fire regime characterizes fire occurrence for a point in the landscape or a landscape as a whole in terms of fire frequency, intensity, season and pattern (Heinselman 1981, Gill 1975), pyrodiversity focuses more explicitly on the spatiotemporal variation of fire by considering the changing mosaic of fire events over time. The fire mosaic combines the visible mosaic (i.e., superposition of fire patches of varying age, frequency, intensity) and the invisible mosaic (i.e., fire-interval temporal sequence of fire patches) as described by Bradstock et al. (2005).

There has been some development of theory on how pyrodiversity might be related to biodiversity. The 'Pyrodiversity-Biodiversity' paradigm states that pyrodiversity begets biodiversity (Martin & Sapsis 1992). Because there is no optimal fire regime that is suitable for all species of a given habitat, landscape or ecosystem, a diversity of fire patterns that allows the co-existence of many taxa, and hence promotes biological diversity is usually advocated (Bradstock *et al.* 1995, Burrows *et al.* 2003). However, this fire management perspective is still being debated among the fire ecology community (e.g., Parr and Andersen 2006), amongst others because most insights come from empirical assessments of the visible fire mosaic only. Only recently, has research started to characterize and analyze the invisible mosaic (Boer *et al.* 2009, Price *et al.* 2005).

Fire and Biodiversity: key knowledge gaps & research priorities

Limitations to address the Pyrodiversity-Biodiversity paradigm

Research into the effects of past fires on current biodiversity patterns is crucial for implementing sustainable conservation management in Mediterranean ecosystems. However, determining what the pyrodiversity requirements are for all organisms to persist over time remains a challenging question because the majority of studies have one or more of the following limitations: (i) Fires are usually studied as isolated events in the landscape and thus researchers investigate a limited range of fire frequencies or fire intervals for their experiments rather than pyrodiversity, which impedes the adoption of their findings to ecosystem-based management. Furthermore, (ii) most of studies are at relatively small spatial scales because there is a lack of objective methods to characterize and quantify pyrodiversity at landscape scale. Hence, the scales considered do not adequately represent either the range of vegetation types in the landscape or the scales at which management decisions are made. Consequently, (iii) fire influence on alpha diversity is relatively well documented whereas impacts of fire on other components of biodiversity such as beta diversity are less well understood. (iv) Fire ecological studies in MTEs generally tackle one group of organisms such as vascular plants or vertebrate animals at a time, while very few studies consider several groups simultaneously (Wittkuhn *et al.* 2011). Moreover, (v) the effects of fires on vegetation are mainly reported at a taxonomic level (e.g., Capitano & Carcaillet 2008, Lavorel *et al.*

1994, Trabaud 1980) while plant functional traits have only started to be considered during the last decade (e.g., Chust et al. 2006, McIntyre et al. 1999, Pausas et al. 2004). Therefore, comparative fire-related studies that may put in evidence convergence trends of vegetation dynamics in response to fire between MTEs are very scarce.

The overall objective of this study

Although fire has long been recognized as a structuring factor in all MTEs, a more quantitative understanding of the importance of variations in fire regimes at a landscape scale is still largely lacking. The purpose of this study is therefore to supply empirical evidence to characterize the Pyrodiversity-Biodiversity paradigm.

Hence, this research aims to answer the following key questions:

- How can we objectively assess pyrodiversity at the landscape level?
- How does the range of pyrodiversity influence plant diversity, from the plot to the landscape level?
- What is the effective contribution of pyrodiversity relatively to other abiotic constraints (e.g., land use, environment) in shaping vegetation patterns?
- Are current fire management strategies adapted to maintain biodiversity?

These questions rely on a more general tacit hypothesis, which states that fire is necessary to the maintainance of Mediterranean biodiversity and that the absence of this key element would generate a loss of Mediterranean-type species.

I will address the above questions based on the comparative study of two Mediterranean-type ecosystems i.e., the Provence region in southern France and the Warren region in southwestern Australia. These regions have contrasting ranges of pyrodiversity resulting from either unplanned wildfires (SE France) or prescribed burning management (SW Australia). Furthermore, this research seeks to identify potential trends of ecological convergence with respect to fire between the two Mediterranean biomes, using plant functional traits as ecosystem structural traits. If the latter hypothesis is verified, linking functional diversity to the range of pyrodiversity would have important applied significance for evaluating large-scale ecosystem dynamics in other fire-prone Mediterranean areas of the world where data availability is limited.

2. Thesis outline and methodology overview

Every chapter of this thesis could be read independently but is part of a general framework designed to address the Pyrodiversity-Biodiversity paradigm from multiple perspectives. I will firstly attempt to characterize pyrodiversity at the landscape level (Chapter 3), which set up the experimental basis of the study of fire-vegetation relationships in the next sections (Chapters 4, 5 and 6). A discussion of the results with respects to the pyrodiversity-biodiversity paradigm and several propositions towards fire management and conservation issues are finally presented in a synthesis (Chapter 7). This chapter summarizes the framework of the thesis and introduces the main methods used in this study, which are further detailed in every chapter.

Preliminary insight of the methodology

The EBONE protocol

In contrast to the characterization of landscape fire regimes (Chapter 3) whose methodology has been especially elaborated for the purpose of this study, I based the sampling and monitoring of vegetation on pre-existing European protocol designed for biodiversity surveillance (BioHab; Bunce *et al.* 2005). I participated to trial this sampling methodology in Mediterranean-type ecosystems and participated in the improvement of this protocol, which has been updated in the course of the FP7-EU EBONE project (Bunce *et al.* 2010). Consequently, some minor inconsistencies may appear in the codification or terminology between my methodology and the last EBONE protocol update as I used a former version (Bunce *et al.* 2008). The EBONE protocol initially designed to monitor habitat and biodiversity at landscape scale throughout Europe and EU-Mediterranean areas was expanded to Mediterranean regions outside Europe (e.g., South Africa, Israel, Southwestern Australia).

The basic survey area is 1km^2 within which, general habitat categories (hereafter termed GHC) are simultaneously mapped and described. (Note: when referring to site or landscape quadrat, I consider the mosaic of habitats encapsulated into a 1km^2 square unit). Preparatory work preceding fieldwork was dedicated to delineate the major aerial elements (> 400 m^2) within the landscape quadrat using aerial photograph, map or satellite images. The EBONE protocol has been designed to map aerial, linear as well as points elements, however I decided to focus only on aerial elements for time limitations reasons. For information, I estimated the full assessment of a $1km^2$ landscape quadrat, including preparatory work, habitat field description and vegetation recording, and laboratory work (e.g., plant identification, GIS layers update) to ca. 4 days.

The determination of GHCs within each site is based upon a sequence of five major categories (Urban, Cultivated, Sparsely Vegetated, Tree and Shrubs, Herbaceous). Except for the Urban, Crop and Natural non-vegetated categories, the other main categories are subdivided into Life Forms categories with distinctive qualifiers used to describe the composition of each habitat. The life form codification used in EBONE is derived from Raunkier's (1934) classification of plant functional traits. Habitats encountered in the field were further differentiated according to their vegetation structure (i.e., different layering of dominant life forms) and composition (i.e., more than 20% cover difference in key dominant life forms). The dominant life forms (>10% cover - layer view) and associated plant species occurring within this habitat were identified and their abundance recorded. Besides vegetation assessment, environmental conditions (e.g., soil profile, micro-climate) and past/current land management activities (e.g., tree plantation, herbivore grazing, abandoned crop) were also recorded for each element. An exhaustive list of GHCs and related Life Forms as well as environmental/management qualifiers can be found in Bunce *et al.* (2010). Pictures of several GHCs are also provided on the EBONE website:

http://www.ebone.wur.nl/UK/Project+information+and+products/General+Habitats+Categories/

Application of the EBONE methodology

The EBONE approach was deemed appropriate to cross the information on both vegetation and fire patterns at the community level (i.e., habitat) and landscape level (mosaic of habitats). The 1km scale permitted indeed to encompass the size range characterizing the fire patterns observed in the two study environments without omitting small fire scars while allowing to consider their overlap with extensive fires.

The preparatory work also involved updating existing fire maps with aerial photograph and satellite images. The fire contours were further verified during field assessments. In addition to the survey of habitats conformed to the EBONE protocol, comprehensive surveys of plant species were conducted within the landscape quadrat. Four $400m^2$ plots in each landscape quadrat were nested within different fire regime situations in order to complete our multi-scale approach to the species level. In each plot, I also assessed the layer structure of the vegetation by recording the abundance of dominant plant species in the different strata (i.e. below 0.5m; 0.5-2m; 2-5m; over 5m strata). The composition and abundance of life forms was also assessed at the plot level. Abundance of species and life forms at the plot level were recorded with the Braun-Blanquet method.

The two study areas i.e., the southeast of France (SF) and the southwest of western Australia (SWWA) were surveyed with the same protocol design. For logistic reasons and time limitation the sampling effort was concentrated in SF where 40 sites were visited (10 sites in SWWA).

Methodology framework overview

Apart from questioning the pyrodiversity-biodiversity paradigm this research aims to provide scope for biodiversity benefits from active fire management in MTEs. Both the characterization of pyrodiversity at operational level and the quantification of fire effects on vegetation at the species, habitat and landscape level will contribute to enhance fire management for biodiversity conservation (Fig. 2.1).

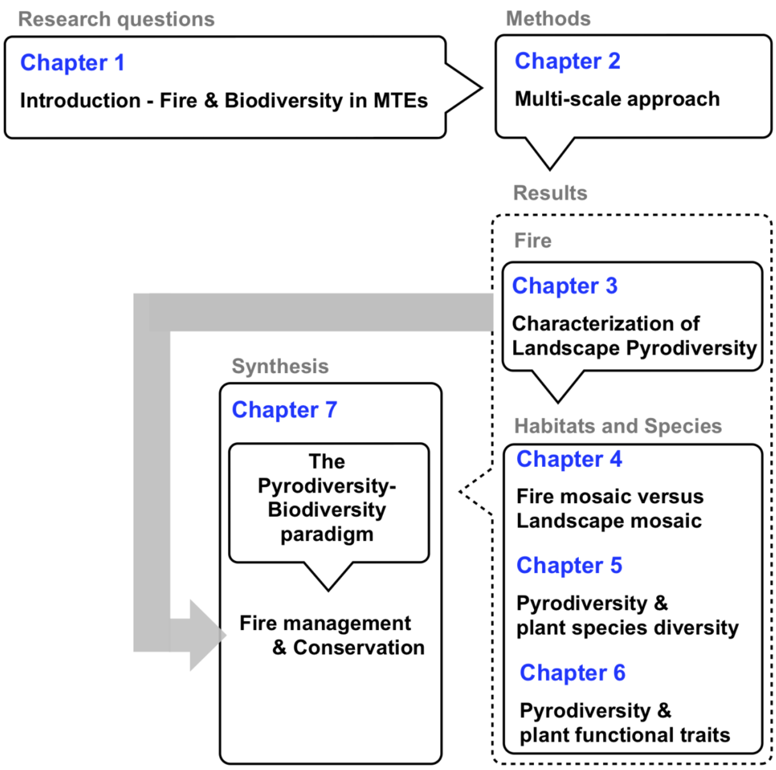


Fig. 2.1 Thesis framework

The following sections provide an outline of the methodological framework used in this research. A synopsis of the main objectives and related hypotheses of each chapter is presented in the following sections (pp. 34, 36, 38 and 40) and I summarized the methods used in each chapter with synthetic figures (pp. 35, 37, 39 and 41).

Fire mosaics in the two Mediterranean study areas

The two Mediterranean regions considered in this study support different landscape fire regimes. Fire mosaics in southern France (SF) are essentially originating from small-unplanned fires characterized by a relatively long fire return interval (Fig. 2.2). Conversely, fire mosaics in the southwest of Western Australia (SWWA) are essentially composed of large recurrent planned fires characterized by a relatively short fire return interval (Fig. 2.2).

These contrasted fire situations offered a tremendous opportunity (i) to compare the pyrodiversity of two MTEs with different fire management strategies and (ii) to relate the contrasts or similarities observed in their floristic responses to pyrodiversity.

Chapter 3 - Quantifying Landscape pyrodiversity

Objectives:

I sought to understand how fire patterns in the two study areas are organized in space and in time, and to identify differences and similarities between those two MTEs.

Hence, the objectives of this chapter were
(1) to determine which descriptors could be used to capture most of the temporal and spatial characteristics of the fire mosaic.
(2) to quantify these descriptors of fire patterns at the landscape level in two contrasting environments.
(3) to identify pyrodiversity replicates in both study areas for further comparison of ecological responses and biodiversity patterns.

Hypotheses:

I envisage that fire mosaics can be described using spatial metrics computed from temporal descriptors of the fire history at each location in the landscape.
Despite the disparate management regimes we hypothesize that the two Mediterranean environments form a pyrodiversity continuum where fire mosaics with similar characteristics might result in the same landscape patterns and ecological responses.

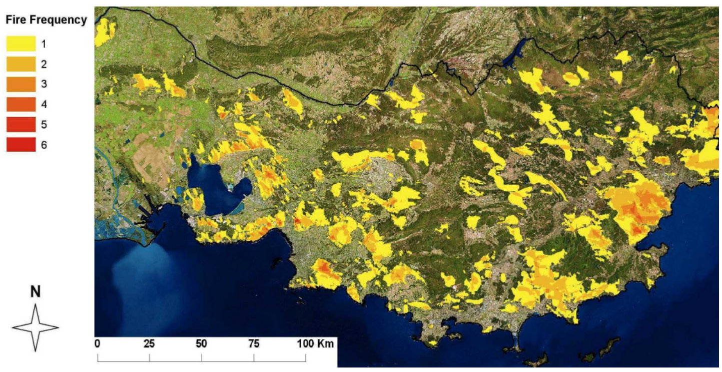
Methods (cf. Fig. 2.3):

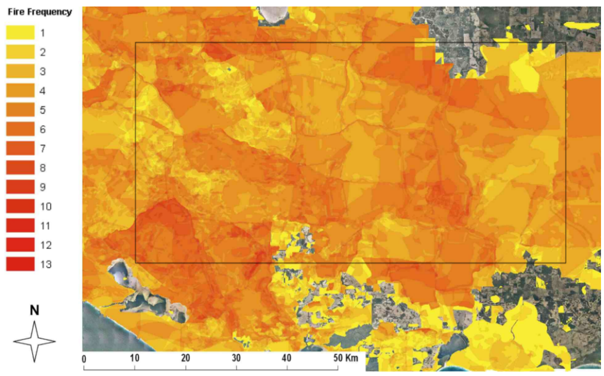
I analyzed the spatiotemporal variation of fire by considering a temporal sequence of fire patterns (i.e., fire frequency and time-since-fire) and secondly, by performing a spatial analysis of this temporal sequence using landscape metrics and basic statistics. I used a $1km^2$ grid template to select a sample of 1000 fire mosaics in each study region. After computing the statistics for each $1km^2$ fire mosaic, I further classified those mosaics according to their degree of complexity to express the pyrodiversity gradient in each Mediterranean area.

Fig. 2.2 - Fire mosaics in the two Mediterranean study areas

Southeastern France

Southwestern Australia



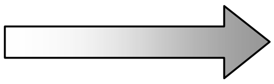


- Fine-grain scale fire mosaics
- Low to medium fire frequency
- Fire suppression management

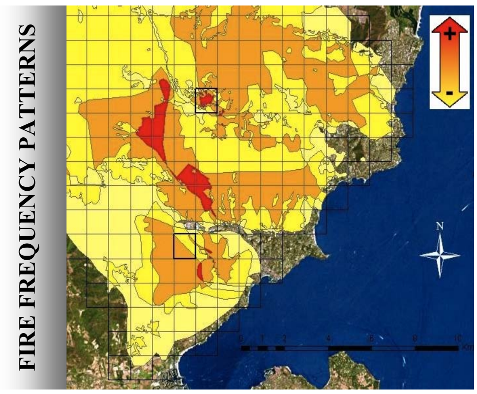
- Large-grain scale fire mosaics
- High fire frequency
- Active prescribed fire management

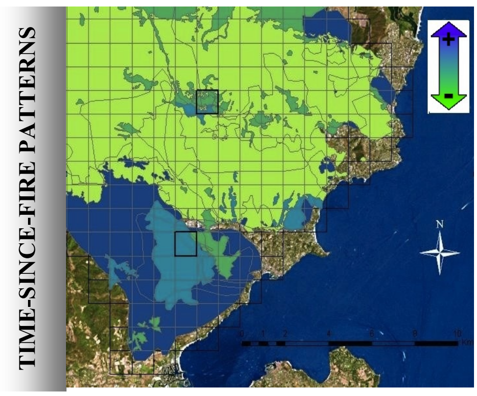
Fig. 2.3 - Quantifying Landscape pyrodiversity (Ch. 3)

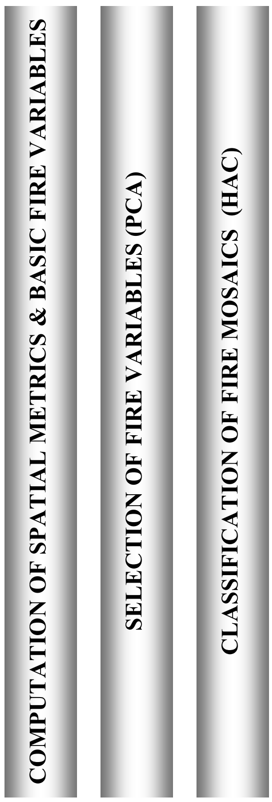
Spatial analysis of fire temporal attributes (frequency and time-since-fire) within 1km² fire mosaics.



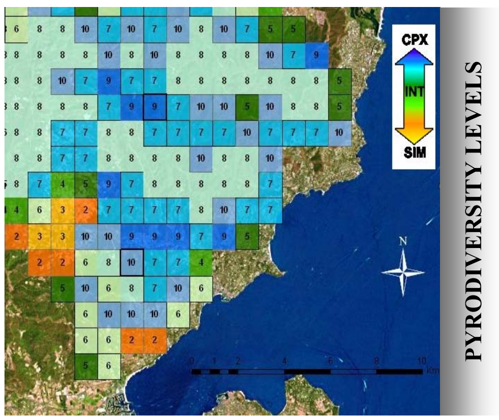
Characterization of Pyrodiversity in the two study regions.







10 pyrodiversity groups distributed over 3 main classes of fire spatiotemporal heterogeneity i.e., simple (SIM), intermediate (INT) and complex (CPX).



Chapter 4 - Fire Mosaic versus Landscape Mosaic

This chapter investigates the role played by fire in shaping landscape patterns, considering successively the composition, the spatial heterogeneity and the diversity of the landscape mosaic. The purpose of the present chapter is to quantify the contribution of fire and land use disturbances on landscape patterns in a Mediterranean area (i.e., south-eastern France) and to compare their relative importance to that of background environmental heterogeneity (terrain, climate, soils).

Objectives:

This chapter divided into two main sections: (i) the study of fire-induced land cover changes in southern France over a 20-year period considering large landscape scale (>1km^2) and (ii) at a finer landscape scale (<1 km^2) the interplay of abiotic factors on the composition and spatial configuration of landscape mosaics.

Hence, the objectives of this chapter were:
(1) to characterize the role of fire in driving broad-scale landcover transitions and fine-scale composition and spatial configuration of the mosaic of habitats.

(2) to assess how fire, environmental heterogeneity and land use relate to observed changes in composition and spatial arrangement of landscape patterns.

(3) to verify the hypothesis that increasing complexity of disturbance patterns has beneficial rather than impoverishing impact on the landscape mosaic diversity (Heterogeneous Disturbance Hypothesis; Warren et al. 2007).

Hypotheses:

I firstly hypothesize in this chapter that fire is the primary agent that determines the spatial configuration of habitats within the landscape mosaic whereas their composition is mostly determined by environmental conditions and land use practices.
Given that the probability that a large number of species can find suitable niches in a heterogeneously disturbed landscape is greater than in a landscape with uniformly distributed disturbance patches, we hypothesize that high pyrodiversity promotes landscape mosaic diversity.

Methods (cf. Fig. 2.4):

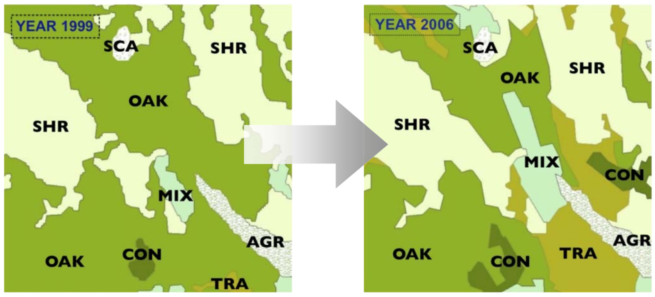
I characterized successively the broad-scale effects of fire on landcover change (A and B) and the role played by fire in shaping the mosaic of habitats at finer scales (C). In the first case, I used land cover maps to quantify landscape changes at a regional scale. In the latter case I focused on general habitats categories (GHCs) developed within the EBONE protocol (Bunce *et al.* 2005).
I also quantified the contribution of fire to landscape heterogeneity into a general context where human influence and environmental gradients are considered (cf. Venn diagram). Finally, I examine the influence of pyrodiversity on the diversity of landscape mosaics with considering the richness of habitats.

Fig. 2.4 - Fire Mosaic versus Landscape Mosaic (Ch. 4)

BROAD LANDSCAPE SCALE
(3km x 3km landscape blocks)

(A) Fire influence on land cover changes

- Selection of 50 landscape blocks with different levels of pyrodiversity (UNB, SIM, INT and CPX), various environmental conditions and land management.
- Analysis of compositional changes between 1988,1999 and 2006 based on 12 land cover categories (e.g., urban and agricultural areas, oak and coniferous forests, shrublands, etc)



(B) Fire effects on land cover transitions

Spatial analysis of landscape mosaics between 1999 and 2006. Characterization of land cover changes in spatial configuration (using landscape metrics) and composition in relation to fire patterns using co-inertia Analysis (CIA).

Analysis of land cover changes.
Legend: agricultural land (AGR), shrublands (SHR), scattered vegetated systems (SCA; habitats with clump of trees/shrubs), vegetated systems in transition (TRA; i.e., seral or interfire habitat, oak forests (OAK), coniferous forests (CON) and mixed forests (MIX).

FINE LANDSCAPE SCALE
(1km x 1km landscape quadrats)

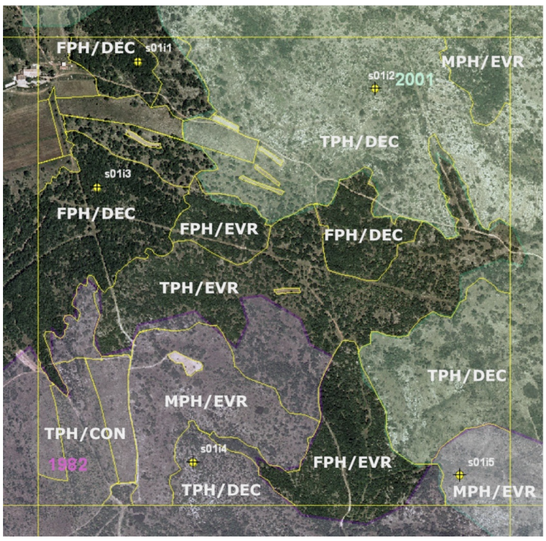
(C) Drivers of landscape heterogeneity - Focus on the mosaic of habitats.

(1) Sampling of 40 landscape quadrats (1km^2).

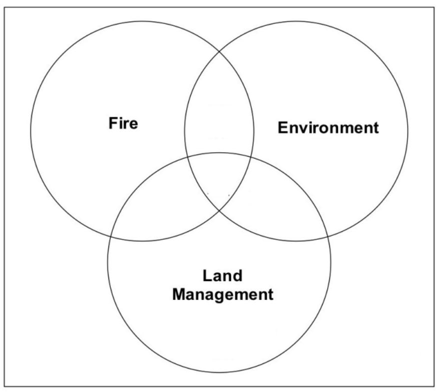
(2) Characterization of the (i) composition of the mosaic of habitats (GHCs) using typology derived from Life Forms classification, (ii) spatial heterogeneity of mosaic of habitats with landscape metrics (e.g., shape index, Shannon diversity index, edge density, aggregation index, etc)

(3) Characterization of past/current land management activities, environmental conditions (soil, topography, climate) and fire spatio-temporal history for each 1km^2 landscape quadrat.

(4) Quantification of the respective contribution of the three main abiotic factors in determining the composition and spatial arrangement of habitats within 1km^2 landscape quadrats using redundancy analysis (RDA) and variance partitioning.



Landscape quadrat - Habitats & Fire patterns



Venn diagram - RDA variance partitioning.

(5) Analysis of the effects of increasing pyrodiversity on the richness of habitats within 1km2 landscape quadrats using the three main classes of pyrodiversity mentioned previously (simple, intermediate and complex fire mosaics).

Chapter 5 - Pyrodiversity and Plant species diversity

I successively consider in this chapter (i) "inventory diversity" (i.e., alpha and gamma diversity) to describe fire influence on species richness and species-abundance at local and regional scales and (ii) "differentiation diversity" (i.e., beta diversity) for compositional similarity between landscape mosaics of different pyrodiversity levels (see Jurasinski *et al*. 2009 for definitions of inventory and differentiation diversity).

Objectives:

I sought in this chapter to address the pyrodiversity-biodiversity paradigm from a taxonomic perspective. Hence, I framed my research objectives as follows:

(1) testing the va1idity of the intermediate disturbance hypothesis at the plot level, considering the temporal effects of fire (fire frequency and time-since-fire) at a single location in the landscape on species diversity.

(2) assessing the effects of increasing landscape pyrodiversity (i.e., spatiotemporal heterogeneity of the fire mosaic) on alpha diversity of plant species.

(3) testing the va1idity of the heterogeneous disturbance hypothesis by characterizing the effects of landscape pyrodiversity on beta diversity.

Hypotheses:

I hypothesize that south-eastern France and south-western Australia exhibit different ecosystem resistance to fire partly because of their different range of pyrodiversity. Consequently, marked differences in their post-fire responses of alpha plant diversity should be observed, with the flora of SWWA being less impacted by high fire frequencies.

However, I hypothesize that both ecosystems show similar responses of beta diversity because high beta diversity will be correlated with fire mosaics of high pyrodiversity (i.e., complex fire mosaics) according to the heterogeneous disturbance hypothesis.

Methods (cf. Fig. 2.5):

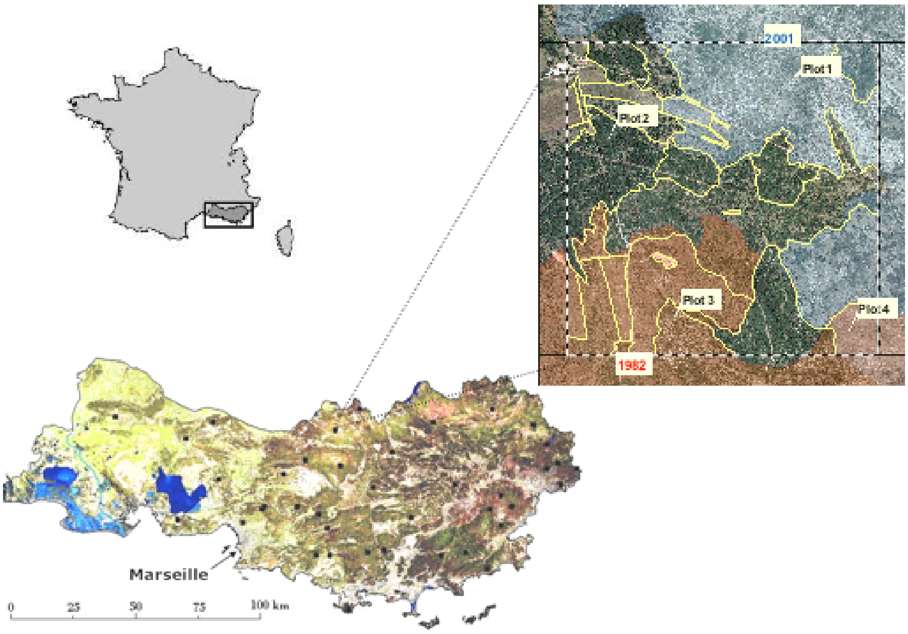
A total of 200 plots (160 in south-eastern France and 40 in south-western Australia) were surveyed during this experiment. I examined the plant diversity both within-habitats (alpha diversity) and among-habitats (beta diversity) and compare the effects of fire at each level between the two Mediterranean areas.

Fig. 2.5 - Pyrodiversity and Plant Species diversity (Ch. 5)

VEGETATION SURVEY PROTOCOL

(A) Vegetation surveys were conducted in 40 quadrats in SF and 10 quadrats in SWWA.
(B) 4 plots ($400m^2$) were selected per $1km^2$ quadrat to capture the range of fire history characterizing the site.
(C) Exhaustive assessment of the composition and the abundance of vascular plant species were conducted.

Right figure shows a zoom of a $1km^2$ quadrat selected from the French study area and depicts how plots are nested within different habitats (yellow borders) and fire scars (blue and red patches)



FIRE AND INVENTORY DIVERSITY

(D) Comparison of species inventory diversity between SF and SWWA.

(1) Comparison of alpha diversity and gamma diversity performed with Shannon diversity accumulation curves based on two equally-sized sub-samples of the two regions.

(2) Influence of a single fire regime on alpha plant diversity:
effects of fire frequency and time-since fire on species diversity (Quantile regressions)

(3) Influence of the fire mosaic on alpha plant diversity:
species diversity responses to increasing heterogeneity of the fire mosaic (ANOVAs)

FIRE AND DIFFERENTIATION DIVERSITY

(E) Comparison of species differentiation diversity between SF and SWWA.

The variations in species composition/abundance across different sites (beta diversity) were assessed using the Bray-Curtis dissimilarity index (modified version of the Sorenson's similarity measure).

I characterized the influence of pyrodiversity on species compositional variations across $1km^2$ landscape mosaics with an analysis of similarity (ANOSIM). For each study region, pairwise comparisons of mean beta diversity between pyrodiversity groups were performed.

Chapter 6 - Pyrodiversity and Plant functional traits

This chapter emphasizes on the relationship between pyrodiversity and the variability of functional diversity within and among habitats across the landscape. In order to capture the range of plant functional traits (PFTs) that contribute to functional diversity, I simultaneously considered life forms (Raunkier 1934) and specific post-fire regenerative traits (i.e., resprouter and seeder species; Pausas and Verdu 2005).

Objectives:

This chapter has three main objectives:

(1) to determine and compare the influence of fire frequency on (i) alpha diversity of life forms and (ii) richness of regenerative traits in the two Mediterranean environments.

(2) to examine the post-fire trends of alpha functional diversity according to time-since-fire.

(3) to quantify the pyrodiversity-functional diversity relationship at landscape level by considering landscape mosaics of increasing pyrodiversity and how responds beta trait diversity (i.e., life forms composition among habitats).

Hypotheses:

I hypothesize that the two Mediterranean regions exhibit contrasting trends of alpha functional diversity, whether considering life form traits or regenerative traits, as the flora of SW Australia is highly resilient to fire (i.e., recurrent fires might not affect the key-structural species).

However, similar trends of beta functional diversity in SF and SWA are likely to be observed because high pyrodiversity will promote heterogeneous landscape mosaics and thereby maximize the diversity of life forms among habitats.

Methods (cf. Fig. 2.6):

Dominant plant species and their associated functional traits (i.e., life form/regenerative trait) were recorded in each habitat within 1km^2 landscape quadrats.

First, I explored the relationship between life form diversity and fire frequency/time-since-fire at the habitat level. Similarly, I examined the differences of plant regenerative traits richness and abundance between the two Mediterranean areas. In a second step analysis, I investigate the effect of landscape pyrodiversity on functional diversity among habitats using life forms as a filter of plant trait diversity. I measured compositional dissimilarities between habitats of similar pyrodiversity and derived beta diversity responses to the gradient of pyrodiversity in south-eastern France and south-western Australia.

Fig. 2.6 - Pyrodiversity and Plant functional traits (Ch. 6)

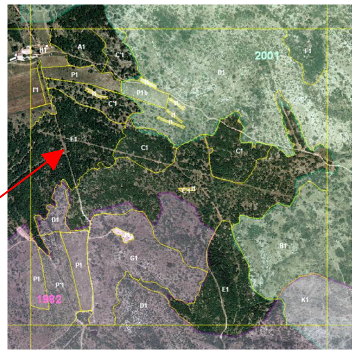
- 50 1km^2 quadrats (40 in SF and 10 in SWWA) were surveyed for recording PFTs.

FUNCTIONAL TRAITS ASSESSMENT

(A) Life forms (LFs)

(1) Recording of dominant life forms (>10% cover) in each habitat of the 1km^2 landscape quadrat.
(2) Identification of LFs based on the EBONE protocol classification (Bunce *et al.* 2008, 2010)

Life Forms	%	Species	%
FPH DEC	60	*Q. pubescens*	60
TPH DEC	30	*A. campestre*	20
TPH DEC	30	*A. ovalis*	10
LPH EVR	10	*L. etrusca*	10
…			



(B) Regenerative Plant Functional Traits (PFTs)

Attribution of fire-response traits to each species recorded: (i) resprouter (e.g., *Q.pubescens*), (ii) seeder (e.g., *P. halepensis*), (iii) resprouter-seeder (*E. arborea*) and (iv) colonizer (e.g., *A. ovata*).

ALPHA TRAIT DIVERSITY

(C) Fire effects on the diversity of life forms

Influence of fire frequency and time-since-fire on within-habitat diversity of LFs. Comparison of diversity trends between the two Mediterranean regions with quantile regression curves.

(D) Fire effects on richness and abundance of regenerative PFTs

Respective influence of fire frequency and time-since-fire on within-habitat diversity of regenerative PFTs. Comparison of diversity trends between the two Mediterranean regions with two-way ANOVAs.

(E) Post-fire successional evolution of combined PFTs

Combination of main life forms categories (i.e., trees, shrubs and herbs) with fire-response traits. Characterization of the influence of time since the last fire on the richness of combined PFTs.

BETA TRAIT DIVERSITY

(F) Effects of pyrodiversity on functional diversity among habitats

Differences in life forms composition between habitats were measured with Bray-Curtis similarity index.

The distributions of dissimilarity indices for each class of pyrodiversity (i.e., UNB, SIM, INT and CPX) were further compared and graphically interpreted (histograms of frequency of observation).

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3. Characterization of landscape pyrodiversity : contrasts and similarities between SW Australia and SE France.

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Introduction

Pyrodiversity describes the spectrum of fire regimes within any given landscape and refers to the variability in recurrence, intensity, seasonality and dimensions of fire patterns across that landscape (Martin and Sapsis 1991). Pyrodiversity in all fire-prone systems is determined to a large extent by climatic conditions and terrain characteristics but also increasingly by human influences as many of the areas concerned come under increasing pressure from population growth and modified land use (Abbott and Burrows 2003; Di Castri et al. 1981; Moreno and Oechel 1994). Pyrodiversity is also closely linked to the spatial distribution and arrangement of vegetation communities of different seral stages, structure and species composition (Lloret et al. 2002). Maintenance of pyrodiversity is thus central to the conservation of ecosystems associated with high ecological value (Àlvarez et al. 2009).

Mediterranean-type ecosystems (MTEs) are located in the mid-latitudes of the five continents. These biodiverse systems, dominated by evergreen shrublands and forests (Cowling et al. 1996), share similar climates typified by generally wet winters and a characteristic summer drought that in turn makes these areas highly fire-prone (Di Castri et al. 1981; Moreno and Oechel 1994). Fire is an integral component of MTEs, affecting key ecological processes and having a pronounced influence on vegetation patterns and soil surface conditions (Odion and Davis 2000; Turner et al. 2004). Fire has shaped Mediterranean landscapes for millennia and has interacted with other constraining abiotic factors (e.g., climate, terrain, soils) to produce the present mosaic-like vegetation patterns (Diaz-Delgado et al. 2004; Pausas 2006). A long history of human land use and associated disturbances (i.e., clearing, grazing, burning) has further shaped current vegetation patterns of most MTEs (Naveh 1975; Trabaud and Galtié 1996).

Elucidating relationships between landscape patterns and ecological disturbances is important to develop our understanding of basic landscape dynamics and to predict further changes in landscape structure (Turner 1989; Gustafson 1998). Consequently, it is also essential to measure patterns and disturbances at adequate spatial and temporal scales, especially when considering scale-dependent process rates (e.g., litter decomposition; seedling mortality; seed dispersal), which are affected by disturbances with wide impact such as fire (Turner 1989; Turner et al. 1994). Landscape patterns can, to some extent, control burning patterns through the spatial arrangement of flammable biomass (Nunes et al. 2005) but the spatial heterogeneity of fire patterns may in turn also influence a variety of ecological processes and post-fire distribution of biomass. Some of these effects are highly scale-dependent, as illustrated by the post-fire regeneration strategies of some plants (Turner and Romme 1994). For example, where a plant can only regenerate from seed, the size of the burned patch or the distance to the nearest unburned area will condition its ability to re-establish whereas the recovery of plants that can resprout from underground organs or from epicormic buds will be mostly determined by the severity of the fire within the patch.

In fire prone environments such as MTEs, manipulating the fire regime has been proposed as an ecological management practice. By changing some aspects of the fire regime such as the timing, intensity or spatial pattern, fire managers intend to achieve multiple objectives including fire hazard reduction and biodiversity conservation. Given that no single fire regime is desirable for all species or communities (Bradstock et al. 2005), some fire ecologists have advocated high pyrodiversity under the assumption that it promotes high biodiversity (Russell-Smith et al. 2002). However, the assumption that 'pyrodiversity begets biodiversity' has recently been questioned by Parr and Andersen (2006), as the link between pyrodiversity and biodiversity is not yet well established in the scientific literature. Indeed, there is currently no objective and quantitative methodology to either characterize or monitor pyrodiversity at the landscape level.

