RESEARCH ARTICLE

Characterization of landscape pyrodiversity in Mediterranean environments: contrasts and similarities between south-western Australia and south-eastern France

Nicolas Faivre · Philip Roche · Matthias M. Boer · Lachie McCaw · Pauline F. Grierson

Abstract Landscape pyrodiversity encapsulates the range of spatiotemporal variability in disturbance by fire. There is a widely-held view that diversity in fire regimes promotes biological diversity (i.e., the Pyrodiversity–Biodiversity paradigm). However, this relationship needs to be examined more carefully as pyrodiversity at the landscape scale remains poorly defined and difficult to quantify. Here, we used a novel approach to analyze landscape pyrodiversity by selecting and quantifying appropriate descriptors of fire variability at the landscape level. We characterized and classified observed fire mosaics at the 1 km scale using temporal attributes (fire frequency, time-since-fire and mean fire interval) and a variety of spatial attributes derived from landscape metrics. We trialed our approach on a 50-year record of fire patterns in two Mediterranean environments; (1) in southern France where fire regimes are dominated by unplanned ('wild'-)fires and (2) in south-west Australia, where fire regimes are dominated by planned fires. We found that the landscape pyrodiversity of both regions was expressed by distinct gradients of both fire frequency and spatial diversity of fire patterns. As expected, the two environments were significantly different in landscape pyrodiversity, with contrasting mean fire frequency and mean time-since-fire patterns. However, we also found similarities between southern France and south-west Australia in the composition and configuration of their spatial fire patterns. Our results show that these two Mediterranean environments form a pyrodiversity continuum despite the disparate management regimes. Our findings also demonstrate that a quantitative characterization of pyrodiversity is central to developing new perspectives and practical tools for biodiversity conservation in fire-prone landscapes.

Keywords Fire regime · Fire mosaic · Landscape ecology · Spatiotemporal analysis · Prescribed burning · Wildfire · Pyrodiversity–biodiversity paradigm

