Original article

Resistance to wildfire and early regeneration in natural broadleaved forest and pine plantation

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ABSTRACT

The response of an ecosystem to disturbance reflects its stability, which is determined by two components: resistance and resilience. We addressed both components in a study of early post-fire response of natural broadleaved forest (*Quercus robur*, *Ilex aquifolium*) and pine plantation (*Pinus pinaster*, *Pinus sylvestris*) to a wildfire that burned over 6000 ha in NW Portugal. Fire resistance was assessed from fire severity, tree mortality and sapling persistence. Understory fire resistance was similar between forests: fire severity at the surface level was moderate to low, and sapling persistence was low. At the canopy level, fire severity was generally low in broadleaved forest but heterogeneous in pine forest, and mean tree mortality was significantly higher in pine forest. Forest resilience was assessed by the comparison of the understory composition, species diversity and seedling abundance in unburned and burned plots in each forest type. Unburned broadleaved communities were dominated by perennial herbs (e.g., *Arrhenatherum elatius*) and woody species (e.g., *Hedera hibernica*, *Erica arborea*), all able to regenerate vegetatively. Unburned pine communities presented a higher abundance of shrubs, and most dominant species relied on post-fire seeding, with some species also being able to regenerate vegetatively (e.g., *Ulex minor*, *Daboecia cantabrica*). There were no differences in diversity measures in broadleaved forest, but burned communities in pine forest shared less species and were less rich and diverse than unburned communities. Seedling abundance was similar in burned and unburned plots in both forests. The slower reestablishment of understory pine communities is probably explained by the slower recovery rate of dominant species. These findings are ecologically relevant: the higher resistance and resilience of native broadleaved forest implies a higher stability in the maintenance of forest processes and the delivery of ecosystem services.

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1. Introduction

Fire is one of the major disturbances affecting ecosystems. Fire can impact an ecosystem directly, by damaging plant tissues or by causing considerable changes to the habitat, such as the destruction of vegetation strata or alteration of microclimatic patterns, rendering it unsuitable for fauna. Indirect impacts from fire may include soil erosion, deregulation of local climate or changes in the composition of natural communities (Neary et al., 1999; Brown and Smith, 2000; Eugenio and Lloret, 2004; De Luis et al., 2006).

The ability of an ecosystem to return to the pre-disturbance condition, that is, ecosystem's stability, is mainly determined by two components: resistance and resilience (Halpern, 1988; McCann, 2000). Resistance can be defined as the degree to which an ecosystem variable (e.g., canopy cover, vegetation composition or species richness) remains unchanged in the face of disturbance, and resilience measures the rate of recovery to the pre-disturbance value (Halpern, 1988; Lavorel, 1999; McCann, 2000; Diaz-Delgado et al., 2002). Regarding fire disturbance, forest resistance to fire is particularly associated with the susceptibility of dominant trees and forest structure to fire (Brown et al., 2004; González et al., 2006; Fernandes, 2009). Forest resilience on the other hand is associated with the traits of species in the plant community, namely their ability to recolonize the post-fire environment through seed germination or bud sprouting (Pausas and Vallejo, 1999). The time required for post-fire reestablishment and the patterns of post-fire succession vary among forest types, being much dependent on the composition of communities prior to fire, and on the fire regime, as very severe or frequent fires may delay or impede recovery (Lavorel, 1999; Brown and Smith, 2000; Domínguez et al., 2002; Gracia et al., 2002).

While forests may eventually recover to the pre-disturbance state, changes in ecosystem processes, immediately after fire and during the interval of recovery, could affect the delivery of forest services (e.g., soil protection, carbon sequestration, stabilization of

hydrological regime). For example, the loss of litter and ground vegetation may contribute for a decrease in rainfall infiltration to groundwater systems and an increase in surface runoff (Neary et al., 2009). In turn, this may affect the supply and quality of clean water and also contribute for soil erosion due to runoff.

Forests response to fire has been assessed through different approaches in various studies, from empirical observations (Rigolot, 2004; Ordóñez et al., 2005; Moreira et al., 2009; Fernandes et al., 2010; Catry et al., 2010) to large-scale analyses, using published data and GIS tools (González et al., 2006; Fernandes et al., 2008; Fernandes, 2009; Silva et al., 2009). Approaches to the study of post-fire regeneration include analyses of tree recovery (Gracia et al., 2002; Broncano et al., 2005; Calvo et al., 2008; Moreira et al., 2009) and of understory vegetation reestablishment (Domínguez et al., 2002; Calvo et al., 2003; Ladd et al., 2005; Buhk et al., 2006; Baeza et al., 2007). All these studies provide important, but nevertheless partial approaches to the understanding of forests response to fire and the ecological effects of fire disturbance, as most focus either on the resistance or on the resilience of forest systems, or are restricted to a single forest type. Moreover, most empirical data on forest resistance to fire were collected in the context of prescribed fires (Rigolot, 2004; Fernandes et al., 2008).