At the patch level, the fire-biodiversity relationship is based on the intermediate disturbance hypothesis (IDH) proposed by Grime (1977), which states that diversity of biological communities will be highest at sites that have experienced intermediate levels of disturbance. In the case of fire disturbance, we should then observe the highest biodiversity in areas burnt by fires of intermediate size or intensity, at intermediate frequencies and intermediate time since the last fire event. Although IDH is widely accepted as an explanation for species diversity patterns at the patch level, Schwilk et al. (1997) drew attention to the fact that this relationship is sensitive to scale. At the landscape level, the mosaic concept is the underlying premise of the Pyrodiversity-Biodiversity paradigm, and refers to finding the appropriate range of pyrodiversity to maintain a diversity of habitat conditions so that global landscape diversity will be maximized (Duelli 1997). Most of the current understanding of the pyrodiversity-biodiversity relationship has come from single observations at relatively small spatial scales (i.e., alpha diversity) or from single fire events at larger scales. Tackling the pyrodiversity-biodiversity relationship at the landscape level poses additional difficulties due to the spatial variability of other constraints (i.e., land management, topography, soil and climatic conditions). Consequently there is currently a lack of knowledge on how to quantify pyrodiversity and, in particular, which spatial attributes to use (Parr and Andersen 2006). Current descriptions and quantifications of the effects of fire on vegetation may not be appropriate for landscape-level ecological studies (i.e., beta and gamma diversity) which in turn provides a challenge of how to interpret the pyrodiversity requirements for biodiversity conservation when studying whole landscapes over time. When considering both visible (i.e., time-since-fire) and invisible (i.e., fire interval) fire mosaics, the focus should not only be on temporal or physical attributes of fire but also on spatial attributes expressing the shape, configuration or spatial composition of fire patterns (Bradstock et al. 2005; Reilly et al. 2006).

Here, we propose a conceptual and practical methodology for the study of fire mosaics from a landscape ecology perspective. We develop a protocol for objective characterization of pyrodiversity in MTEs based on two case studies, one in south-west Western Australia (SWWA) and another in southern France (SF). Comparing MTEs on different continents offers the opportunity to trial our methodology in contrasting environments and to evaluate its performance in a wider range of circumstances by considering pyrodiversity resulting from fire regimes dominated either by unplanned fires (in France) or planned fires (in Australia). We sought to understand how fire patterns in the two study areas are organized in space and in time, and to identify differences and similarities between those two MTEs. Defining the diversity of fire patterns across space and time, hereafter termed 'landscape pyrodiversity', is a necessary first step if we are to improve our understanding of the relationship between the diversity in fire disturbance and biodiversity at patch to landscape scales. We envisage that fire mosaics can be described using spatial metrics computed from temporal descriptors of the fire history at each location in the landscape. As some of the metrics can be expected to be strongly correlated, we also develop criteria for the selection of those metrics that provide most information. For example, a fire mosaic representing a large number of fires can be expected to hold a greater range of fire ages (i.e., old and recent fires) and thus to feature less aggregate but more diverse spatial patterns. Hence, the objectives of this study were firstly to determine which descriptors could be used to capture most of the temporal and spatial characteristics of the fire mosaic, and secondly to quantify these descriptors of fire patterns at the landscape level in two contrasting environments. Finally, we also sought to identify pyrodiversity replicates in both MTEs for which we will compare ecological responses and biodiversity patterns in a forthcoming paper.

Materials and methods

Study regions

Our first region was located in the southeast of France (Provence), consisting of 1.1 Mha of mixed forests and evergreen shrublands across the districts of Bouches-du-Rhône and Var (Fig. 3.1). The climate is subhumid/humid Mediterranean with mean annual rainfall of 500–1,000 mm and mean annual temperature ranging from 9 to 21°C (MeteoFrance data records, meteorological station of Le Luc, Var). The Provence region is characterized by high heterogeneity in topography and bedrock. Fire patterns are characterized by relatively infrequent and small fires, forming fine grain mosaics. As in most countries of the Mediterranean Basin, fire management efforts in France are mainly directed towards fire prevention and suppression. Despite this effort, over the last 30 years there has been a general trend of increasing fire frequency and burned area in Spain, Portugal, Greece and other Mediterranean countries (Vélez 1997; Dimitrakopoulos and Mitsopoulos 2006). In France, the emphasis on fire prevention and suppression has stabilized fire numbers since the 1980s, but has had limited impact on the incidence of large fires burning under extreme weather conditions (Rigolot and Roche 2009). In the Mediterranean Basin controlled burning is used marginally or not at all. Management agencies in France began using prescribed burning in the early 1990s but the annual treated area is currently only about 10,000 ha for the whole country (Rigolot 1998). The average annual area burnt in France has decreased over the 1973-2010 period; since 1990 the annual extent of fire has decreased from 7,600 to 4,725 ha (French PROMETHEE database on forest fires). However, in the Mediterranean Basin as a whole, the incidence of large and damaging fires (e.g., size of 20,000 ha) has become more frequent (Moreira and Russo 2007). While the main reason for the increase in fire incidence over the last few decades has probably been land use change (e.g., fuel accumulation resulting from abandonment of cultivated fields), changes in climatic factors and an increase in ignition sources should be also considered (Rego 1992; Lloret et al. 2002; Mouillot et al. 2003; Moreira and Russo 2007).

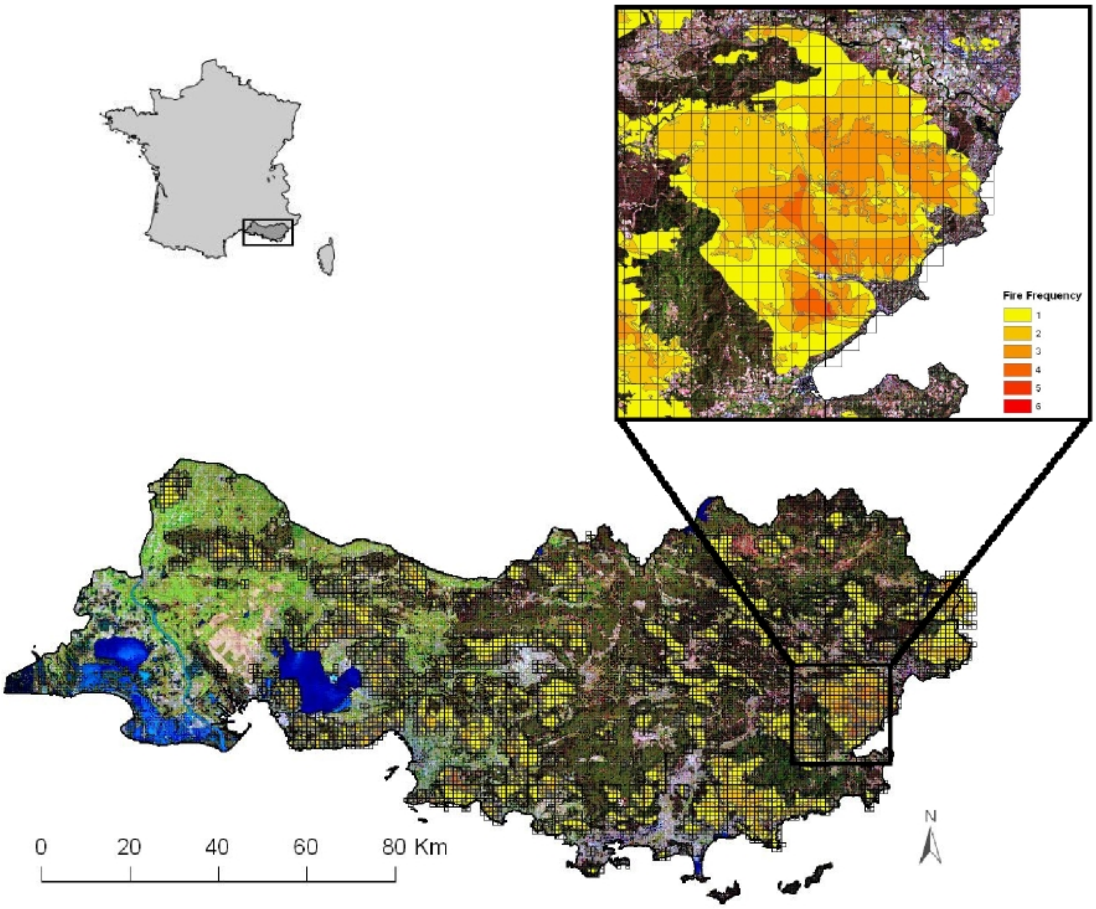

Fig. 3.1 Location of the study area in the French Provence.
Fire patterns over the 1960–2008 period have been unified and the 1 km-grid used in the study protocol and are superimposed on a Landsat satellite image (bottom figure). Fire patterns in Provence are very fragmented within the region and concentrated around major urban areas. A zoom of a smaller area located in the East of the study region (top-right panel) shows spatial variation in fire frequency within 1 km2 sample areas, represented as a colour gradient from yellow to red for 1–6 fires over the 1960–2008 period.

Our second study area was located in the Warren Region in the southwest of Western Australia, consisting of 0.5 Mha of forest, woodland and shrub- land with exceptional landscape richness and local endemism (Wardell-Johnson and Horwitz 1996) across the districts of Walpole and Denmark (Fig. 3.2). The climate is humid/perhumid Mediterranean, with mean annual rainfall in the 700-1,400 mm range and mean annual temperatures ranging from 9.5°C for inland locations to 20°C at coastal locations (Bureau of Meteorology data records, North Walpole meteorological station). In SWWA, analysis of Pliocene sediments provides evidence of fire occurrence, mainly resulting from lightning ignition, over at least the last 2 million years (Atahan et al. 2004).

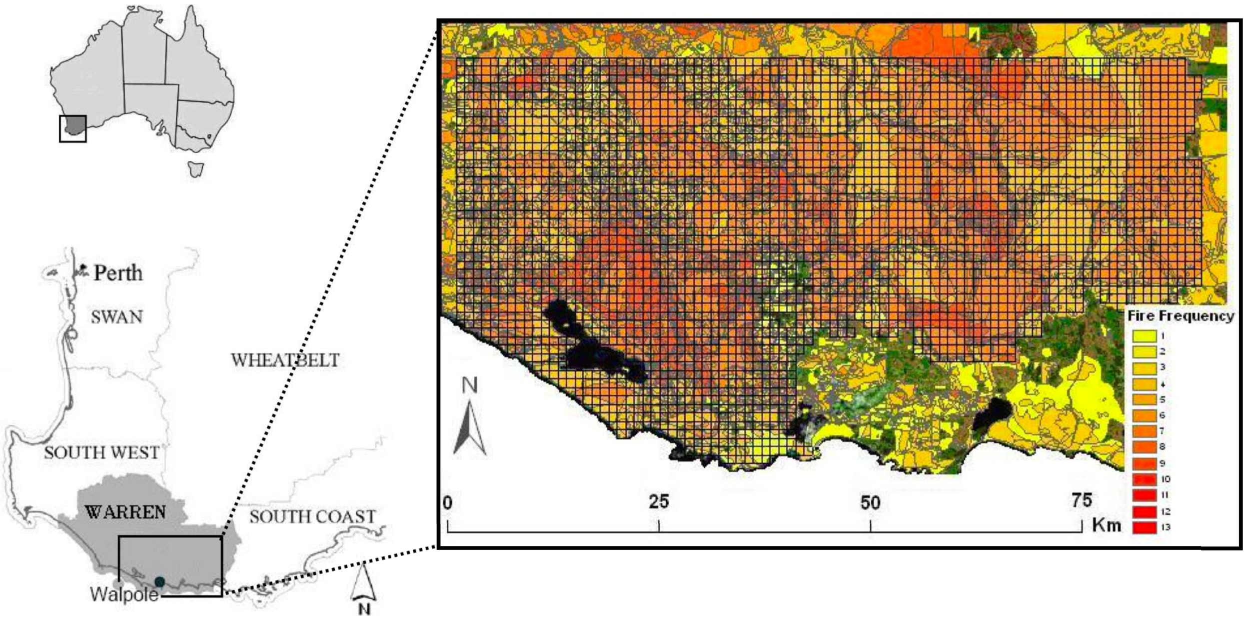

Fig. 3.2 Location of the study area in the Warren Region of south-west Western Australia. Fire patterns over the 1960–2008 period have been unified and are represented with a colour gradient from yellow to red for 1–13 fires. Spatial distribution of fire patterns in SWWA mimics the forest blocks template for prescribed burning management. The 1km-grid mapping of fire mosaics is also displayed and superimposed on a Landsat satellite image to illustrate the spatial variation in fire frequency within 1km^2 sample areas over the 1960–2008 period (right figure panel).

Before European settlement, fire regimes were characterized by very frequent (i.e., sub-decadal fire intervals) low- intensity fires, influenced by traditional aboriginal use of fire that had developed over a period of ca. 60,000 years (Abbott 2003; Bowman 2003 but see Wardell-Johnson et al. 2004). From 1826, colonization by Europeans resulted in commercial exploitation of forests for timber, clearing for agriculture, grazing and mining, which considerably fragmented the landscape and disrupted the earlier aboriginal burning practices (McCaw and Hanstrum 2003). Since the 1900s, the use of fire in association with agricultural clearing and from the1960s the widespread use of prescribed fire for fuel reduction has largely obliterated pre-existing fine-grained habitat mosaics (Bowman 2003). Current fire regimes in SWWA are characterized by a dominance of prescribed (planned) burns of low to moderate intensity at an approximately decadal frequency but including occasional, large (between 103 and 104 ha), high intensity, wildfires. Since the early 1960s, approximately 80% of the annual fire extent within the Warren Region results from planned fires (Boer et al. 2009). However, the high level of prescribed burning applied during the 1960s and 1970s has declined in recent times such that the annual area treated in the 1990s was only half that of the

1970s. There is some evidence that the reduction in prescribed burning rate since the 1980s has resulted in a greater incidence of large unplanned fires (Boer et al. 2009). From the early 1960s to the 2000s, mean interval between fires increased in this region from 4 years up to 9 years (Wittkuhn et al. 2009), which has resulted in a general coarsening of old fuel age patterns across SWWA. Current fire management seeks to create a finer grain fire mosaic, which is considered beneficial to biodiversity conservation (Burrows 2008; Boer et al. 2009).

Spatial analysis of fire mosaics in Provence and SWWA

We analyzed the spatiotemporal variation of fire disturbance firstly by considering a temporal sequence of fire patterns and secondly, by performing a spatial analysis of this temporal sequence using landscape metrics and basic statistics. Existing digital fire atlases from the French Regional District of Agriculture and Forestry (DDAF), the French National Forestry Office (ONF) and the Western Australia Department of Environment and Conservation (DEC; Hamilton et al. 2009) were used. Our analysis focused on fires recorded and mapped from 1960 to 2008. Approximate fire contours that concerned old fire events (i.e., before 1990) have been corrected using aerial photos and satellite images (e.g., delineation of unburned areas and fire boundaries adjustment were performed). Patterns of historical fires were characterized in detail within a random sample (n = 1,000) of 1 km^2 grid cells. A 1 km^2 grid size was deemed appropriate as it provided a sufficiently large sample from which to randomly select grid cells for statistical analyses and was found to be compatible with the grain size of fire mosaics in the two study regions. In addition the 1 km^2 grid size ensures compatibility with habitat and biodiversity data currently being compiled across Europe and across MTEs worldwide in the frame of the EBONE project (Bunce et al. 2008).

For our study, we acquired data at the 1 km^2 scale by converting initial vector layers to raster layers of 50 m resolution. Based on a sequence of 49 layers of annual fire scars (i.e., covering the 1960–2008 period), the following temporal fire attributes were extracted for all 50 m 9 50 m grid cells within every 1 km x 1 km square: (1) fire frequency or the number of fires over the observation period (mean, maximum and range), (2) time since the last fire (mean, maximum and range) and (3) mean fire interval (mean and maximum). Zonal statistics were then applied to the whole landscape to obtain a value for each 1 km quadrat. ArcGIS 9.3 software (ESRI 2008) was used for all digital map analyses.

Over recent decades numerous metrics have been developed to quantify the topology of categorical maps. Landscape patterns can be described using three broad types of metrics: composition metrics, aggregation metrics and shape complexity metrics (Gustafson 1998). As pyrodiversity depends to a certain extent on the inherent heterogeneity of the environment (e.g., topography, land use), in a second round of analysis we focused on spatial fire attributes and applied a limited set of landscape-level metrics to analyze the pattern of the entire landscape fire mosaic as of 2008. For this second round of analyses we selected those metrics that most effectively captured independent components of landscape pattern (i.e., shape, configuration and diversity) (Li et al. 2005; Cushman et al. 2008; Peng et al. 2010) and to express the spatial and temporal heterogeneity of fire patterns. Using the FRAGSTATS 3.3 software package (McGarigal and Marks 1995) the following landscape-level metrics were computed for the fire mosaic represented in each 1 km^2 sample: Simpson's Diversity Index (SIDI), the Aggregation Index (AI) and the Edge Density index (ED). The SIDI is a composite measure of patch richness and patch evenness and reflects the variability in composition of the fire patches within the 1 km x 1 km sample area; the AI measures the extent to which 50 m x 50 m grid cells of similar fire parameter values within the 1 km^2 area are aggregated and provides an index of the overall clumpiness of the fire mosaic; and the ED is a shape index that indicates whether the fire boundaries tend to be simple and compact or irregular and convoluted. SIDI, AI and ED were computed both for the fire frequency map and for the time-since-fire map in order to capture the visible (i.e., time-since-fire patterns) as well as invisible (i.e., areas of varying fire interval) fire mosaics. As for the other parameters, we applied zonal statistics within each 1 km2 sample area to compute the mean, maximum and range values for each landscape metric. For the remainder of the paper we refer to the mean of Simpson's diversity calculated from fire frequency as mean $SIDI_{Freq}$, for time-since-fire patterns as mean $SIDI_{Tsf}$, and so on for the other landscape indices.

Variability of fire mosaics in Provence and SWWA

A random set of 500 1km x1 km quadrats was collected from both study areas to represent the full range of variation in fire mosaics present in both environments. A principal component analysis (PCA) was used in order to summarize the variability of the metrics among the 1 km^2 sample areas and to analyze correlation patterns between variables. Data were standardized and centered beforehand to equalize variables measured on different scales.

All statistical analyses were performed in R (R Development Core Team 2009). The R package ‘ade-4’ was used for the multivariate analyses.

Based on the PCA results, we selected a reduced set of variables. The distributions of the fire history variables were skewed, so we used box plots to express the dispersion around the median rather than considering the mean of each variable. From the previous PCA and the box plots, we focused on the variables that (1) expressed most of the variability of the fire mosaics and (2) were not redundant with another variable. A second PCA was then performed with a reduced set of five selected variables. We sought to classify the fire mosaics from France and Australia into homogeneous groups according to these five fire attributes.

We conducted a hierarchical agglomerative clustering (HAC) on the combined data from SE France and SW Australia; this HAC was based on a Euclidean distance matrix computed from the first three principal components of the second PCA. The Ward criterion (Ward 1963) was used to cluster by successive pairwise agglomeration of the samples that presented similar fire characteristics. The Ward criterion ensures that one will find, at each step, a local minimum of the intra-group inertia (sum of the inertia of the different clusters). After examination of the clustering, we cut the classification tree into nine groups of increasingly complex fire patterns (i.e., three simple, three intermediate and three highly complex types of fire mosaic). We then projected the nine groups onto the PCA factorial map in order to visualize their position and their degree of overlap in the pyrodiversity variable space. The distribution of the variables for each group was quantified and compared using box plots for the variables previously selected and illustrated with aerial photos superimposed by fire frequency patterns.

Results

Descriptors of pyrodiversity in time and space

The first component of the PCA was associated with variables describing spatial patterns, while the second component was associated with temporal variables (Fig. 3.3). Time-since-fire was positively correlated to mean fire interval, but negatively correlated with fire frequency. When considering frequency-based spatial metrics, edge density and Simpson’s diversity were negatively correlated to the aggregation index. This was not the case for all the spatial metrics based on time-since-fire patterns as edge density (mean ED_{Tsf})

was correlated with the range of time-since-fire. Fire frequency range was also correlated with Simpson's diversity (mean $SIDI_{Freq}$). Several variables describing mean, maximum and range values of spatial metrics appeared to be redundant (e.g., range ED_{Freq} and max ED_{Freq} overlapping mean ED_{Freq}). Moreover, we found the spatial metrics calculated from fire frequency maps and time-since-fire maps to be highly correlated (e.g., mean AI_{Tsf} and mean AI_{Freq}), except for the edge density metric.

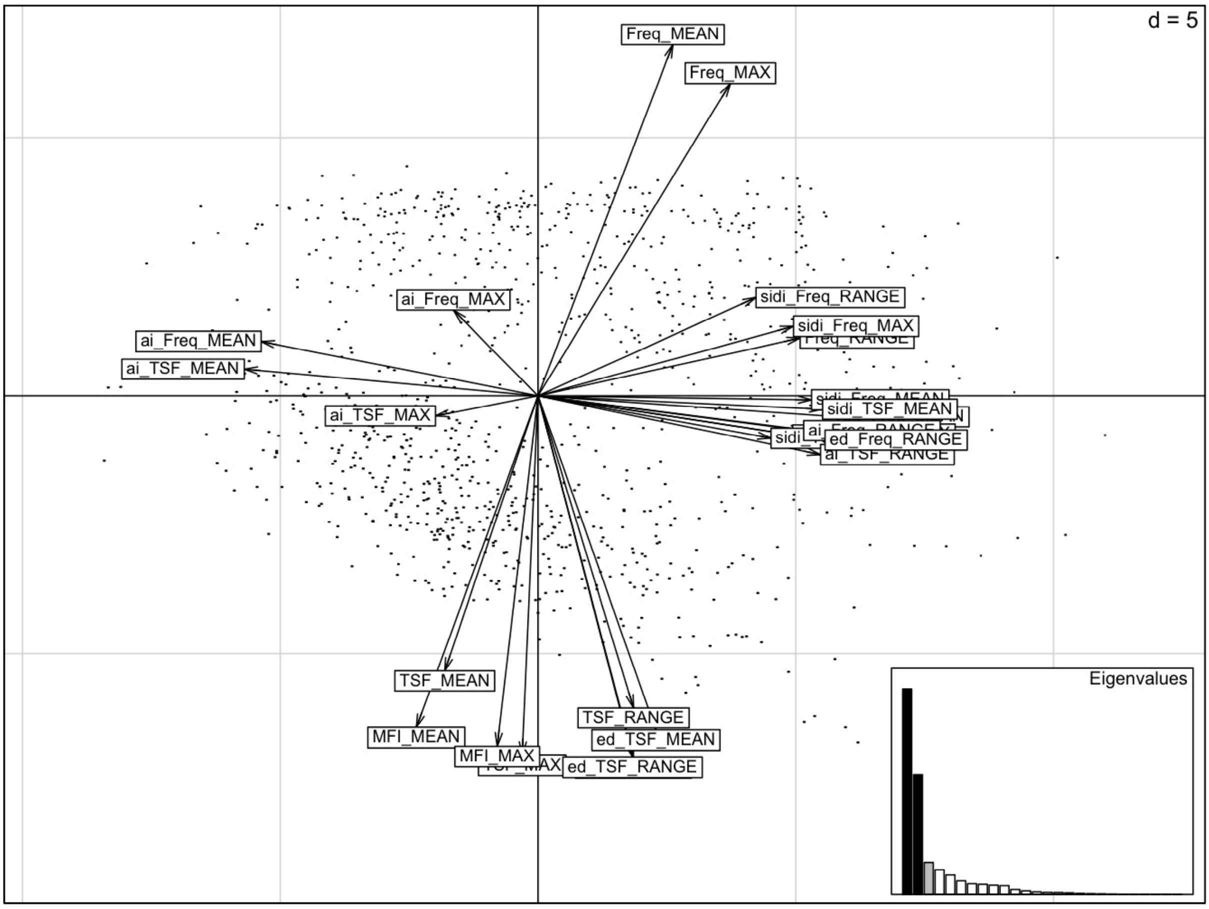

Fig. 3.3 PCA biplot showing the ordination of 1 km^2 samples (points) along the first two principal axes (ca. 69% of the samples variability).
Passive vectors for each of the 26 variables are super-imposed onto the ordination plot. Vector labels refer to the mean, range or maximum of Time- since-fire (TSF), fire frequency (FREQ), Mean Fire Interval (MFI), Simpson Diversity Index (SIDI), edge density (ED), and Aggregation Index (AI), within each 1 km2 sample area.

Based on the strong correlations between several variables, most of the variability of pyrodiversity at landscape scale can be expressed by a reduced set of variables with little loss of information (Fig. 3.4). A co-inertia analysis based on the two PCA datasets followed by a Monte–Carlo permutation test confirmed that the reduced set of variables was significant in capturing a major fraction of the variation in fire patterns (RV coefficient = 0.78; simulated P value = 0.001). Hence, the following variables were retained for subsequent analyses: mean fire frequency, mean time-since-fire, mean Simpson's spatial diversity and mean spatial aggregation based on frequency patterns, and mean edge density based on time-since-fire patterns.

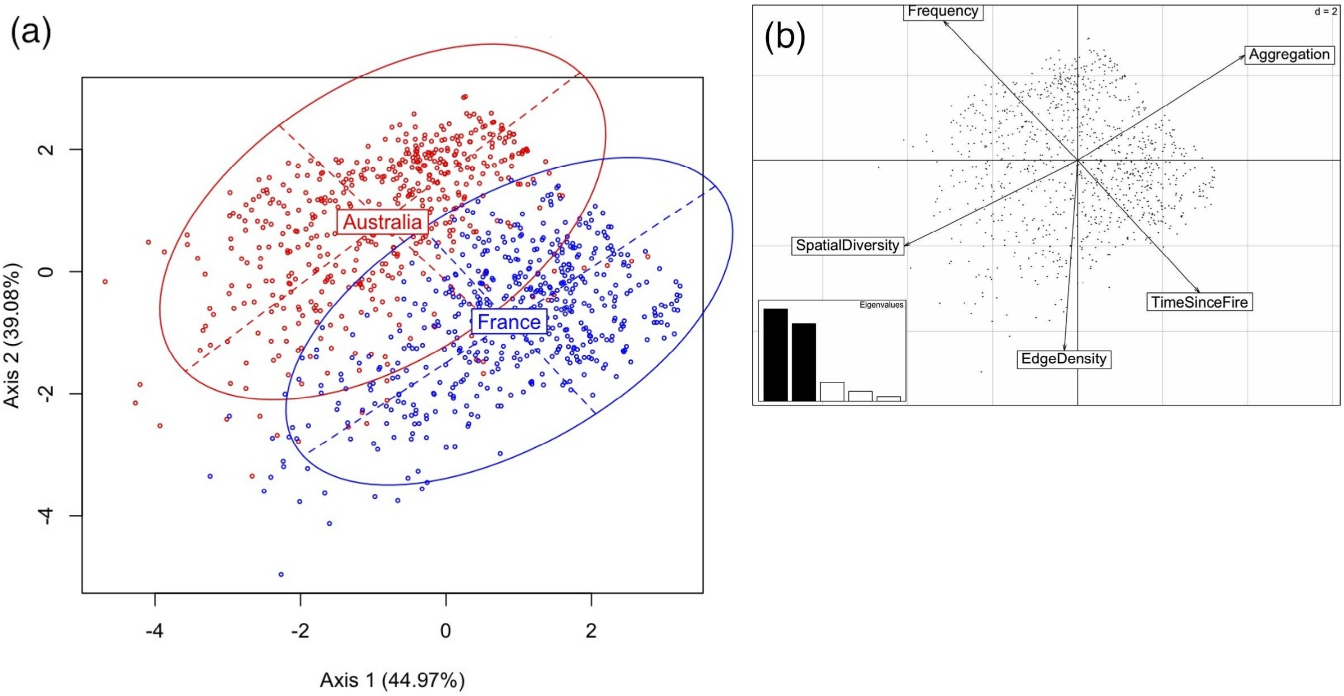

Fig. 3.4 PCA ordination plot (a) summarize samples dispersion by the five selected variables for the two study regions.
Individual 1 km^2-squares are identified by circles. Dispersion ellipses depict the distribution of the cloud for each study area and contain ca. 95% of the samples. The two distributions are clearly separated along the temporal gradient but have comparable variability among the spatial gradient. The two regions share samples with common pyrodiversity attributes. The five variables (i.e., mean Freq, mean TSF, mean SIDI$_{Freq}$, mean AI$_{Freq}$ and mean ED$_{TSF}$) are represented by arrows overlaid on the PCA multivariate space (b)

Pyrodiversity comparison of the study areas

Based on the PCA computed from the reduced set of pyrodiversity variables, fire mosaics of the two study regions were clearly separated from one another in the space of the first two PCA axes, with most of the dispersal caused by the temporal patterns of fire within the 1 km^2 sample areas (fire frequency and time-since-fire) (Figs. 3.4, 3.5). Over the observation period from 1960 to 2008, mean fire frequency (1.5 fires) and time-since-fire in Provence (21.6 years) were significantly different from those in the SWWA (mean fire frequency of 5.1 with time since fire of 7.1 years) (Fig. 3.5). The mean fire interval for the study area in Provence was 21 years and significantly longer than in SWWA (i.e., 9 years).

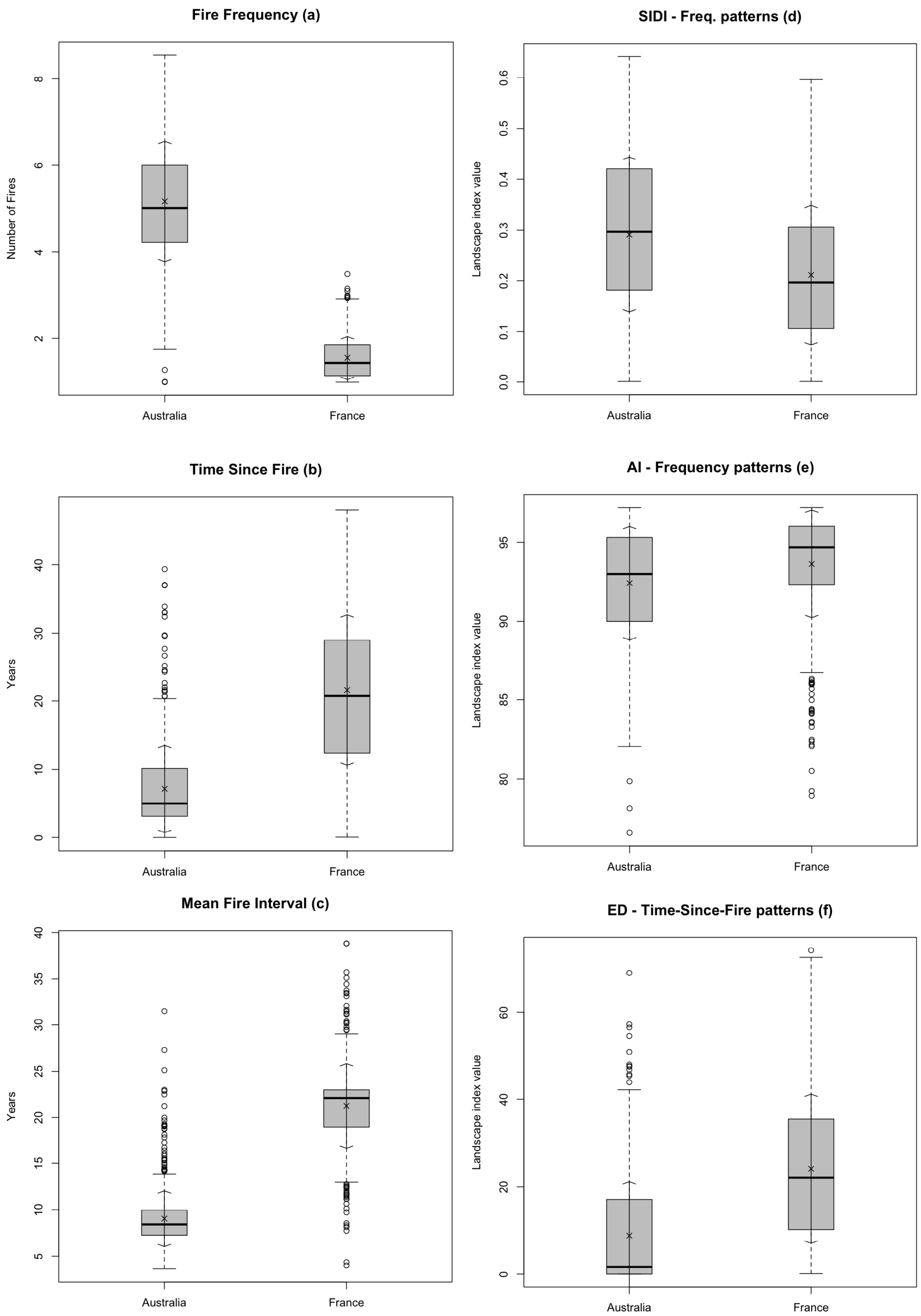

Fig. 3.5 Comparison of spatiotemporal attributes of fire mosaics in the two study regions illustrated by boxplots and using t-test analysis on the main spatial and temporal parameters of the fire mosaic [i.e., fire frequency (a), time-since- fire (b), mean-fire-interval (c), SIDIFreq (d), AIFreq (e) and EDTSF (f)]. Boxplots summarize the variance of the sample distribution on both side of the median for each variable. The mean is represented by a cross and the standard deviation is represented by two arrows. Results of two sample t-tests showed the two study regions to be significantly different ($P < 0.001$) for all six variables.

In the two study areas, fire frequency patterns had similar spatial heterogeneity (Figs. 3.4, 3.5). Fire mosaics within the 1 km^2 sample areas in the French and Australian study regions had comparable mean values for the spatial diversity metric (0.21 compared to 0.29). Differences were more obvious for the time-since fire patterns (Fig. 3.5): French fire mosaics presented a higher edge density than Australian fire mosaics (24.1 compared to 8.8 for the mean edge density index).

However, the two study regions also shared a common set of fire mosaics, corresponding to the intersection of the two dispersion ellipsoids in the multivariate space (Fig. 3.5). Samples within the overlapping zone included both mosaics dominated by prescribed fire and wildfire with fire frequencies of three to five fires over the 49 years observation period, which corresponds to relatively high-fire frequencies in France and relatively low fire frequencies in SWWA. Both diverse and aggregated mosaics could be identified in this shared space (Fig. 3.4).

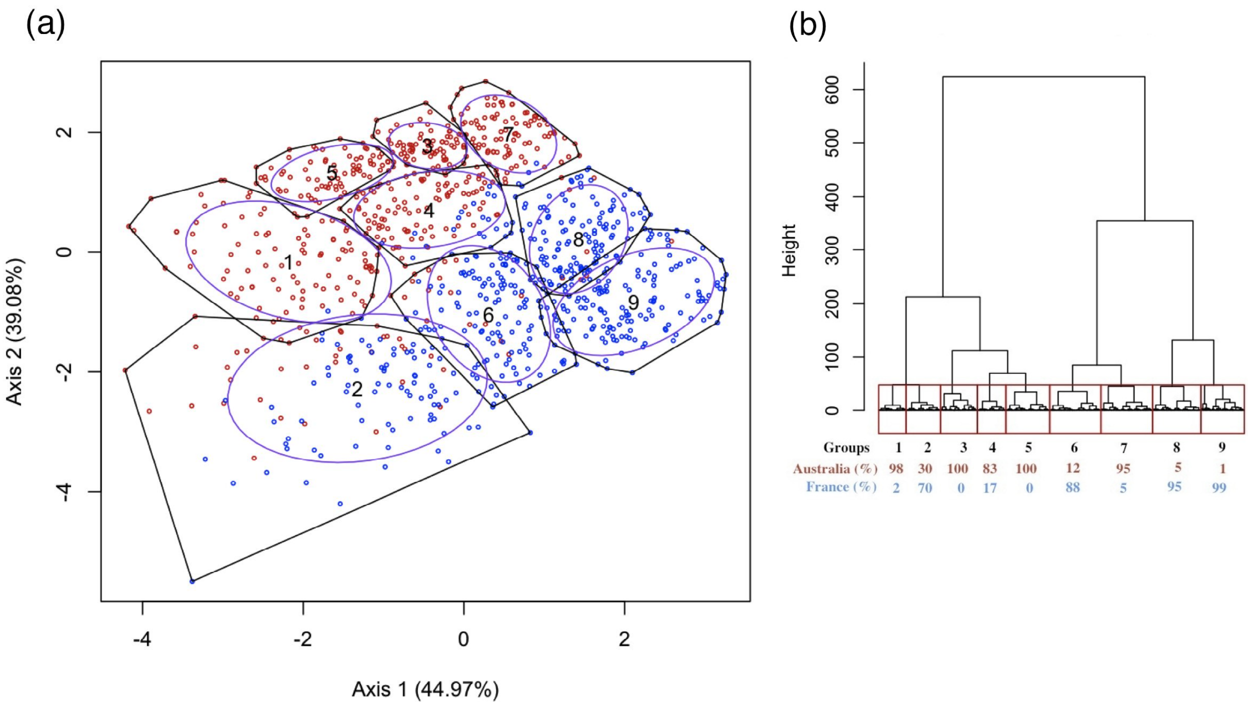

Fig. 3.6 Grouping of the 1 km^2 fire mosaics samples by hierarchical agglomerative clustering (a). 75% confidence ellipses are superimposed on the PCA plot and represent the probability for a chosen sample to belong to a particular cluster. The dendrogram (panel b) depicts the partitioning of the 1,000 samples into nine clusters. Distribution of both study areas samples within each group (i.e., percentage of compo- sition) is specified below the dendrogram

The majority of the nine clusters resulting from the HAC classification contained exclusively 1 km^2 sample areas from either Provence or SWWA (see dendrogram in Fig. 3.6). The two study regions presented contrasted aggregated fire mosaics, mainly due to the significant differences in fire frequency (Fig. 3.6). However, we also observed more interspersion between the two environments when fire mosaics presented high edge density and high spatial diversity (Figs. 3.6, 3.7).

