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Fire effects on the seed bank of three Mediterranean shrubs: implications for fire management

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Abstract To evaluate fire effects on the soil seed bank of a Mediterranean heathland, soil and litter samples were collected under the three dominant shrub species (*Erica australis* L., *Erica umbellata Loefl.* ex L., and *Pterospartum tridentatum* (L.) Willk) before and after an experimental fire. Target plants were selected near to 12 points regularly spaced in a grid layout in a 50 × 50 m plot. Soil heating by the fire was estimated using thermocouples installed at 1.5 cm depth. The soil seed bank was dominated by *E. australis* and *E. umbellata*. *Erica australis* having statistically significantly higher germination densities under their conspecific shrubs. *Pterospartum tridentatum* was extremely underrepresented in the viable seed bank, despite being the dominant species in the vegetation. Fire did not produce significant differences in the overall germination, but post-fire germination density of *E. australis* was related to maximum temperatures recorded at 1.5 cm depth. Special focus was given to the seed bank of the obligate seeder *E. umbellata* and its possible implications in population regeneration after recurrent fires. There was, however, no evidence that current fire frequency would imply a risk of population decline, since *E. umbellata* seed bank is abundant despite the scarcity of adult shrubs.

Keywords *Erica umbellata* · *Erica australis* · *Pterospartum tridentatum* · Heathland · Soil seed bank · Experimental fire · Temperature

Introduction

Heathlands currently occupy extensive areas of the Mediterranean region, covering a total surface of over 110.000 km^2 (Calvo et al. 2012). These formations are typically affected by fires and, in Portugal, represent the most fire-prone land-cover type (Silva et al. 2009). While heathlands are treated as important ecosystems for nature conservation in Northern Europe, in the Mediterranean they are generally considered marginal

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lands with low productivity and economic value, often representing a degradation state of the climax vegetation (Calvo et al. 2012). Nonetheless, it is increasingly recognized that Mediterranean heathlands provide key ecosystem services, especially in relation to traditional products from grazing by sheep and goats and bee keeping.

Mediterranean heathlands are mainly composed of Ericaceae (*Erica* and *Calluna* genera) and, to a lesser degree, by Leguminosae and also Cistaceae families. These families are well adapted to fire-prone environments, since they present traits that allow them to cope with repeated fires, persisting after fires at the individual level by resprouting (resprouters) and/or at the population level through an in situ seed bank (seeders) (Paula and Pausas 2008).

The main species addressed in this study—*Pterospartum tridentatum* (L. Willk) (Leguminosae), *Erica australis* (L.), and *Erica umbellata* (Loefl. ex L.) (Ericaceae)—are common species in Portuguese and Spanish heathlands. *P. tridentatum* is a legume with hard-coated seeds (physical dormancy), and its germination is known to be stimulated by fire (Valbuena and Vera 2002; Rivas et al. 2006; Vasques et al. 2012). Erica species have small seeds that have the ability to remain viable for many years in the soil (Thompson and Band 1997; Gimingham 1972). *Erica australis* seeds that may present physiological dormancy, with ability to produce persistent seed banks, are known to be stimulated by fire (Cruz et al. 2003; Vera et al. 2010; Vasques et al. 2012), but can also show decreased germination after fire in the soil seed bank (Valbuena et al. 2001). While both *P. tridentatum* and *E. australis* are also strong post-fire resprouters (Paula and Pausas 2008), *E. umbellata* is an obligate seeder and therefore relies exclusively on the soil seed bank for post-fire regeneration. Persistency of the seed bank is not consensual between different populations (Paula et al. 2009) and although heat has been reported as a poor germination stimulus (Vasques et al. 2012), exposure to smoke showed increased germination percentage (Moreira et al. 2010).

The spatial variability in plant recruitment after fire has been studied in several habitats. For example, the post-fire establishment of *Pinus halepensis* occurs mainly around mature trees, while shrubs and herbs are mostly recruited in gaps and shrub patches (Eshel et al. 2000). A study in a Mediterranean shrubland showed that while soil seed banks of herbs were spatially related to the patterns in the vegetation, the soil seed bank of woody shrubs was not (Torres et al. 2013). However, to date no studies were found that explore fine scale of soil seed banks in relation to the distribution of aboveground shrub species.

