



Post-fire plant diversity and abundance in pine and eucalypt stands in Portugal: Effects of biogeography, topography, forest type and post-fire management



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ABSTRACT

This study concerned the mid-term regeneration of the woody understory vegetation of pure and mixed stands of *Pinus pinaster* Ait. and *Eucalyptus globulus* Labill. in northern and central Portugal following wildfires in 2005 and 2006. Pine and eucalypt stands are the most widespread and most fire-prone forest types in Portugal. The main aim was to investigate the importance of biogeography, topography, forest type and post-fire management operations in explaining the patterns in shrub diversity (species richness) and abundance (cover). To this end, 284 study sites in four distinct biogeographic regions were sampled 5 to 7 years following the last wildfire. At each site, the presence and cover of individual shrub species were estimated using 4 sub-plot of approximately 10 m² each. The entire data set was analyzed by means of GLM using a total of seven explanatory variables: biogeographic region, forest type, three types post-fire management operations (soil tillage, tree harvesting, and shrub clearance), and two topographic variables (slope angle and elevation). The GLM analysis was also done for the individual biogeographic regions.

Biogeographic region and slope steepness were key factors explaining shrub species richness, albeit the role of slope angle was possibly linked to the intensity of past land use.

Biogeographic region equally played a significant role in explaining the cover of all shrubs together as well as of the shrubs of Leguminosae and Cistaceae. All three types of post-fire management operations appeared to hamper the recovery of resprouters and Leguminosae, whereas just tree harvesting and shrub clearance (but not soil tillage) negatively affected the cover of seeder species. These impacts of post-fire management operations had a noticeable region-specific component, being more relevant in the less productive biogeographic regions.

Also the role of forest type depended strongly on biogeographic region. It was only significant in the South Mediterranean region, where pine plantations had a higher total shrub cover as well as higher covers of seeders and Cistaceae. Possibly, however, this significant role of forest type could be due to the lower incidence of shrub clearance in the pine stands.

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1. Introduction

Forests are of the utmost importance for mankind as they provide a vast number of ecosystem services such as regulation of water fluxes, protection against soil (fertility) losses and conservation of plant and animal biodiversity (European Commission, 2010). According to the insurance hypothesis (Bengtsson et al., 2000; Folke et al., 1996), the present and future ecosystem services provided by forests (and other ecosystems) depend heavily on

their biodiversity as their biodiversity is fundamental to an ecosystem's resistance and resilience against disturbances. A large number of plant species is considered essential for the continued provision of services by ecosystems, even if these species appear to be partially redundant in terms of ecosystem functioning (Isbell et al., 2011). Ecosystem resilience is of particular relevance for fire-prone forests such as the planted pine and eucalypt forests studied here, including because fire frequency in Portugal is not expected to reduce substantially in the near future (Fernandes et al., 2013; Moreira et al., 2011). The understory vegetation of western Iberian eucalypt and pine stands deserve special mention for their key role in the ecosystem service of water flux regulation

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and erosion protection, especially during the early stages of the so-called window-of-disturbance (e.g. Fernandez et al., 2011; Prats et al., 2012, 2013) and with important implications for long-term land-use sustainability (e.g. Grigal, 2000). Conservation of present and future biodiversity is also relevant from an economic point of view, as biodiversity constitutes an important aspect in forest certification schemes such as FSC (Forest Stewardship Council) and, thus, in valorization of forest products.

A variety of factors is likely to affect the cover and floristic composition of the understory vegetation in burned forest plantations. Biogeographic regions, which encompass climatic, edaphic and topographic conditions, constitute limits to the distribution ranges of native species (e.g. Abella and Covington, 2006; Lobo et al., 2001). Also topographic factors have often been pointed out as key variables in explaining floristic patterns, albeit not in a consistent manner. For example, Pausas (1994) found that woody species richness was negatively correlated with elevation in high-elevation mountain ranges, while Lobo et al. (2001) found the opposite for the Iberian Peninsula. In the case of forests, the species richness of the understory has been associated to the predominant tree species of the overstory (Suckling et al., 2001). However, it is often unclear if the role of forest type is due to direct or indirect effects, resulting for example from competition by the tree species, alterations in abiotic conditions (e.g. pine needle cast) or differences in forestry practices (Cavard et al., 2011; Macdonald and Kurulok, 2007). Management operations carried out following wildfires can be a major driver in the regeneration of the understory vegetation from the direct fire effects, both in terms of its cover and its species diversity (Vallejo and Alloza, 2012). A wide range of management operations have been applied in recently burnt areas, ranging from tree harvesting, to soil tillage in preparation of new plantations, to restoration actions such as seeding. All such operations can be expected to affect vegetation persistence and/or (re-)colonization following wildfires (Hartley, 2002).