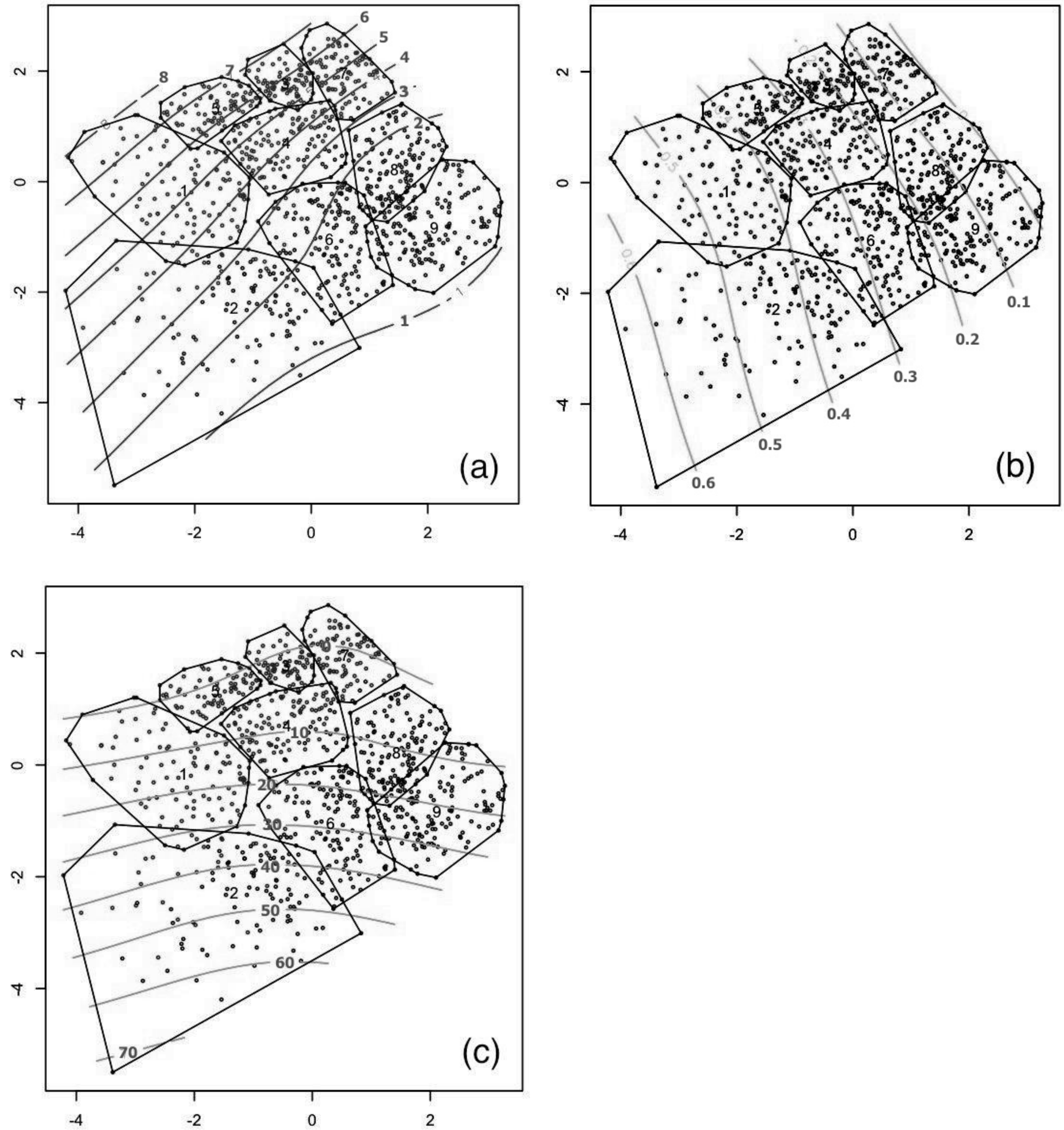

Fig. 3.7 Visualization of the cluster distribution along three main gradients defined by (a) mean FREQ, (b) mean $SIDI_{Freq}$, and (c) mean ED_{TSF}. The isolines on each panel give the values for each variable/index mentioned below

In three of the clusters (i.e., groups 2, 4 and 6) fire mosaics from both study regions were well represented (Fig. 3.6). These groups were characterized by a great variability in fire frequency associated with a high spatial diversity in their fire frequency patterns. We also found a relatively high interspersion of samples from the two study areas when these samples were characterized by high edge densities in their time-since-fire patterns (Fig. 3.7).

Pyrodiversity levels

Decomposition of the fire regime into spatial and temporal parameters allowed us to express the full range of pyrodiversity and to classify each group along a gradient of increasing heterogeneity in fire patterns. Groups 1 and 2 had the greatest pyrodiversity and were relatively dispersed (in multivariate space), while groups 3, 5 and 7 had lower pyrodiversity and were more aggregated in multivariate space (Fig. 3.6). Groups 4, 6, 8 and 9 exhibited intermediate levels of pyrodiversity (Fig. 3.6). In this study, high pyrodiversity was the result of high variability in time-since-fire and fire frequency combined with high values of spatial diversity. In contrast, low pyrodiversity levels corresponded with relatively short mean fire intervals and low scores of edge density. Almost half of the SWWA fire mosaics belonged to low-pyrodiversity groups (i.e., 242 samples), while 30% were characterized by high pyrodiversity (i.e., 135 samples). In contrast, 80% of the Provence fire mosaics (i.e., 410 samples) were characterized by intermediate pyrodiversity (Fig. 3.6).

Discussion

Descriptors of landscape pyrodiversity

Fire regimes are often described by the type, intensity, size, frequency and season of fire (Gill 1975; Heinselman 1978). More recently fire regimes have also been characterized according to the spatial pattern of fire occurrence (e.g., Bradstock et al. 2005; Burrows 2008). However, attempts to characterize pyrodiversity and its relationship to biodiversity have been largely speculative or restricted to the stand level owing to the difficulties associated with selection of appropriate scale and relevant landscape descriptors when quantifying spatial complexity of fire (Thode 2005; Driscoll et al. 2010). To our knowledge, this is the first study to develop a methodology to simultaneously consider spatial and temporal aspects of fire mosaics and to apply existing spatial analyses tools from landscape ecology to characterize the spatiotemporal complexity of fire regimes at the landscape level. The 1 km scale of our analysis is arbitrary, but a reasonable choice given it's common use for measuring landscape vegetation patterns (Bunce et al. 2008). However, we recognize that the characterization of pyrodiversity at other spatial sampling scales may result in different conclusions and that a single scale may not be appropriate for studying all biodiversity responses to pyrodiversity. The list of descriptors used in this trial was not exhaustive, and incorporation of additional variables such as fire intensity and seasonality would strength the framework. As knowledge of the linkages among fire patterns, processes and species improves, further research may assist in identifying appropriate scale to address the Pyrodiversity-Biodiversity paradigm and the most relevant fire parameters to consider for each situation. For example, a recent study of multiple taxonomic groups in the Warren Region of SWWA demonstrated a high degree of resilience to the sequence of fire intervals over a 30 years period (Wittkuhn et al. 2011).

The descriptors used in this methodology to quantify landscape pyrodiversity permitted us to better understand the relationships within and between spatial and temporal attributes. Firstly, there is a clear opposition between the gradient of fire frequency and the gradient of time-since-fire, suggesting that fires are selective in where they occur. Thus, areas that have previously experienced fires at short intervals are unlikely to be long unburnt areas (i.e. to have high TSF values. This observation is consistent with other findings and is either related to the inherent variation in the flammability of vegetation types (Dimitrakopoulos and Papaioannou 2001; Nunes et al. 2005) or to other constraining environmental parameters such as altitude, slope, climate, and distance to urban areas (Diaz-Delgado et al. 2004). Secondly, the orthogonality between the spatial and temporal gradients indicates that the complexity of fire temporal history was not associated to the spatial heterogeneity of the fire mosaic. Fire mosaics with a high number of fires can be either spatially aggregated or show a high diversity of different age burn patches. Surprisingly, the edge density variable did not behave similarly to spatial diversity and aggregation according to the samples' mapping in the multivariate space (see Fig. 3.3). The edge density was dependent on the type of fire maps, whether we were considering fire recurrence patterns or on the last fire event, as the encompassing pattern. We believe this may be explained by the fact that fire mosaics in Provence are characterized by low number of fires of disparate ages and relatively small size. Consequently, in Provence the edge creation associated with fire frequency patterns, does not vary at the 1 km scale because of the small number of fire events. However, when considering time-since-fire patterns, the edge creation is more influenced by the age differences of the patches composing the fire mosaic.

Finally, we found that some of the attributes used to characterize fire mosaics were strongly correlated and to a certain extent redundant (e.g., the range of fire patterns frequency was associated with the spatial diversity). Consequently, not all fire attributes need to be considered when assessing landscape pyrodiversity. These findings justify the need to consider spatial variables based on both fire frequency and time- since-fire patterns, in particular when linking disturbance patterns with ecological processes that respond to fire return intervals or the extent or grain of the burnt area (e.g., local species extinction or post-fire recolonization).

Pyrodiversity in SWWA and southern France

We expected to find a clear contrast between fire mosaics in Provence and SWWA because of inherent differences in fuel age distribution, topography, vegetation structure and fire management practices. A two-sample t test confirmed that the fire regimes of the two study regions are significantly different ($P < 0.001$).

The use of prescribed burning has strongly influenced the shape and recurrence of fire patterns in SWWA over the last 50 years (Boer et al. 2009). For example, in SWWA the Department of Environment and Conservation large blocks of forest (102-103 ha) may be ignited in a single day using incendiaries dropped from aircraft. The temporal spacing of fires combined with flat terrain and a relatively fixed template of forest blocks delineated by a sparse network of roads has tended to aggregate fire mosaics. However, the range of frequencies with which prescribed fire is applied has also created high spatial diversity of fire patterns within the landscape. The combination of these two factors has resulted in a landscape that is characterized by areas of either high or low pyrodiversity, but with few areas of intermediate pyrodiversity.

In contrast, fire mosaics in the French study region were characterized by greater variation in time-since-fire values than those in SWWA. Also, fires in Provence were generally much smaller in area than in SWWA over the observation period (1960-2008). This resulted in more fragmented fire mosaics in France, with relatively large numbers of small patches of different fuel age within the 1 km^2 sample areas. Although the range of fire frequencies was much smaller than in the SW Australian study region, fire mosaics in the

French study region also showed high spatial variability which likely results from the variation in topography and land use characterizing SE France.

Despite the differences of the fire mosaics in the two study regions the multivariate clustering did not show a dichotomy of the 1 km^2 sample areas from both regions, implying that there are landscapes of similar pyrodiversity in these two Mediterranean environments. The two ellipses delineating the distribution of the sample areas from both study regions in pyrodiversity space (Fig. 3.4) have a strikingly similar shape (i.e., axes length and orientation), but occupy different locations along the fire frequency gradient. This finding suggests that the spatiotemporal patterns of intensively managed fire mosaics in SWWA are often undistinguishable from patterns resulting exclusively from unplanned fires. The current policy of active management by prescribed fire in SWWA (Burrows 2008) appears to provide a disturbance regime that shares key spatiotemporal patterns with unmanaged regimes in other MTEs, suggesting that there is scope for effectively managing for both biodiversity conservation and wildfire hazard reduction in this environment (Boer et al. 2009). The fact that landscapes subject to similar disturbance regimes can be identified across different MTEs, despite strong environmental contrasts between the study regions and taxonomic differences in their biota (Pignatti et al. 2002), also provides prospects for more fundamental studies into ecological responses to disturbance.

Potential applications in fire and conservation management

Sustainable management of fire-prone environments seeks to produce a wide range of fire regimes in order to create or maintain an appropriate variety of habitats and thereby conserve the diversity of species and communities in the management area (Burrows and Wardell-Johnson 2004). Our approach to assessing landscape pyrodiversity can help identify areas of high conservation priority and thereby guide the design of adequate conservation measures. In SWWA, our methodology could be readily used to monitor the diversity of actively managed fire mosaics over time and space. Objective descriptors of fire mosaics could be applied to the Fire Mosaic Project in the Warren Region initiated by DEC in 2002 that aims to enhance biotic diversity at the landscape scale by creating and perpetuating a fine scale mosaic of patches of variable size intensity and time since fire (Burrows and Wardell-Johnson 2004). In addition, objective quantification of pyrodiversity could contribute to the design of better regional fire management plans by clarifying the trade-offs between fire hazard reduction and maintenance of the ecological infrastructure for the dispersal of biota (Malanson and Cramer 1999; Boer et al. 2009).

Conservation decisions and practical management of biodiversity require adequate information at the species, community and habitat levels. However, for the landscape level this type of information is often incomplete, fragmented and collected according to different sampling schemes, which impedes the sharing of such information among different management agencies/ countries (Vogiatzakis and Mannion 2006; Driscoll et al. 2010). Our methodology may facilitate the exchange of information among agencies by providing a protocol for the objective quantification of pyrodiversity. In more fundamental (landscape) ecological research the proposed method could be used to identify environmental analogues (i.e., sample areas) of similar spatiotemporal fire disturbance patterns across different fire-prone environments. Cortina and Vallejo (1999) have previously summarized some of the benefits that have come from comparisons of MTEs in terms of land rehabilitation. Comparisons of biodiversity across different MTEs could be made more reliable if observations can be made at sites of comparable disturbance history. Our approach could be also applied to other fire-prone areas in order to determine the role played by fire as a factor controlling the heterogeneity of floristic patterns and to evaluate the relevance of prescribed burning to manage fire mosaics at local and regional scales if long unburned sites were available as reference.

One of the most striking differences between the landscapes of Australia and the Mediterranean Basin (Pignatti et al. 2002) concerns their very different grain (Wiens 1989). While vegetation types often change abruptly over short distances in the Mediterranean Basin, vegetation of similar composition and structure is often widespread over large areas in Australian MTEs due to flat terrain and more gradual environmental gradients. Although fire has long been recognized as a structuring factor in all MTEs, a more quantitative understanding of the role fire plays in this landscape ecological convergence is still largely lacking. We suggest that objective characterizations of pyrodiversity could be a useful first step in building that knowledge base.

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4. What drives diversity of Mediterranean landscape mosaics? The relative contribution of fire, environment and land use.

Ecography - prepared for submission

Introduction

Landscapes of southeastern France (Provence), and more generally in the Mediterranean Basin, often consist of fine-grained mosaics of natural, semi-natural and anthropogenic habitats. The macroscale physiographic variation across the Provence region is the product of major climatic gradients and a complex geomorphological evolution involving tectonic and volcanic activity (diCastri et al. 1981; Naveh and Lieberman 1984). However, as highlighted by many paleological studies, the microscale (< $1km^2$) diversification of habitats in Provence can be mainly attributed to a long history of human activities such as cultivation, irrigation, livestock grazing, clearing and burning in the region (Naveh 1982, Le Houerou 1981). Natural disturbances such as wildfires have also played and continue to play a role in shaping landscape patterns (Pausas and Vallejo 1999, Trabaud and Galtié 1996).

The diversity of habitats and patchiness of habitat mosaics found in Mediterranean landscapes contributes to its exceptionally high biodiversity (Chust et al. 2006, Harrison 1997). For example, more than 2500 plant species are found in south-eastern France, encompassed by around 149 major phyto-ecological groupings (Braun-Blanquet et al. 1952). Human activities and fire are considered to be the main drivers of recent change in landscape patterns (Barbero et al. 1990). However, the diversity of habitats composing these landscape mosaics is thought to be attributed to the high topographical and climatic heterogeneity of the region (Cowling et al. 1996). How vegetation dynamics and plant diversity patterns are controlled by these abiotic constraints is still little understood because of the complex interplay between landuse change, disturbance and the physical environment across the region (Scarascia-Mugnozza et al. 2000). Landscapes in southeastern France, and more generally in the northern Mediterranean Region, have experienced increasing urban pressure and widespread agricultural abandonment since ca. 1950s (Tatoni et al. 2005). Consequently, these landscapes have successively suffered from land degradation caused by intense urbanization and biodiversity loss consecutive to landscape homogenisation, which currently translates into a complex array of diverse vegetation seral stages and complex fuel loads patterns (Mazzoleni et al. 2004, Moreira and Russo 2006).

The process of landscape fragmentation can be defined by (i) a global increase in number of habitat patches with smaller size, (ii) a reduction in the amount of habitat types and (iii) an increase in habitat isolation (Fahrig 2002). Landscape fragmentation is a serious threat to biological diversity (Saunders et al. 1991) and concerns all Mediterranean biomes that are currently experiencing intensive land clearing for agriculture purposes (e.g., south-western Australia; Hobbs 1993) or increasing urbanization (e.g., Mediterranean Basin and southern California; Underwood et al. 2009). The study of landscape spatial structure and composition is of central importance in understanding the effects of fragmentation on population dynamics (Fahrig 1994). In order to conserve landscape spatial structure and its associated diversity of habitats, it is essential to acquire a global understanding of the relative contribution from environmental factors, disturbance regimes and land use practices in shaping current Mediterranean landscape mosaic patterns.

Landscape biodiversity, defined here as diversity of habitats composing a landscape mosaic, relies on structural parameters (i.e., habitat composition, size and shape) and functionally on metacommunity dynamics involving plant colonization and extinction processes. Therefore, landscape-scale disturbance such as fire or land use can strongly impact landscape biodiversity. In some cases, both fire and land use may contribute to increase landscape heterogeneity by creating a mosaic of vegetation patches in different successional stages (Lloret et al. 2002). Alternatively, landscapes may be homogenised by disturbances when their magnitude, intensity, or frequency exceeds certain thresholds: particular habitats may loose their functional role due to excessive fragmentation of patches (Fahrig 2003) and even disappear from the mosaic (Turner et al. 1994). The challenge consists in determining the range of disturbances (e.g. fire and land use) that is either required or desirable to maximize or maintain the number and size variation of mosaic patches and the number of biotope types per unit area.

The goal of the present chapter is to quantify the contribution of fire and land use disturbances on landscape patterns in a Mediterranean area (i.e., south-eastern France) and to compare their relative importance to that of background environmental heterogeneity (terrain, climate, soils). This chapter is divided in two sections: (i) the study of fire-induced land cover changes in Provence over a 20-year period considering large landscape scale (>1km^2) and (ii) at a finer landscape scale (<1 km^2) the interplay of abiotic factors on the composition and spatial configuration of landscape mosaics. The objectives were: (i) to characterize the role of fire in driving broad-scale landcover transitions and fine-scale composition and spatial configuration of the mosaic of habitats; (ii) to assess how fire, environmental heterogeneity and land use relate to observed changes in composition and spatial arrangement of landscape patterns. In a final step, we propose (iii) to verify the hypothesis that increasing complexity of disturbance patterns has beneficial rather than impoverishing impact on the landscape mosaic (Heterogeneous Disturbance Hypothesis; Warren et al. 2007). When considering a landscape with high pyrodiversity (i.e., landscape fire regime with complex spatiotemporal variability), different younger successional stages are present simultaneously. Hence, the probability that a larger number of species can find suitable patches in a heterogeneously disturbed landscape is greater than in a landscape with uniformly distributed intermediate disturbance. A better understanding of the relationship between pyrodiversity and landscape biodiversity at an operational level is required for the design and implementation of landscape-scale conservation policies in southeastern France but also in other fire-prone ecosystems (Driscoll et al. 2010).

Material and Methods

Study area

The study region is located in Provence, south-eastern France. The landscape consists of a complex mosaic of urban and rural areas juxtaposed with patches of semi-natural and natural vegetation that have a long history of both natural and anthropogenic disturbance. Our study focused on a 1.1 Mha area within the Departments of Bouches-du-Rhône and Var (Fig. 4.1). According to the environmental climatic stratification of Europe, the area is classified as Mediterranean North and Mediterranean Mountain (Metzger et al. 2005). The climate is strongly seasonal with dry and hot summers and moist and cool autumns and winters. The area is characterised by occasional and violent precipitation events, large year-to-year variability of total rainfall, as well as frequent strong dry winds that favour the spread of forest fires. The broader region of south-eastern France is characterized by strong variation in elevation (0-1700m a.s.l.), terrain types and substrates (e.g., limestone, acidic soils, dolomites, marl and sediments). Therefore, climatic heterogeneity in the region can be further described as a series of ‘etages’ in relation to thermal differences along altitudinal gradients (i.e., thermo-, meso- and supra- Mediterranean climatic types; Médail and Quézel 2003; Table 4.1).

The natural vegetation is a mixture of (i) extensive woodlands dominated by both evergreen (*Quercus suber* and *Quercus ilex*) and deciduous (*Quercus pubescens*) oak species, Aleppo pine (*Pinus halepensis*) forests and evergreen sclerophyllous shrublands of many forms; (ii) tall sclerophyll shrublands mainly found on acidic substrates ("*maquis*"); and (iii) middle height shrublands, generally occurring on calcareous substrates ("*garrigue*").

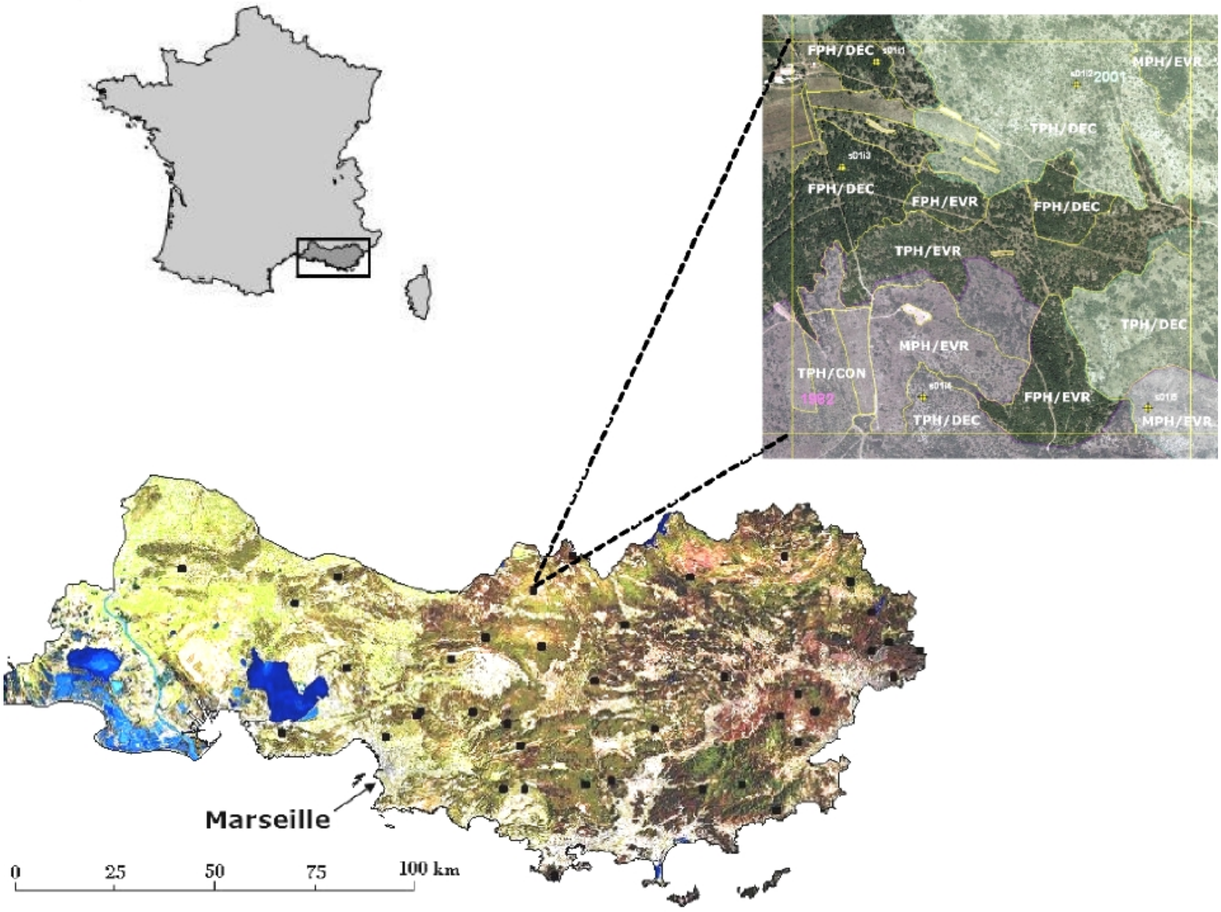

Fig. 4.1 Location of the study area in the Provence, south-eastern France.
The grey surface is zoomed out to display the location of the 40 1km^2 quadrats (i.e., black squares) sampled for vegetation surveys (mapping and description of habitats). A snapshot of one particular site shows the composition of habitats encountered (see Table 4.1 for codification) and the associated fire mosaic (fire patterns from 19822 and 2001) overlaid on an aerial photography of 2008.

These ecosystems are thought to have co-evolved with fire and the vegetation dynamics are hypothesized to be largely determined by fire regimes (Trabaud 1982). Most fires (95%) in this region are unplanned and result from human activity. The current fire regime is characterized by relatively low mean fire frequency (ca. 1.5 fires per 50 years period) and dominance of relatively small fires (10^1-10^2 ha) resulting in fine-grained mosaics (Faivre et al. 2011).

Landcover change analysis – regional scale

Global changes in landscape patterns were assessed by comparing landscape composition from 1988, 1999 and 2006. Data were compiled using Corine Land Cover (Coordination of Information on the Environment) typology and national inventory maps from CRIGE-PACA (Center for Geographical Information of the Provence-Alpes-Côte d'Azur administrative region; www.crige-paca.org). These regional land cover maps have been derived from aerial photo interpretation plus 30 m resolution Landsat imagery for 1988 and 1999 (30m) and 20 m resolution Spot imagery for 2006. The land cover typology was simplified to retain only 13 categories: urban areas (URB), agricultural land (AGR), wetlands (WET), water bodies (WAT), open and non-vegetated habitats (OPE), pastures (PAS), shrublands (SHR), scattered vegetated systems (SCA; vegetated habitats with clump of trees/shrubs), vegetated systems in transition (TRA; i.e., seral or interfire habitat considered as transient), oak forests (OAK), coniferous forests (CON) and mixed forests (MIX).

In order to relate land cover patterns to spatiotemporal patterns of fires we sampled a total of 100 blocks of 3 km x 3 km each that were randomly selected from the study area. As our focus was on vegetated areas where fires can potentially occur, we excluded blocks that had >50% of the total block area classified as urban, agricultural, or water, from our analysis. Of the 50 blocks remaining, 15 have not burned over the last 50 years, 17 blocks have had at least one fire in the last 5 years (i.e., between 1999 and 2006) and 18 blocks have had at least one fire more than 5 years ago (i.e., before 1999). After describing the general trends of land cover transitions between 1988 and 2006 for the whole set of landscape blocks (Fig. 4.2), we visually compared land cover changes of the main categories for burned and unburned blocks using boxplots (Fig. 4.3).

To characterize fire influence on land cover changes in both composition and spatial configuration a diachronic analysis (i.e., two-dates analysis of land cover maps) was performed to compare landscape patterns from 1999 and 2006. ArcGIS 9.3 software (ESRI) and FRAGSTATS 3.3 software (McGarigal and Marks 1995) were used to compute the following landscape metrics relative to each land cover map: patch diversity (Patch_div), patch richness (Patch_rich), mean patch size (MPS) as well as mean shape index (MSI) to describe the spatial heterogeneity of the landscape mosaic.

Co-inertia analysis (CIA) was used to analyse simultaneously the sites x land cover variables datasets for 1999 and 2006 (Fig. 4.4). CIA is commonly applied in ecological studies for identifying co-relationships in multiple datasets as it performs simultaneous ordinations of two sets of variables for the same individuals (Dray et al. 2003). The optimising criterion is that the resulting sample scores of both datasets are the most covariant (Doledec and Chessel 1994). Co-inertia analysis is very flexible and allows many possibilities for coupling so that its concept can be extended to diachronic analyses where the same variables (e.g., species abundances and environmental variables) are studied at the same sites and at two different dates (Blanc 2000, Dray et al. 2003). A Monte Carlo permutation test (1000 replicates) was used to check the significance of the CIA (i.e., degree of co-structure between matrices). As the composition and structure from the 1999 and 2006 land cover maps were significantly related, CIA was used to graphically summarize land cover transitions within quadrats between 1999 to 2006 (Fig. 4.4) using (i) the location of the site in the CIA multivariate space in 1999 and (ii) a vector showing its change to a future location in 2006 that is proportional to the change in composition and structure. In order to facilitate the interpretation of the CIA diagram we summarized the main land cover transitions of four selected sample sites and described the fire-landscape relations of each case (Fig. 4.5).

Drivers of landscape patterns - Fine scale landscape analysis

An analysis of fine scale landscape mosaics based on the field sampling of vegetation types (i.e., habitats) was performed in 1km^2 quadrats for which fire history, environmental features and land management activities had been characterized. The characterisation of vegetation types followed the EBONE protocol (Bunce et al. 2008) designed to monitor habitat and biodiversity at landscape level across Europe and across MTEs worldwide (see Fig. 4.1). The chosen 1km scale may seem arbitrary but was considered appropriate in our study case to capture the spatial heterogeneity of environmental gradients and land use activities as well as the grain size of fire mosaics across the region. The 1km scale is also the common scale used in landscape ecology for studying landscape patterns according to Formann and Godron (1986). We selected a total of 40 quadrats (1 km x 1 km) using the protocol of Faivre et al. (2011) to characterize landscape pyrodiversity (e.g., clustering of sites with similar fire regime). Briefly, the sample pool was divided into four sub-samples of 10 quadrats each, according to the classification of fire patterns into three main pyrodiversity classes of increasing complexity; thereby the sub-samples were respectively defined by quadrats of complex (CPX), simple (SIM) or intermediate (INT) pyrodiversity, while the fourth sub-sample was used as a reference consisting of quadrats that have not been affected by fire disturbances for the last 50 years or longer (UNB; unburned). Within each pyrodiversity cluster, we further stratified the sample of 1km^2 quadrats according to the variability in soil substrates, relief and climatic conditions present throughout the whole study area. Therefore, each pyrodiversity cluster featured quadrats in different ranges of altitude, located on either limestone or acidic soils (defined as the two main classes of substrate), as well as in thermo, meso and supra-Mediterranean climate-types (Médail and Quézel 2003). Details of the 40 landscape units examined in this study are provided in Table 4.1.

Dataset creation

We produced four datasets for analysis: the first (Y matrix) is a compilation of landscape composition and spatial configuration variables for the 40 1km^2 quadrats, while the three other matrices contain explanatory variables related to fire (X1), background environmental heterogeneity (X2) and land use (X3) explanatory variables per 1km^2 quadrat (Table 4.2).

We used the habitat mapping and identification protocol developed within the EBONE project (Bunce et al. 2008) to characterize the habitats recorded in each quadrat (Fig. 4.1). Field descriptions of habitat composition and mapping of their boundaries were conducted in the Spring and Summer of both 2008 and 2009. The vegetation types present in those habitats were identified on the basis of plant functional types following the classification developed for the EBONE project (Table 4.2). We used the respective surface of each habitat as a measure of its abundance within the 1km^2 quadrat. The spatial pattern of habitats within each 1km^2 quadrat was characterised using landscape patch metrics (McGarigal and Marks 1995). We selected metrics expressing the shape (i.e. mean shape index, mean patch size), the configuration (i.e. number of patches, total edge) and the diversity (i.e. Shannon diversity and evenness indices) of habitat patches (Table 4.2). Care was taken to avoid metrics overly affected by the edge effect inherent to the grid-sampling layout.

Site	Location (Dept)	XMIN	YMIN	Pyrodiversity	Fire years	Bedrock	Climate
s01	Ollières (83)	883000	1843000	INT	1982/2001	Limestone/Clay/Alluvium	SUPRA
s02	Regagnas, Peynier (13)	867000	1828000	INT	1979/1999	Marl/Limestone	MESO
s03	Cuges-les-pins (83)	874000	1810000	CPX	1962/1978/1995/2000	Limestone	MESO
s04	St Julien les Martigues (13)	823000	1823000	INT	1960/1985/2002	Clayl/Limestone	MESO
s05	Saint-Zacharie (83)	875000	1825000	INT	1972/1989	Limestone/Marl	MESO
s06	Le Castellet (83)	879000	1810000	CPX	1962/1996/2001	Limestone/Marl	MESO
s07	Bras (83)	895000	1835000	INT	1991/2004	Dolomitic limestone	MESO
s08	Plan de la Tour (83)	942000	1821000	INT	1970/1980	Granite	THERMO
s09	Pelissane (13)	826000	1853000	CPX	1967/1979/1997/2005	Limestone/Marl	MESO
s10	Ginasservis (83)	881000	1856000	CPX	1979/1989	Limestone/Clay	SUPRA
s11	Maussane les Alpilles (13)	800000	1861000	CPX	1967/1970/1979/1982/1995/2005	Colluvium/Limestone	MESO
s12	Ventabren (13)	838000	1838000	CPX	1967/1970/1979/1982/1995/2005	Limestone/Marl/Clay	MESO
s13	Collobrières (83)	920000	1810000	INT	1962/1990	Phyllades	MESO
s14	Fréjus (83)	959000	1842000	INT	1974/1982	Schists	MESO
s15	Ste Maxime (83)	946000	1828000	CPX	1962/1978/1982/1990/2003	Gneiss	MESO
s16	Saint Raphaël (83)	964000	1836000	CPX	1964/1979/1986/1996	Rhyolits	THERMO
s17	Montauroux (83)	959000	1851000	SIM	1990	Gneiss	MESO
s18	St Raphaël (83)	970000	1842000	SIM	1964	Rhyolits	THERMO
s19	Marseille (13)	847000	1822000	CPX	1967/1968/1969/1970/1977/1989/2006	Dolomitic limestone	MESO
s20	St Antonin sur Bayon (13)	862000	1840000	SIM	1989	Limestone/Clay	MESO
s21	Pontevès (83)	902000	1848000	SIM	2005	Limestone/Alluvium	SUPRA
s22	Mimet (13)	854000	1827000	SIM	1997	Dolomitic limestone	SUPRA
s23	Six-Fours-les-Plages (83)	886000	1790000	SIM	1979	Phyllades	THERMO
s24	Belgentier (83)	899000	1812000	SIM	1960	Limestone/Marl/Alluvium	MESO
s25	Rayol-Canadel sur Mer (83)	937000	1805000	SIM	1990	Micaschists	THERMO
s26	Vérignon (83)	917000	1859000	INT	1985/2008	Limestone/Marl	MOUNT
s27	Le Muy (83)	942000	1832000	CPX	1982/1990/2003	Granite	MESO
s28	La Garde Freinet (83)	938000	1827000	INT	1990/2003	Micaschists	MESO
s29	Comps sur Artuby (83)	939000	1864000	SIM	1984	Limestone/Marl	MOUNT
s30	Besse sur Issole (83)	909000	1824000	SIM	1979	Limestone/Marl	MESO
s31	Lorgues (83)	925000	1836000	UNB	-	Clay/Dolomitic limestone	MESO
s32	Mimet (13)	855000	1828000	UNB	-	Dolomitic limestone	SUPRA
s33	Puits d'Auzon (13)	870000	1845000	UNB	-	Limestone/Clay	SUPRA
s34	Lambesc (13)	836000	1859000	UNB	-	Limestone	SUPRA
s35	Collobrières (83)	929000	1811000	UNB	-	Gneiss/Micaschists	SUPRA
s36	Plan d'Aups (83)	878000	1820000	UNB	-	Limestone	MOUNT
s37	Montrieux (83)	893000	1811000	UNB	-	Limestone/Marl	MESO
s38	Fréjus (83)	963000	1844000	UNB	-	Rhyolits	SUPRA
s39	Tourettes (83)	954000	1858000	UNB	-	Clay/ Limestone	MESO
s40	Saint-Julien (83)	890000	1864000	UNB	-	Limestone	MESO

Table 4.1 Listing of the 40 landscape units of $1km^2$ with details on geolocalization (Lambert IIe coordinates), fire history, macro-climate and geology.

Sites can be localized with their coordinates in Lambert II extended (Xmin and Ymin are the coordinates of 1 km^2 quadrat samples). Fire mosaic spatiotemporal diversity of each site is summarized by the following pyrodiversity levels: UNB (unburned), SIM (simple fire mosaic), INT (intermediate complexity) and CPX (complex fire mosaic). The site geological composition is described by the main geological bedrock categories. Thermo-, meso-, supra- and moutain Mediterranean express the bioclimatic layer (altitudinal gradient) of study sites.

Using a regional database of digitised fire scars we characterized the fire history of each 1 km^2 quadrat since 1960 with three basic fire variables (i.e., time-since-fire, fire frequency, fraction of area burnt) and five additional variables expressing the spatial heterogeneity of the fire mosaic (i.e., Shannon diversity index, aggregation index, mean shape index, total edge, mean patch size, number of fire patches). Fire mosaics were classified into groups of similar pyrodiversity using principal components analysis (PCA) followed by clustering analysis (see Faivre et al. 2011).

Nine additional environmental attributes were computed for each 1 km^2 quadrat using a digitized geological map (1: 200,000) from the Bureau of Geological and Mining Research (BRGM), a digital elevation model (DEM) of 25 m resolution and meteorological data from Meteo France's local stations (http://climatheque.meteo.fr). The geological map was classified into five broad lithology classes (i.e. limestone, siliceous, sediments, marl and clay), which was then used to extract the proportional surface area of each lithology class for the 1 km^2 quadrats. Ten-year means (1987-1996) of annual rainfall and minimum temperature for each quadrat were computed from the monthly records of the nearest meteorological station (i.e., 10 km maximum). Finally, the mean and standard deviation of elevations within each quadrat were extracted from the DEM as a measure of relief.

Land use was summarised as the proportional surface area affected by nine classes of land use/land management: urbanized land, active farmland, abandoned farmland, clearing of shrub layer, grazing, clear-cut, tree plantation, recreation and unmanaged (i.e., natural regeneration). Definitions and codification of variables of each dataset are summarized in Table 4.2.

Statistical analyses

The influence of constraining factors (X1, X2 and X3 matrices) on the composition (abundance scores) and spatial pattern (spatial metrics) of habitats (Y matrix) within the 1km^2 quadrats was analysed with canonical analysis in R (R Development Core Team 2009). In this study redundancy analysis (RDA) was the most appropriate ordination method to study intermediate compositional gradients assuming linear species responses along the environmental gradients (Legendre and Legendre 1998). The R packages 'vegan' and 'simba' were used for multivariate statistics. Further analyses were made on simplified ordination diagrams showing only the most influential variables in order to improve interpretability.