Here we analyze a case study on the response of natural broadleaved forest and pine plantation to a summer wildfire, at an early stage of post-fire recovery. This study was conducted in the first growing season after a single fire event that burned a large area in the Peneda-Gerês National Park (NW Portugal). The area affected was a mosaic of natural broadleaved forest, planted forest and shrublands. This created a singular opportunity to compare the response of natural broadleaved forest and pine plantation to wildfire. We hypothesize that natural broadleaved forest will present higher stability following fire disturbance than pine plantation, due to differences in forests characteristics. In particular we expect differences in resistance to result from differences in the vulnerability of dominant trees and forest structure, and differences in resilience to be associated with species strategies to recolonize the burned environment and with differences in fire resistance.

2. Methods

2.1. Study area

This study was conducted in the Soajo mountain range (max. alt. 1416 m) in the Peneda-Gerês National Park (41° N 8° W), NW Portugal. The climate in the region is temperate submediterranean (Rivas-Martínez et al., 2002; Honrado, 2003). Annual precipitation ranges from 1500 mm in lower regions up to 2800 mm in mountainous areas, and mean temperatures range from 4 °C to 9 °C in January and from 15 °C to 21 °C in July (Honrado, 2003).

In August 2006, a fire burned over 6000 ha in the region, of which more than 4000 ha within the National Park. The fire lasted for over a week producing a mixed-severity mosaic. During this period maximum daily temperatures remained high, >30 °C, and mean relative humidity low, <50%, and precipitation only occurred in the last day when the study area had already burned (climate data available at http://snirh.pt/). It should also be noted that summer periods between 2003 and 2006 were the most severe of the last decade (2000–2009) in terms of fire weather risk (AFN, 2010), and that the summer of 2006 took place after a long period of drought that started in the end of 2004 and lasted until the spring of 2006 (INM, 2009).

Two major areas were affected during the fire: an important natural area, Ramiscal, and an area of planted forest, Mezio (Fig. 1). The dominant trees in Ramiscal were Quercus robur and Ilex aquifolium. Ramiscal is a strict nature reserve due to its high natural value, which results from its important floristic diversity, including some rare remnants of climax communities and unique examples of ancient oaks and hollies (PNPG, 1995; Torres et al., 2001). Q. robur and I. aquifolium are fire resprouters, that is, these species are able to regenerate after fire from vegetative shoots; seed germination also occurs but its importance for species reestablishment after fire is minor (Calvo et al., 2003; Paula and Pausas, 2008; Paula et al., 2009).

The dominant trees in Mezio were Pinus pinaster, Pinus sylvestris, but also Betula celtiberica (Sequeira, 1995). Pine stands were in average 50 years old when the fire occurred (Sequeira, 1995). P. pinaster and P. sylvestris are obligate seeders, that is, these species are not able to regenerate vegetatively but produce seed banks and rely on germination to recolonize post-fire environments. P. pinaster is able to retain seeds in the canopy, while P. sylvestris produces soil seed banks. Due to this difference, seeds of P. sylvestris are more vulnerable to fire (Rodrigo et al., 2004; Fernandes and Rigolot, 2007).
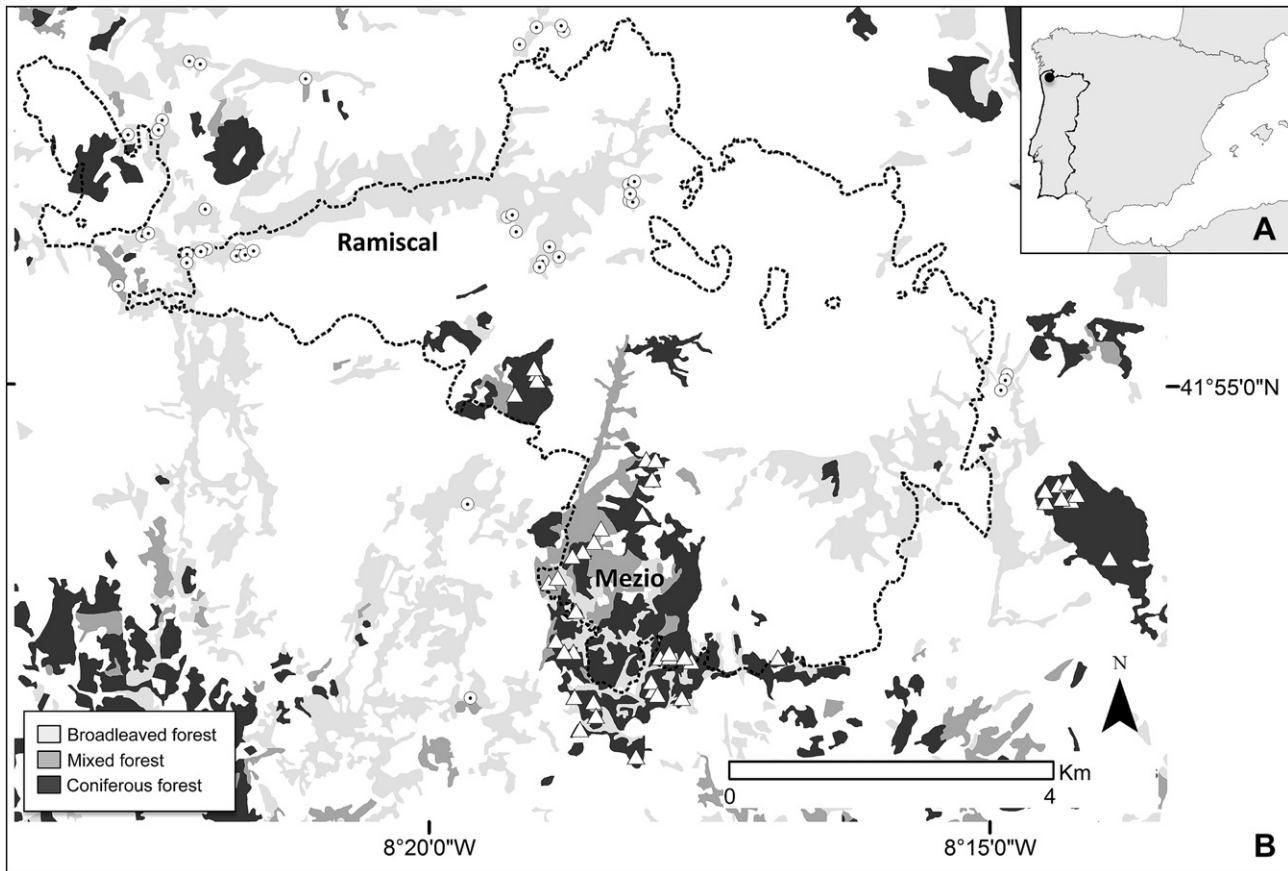
2.2. Sampling methods