Forests in Portugal, like in other parts of southern Europe, have changed profoundly over the past few decades, especially due to the widespread planting of commercial tree species such as *Pinus pinaster* Ait. (for wood production) and eucalypt and, in particular, *Eucalyptus globulus* Labill. (for paper pulp production). At present, planted forests dominated by maritime pine and/or eucalypt constitute approximately 50% of the forested area in Portugal (ICNF, 2013). Since the tree layer of these planted forests is composed of just one or two species, the understory vegetation largely determines these forests' plant species diversity. Bengtsson et al. (2000) considered the understory vegetation of mono-specific plantations as the best indicator of their overall biodiversity and, thereby, of their sustainability. An important drawback of pure and mixed stands of pine and eucalypt is their elevated flammability (Fernandes, 2009; Silva et al., 2009). To reduce their intrinsic fire hazard, pine and eucalypt plantations are typically subjected at regular intervals to reductions of the standing biomass of the understory vegetation, traditionally by grazing and shrub collection for livestock bedding and presently by mechanical shrub clearance and increasingly prescribed burning (e.g. Oliveira, 1999). These fuel management operations, however, can be expected to interfere with the biodiversity of the understory and, thus, with the principles of sustainable management.

The present study is a follow-up of Moreira et al. (2013), which concerned the native and exotic tree species in pure and mixed stands of maritime pine and eucalypt that had burnt 5–7 years earlier and which showed that biogeographic region and post-fire management operations were the most important factors explaining native tree species diversity. This study, on the other hand, concerned the mid-term post-fire regeneration of the woody understory vegetation. The specific objectives of this study were: (i) to describe the patterns in shrub species richness as well as in

their total cover and in the cover of the two main plant functional groups (in terms of fire adaptation strategy) and of the most common families; (ii) to explain these patterns in terms of potential explanatory variables related to biogeographic region, topography, forest type and post-fire management operations.

2. Materials and methods

2.1. Study areas and study sites

Within northern and central Portugal, twenty study areas were selected that according to the Portuguese digital atlas of burnt areas had burnt in 2005 or 2006. The selection of these areas furthermore involved the following criteria: (i) the presence of sufficient numbers of mono-specific and/or mixed stands of eucalypt and maritime pine; (ii) the size of the burnt area (which ranged from 137 to 10,924 ha); (iii) accessibility. The number of pure and mixed eucalypt and pine stands was estimated using the data of the 5th National Forest Inventory (NFI) of 2005–2006 (ICNF, 2013). From the NFI grid points within each area that corresponded to pure and mixed eucalypt and pine stands, up to 30 were selected in a random stratified manner such that the study sites were equally divided over the three forest types as possible. The final selection of the study sites involved a field check in terms of accessibility, indications for the occurrence of a fire in 2005/2006 and the occurrence of a change in forest type following the NFI of 2005–2006, as further detailed in Moreira et al. (2013) and Águas et al. (2014). Sites that were recently planted or sites where the spontaneous vegetation was eliminated by recent forestry operations were not included in this study.

2.2. Field sampling

A total of 284 study sites were sampled between the winter of 2010 and the late spring of 2012, by which time the sites had burnt for the last time between 5 and 7 years earlier. At each site, a sampling plot was laid out that consisted of a circular buffer with a radius of 6.78 m (Fig. 1), using as center the coordinates of the respective NFI grid point. For this study, sampling itself was carried out in four sub-plots with a radius of 1.78 m, whose center was located at 5 m distance from the center of the plot in the four cardinal directions (N, E, S, W). Within each sub-plot, the woody species making part of the understory (further referred to as

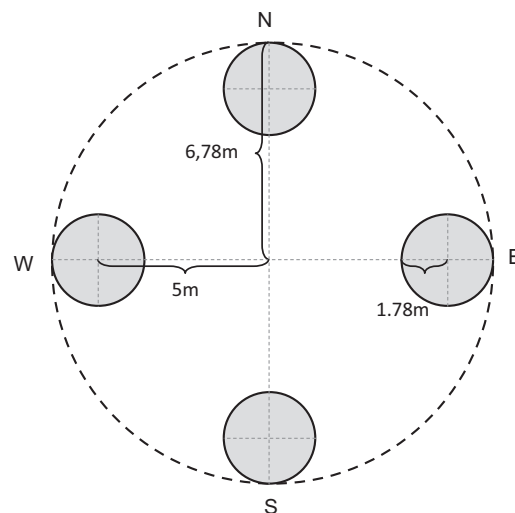


Fig. 1. Schematic view of a sampling plot and its four sub-plots.

“shrub” species) were recorded and their projected aerial cover estimated visually. To this end, 12 cover classes were recognized: 0%, >0–5%, >5–10%, >10–20%, >20–30%, etc.

Evidence of forest management operations that had taken place after the wildfire of 2005/2006 was recorded based on direct observations and, whenever possible, complemented with information provided by land owners and/or forest managers. The following three types of management operations were recognized for their expected impact on the understory: (a) harvesting of burned trees; (b) soil tillage (including harrowing, ploughing, and soil ripping); (c) cutting of the understory vegetation. Furthermore, the elevation and slope angle of the sampling plots were measured in the field.