Datasets		Codification	Definition
Habitat (Y Matrix)	Y1	URB1	Scattered urban areas with surrounding vegetation
		URB2	Dense urban areas
		CUL	Cultivated areas
		SPV	Sparsely vegetated areas
		HER	Grasslands with herbaceous dominance
		ESH	Evergreen small shrubland (0.5-2m height)
		TSH	Tall evergreen shrubland (2-5m height)
		TPH_EVR	Evergreen woodland (2-5m height)
		TPH_MIX	Mixed woodland (2-5m height)
		TPH_CON	Coniferous woodland (2-5m height)
		TPH_DEC	Deciduous woodland (2-5m height)
		FPH_EVR	Evergreen forest (canopy > 5m)
		FPH_MIX	Mixed forest (canopy > 5m)
		FPH_CON	Coniferous forest (canopy > 5m)
		FPH_DEC	Deciduous forest (canopy > 5m)
	Y2	SDI	Shannon's Diversity Index
		SEI	Shannon's Eveness Index
		MSI	Mean Shape Index
		TE	Total Edge
		MPS	Mean Patch size
		NumP	Number of patchs (Patch Richness)
Fire (X1 Matrix)		Fire_freq	Mean number of fires
		Fire_tsf	Mean time since the last fire event
		Burned Area	Total burned area per 1 km^2 grid cell
		Fire_shdi	Shannon's diversity - relative fire patch diversity
		Fire_ai	Aggregation index - degree of like adjacencies
		Fire_te	Total Edge - Perimeter of fire patches
		Fire_mps	Mean patch size - Average fire patch size
		Fire_numP	Number of fire patches
		Fire_msi	Mean Shape Index - measure of shape irregularity
Environment (X2 Matrix)		Limestone	Calcareous bedrock
		Clay	Clay soils
		Siliceous	Metamorphic or volcanic bedrocks
		Marl	Marl soils
		Sediments	Alluvium and Colluvium
		Altitude_mean	Mean Altitude per 1 km^2 grid cell
		Altitude_stdev	Measure of relief heterogeneity
		Rainfall	Average of total annual rainfall
		T°min	Average of minimum yearly temperature
Land Management (X3 Matrix)		URB	Urban construction
		AGR 1	Cultivated area
		AGR 2	Abandoned cultivated area
		CLC	Wood harvesting (Clear cut or selective cut)
		SCL	Shrub layer clearing (fuel break)
		PLA	Plantation of native/exotic species
		REC	Recreational area
		GRA	Herbivory grazing
		UMG	Unmanaged area

Table 4.2 Summary of data sets used in the fine landscape analysis (1 km^2 scale).
Codification and explanation of the different variables considered for the data sets computed in the multivariate analysis are provided. Further details can be found in the Handbook for surveillance and monitoring of European Habitats (Bunce et al. 2005).

Ordination diagrams were created using standard scaling and were inspected visually to assess the correlation between sites and explanatory variables (Fig. 4.6). Significance of the ordination was assessed by calculating the total variance explained by each axis and with a Monte Carlo permutation test (1000 replicates).

A partial RDA was undertaken to understand the relative importance of the explanatory variables (Borcard et al. 1992); this extension of RDA permits measurement of the relative contribution of individual sets of explanatory variables to the variance of the vegetation types (i.e., composition and spatial arrangement of habitats; see Table 4.2). Each explanatory table contained nine variables so that their respective weights were similar in the analysis (Table 4.2). This analysis was done separately for composition variables (Y1 matrix) and structural variables (Y2 matrix) of the response matrix Y (Table 4.2). The use of Hellinger-transformed data prior to partitioning the variance produces yields better accuracy in the estimation of adjusted R-squares values (Peres-Neto et al. 2006). The adjusted R-squares assess variance explained by individual explanatory tables and their combinations. The raw R-squares are also displayed, but these are biased estimates of variation explained by the explanatory tables since the raw R-squares are related to the number of variables (Peres-Neto et al. 2006) Results of variance partitioning including Monte-Carlo permutation tests are presented in Tables 4.3 and 4.4, and graphically summarized by Venn diagrams (Fig. 4.7 and 4.8).

In order to further characterize the role of fire in determining the composition and spatial heterogeneity of the mosaic of habitats, we compared the effects of different levels of pyrodiversity (i.e., unburned-UNB, simple-SIM, intermediate-INT and complex-CPX). Firstly, we used an analysis of similarities (ANOSIM) to investigate the significance of the effects between the different levels of pyrodiversity considering the entire Y matrix (Table 4.5). Then we used non-parametric Kruskal-Wallis test followed by Nemenyi tests (Hollander and Wolfe 1999) to investigate significant differences between pyrodiversity groups of key landscape mosaic variables such as diversity (Shannon diversity index and patch richness), fragmentation (aggregation index and mean patch size) and shape (mean shape index and total edge). Based on the richness of habitats per 1km^2 quadrat (i.e., number of different plant assemblages recorded), we performed species accumulation curves (SAC) and compared the curves of the four pyrodiversity levels (Fig. 4.8). We further use these results to relate the diversity of habitats per 1km^2 quadrat to the associated complexity of the fire mosaic, and thereby conclude on the pyrodiversity-biodiversity at the landscape level.

Results

Influence of fire on regional land cover changes

Regional trends

Over the 19-year period from 1988 to 2006 there has been pronounced change in the land cover distribution in Provence. The main trends in the proportional surface area of the nine land cover classes between 1988, 1999 and 2006 are summarised in Figure 4.2. Increases or decreases in the area under shrubland (SHR) and vegetation in seral stage (TRA) are opposed to increases/decreases in forested areas (oak woodlands-OAK; mixed woodlands-MIX; coniferous-CON). This contrast is particularly strong for the change over the 1999-2006 period. Although a small reduction of agricultural lands and a slight increase of urbanized areas can be noticed, the proportional area of these land cover categories did not show much variation during the 1988-2006 period.

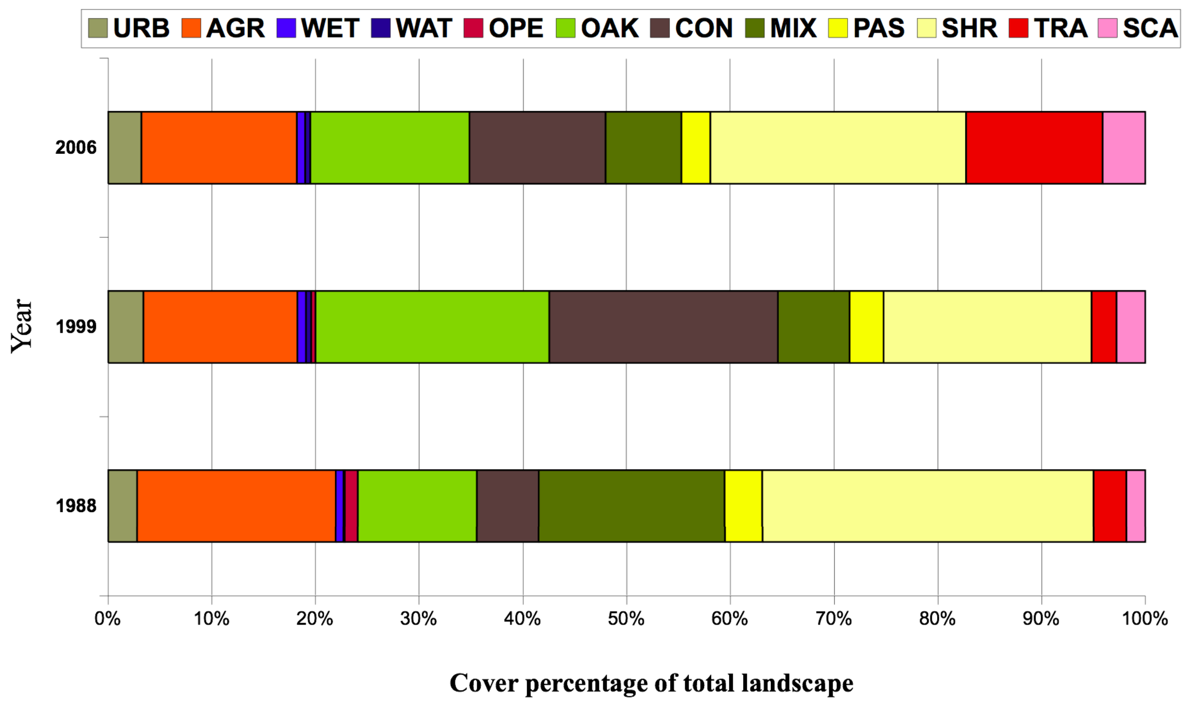

Fig. 4.2 Area of different land cover types measured among 50 landscape mosaics (3km x 3km) in 1988, 1999 and 2006.
Area per land cover category is expressed as the proportion of the whole sample. Land cover types studied are urban areas (URB), agricultural land (AGR), wetlands (WET), water bodies (WAT), open and non-vegetated habitats (OPE), pastures (PAS), shrublands (SHR), scattered vegetated systems (SCA), vegetated systems in transition (TRA), oak forests (OAK), coniferous forests (CON) and mixed forests (MIX).

Considering land cover change within burned landscape mosaics, Fig. 4.3 indicates substantial variations in mean land cover area for all categories except for mixed forests. When considering unburned landscape mosaics, we only noticed variations in mean land cover area within the coniferous stands category.

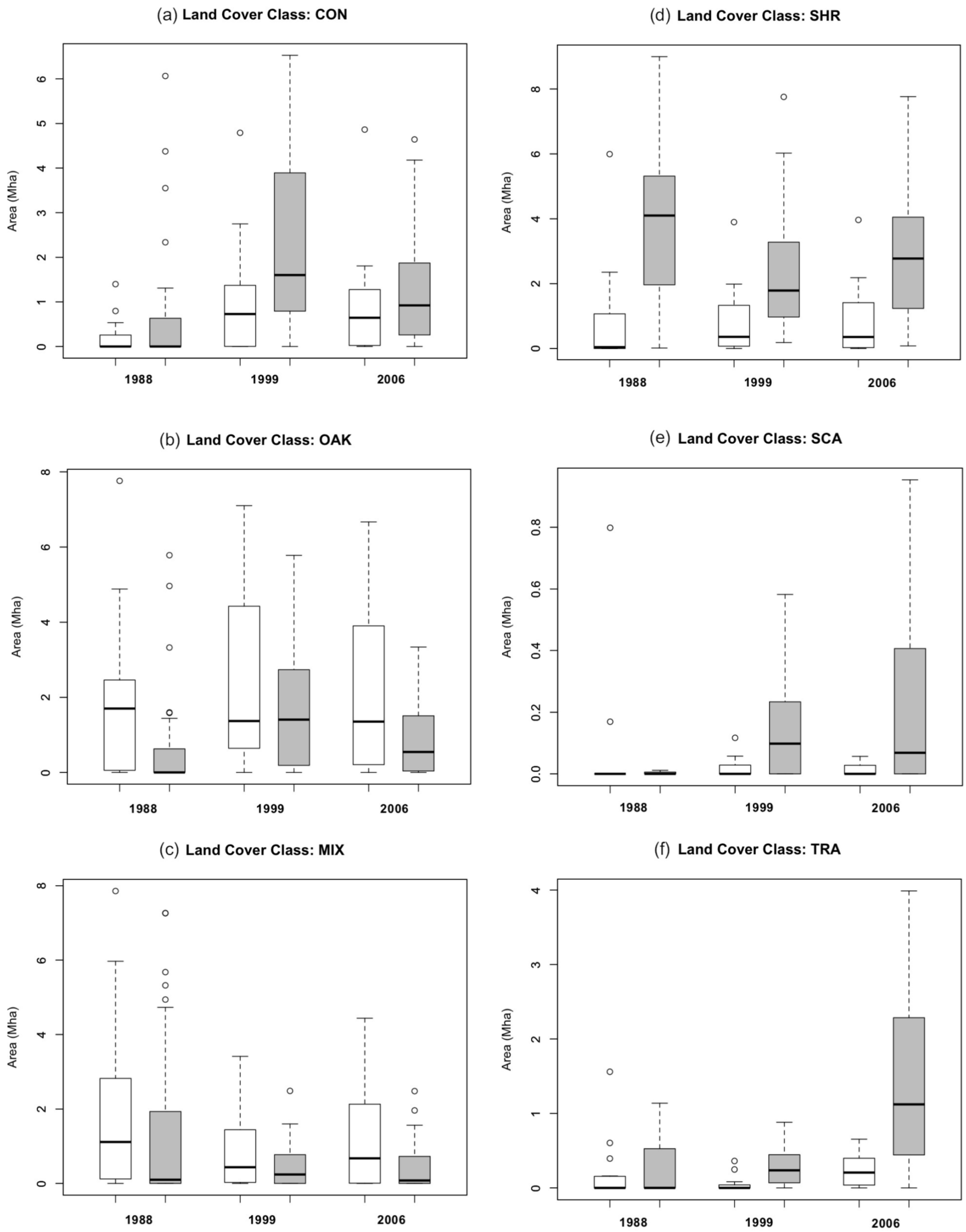

Fig. 4.3 Dominant land cover categories between 1988 and 2006 for burnt (grey) and unburnt (white) samples. In general, landscape mosaics that remained unburned for more than 50 years exhibited low variation in land cover types over the 1988-2006 period. Inversely, the landscape units affected by fire showed stronger variations in composition.

Landscape level trends

We further investigated the influence of fire on variations in land cover using co-inertia analysis. Analysis of the CIA diagram (Fig.4.4) revealed that the major shifts in composition and structure of land cover mosaics occurred in the quadrats that had been affected by fire in the last 50 years. The composition and spatial structure of land cover patterns in 1999 and 2006 were significantly related. The results of a Monte-Carlo permutation test confirmed that the co-inertia analysis presented a good initial summary of the co-structure between the two land cover datasets (*p*-value = 0.001). However, the RV-coefficient of 0.53, which measures the global similarity between the two datasets, expressed a relatively high degree of change in land cover patterns between the two dates.

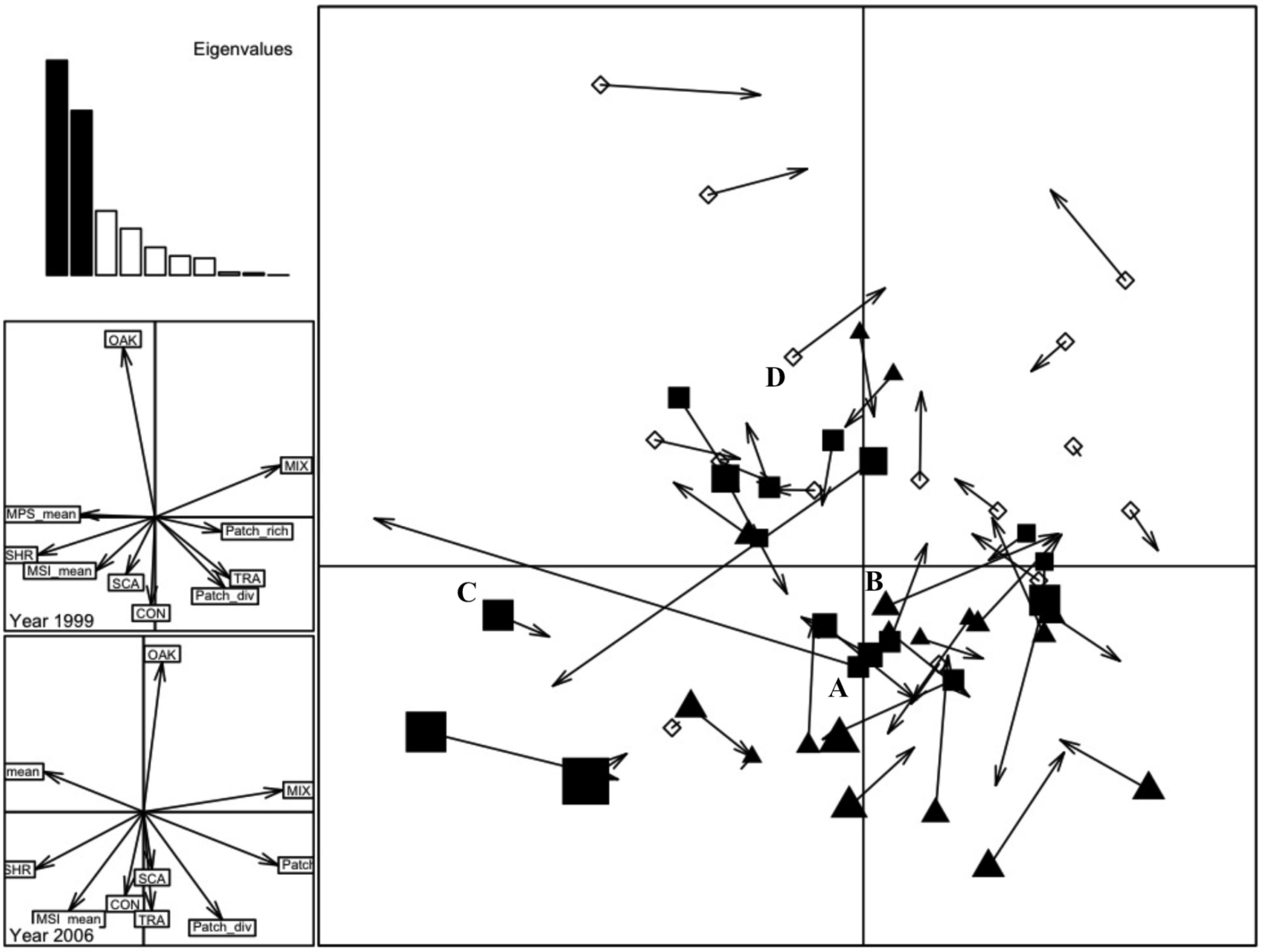

Fig. 4.4 Co-inertia diagram illustrating land cover change between 1999 and 2006.
The co-inertia axes are derived from two PCAs performed on the 1999-landcover dataset and 2006-landcover dataset respectively (see ordinations on the left of main diagram). The first and second co-inertia axes correspond to the most important joint trend between datasets (maximum of covariance) and accounted for 68% of the variance of the co-inertia analysis. Monte Carlo permutation test showed that the two datasets were significantly related. Each landscape mosaic is identified on the main diagram according to its fire history by black squares and triangles (i.e., recent and old fires respectively) and empty diamonds (no fires). The symbol's size expresses the number of fires (i.e., one fire for smaller symbols to six fires for larger ones) that occurred within the landscape unit. Arrows can be interpreted as the sample transitions from 1999 to 2006 and arrows length is proportional to the differences of structure and composition between the two dates.

Overall, the land cover change within unburned quadrats were characterized by short vector lengths while long vector lengths characterized transitions in burnt quadrats, indicating that there was significant divergence in the composition and structure profiles between 1999 and 2006 (Fig.4.4). Moreover the transitions within unburnt quadrats were relatively simple concerning transitions from mixed forests to oak forests (deciduous or sclerophyllous) and vice versa. On the other hand land cover change within burnt quadrats were much more complex and diverse (i.e., multiple orientations of vectors; Fig.4.4). Quadrats burnt between three and six times in the last 50 years, were characterized by higher patch diversity and patch richness than unburnt landscape mosaics. Alternatively quadrats characterized by large patches (MPS index) or complex shape (MSI index) were associated with relatively high fire frequency and often concerned recently burnt landscapes (Fig.4.4). However, there was no clear distinction in land cover structure or composition between old and recently burnt quadrats per se (i.e., when fire frequency was low).

Major changes in land cover patterns at the regional level can be attributed to fire occurence (Fig. 4.5). Where quadrats have been impacted by large extensive fires, forests have been converted to shrubland and there has been an associated decrease in the diversity of land cover types and increase in mean patch size (e.g., case A; Fig. 4.5). In contrast, the heterogeneity in fire patterns has enhanced the creation of transient (or interfire) habitats (TRA; e.g., open-woodlands with shrub understory) while permitting forests to maintain, thus increasing habitat diversity (e.g., case B; Fig. 4.5). In the case of repeated fires, the landscape mosaics tended to remain in a steady-state, generally composed of low shrublands and transitional habitats (TRA; shrublands with scattered trees)(e.g., case C; Fig. 4.5). Finally changes within unburned mosaics mainly consisted of coniferous forests conversion into mixed or oak forests, the small patches being progressively integrated into the main matrix. (e.g., case D; Fig. 4.5).

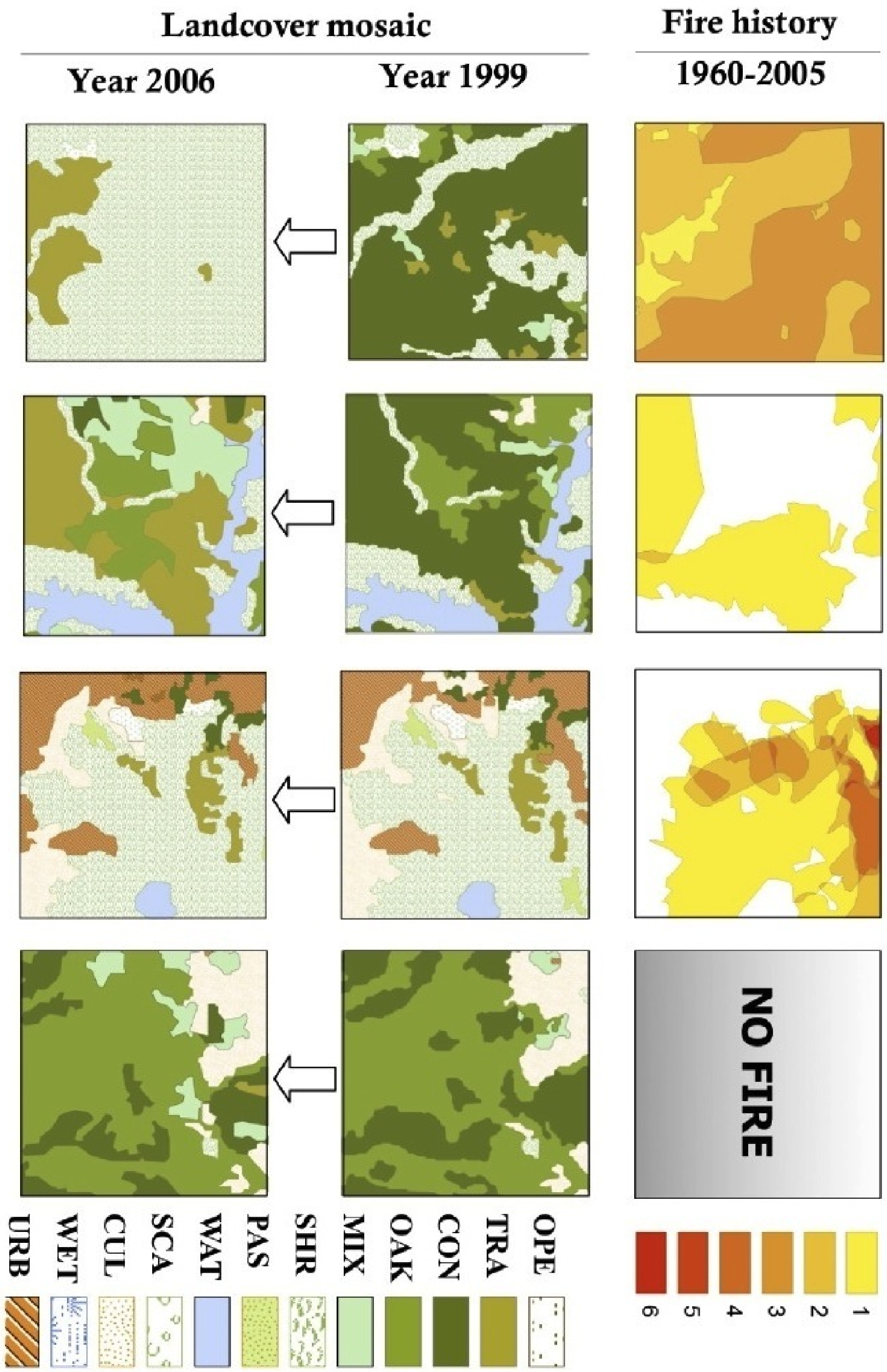

Fig. 4.5 Case studies representing different changes of land cover mosaics during the 1999-2006 period. The land cover change scenarios illustrate landscape diversification versus landscape homogenization processes and their relation to fire frequency patterns.

Drivers of landscape mosaic diversity

Influence of fire, environment and land management

Redundancy analysis allowed us to relate the distribution of landscape patterns according to their composition and structure (sites x habitat variables matrix; Y) to abiotic constraints (sites x explanatory variables; Xtot=X1+X2+X3). The first three axes of the RDA explained 51.2% (i.e., 22.6%, 16,5% and 12,1%, respectively) of the variance in the sites x habitat variables dataset. A Monte-Carlo permutation test for the redundancy analysis under a reduced model showed that the predictor variables matrix (i.e., fire, environment and land management variables) was significantly explaining the variability of landscape patterns (N.perm= 199, F=1.8737, *p*-value=0.005). Figure 4.6 (panels a-b) shows the distribution of sampled quadrats on the two first axes of the RDA according to the composition and diversity of habitat types constrained by the variable table, while the constraining variables vectors on the same axes are shown in panels c-d.

First, landscape mosaics with intermediate and complex levels of pyrodiversity were the most diverse. The diversity in composition and spatial configuration of habitat types, expressed by the isolines (Fig. 4.6), was positively correlated to the heterogeneity of the fire mosaic (Fire_msi and Fire_shdi) but also to anthropogenic factors such as agricultural practices or urbanization (Fig. 4.6). Management practices such as harvesting treatments, planting or grazing had barely any influence on landscape patterns and were mostly associated to homogeneous landscape mosaics. Considering environmental factors, there was an opposite gradient between sites on siliceous substrate and sites on limestone bedrock, the former showing higher diversity in landscape patterns. Quadrats at high elevations had more homogeneous patterns than those at low elevation, while those with strong relief showed higher diversity in landscape patterns than those with little relief.

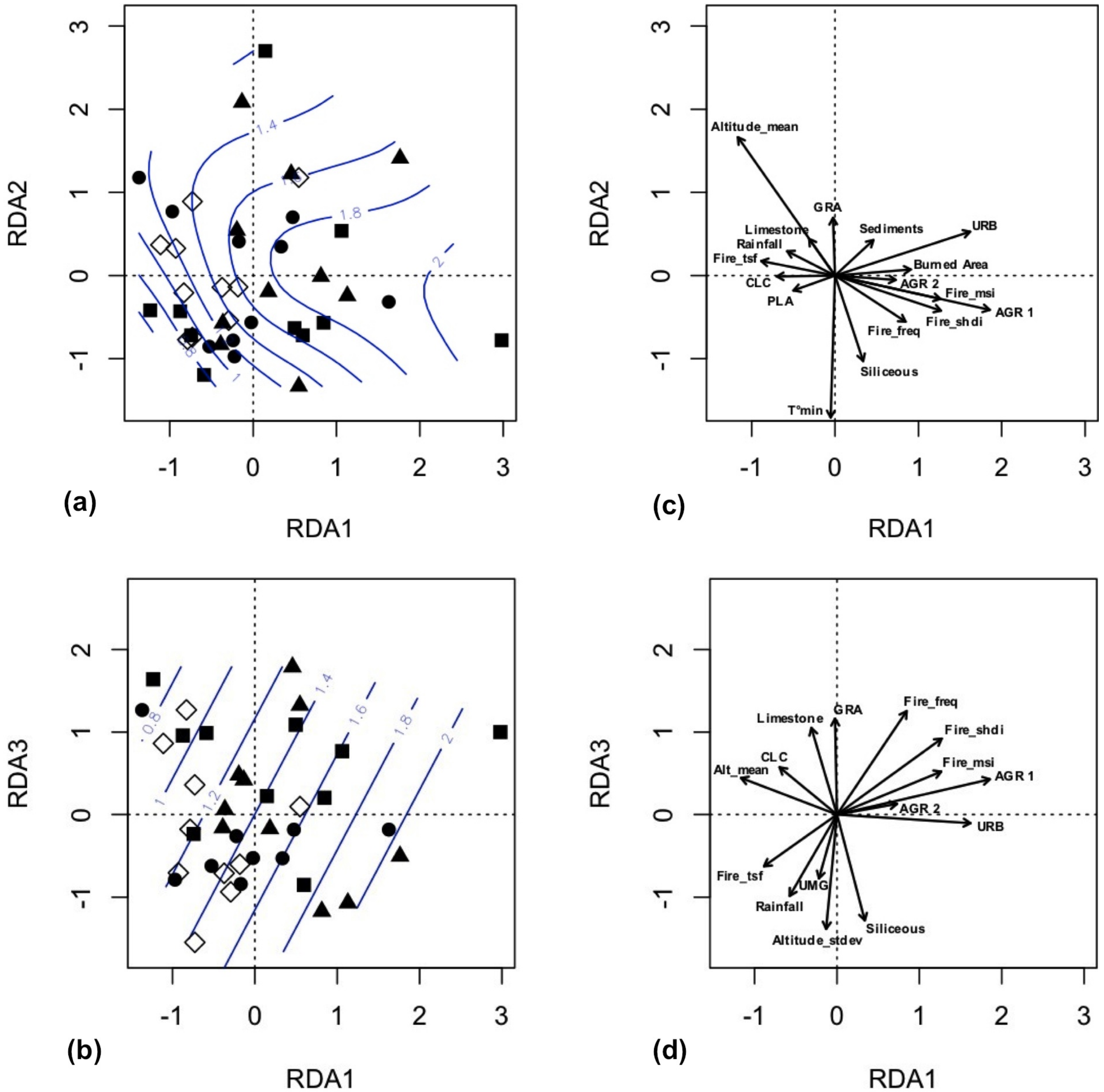

Fig. 4.6 Ordination biplot of study sites on the basis of a redundancy analysis.
The diagram shows the ordination of structure and composition attributes of land cover-land use patches, and explanatory variables (i.e., fire, land use and environment parameters). Diagrams from panels (a) and (b) depict the ordination of landscape mosaic samples, depicted by symbols corresponding to their pyrodiversity levels (i.e., UNB-empty diamonds, SIM-black circles, INT-black triangles and CPX-black squares). Isolines displaying the SHDI of habitat types are overlaid on the diagram using the envfit function of the vegan package. Panels (c) and (d) describe the ordination of explanatory variables represented by arrows. The first three RDA axes accounted respectively for 22.6%, 16,5% and 12,1% of total inertia. Permutation test for RDA under reduced model returned a significant effect (R^2= 0.845; *p-value* < 0.005) of fire, environment and land management constraints. Codes used in the RDA diagram to describe explanatory variables are mentioned in Table 4.1.

Deterministic factors of landscape mosaics

The relative contribution of abiotic variables (X1, X2 and X3 matrices) to habitat composition and spatial configuration was quantified using partial variance partitioning (Fig. 4.7,4.8). The adjusted R square values estimated from variance partitioning can be interpreted as the percentage of variance explained by the three constraining tables, individually or combined (Peres-Neto et al. 2006; Appendices 2 and 3). We found that environmental factors explained 28% of the variability in vegetation types composition of the 1km^2 quadrats (p-value < 0.001) and were therefore the predominant factor that determined the composition of vegetation types within the 1km^2 mosaics (Fig. 4.7, Table 4.3). Fire alone also explained a substantial part (8%) of compositional patterns variability within the landscape mosaics but additional part (4%) of this variability was explained only by its interaction with environmental factors.

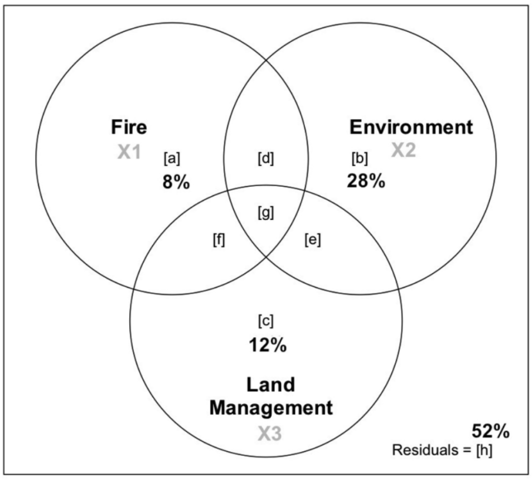

Fig. 4.7 Venn diagram showing the partitioning of variation in landscape patterns composition

The influence of land management alone appeared to be stronger than the fire one (12% of explained variance). All abiotic factors together explained a substantial and significant part of the total variability in habitat composition (47%).

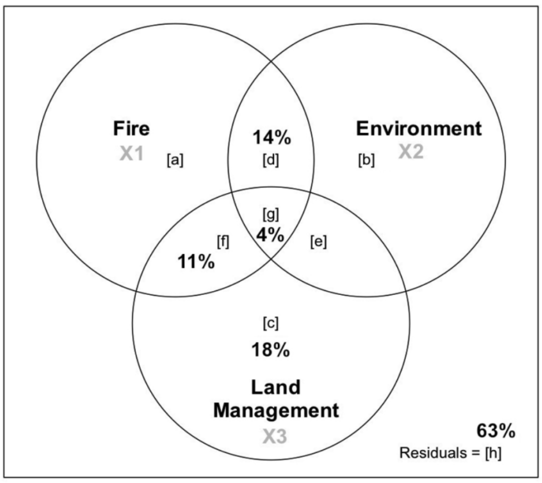

Fig. 4.8 Venn diagram showing the partitioning of variation in landscape spatial heterogeneity

Based on our analysis of the contribution of abiotic factors to the spatial configuration of the habitat mosaic (Fig. 4.8, Table 4.4) we found that land management is the only factor having significant influence (18% of explained variance; p < 0.05).

However, the differences in spatial configuration resulted to great extent from the interaction of fire and land management (18%) on the one hand and fire and environmental factors (11%) on the other hand. However, the amount of unexplained variation (i.e., Fig. 4.7 and 4.8; fraction (h)) is relatively high (> 50%), meaning that the set of variables considered in this study is not exhaustive.

	Df	R.square	Adj.R.square	Testable	F	Pr (>F)
Composite fractions:						
[a+d+f+g] = X1	9	0.3195	0.1154	TRUE	1,565	**
[b+d+e+g] = X2	9	0.4704	0.3115	TRUE	2,960	***
[c+e+f+g] = X3	9	0.2944	0.0827	TRUE	1,390	*
[a+b+d+e+f+g] = X1+X2	18	0.6507	0.3514	TRUE	2,616	***
[a+c+d+e+f+g] = X1+X3	18	0.5684	0.1985	TRUE	1,436	*
[b+c+d+e+f+g] = X2+X3	18	0.6738	0.3943	TRUE	2,570	***
[a+b+c+d+e+f+g] = All	27	0.8382	0.4742	TRUE	1,833	**
Individual fractions:						
[a] = X1 | X2+X3 = 8%	9	-	0.0798	TRUE	1.073	**ns**
[b] = X2 | X1+X3 = 28%	9	-	0.2757	TRUE	2,392	***
[c] = X3 | X1+X2 = 12%	9	-	0.1228	TRUE	1,328	**ns**
[d]	0	-	0.0359	FALSE	-	-
[e]	0	-	-0.0397	FALSE	-	-
[f]	0	-	-0.0400	FALSE	-	-
[g]	0	-	0.0397	FALSE	-	-
[h] = Residuals	-	-	0.5258	FALSE	-	-
Controlling one table X:						
[a+d] = X1 | X3	9	-	0.1157	TRUE	1,481	*
[a+f] = X1 | X2	9	-	0.0398	TRUE	1,204	**ns**
[b+d] = X2 | X3	9	-	0.3116	TRUE	2,714	***
[b+e] = X2 | X1	9	-	0.2359	TRUE	2,212	***
[c+e] = X3 | X1	9	-	0.0831	TRUE	1,345	**ns**
[c+f] = X3 | X2	9	-	0.0827	TRUE	1,456	*
Signif. codes: '***' 0.001; '**' 0.01 ; '*' 0.05						

Table 4.3 Variance partition table associated to Venn diagram (Fig. 4.7)

	Df	R.square	Adj.R.square	Testable	F	Pr (>F)
Composite fractions:						
[a+d+f+g] = X1	9	0.4455	0.2791	TRUE	2,678	*
[b+d+e+g] = X2	9	0.3035	0.0946	TRUE	1,452	**ns**
[c+e+f+g] = X3	9	0.4206	0.2468	TRUE	2,419	*
[a+b+d+e+f+g] = X1+X2	18	0.5617	0.1860	TRUE	1,728	**ns**
[a+c+d+e+f+g] = X1+X3	18	0.6604	0.3694	TRUE	4,423	**
[b+c+d+e+f+g] = X2+X3	18	0.6681	0.3837	TRUE	2,181	**ns**
[a+b+c+d+e+f+g] = All	27	0.8041	0.3635	TRUE	2,572	*
Individual fractions:						
[a] = X1 | X2+X3 =	9	-	-0.0202	TRUE	1,056	**ns**
[b] = X2 | X1+X3	9	-	-0.0058	TRUE	0,616	**ns**
[c] = X3 | X1+X2	9	-	0.1774	TRUE	3,134	*
[d]	0	-	0.1428	FALSE	-	-
[e]	0	-	-0.0872	FALSE	-	-
[f]	0	-	0.1116	FALSE	-	-
[g]	0	-	0.0448	FALSE	-	-
[h] = Residuals	-	-	0.6364	FALSE	-	-
Controlling one table X:						
[a+d] = X1 | X3	9	-	0.1226	TRUE	1,648	**ns**
[a+f] = X1 | X2	9	-	0.0914	TRUE	1,374	**ns**
[b+d] = X2 | X3	9	-	0.1369	TRUE	1,740	**ns**
[b+e] = X2 | X1	9	-	-0.0931	TRUE	0,618	**ns**
[c+e] = X3 | X1	9	-	0.0902	TRUE	1,476	**ns**
[c+f] = X3 | X2	9	-	0.2891	TRUE	2,564	*
Signif. codes: '***' 0.001; '**' 0.01 ; '*' 0.05						

Table 4.4 Variance partition table associated to Venn diagram (Fig. 4.8)

The tables summarize the respective influence of fire parameters (i.e., Matrix X1), environmental factors (i.e., Matrix X2) and land management variables (i.e., Matrix X3) on the habitat composition (Table 4.7) and spatial heterogeneity of 40 landscape 1km^2 units (i.e., Matrix Y1). The fraction [a] describes the part of variance explained by fire only when the environment and land management parameters are controlled. The same logic applies to [b] and [c]. Fractions [d], [e] and [f] correspond to the part of variance explained by the two-ways interactions between fire, environment and land management while [g] relates to the interaction of the three factors.

Pyrodiversity and landscape pattern diversity

Composition and diversity of vegetation types related to pyrodiversity

ANOSIM shows that landscape patterns associated to intermediate/complex fire mosaics are significantly different in both composition and structure in vegetation types from simple/long unburned fire mosaics (Table 4.5). There are thus two distinct groups of pyrodiversity in which similar effects on the composition and spatial configuration of landscape mosaics can be observed.