Understanding the fine scale relationship between soil seed bank distribution patterns and the shrub species in the vegetation may be valuable for predicting post-fire vegetation composition, specifically in relation to the regeneration of obligate seeders. High recovery of the vegetation due to resprouting of the dominant species can leave little opportunity for seedlings of obligate seeder species like *E. umbellata* to establish, mature, and produce seeds (Rego et al. 1991; Fernández et al. 2013; Fernández and Vega 2014. If seed distribution of obligate seeders is highly associated with the spatial distribution of the mother plants, the risk of local extinction greatly increases with increasing fire recurrence, given that soil seed banks become progressively exhausted (e.g., Ferrandis et al. 1999; Ottewell et al. 2009; Calvo et al. 2012). The understanding of the post-fire vegetation dynamics, particularly in respect to fire-interval, is essential in fire-prone ecosystems like Mediterranean heathlands that are often managed by prescribed fires for decreasing wildfire risk or creating pastures for grazing (Fernandes et al. 2013).

This study intends to analyze how fire (management) may affect the potential for the community to regenerate from the seed bank. The specific objectives are to

1. assess the representativeness of the three main species of the aboveground vegetation in the seed bank sampled under the different shrubs and the implications in terms of the post-fire community regeneration and
2. evaluate the impact of fire on the seed bank of the main species, using several fire severity estimations.

Materials and methods

Study site

The study site was a heathland located in Central Portugal, near Castanheira de Pêra. This habitat can be classified under the Natura 2000 classification heathland type 4030, with co-dominance of *Erica umbellata, Erica australis*, and *Pterospartum tridentatum* (Aguiar and Capelo 2000; ICNF 2013).

The study site comprises a series of plots where experimental fires have been carried out during the last decades. The plot studied here had not been burned for 8 years (Viegas, D. X., pers.comm.). It was approximately 50 × 50 m, with a slope angle of 8 % and NE aspect. By the time of this study, the aerial fuel load of the plot was estimated to be 35 ton ha^{-1} of mainly fine fuel provided by the shrub canopies. *Pterospartum tridentatum* clearly had the highest cover (60–70 %), followed by *Erica australis* (~30 %) and sparse individuals of *Erica umbellata* (<10 %), resulting in a continuous shrub cover (~100 %). The cover of other woody species, like *Halimium* spp. and *Cistus* spp., was not representative in the plot, although they were present in the vicinity (Supplementary Material 1).

Experimental layout and field sampling

In the study plot, 12 sampling points were established in a grid layout, and each of them was equipped with a thermocouple, buried at 1.5 cm depth (EL-USB-TC, Lascar Electronics) (Fig. 1). Within a 1.5 m radius from each thermocouple, one specimen of at least two or, if present, of the three dominant shrub species (*P. tridentatum*, *E. australis*, and *E. umbellata*) was selected. Even though the distance between the selected shrubs was small, the overlap area between their canopies was minimal. As illustrated in Fig. 1, 12 *P. tridentatum*, 10 *E. australis*, and 6 *E. umbellata* specimens were selected, roughly reflecting the relative abundance of the three species.

Before the experimental fire, the selected plants were described in terms of height and canopy diameter.

Samples of the seed bank in the soil and litter were taken from below the canopies of the target shrubs, before and after the experimental fire. To this end, the litter layer and upper 3 cm (Maia et al. 2012; Traba et al. 2004) of the mineral soil were collected separately over a square area of 625 cm^2 (a 25 × 25 cm square). This sampling area was positioned such that one of its corners coincided with the center of the canopy, and was marked with pins at the three other corners to avoid overlap in pre- and post-fire sampling areas.

Immediately after the fire, the ash layer (post-fire "ash" samples were often a mixture of unburnt, scorched, and burnt litter and ashes. Hereafter it will be referred to as "ash") and the upper 3 cm of the mineral soil were also collected separately from an adjacent square area of 625 cm^2.