We sampled 80 belt transects (50 m × 10 m): unburned broadleaved forest ($n = 20$), burned broadleaved forest ($n = 20$), unburned pine forest ($n = 20$), and burned pine forest ($n = 20$) (Fig. 1, Table A1 in Supplementary material). Broadleaved belt transects were dominated by oak, Q. robur, and holly, I. aquifolium, and pine belt transects by P. pinaster and P. sylvestris. The location of belt transects was determined prior to field sampling using land cover maps and orthophotomaps in ArcGIS 9.0 software. Belt transects in burned forest were arranged to cover as much as possible the burned area (given forest patches distribution and accessibility constraints) and unburned belt transects were located in the proximity of the burned area. Data were collected during the first growing season in April and May 2007.

We surveyed all pole-sized and larger trees (height ≥ 1.3 m (breast height) and DBH (diameter at breast height) ≥ 10 cm) and live saplings (height ≥ 1.3 m and DBH < 10 cm) along each transect (500 m²). We collected data on tree species, height, DBH and identified dead trees (trees without any green foliage or buds). Live saplings were counted along each belt transect. Frangula alnus and Pyrus cordata were surveyed as trees whenever they presented tree morphology. Young tree seedlings (height <0.50 m) were counted in five squares of 4 m² (2 m × 2 m) located in the corners and centre of one 100 m² plot (10 m × 10 m) placed at the centre of each belt transect. Cover percentage of understory vascular plant species (excluding trees) was determined in five squares of 1 m² (1 m × 1 m), each located within a 4 m² square, using the Braun−Blanquet's cover scale (Kent and Coker, 1994): + (<1%); 1 (1−5%); 2 (6−25%); 3 (26−50%); 4 (51−75%), 5 (76−100%). Species taxonomy follows Franco (1984), Castroviejo (1986−2009), and Franco and Afonso (1994, 1998). Data on species traits follows Paula and Pausas (2008) and Paula et al. (2009). Fire severity at surface and canopy levels in each belt transect was evaluated on-site through a qualitative scale of fire damage (Turner et al., 1999; USDI, 2001) (Table 1).

2.3. Data analysis

We assessed fire resistance, through the analysis of data on fire severity, tree mortality (percentage of dead trees per belt transect) and sapling persistence (number of live saplings per belt transect). We used the generalized Fisher's exact test to assess the relationship between fire severity classes at surface and canopy levels and forest type (note that apart from these analysis, broadleaved and pine forests were always tested separately), using an algorithm developed for contingency tables larger than 2 × 2 (Mehta and Patel, 1983, 1986) available in the R statistical software system (www.cran.r-project.org).

Fig. 1. (A) Study area location in NW Portugal (black circle). (B) Forest cover in the study area and distribution of belt transects. Belt transects in broadleaved forest are represented by circles and belt transects in pine forest by triangles, the dashed line limits the burned area. Unburned belt transects are located outside the burned area. Broadleaved forest patches are either dominated by a single species or by more than one broadleaved species. Coniferous forest patches are either dominated by a single species or by more than one coniferous species. Mixed forest patches are composed by broadleaved and coniferous species. Belt transects in broadleaved forest were always dominated by *Quercus robur* or *Ilex aquifolium*, belt transects in pine forest were always dominated by *Pinus* spp.