	X	Y	mean.x	mean.y	diff	sig	sigs
1	INT	CPX	0.6836	0.7092	-0.02570	0.191808	ns
2	INT	SIM	0.6836	0.6148	0.06878	0.006993	*
3	CPX	SIM	0.7092	0.6148	0.09448	0.000999	*
4	INT	UNB	0.6836	0.5962	0.08732	0.000999	*
5	CPX	UNB	0.7092	0.5962	0.11302	0.000999	*
6	SIM	UNB	0.6148	0.5962	0.01854	0.229770	ns

Table 4.5 Analysis of compositional similarities between subsets of different pyrodiversity. The table shows the ANOSIM results for the four categories of pyrodiversity considered (i.e., UNB, SIM, INT, CPX). Measures of similarity were performed using the Bray-Curtis dissimilarity index.

The Kruskal-Wallis tests preformed on selected variables describing landscape heterogeneity indicated that pyrodiversity had a significant effect on the patch richness of the landscape mosaic (NumP; chi-squared = 11.3449, p-value =0.01) and the mean patch size (MPS; chi-squared = 11.6312, p-value =0.00876). A post-Hoc Nemenyi test indicated that quadrats of complex/intermediate levels of pyrodiversity were significantly different from the unburned quadrats for these two variables (alpha=0.05).

Habitat accumulation curves representing the cumulative richness of habitats per sampled quadrat (Fig. 4.9) showed that the maximum richness in habitats was obtained at complex levels of pyrodiversity whereas the miminum richness in habitats was associated to unburned landscape mosaics.

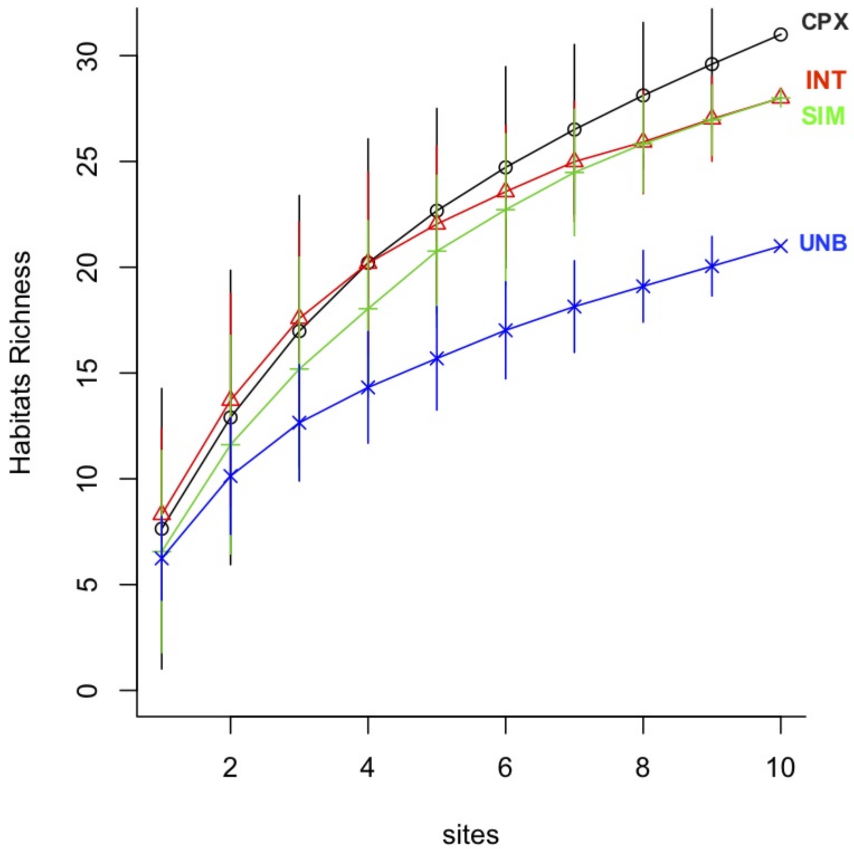

Fig. 4.9 Accumulation curves describing the accumulated richness in vegetation types according to the degree of pyrodiversity.

Discussion

Fire and the shifting landscape mosaic

Substantial land cover conversions occurred over a 20-yr time window in southeastern France. Most of the changes reflect a shift in the relative proportion of forest land covered by conifers, mixed and broadleaved forests, and seral land cover types such as transitional shrub lands. From 1999 to 2006 the proportion of CON and OAK decreased and the proportion of TRA increased. This pattern is not consistent with the classical successional pattern

SHR→TRA→CON→MIX→OAK (Médail and Quézel 2003). We thus interpret these changes as being the result of disturbance events such as fire. The co-inertia analysis of landscape quadrats between 1999 and 2006, confirmed that the landscape blocks with the higher rate of change were the burnt ones. When we analysed the proportional areas of land cover types along time series separating burned and unburned landscape mosaics, we observed an obvious difference between the proportional areas of wooded and shrubby land covers of burnt and unburnt blocks. Fire has an effect on the compositional change of habitats at the landscape level by promoting shrublands and coniferous woodlands while reducing the cover of broadleaved forest. The variability in successional trajectories of disturbed landscape blocks expressed by the co-inertia diagram also indicated that successional trajectories are not easily predictable according to the recurrence of fire events. A comprehensive review of post-fire landscape dynamics demonstrated that disturbed ecological systems recover deterministically through succession (Turner et al. 1993). Where disturbance interval is long relative to recovery time and a small proportion of the landscape is affected, the system is in a steady-state and exhibits low variance over time (e.g., broadleaved oak forested areas). However, where disturbance interval becomes much shorter than the lifespan of dominant organisms and a large proportion of the landscape is affected, the landscape mosaic will switch to another state defined by new successional trajectories (the theory of the shifting mosaic steady state; Bormann and Likens 1979).

Abiotic constraints of landscape heterogeneity

Abiotic factors are usually expected to determine the landscape-scale distribution of vegetation types (Pearson and Dawson 2003). Within the same study region, Roche et al. (1998) found that both environmental and land use factors controlled the patterns of woody species cover. Here, we arrived to similar conclusions as those factors explained 40 % of the variability of landscape composition in habitat types. The biophysical variables studied, particularly mean minimum temperature, mean elevation, rainfall and lithology, had a predominant influence in determining the composition of landscape patterns. For example, we observed a strong dichotomy between landscape mosaics on limestone and siliceous substrates, with the latter bedrocks being associated with higher diversity in habitat types. Altitudinal and geomorphological (topographic and landform) gradients control the variations in temperature, water and solar radiation, and thereby the availability of resources that regulate vegetation growth and distribution within the landscape matrix (Viedma and Melia 1999, Villers-Ruiz et al. 2003). Other recent Mediterranean studies reported the importance of biophysical variables, including lithology, temperature, precipitation and distance from the sea in explaining the differentiation of landscape patterns (Fellicisimo et al. 2002, Serra et al. 2008). Land management in the Provence region greatly contributed to the differences in composition (12%) and spatial configuration (18%) observed during the last 50 years between landscape mosaics. Land abandonment and intensification of agricultural practices, urbanisation of coastal plains and urban settlement in rural areas have been identified as the main causes of those land cover changes (Antrop 2004, Baudry and Tatoni 1993). The RDA results confirmed this trend by demonstrating the strong correlation between the spatial distribution of urban and cultivated areas and landscape mosaic diversity. More precisely, the modification in the organization of Provencal landscapes is a direct consequence of the fragmentation of natural vegetated systems (Tatoni et al.2005) due to (i) intense urbanisation, notably the diffuse housing among the coastal peri-urban belt, and (ii) progressive replacement/isolation of forested areas by vineyard- and orchard- dominated systems development among agricultural plains. This fragmentation phenomenon was found to accelerate the differences in shape, size and edge within landscape mosaics in Provence (Tatoni et al.2005). Similarly, our findings indicate that land use is responsible for nearly 20% of the variability of spatial heterogeneity. Although the influence of environmental heterogeneity on landscape composition is overriding the influence of fire and landuse, fire remains a major driver of landscape spatial heterogeneity at the landscape scale.

Fire is an inherent feature of Mediterranean Provence ecosystems contributing to pattern and diversity of plant assemblages within natural and semi-natural landscapes (Naveh 1994, Trabaud and Galtié 1996). Fire recurrence and severity have been described as driving forces that initiate cycles of vegetation succession and regulate patch dynamics within the mosaic of habitats (Turner et al.1994, Lloret et al. 2002). Here, we observed higher rates of transition between habitats associated to burned landscape mosaics, translating into either diversification or homogenization (spatial simplification) processes (Fig. 4.5). We found that the inherent heterogeneity characterizing these landscape patterns was positively correlated with the fire mosaic shape irregularity and diversity in fire frequency patterns. Moreover, landscape mosaics that had experienced fires over the last 50 years were associated with higher patch diversity, richness and interspersion than areas that remained unburned. These findings suggest that fire has a secondary (or subsidiary) influence on landscape composition in Provence, but remains the predominant factor influencing the spatial arrangement of natural and semi-natural habitats in the landscape mosaic through its strong interaction with environmental conditions and land use activities. Earlier Mediterranean studies (Viedma et al. 2006, Baeza et al. 2007) reported similar results while precising the importance of the pre-fire habitat composition (i.e., dominant types of vegetation) in determining future patterns of vegetation.

The ecological patterns in Provencal forests reflect the strong interaction between edaphic, climatic, natural and anthropic constraints (Médail 1996). We demonstrated in this study that these interactions had mainly implications on the spatial configuration of landscape patterns (Fig.4.7b). Fire and land use are indirectly related and contribute together to the heterogeneity of Provencal landscapes (Roche et al. 1998). Indeed, we currently observe among coastal areas an expansion of the wildland-urban interface (consecutive to intense urbanization), which has been related to the increase of fire ignitions (Lampin-Maillet et al. 2010, Syphard et al. 2008) and that are together responsible for the patchiness of actual landscape mosaics.

Pyrodiversity and landscape mosaic diversity

The question of how fire controls landscape diversity is complicated by the strong interplay between all abiotic constraints as mentioned previously but also by the multi-scale effects of fire (i.e., on landscape homogenization/diversification as well as on plant community regeneration strategies). Nevertheless, no single fire regime or history is optimal for all species or communities whether we consider local or landscape scales (Bradstock et al. 2005). If landscape diversity is defined as the combination of the number of vegetation types (or landscape richness) and the degree of spatial heterogeneity, then high pyrodiversity is thought to promote landscape diversity (Russell-Smith et al. 2002, Burrows and Wardell-Johnson 2004). The RDA results (Fig. 4.6) supports this idea as landscape diversity was positively correlated with fire frequency, the spatial heterogeneity of the fire mosaic (shape and patch diversity) and the burned area. Our findings further support the Heterogeneous Disturbance Hypothesis (HDH; Warren et al. 2007) as we found the higher richness in vegetation types associated with the more complex fire mosaics (Fig. 4.7). Indeed, the most diverse landscape patterns result from heterogeneous disturbance patterns that produced a high number of vegetation types of varying size and composition (Turner 2010). Moreover, complex fire mosaics are more likely to be composed by recent fires, which in turn created new regeneration niches originating new habitats within the landscape mosaic. However, Turner (1994) drew our attention to the fact that post-fire landscape heterogeneity is a function of the size of fire-created patches. As illustrated in figure 4.5, recurrent and extensive fires are more likely to generate homogeneous landscape patterns characterize by widespread shrubland coverage.

Implications for landscape-level conservation management

Understanding how fire interacts with other processes to shape current landscape patterns and their respective biodiversity is becoming increasingly important as climates change, as the wildland–urban interface expands and as human influence on fire regimes increases. It is clear that some amount of pyrodiversity is needed for biodiversity conservation (Driscoll et al. 2010). Land alteration and/or management practices that decrease landscape complexity (compositional or structural), such as fire suppression (e.g. in North America or Australia), or land abandonment (e.g. in the Mediterranean Basin), may create landscapes that are prone to larger, more intense fires (Keeley 2002, Lloret et al. 2002). In France, a strong fire suppression policy since the 1980s has led to reduction in the annual incidence and extent of fire. This suppression policy has already led to a decrease in the variability of fire disturbance events (Rigolot 1997). Consequently the area occupied by landscape mosaics of high structural and compositional diversity resulting from fire mosaics of intermediate complexity is diminishing. Furthermore, fire permits to reinitialize successional trajectories within the landscape as demonstrated earlier (Fig. 4.5). Consequently, the suppression of fires from the landscape is likely to alter the dynamic equilibrium of landscape mosaics (i.e., suppression of early stages of forest dynamics) and may lead to homogeneous landscape patterns composed of mature deciduous forests. The progressive disappearance of open woodlands and shrublands may cause deleterious effects on the Mediterranean biota across the region such as a loss in birds diversity (Prodon 2000).

The key management questions yet to be addressed are (i) how much pyrodiversity is required to meet biodiversity requirements at the landscape level while maintaining fire hazard the lowest to preserve life and property? and (ii) how do we translate this core information into practical fire management? This information is essential as the importance of landscape-scale fire regimes become more evident and as policies more explicitly require biodiversity to be incorporated into management (Driscoll et al. 2010, Clarke 2008). Depending on targeted conservation objectives (i.e., limitation of rare species extinction risk, maximizing species diversity, post-fire site rehabilitation), conservation agencies need to be able to adapt their fire policy, whether using prescribed burning as a surrogate for wildfires or by re-thinking the current fire suppression policy to meet biodiversity conservation objectives. Ongoing research upon the scope of pyrodiversity-biodiversity linkages is going to play a determining role in building that integrated fire management in southeastern France.

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5. Floristic comparison of contrasted fire-prone Mediterranean ecosystems from a landscape-level perspective.

Conservation Biology - prepared for submission

Introduction

The striking floristic richness and structural diversity that characterize Mediterranean environments is the product of palaeogeographical (Verlaque et al. 1997) and ecological conditions (Quézel 1985), long evolutionary processes in which natural disturbances like fire played a role as selective forces (Naveh 1975) and human caused disturbances acted as a filter of environmental complexity (Le Houerou 1981). This rich diversity also shows closer interrelations than any other climatic areas in the world between its major landscapes, their associated flora and the human activities that have been moulding them for nearly 10 000 years (Pons & Quézel 1985; Thirgood 1981). Fire has also contributed and continues to play a significant role in the evolution of Mediterranean biota but also in the diversification of natural, semi-natural and agro-pastoral landscapes (Di Castri et al. 1981; Naveh 1975). Wild- or prescribed fires influence the vegetation and its biodiversity across a wide range of scales (Reilly et al. 2006). In the absence of disturbances such as fire, landscapes of Mediterranean areas would tend to less diverse and more homogeneous patterns dominated either by forests or shrublands according to water availability constraints.

Mediterranean areas throughout the world are unique but fragile ecosystems that have suffered for most of them, from land conversion caused by agriculture intensification and urbanization, landscape homogenisation and detrimental changes in their disturbance regimes (Mazzoleni et al. 2004; Moreira & Russo 2006). Consequences for alpha and beta diversity might be local species extinction and globally a loss that might be irreversible. In the context of conserving that biodiversity, it becomes essential to acquire a global understanding of the relationships between disturbances such as fire and floristic diversity from local to regional scales. At small scales (i.e., stand level), the general opinion in the literature follows the precept of the ‘‘intermediate-disturbance hypothesis” (IDH; (Grime 1973) stating that the species diversity-disturbance relationship should peak at intermediate levels of disturbance.

The IDH postulates that intermediate disturbance levels prevent competitively dominant species from excluding other species from the community, and that there is a trade-off between species' ability to compete and their ability to tolerate disturbance. At low levels of disturbance, floristic diversity is low because only the best competitors persist. Similarly, when disturbances are very intense or frequent, few species can persist or repeatedly colonize after every disturbance. At larger scales (i.e., landscape, regional level), regional diversity of plant communities varies according to the 'mosaic concept' (Duelli 1997), which advocates that regional landscape diversity, which relies on structural parameters such as habitat variability and landscape heterogeneity, is promoted by increasing complexity of disturbances patterns (Chapter 4).

However, diversity-disturbance relationships can behave differently than contemporary consensus would suggest. The premise that intermediate disturbance produces maximum diversity has been found to be valid only under conditions of intermediate productivity (Grime 1973; Huston 1999). Secondly, peaked diversity relationships have the greatest odds of being observed when sampled areas are small and when few disturbance levels are examined (Mackey & Currie 2001). Although the logic of the intermediate disturbance hypothesis is sound when considering locally the effect of a single fire regime, it is necessary to examine if plant species diversity patterns response to natural disturbance support this prediction when considering the spatio-temporal fire mosaic. For instance, does a loss of biodiversity at the stand level (i.e., temporary absence of a species group from a localized area) translate into a global loss of biodiversity at the landscape level considering the mosaic of different habitats composing that landscape?

Pyrodiversity describes the spectrum of fire regimes within any given landscape and refers to the variability in recurrence, intensity, seasonality and dimensions of fire patterns across that landscape (Martin & Sapsis 1991). Most of the literature on the pyrodiversity-biodiversity relationship deals with alpha and/or gamma diversity as being less enigmatic concepts to tackle than beta diversity (Novotny & Weiblen 2005). In the present contribution we intend to address the pyrodiversity-biodiversity paradigm (Parr & Andersen 2006) by studying how landscape pyrodiversity (i.e., diversity of fire patterns across space and time) influence plant species diversity. According to the terminology used by Jurasinski et al. (2009), we successively consider in this study (i) "inventory diversity" to describe species richness and species abundance distributions within samples at local (i.e., alpha diversity) and regional (i.e., gamma diversity) scales and (ii) ‘‘differentiation diversity’’ for species compositional similarity between habitats of the same landscape mosaic (i.e., beta diversity). Using a pre-existing protocol to characterize landscape pyrodiversity (Faivre et al. 2011), we based our diversity analyses on two contrasting case studies, one in south-west Western Australia (SWWA) and another in southern France (SF). Comparing Mediterranean type ecosystems (MTEs) on different continents offered the opportunity to study a wider range of circumstances by considering fire regimes dominated either by unplanned fires (in France) or planned fires (in Australia).

The two study environments present contrasting fire management history (Faivre et al. 2011) but also marked differences in plant species responses to fire (i.e., resistance and resilience capacities). Moreover, the prescribed burning management in SWWA has generated coarse grained fire mosaics characterized by short fire return intervals while SE France exhibit finer grained fire mosaics with longer fire return interval (Boer et al. 2009; Faivre et al. 2011). Given that the range of floristic diversity patterns is dependent on the disturbance regime characterizing those Mediterranean biomes (Pignatti et al. 2002), we may ask whether planned fires and unplanned fires will have similar effects or not on plant diversity. We hypothesize that plant diversity within habitats (i.e., alpha diversity) will not vary the same in the two environments according to fire frequency or time-since-fire because of different levels of species adaptation to fire. However, we shall expect similar patterns of beta diversity between SWWA and SF as fire contributes to increase landscape heterogeneity by differentiating the mosaic of patches in different successional stages (Lloret et al. 2002), which would maximize floristic diversity at the landscape scale.

We framed our research objectives around the comparison of these fire-contrasted MTEs and according to the following topics: (i) testing the validity of the intermediate disturbance hypothesis at the alpha level while assessing successively the effects of fire frequency and time-since fire. We also propose (ii) to examine the relationship between the complexity of the spatio-temporal fire mosaic and resulting alpha diversity considering a gradient of pyrodiversity levels. In a further step, (iii) we investigate how beta diversity (i.e., degree of differentiation in species composition between communities from different sites) is influenced by landscape pyrodiversity. Finally, we discuss the implications of our findings to the sustainable conservation of plant diversity in these two MTEs while addressing the pyrodiversity-biodiversity paradigm.

Material and Methods

Study regions

Our first study area overlays two districts (i.e., Bouches-du-Rhône and Var) from the Provence-Alps-French Riviera administrative region in the south-east of France (Fig. 5.1). The climate is classified as Mediterranean North and Mediterranean Mountain bioclimates according to environmental climatic stratification of Europe (Metzger et al. 2005), with mean annual rainfall of 600-1000 mm and mean annual temperature ranging from 9°C to 21°C (MeteoFrance data records). The study area is characterized by high heterogeneity in geology and topography and consists of 1.1. Mha of mixed forests and evergreen shrublands across the districts of Bouches du Rhône and Var. Natural vegetation is a mixture of (i) extensive woodlands dominated by both evergreen (*Quercus suber* and *Quercus ilex*) and deciduous (*Quercus pubescens*) oak species, Aleppo pine (*Pinus halepensis*) forests and evergreen sclerophyllous shrublands of many forms, (ii) tall sclerophyll shrublands mainly found on acidic substrates and termed "*maquis*", (iii) middle height shrublands, generally occurring on calcareous substrates and termed "*garrigue*".

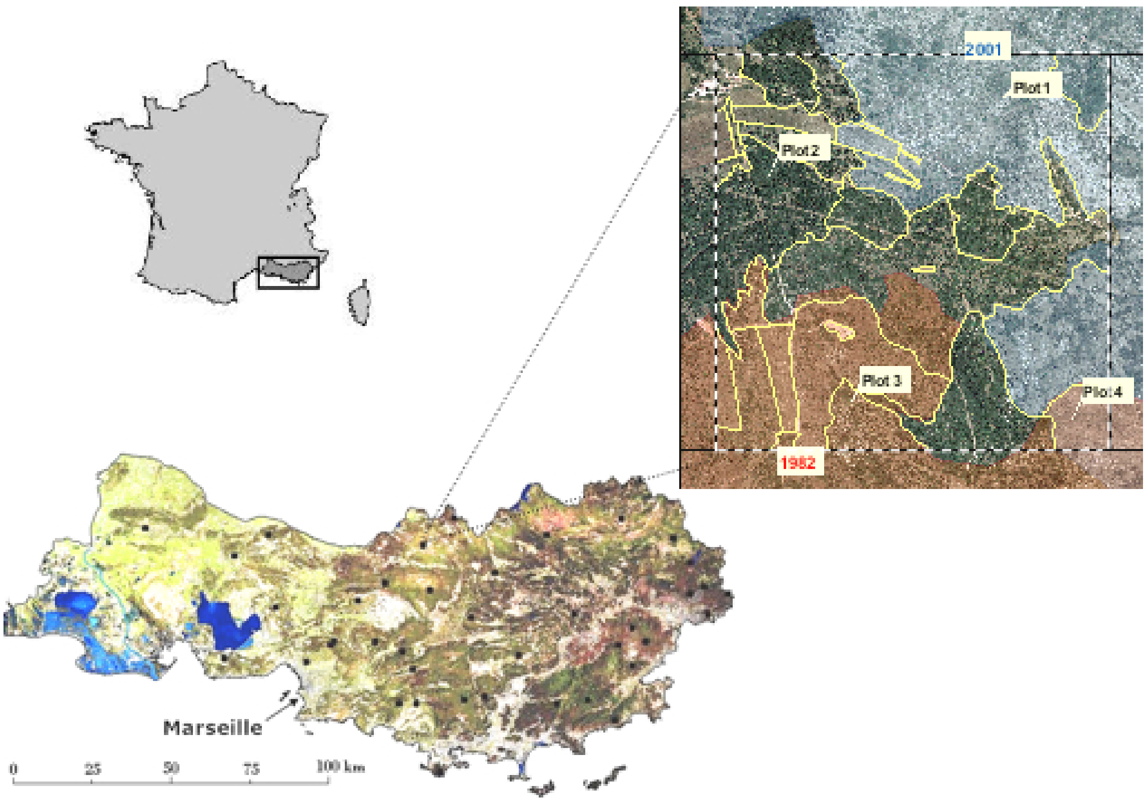

Fig. 5.1 Location of the study area in the Provence, southeastern France. The grey surface corresponds to the administrative districts of Bouches du Rhône and Var where the experiment was conducted. The 40 sites corresponding to 1km^2 grid cells are depicted by black squares. A zoom on one selected site in the North of the study region (top-right panel) shows the sampling design of a 1km^2 grid cell including plots location, habitats delineation as well as the fire history overlaid on an aerial photography of 2008.

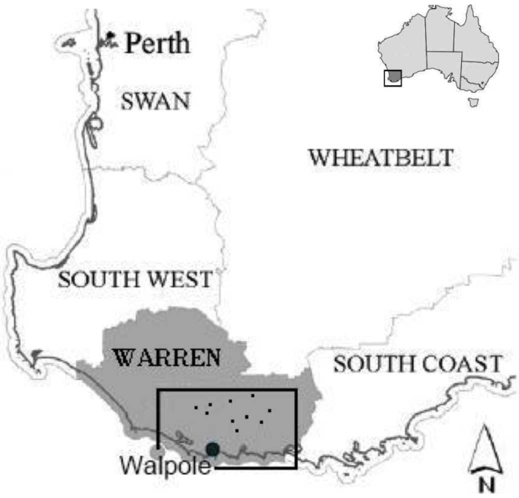

Fig. 5.2 Location of the study region in Western Australia. The figure displays the location of the Warren region (grey surface) and provides the locations of the 10 sampled sites (i.e., 1km^2 grid cells) shown by black points. Similar protocol as in SE France for monitoring species diversity and mapping fire patterns has been undertaken (see Fig. 5.1)

The second study area, located in the Warren biogeographic region of SWWA (Figure 5.2), features a Mediterranean-type climate with considerable climatic variations in temperature and rainfall with gradients from both south to north and west to east (i.e., mean annual rainfall ranges from 700 to 1100 mm; Australian Bureau of Meteorology).

The region is marked by an ancient geological history encompassing prolonged leaching and erosion, deposition and lateritization of the land surface (Wardell-Johnson & Horwitz 1996). Perhaps the most striking feature of this region is the lack of topographic relief (< 300m a.s.l) and apparent homogeneity as exemplified by the regional dominance of three widely distributed overstorey eucalypts: jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*) and karri (*E. diversicolor*) across a range of climatic and edaphic gradients (Wardell-Johnson G. et al. 1997). The sclerophyllous understorey comprises a rich diversity of woody shrubs and perennial and annual herbs termed “kwongan” (Pate & Beard 1984).

Characterization of landscape pyrodiversity

Our analysis focused on fires recorded and mapped from 1960 to 2008 in both study areas. Existing digital fire atlases from the French Regional District of Agriculture and Forestry (DDAF), the French National Forestry Office (ONF) and the Western Australia Department of Environment and Conservation (DEC; Hamilton et al. 2009) were used. We analyzed the spatiotemporal variation of fire disturbance firstly by considering the 1960-2008 temporal sequence of fire patterns and secondly, by performing a spatial analysis of this temporal sequence using landscape metrics and basic statistics. Historical fire patterns were characterised in 1km^2 grid cells, which were further classified according to the heterogeneity of their fire mosaic, from simple (i.e., low fire frequency, regular fire boundaries) to complex fire mosaics (high fire frequency, irregular fire boundaries). An exhaustive description of the methods used to characterise landscape pyrodiversity in each study area can be found in Faivre et al. (2011). A total of 50 sites (i.e., 1km^2 grid cells) were selected (40 sites in SE France and 10 sites in SW Australia). In each country, sites were selected to capture the spatiotemporal variability of fire patterns and were equally distributed among four levels of pyrodiversity (SIM, simple; INT, intermediate; CPX, complex; UNB, unburned since 50 years or more).

Vegetation sampling procedure

We considered a biogeographical perspective for both regions of interest before reducing the study areas extent to administrative districts. For instance, in SWWA, we used the template of Landscape Conservation Units and Ecological Vegetation Systems (Mattiske & Havel 1998) to delimit a relatively homogenous subregion within the Warren Region with regards to geology, biota, and climatic differences. Site selection in this subregion was further stratified to encapsulate these environmental variations as well as the variability in the fire regime.

Vegetation was surveyed in each site by assessing vascular plant species within four plots of 400 m^2 (radius of ca. 12m). The four circular plots selected per site were nested in different types of vegetated habitats so as to capture both the inherent vegetation diversity (i.e., variability of plant communities) and the fire history of the selected site (Fig. 5.1). For instance, preference was firstly given to nest plots within habitats characterized by different time-since-fire or that experienced different fire frequencies. When possible, we selected one plot per site within a remnant habitat that did not burned since at least 50 years. The remaining plots were selected within habitats dominated by different key species (e.g., pine forests, deciduous oak forests, ericaceous shrublands, heathlands). All survey plots in this study were assessed during the main flowering period in spring (May/June in SF and November/December in SWWA) to enable accurate identification of vascular plants.
The cover-abundance of each plant species was recorded using the Braun-Blanquet scale (i.e. +, <5% (rare species); 1, <5% (frequent species); 2, 5–25%; 3, 25–50%; 4, 50–75%; 5, >75%). Species nomenclature follows respectively Paczkowski and Chapman (2000) for SWWA and Kerguélen (1993) for SF.

Each plant species encountered during the vegetation surveys was also characterised using life forms attributes adapted from Raunkiaer's (1934) functional traits. This complementary information was collected in order to determine which plant functional groups contributed for the high species diversity in the two regions (Figure 5.3). The life forms categories include forest phanerophytes (tree>8m; FPH), tall phanerophytes (tree<8m or shrub>2m; TPH), multi-stemmed trees/tall shrubs (tree<8m or shrub>2m; MLT), multi-stemmed shrubs (0.5-2m; MLS), mid phanerophytes (0.5-2m; MPH), low phanerophytes (<0.5m; LPH), chamephytes (SCH), herbaceous geophytes (HER/GEO), herbaceous therophytes (HER/THE), herbaceous leafy hemicryptophytes (HER/LHE) and miscellaneous herbaceous (HER-others). Complete description of each class can be found in Bunce et al. (2005).

Diversity analyses

Inventory diversity

Initially, we selected a subsample of 40 plots per study area and investigated their diversity profiles by calculating their Shannon diversity index (Peet 1974; Shannon 1948). We calculated Shannon diversity accumulation curves with random permutations of accumulated plots, which enable to visually assess the differences in alpha and gamma diversity between the two regions. The method is similar to that designed for species richness accumulation curves (Colwell et al. 2004) with replacing the number of species encountered per sample by their diversity.

Secondly, we investigated the trends in plant species alpha diversity in relation to fire frequency and time-since-fire by performing a polynomial quantile regression on diversity values from each plot (160 plots in SE France and 40 plots in SWA; Fig. 5.4 and Fig. 5.5). The Shannon index (H_s) is not itself considered as a measurement of diversity (Jost 2006), but rather gives the uncertainty in the species identity of a sample. Therefore, we used the exponential of H_s as a measure of true diversity instead of the raw Shannon entropy because it expresses the number of effective species when considering multiple, unequally-weighted communities (Jost 2006). As we found a strong relation between fire frequency and alpha diversity in SE France, we sought to reduce this effect by considering diversity trends with time-since-fire for plots burned less than three times between 1960 and 2008. The polynomial quantile regressions were performed using “quantreg” package in R statistical software (R Development Core Team 2009).

After linking alpha diversity to the local-scale attributes of the fire regime (i.e., fire frequency and time-since-fire) we further investigate how landscape-scale parameters of the fire mosaic (i.e., spatial configuration and diversity in temporal patterns) were influencing the alpha diversity of plant species. Using a gradient of landscape pyrodiversity ranged in four levels of increasing fire spatiotemporal diversity (UNB; SIM; INT and CPX), we performed separately for each study area a one-factor ANOVA (after assumptions of normality and constant variance were checked) to test the differences in true alpha diversity (i.e., exp(H_s)) between plots from sites with different treatments. Additional Tukey HSD test permitted to test all pairwise comparisons of alpha diversity means among the four levels of treatment when ANOVA results showed significant difference (Table 5.1).

Differentiation diversity

Differentiation diversity or beta diversity is commonly thought to mean a change in species composition/abundance across different sites (Magurran 2004). We examine the distinctness of species assemblages among habitats by measuring their composition dissimilarities (i.e., pairwise comparisons between all pairs of 400m^2 plots). As our data were quantitative rather than presence/absence, we used a modified version of the popular Sorenson’s similarity measure called the Bray-Curtis index. We refer in the following to this dissimilarity index as a beta diversity measure (Magurran 1988):

$$C_N = \frac{2jN}{(N_a + N_b)}$$

Where N_a = the total number of individuals in site A; N_b = the total number of individuals in site B; and 2jN = the sum of the lower of the two abundances for species found in both sites.

We used a one-way analysis of similarities (ANOSIM; Clarke 1993) to test the null hypothesis that there is no difference in community composition/abundance among sites of different groups (i.e., 4 levels of pyrodiversity). A test statistic R was recomputed under permutation of the sample labels, and the significance level was found by referring the observed R-value to its permutation distribution resulting from 1000 runs. The ANOSIM statistic *R* is given by the formula:

$$R = \frac{(r_B - r_W)}{(N(N-1)/4)}$$

Where N is the total number of sampled sites and r_B and r_W are respectively the differences of mean ranks between groups and within groups. ANOSIM results are presented with boxplots in figure 5.7.

As previously for the standard ANOVA, we performed post-ANOSIM test to compare pyrodiversity groups regarding their mean similarity in species composition. For each group dissimilarities between all plots were calculated with the Bray-Curtis index. Resulting distance matrices were then compared between each pair of groups and a Bonferroni correction applied to correct for multiple testing. The comparison matrix showing the connections between groups is provided in Table 5.2. The *R*-packages “vegan” and “simba” were used for this section (R Development Core Team 2009).

Results

“Inventory diversity” of plant species

Species diversity in the two environments

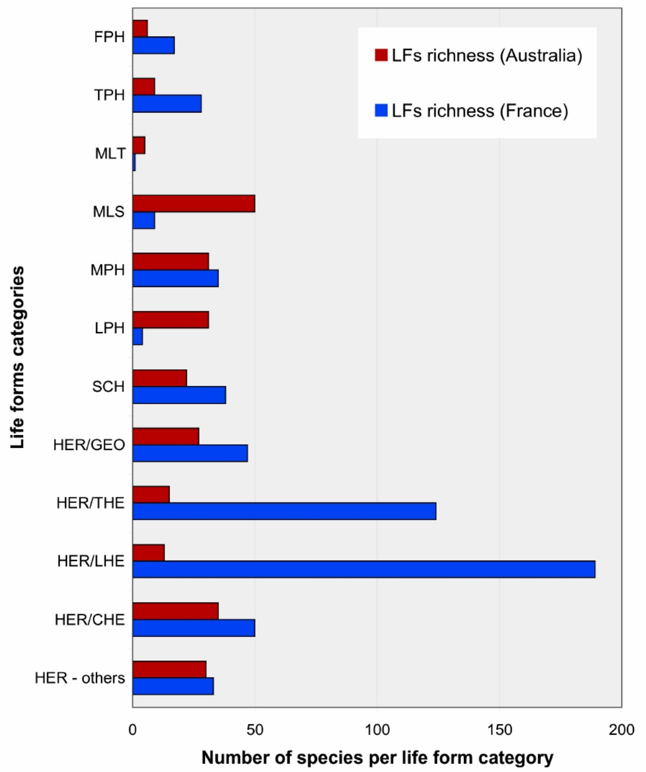

Fig. 5.3 Distribution of plants species among life forms categories in SF and SWWA.

We recorded about 600 plant species in France and 300 in Australia. In south-eastern France, this specific richness can be mainly imputed to the high number of herbaceous species with nearly 125 therophytes and 200 leafy hemicryptophytes (Fig.5.3). In SWWA, species richness comprised a broader variety of life form categories including herbaceous plants such as geophytes and caespitose hemicryptophytes and multi- and single stemmed shrubs and chamephytes (Fig.5.3).

The most species-rich families included the Fabaceae, Myrtaceae, Proteaceae and Poaceae in Australia and Asteraceae, Fabaceae, Poaceae and Lamiaceae in France.

When comparing the diversity profiles of both environments, we found higher alpha diversity within the 400m^2 plots in SW Australia than in SE France (Fig. 5.4a). Species-area curves showed that diversity increases more rapidly in Australia than in France when increasing the area sampled (Fig. 5.4). We found that gamma species diversity, summarized by the plateau of the accumulation curves, was significantly higher in the Warren region than in Provence (Fig. 5.4a). Considering the composition in life forms per plot, we also noticed higher diversity scores at the alpha level in SW Australia. Nevertheless, the two ecosystems shared similar profiles of life forms diversity when increasing the area sampled (Fig. 5.4b).

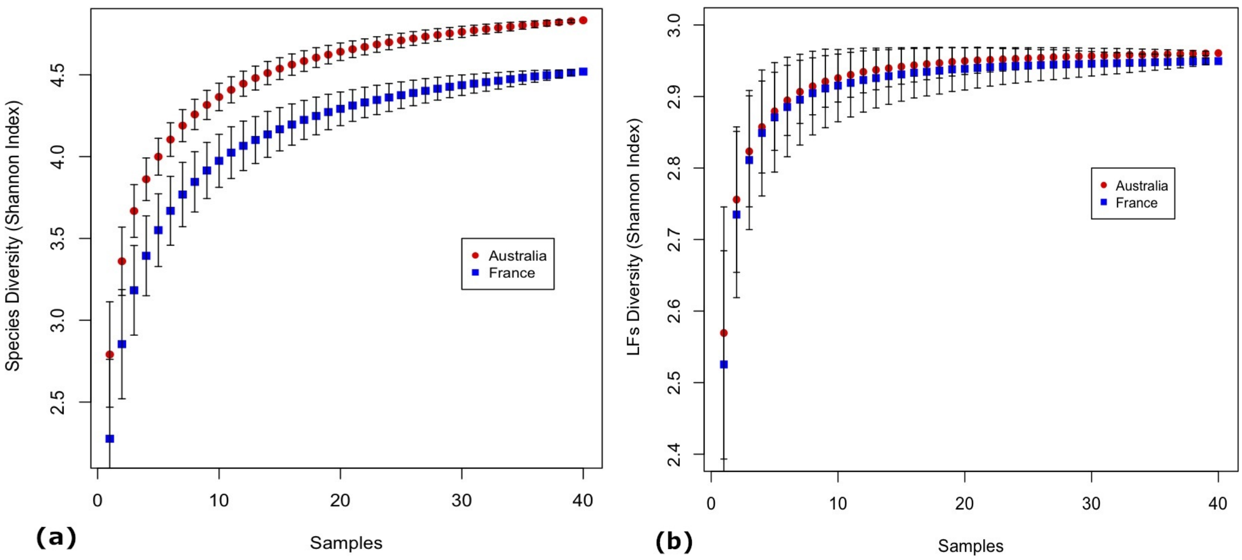

Fig. 5.4 Diversity accumulation curves.
Accumulation curves were calculated for a subsample of 40 plots randomly selected in each study area. The diversity is expressed by the Shannon index calculated from species abundance data (panel a) and from life forms abundance data (panel b).