2.3. Data analysis

This study analyzed the following response variables: (1) species richness (number of woody species); (2) total cover of the shrub species; (3) total cover of the shrub species classified as resprouters; (4) total cover of the shrub species classified as seeders; (5) cover of individual shrub families and, in particular, the Leguminosae, Cistaceae, and Ericaceae for occurring most frequently in the data set. The classification in seeders and resprouters was based on the species' post-fire regeneration strategies as reviewed by Paula and Pausas (2008) and Paula et al. (2009), including under resprouters both facultative and obligate resprouters (coded as S and R in Annex 1). In case a species' strategy was not specified in Paula and Pausas (2008) or in Paula et al. (2009), it was determined by observations during the field work.

The above-mentioned response variables were modeled by means of Generalized Linear Modeling (GLM), using IBM SPSS v.19 for Windows. In the case of species richness, this was done using a Poisson distribution with a log link, following Moreira et al. (2013); in the case of the various cover variables, it involved a Tweedie distribution with a log link for providing the best fit in most instances.

A total of seven explanatory variables were considered for model selection in GLM. Organized by measurement scale, they were: (A) categorical variables: – (1) biogeographic region; (2) forest type (mono-specific eucalypt plantation; mono-specific maritime pine plantation; mixed eucalypt-pine stand); (B) binomial variables, associated to post-fire management operations: (4) soil tillage; (5) tree harvesting; (6) shrub clearance; (C) continuous variables: (7) slope angle; (8) elevation. The biogeographic region of the study sites was derived from the maps by Rivas-Martínez and Rivas-Saenz (1996–2009). The following four regions were included in this study: (1) the Atlantic European Region, Cantabro-atlantic Sub-region (hereafter “Atlantic”); (2) the Mediterranean Region, Coastal-Lusitano Andalusian Sub-region, Sado-Divisorian Province (hereafter “Coastal”); (3) the Mediterranean Western Iberian Sub-region, Carpetano Leonese Province (hereafter “North Mediterranean”); (4) the Mediterranean Western Iberian Sub-region, Luso-Extremadurensis Province (hereafter “South Mediterranean”). As shown in Fig. 2, however, the study sites that were located in the inland part of the Coastal-Lusitano Andalusian Sub-region (“Coastal”) were included here in the “South Med.” region (Annex 1). Model selection in GLM involved the stepwise backwards selection procedure, starting with all seven exploratory variables (Myers, 1990; Quinn and Keough, 2002). The percentage of deviance explained by each model was calculated as proportion of the deviance explained by the intercept-only model.

GLM was not only done for the entire data set but also for each of the four individual biogeographic regions separately to detect region-specific effects of forest type, management operations and topographic factors.

3. Results

3.1. Overall description of the data set

Roughly half of the sampling plots concerned mono-specific eucalypt plantations (46%), whereas the rest of the plots was about evenly distributed over mono-specific maritime pine plantations (30%) and mixed eucalypt-pine stands (25%) (Table 1). Almost 70% of the sampling plots had undergone tree harvesting after the 2005/2006 fire, whilst similar amounts of plots had undergone either soil tillage (17%) or shrub clearance (14%).

Shrubs were encountered in almost all sampling plots (99%) and had, on average, attained an elevated cover (87%) over the 5 to 7 years after the last fire (Annex I). A total of 64 shrub species were found in the 284 sampled plots, with a mean species richness of 7 species per sampling plot. Resprouter species were present in basically all sampling plots (97%), whilst seeder species occurred somewhat less frequently (81%). The resprouters were clearly more abundant than the seeders, with a mean cover of 68% as opposed to 32%. The cover of the resprouters was by and large due to obligate resprouter species, as facultative resprouters were insignificant in terms of cover.

The three most frequent families in the data set were the Leguminosae (93%), Ericaceae (80%) and Cistaceae (51%) (Annex I). In the same order, they were also the most abundant families, with a mean cover of 37%, 28% and 13%, respectively. The most common species of each of these three families were *Pterospartum tridentatum* (Leguminosae), *Calluna vulgaris* (Ericaceae) and *Cistus ladanifer* (Cistaceae). They were present in 48%, 48% and 14% of the sampling plots, respectively. Worth referring was the contrast in post-fire strategies among the three families. All shrub species pertaining to the Leguminosae family corresponded to resprouters (i.e. obligate or facultative resprouters), whereas all Cistaceae species were seeders. By contrast, the Ericaceae species included both resprouters and seeders.

3.2. Key factors explaining shrub species richness and shrub cover

The shrub species richness could be explained to a significant extent by biogeographic region and slope angle, with the resulting GLM accounting for 23% of the total variation (Table 2). The role of biogeographic region reflected clear differences in mean shrub species richness, ranging from 9 in the Coastal and South Mediterranean regions to 7 in the Atlantic region (Annex I) and 5 in the North Mediterranean region. The role of slope angle corresponded to a tendency for the number of shrub species to increase with increasing with slope steepness.

The total shrub cover was explained best by a GLM that included biogeographic region, post-fire management and elevation as significant factors. Together, these three factors explained 23% of the variation. The importance of biogeographic region was due to a marked contrast in total shrub cover between the North Mediterranean region (60%), on the one hand, and, on the other, the Coastal and South Mediterranean regions (95% and 113%, respectively). The role of post-fire management reflected a negative impact of all three management types on total shrub cover, while the effect of elevation corresponded to a decrease in total shrub cover with increasing elevation.