We performed Spearman's rank correlation tests to investigate the potential association between fire severity and three environmental variables: slope, aspect, and elevation. Aspect is a circular variable and was transformed in a measure of northness = cosine (aspect) (Blake and Schuette, 2000). We compared tree mortality and sapling persistence between burned and unburned belt transects using the Welch test for two samples, which is an alternative to the *t*-test recommended when homocedasticity is not verified (Grissom, 2000; Quinn and Keough, 2002).

The resilience of forest communities was assessed using three different approaches. First, we determined the number of species shared between burned and unburned communities in each forest type. Second, we compared diversity between burned and unburned plots using three diversity measures: plant species richness (S), the Shannon-Wiener diversity index ($H = -\sum p_i \ln p_i$) and evenness ($H/\ln(S)$). For this analysis percentage cover classes were transformed to midpoint values (+ (0.1%); 1 (2.5%); 2 (15%); 3 (37.5%); 4 (62.5%); 5 (87.5%)), and diversity values were compared using two-tailed *t*-tests. Third, mean values of seedling abundance per plot were compared using a two-tailed *t*-test.

The Shannon–Wiener index was calculated using the EstimateS software (Colwell, 2005). Statistical analyses were performed using the R statistical software system (www.cran.r-project.org).

Table 1
Qualitative scale of fire severity at the surface level and the canopy level.

Fire severity	Substrate condition	Canopy condition
Unburned	Not burned	Not burned
Scorched	Litter partially scorched. Duff scarcely affected.	Tree canopy retains green foliage. Some leaves and small branches scorched, leaves still attached to supporting twigs.
Low severity	Litter charred to partially consumed. Duff only charred in the upper layer. Woody debris is partially burned and logs are scorched but not charred.	Some leaves and twigs consumed. Larger branches are undamaged.
Moderate severity	Litter mostly to entirely consumed. Duff deeply charred, but underlying mineral soil is not visibly altered. Woody debris is mostly consumed and logs are deeply charred.	Partial mortality at the canopy level. Leaves and small branches consumed, larger branches persist.
High severity	Litter and duff completely consumed. Mineral soil visibly altered, often reddish. Sound logs are deeply charred.	Total mortality at the canopy level. Some larger branches and trunk may persist but severely burned.

Table 2

Percentage of burned belt transects in each class of fire severity at the surface level and at the canopy level. Fire severity was independent of forest type at the surface level but not at the canopy level (surface level, $p > 0.05$; canopy level, $p = 0.03$; absolute frequencies were used in Fisher's exact tests). S — scorched, L — low severity, M — moderate severity, H — high severity; see Table 1 for details on classes of fire severity.

Fire severity class	S	L	M	H
Surface				
Broadleaved ($n = 20$)	10%	55%	35%	0%
Pine ($n = 20$)	0%	55%	45%	0%
Canopy				
Broadleaved ($n = 20$)	25%	60%	15%	0%
Pine ($n = 20$)	35%	20%	25%	20%

3. Results

All belt transects presented a closed canopy (>30% cover) before fire, the exceptions were two belt transects in broadleaved forest that presented an open structure (one was lightly burned and the other moderately burned). The mean canopy height varied between 6 m and 10 m in broadleaved belt transects and between 8 m and 14 m in pine belt transects. Mean DBH of trees was 31.5 ± 0.74 cm in broadleaved belt transects and 24.5 ± 0.20 cm in pine belt transects, and mean tree density was 28 ± 2.0 ha^{-1} in broadleaved forest and 79.6 ± 6.2 ha^{-1} in pine forest.
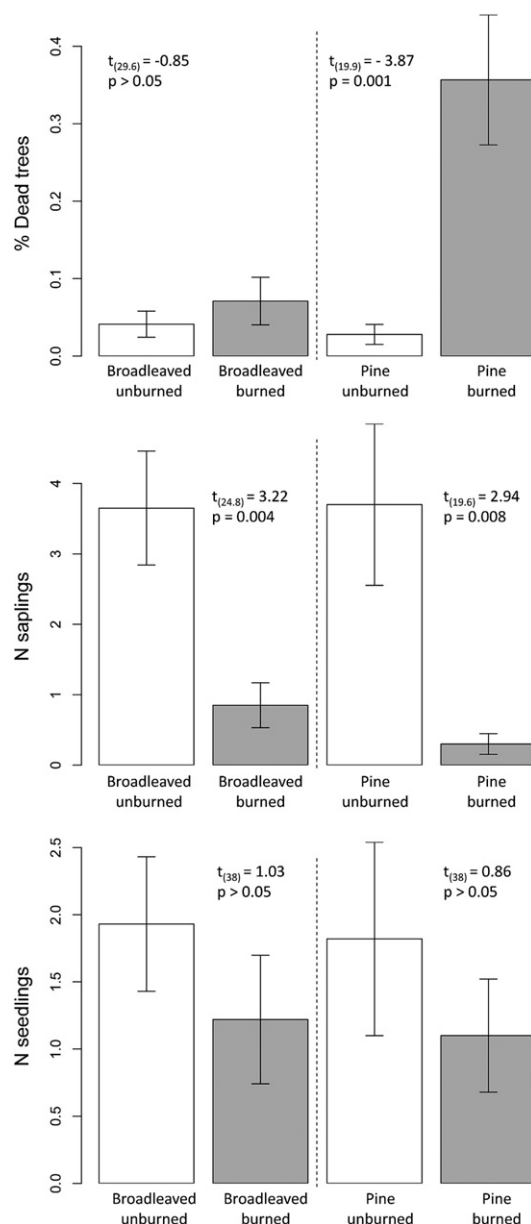
3.1. Fire resistance