Fire severity estimations

At each sampling point (Fig. 1), a thermocouple (EL-USB-TC, Lascar Electronics) linked to a data logger was installed at a depth of 1.5 cm in the soil. The samples collected under the two or three target shrubs of each sampling point were assumed to have experienced the same temperatures. For each sampling point, the maximum temperature recorded by the thermocouple during fire was computed. Two of the 12 thermocouples were malfunctioning during the experimental fire.

Furthermore, the diameters of the five thinnest branches of each target specimen were measured at 1 cm below the tip of the branch (see Maia et al. 2012b). Additionally, the volume of litter consumed by the fire was also estimated, as the difference between the volume of litter (pre-fire) and the volume of ashes (post-fire) collected under each of the target plants. The amounts of litter and ashes were computed as l m^{-2} (volume was estimated with a measuring cup).

Seed bank assessment

The composition and density of the seed bank was evaluated by the indirect method (seedling emergence), which was considered to be adequate for the first 5 cm of soil (Price et al. 2010). This method may underestimate seed densities and richness compared with the direct observation (Gross 1990), but the viable portion of the seed bank, which effectively influences the post-fire community, will be able to germinate.

The litter, ash, and soil samples were transported to a greenhouse, where the bigger rocks and wood debris were removed manually before measuring the volumes of the litter and ash samples. Each individual sample was then spread over a 3-cm-thick layer of vegetable substratum in an aluminum tray that had been perforated to allow for water drainage. In addition, 15 trays containing only turf were also placed in the greenhouse, in order to control for possible weed contamination. Five of the 127 trays suffered an accident at the beginning of the experiment.

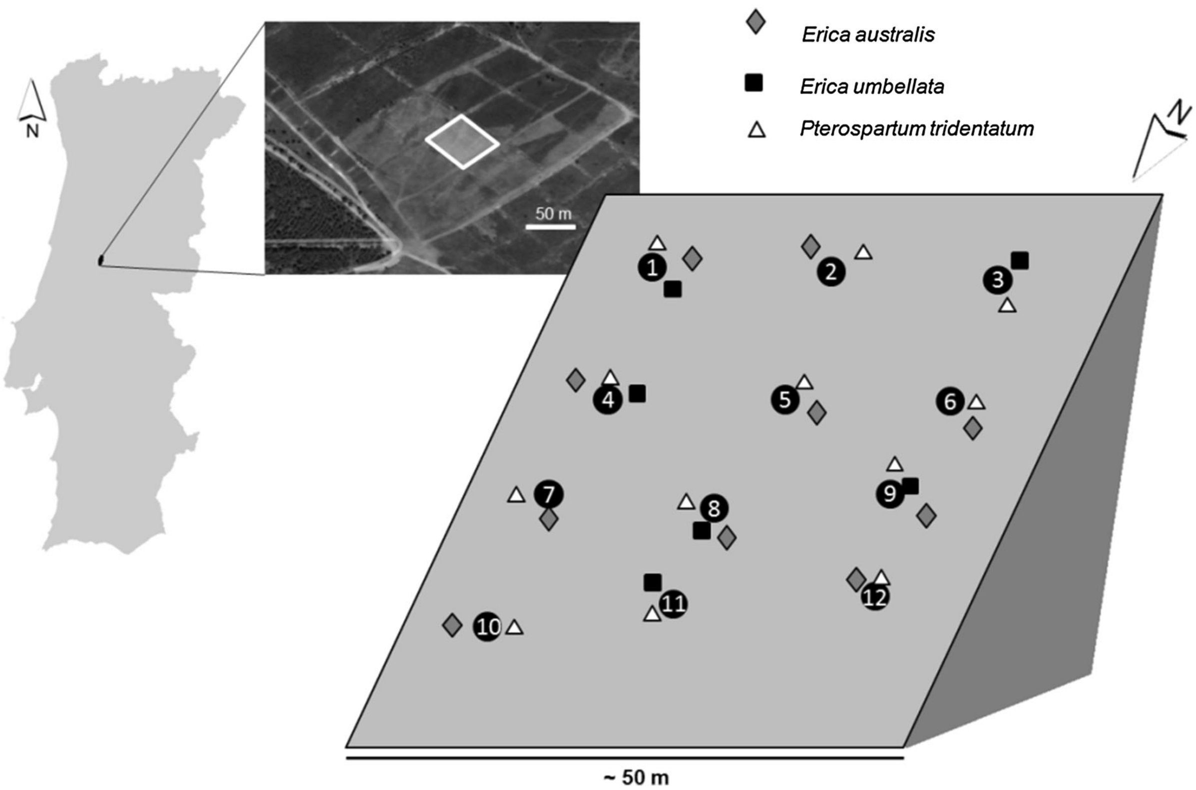

Fig. 1 Location of the study site and plot as well as schematic view of the experimental set-up comprising 12 sampling locations with two or three target plants and equipped with thermocouples