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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 (Álvarez 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 organised 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. 1a). 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
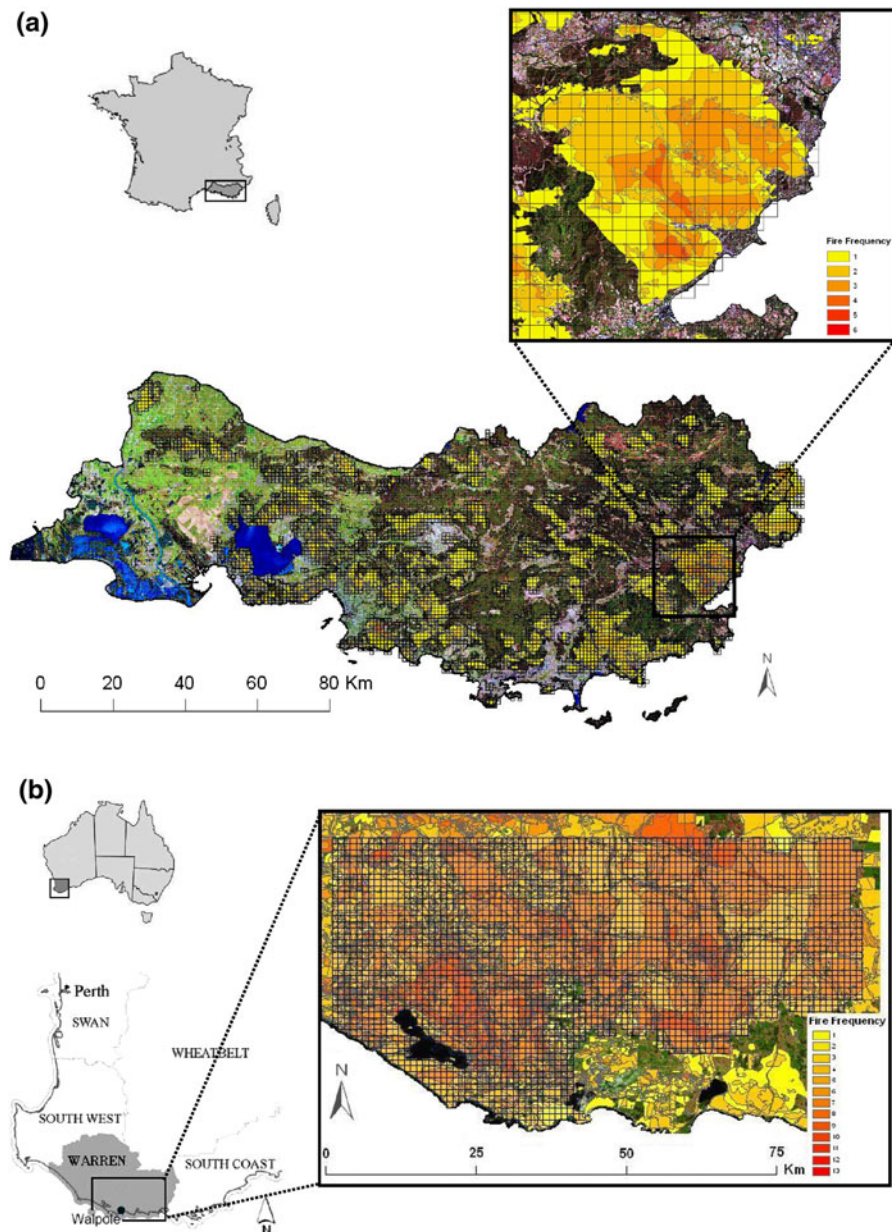
Fig. 1 **a** Location of the study area in the French Provence. Fire patterns over the 1960–2008 period have been unified and the 1 km-grid used in the study protocol and are superimposed on a Landsat satellite image (*bottom figure*). Fire patterns in Provence are very fragmented within the region and 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. **b** 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 1 km-grid mapping of fire mosaics is also displayed and superimposed on a Landsat satellite image to illustrate the spatial variation in fire frequency within 1 km² sample areas over the 1960–2008 period (*right figure panel*)

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).

Our second study area was located in the Warren Region in the south-west of Western Australia, consisting of 0.5 Mha of forest, woodland and shrubland with exceptional landscape richness and local endemism (Wardell-Johnson and Horwitz 1996) across the districts of Walpole and Denmark (Fig. 1b). 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). 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 ∼60,000 years (Abbott 2003; Bowman 2003 but see Wardell-Johnson et al. 2004). From 1826, colonisation 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 the 1960s 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 10^3 and 10^4 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 characterised 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 × 50 m grid cells within every 1 km × 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 × 1 km sample area; the AI measures the extent to which 50 m × 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 km^2 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 1 km × 1 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.,
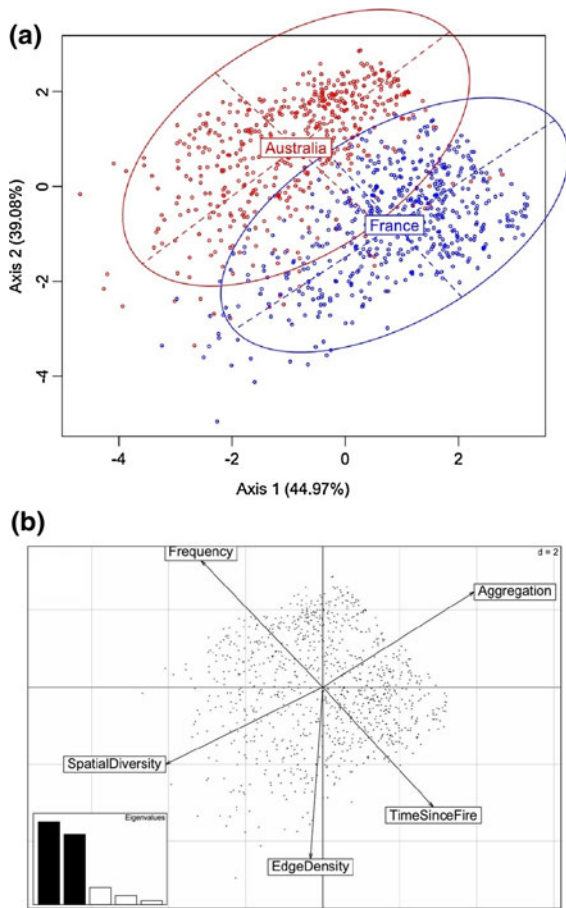
three simple, three intermediate and three highly complex types of fire mosaic). We then projected the nine groups onto the PCA factorial map in order to visualize their position and their degree of overlap in the pyrodiversity variable space. The distribution of the variables for each group was quantified 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. 2). 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. 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). 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.