There were no differences in fire severity at the surface level between forest types. In broadleaved forest the canopy layer was less damaged by fire than in pine forest, fire severity was low in most belt transects and none presented signs of heavy burning (Table 2, Table A1 in Supplementary material). Fire severity at both strata was not related ($p > 0.05$) with any tested environmental variable (slope, northness, and elevation) in burned broadleaved forest but was positively related with slope (surface level: $\rho = 0.6$, $p = 0.005$; canopy level: $\rho = 0.67$, $p = 0.001$) in burned pine belt transects.

No differences in the percentage of dead trees were found between burned and unburned belt transects in broadleaved forest (Fig. 2). Mortality was zero in thirteen broadleaved burned belt transects and reached a maximum of 44% in two belt transects. Tree mortality was significantly higher in burned pine belt transects when compared to unburned belt transects (Fig. 2). Total mortality (100%) at the canopy level was recorded in four burned pine belt transects and none presented zero mortality. Live sapling abundance was significantly lower in burned belt transects than in unburned belt transects in both forest types (Fig. 2).

3.2. Composition of understory communities

We recorded a total of 54 and 68 plant taxa in unburned and in burned plots respectively in broadleaved forest, and a total of 31 taxa in both unburned and burned plots in pine forest (Table A2 in Supplementary material). Some plants could not be identified at the species level, but we could ascertain that they corresponded to different taxonomic units. Therefore they will be referred as species hereafter. Understory communities in unburned plots in broadleaved forest were dominated by perennial herbs (e.g., *Arrhenatherum elatius*, *Asphodelus ramosus*) and woody species (e.g., *Hedera hibernica*, *Erica arborea*), all capable of vegetative regeneration (Table 3). Woody species, namely shrubs, were more represented in unburned plots in pine forest, than in broadleaved forest. Most dominant species in unburned pine forest relied on post-fire seeding (i.e., the germination of seeds is stimulated during fire or by

Fig. 2. Tree mortality (% dead trees per belt transect), number of live saplings (500 m^2) and number of seedlings (4 m^2) in unburned and burned plots. Mean values and standard errors are indicated for each group. Significant results with $p < 0.05$, $n = 20$ for all forest groups.

post-fire environmental conditions) to recolonize burned environments and some were also capable of vegetative regeneration (e.g., *Ulex minor*, *A. elatius* and *Daboecia cantabrica*). Note that all species in Table 3 can regenerate from seed, but only some present a post-fire seeding strategy. Two perennial herbs, false oat-grass, *A. elatius*, and bracken, *Pteridium aquilinum*, dominated burned plots in both forest types. However, in contrast with pine plots, which were deprived of other dominant species (i.e., mean percentage cover ≥ 1%), broadleaved plots were dominated by other species, mostly perennial herbs with the ability to regenerate vegetatively (e.g., *Anemone trifolia*, *Scilla monophyllus*). The similarity in the floristic composition of unburned and burned plots was higher in broadleaved forests: 42 of the 54 species (78%) found in unburned plots were also found in burned plots; in pine forest, 15 of the 31 species (48%) found in unburned plots were also found in burned plots.

Table 3

Dominant species (mean percentage cover ≥1%) in understory communities with mean percentage cover and standard error, life form (LF), biological traits (BT), vegetative regeneration ability (Veg.Reg.) and post-fire seeding (Seeder). Life forms: annual forb (Af), perennial graminoid (Pg), perennial forb (Pf), geophyte (G), liana (L), low shrub (lS), shrub (S), large shrub (LS), tree (T). Biological traits: woody species (W), perennial herbs (P), annual herbs (A). Vegetative regeneration ability and post-fire seeding: yes (+), no (−), published data not conclusive or data not found in literature (?).