All 122 trays were then placed in a greenhouse on May 29, 2010 for a period of 10 months under ambient temperature and natural photoperiod. The germination trays were watered as needed by means of sprinklers connected to an artesian well.

The seedlings that emerged in each tray were counted at 1- to 2-weekly intervals and were all marked with metal pins to avoid double counts. Seedlings were removed and discarded as soon as they could be identified. Where identification was difficult, seedlings were transplanted to individual pots to allow growth and subsequent identification. During the experiment, the individual trays were also photographed at monthly intervals to have a documented record and, if needed, clarify possible doubts about species identification. In a few cases, species identification of *Erica* spp. seedlings was not possible due to seedling mortality, so those samples could not be included for *E. australis* and *E. umbellata* statistics.

Data analysis

Data analyses were carried out with IBM SPSS version 19. Assumptions for parametric analyses could not be met, even after performing various data transformations.

The comparison of densities of *Erica australis*, *E. umbellata*, and *P. tridentatum* seedlings, between the three sampling locations (EAU, EUM, PTR), was done with the Kruskal–Wallis test. *Post hoc* pairwise comparisons were carried out using the Mann–Whitney U-test in the individual pairs, correcting α by the Holm's sequential Bonferroni method (Holm 1979).

The differences between pre- and post-fire germination densities were analyzed by means of univariate General Linear Models (GLMs) performed on the rank data, using sampling time (pre–post-fire) as a fixed factor and sampling point (1–12) as a random factor. To analyze the differences in the samples collected before and after fire for the different target species

(EAU, EUM, PTR), Mann–Whitney U was used instead.

The Spearman correlation coefficient was used to test the relation between pre-fire and post-fire seedling density and vegetation measurements (shrub height, shrub diameter, litter volume collected under each shrub). The relation between the proportional changes in seedling density after fire and fire severity estimations (maximum temperature recorded, mean twig diameter, and consumed litter volume) was also tested, for the different target species.

The lack of reliable data in 2 of the 12 thermocouples reduced the sample size for the correlations between post-fire germination densities and temperature data. The 12 PTR samples were reduced to 10, the 10 EAU to 7, and the 6 EUM samples were reduced to 4.

Results

Before the experimental fire—seed bank under the three target species, relation with plant size and litter volume

Seed germination from the litter samples revealed a poor relation with the canopy species, for all of the three target species, and was highly variable. *Erica umbellata* was the only species to exhibit much higher seedling density under the same species canopy but without statistically significant differences ($p > 0.1$) (Fig. 2a; Table 5).

The seed bank of the topsoil revealed a clearer association with the canopy species, compared to the seed bank in the litter. This was specifically the case of *Erica australis*, with significantly higher germination density in the samples collected under EAU than in other locations ($p < 0.05$). An analogous pattern, although not statistically significant, was found for *E. umbellata*. *P. tridentatum* seedlings were, as in the litter layer, scarce at all sample locations (Fig. 2b; Table 5).

The size of the shrubs was variable, but the diameter of the canopy always exceeded the sampling area (Table 1). The seed density in the litter was related to the canopy size but the relation was not the same for the three target species (Table 2). The seed bank of *E. umbellata* was significantly related with canopy diameter ($\rho = 0.975$; $p < 0.05$), its density increasing with increasing canopy diameter. By contrast, the density of *E. australis* seedlings appeared to be negatively related with the height of the shrubs before ($\rho = -0.676$; $p < 0.1$). The amount of litter covering the soil also varied between and within species (Table 1), but seedling densities were not related with litter volume. The density of seedlings in the soil samples was in no case related with plant size (Table 2).