Fire influence on alpha diversity: time and frequency effects.

Figure 5.5 indicates that the two ecosystems exhibit contrasted alpha diversity profiles among the gradient of fire frequency. Medium diversity values (i.e., 0.5 quantile) in SW Australia were insensitive to the number of times burnt. However, when considering the maxima of diversity values (i.e., 0.9 quantile), we observed a peaked relationship between fire frequency and alpha diversity. Alpha diversity increases until fire frequency reach three fires in 48 years and decreases progressively hereafter. We also noticed that alpha diversity in plots burnt 8 times (maximum fire frequency) was still higher than for plots unburnt in 48 years (Fig. 5.5a). In SE France, alpha diversity exhibited greater variation in relation to fire frequency even when considering plots with medium levels of diversity (i.e., 0.5 quantile) (Fig. 5.5b). Interestingly, when looking at the plots with the highest diversity (i.e., 0.9 quantile) we observe the similar peaked relationship as in SW Australia corresponding to a fire frequency of three fires (Fig. 5.5b). However, all the diversity curves reach minimum values after four fires in SE France.

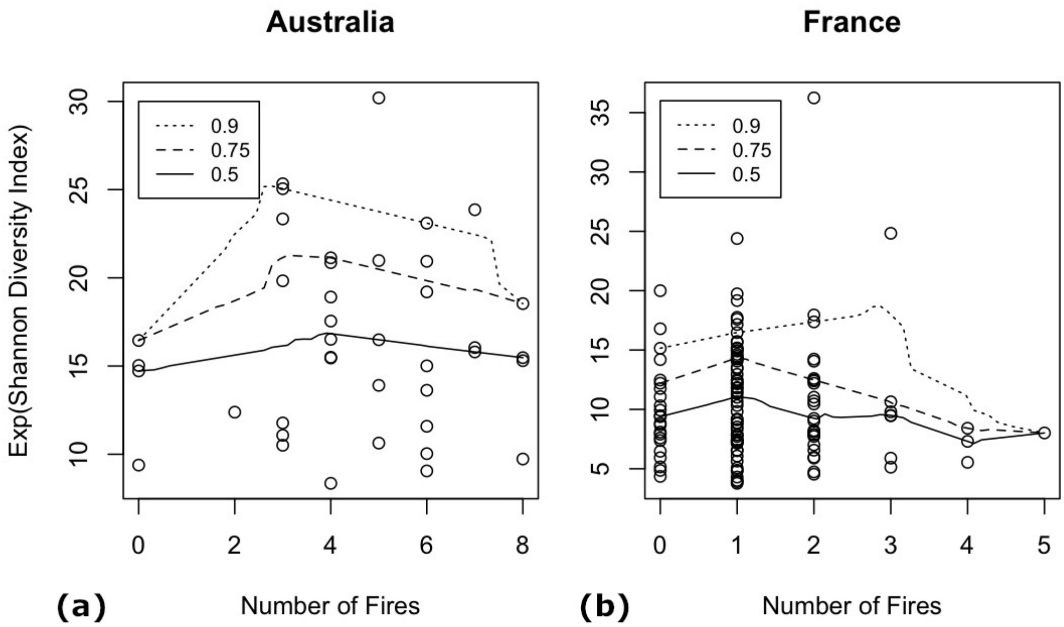

Fig. 5.5 Evolution of alpha diversity according to fire frequency. The curves correspond to the polynomial quantile regressions of 400m^2 plots diversity while considering simultaneously 0.5, 0.75 and 0.9 quantiles. Regression curves are respectively displayed Australia (panel a) and France (panel b).

Species alpha diversity varied according to time-since-fire, which translated by a global decline with age in the two study areas (Fig 5.6). However we noticed for SW Australia a slight increase of species diversity in the 5 years following the occurrence of a fire before decreasing progressively between 5 and 15 years (Fig. 5.6a). In SE France, we also recorded the highest rates of species alpha diversity just after a fire but we observed a significant decline of diversity during the first 5 years (Fig. 5.6b). In contrast to Australia, alpha diversity did not show strong variations after 5 years as indicated by the 20-years plateau in figure 5.6b.

Despite the insufficient number of long unburned plots, our results suggest that alpha diversity declined to minimum values after 35 years in the two regions.

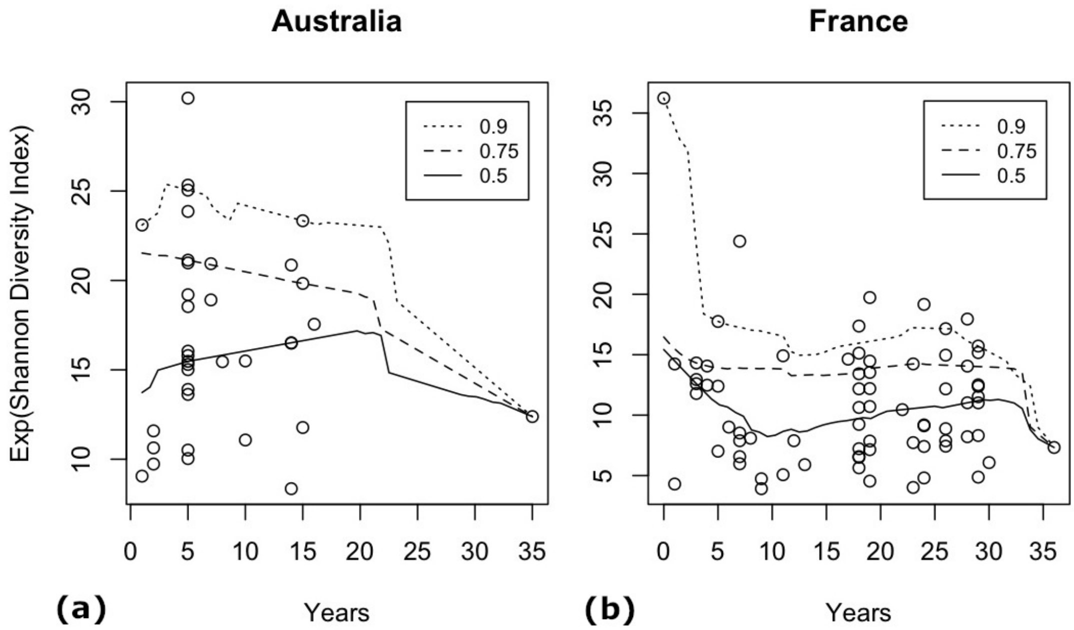

Fig. 5.6 Evolution of alpha diversity according to time-since-fire. The curves correspond to the polynomial regressions of 400m^2 plots diversity while considering simultaneously 0.5, 0.75 and 0.9 quantiles. Regression curves are respectively displayed for Australia (panel a) and France (panel b).

Impacts of landscape-scale disturbances on local diversity patterns

The results of one-way ANOVA indicated that both the variability of fire patches resulting from diverse fire frequency/time-since-fire and their spatial configuration within the fire mosaic exert a strong influence on the plant species diversity that is observed locally within the corresponding mosaic of vegetated habitats. This influence was close to the significance threshold (α =0.05) when considering the Australian study region (F=2.554; p-value=0.07) and was highly significant with regards to the French study region (F=3.236; p-value=0.02).

The post-ANOVA Tukey test performed for SE France (Table 5.1) showed that landscape mosaics with complex fire spatiotemporal patterns had significantly higher alpha diversity profiles than long unburned (i.e., 48 years) landscape mosaics.

Tukey HSD test				
Pyrodiversity levels	Diff	lwr	upr	p adj
INT-CPX	2.892	-0.2391	6.0234	0.0815 .
SIM-CPX	3.062	-0.0684	6.1941	0.0577 .
UNB-CPX	3.237	0.1060	6.3687	0.0397 *
SIM-INT	0.170	-2.9407	3.2821	0.9989
UNB-INT	0.345	-2.7661	3.4566	0.9916
UNB-SIM	0.174	-2.9369	3.2859	0.9988
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1				

Table 5.1 Results of Tukey-HSD test
The table summarize the differences between pyrodiversity levels (i.e., complex (CPX), intermediate (INT), simple (SIM) fire mosaic and unburned mosaic (UNB)) on alpha diversity.

"Differentiation diversity" within the landscape mosaic

In southeastern France, we found a significant differentiation in species composition among the different levels of pyrodiversity considered (Fig.5.7a; *p*-value=0.001; *R*=0.08). The low value of the R statistic indicated that plots from sites of different pyrodiversity shared globally a common pool of species. However, results of fig. 5.7a show that beta diversity (i.e., dissimilarities in species composition/abundance) is higher within sites characterized by complex fire mosaics than those characterized by intermediate or simple fire mosaics and that beta diversity of long unburned sites was the lowest. We can also notice that beta diversity of sites associated to intermediate pyrodiversity was lower than beta diversity of those associated with simple or complex pyrodiversity. Similar observations were ascertained for southwestern Australia despite no significant differences could be inferred (Fig. 5.7b; *p*-value=0.137).

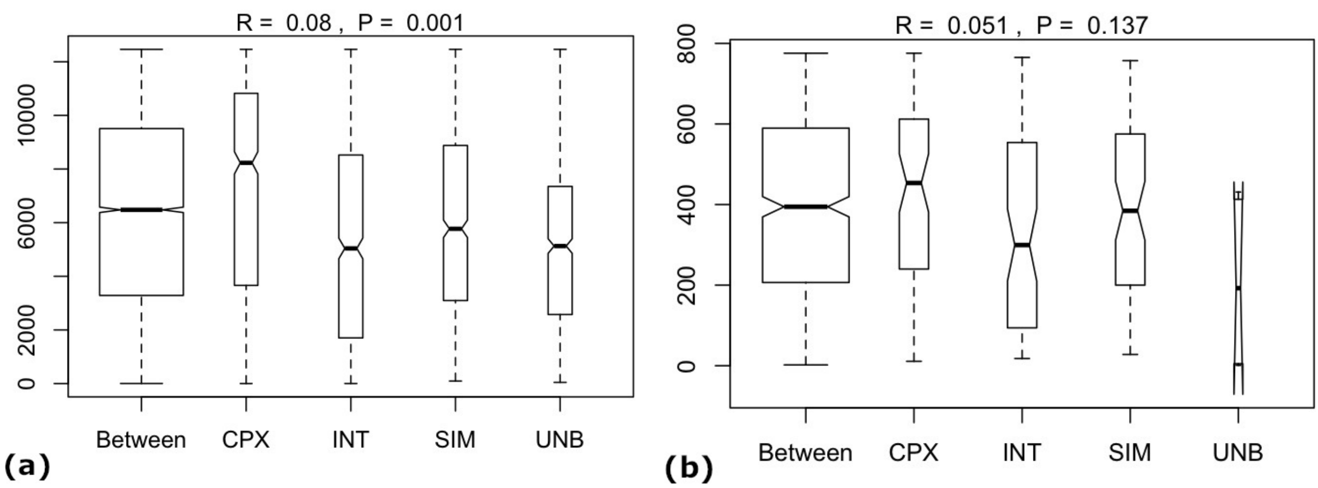

Fig. 5.7 Analysis of similarity (ANOSIM) results.
The boxplots depicts dissimilarities in species composition inter and intra sites (i.e., 1km^2 grid cells) belonging to the same class of pyrodiversity. The analysis has been performed for the 40 sites in France (panel a) and the 10 sites in Australia (panel b).

The mean pairwise comparisons between pyrodiversity groups computed for SE France confirmed that dissimilarities in species composition were significantly higher between plots of sites typified by complex pyrodiversity (Table 5.2). Differences of beta diversity were more contrasted between complex and simple pyrodiversity groups (i.e., p-value <0.01) than between complex and intermediate/unburned pyrodiversity groups (i.e., p-value <0.05).

	X	Y	mean.x	mean.y	diff	*p*-value	sigs
1	**INT**	**CPX**	0.789	0.840	-0.051	0.0019	**
2	INT	SIM	0.789	0.811	-0.022	0.1278	ns
3	**CPX**	**SIM**	0.840	0.811	0.028	0.0249	*
4	INT	UNB	0.789	0.801	-0.012	0.2497	ns
5	**CPX**	**UNB**	0.840	0.801	0.038	0.0029	**
6	SIM	UNB	0.811	0.801	0.009	0.2617	ns

Table 5.2 Post-ANOSIM test - Effects of pyrodiversity on Beta diversity in SE France The table summarizes the differences in mean composition dissimilarity (Bray and Curtis metric) between multiple sites affected by four different treatments of pyrodiversity. X and Y are the subset identifiers for one of the compared treatments. The difference in average distance between the respective means of X and Y is also indicated (i.e., diff). The significance of the difference in mean dissimilarities is notified by corresponding p-value and associated significance flag (i.e., sigs).

Discussion

Fire influence on “inventory diversity”

Our findings indicate that southeastern France and southwestern Australia share a similar peaked relationship when considering alpha diversity among fire frequency. We observed maximum plant species diversity within plots subject to intermediate fire frequencies (i.e., 1-2 fires in SE France and 2-4 fires in SW Australia), as predicted by the intermediate disturbance hypothesis (Grime 1973). However, floristic diversity showed less variation with increasing fire frequency in SW Australia than in SE France. This may be attributable to the sample size of Australian sites, which was lower and resulted in low statistical power. Another explanation is that peaked richness relationships are more likely to occur when disturbances are unplanned (i.e., wildfires) rather than planned (i.e., controlled fires) because their size, intensity being kept at constant levels in the latter case (Mackey & Currie 2001). Finally, we may hypothesize that the SWWA flora itself and its ability to recover very fast after fire is responsible for the diversity trends observed, as species diversity is strongly associated with ecosystem resiliency (Naeem & Li 1997). Burrows et al. (2008) examined the post-fire juvenile periods of plants from the Jarrah forests of SWWA and concluded that most of plant species flowered within 36 months after a fire. Furthermore, plant species present before the fire were also present afterwards as surviving stems or resprouts, thus maintaining the pre-fire composition of individual species. Similar observations have been noticed in the south-east of France with the maintenance of key-structural plant species after fire (Schaffhauser 2009).

The previous results also show that alpha diversity of vascular plants was influenced by time-since-fire in the two study areas, but to a lesser extent in SW Australia. In SE France, diversity was the greatest in the youngest burned stands (0-3 years) due to the presence of (i) invading herbaceous and heliophylous species (e.g., *Psoralea bituminosa*, *Argyrolobium zanonii* and *Aphyllanthes monspelliensis*) (ii) resprouting shrub species (e.g., *Quercus coccifera* and *Erica arborea*) or fire-induced seed-germinating species (e.g., *Cistus albidus*) and (iii) pionner species (e.g., *Pinus halepensis*). With increasing time-since-fire (5-30 years), diversity declines steeply followed as pioneer species are rapidly replaced by late successional tree/shrub species such as *Quercus ilex* and *Phyllirea latifolia*. These findings are in accordance with previous studies in the same area (Bonnet & Tatoni 2003; Capitanio & Carcaillet 2008). In SW Australia, species diversity was slightly delayed over time (i.e., 3-5 years) and is likely to be associated to the dominance of shrub species that have a slower growth. Conversely to SE France, we did not observe the peak of diversity corresponding to herbaceous species as this group is less represented in SW Australia (Fig. 5.3). Species diversity in SWWA then declines gradually between five and twenty years. This observation can be mainly attributable to the maintenance of a greatest species suite than in France, which is the result of more diversified post-fire regeneration strategies (Pignatti et al. 2002).

Our results also suggest that fire influence on species inventory diversity is not only valid at local scale but also at the landscape level. We found that more complex fire mosaics (i.e., fire patterns of different age, frequency and patchiness) are associated to higher alpha diversity of plant species encountered within the associated mosaic of habitats. Contrastingly, mosaic of habitats left unburned for more than 50 years exhibited the lowest alpha diversity. At the landscape scale, species richness is promoted by habitat heterogeneity because after a fire, species with differing resources requirements and competitive abilities are more likely to coexist in a wider range of habitats (Reilly et al. 2006). In both SWWA and SF, unburned and unmanaged landscapes mosaics were mostly composed of large habitat patches with similar species composition. Consequently off-site immigration processes are restricted as well as the maintenance of plant species unable to cope with these physical conditions (e.g., reduction of light availability), which explains the low alpha diversity value found in those landscapes.

Pyrodiversity and "differentiation diversity"

This study demonstrates that landscape pyrodiversity has a clearly discernible influence on the degree of compositional change between and within mosaic of habitats within the landscape. In southeastern France, beta diversity was significantly related to the degree of complexity of the fire mosaic but this was not the case for southwestern Australia. The results indicate that complex fire mosaics are associated with greatest differentiation of plant species within the landscape. As demonstrated in the previous chapter (Chapter 4), patch diversity of a given landscape mosaic (i.e., Shannon diversity based on vegetation types composition) is positively correlated with fire frequency, the spatial heterogeneity of the fire mosaic (shape and patch diversity) and the burned area. Moreover, complex fire mosaics are more likely to be composed by recent fires, which in turn create new regeneration niches originating new habitats within the landscape mosaic. Thus, high pyrodiversity promotes landscape heterogeneity (i.e., vegetation types of varying size, layer structure, and composition) and thereby high beta diversity (Burrows & Wardell-Johnson 2004; Russell-Smith et al. 2002).

The differences observed between our two study areas with regard to beta diversity can be related to their contrasted post-fire successional pathways. Fire succession in southwestern Australian plant communities generally follows the initial floristic composition model (Egler 1954), characterised by a very rapid recovery of plant cover and biomass after only 5-10 years (Bell et al. 1989; Burrows & Wardell-Johnson 2003). The post-fire forest environment is almost immediately populated by rootstock regeneration of pre-fire species, which reduce considerably the creation of new regeneration niches for off-site colonizers. In contrast, three distinct stages of post-fire vegetation dynamics characterized by different species composition or importance can be observed in southeastern France (Capitanio & Carcaillet 2008). An initial stage, somewhat similar to what occured in SW Australia, characterised by an intense regeneration of pre-fire species involving shrubs (e.g., *Q. coccifera*, *U.parviflorus*, *C. albidus*), tree resprouts and seedlings (e.g., *P. halepensis*, *Q. ilex*) and the presence of short-lived herbaceous species. The second transitional stage starting ca.15 years is defined by the dominance of shrubs in the understorey while Aleppo pine and evergreen oak species are well established. After 50 years, a shift in dominance from pine to mixed evergreen-deciduous oak vegetation occurs in an advanced stage of succession. The differences observed in fire succession explain how the transient vegetation stages in SE France are more likely to enhance the variability of beta diversity than in SW Australia.

Applying the Pyrodiversity-Biodiversity paradigm to conservation management

Although the logic of the Intermediate Disturbance hypothesis (IDH) is sound to explain the pyrodiversity-biodiversity paradigm at the patch scale, our findings advocate that the Heterogeneous Disturbance Hypothesis (Warren et al. 2007) when considering multi-patch or landscape scale. This precept suggests that biodiversity is maximized where multiple kinds, frequencies, severities, periodicities, sizes, shapes, and/or durations of disturbance occur across the landscape in a spatially and temporally distributed fashion. In this study, we demonstrated that the more heterogeneous/complex the fire mosaic was, the greatest were the alpha and beta diversity recorded within the associated landscape mosaic. Indeed, where a heterogeneous disturbance regime exists, species can partition the varied conditions so that a multitude of species can coexist along gradients of disturbance and succession (Turner 2010; Warren et al. 2007). Nevertheless, the comparison between the two study regions highlighted the limits of applicability of the HDH. Whether we consider planned or unplanned disturbances, the range of intensity, spatial configuration and temporal patterns encapsulated by the disturbance regime is significantly different (Faivre et al. 2011), which was found in this study to have a significant impact on landscape-scale plant diversity (SE France) or not (SW Australia).

In southwestern Australia, the current prescribed burning management policy implemented on ca. 5-years intervals is efficient in conserving the peak of species diversity at the alpha level. However the uniformity of burning spatial patterns superimposed on forest blocks associated with the high resilience of the flora to fire can have reversible impacts on biodiversity (Wittkuhn et al. 2011). Consequently, fire management recently evolved towards the integration of landscape-scale biodiversity as exemplified by the Fire Mosaic Project initiated by DEC in the Warren Region in 2002 that aims at enhancing biotic diversity at the landscape scale by introducing much smaller prescribed burns of more variable intensity than used in the rest of the district (Burrows & Wardell-Johnson 2004).

In southeastern France, similar conservation issues with respect to fire management may arise in the following decades as the fire suppression policy is changing the fire patterns within the landscape. We already observe fire mosaics essentially composed of small-size fires (i.e., fires rapidly stopped after their ignition) and large intense fires that went out of control, which is likely to result in a decrease of landscape pyrodiversity (Rigolot 1997). Consequently, if locally, alpha diversity is maintained, we shall expect a global loss of beta diversity consecutive to the homogenization of the mosaic of habitats at the regional level.

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6. Plant functional responses to landscape pyrodiversity in MTEs

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Introduction

Although many efforts have been dedicated to the protection and conservation of plant species, we are currently facing a loss of biodiversity around the world, with some of the most threatened habitats being in Mediterranean-Type Ecosystems, MTEs (MEA 2005). Understanding how variations of biodiversity will affect ecosystems processes becomes essential (Diaz & Cabido 2001) if we want to preserve the ecosystem services essential for human well-being (Diaz et al. 2005). The relationship between biological diversity and ecosystem functioning has been well studied since the mid-90s, particularly for more temperate ecosystems (Hector et al. 1999; Tilman et al. 1997). Nevertheless, biological diversity is often evaluated through species composition or relative abundance without consideration of other aspects of biodiversity, such as functional diversity (Hooper et al. 2005). However, the Biodiversity-Ecosystem Function paradigm (Naeem 2002) contends that any given ecosystem process is a function of biodiversity and the functional traits of the organisms involved (Costanza et al. 1997), as well as associated biogeochemical processes, and the abiotic environment. Consequently, the consideration of both functional diversity and functional composition is essential to predict how species will survive to human and natural disturbances and maintain the properties of an ecosystem (Diaz & Cabido 2001).

Mediterranean-climate regions of the world show exceptionally high plant diversity with a high level of rare and locally endemic taxa (Cowling et al. 1996). The different floristic assemblages observed within all MTEs are directly related to their biogeomorphological history, their intrinsic ecosystems processes and human/natural disturbances (Di Castri et al. 1981; Pignatti 1978). Despite strong taxonomic differences, the vegetation patterns of MTEs share common life form traits and similar morphological adaptations to fire (Barbour & Minnich 1990; Cowling & Campbell 1980). Consequently, the comparative study of functional traits of two (or more) MTEs is a promising way of examining how landscape-scale disturbances such as fire controls vegetation dynamics and if convergence trends between fire-prone systems can be identified. Moreover, simplifying the great diversity of plant species into a reduced set of functional traits allows examination of vegetation dynamics more precisely by differentiating the influence of biophysical constraints intrinsic to each ecosystem from those related to disturbance-related processes such as plant mortality and recruitment.

Fire is considered one of the main drivers of plant diversity in MTEs (Di Castri et al. 1981). Plant communities in MTEs are considered to have high resilience to fire and are adapted to fire regimes through plant traits such as resprouting, seed germination by heat-shock and smoke and fruit serotiny (Gill 1981; Keeley & Keeley 1981; Paula S. et al. 2009; Pausas et al. 2004). Functional diversity defines the variability of groups of species that use the same resources and respond to the environment in a similar way (Diaz et Cabido 2001). Each plant trait is expected to play a specific function role that contributes to the sustainability of ecosystem processes. Sclerophylly is one of the distinctive features characterizing most Mediterranean shrublands and this trait has primarily been interpreted as an adaptive response to low water availability during seasonal drought and/or to low fertility soils (Cunningham et al. 1999; Lamont et al. 2002), both of which also may influence fire risk. Consequently, the identification and estimation of PFTs abundance is of primary importance to the assessment of ecosystem function (Gitay & Noble 1997) and to predict long-term vegetation dynamics.

Here, we investigate the relationship between fire and functional diversity within habitats and across the landscape (i.e., mosaic of habitats) in MTEs. In order to capture the range of plant functional traits (PFTs) that contribute to functional diversity, we simultaneously consider life forms attributes derived from Raunkier (1934) functional traits and specific post-fire regenerative traits (Pausas & Verdú 2005). Whereas the former focuses on growth forms and position and type of the perennating bud (e.g., chamephytes and therophytes) and leaf retention attributes of shrubs and trees (e.g., deciduous and coniferous), an examination of regenerative traits provides insight into capacity to both withstand and recover after fire (e.g., resprouting capacity). We trialed our approach in two MTEs of contrasting fire management: (1) southern France, where fire regimes are dominated by wildfires and (2) south-west Australia, where fire regimes are dominated by planned fires. While these two regions differ in terms of fire return interval they feature similarities in their spatial fire patterns (Faivre et al. 2011).

We hypothesize that the two MTEs (southern France and south-west Australia) will exhibit contrasting functional diversity patterns at the habitat level, whether we consider life form or regenerative traits, because ecosystems of south-west Australia are highly resilient to fire (Bell 2001; Wittkuhn et al. 2011). Consequently, we expect a decrease in PFT diversity with increasing fire frequency in southern France whereas PFT diversity in south-west Australia would be less affected. Similarly, we might observe greater fluctuations of functional diversity in southern France with increasing time-since-fire. When considering beta functional diversity (i.e., compositional similarities among habitats), we expect the two regions to respond similarly to landscape pyrodiversity, with the more diverse landscape mosaics resulting from the more heterogeneous fire mosaics. Consequently, this study has several nested objectives. We sought to: (i) characterize and compare the influence of fire on functional diversity in two fire-prone MTEs, (ii) investigate functional diversity response by simultaneously analyzing the effects of fire on life form PFTs and regenerative PFTs, and finally (iii) examine the pyrodiversity-functional diversity relationship both within habitats and among habitats.

Material and Methods

Study areas

Our study focused on two regions, one located in the south-west corner of Western Australia and the second in the north-west Mediterranean basin. These regions feature a Mediterranean-type climate with pronounced bi-seasonality and variability of total rainfall (i.e., dry and hot summers and moist and cool autumns and winters). The first study area, located in the Warren region (SW Australia) is characterized by considerable climatic variations in temperature and rainfall (e.g., mean annual rainfall ranges from 700 to 1100 mm; Australian Bureau of Meteorology). The Warren region is marked by an ancient geological history encompassing prolonged leaching and erosion, deposition and lateritization of the land surface (Wardell-Johnson & Horwitz 1996). The lack of topographic relief within the Warren mostly explains the apparent homogeneity of plant species assemblages as exemplified by the regional dominance of three widely distributed overstorey eucalypts: jarrah (Eucalyptus marginata), marri (Corymbia calophylla) and karri (E. diversicolor) across a range of climatic and edaphic gradients (Wardell-Johnson et al., 1997). The sclerophyllous understorey comprises a rich diversity of woody shrubs and perennial and annual herbs. High fire frequencies, along with often intense fire conditions, have had a strong influence on the floristic composition by eliminating fire sensitive species and enhancing fire-resistant or tolerant species, leading to two major fire-response syndromes: resprouters and reseeders (Gill 1981). In the forest-dominated communities and similarly in the shrub-dominated kwongan (heathland) ecosystems of the southwest, the proportion of resprouting species represent ca. 65-75% of the flora while reseeders represent ca. 25-30% and a few percentage of the taxa combine both traits (Bell 2001; Burrows & Wardell-Johnson 2003). The high proportion of resprouters in SW Australia indicates that the postfire plant recovery of aboveground biomass is very rapid in these ecosystems (i.e., 5-10 years) compared to other Mediterranean-climate regions (Burrows & Wardell-Johnson 2003).

The second study area is located within the Provence-Alps-French Riviera administrative region in the south-east of France. The climate is classified as Mediterranean North and Mediterranean Mountain bioclimates according to environmental climatic stratification of Europe (Metzger et al. 2005), with mean annual rainfall of 600-1000 mm (MeteoFrance data records). The study area is characterized by high heterogeneity in topography and bedrocks and consists of 1.1. Mha of mixed forests and evergreen shrublands. The common vegetation assemblages encountered in this region are extensive evergreen and deciduous oak woodlands and Aleppo pine (Pinus halepensis) forests mixed with evergreen sclerophyllous shrublands of varying structure and diversity (Trabaud & Lepart 1980). Most fires (95%) occuring in Provence are unplanned and caused by human activities. Current fire regime is characterized by an average minimum fire interval of 26 years and a relatively low mean fire frequency (ca. 1.5 fires per 50 years period) (Faivre et al. 2011). Effective fire prevention and suppression management has significantly reduced the number and the extent of fires across the region (Rigolot & Roche 2009). Consequently, fire mosaics exhibit fine-grained patterns dominated by relatively small fires (10^1-10^2 ha) interspersed with large fire scars that resulted from extreme wildfire events.

Sampling and measurements

In the present study we tackle functional diversity by simultaneously considering life forms (or growth forms) PFTs and regenerative PFTs (see Lloret et al. 2003 for similar approach).

Vegetation sampling was performed at a fine landscape scale with considering mosaics of habitats of 1km^2 (hereafter named quadrats). We selected a total of 40 quadrats in SE France and 10 quadrats in SW Australia. Quadrat location was chosen to encompass the variability of fire history and the environmental heterogeneity in soil substrates, relief and climatic conditions characterizing each study area. Thus, the sample pool in each Mediterranean region was divided into four pyrodiversity classes of increasing complexity based on the protocol defined by Faivre et al. (2011) to characterize landscape pyrodiversity (i.e., clustering of sites with similar fire regime). Three sub-samples (10 sites in SE France, 3 sites in SW Australia) were defined by quadrats of complex (CPX), simple (SIM) and intermediate (INT) pyrodiversity, while the fourth sub-sample (10 sites in SE France, 1 site in SW Australia) was used as a reference consisting of quadrats that have not been subjected to fire for the last 50 years or longer (UNB; unburned).

Habitat surveys and recording of life forms in each quadrat followed the EBONE protocol (Bunce et al. 2008), which was designed to monitor biodiversity at landscape level across Europe and across MTEs worldwide. We assessed the composition and abundance of all life forms (and corresponding plant individuals) exceeding 10% of cover per habitat. For example, Allepo pine was recorded as FPH/CON for coniferous forest phanerophyte. We paid special attention in covering all the range of life forms PFTs in the two study regions by completing the EBONE classification with life form and leaf retention traits encountered in Australia such as multi-stemmed evergreen tall phanerophytes (e.g., Banksia attenuata; MLT/EVR) or forest phanerophytes with modified evergreen leaves (e.g., Nuytsia floribunda; FPH/MLE).

Detailed information and species examples related to the life form traits used to characterize plant functional types are provided in Table 6.1 (see also Bunce et al. 2005).

	Plant category	Life Forms (EBONE)	Level 1
Woody plants	Tree	Forest phanerophyte (> 5m)	**FPH**
		Tall phanerophyte (< 5m)	**TPH**
	Multi-stemmed tree/shrub	Multi-stemmed tree (< 5m) Multi-stemmed tall shrub (> 2m)	**ML T**
		Multi-stemmed shrub (< 2m)	**MLS**
	Shrub	Tall shrub (> 2m)	**TPH**
		Medium shrub (0.5-2m)	**MPH**
		Low shrub (< 0.5m)	**LPH**
		Dwarf shrub - chamephyte	**SCH**
	Palm, Grass tree and Fern tree	Stem rosette phanerophyte	**SRP**
	Cycads	Basal rosette phanerophyte	**BRP**
Non-woody plants	Grass, Sedge	Caespitose hemicryptophyte	**HER/CHE**
	Perennial forb	Leafy hemicryptophyte	**HER/LHE**
	Perennial forb	Geophyte	**HER/GEO**
	Annual and biennial forbs	Therophyte	**HER/THE**
	Rush	Helophyte	**HER/HEL**
	Fern, Moss and Lichen	Epiphyte	**HER/EPI**
	Succulents	Succulent herb	**HER/SUC**
Woody or not	Vine	Climbing shrub or herb	**CLI**

Leaf retention trait (EBONE)	Level 2
Evergreen broad leaves	**EVR**
Evergreen small leaves	**EVS**
Ericoid leaves	**ERI**
Non-leafy evergreen leaves	**NLE**
Modified leaves evergreen	**MLE**
Coniferous	**CON**
Winter deciduous	**DEC**
Summer deciduous	**SUM**

Taxonomic examples from southeast France and southwest Australia	
FPH/MLE	e.g., *Nuytsia floribunda*
TPH/DEC	e.g., *Ulmus minor*
MPH/EVR	e.g., *Cistus albidus*, *Petrophile diversifolia*
MLT/ERI	e.g., *Erica arborea*
MLS/NLE	e.g., *Calicotome spinosa*, *Daviesia incrassata*
LPH/EVR	e.g., *Lonicera implexa*, *Bossiaea ornata*
SCH/EVS	e.g., *Thymus vulgaris*, *Andersonia sprengelioides*
SRP/EVR	e.g., *Xanthorrhoea gracilis*
BRP/EVR	e.g., *Macrozamia riedlei*
HER/CHE	e.g., *Brachypodium retusum*, *Lomandra heterophylla*
HER/LHE	e.g., *Crepis vesicaria*, *Stylidium schoenoides*
HER/THE	e.g., *Trifolium angustifolium*, *Linum trigynum*
HER/GEO	e.g., *Asphodelus albus*, *Thelymitra macrophylla*
HER/HEL	e.g., *Gahnia trifida*
HER/EPI	e.g., *Asplenium adiantum-nigrum*, *Pteridium aquilinum*
HER/SUC	e.g., *Sedum anopetalum*
CLI	e.g., *Hedera helix*, *Billardiera floribunda*

Table 6.1 Life forms categories used for PFTs recording and related examples. LFs categories are derived from Raunkiaer's classification of growth forms and leaf retention traits. LFs were recorded using code1 and code2 to describe woody plants and code1 for other taxa. While code1 describes the general plant life forms, code2 give a precison on the photosynthetic component (for leaf size categories see Raunkier 1934 and Webb 1959). Examples of taxa encountered in the two Mediterranean ecosystems are provided for different types of life forms. Further information on LFs and their habitat preferences can be found in the Ebone's handbook for monitoring habitat and biodiversity (Bunce *et al.* 2005).

In addition, we also considered regenerative PFTs. Two main fire response traits have been identified in Mediterranean areas, (i) the resprouting capacity and (ii) the propagule-persistence capacity (Pausas et al. 2004). Therefore we attributed to every plant taxa recorded during the field surveys (over 10% of cover) one of these two traits (i.e., OR: obligate resprouters and OS: obligate seeders), or both (i.e., RS: facultative species). Colonizer species (i.e., neither resprouter or seeder) were not represented enough to be taken into account.

Statistical analysis

True functional diversity based on the exponential of the Shannon index was calculated for life form PFTs in order to characterize the influence of fire frequency and time-since-fire at the habitat level. We used the exponential of Shannon entropy as a measure of true diversity instead of the raw Shannon entropy because it expresses the number of equally-common species or life forms within a community (Jost 2006; MacArthur 1965) rather than the uncertainty in the species or life form identity of a sample. We explored the relation between life form diversity and fire frequency/time-since-fire using polynomial quantile regression performed with R statistical software (R Development Core Team 2009).

The behaviour of each regenerative PFT was examined by two-way ANOVAs to investigate if the differences of richness or cumulative cover per habitat observed between the two areas were related to the ecological characteristics of the regions or to the effects of fire (Table 6.2). This analysis was complemented by one-way ANOVAs performed for each regenerative PFT separately for each region. Results are mentioned within the text.

In addition we provided graphical insight to assess visually where the changes of richness/abundance of regenerative PFTs per habitat occur according to fire frequency and time-since-fire.

Life form and regenerative PFTs were finally analyzed together by grouping life forms into trees, shrubs and herbs categories, each of those being associated to resprouting (R+) or non-resprouting (R-) abilities. We explored graphically the post-fire successional evolution of these combined PFTs over time. .

In a second step analysis, we investigated the effect of landscape fire patterns (i.e., landscape pyrodiversity) on the diversity of PFTs among habitats. We used the composition of life form PFTs of all habitats per 1km^2 quadrat to derive Bray-Curtis dissimilarity index (Bray & Curtis 1957) as a measure of functional beta diversity. This index is bound between 0 and 1, where 0 means that the two habitats of the same quadrat have the same LFs composition, and 1 means that they do not share any species. Compilation of Bray-Curtis dissimilarity indices allowed us to plot density histograms for each pyrodiversity level in the two study regions.

Furthurmore, we quantified the variations of life forms frequencies within landscape mosaics subjected to contrasting pyrodiversity level and we explored graphically the decreases and increases in life form frequency along the pyrodiversity gradient for both study areas

Results

Plant functional response to fire frequency and time since fire

Diversity trends of life form PFTs in SE France and SW Australia

The two Mediterranean regions showed different trends of life forms diversity according to fire frequency (ANOVA; F= 5.979 and p-value= 0.0148). The effect of fire frequency on the diversity of life forms in each environment was significant (ANOVA; F= 6.365 and p-value= 0.0119). Life form diversity in SE France gradually decreased when the number of fires increases and significantly declined after four fires (Fig.6.1a). Life form diversity was greatest within habitats that had burned only once in the last 50 years. Nevertheless, long unburned habitats were also characterized by varying life form diversity. In SW Australia, there was no clear linkage between fire frequency and life form diversity (Fig. 6.1b). However, we observed the greatest range and maxima of life form diversity at intermediate levels of fire frequency (i.e., 4-5 fires).