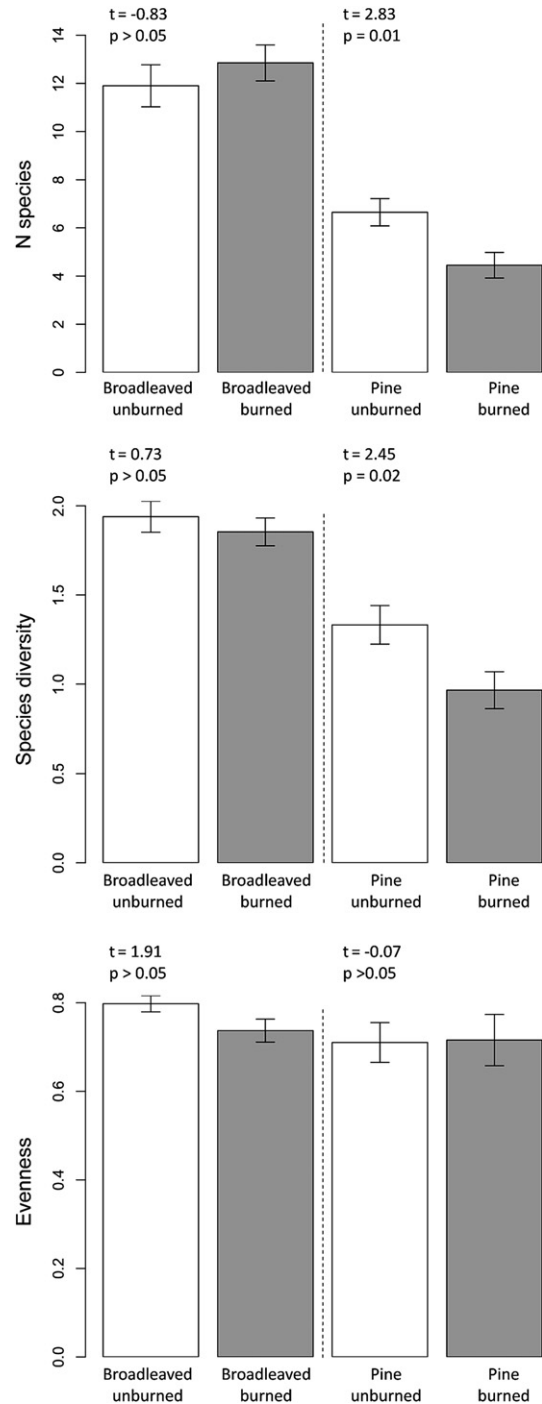|	Mean	SE	LF	BT	Veg.Reg.	Seeder[a]
Broadleaved forest − unburned plots						
Arrhenatherum elatius	4.5	0.7	Pg	P	+	+
Hedera hibernica	3.6	1.6	L	W	+	−
Erica arborea	3.3	1.6	S	W	+	?
Asphodelus ramosus	2.1	1.0	G	P	+	−
Rubus spp.	1.9	0.7	L	W	+	−
Agrostis curtisii	1.6	0.7	Pg	P	+	+
Pteridium aquilinum	1.5	0.2	G	P	+	−
Pyrus cordata	1.3	0.6	LS	W	+	−
Frangula alnus	1.2	0.4	LS	W	+	−
Ranunculus bolbosus sl.	1.2	0.6	Pf	P	+	?
Broadleaved forest − burned plots						
A. elatius	8.6	2.1	Pg	P	+	+
P. aquilinum	6.4	2.8	G	P	+	−
Rubus spp.	3.4	1.7	L	W	+	−
Ceratocapnos claviculata	3.0	1.4	Af	A	−	+
Anemone trifolia	2.0	0.5	G	P	+	?
Scilla monophyllos	1.7	0.4	G	P	+	−
Anthoxanthum odoratum	1.6	0.7	Pg	P	+	?
A. curtisii	1.6	0.7	Pg	P	+	+
E. arborea	1.5	0.9	S	W	+	?
Saxifraga spathularis	1.5	0.9	Pf	P	+	?
Pine forest − unburned plots						
Ulex minor	4.8	1.6	S	W	+	+
A. elatius	4.2	1.6	Pg	P	+	+
A. curtisii	3.8	1.1	Pg	P	+	+
E. arborea	2.2	1.0	S	W	+	?
Erica umbelata	1.6	0.8	lS	W	−	+
P. aquilinum	1.6	0.4	G	P	+	−
Pinus pinaster	1.3	0.4	T	W	−	+
Calluna vulgaris	1.1	0.8	lS	W	?	+
Daboecia cantabrica	1.0	1.0	lS	W	+	+
Pine forest − burned plots						
A. elatius	6.4	2.5	Pg	P	+	+
P. aquilinum	1.2	0.4	G	P	+	−

[a] Seeder data for the following species were based on available data for similar species (in brackets): *P. cordata* (*Pyrus spinosa*), *C. claviculata* (*Fumaria densiflora*, *Fumaria macrocarpa*, *Fumaria officinalis*), *Scilla monophyllus* (*Scilla automnalis*).

Diversity measures in burned and unburned plots in broadleaved forest were not significantly different. In the case of pine forest, burned plots were less rich and diverse than unburned plots (Fig. 3). Seedling abundance was not significantly different in burned and in unburned plots in both forests (p > 0.05) (Fig. 2).