Experimental fire—fire severity estimations

The temperatures recorded during the experimental fire were quite variable along the plot, but did not exceed 71.5 °C (Fig. 3; Table 3). After fire, the canopies of the shrubs were completely burned; however, the litter was only totally consumed in one sample under *P. tridentatum* (Table 3). Mean twig diameter of the individual species was variable (Table 3); in EAU, the maximum was twice as high as the minimum, in EUM the maximum was threefold the minimum, and in PTR the maximum was nine times higher than the minimum (Table 3). However, twig diameter was not related with soil temperatures or with the amount of consumed litter (Supplementary Material 1).

After the experimental fire—relations between germination densities and the fire-related variables

Fire markedly decreased the overall density of seedlings germinating from the litter samples of both *Erica* species, but not of *P. tridentatum* (Table 5). However, the germination densities of the different species were not related with the same fire severity indicators (Table 4a). In particular, the densities of *P. tridentatum* and *E. umbellata* seedlings in the soil were positively correlated with the volume of remaining ashes. *E. umbellata* density was also negatively related to twig diameter, while the density of *E. australis* seedlings was negatively related to the maximum temperature recorded at 1.5 cm depth (Table 4a).

Despite the absence of a significant impact of fire in the overall germination in the soil (Table 5), there was some suggestion that the heterogeneous fire severity promoted differential effects on the germination of *E. australis* in the soil samples. The