The best GLMs for the resprouter as well as seeder cover closely resembled that for the total shrub cover, as they involved the same three significant explanatory variables and accounted for comparable fractions of the total variation (17% and 23%, respectively). Furthermore, also resprouter and seeder cover were clearly lower in the North Mediterranean region than in the other regions (43% vs. 69–84% and 8% vs. 28–49%). Nonetheless, the biogeographical

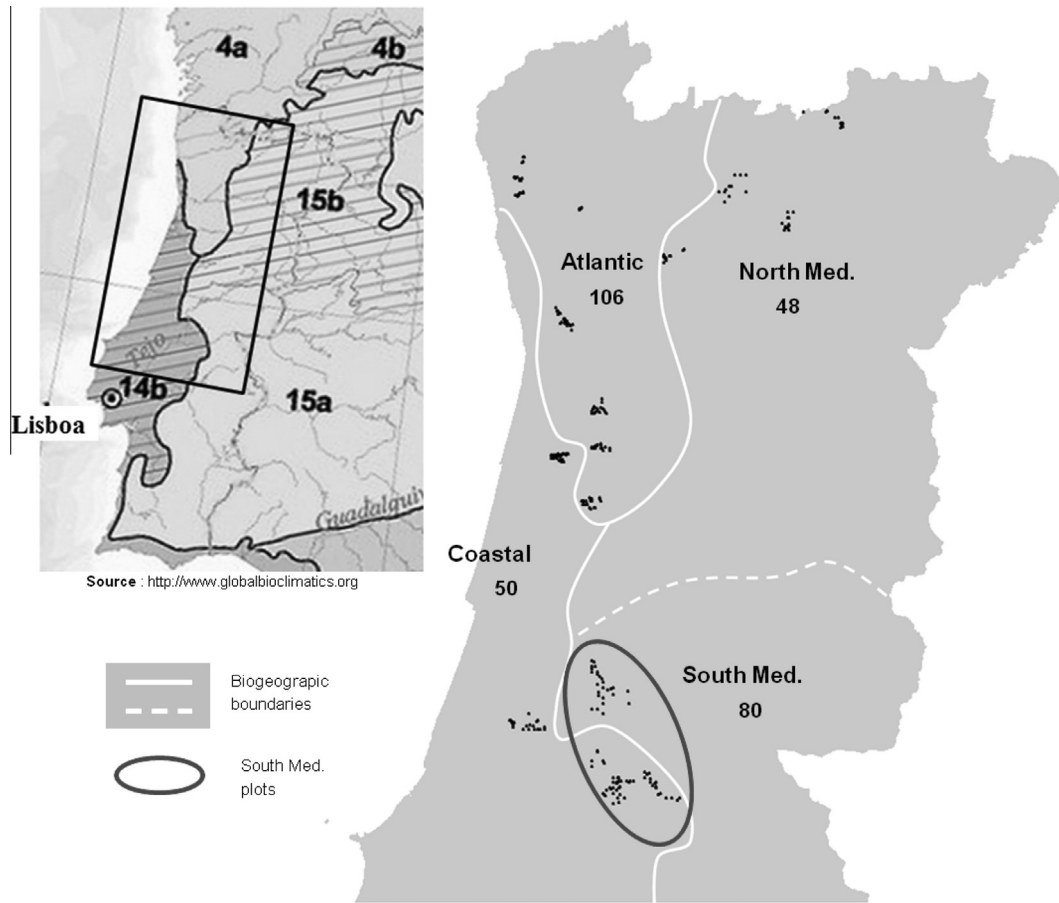


Fig. 2. Biogeographic regions of study area. Dots in the main figure are sampling plots and sample numbers are indicated for each region. Upper left corner inset is an excerpt of the original cartography, for the Western Iberian Peninsula (www.globalclimatics.org). 4a – Atlantic European Region, Cantabroatlantic Subregion; 14 and 15 – Mediterranean Region 14b – Coastal–Lusitano Andalusian sub region, Sado–Divisorian province; 15 – Mediterranean Western Iberian sub region; 15a – Luso–Extremadurensis province; 15b – Carpetano Leonese province. These designations correspond, respectively to the designations in the main figure: Atlantic, Coastal, South Mediterranean and North Mediterranean. The South Mediterranean region included the plots sampled in the Luso–Extremadurensis province, and also the most inland plots of the Coastal–Lusitano Andalusian sub-region.

pattern in resprouter (and that in total shrub cover) cover differed from that in seeder cover in that its mean cover was highest in the Coastal region instead of in the South-Mediterranean region. The resprouter cover also revealed a distinct response to post-fire management than the seeder cover (and the total shrub cover). While the resprouter cover, like the total shrub cover, was negatively affected by all three types of management operations, the seeder cover was not significantly impacted by either soil tillage or tree harvesting.