4. Discussion

4.1. Fire resistance

Fire was equally severe at the surface level in the two types of forest as suggested by the lack of differences in the frequency of classes of fire severity and the considerable sapling mortality (inferred from sapling persistence). Moisture of extinction of dead fuels in broadleaved deciduous forest is lower than in pine forest (Fernandes, 2009), therefore we would expect to find lower fire severity at the surface level in broadleaved forest. However, due to the dry weather conditions that preceded this fire, dead fuels in both types of forest probably had low moisture content. The effect of slope in fire severity was detected in pine forest but not in broadleaved forest. In pine forest, half of the burned belt transects were located in gentle slopes (slope ≤20%). In broadleaved forest, only two belt transects were located in gentle slopes and more than

Fig. 3. Species richness, Shannon−Wiener diversity and evenness in understory communities. Mean values and standard errors are indicated for each group. Significant results with $p < 0.05$, $n = 20$ for all forest groups, df = 38.

half were located in steep slopes (slope ≥40%). Fire spread down slope across much of the surveyed area, both in broadleaved and pine forest. Under these conditions (i.e., fire spreading down slope) the effect of slope angle on fire intensity and consequently on fire severity is less detectable than if fire spreads up slope (Rothermel, 1983). Still, the effect of slope was detected in pine forest but not in broadleaved forest, which may be due to a larger variation in the steepness of slopes in the surveyed pine forest.

At the canopy level, the lower resistance to fire of pine stands might be explained by the characteristics of dead and live fuels, and

by forest structure. The large amount and piled arrangement of fine fuels, fuels chemical composition (e.g., resins), and low water content are all characteristics that potentiate fire intensity. In addition, fire progression into the canopy is further potentiated by the existence of ladder fuels (e.g., lower dead branches, suspended needles) that promote the vertical progression of fire (Bond and van Wilgen, 1996; Fernandes and Rigolot, 2007; Ormeño et al., 2009; Fernandes, 2009). Canopy structure should also be considered since it affects fire progression through its effect on local variables, such as wind speed and dead fuels moisture (Fernandes, 2009). In our study, pine belt transects presented a structure more dense than broadleaved belt transects, as revealed by values of mean tree density. Denser forests are less exposed to wind, tend to maintain lower temperatures due to shade, and higher relative humidity due to reduced evaporation (Whelan, 1995), all factors that contribute to decrease fire intensity and fire spread. However, when ladder fuels exist, as was the case in our belt transects, the risk of fire crowning is also higher in dense forests (Fernandes, 2009; Fernandes et al., 2010). Moreover, in comparison to broadleaved forest, fuels in pine forest tend to have lower moisture content, which contributes to higher heat release rates (Bond and Midgley, 2001; Castro et al., 2001; Dimitrakopoulos and Papaioannou, 2001; Fernandes, 2009), and a higher load of small fuels (e.g., pine needles, dried grasses) that promote fire spread.

Differences in fire resistance of surface and canopy strata within broadleaved forest could be due to differences in fire intensity along the vertical gradient between ground and canopy. During fire, temperature tends to be higher at the surface level and to decrease with height (Whelan, 1995). In addition, under dry weather conditions, dead fuels at the surface level probably had lower moisture content than live foliage in the canopy. Finally, larger trees tend to be more resistant than saplings to fire damage due to a thicker bark (Fernandes and Rigolot, 2007; Fernandes et al., 2008).

Overall, differences in forest response, suggest a higher resistance of natural broadleaved forest to fire. These results are in agreement with other studies that also report a higher resistance of broadleaved species in relation to coniferous species (Wang, 2002; Catry et al., 2010; Fernandes et al., 2010). Besides differences in the characteristics of broadleaved and pine forests, variation in local environmental conditions and in weather conditions during fire could have also played a role in forest response to fire. While weather conditions were somehow uniform during fire, as described in methods, our sampling did not fully control the effect of environmental variables, because it was restricted by the conditions found in the study area. However, exploratory analyses only revealed an effect of slope in pine forest, suggesting that variation of local environmental conditions was probably less important than forest characteristics to explain forest responses to fire.

4.2. Community reestablishment

Broadleaved communities were dominated by perennial herbs, such as *A. elatius*, *A. ramosus*, and *P. aquilinum*, which are able to regenerate from stem bases or storage organs located belowground, and by woody species with the ability to resprout from vegetative buds, such as *H. hibernica*, *E. arborea* and *Rubus* spp. (Trabaud, 1982; Domínguez et al., 2002; Calvo et al., 2003). The observed increase in the abundance of perennial and annual herbs in burned plots has been described as an opportunistic and transient process promoted by a reduced competitive pressure from woody species, which produce shade and compete for nutrients, and by the sudden availability of nutrients resultant from the incineration of organic matter (Trabaud, 1982; Naveh, 1994; Calvo et al., 2002, 2003). As plant cover is re-established the species that first benefited from post-fire conditions will tend to regress and species richness is expected to return to pre-fire values (Trabaud, 1982; Guo, 2001;

Keeley et al., 2005). The great similarity between communities in burned and unburned plots in broadleaved forest is consistent with the process of autosuccession (i.e., community reestablishment through resprouting of surviving plants or germination of surviving seeds) described in Mediterranean ecosystems (Hanes, 1971; Buhk et al., 2006; Núñez et al., 2008).