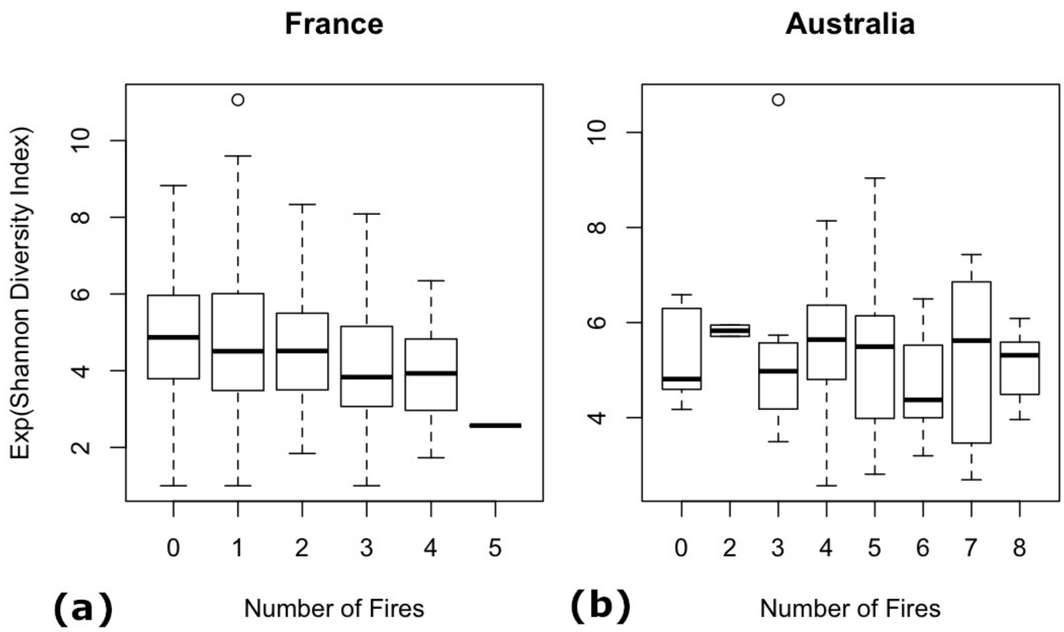


Fig. 6.1 Functional diversity response to fire frequency in SE France and SW Australia Boxplots describe the range of functional diversity according to fire frequency. The diversity is expressed as the exponential of the Shannon index (i.e., true diversity) based on the abundances of life forms per habitat of the 1km^2 quadrat.

The LFs diversity index (i.e., exp(Shannon index)) was not significantly influenced by time-since fire (ANOVA; F= 0.2173; p-value= 0.6413). However, the two regions showed a net increase of LFs diversity in the first five years after fire (Fig. 6.2). LFs diversity curves of the two regions showed contrasting trends according to time-since-fire as confirmed by the one-way ANOVA (F= 5.979; p-value= 0.0148). In SE France, the diversity of life forms within habitat showed a second peak between 10 and 15 years after fire (Fig. 6.2a) whereas we observed a relatively stable trend after 5-10 years in SW Australia (Fig. 6.2b).

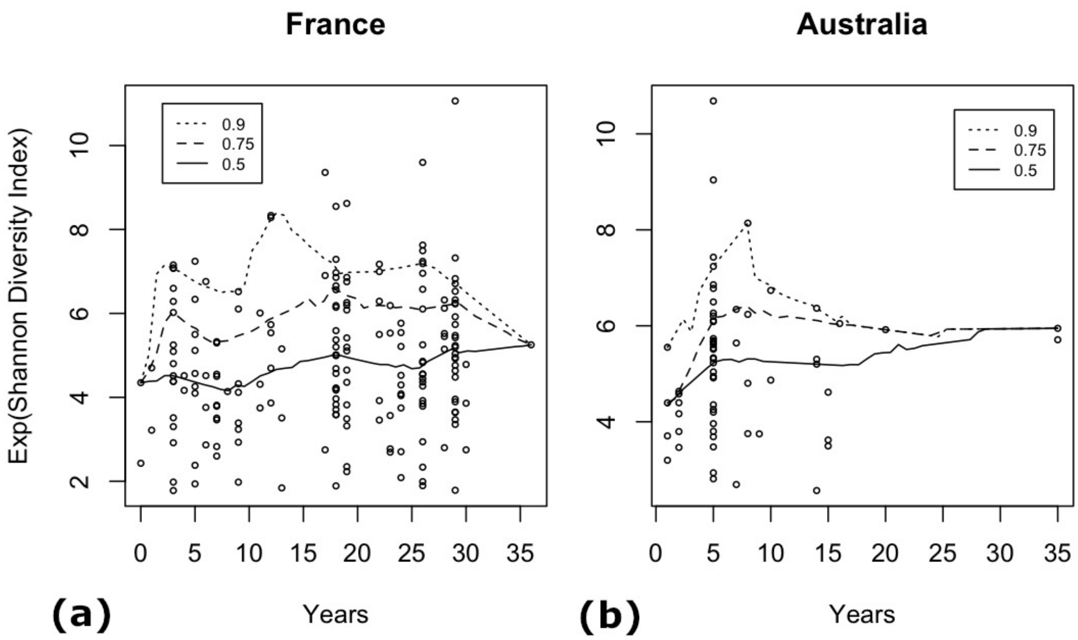


Fig. 6.2 Variations of functional diversity with time-since-fire in SE France and SW Australia
The curves correspond to the polynomial regressions of life forms diversity measured per habitat per 1 km^2 quadrat while considering simultaneously 0.5, 0.75 and 0.9 quantiles.

Influence of fire frequency and time-since fire on regenerative PFTs

The results of the two-way ANOVA performed on the richness of regenerative PFTs (Table 6.2) indicated significant differences between the two ecosystems in the effect of fire frequency on the richness of obligate resprouters (OR) and to a lesser extent on the richness of obligate seeders (OS). There was a pronounced decrease (by 50%) of the number of OR species with increasing fire frequency in SW Australia (Fig. 6.3a-b) while the richness of OR species in SE France decreased slightly (by 20%). SW Australia also exhibited varying richness of seeder species according to fire frequency than SE France, where OS richness remained relatively constant.

Regenerative PFTs	Country		FREQ		TSF		Country x FREQ		Country x TSF	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
OR richness	75.60	***	36.29	***	26.68	***	9.83	**	0.96	**ns**
OR abundance	92.93	***	11.75	***	3.71	**ns**	1.41	**ns**	2.34	**ns**
OS richness	28.16	***	5.61	*	9.25	**	0.37	**ns**	0.02	**ns**
OS abundance	8.79	**	2.21	**ns**	0.06	**ns**	0.21	**ns**	2.16	**ns**
RS richness	553.6	***	0.29	**ns**	0.57	**ns**	0.14	**ns**	0.08	**ns**
RS abundance	469.2	***	0.22	**ns**	0.01	**ns**	3.39	**ns**	5.26	*

Table 6.2 Two-way ANOVAs of the effect of fire frequency, time-since-fire and country on PFTs abundance and richness

In both regions, separate one-way ANOVAs revealed that fire frequency significantly impacted the richness of resprouting species (p-value <0.05), which was not the case for seeder species (OS). Nevertheless, we observed a greater richness of OS species within burned habitats than within unburned ones. As for seeder species, the richness of facilitative species (RS) in both regions exhibited no significant variations (one-way ANOVAs; p-value >0.05) as fire frequency increased.

The abundance of regenerative PFTs responded similarly to the richness of regenerative PFTs according to fire frequency/time-since-fire in the two study areas (Fig. 6.3). We noticed however that OR species exhibited the lowest richness at high fire frequencies (i.e., five fires within 50 years) while maintaining a high abundance.

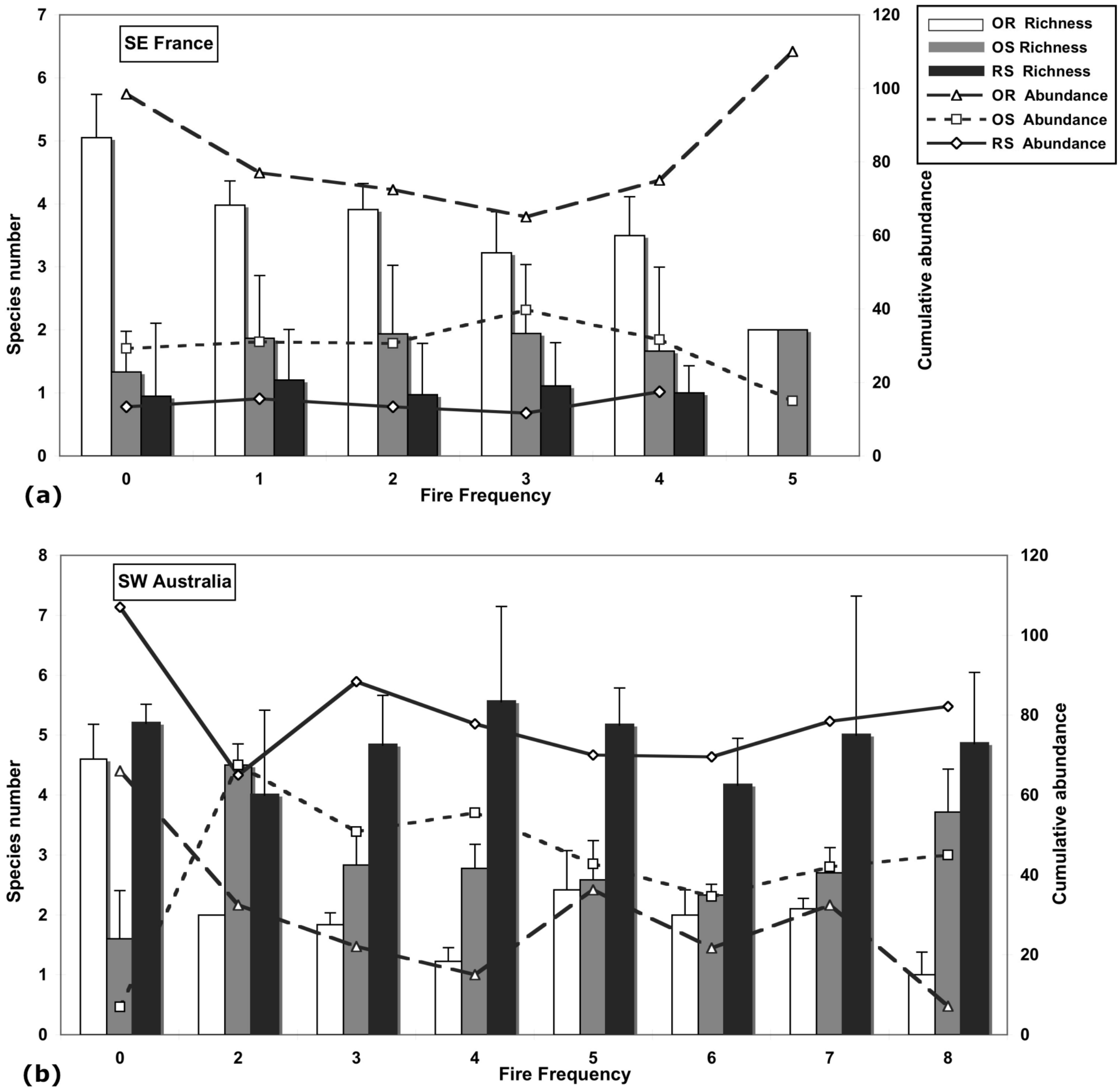


Fig. 6.3 Variations in PFTs richness and abundance with fire frequency.
PFTs richness is displayed with histograms (mean ± SE) corresponding to obligate resprouters (OR), obligate seeders (OS) and resprouter-seeder species (RS). Curves show the mean cumulative abundance (second Y axis) per regenerative PFTs.

When examining the behaviour of regenerative PFTs richness/abundance with time-since-fire, resprouters and seeders exhibit opposite trends across both regions (Fig. 6.4a-b), whereby richness/abundance of obligate seeders increased in the first post-fire period (i.e., 0-15 years), but are progressively replaced by obligate resprouters in the later stages of succession (i.e., 15-50 years).

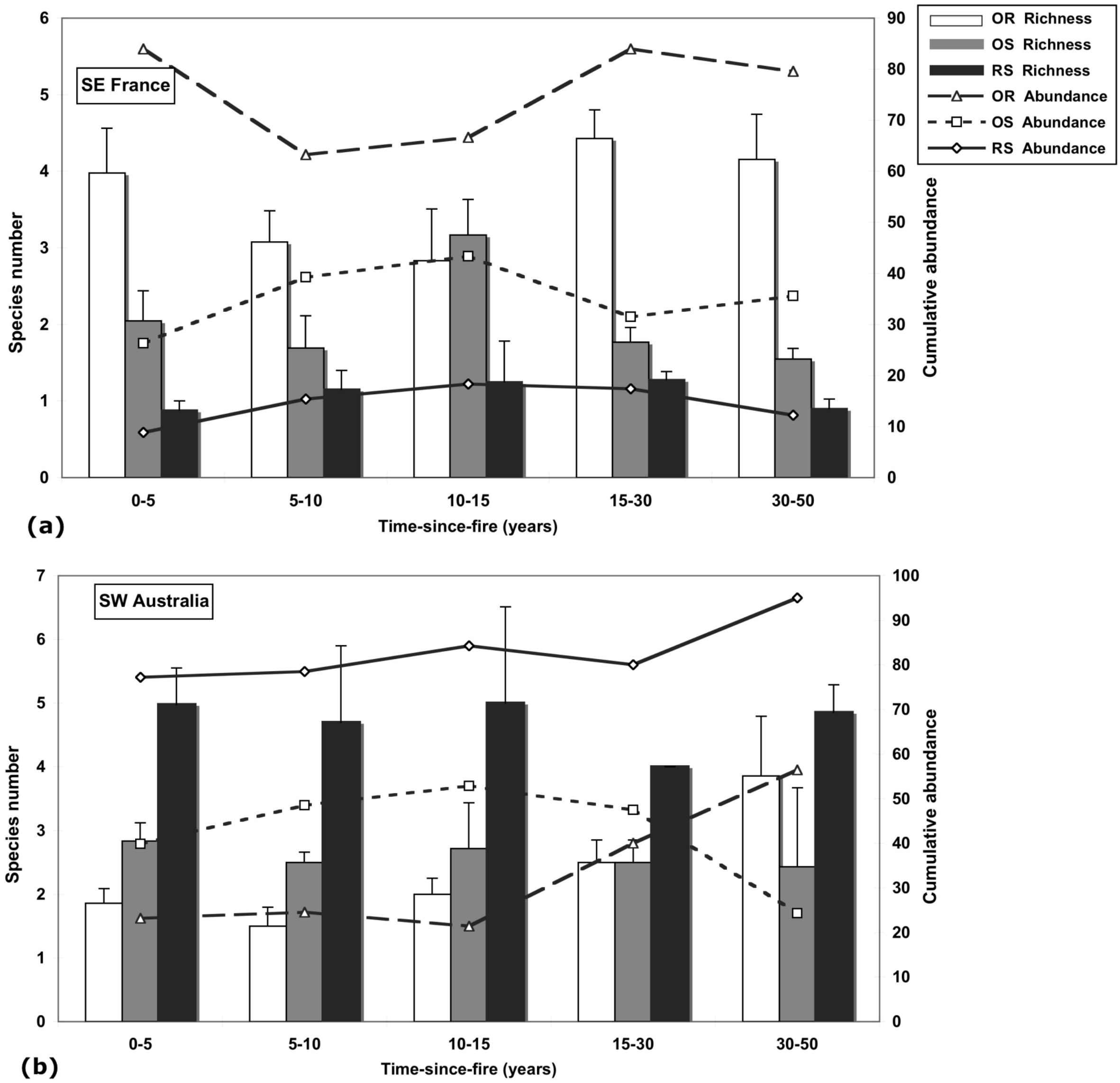


Fig. 6.4 Variations in PFTs abundance and richness according to time-since-fire. PFTs richness is displayed with histograms (mean ± SE) corresponding to obligate resprouters (OR), obligate seeders (OS) and resprouter-seeder species (RS). Curves show the mean cumulative abundance (second Y axis) per regenerative PFTs.

The results of one-way ANOVAs performed for each study area confirmed the significant influence of time-since-fire on the richness of regenerative PFTs (p-value <0.01) in SE France but not in SW Australia, possibly due to a lower sample size. No significant inference was made with respect to regenerative PFTs abundance, except for the abundance of resprouter-seeder species that showed contrasted trends with time-since-fire between both regions (Table 6.2).

Plant functional response after disturbance over a 50-yr period

We observed a net increase in the cover percentage of OR/RS trees from ca. 5-10 years in both Mediterranean ecosystems (e.g., Q. ilex and Q. suber in SE France; E. marginata and C. calophylla in SW Australia) as shown in Figure 6.5. Abundance of OS trees in SE France also increased from ca. 5-10 years since fire (e.g., P. halepensis) to reach maximum values after ca. 30-50 years. In contrast, OS trees in SW Australia were mostly present in the early post-fire stages (0-10 years). In SE France, OR/RS shrubs globally maintain their abundance during the whole period considered whereas OS shrubs abundance seemed to be related with the abundance of tree species as the cover of OS shrubs start diminishing when the cover of both OR/RS and OS trees increase (Fig. 6.5a).

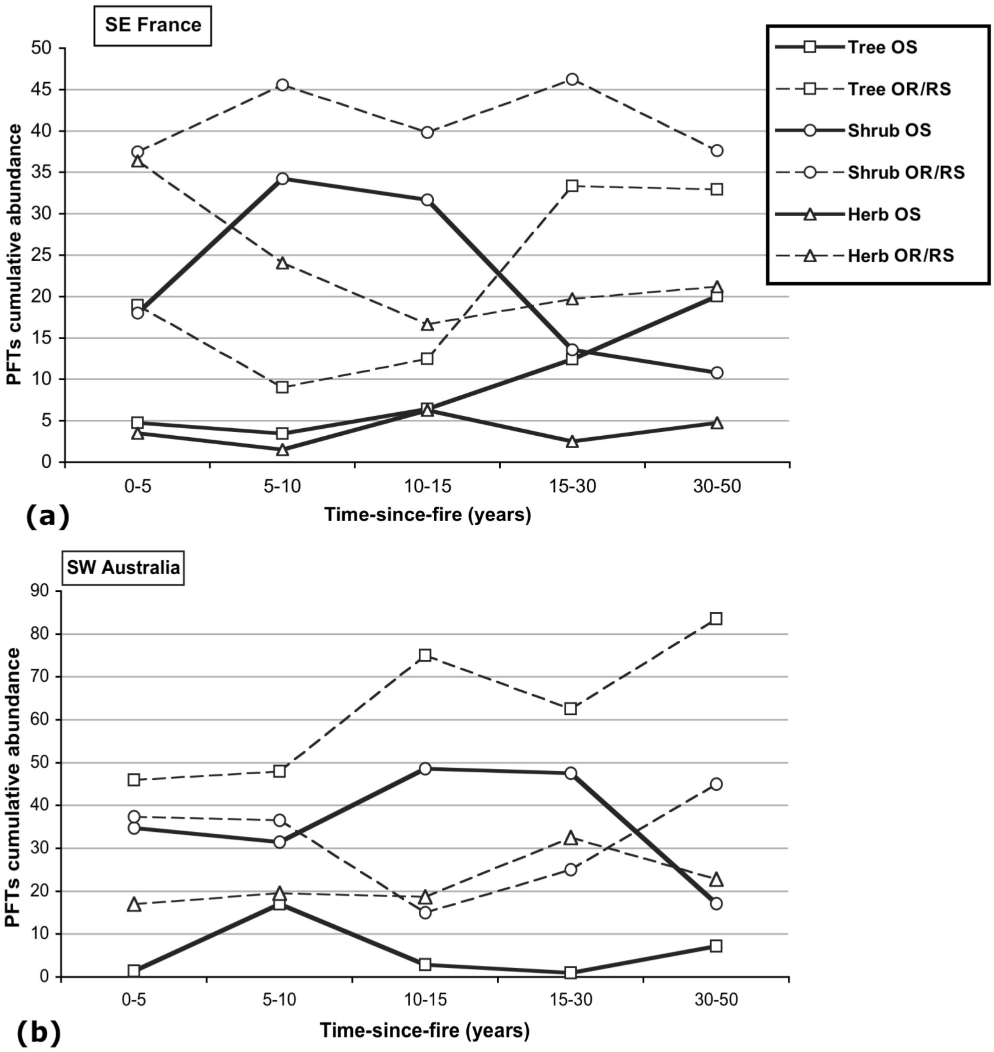
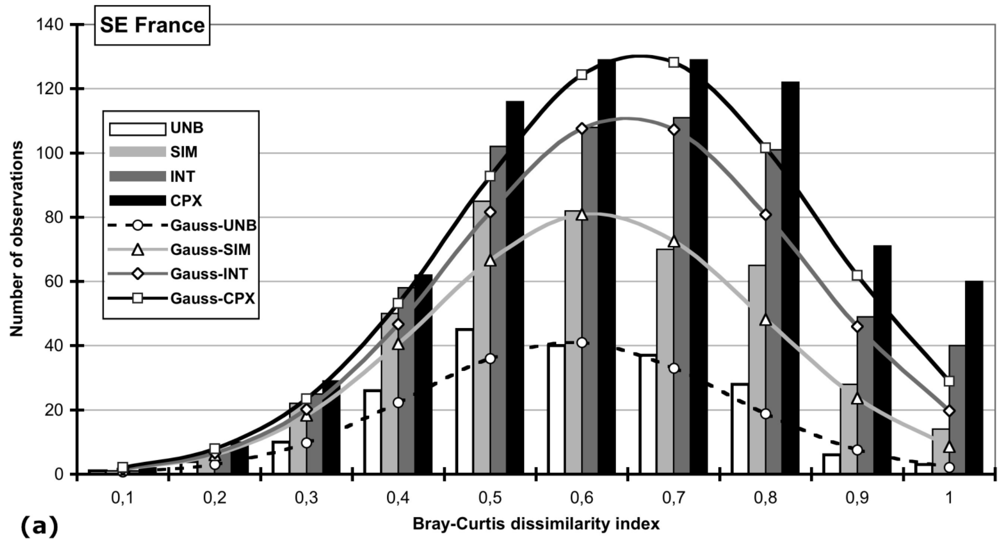


Fig. 6.5 Variations in cumulative abundance of combined PFTs with time-since-fire. Curves represent the mean variations of cumulative abundance (sum of cover percentage of species) for SE France (a) and SW Australia (b). Combined PFTs are defined by the regenerative strategies i.e., resprouter (OR/RS) or non-resprouter (OS) traits of main growth forms i.e., trees, shrubs and herbs.

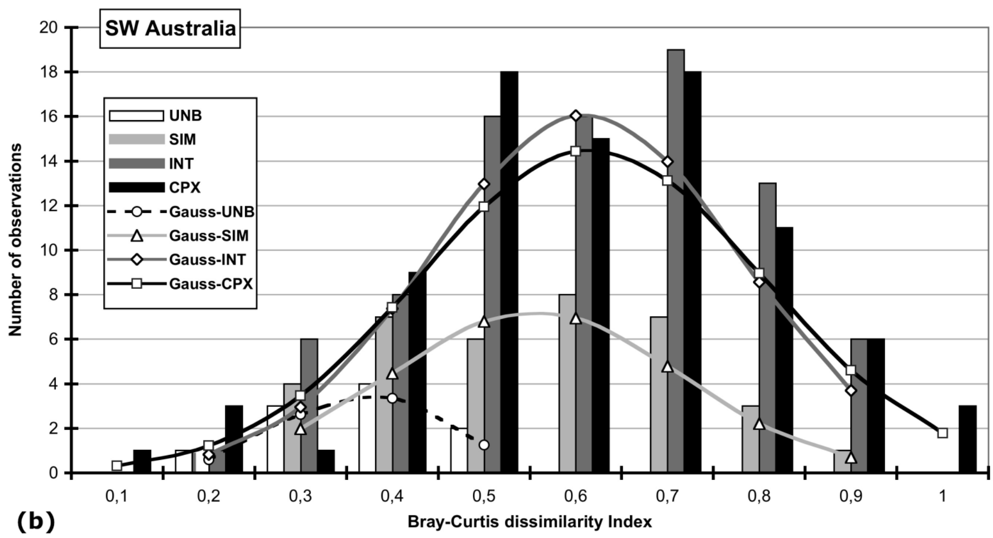
In SW Australia, we observed opposite trends between OS and OR shrubs with the former being dominant over the latter from 10 to 30 years after fire before OR shrubs start to replace OS shrubs (Fig. 6.5b). OR/RS herbaceous showed contrasted behaviors in the two study regions. In SE France, we noticed a decrease (0-15 years after fire) in their respective cover followed by a plateau where OR/RS herbaceous managed to maintain over time. OR/RS herbaceous was not significantly affected by fire.

Influence of landscape pyrodiversity on beta functional diversity

Beta functional diversity was increasing with the level of pyrodiversity across both regions (Fig. 6.6a-b). We found that mosaics of habitats subjected to heterogenous fire patterns (i.e., complex pyrodiversity) were characterized by the greatest beta diversity of life form PFTs.



(a)



(b)

Fig. 6.6 Effects of pyrodiversity on Beta trait diversity.
Histograms represent the distribution of Bray-Curtis dissimilarity indices calculated among habitats of each 1km^2 quadrat. Gaussian curves approximate trends of functional diversity for each pyrodiversity level (UNB-unburned; SIM-simple; INT-intermediate; CPX-complex) in the two study regions.

However, beta diversity response to pyrodiversity was more pronounced in SW Australia with unburned landscape mosaics being significantly less heterogeneous (i.e., low values of dissimilarity index) than burned landscape mosaics (Fig. 6.6b). Gaussian approximation of beta diversity patterns confirmed that functional diversity in SE France responded gradually to the pyrodiversity gradient (Fig. 6.6a) whereas simple, intermediate and complex pyrodiversity levels had relatively similar effects on beta functional diversity in SW Australia.

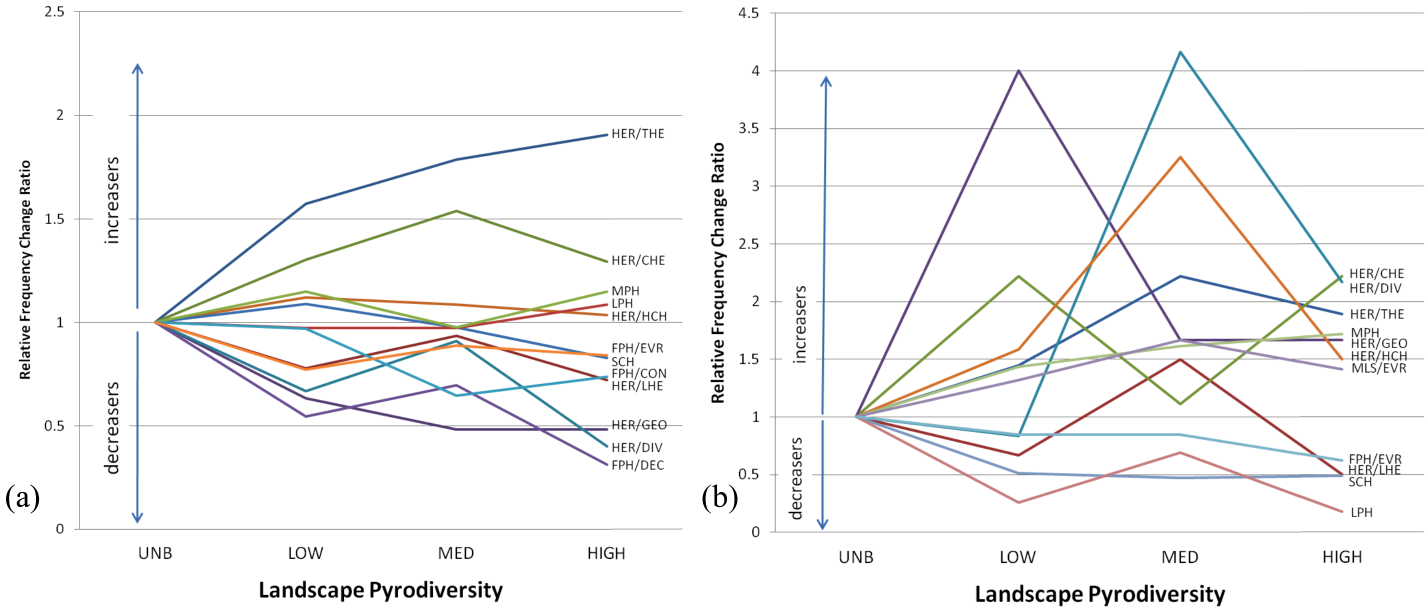


Fig. 6.7 Variation of Life form frequencies along the pyrodiversity gradient. The relative frequencies of the life forms are expressed as the ratio of the frequency of the life form for a given level of pyrodiversity divided by the frequency in unburned vegetation (UNB). The decreasers are the life-forms showing a decreasing ratio (<1) along the pyrodiversity gradient. The increasers are the life-forms showing an increasing ration (>1) along the pyrodiversity gradient. The curves are displayed for southeastern France (a) and southwestern Australia (b).

The trends of life forms frequencies expressed in Fig. 6.7 indicate that life forms frequencies exhibit strong variations in both Mediterranean areas according to the level of landscape pyrodiversity. Despites differences in the life form pools, similar trends can be observed in the two Mediterranean environments: herbaceous therophytes (HER/THE), caespitose hemicryptophytes and mid-phanerophytes (MPH) increase whereas forest phanerophytes (FPH), leafy hemicryptophytes (HER/LHE) and chamephytes (SCH) decrease along the pyrodiversity gradient. It can also be observed that some life forms exhibit different trends in the two ecosystems such as low phanerophytes (LPH) or geophytes (GEO).

Discussion

Fire and life forms diversity

Fire regime had a major influence on the diversity of life form and regenerative PFTs. The results point to the fact that the diversity of life forms encountered in the two MTEs is more dependent on the time since the last fire rather than on fire recurrence. The range of life form diversity was slightly changed when increasing fire recurrence as we observed particular groups of life forms to be alternatively favored by specific level of pyrodiversity. This finding accords with Gill (1981), who commented that plants, and therefore life forms, are not adapted to fire but to a particular fire regime (Fig. 6.7), which includes fire frequency and intensity as well as attribute influencing the patterning and extent of any given fire. In the two Mediterranean study areas, increasing pyrodiversity differentiate the profile of life forms recorded within the landscape (Fig. 6.7). At low levels of pyrodiversity (i.e., long fire interval), the diversity of life forms is supported by sclerophyllous dwarf shrubs (chamephytes) and trees (phanerophytes), and perennial herbs (leafy hemicryptophytes) whereas at higher levels of pyrodiversity (i.e., short fire intervals), the diversity is mostly supported by perennial (caespitose hemicryptophytes) and annual (therophytes) herbs, and shrubs (mid-phanerophytes). Therefore high pyrodiversity promotes vegetation dominated by shrubs and grasses by reducing the abundance of other life forms. A landscape-scale simulative study of fire effects on the distribution of functional groups in Southern California arrived to similar conclusions (Syphard et al. 2006). We further noticed that beyond a certain threshold (i.e., four fires within 50 years) recurrent fires significantly reduced the diversity of life forms in southern France (Fig. 6.1a).

Life form diversity changed consistently according to time since fire. In both Mediterranean areas, we noticed the higher values of LFs diversity in the early stages after fire (ca. 5 years). This peak in LFs diversity is the result of the coexistence of annual and biennial herbs (therophytes) with perennial herbs (leafy hemicryptophytes), sedges and grasses (caespitose hemicryptophytes), and climax-woody species (phanerophytes). This coexistence is facilitated by the opening of the vegetation and nutrients release generated by fire, which enables the establishment of annuals from exogenous sources, and the germination of perennial herbs from seed bank (Bell & Koch 1980; Trabaud & Lepart 1980). In SE France, a second peak of

LFs diversity was observed around 15 years after fire. Between 5 and 15 years after fire, there is a vigorous regrowth of the understorey, generally represented by a few LFs (i.e., low- and mid-phanerophytes with evergreen leaves), which eliminates the different herbaceous LFs from the ground layer. This mid-layer strata does not always persist with the closing of the canopy like in SW Australia, and we noticed progressively the apparition of herbaceous climbers (e.g., *Hedera Helix*), herbaceous pteridophytes (e.g., *Pteridium esculentum*) as well as shade-tolerant hemicryptophytes (e.g., *Viola scotophylla*).

Fire and regenerative PFTs

We found in both study areas that increasing fire frequency leads to a decline in the abundance of obligate seeders (OS species), while species able to resprout (i.e., OR and RS species) manage to persist over time (Fig. 6.3a-b). When fires are recurrent, the inter-fire interval becomes shorter than the time that fire-sensitive species need to produce viable seeds or to accumulate a critical seed store for self-replacement (Bell 2001). In contrast, although consecutive fires may reduce the capacity to resprout from fire of some individuals (Vilà & Terradas 1995), most resprouting species will remain at the site or even be promoted after highly frequent burning (Keeley & Zedler 1978; Trabaud 1990). The convergence trends between the two biomes observed for the abundance were not always verified for the richness of regenerative PFTs. In SW Australia, we still noticed a high richness within the group of seeder species at high fire frequencies whereas it declined significantly after four fires in southern France. With regards to species relying on canopy seed bank, the fact that serotiny is more widespread within SW Australian community (Bell et al. 1993; e.g., *Banksia* spp., *Hakea* spp.) than in the Mediterranean Basin may explain why seeders are less likely to persist at high disturbance frequency in SE France. The previous observation may also be attributed to the differences in intensity associated with prescribed burning in SW Australia and wildfires in SE France. Indeed, seed survival and germination ability of species vary according to fire intensity (Buhk et al. 2007). Unplanned fires generally generate a higher heat release than prescribed burns, which destroys shallow-buried seeds and can therefore significantly reduce the seeders pool (De Luis et al. 2005), which is the case in SE France (e.g., *Cistus* spp., *Ulex parviflorus*).

The richness and abundance of regenerative PFTs were significantly related to time-since-fire in both Mediterranean environments. However, contrasting post-fire succession patterns seemed to characterize plant communities of the two regions. Within the first 10 years after fire, we observed considerable change of the vegetation profiles in southeastern France whereas the fire response seemed to be shifted back in time (i.e., beyond 10-15 years) in south-west Australia (Fig. 6.5). In the first case, the results provide evidence that resprouting herbaceous (e.g., *Brachypodium retusum*, *Carex divisa*) and resprouting shrubs (e.g., *Quercus coccifera*, *Erica arborea*, *Pistacia lentiscus*) are prominent within the first post-fire succession stage (0-5 years) before being associated to seeder shrubs (e.g., *Cistus* spp., *Fumana* spp.) in a second phase (5-10 years). As the tree coverage of resprouting species (e.g., *Quercus ilex*, *Quercus suber*) and seeders (e.g., *Pinus* spp.) increased, the community structure changes again before stabilizing at around 30 years. The major difference exhibited by SW Australia is that structuring tree species (*Eucalyptus* spp.) are not killed by fire as their regenerative strategies and resistance capacities to disturbance are strongly fire-associated (i.e., thick bark, underground lignotuber, encapsulated seeds), which contrasts to species of the Mediterranean Basin. In addition, facultative species (propagule persistent species than can resprout after fire) are very common in SW Australia compared to SE France (see Fig. 6.4) and recover very rapidly (Burrows & Wardell-Johnson 2003). Consequently, no major change of plant regenerative profiles was noticed in SWWA within the 5-10 years following a fire. As time since fire increases (10-15 years), major variations in abundance concerned the understorey species while the coverage of resprouting trees gradually increased with time. After 10-15 years, propagule persistent shrubs become more abundant than respouting shrubs due to better nutrient retention efficiency (Cowling & Lamont 1985; Lamont 1985). Nevertheless, in older stands (30-50 years since the last fire) resprouters dominate the community as the survival of seeders becomes critical (i.e., exhausted seedbank, fire-dependent germination).

Alpha and beta trait diversity in MTEs

A striking feature of both MTEs studied here is the wide spread of life form traits among different vegetation types. The great LFs diversity is not only the result of fire influence as unburned habitats also presented various LFs, part of them being in common with burned habitats. For instance, in SWWA, species/LFs may colonize unburned areas through mass flowering stimulation like *Macrozamia* spp. (BRP/EVR), *Drosera* spp. (HER/CLI) or *Xanthorrhoea gracilipes* (SRP/EVR) (Pignatti et al. 2002). Nevertheless our results provide evidence of the linkages between fire and alpha trait diversity.

Alpha functional diversity approached from a life form perspective, and measured at the habitat level, follows similar trends than species diversity (see Chapter 5). The higher diversity of life forms encountered within burned habitats is found at intermediate levels of disturbance frequency (i.e., 1-2 fires in SE France; 4-5 fires in SW Australia) as predicted by the IDH (Intermediate Disturbance Hypothesis; Grime 1977). Similarly to species diversity, a peak of functional diversity is observed within the first 5 years after fire. At the landscape level, we found that landscapes characterized by the more complex fire spatiotemporal patterns exhibited the greatest beta functional diversity. This findings supports the Heterogenous Disturbance Hypothesis (HDH) proposed by Warren et al. (2007), which suggests that beta diversity will be enhanced when the frequency, periodicity, shape and size of the disturbance regime vary spatially and temporally across the landscape. The HDH was verified in the two Mediterranean environments but with some subtle differences. Nevertheless, we found that the distributions of beta trait diversity patterns of the four pyrodiversity classes were more interspersed in SE France than in SW Australia. Beta trait diversity was clearly differentiated between unburned landscape mosaics, landscape mosaics of simple pyrodiversity and landscape mosaics of intermediate/complex pyrodiversity in the SE of France. The fact that we found higher dissimilarities between landscape mosaics of the same pyrodiversity treatment in SE France can be attributed both to sample size effect and to the high environmental heterogeneity characterizing southern France landscapes. As pointed out by Pignatti et al. (2002), the region of southern France shows higher variability of bedrock, climatic conditions and topography, resulting in fine grain matrix of different vegetation types, rather than in SW Australia, the same type of vegetation is often widespread over large distances due to a lack of environmental heterogeneity.

Implications for biodiversity conservation in fire-prone systems

The life form classification implemented within the EBONE project is proving to be a reliable approach to predict the pyrodiversity-biodiversity relationship at different spatial scales. Nevertheless, we recognize that considering life forms separately or in addition to regenerative traits might not be applicable to study essential features of the flora in relation to other kinds of phenomena as we only captured some of the dimensions of ecological variation (Westoby et al. 2002). From a functional perspective, conservation practices should target plant species of which functional traits will maintain the desired ecosystem properties. For example, the presence of trees with complex aboveground woody structures and extensive root systems (e.g., mallee trees in south-west Australia) has important effects on soil erosion, water and sediment retention. Similarly, ecosystem resilience and resistance to disturbance (e.g., fire or grazing) are strongly dependent on the traits of the dominant plant species so that communities dominated by fast-growing plants with high vegetative regeneration capacity tend to have high resilience (Diaz and Cabido 2001). Consequently, in fire-prone ecosystems, our results suggest that sustainable conservation strategy requires a framework based on (i) maintaining the adequate range of fire return interval to enable the co-occurence of seeders and resprouters, (ii) conserving spatial fire mosaics with the more heterogeneous frequency and time-since-fire patterns to counteract the extinction of life forms within the landscape, and finally (iii) controlling the recurrence of extensive stand-replacing fires to reduce the threat to propagule persisters relying on dormant seeds.