The GLM results differed notably between the three most common families. In the case of the Ericaceae, none of the seven explanatory variables could account for a significant fraction of the cover variation. The best GLM for the Leguminosae cover was similar to that for the resprouter cover, as the different biographic regions and the three post-fire management operations had analogous significant effects and as the explained variance was almost identical (16%). The best GLM for the Cistaceae cover, however, was the only one in the present study that included forest type as significant factor. This role of forest type coincided with a higher Cistaceae cover in mono-specific maritime pine plantations than in mono-specific eucalypt plantations or mixed eucalypt–pin stands. The Cistaceae cover further stood out amongst the different covers analyzed here (including that of Ericaceae) in that its mean value was not clearly lowest in the North Mediterranean region.

3.3. Key factors for the individual biogeographic regions

The significant role of slope angle in explaining shrub species richness in the entire data set appeared to be highly region-specific (Table 3). In fact, the general pattern of increasing richness with increasing slope angle was only verified for the South Mediterranean region. This region combined relatively steep slopes of, on average, 17.8° (Table 1) with a comparatively high shrub species richness of, on average, 9 species (Annex 1). The species suit of the South Mediterranean region furthermore included a comparatively large number of characteristic species, i.e. species that occurred clearly more frequently in one region than in the other three regions (10% vs. 2–5%). From the ten characteristic taxa of the South Mediterranean region, the following four were almost exclusively found there: *Cistus monspeliensis*, *Ulex airensis*, *Ulex jussiaei* and *Lavandula* spp.

Also in the case of the second topographic factor, elevation, there were clear discrepancies between its relevance in the entire data set and its importance in the individual biogeographic regions. The significant decrease in both total shrub cover and resprouter cover with increasing elevation was found for only one out of four biogeographic regions. By contrast, this same elevation–cover relationship was significant for the resprouters in three of the regions.

Table 1
Summary of the variables used in the analysis. Frequency (%) of forest type, management operations and mean and coefficient of variation of the topographic variables (slope and elevation) in each Biogeographic Region. Relative frequency of the plots sampled in each region is given in the first line of the table. Frequency of post-fire management operations by forest type is given for the four biogeographic regions. pin – pine plantations, euc – eucalypt plantations, mix – mixed forests.

	Frequency (%)				All regions
	Atlantic 37.3	Coastal 17.6	NorthMed 16.9	SouthMed 28.2	
<i>Forest Type</i>					
Pine	17.9	10.0	72.9	31.3	29.6
Eucalypt	45.3	62.0	18.8	52.5	45.8
Mixed	36.8	28.0	8.3	16.3	24.6
<i>Post-fire Management</i>					
Soil tillage	19.8	32.0	12.5	6.3	16.9
pin	21.1	20.0	0.0	0.0	
euc	27.1	38.7	44.4	11.9	
mix	10.3	21.4	50.0	0.0	
Tree harvest	60.4	88.0	60.4	72.5	68.7
pin	57.9	100.0	57.1	68.0	
euc	54.2	83.9	66.7	76.2	
mix	69.2	92.9	75.0	69.2	
Shrub clearance	11.3	18.0	0.0	23.8	14.1
pin	15.8	20.0	0.0	8.0	
euc	8.3	9.7	0.0	38.1	
mix	12.8	35.7	0.0	7.7	
At least one operation	74.5	94.0	64.6	75.0	76.4
<i>Topography</i>	Mean (c.v.)				
Slope (°)	15.3 (0.5)	11.2 (1.0)	17.3 (0.4)	17.8 (0.5)	
Elevation (m)	344.2 (0.7)	147.3 (0.5)	556.8 (0.3)	282.8 (0.3)	

Table 2

Generalized linear models for each of the response variables: richness of Woody species in the understory layer and plant cover variables. *P* values of the model (partial or omnibus) are given with asterisks – $p < 0.05$ (*) – $p < 0.01$ (**) – $p \ll 0.01$ (***); + and – signs indicate significant differences (between Biogeographic region, forest Type) or significant correlation sign (slope or elevation); for the post-fire management it indicates significant differences between plots with and without evidences of the specific management operation.

Variables	Shrub species richness	Cover					
		Total Shrub	Post-fire regeneration		Families		
			Resprouters	Seeders	Leguminosae	Cistaceae	Ericaceae
Biogeographic Region	***	***	**	***	***	***	n.s.
Atlantic	+		+	+	+		
Coastal	++	+	+	+			
NorthMed						+	
SouthMed	++	+	+	++	+	+	
Forest type	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
Pine						+	
Euc							
Mix							
Post-Fire Management	n.s.					n.s.	n.s.
Soil tillage		*** (–)	** (–)	n.s.	* (–)		
Tree harv		** (–)	** (–)	n.s.	* (–)		
Shrub clear		*** (–)	** (–)	** (–)	** (–)		
Topography					n.s.	n.s.	n.s.
Slope angle	* (+)						
Elevation		** (–)	** (–)	~* (–)			
Omnibus test <i>p</i>	***	***	***	***	***	***	n.s.
% Variance Explained	26.2	23.2	17.2	22.8	15.6	19.9	–