Pyrodiversity comparison of the study areas

Based on the PCA computed from the reduced set of pyrodiversity variables, fire mosaics of the two study

Fig. 2 PCA biplot showing the ordination of 1 km² 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

Fig. 3 PCA ordination plot (**a**) summarize samples dispersion by the five selected variables for the two study regions. Individual 1 km²-squares are identified by *circles* (in color version: *red* for SW Australia and *blue* for SE France). 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**)

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 km² sample areas (fire frequency and time-since-fire) (Figs. 3, 4). 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. 4). The mean fire interval for the

study area in Provence was 21 years and significantly longer than the mean fire interval for SWWA (i.e., 9 years) (Fig. 4).

In the two study areas, fire frequency patterns had similar spatial heterogeneity (Figs. 3, 4). Fire mosaics within the 1 km² 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. 4): 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. 4). 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).

The majority of the nine clusters resulting from the HAC classification contained exclusively 1 km² sample areas from either Provence or SWWA (see dendrogram in Fig. 5). The two study regions presented contrasted aggregated fire mosaics, mainly due to the significant differences in fire frequency (Fig. 5). However, we also observed more interspersion between the two environments when fire mosaics presented high edge density and high spatial diversity (Figs. 5, 6). In three of the clusters (i.e., groups 2, 4 and 6) fire mosaics from both study regions were well represented (Fig. 5). 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. 6).