In south-west Australia, the short fire return interval (5 years) imposed by prescribed burning management may reduce the range of functional diversity as the variability in regenerative traits within habitats expressed beyond 10 years after disturbance. Increasing the fire return interval in some places (patch mosaic burning) while keeping the hazard of fire propagation at low levels in the meantime would significantly increase the variety and abundance of seeders within the landscape matrix. This would translate by introducing in the landscape much smaller prescribed burns of more variable intensity than used in the rest of the region. A landscape-scale experimentation (Fire Mosaic Project; Burrows & Wardell-Johnson 2004)) has already been initiated in 2002 by DEC (Department of Environment and Conservation) to tackle the previous issues. In SE France, the situation is different as the emphasis is laid on fire suppression to reduce fire hazard for life and property as the wildland-urban interface increases (Rigolot and Roche 2009). However this fire management policy has already modified landscape pyrodiversity with the progressive suppression of intermediate fire mosaics (Rigolot 1997). Prescribed burning might be an alternative to reverse the homogenization of fire patterns but its use remains marginal in SE France and little research has documented its impacts and implications within an anthropogenic context.

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7. Thesis synthesis

Landscape pyrodiversity encapsulates the range of spatiotemporal variability of disturbance by fire. There is a widely-held view that diversity in fire regimes promotes biological diversity (i.e., the Pyrodiversity-Biodiversity paradigm). My research has addressed this paradigm in two Mediterranean biomes (i.e., southeastern France and southwestern Australia) from a landscape ecology perspective. To do so, I have developed a methodology for the objective and quantitative characterization of landscape pyrodiversity and applied it in two fire-prone regions (Chapter 3). Application of the methodology in SE France provided evidence that pyrodiversity significantly influences the landscape patterns, either contributing to their diversification or homogenization (Chapter 4). High landscape pyrodiversity enhances the richness of habitats within a landscape mosaic depending on its level (Chapter 4), which was shown to contribute to increased plant species diversity (Chapter 5) and functional diversity (Chapter 6) among the habitats of that mosaic. Within-habitat plant diversity was also maximized when landscape fire regimes were complex in space and time as these regimes offer intermediate disturbance conditions (Chapter 5).

Below, I discuss the implications of the main results of my study for the ecological understanding of fire in SE France and SW Australia. I also evaluate the validity of the Pyrodiversity-Biodiversity paradigm into the context of Mediterranean-type ecosystems (MTEs) and discuss the potential for biodiversity benefits or threats from current fire management strategies in the two study areas.

Implications of findings for other Mediterranean-type ecosystems

In Chapter 3, a novel approach was developed to analyze landscape pyrodiversity by selecting and quantifying appropriate descriptors of fire variability at the landscape level. Using landscape ecology metrics applied to the fire history mosaic, I characterized and classified fire diversity in space and time. The descriptors used were derived from the observed fire mosaics at the 1 km scale and consist of temporal variables (fire frequency, time-since-fire and mean fire interval) as well as a variety of spatial attributes derived from landscape metrics (edge density, aggregation index, diversity index). This approach was trialed on a 50-year record of fire patterns in two Mediterranean environments; (1) in southeastern France where fire regimes are dominated by unplanned fires and (2) in southwestern Australia, where fire regimes are dominated by planned fires. Multivariate analysis of the fire mosaic metrics separate out distinct gradients of both fire frequency and spatial diversity of fire patterns in both regions. The temporal spacing of prescribed fires (e.g., FRI of 9 years) combined with the relatively fixed template on which they are applied resulted in coarse-grained fire mosaics in the SWWA study region. Conversely, fire mosaics in the French study area consisted of fragmented scars characterized by greater variation in time-since-fire (i.e., average of 21.6±11.0 years over a 48-year period) and a lower range of fire frequency values (i.e., average of 1.5±0.5 fires over a 48-year period) than those in SWWA. Besides these strong differences, there were also similarities between the profiles of pyrodiversity between southeastern France and southwestern Australia (Chapter 3). We found pyrodiversity analogues in between regions that share a common set of fire mosaics characterized by disturbance regimes with similar spatiotemporal complexity. Despite the different origins of the fires events in SWWA and Southeastern France, the fire patterns similarities allowed building a pyrodiversity continuum.

Contrasts and similarities between fire regimes in MTEs - the Pyrodiversity continuum perspective

Mediterranean-type ecosystems across the globe exhibit various and contrasting fire regimes; however, results from this research suggest that their fire regimes could be described using the pyrodiversity quantification protocol defined (chapter 3) allowing to form a pyrodiversity continuum that can be mapped along two orthogonal axes: (i) a first axis expressing the gradient of spatial complexity of fire mosaics (spatial component) and (ii) a second axis expressing length of fire return intervals (temporal component). The first axis predicts how these patterns are organized in space (i.e., patchiness, extent, shape) whereas the second axis emphasizes the variability of fire frequency and time-since-fire patterns within the mosaic. The conceptual diagram presented in Fig. 7.1 is inspired by the ordination of fire mosaics of SE France and SW Australia in the multivariate space (PCA) defined by fire spatial and temporal variables as described in Chapter 3. Based on the characterization of landscape pyrodiversity developed in this study for SW Australia and SE France (Chapter 3), the results obtained for the two regions suggest that the pyrodiversity of all MTEs worldwide could be mapped along the same spatial and temporal axes.

Most of the variability of pyrodiversity at landscape scale can be adequately expressed using a reduced set of variables (mean fire frequency, mean time-since-fire, mean Simpson's spatial diversity and mean spatial aggregation based on frequency patterns and mean edge density based on time-since-fire patterns) with little loss of information. The range of pyrodiversity characterizing each MTE could be illustrated using dispersion ellipsoids within the pyrodiversty space. The position, width and orientation of each ellipse are based on results of this study (Chapter 3) and on literature sources reporting historical data on fire regimes and their spatial complexity.

Hence, the diagram presented in Fig. 7.1 was built according to the following assumptions:

- The axes of the dispersion ellipsoids are parallel with the temporal and spatial axes of the diagram (Faivre et al. 2011; Chapter 3).
- Ellipses have similar shapes (i.e., axes length and orientation) but occupy different locations along the temporal gradient (Faivre et al. 2011; Chapter 3).
- Fire mosaics resulting from planned fires (e.g., SW Australia) are more likely to exhibit a smaller range of spatial diversity (i.e., edge density) than those resulting from unplanned fires (e.g., SE France) because the spatial planning of prescribed burns is usually based on fixed templates of treatment blocks (Faivre et al. 2011; Chapter 3).
- Differentiation of ellipses among the spatial axis has to express the variations in topography and land use characterizing each MTE as the spatial configuration of fire patterns is strongly influenced by terrain and land use (Mouillot et al. 2003).

Fire regimes in the MTEs are differentiated according to their fire return interval. Fire regimes in California contrast strongly between southern California and Baja California with substantial differences in fire frequency and burned area (Keeley & Fotheringham 2001). Fire frequency in Baja California is up to five times greater than in southern California. However, Keeley et al. 1999 reported a general reduction of fire return intervals in southern California since the 1950s (from ca. 30-225 years to ca. 30-80 years). A similar range of fire return intervals has been observed within the Mediterranean Basin (ca. 25-130 years; Piñol et al. 1998). Gonzalez et al. (2005) reported fire return intervals of 7 to 62 years in central Chile for the 1900-2000 period. In contrast, Mediterranean regions submitted to active prescribed burning management such as Southwest Australia (Boer et al. 2009) or South Africa (Van

Wilgen et al. 2010) are characterized by much shorter fire return intervals (ca. 6-9 years in SWWA and ca.10-13 years in SA).

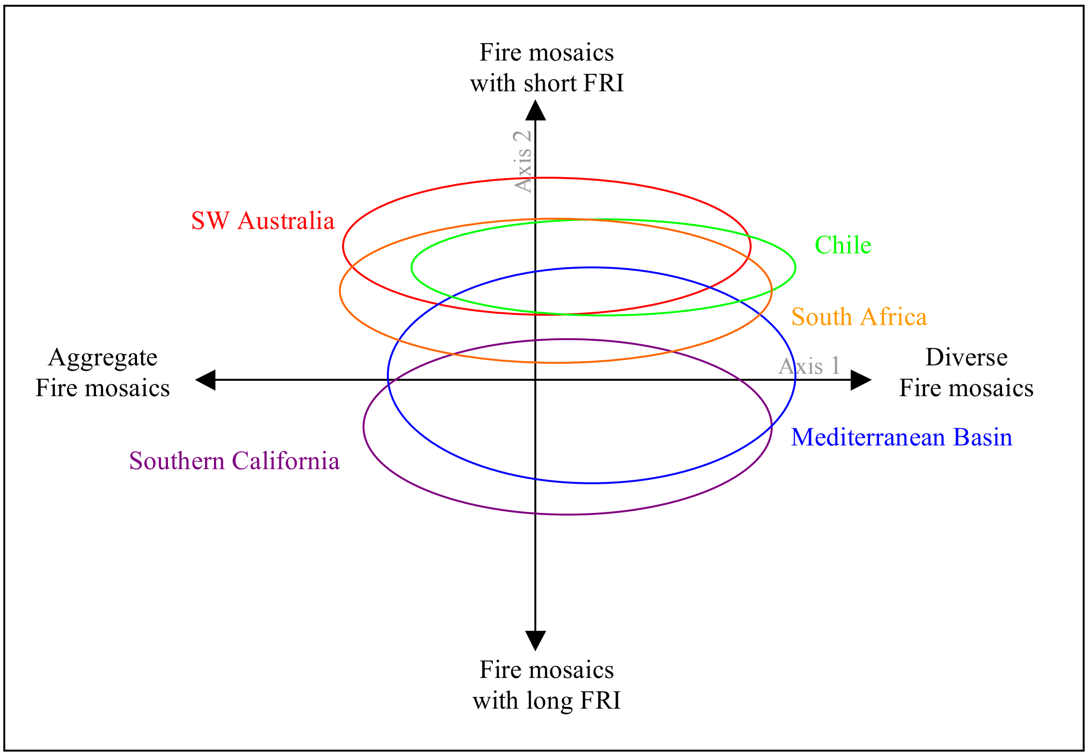

Fig. 7.1 Conceptual diagram of the pyrodiversity continuum unifying the five MTEs. Dispersion ellipses depict the distribution of the cloud (95% confidence) of fire mosaics for each Mediterranean area (from ca. 1960s until today). The distributions are clearly separated along the temporal gradient (Axis 1) but have comparable variability among the spatial gradient (Axis 2). The intersection of dispersion ellipsoids shows that some Mediterranean areas share a common set of fire mosaics characterized by similar pyrodiversity profiles.

With respect to the position of ellipses on the first axis, it was assume that the spatial configuration of fire mosaics is related to the type of fire management and the level of heterogeneity in environmental conditions characterizing each MTE. Topographic heterogeneity of the Mediterranean Basin, South Africa and California is intermediate between those of Chile (very high) and Australia (low-moderate) (Cowling et al. 1996). In addition contemporary fire mosaics in the Mediterranean Basin and southern California are mostly dominated by unplanned fires of relatively small extent (10-10^3 ha) and relatively high spatial complexity enhanced by the complex and heterogeneous matrix of land use patterns (Keeley & Fotheringham 2001, Baeza et al. 2007). Inversely fire mosaics that are primarily created by planned fires (e.g., South Africa and Southwest Australia) are more spatially aggregated because burning patterns are usually designed from a fixed layout of existing fire breaks (e.g., roads, forest blocks).

We may expect the flora of each Mediterranean biome to hold some signature of the pyrodiversity profile of that region. Pyrodiversity is dynamic and subject constant change, for example caused by changing climate conditions (Pausas 2004) or changing fire suppression or prescribed burning strategies. Therefore, there is a pressing need to determine whether contemporary pyrodiversity profiles are likely to create or maintain the suit of environmental circumstances that allows long-term conservation of each MTE's biodiversity. Parr and Andersen (2006) have recently draw attention to this challenge under the Pyrodiversity-Biodiversity paradigm and questioned the key assumption of the paradigm that pyrodiversity begets biodiversity?

Does pyrodiversity begets biodiversity?

What would be the consequences for landscape, habitat or species diversity if uniform fire regimes (i.e., constant fire return-interval, similar burning extent) were applied to an entire landscape? Our perception of the effects of fire on the environment depends on the scale we consider this phenomenon (Naveh 1990). A single fire event may have severe short-term impacts on the diversity of plant species, killing most of obligatory seed regenerating plant species, but if we extend the time window it appears that fire may be the only way to ensure reproduction through stimulating regeneration (e.g., Cistus spp.) or facilitating off-site establishment (e.g., Pinus halepensis). Similarly, when considering different spatial scales, the effects of fire on the diversity of a forest stand may be compensated at the regional scale by the occurrence of similar taxa in other habitats. Consequently, in this study I sought to apply an integrative and multidimensional approach based on the previous characterization of landscape pyrodiversity (Chapter 3) in order to address the effects of varying fire regimes on landscape heterogeneity (Chapter 4), species diversity (Chapter 5), and functional diversity (Chapter 6). The background hypothesis of this research states that the biodiversity associated to Mediterranean flora and habitats would not be maintained in the absence of fire.

Conceptual framework of the pyrodiversity-biodiversity paradigm

To answer the question whether pyrodiversity begets biodiversity I propose a conceptual framework presented in Fig. 7.2. The diagram organises three existing hypotheses on disturbance-biodiversity relationships that have been addressed in this thesis in a single multiscale framework. The diagram thus illustrates how biodiversity relates to variations of fire at species level (i.e., species diversity of 400 m^2 plots), habitat level (i.e., species diversity among habitats) and landscape level (i.e., diversity of habitats over the entire landscape). In addition, I compare the idealized curves corresponding to each hypothesis to the results obtained in this research.

Regional level

If landscape diversity (i.e., gamma diversity sensu Whittaker 1972) is defined as the combination of the number of vegetation types (or landscape richness) and the degree of spatial heterogeneity, this study provides evidence that high pyrodiversity promotes regional landscape diversity (Chapter 4). In SE France, fire reinitialized the classical post-disturbance successional pattern Shrubland → Transient woodland → Coniferous forest → Mixed forest → Deciduous/Evergreen oak forest (Médail and Quézel 2003) and introduced variability in successional trajectories observed in different parts of the landscape. At low levels of pyrodiversity (i.e., resulting from relatively small fires and long fire intervals), the system is relatively stable and exhibits low variance over time resulting from the convergence of all landscape elements toward the oak forest stage. Given the small amount of fire disturbances, the compositional and spatial organization of the resulting mosaic of habitats may change at some locations in a landscape but the overall the proportion of the landscape in each successional stage is relatively constant (Fuhlendorf & Engle 2004). Hence, the landscape would be dominated by forest habitats and the biodiversity associated to mature forests will become more common. In this case the mechanisms of species competitive exclusion apply and the system will exhibit a regional diversity depending on variability of substrates and on management (Chapter 4; Fig. 7.2). However, when a larger proportion of the landscape is affected by fire and the interval between disturbances becomes shorter (i.e., medium levels of pyrodiversity), the regional landscape mosaic will switch to initial stages of the post-disturbance succession creating of mosaic composed of the different successional stages (the theory of the shifting mosaic steady state; Bormann and Likens 1979; Fig.7.2). The results of this study demonstrated that the diversity of habitats within the landscape mosaic is positively correlated with fire frequency, the spatial heterogeneity of the fire mosaic (shape and patch diversity) and the burned area (Chapter 4). Indeed, increasing pyrodiversity will increase landscape patchiness and habitat diversity at the regional scale (Turner et al. 2010; Chapter 4) while promoting diversity associated with initial stages of the dynamics and suitable niches for species able to occur outside their core habitat (Mass effect; Schmida & Wilson 1985; Fig. 7.2). Species having resistance or/and resilience strategies will also be favored. Regional landscape diversity is predicted to increase with pyrodiversity up to a certain threshold determined by the mechanisms of compensation between landscape diversification (niche differentiation) and landscape homogenization (habitat isolation) in the case of recurrent and extensive fires (Turner et al. 1994; Chapter 4; Fig. 7.2).

Habitat level

The variability of habitat composition within the landscape mosaic was found to be determined to a great extent (ca. 50%) by abiotic factors including environmental conditions (soil, topography and climate), land use (agricultural and forestry activities, urbanization) and fire (Chapter 4). Although environmental heterogeneity was the dominant factor determining landscape composition in terms of habitat types, fire was found to be the main driver of heterogeneity in the spatial configuration of habitats in the landscape outside agricultural and urban dominated areas (Chapter 4). The results of this study further support the heterogeneous disturbance hypothesis (HDH) proposed by Warren et al. (2007). The HDH states that 'biodiversity is maximized in habitat mosaics where multiple kinds, frequencies, severities, periodicities, sizes, shapes, and/or durations of disturbance occur concomitantly in a spatially and temporally distributed fashion. According to the HDH, the more heterogeneous the fire mosaic is in space and time, the greater the probability to simultaneously observe different stages of succession of varying species composition and therefore the higher the resulting beta diversity. This hypothesis was supported by results of this study for species diversity (Chapter 5) and functional diversity (Chapter 6). Beta diversity was lowest in undisturbed habitat mosaics, independently of whether plant species or plant traits were considered; this makes sense as undisturbed habitats offer limited conditions for species establishment from off-site locations but also prevent non-competitive species to persist. Furthermore, I found that beta diversity of plant traits increased proportionally with the level of pyrodiversity (see Fig. 6.6, Chapter 6; Fig 7.2). Beta diversity of plant species was also greater for landscape mosaics associated with complex fire mosaics (i.e., interspersed fire scars of varying age, high edge density) (Chapter 5). High pyrodiversity provides a wider range of habitat conditions with contrasted light availability, soil decomposition rates and resources. Hence, species can partition the diverse available resources and coexist along different successional pathways in different parts of the landscape, which contributes to increase beta diversity (Reilly et al. 2006; Fig 7.2).

Species level

At the species level, similar trends of alpha diversity with respect to fire frequency were observed in the two study areas. The results put in evidence that southeastern France and southwestern Australia share similar peaked relationship for variation in plant species diversity with fire frequency but at different levels (Chapter 5; Fig. 7.2). Maxima of alpha diversity were observed at low levels of fire frequency (i.e., 1-2 fires) in SE France and at moderate levels of fire frequency (2-4 fires) in SW Australia over the 1960-2008 period. These results are coherent with the intermediate disturbance hypothesis (IDH; Grime 1973). The rationale behind the IDH is that plant communities submitted to intermediate frequencies of disturbance are more species-rich than others. At low fire frequency levels, the competitive exclusion principle would apply, as each available niche within the landscape mosaic will be dominated by a small sub-set of the species pool composed of plants able to persist in the long absence of fire (Fig. 7.2). At intermediate levels of disturbance, processes of colonization and dispersal are maximized between habitats and would enhance species coexistence (Roxburgh et al. 2004) as the community benefits from the income of pioneer species while fire-resistant species regenerate from site. Analysis of functional traits in SE France and SW Australia (Chapter 6) revealed that habitats subjected to intermediate fire frequency showed a wider range of diversity than the others. Those results are consistent with the IDH's prediction that fires must be frequent enough to insure that competitive exclusion does not occur over the whole area but not too frequent to prevent the extinction of fire-sensitive species (Sousa 1984).

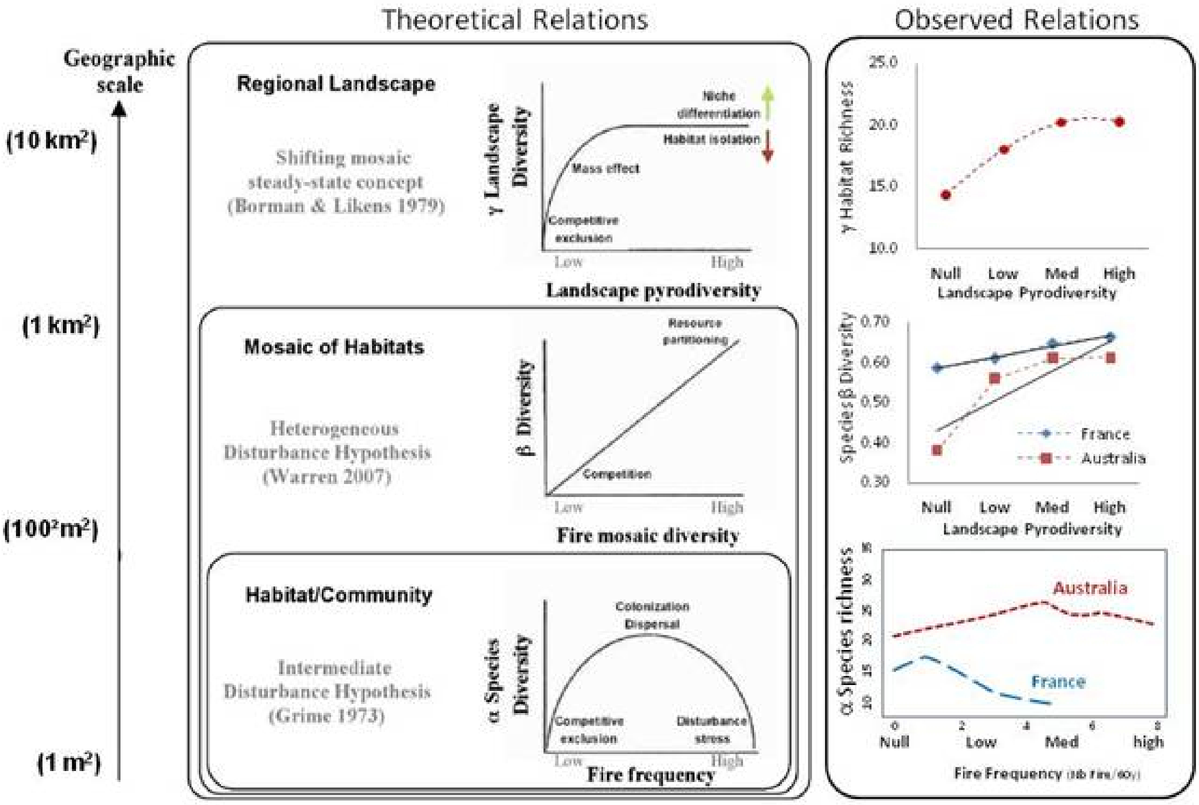

Fig. 7.2 Synthetic multi-scale representation of the Pyrodiversity-Biodiversity paradigm
The diagram successively considers the effects of fire on a single community, a mosaic of habitats and a regional landscape. Associated hypotheses that explain the pyrodiversity-biodiversity paradigm at each geographical level are indicated. Theoretical relationships between pyrodiversity and biodiversity are summarized graphically by idealized curves, which are further supported by the results of the study. Empirical curves of alpha and beta diversity (linear bray-curtis approximation) display the trends observed in SE France (blue) and SW Australia (red) while gamma diversity curve represent habitat richness in SE France.

A generalized Pyrodiversity-Biodiversity paradigm for MTEs?

This research verified that the influence of fire on plant diversity is highly scale-dependent as the effects of a fire disturbance sequence at a single location in the landscape are significantly different from the effects of the spatiotemporal mosaic characterizing that landscape (Fig.7.2). Nevertheless, the hypothesis that landscape pyrodiversity begets plant species diversity within and among habitats was found to be true. Landscape mosaics characterized by complex fire-frequency patterns showed the greatest alpha, beta and gamma diversity of plant species (Chapter 5; Fig. 7.2). This finding for plant species diversity may be generalized to plant functional diversity. However, I noticed a lower variation of plant life form richness according to fire frequency than for species taxa in the two study environments (Chapter 5 & 6). The lower variation of plant life form richness following disturbance can easily be explained by a high degree of redundancy of species with each life forms (e.g. the appearance or disappearance of some species within the same life form will have no effect on the overall life form richness). This result confirms the high resilience to fire of both Mediterranean ecosystems (Lavorel 1999, Wittkuhn et al. 2011). Furthermore, both species diversity and functional diversity were significantly influenced by time-since-fire at the local level. As a consequence, landscape mosaics that are highly diverse in fuel age (i.e., time-since-fire) are likely to feature the greatest plant diversity, providing further support for the hypothesis that pyrodiversity begets biodiversity.

The results showed that the two Mediterranean study areas have different resilience to fire although both ecosystems exhibit similar profiles of life forms along the pyrodiversity gradient (Chapter 6). Ecosystems of SE France can be characterized by low resistance and medium resilience whereas ecosystems of SW Australia are highly resistant and resilient. SE France plant functional diversity was fairly similar for unburnt areas and areas that burned one to three times over the observation period but significantly lower for areas that burned four or more times. In contrast plant functional diversity in SW Australia appeared insensitive to the number of fires; plant functional diversity was similar for areas burnt once and up to eight times since 1960 while burnt areas in general tended to have higher plant functional diversity than unburnt areas (Chapter 6). Most of plant species occurring in SWA exhibit various regenerative strategies and resistance capacities to disturbance. For instance, seeder-resprouter species are very common in SW Australia compared to SE France (Chapter 6) as many taxa feature more than one response strategy to fire (i.e., thick bark, underground lignotuber, encapsulated seeds), which contrasts to species of the Mediterranean Basin. Overall, if functional diversity is not strongly affected by recurrent fires this study put in evidence that life forms were not adapted to fire *per se* but to a particular level of pyrodiversity (Chapter 6).

Though, fire is an inherent aspect of Mediterranean type ecosystems, their resilience to fire has been shown to be reduced if fires are too frequent (Baeza et al. 2007) or intense (Capogna et al. 2009). Recurrent fires can cause a decrease of soil fertility by altering nutrient cycling and may result in lower resilience capacity of the ecosystem (Duguy et al. 2007). Consequently, promoting high landscape pyrodiversity implies to maintain the multi-age structure of fire mosaics with contrasting fire return intervals as well as keeping areas unburnt. Species individuals that have no specific fire-functional traits require long fire-free periods for successful reproduction and potential dispersal (Ooi et al. 2006). These fire-avoider species are usually associated with long unburned habitats such as the deciduous and evergreen forests occurring in the Mediterranean Basin (e.g., *Cephalanthera* sp., *Epipactis* sp., *Polygonatum* sp. and *Neottia nidus-avis*) and greatly contribute to the high regional diversity that characterizes Mediterranean ecosystems (Quézel and Médail 2003).

Fire affects vegetation dynamics and helps to maintain the diversity of plant communities and landscapes (Moreno & Oechel 1994; Trabaud & Galtié 1996). However, the influence of fire on the distribution and composition of vegetation patterns is moderated by interactions with the physical environment (climate, topography, soil) and land use (Fellicisimo et al. 2002; Roche et al. 1998; Serra et al. 2008). The results of this study show that in SE France, fire has a subsidiary influence on the composition of vegetation types within the landscape, but is the predominant factor influencing the spatial arrangement of vegetation habitats within the landscape mosaic (Chapter 4). It is likely that the relative contribution of abiotic constraints to shaping biodiversity will differ substantially among other MTEs due to strong differences in environmental heterogeneity (e.g., high heterogeneity in topography and bedrock in the Mediterranean Basin versus homogeneous terrain parameters in SW Australia), different impacts from land use (e.g., urbanization in California versus land clearing for agriculture in SW Australia) and contrasting fire management strategies (i.e., interventionist using prescribed burning or protectionist by strong fire suppression). In order to design effective management strategies for long-term conservation of biodiversity in a particular environment it is essential to quantify the relative contribution of pyrodiversity in determining floristic diversity; such knowledge is currently lacking in many MTEs.

Towards enhancing fire management

Preservation of the largest possible number of native species in a region is a key goal of biological conservation (Murphy 1989). This goal of maximizing regional diversity can only be achieved by maintaining both alpha and beta diversity. Given that objective and the impacts of fire thereon, what fire mosaics need to be applied or maintained across the region to maintain the global diversity of vegetation communities? This is a key question for contemporary fire management. Here, I will briefly review key aspects of current fire management approaches in MTEs and discuss how my results could be used to enhance long-term biodiversity outcomes.

Effects and effectiveness of current fire management

Reducing the frequency and extent of major fires that threaten life, property and economic assets is the primary concern of current fire management policies in MTEs; however, environmental policies also require biodiversity conservation to be incorporated into management (Clarke 2008; Driscoll et al. 2010). The spatial assessment and management of fuels distribution across the landscape are central (i) to develop fire hazard maps and models to facilitate further fire suppression efforts and/or (ii) to implement preventive burning to reduce the extent and severity of potential wildfires.

The use of fire as a tool: implications for biodiversity

Prescribed burning has been extensively used and promulgated as an effective fire protection tool in several MTEs (e.g., SW Australia, South Africa). The effectiveness of prescribed fire to mitigate wildfire hazards or maintaining ecological values remains unquantified for many environments (but see, Boer et al. 2009; Fernandes & Botelho 2004; King et al. 2006; McCaw et al. 2008; Moritz et al. 2004; Parr & Andersen 2006). The first concern is directed towards the ability of prescribed burning to significantly reduce the occurrence of large damaging wildfires. Although some studies (Boer et al. 2009; King et al. 2006) provide quantitative evidence for the effectiveness of prescribed burning in reducing the annual extent of unplanned fires, it is argued that the impact of prescribed burning is strongly diminished under extreme fire weather conditions (Bradstock 2008; Moritz et al. 2004). To achieve significant decreases in the extent of unplanned fires requires both a relatively short interval between burns (i.e., inhibition period of up to 4 years) and treating a fairly large proportion of the landscape (e.g., managers aim at maintaining fine surface fuel quantity below 8-9 t ha^{-1} about over 60-70% of the treated forest blocks of southwestern WA; Burrows 2008). Though the effectiveness of prescribed burning in providing protection to life and property is fairly well documented, it is uncertain how well existing burning strategies cater for long-term conservation of plant diversity.

Southwestern Australia has experienced extensive and recurrent prescribed burning since the 1960s. However, over this period prescribed burning has not been detrimental to plant species or functional diversity (Wittkuhn et al. 2011). Indeed, my research provides evidence that the current policy of active management by prescribed fire appears to provide a disturbance regime that shares key spatiotemporal patterns with unmanaged regimes in other MTEs such as the Mediterranean Basin (Chapter 3). Moreover, the diversity of both plant species and life forms was higher in habitats burned up to eight times in 48 years than in unburned habitats (Chapters 5 & 6). However, most of the variations in fire-response traits (resprouter and seeder species) occurs about 10 years after a fire in the Jarrah forest and mallee-shrub systems (Chapter 6). Therefore, if the fire-return interval is maintained below this threshold over a large area, seeder species may not be able to re-establish within surrounding refugia areas and may become extinct. Syphard et al. (2006) made similar observations in Californian chaparral and noticed a significant decline of obligate seeders when the fire-return interval was shorter than 17 years. A precautionary approach would be to nest finer-grained fire mosaics within the coarse-grained fire network to preserve remnant patches (ecological benefits) while serving as fire cutblocks to mitigate the bushfire risk (fire safety benefits). In SW Australia, the Department of Environment and Conservation (DEC) has already been experimenting with more patchy prescribed burns of varying intensity in the context of the Fire Mosaic Project, initiated in the Warren Region in 2002 (Burrows & Wardell-Johnson 2004).

Consequences of fire suppression policies on biodiversity

Fire fighting and fire prevention policy in France has demonstrated its effectiveness in reducing both the number of wildfires (21%) and the total area burned (53%) since the 1990s (Alexandrian 2010). Fires are more rapidly detected and stopped as a result of pre-emptive methods such as regional forest development plans for fire prevention (e.g., improvement of access road; DFCI network) and significant firefighting resources. Fires in the 10^1-10^2 ha range remain most frequent since the 1950s, however the occurrence of extensive wildfires (i.e., >10^3 ha) did not decrease over the last 30 years (Rigolot and Roche 2009). Similar observations were reported in California where fire suppression was ineffective in reducing the frequency of fires larger than ca. 4000 ha (Moritz 1997). Consequences of fire suppression on fire patterns in SE France (and potentially in other MTEs with similar fire management strategy) are an increase of both small and large fire scars in the landscape while scars of

intermediate size are disappearing. It is likely that this fire policy would result in a decline of pyrodiversity in the long term (Hubert et al. 1991), and cause a substantial decrease of beta and gamma diversity in Provencal landscapes. Rigolot (1997) claimed that the use of prescribed burning in such context would be a valuable management tool to reintroduce the range of fire seasonality, patchiness and intensity that are required to maintain biodiversity.
Nevertheless, the implementation of prescribed burning in Provence is restricted, mainly for safety reasons, to ca. 30-50 ha each burn, which puts its application at a regional scale into perspective. To be effective and maintain pyrodiversity across the landscape, prescribed burning would need to treat areas in the 10^2-10^3 ha size range (i.e., medium-size fires), but this would be difficult to implement given the relatively high population density and fine-grained pattern of land use in the region. The use of prescribed burning for meeting conservation objectives in Mediterranean ecosystems under high anthropogenic pressure, such as the northern Mediterranean Basin and southern California, will remain difficult to achieve because of priorities given to human life and property. The necessity for a more wide spread use of prescribed burning is not yet accepted in SE France given the many sociologic misgivings and environmental policies that stressed the negative impacts of fire.

Areas identified as priorities for further fire research

A basic premise of natural disturbance ecology asserts that when an ecosystem is managed within its historical range of disturbance variability, it will remain diverse, resilient, productive and healthy. My research provides further evidence for linkages between pyrodiversity and biodiversity. I provide an objective methodology to examine how fire regimes impact plant diversity in each piece of any given landscape mosaic. However, many uncertainties remain as to what are the most appropriate fire regimes to achieve specific conservation objectives.
In particular, I would recommend future research to focus on the following topics and research questions:

- As I use a retrospective approach to characterize current landscape pyrodiversity, the next step would be to implement a long-term monitoring of pyrodiversity and of the associated biodiversity patterns at a regional scale.

This would permit (i) to quantify the influence of climate change and land use - land cover change on landscape pyrodiversity, (ii) to drive integrated fire management towards specific objectives to maintain landscape pyrodiversity (e.g., reduction of fire extent, increase of fire-return intervals) in targeted areas and (iii) to allow for early warning of extinction risk of endangered species in the case of strong alteration of landscape fire regimes.

- Conserving biodiversity and protecting human life and property from wildfires are not incompatible objectives as illustrated in southwestern Australia. Nevertheless the compromise needs to be defined in order to apply the appropriate fire regime. Simulation modeling affords a capacity for experimentation, beyond what is empirically possible in terms of temporal and spatial scales and is therefore essential to explore the consequences of different management options for both biodiversity conservation and the mitigation of wildfires risk.

- I focussed in this study on the effects of pyrodiversity on the structure and composition of the landscape mosaic. Using a similar retrospective approach to characterize the spatiotemporal evolution of landscape patterns (e.g., spatial arrangement and composition of vegetation biomass over a 50-year period) would provide useful insight on how land cover and land use change influence pyrodiversity.

- Research on fire impacts on biodiversity has largely focused on impacts on declared rare flora and threatened ecological communities. Few studies have evaluated the pyrodiversity-biodiversity paradigm on a wide range of taxonomic groups (vascular plants, macrofungi, ground-dwelling invertebrates and vertebrates (but see Wittkuhn et al. 2011). Consequently, future studies need to broaden the range of taxonomic groups examined and to select relevant functional types that could be used as pyrodiversity indicators.

- Related to the previous research challenge: the plant functional types approach used in this study was found to be reasonably successful for predicting plant responses to fire. Driscoll et al. (2010) suggest that it may also be possible to identify a set of common traits for other taxonomic groups to study how fire influences wildlife diversity.

- The implications for biodiversity of interactions between human-induced global change (e.g., climate, [CO_2], land use) and abiotic controls (e.g., environment, fire) are vast and difficult to assess. Hence, the importance in fire research of including long unburned habitats (preferably unmanaged) as reference sites into pyrodiversity-biodiversity analyses is critical if we want to separate the role of fire from the influence of other factors in determining plant diversity. This is also essential if future studies address the influence of fire on the floristic convergence patterns between Mediterranean biomes.

- Finally fire research addressed only recently the impact of fire and fire management on carbon emissions and sequestration tradeoffs at various temporal and spatial scales. Specific kinds of questions could include how different fuel treatments (preventive prescribed burning versus active fire suppression) impact the resulting above- and below-ground carbon sequestration at both local and landscape scales.

General conclusion

This thesis has provided a first comprehensive characterization of the Pyrodiversity-Biodiversity paradigm at multiple scales in two contrasting Mediterranean-type ecosystems. As knowledge of the linkages among landscape fire regimes, ecosystem processes and species improves, this research provides a reference to quantify landscape pyrodiversity and characterize its effects on several aspects of floristic diversity.

Overall, this study supported the hypothesis that pyrodiversity begets plant diversity from the species to the landscape level. My research also highlighted the need for improved knowledge of the pyrodiversity requirements of other taxonomic groups to improve our understanding of the ecological role of fire and develop an appropriate and integrated fire management approach in fire-prone landscapes.

Epilogue

Fire is definitely a hot topic surrounded by many misbelieves from the public side and a burning issue much debated by the scientific community. This diversity of opinions enriches our cultural, social and ecological perception of this phenomenon. This research helps in our understanding of the contribution of fire to the exceptional floristic richness found in Mediterranean-type ecosystems. Such areas need a minimum amount of pyrodiversity to maintain the variety of habitats and the diversity of their flora. Unfortunately human societies have nowadays a harsh dilemma to deal with the environment as we see it today is the product of fire, but we cannot tolerate fire in this environment to the degree that we have lived with it in the past or to the degree that is required to maintain biodiversity.

Thus, in a way, fire challenges how we connect to our environment and questions how we perceive Nature. Legislation and incentives that support excessive protectionism and overlook the historical importance of the fire regime do not contribute to save this natural legacy. To the other extreme, excessive human interventionism that begets inappropriate fire management strategies may lead to reversible impacts on biodiversity. The preliminary consultation with the public community, the political powers and the scientific community is a necessary first step to find the right balance between a protectionist perception and a stewardship approach of fire in the future.

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