The various GLMs for the individual biogeographic regions equally revealed that the relevance of all three types of post fire management operations was markedly region-specific, since none of the significant management-cover relationships in the entire data set applied to more than two out of four regions. Even so, soil tillage and shrub clearance tended to have a more widespread impact than tree harvesting, playing a significant role in two regions instead of one. While soil tillage was especially relevant in the Atlantic and North Mediterranean regions, shrub

clearance was particularly important in the Atlantic and South Mediterranean regions, both types of operations producing significant reductions in total shrub cover, resprouter cover and Leguminosae cover. Shrub clearance also diminished the seeder cover in the South Mediterranean region in a significant manner. Among these three regions, the North Mediterranean region stood out for its clearly lower mean values of total shrub, resprouter and Leguminosae cover; in turn, the South Mediterranean region had similar mean resprouter and Leguminosae covers than the Atlantic

Table 3

Generalized linear models for the effects of forest type, post-fire management and Topography, for the individual biogeographic regions. The biogeographic regions for which the explanatory variables (rows) are significant in explaining the variability of the response variables (columns) are indicated as follows: Atl (Atlantic), Nmed (North Mediterranean), Smed (South Mediterranean). *P* values of the effect are given with asterisks, following the abbreviation of the Biogeographic Region where the effect is statistically significant. $p < 0.05$ (*) – $p < 0.01$ (**) – $p < 0.001$ (***). + and – signs indicate significant differences between plots with and without evidences of the specific management operation or significant correlation sign (slope or elevation).

Variables	Shrub species richness	Cover				
		Total Shrub	Post-fire regeneration		Families	
			Resprouters	Seeders	Leguminosae	Cistaceae
Forest type		Smed*		Smed*		Smed**
Pine		+		+		+
Euc		–				–
Mix						
Post-fire management						
Soil tillage		Atl (–)** Nmed (–)**	Atl (–)*** Nmed (–)*		Atl (–)**	Coast (–)**
Tree harvest		Nmed (–)*	Atl (–)**	Nmed (–)* Smed (–)*		
Shrub clear	Smed (–)*	Atl (–)** Smed (–)***	Atl (–)** Smed (–)*	Smed (–)**	Atl (–)** Smed (–)**	
Topography						
Slope angle	Smed (+)***	Smed (+)**		Nmed (–)*		
Elevation		Nmed (–)**	Atl (–)* Coast (–)* Nmed (–)*	Smed (–)*	Nmed (–)*	Smed (–)**
% Variance Explained						
Atl	–	12.5	24.5	–	11.5	–
Coast	–	–	8.8	–	–	–
Nmed	–	25.3	12.7	15.9	7.3	–
Smed	21.4	28.8	11.7	21.2	9.3	11.6

regions but a noticeably higher mean total shrub cover (113% vs. 76%). Worth noting, however, was that shrub clearance was not observed at any of the 48 study sites in the North Mediterranean region. Furthermore, the Coastal region deserved special mention for the exceptional lack of impact of post-fire management on its shrub cover, except in the case of the Cistaceae cover. At the same time, however, post-fire management was more frequent in the Coastal region than in any of the other three regions, with 94% as opposed to 65–75% of the study sites having been subjected to one or more types of management operations. In spite of these frequent operations, the Coastal region had the highest resprouter cover of all four biogeographic regions (84% vs. 43–73%).

Forest type was of greater relevance in the region-specific GLM's than in the overall GLM's, playing a significant role not just in case of the Cistaceae cover but also in the case of the total shrub cover and of the seeder cover. Nonetheless, the statistical significance of forest type was restricted to a single biogeographic region, the South Mediterranean one. The mono-specific maritime pine had a positive effect on all three cover categories in the region, while the mono-specific eucalypt plantations had a negative effect on total shrub cover and Cistaceae cover but not on seeder cover. These effects were well-illustrated by the mean values of total shrub cover (pine: 142%; euc: 71%), seeders (pine: 71%; euc&mix: 37–50%) and Cistaceae (pine: 37%; euc: 13%).

4. Discussion

4.1. Factors affecting shrub species richness

The shrub species richness of mono-specific and mixed stands of maritime pine and eucalypt in northern and central Portugal was significantly influenced by biogeographic region. The important role of biogeographic units in biodiversity patterns was also pointed out by previous studies (e.g. Moreira et al., 2013; Ihaddaden et al., 2013). Mean shrub species richness was highest in the Coastal and South Mediterranean regions, but the regions' identical figures could well have different origins. The high diver-

sity in the Coastal region could be due to reduced inter-specific competition, reflecting the region's mild temperatures and elevated rainfall and, thus, limited water stress. By contrast, the high diversity in the South Mediterranean could be due to habitat diversity, reflecting the region's irregular topography as indicated by its variability in slope angle (Lobo et al., 2001; Wohlgemuth, 1998).

The mean values of shrub species richness presented here were much lower than the richness figures of prior studies in the Iberian Peninsula and surrounding Mediterranean regions (Ihaddaden et al., 2013; Lobo et al., 2001; Pausas and Carreras, 1995). This could be due to the reduced size of the area sampled in each plot (approximately 40 m²), especially since species richness assessment typically depends strongly on spatial scale (Vetaas and Ferrer-Castán, 2008). This methodological aspect was also supported by the fact that the present figures of shrub species richness per biogeographic region were comparable to those of the study by Santana et al. (2011) on cork oak forests in Portugal.