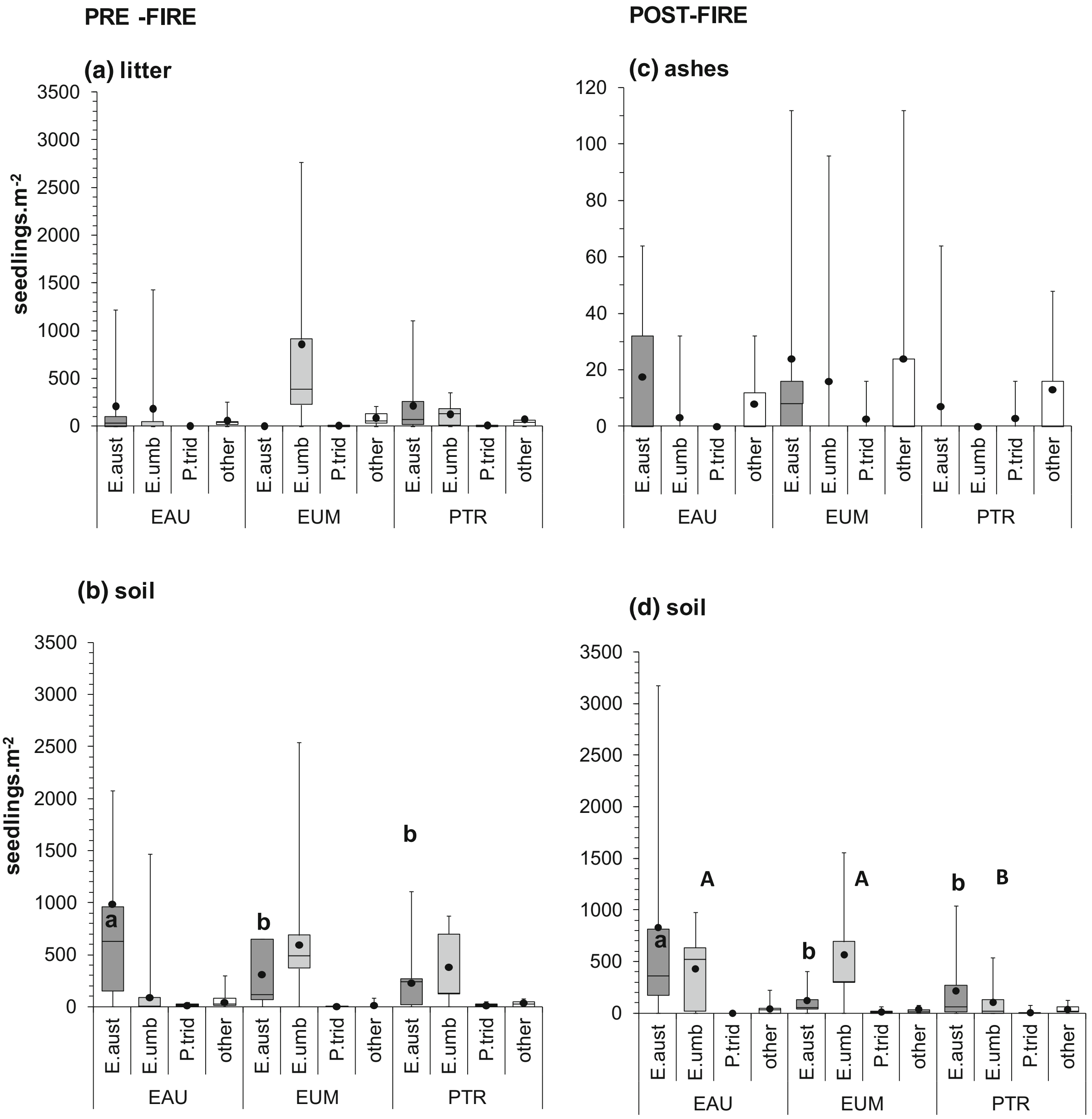

Fig. 2 Boxplot of germination densities from the litter and soil samples collected before (**a** and **b**) and after the fire (**c** and **d**) below the canopy of the target species. Target species: *EAU E. australis*, *EUM E.* ***umbellata***, PTR *P. tridentatum*. Different lower case letters indicate statistically significant differences in seed density (only occurring for *E. australis* seeds), between samples collected below the different target species' canopies. *Different capital letters* indicate statistically significant total seed density between target species samples. *Black dots* are means. Note the difference in the *y-axis* scale on **c**)—max 120

germination of *E. australis* seemed to be enhanced with exposure to temperatures up to 40.5 °C, but increasingly inhibited by higher temperatures (Fig. 4). Moreover, the proportional change in *E. australis* seedling density after fire was negatively related with the maximum temperature ($\rho = -0.857$, $p = 0.014$; $N = 7$) (Table 4b).

Table 1 Description of the target sample points before the experimental fire

	EAU ($n = 10$)			EAU ($n = 6$)			PTR ($n = 12$)		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Plant height (cm)	100	148	170	60	92	120	80	102	130
Canopy diam (cm)	90	930	200	30	83	120	80	118	200
Litter amount (l m^{-2})	11.2	14.9	16.0	6.4	12.8	14.4	9.6	15.1	19.2

Minimum (min), mean, and maximum (max) values of plant size and litter amount of the three target species

EAU Erica australis, *EUM Erica umbellata*, *PTR Pterospartum tridentatum*

Table 2 Spearman correlations between measures of the vegetation and germination densities in the samples collected before the fire

Pre-fire vegetation								
	Target species	N	Litter/ash			Soil		
			Height	Canopy diam	Litter volume	Height	Canopy diam	Litter volume
Seedlings m^2 before fire	EAU	8–10	−0676 ∼s	−0.512 ns	0.277 ns	−0.132 ns	0.117 ns	−0.135 ns
	EUM	5	0.308 ns	0.975*	−0.154 n.s	0.316 ns	0.300 ns	−0.103 ns
	PTR	9–10	0.230 ns	0.588 ∼s	0.441 ns	−0.184 ns	−0.525 ns	−0.409 ns

Only seed banks of the target species are considered (EAU *Erica australis*, EUM *E. umbellata*, PTR *Pterospartum tridentatum*)