Pine understory communities were in a less advanced stage of recovery, despite the fact that unburned communities were dominated by species, such as *U. minor*, which presented both a post-fire seeding strategy and the ability to regenerate vegetatively, or by species with at least one of these traits. The lower resilience observed in pine forests may result from two factors, the slower recovery rate of dominant plants in pine plots, and the higher intensities during fire, which may have caused the destruction of regenerative tissues and reduced seed viability. With regard to the first factor, woody species require more time than perennial herbs to develop new tissues, and seed germination also requires more time to start than vegetative regeneration (Domínguez et al., 2002; Calvo et al., 2002, 2003). Moreover, the soil seed bank in a pine community in this region has been found to be poor in herb species (Calvo et al., 2003), which may also explain the low diversity values. High temperatures may also have had an impact, as suggested by seedling germination patterns in pine forest (see next paragraph).

Seedling abundance did not differ between burned and unburned belt transects in both types of forest. We did not expect to find differences in seedling abundance in broadleaved forest because *Q. robur* and *I. aquifolium* are resprouter species. But we expected to find more seedlings in burned pine belt transects, because *P. pinaster* and *P. sylvestris* rely on seeds to recolonize post-fire environments, and have been reported to start recruitment immediately after fire (Valbuena et al., 2001; Fernandes et al., 2005; Calvo et al., 2008). The reason for the low abundance of seedlings was probably a reduced stock of viable seeds, particularly in *P. sylvestris* plots (60% of burned plots). *P. sylvestris*, contrary to *P. pinaster*, does not retain seeds in the canopy, the seeds are released after maturation and germinate during the spring (Reyes and Casal, 1995; Núñez et al., 2003; Tapias et al., 2004). If a summer fire occurs, it will kill the seedlings and reduce the viability of the remaining seeds (Núñez et al., 2008).

Overall, plots in broadleaved forest were in a more advanced stage of recovery than plots in pine forest, suggesting a higher resilience of broadleaved forest at early stages of post-fire recovery. Recovery capacity after fire depends both on fire severity and on the regenerative ability of species present in plant communities. Because communities in pine forest experienced higher fire intensities, they were more altered after fire and had to invest more in post-fire recovery.

The higher resilience of understory communities in broadleaved forests is in agreement with other studies, Domínguez et al. (2002) and Calvo et al. (2003) compared post-fire regeneration in pine and oak forests in the first years after fire and reported a faster post-fire regeneration of oak communities as well. In our study it was not possible to compare forest recovery in the following years, because pine plantations were logged just after field sampling. Nevertheless, a later visit to the study area about two years after the fire, in November 2008, confirmed the ongoing regeneration of broadleaved forest.

4.3. Implications for conservation

Governments' reaction to more frequent and severe fires has mainly consisted in fire suppression and preventive silviculture. Although these measures are important, they present two major weaknesses, first they are costly (over € 475 million were spent between 2000 and 2004 in Portugal (DGRF, 2007)) and second, and most important from an ecological perspective, they do not address

a critical issue, inadequate forest planning and management. A way of approaching this issue is to promote forest management policies that aim at ecosystem stability.

Here we have presented a case study where we compared the response to wildfire of natural broadleaved forest and pine plantation. We discussed differences in response patterns at early stages of post-fire recovery in the light of differences in fire resistance and resilience. The lower susceptibility of natural broadleaved forests to fire disturbance is ecologically relevant because it implies a higher stability in the maintenance of ecosystem processes and forest services. Analyses of recent trends and scenarios of land use change in Europe agree towards an increase of forest cover in the next decades through natural regeneration, mostly due to farmland abandonment (Moreira et al., 2001; Lloret et al., 2002; Poyatos et al., 2009; Verburg and Overmars, 2009). The expansion of naturally regenerated forest may contribute to restore biodiversity and the condition of many ecosystem services, such as carbon sequestration, soil formation, and regulation of the hydrological cycle (Rey Benayas et al., 2007; Chazdon, 2008). However it may also contribute to increase fire risk due to fire-prone shrub encroachment during the first stages of secondary succession (Rey Benayas et al., 2007). Therefore, management interventions to accelerate broadleaved forest regeneration and reduce fire hazard should be regarded as priority measures in fire-prone regions. In addition, new plantations should also include a higher representation of broadleaved species as a way of increasing the resistance of forests to fire (Pausas et al., 2004).

Acknowledgments

Appendix. Supporting material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.actao.2010.09.008.

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