Biogeographic Region was also found to be a key factor in determining woody species composition. The specific composition revealed a clear pattern, which followed the species ecological range (SPB, 2012–2013). For example, *Erica arborea* and *Ulex europaeus* were more frequent in the Atlantic region, while the South Mediterranean sites were comparatively more represented by species typical of Mediterranean communities, like *Lavandula* spp., *Ulex airensis*, *Halimium ocyroides*, *Cistus monspeliensis* and *Cistus ladanifer* (Annex 1).

The shrub species richness in this study also depended significantly on slope angle, both in the entire data set and in the South Mediterranean region. A significant relationship between slope angle and woody plant species was also found by Sharma et al. (2009) but it was opposite to that found here, with tree species richness decreasing with increasing slope angle. Sharma et al. (2009) interpreted their results as reflecting a decrease in establishment potential of the tree species on steeper slopes. Possibly, in the present case the role of slope angle was indirect, as a key factor shaping land-use intensity (Lobo et al., 2001). In the past, land use would have been less intensive on the steeper slopes, as the

slopes' difficult access implied greater efforts and as their productivity was more marginal (Porto et al., 2011; Santana et al., 2011). Even in recent times as studied here, soil tillage – typically the most costly management option – was less frequent on the steeper slopes. Possibly, however, the role of slope angle in this study reflected past rather than recent land-use patterns, since post-fire soil tillage was not found to have a significant influence on shrub species richness. The shrub species richness in the pure and mixed pine and eucalypt stands studied here was not significantly related to forest type. Likewise, the richness in native tree species in the same data set could not be explained to a significant extent by forest type (Moreira et al., 2013). These results would seem to go against the findings by Brockerhoff et al. (2008), whose review indicated that species richness would typically be higher in native forest than in exotic plantations. A possible explanation would be that not only the mixed and pure eucalypt stands but also the pure pine stands were planted forests and, thus, must have undergone considerable human intervention during the past century. Especially in the case of the mixed and pure pine stands, past human disturbance could have included regular thinning, shrub removal (e.g. as stable material) and grazing activities. In terms of management operations following the 2005/2006 fires, however, no obvious differences were found between the three forest types studied here. This lack of differences could, at least in part, be an artifact resulting from the decision to exclude the study sites that had recently suffered major impacts of management operations (see Section 2.2).

4.2. Factors influencing shrub cover

The cover of (part of) the woody understory vegetation 5–7 years after the latest wildfire was found here to vary significantly with biogeographic region as well as with topographic factors and with the type of post-fire management operations. Apparently, while biogeographic setting in combination with topographic conditions defined the potential for post-fire re-recovery of the shrub species, their two principal regeneration strategies and two of their most common families (i.e. Leguminosae and Cistaceae but not Ericaceae), post-fire management options determined the extent to which this potential was achieved. From the two topographic factors considered in this study, elevation had a more consistent and widespread impact on shrub cover than slope angle, which contrasted with the factors' impacts on shrub species diversity. The decline in total or partial shrub cover in this study agreed well with the decrease in forest understory cover with elevation reported by Coll et al. (2010).

There was a marked contrast in the relevance of post-fire land management for the cover of the seeders than for the cover of the resprouters, especially in the entire data set. Seeder cover was hampered in a significant manner by shrub clearance and, in two out of four biogeographic regions, tree harvesting but not by soil tillage. Resprouter cover, however, was affected significantly by all three types of post-fire management operations. This differential effect of soil tillage on the cover of resprouters (as well as the Leguminosae family) could well be longer lasting than the period of 5–7 years following fire studied here, as soil tillage would easily produce major damage to the root systems of the resprouter plants and, thereby, seriously interfere with their capacity to recover from the damage by the fire and their resilience to possible adverse post-fire conditions. In the case of the obligate resprouter species, an aggravating factor is their typically low dispersal rate and, thus, reduced potential for re-colonization (e.g. Pausas and Vallejo 1999). In the case of the seeder species, the lack of relevance of soil tillage 5–7 years after the last fire fitted in well with their preferential allocation of resources to seed production and, hence, with their elevated capacity to regenerate from the soil seed bank

and/or from external seed sources (e.g. Verdú, 2000; Pausas and Paula, 2011).

Although the above-mentioned differential impacts of three types of management operations made much sense, two aspects of the present data set deserve special mention as they might have contributed to an underrating of the role of soil tillage and, at the same time, to an overrating of the importance of tree harvesting and shrub clearance. In the first place, sites that had recently been subjected to soil tillage were excluded from study, whereas sites that had recently undergone tree logging or shrub clearance were not. In the second place, for the majority of study sites that had been tilled less recently it was difficult to estimate when this soil tillage had taken place. Therefore, the present analyses could very well have included sampling plots that had been tilled before the 2005/2006 fire and, consequently, where especially resprouter species would have had more time to regenerate following soil tillage and before the fire.