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

Fig. 4 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**), SIDI$_{Freq}$ (**d**), AI$_{Freq}$ (**e**) and ED$_{TSF}$ (**f**)]. The *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
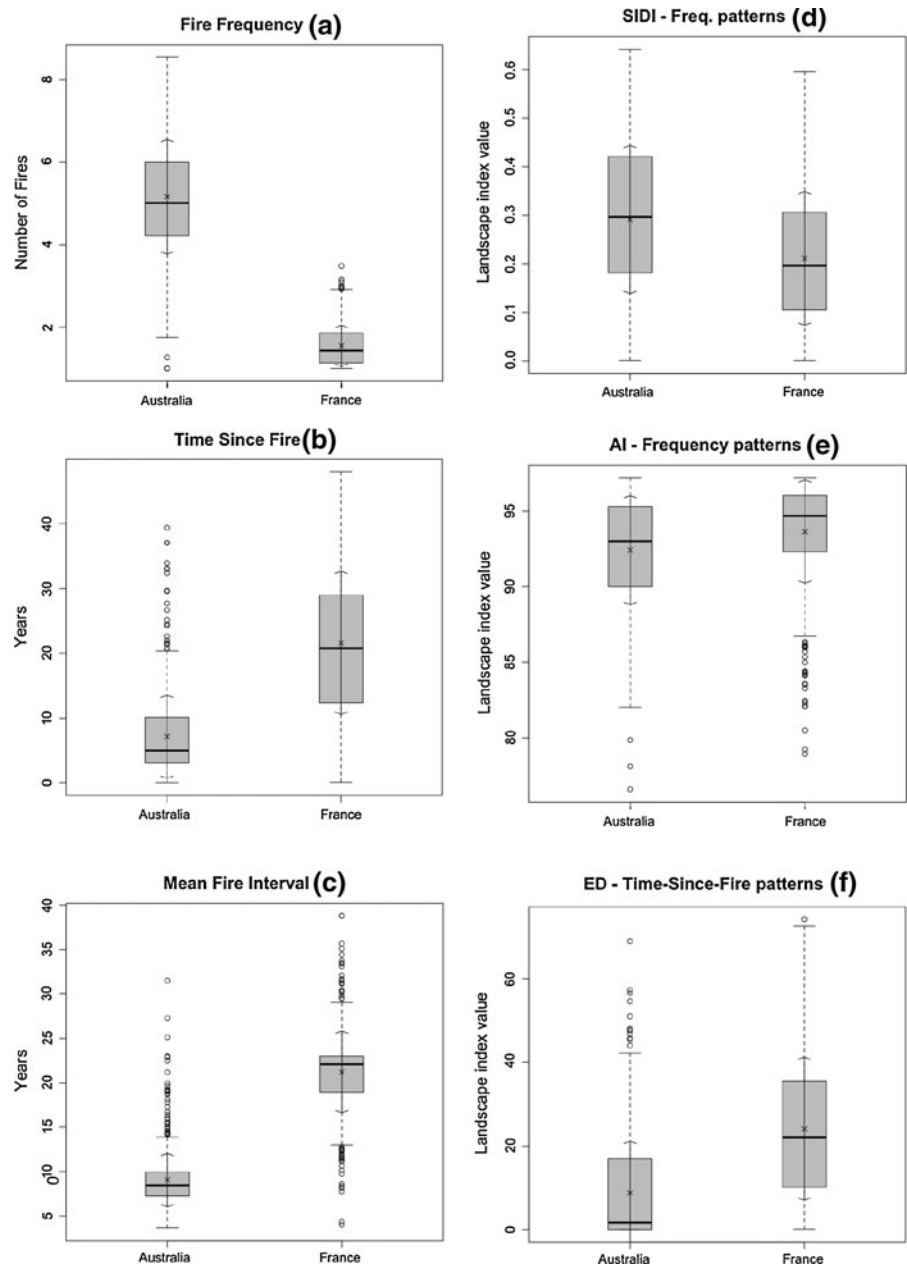
pyrodiversity and were relatively dispersed (in multivariate space), while groups 3, 5 and 7 had lower pyrodiversity and were more aggregated in multivariate space (Fig. 5). Groups 4, 6, 8 and 9 exhibited intermediate levels of pyrodiversity (Fig. 5). In this study, high pyrodiversity was the result 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. 5).
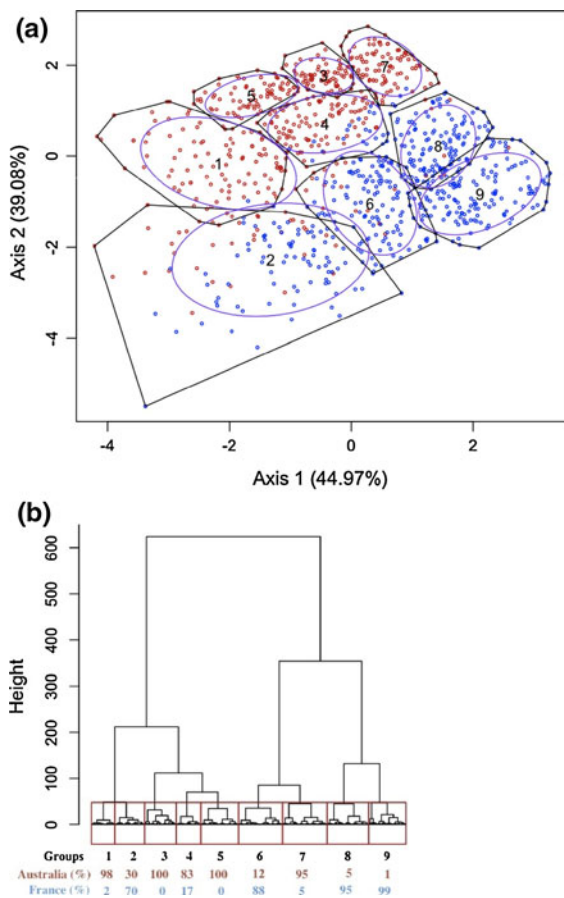
Fig. 5 Grouping of the 1 km^2 fire mosaics samples by hierarchical agglomerative clustering (**a**). 75% confidence ellipses are superimposed on the PCA plot and represent the probability for a chosen sample to belong to a particular cluster. The dendrogram (panel b) depicts the partitioning of the 1,000 samples into nine clusters. Distribution of both study areas samples within each group (i.e., percentage of composition) is specified below the dendrogram