Forest type also was a limited relevance for the shrub cover, except in the case of the South Mediterranean region where total shrub cover, seeder cover and Cistaceae cover were, on average, higher in mono-specific Maritime Pine plantations than in pure or mixed stands of eucalypt. The effects of forest type on total shrub cover and seeder cover, however, could be indirect and be associated to impacts of post-fire management. Namely, shrub clearance was more frequent in the eucalypt stands of the South Mediterranean region than in those of the other regions, and shrub clearance was found to negatively affect both total shrub and seeder cover in the South Mediterranean region. In the case of the Cistaceae cover, the significant relation with forest type found could reflect competition (or other interactions) with the pine and eucalypt trees or differences in land-use history of the pine and eucalypt plantations prior to the 2005/2006 fires. The former explanation is perhaps less likely, as similar impacts would have been expected for the other native plant groups (see Chu et al., 2014). The latter explanation could involve repeated grazing and/or shrub clearing, leading to progressive impoverishment of the soil seed bank and, thus, the regeneration potential of Cistaceae species.

The Ericaceae family stood out for the lack of significant relations with any of the seven explanatory variables included in this study, not even with biogeographic region. This could be due to the broad distribution range of this family throughout the Portuguese territory (SPB, 2012–2013). Another explanation could be that the Ericaceae species encountered in this study included both seeders and resprouters, unlike the Leguminosae species (all resprouters) or the Cistaceae species (all seeders). Possibly, separate analysis of the resprouter and seeder species of Ericaceae would have yielded similar results as presented here for all resprouter/seeder species together, shedding further light on variability in vulnerability to disturbance regimes within the same family. Since this family is composed by post-fire seeders and resprouters (Annex 1) (Paula and Pausas, 2008), it may also explain why Ericaceae cover was unrelated with post-fire management operations – resprouters species, like *Arbutus unedo* and *Erica australis*, would be negatively affected by all management operations, but obligate seeders, like *Calluna vulgaris* or *Erica umbellata*, might not be significantly affected by soil tillage. A further step would be to repeat the GLM analyses for individual species (those occurring frequently enough in the data set). Especially a better understanding of management-impacts would seem of interest for the protection of specific taxa and, thereby, for increasing the value of mono-specific and mixed eucalypt and pine plantations, namely by adding to their biological value (Sharma and Henriques, 2005), by increasing their potential for forest conversion into native forests (Moreira et al., 2013), and by diversification of forest products (FSC, 2012).

4.3. Management implications and further research

While this study did not address the effect of management operations on the growth of the main tree species, it showed clearly that management operations had negative impacts on the understory communities of pure and mixed pine and eucalypt plantations. Future research should focus in the analysis of the efficacy of typical management operations for attaining certain management goals. For example, cases of fertilization for eucalypt growth (e.g. Madeira et al., 2011) or harrowing for eliminating competition and increase tree growth (e.g. Carneiro et al., 2008) did not lead to the expected outcome, but have hampered spontaneous vegetation structure and diversity. In other situations, mechanical soil preparation has increased the survival rates and growth of planted tree seedlings (Prévosto et al., 2012), but on the contrary did decrease the diversity of trees (Prévosto et al., 2011), like Moreira et al. (2013) also verified.

Conservationist (biodiversity, resilience, provision of ecosystem services) and productivity (economic income: timber production, pay per services, forest certification) perspectives can co-exist in a sustainable forestry scheme (Bullock et al., 2011; Maes et al., 2012). A possibility is to designate areas exclusively for forest conservation, in the forest matrix (Bengtsson et al., 2000; Fischer et al., 2006), which is moreover, one of the requisites for the attribution of forest certification labels (principle 6 – FSC 2012). As this study suggests, such areas could be the steepest slopes, where (1) species richness is higher, (2) management operations are more expensive and less likely to produce high economic revenue, while (3) being potentially more damaging, namely by leading to high soil erosion rates (see Martins et al., 2013).

5. Conclusions

The main conclusions of this study into the woody understory vegetation of Maritime Pine and eucalypt in northern and central Portugal that had burnt five to seven years earlier by wildfires were as follows:

1. Shrub species richness could be explained to a significant extent by biogeographic region and slope angle but not by post-fire management operations (soil tillage, tree logging, shrub clearance) or by forest type. The – unexpected – increase in shrub species richness with increasing slope steepness was possibly due to less intense land use on steeper slopes, especially in the period before the last wildfires, than to differences in ecological conditions *per se*.
2. Total shrub cover was significantly related to biogeographic region and, at the same time, notably hampered by management operations after the last fire.
3. The covers of seeders and resprouters contrasted sharply in their response to post-fire management operations in that resprouter cover was significantly affected by all three types of operations, while seeder cover was significantly affected by tree harvesting as well as shrub clearance but not by soil tillage.
4. The negative impacts of post-fire management operations on shrub cover typically had a strong region-specific component, with the impacts being more pronounced in the less productive biogeographic regions with their more marginal ecological conditions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.08.030>.

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