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 characterised 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

Fig. 6 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
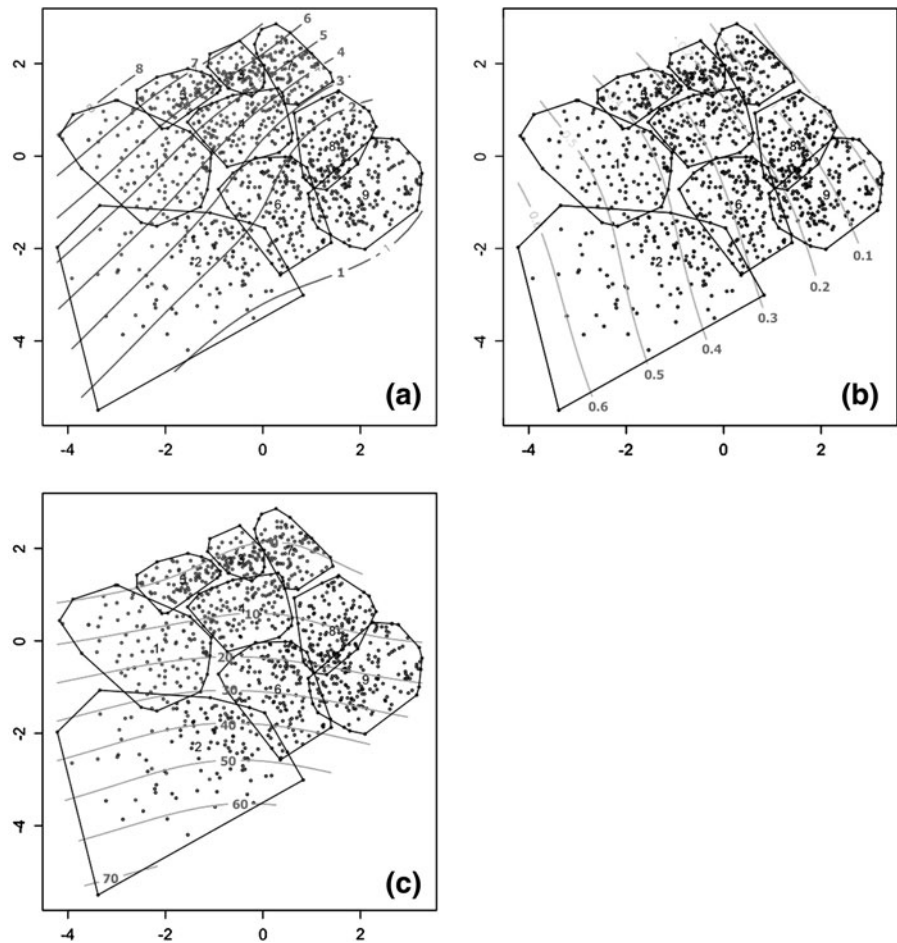
density variable did not behave similarly to spatial diversity and aggregation according to the samples' mapping in the multivariate space (see Fig. 2). The edge density was dependent on the type of fire maps, whether we were considering fire recurrence patterns or on the last fire event, as the encompassing pattern. We believe this may be explained by the fact that fire mosaics in Provence are characterised 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 (10^2–10^3 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 characterised 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) 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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