P values lower than 0.1 are marked with ∼s and those lower than 0.05 with *

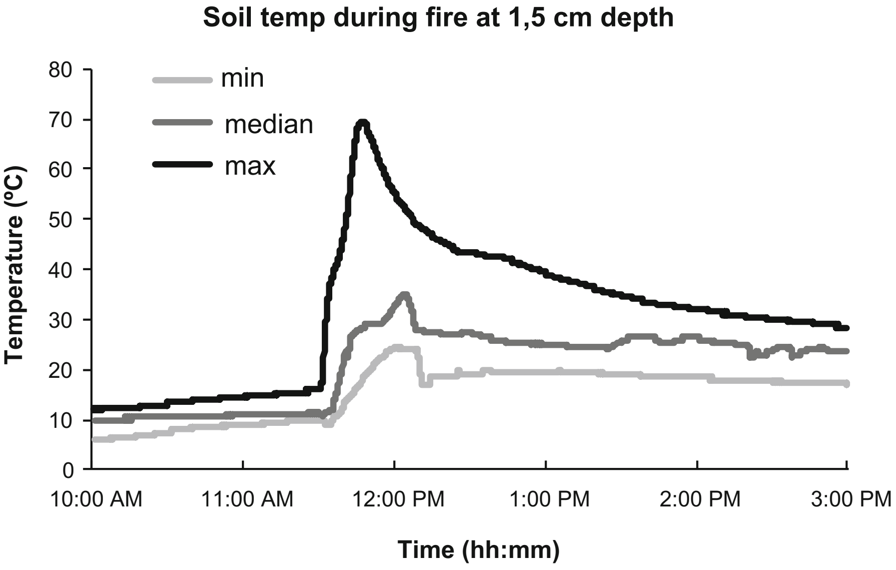

Fig. 3 Soil temperatures recorded in the plot. The experimental fire began approximately at 11.30. Post-fire sampling and recovery of the thermocouples began at 3 pm

Table 3 Fire severity variables estimated for the individual target plants and at the plot scale (overall)

	EAU ($n = 8/10$)			EUM ($n = 5/6$)			PTR ($n = 10/12$)			Overall		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
Twig diam (mm)	7.4	10.7	15.9	5.9	9.6	17.6	1.3	5.8	9.7			
Max temp (°C)	24.5	46.3	71.5	28.0	43.8	69.5	24.5	43.9	71.5	24.5	43.9	71.5
Time > 30 °C (min)	0.0	118.1	294.0	0.0	80.6	225.0	0.0	95.3	294.0	0.0	95.3	294.0
Time > 50 °C (min)	0.0	10.0	34.0	0.0	8.8	26.0	0.0	8.0	34.0	0.0	8.0	34.0
Ash amount (l m^{-2})	4.0	7.0	12.8	0.8	4.4	9.6	0.0	7.6	25.6	0.0	5.0	25.6
Cons litter (l m^{-2})	8.0	17.4	24.0	12.8	19.3	31.2	1.6	21.5	44.8	1.6	19.5	44.8

Target species: *EAU E. australis*, *EUM E. umbellata*, *PTR P. tridentatum*. Overall values for consumed litter amount include all 28 litter samples (12 PTR, 10 EAU, and 6 EUM)

Table 4 Spearman correlations between post-fire measures and a) post-fire seedling densities and b) proportional changes in seedling densities after fire

Fire severity estimations								
	Target species	N	Ash			Soil		
			Max tem.	Twig diam	Ash volume	Max tem.	Twig diam	Ash volume
(a) Seedlings m^2 before fire	EAU	7–10	0.273 ns	−0.038 ns	0.252 ns	−0.786*	−0.561 ns	0.420 ns
	EUM	4–6	–	−0.131 ns	0.393 ns	−0.400 ns	−0.900*	0.900*
	PTR	10–12	–0.174 ns	−0.097 ns	0.099 ns	0.130 ns	−0.002 ns	0.594*
(b) Δ/pre-fire seedlings m^2	EAU	7–9	0.430 ns	0.364 ns	0.099 ns	−0.857*	−0.427 ns	−0.050 ns
	EUM	4–5	0.316 ns	–	−0.406 ns	−0.600 ns	−0.086 ns	0.551 ns
	PTR	7–9	0.356 ns	−0.456 ns	0.252 ns	−0.204 ns	–	–

Only seed banks of the target species are considered (*EAU Erica australis*, *EUM E. umbellata*, *PTR Pterospartum tridentatum*). *P* values lower than 0.05 are marked with *. − means that Spearman correlation is 0

Discussion

Seed bank variability in relation to vegetation characteristics and species dispersal mechanisms

The review of Bossuyt & Honnay (2008) has shown that, among a wide variety of ecosystems, heathlands are the ecosystem which can better rely on the germination from the soil seed bank for post-disturbance community restoration. They have pointed out the overwhelming dominance of Ericaceae seeds in relation to other species in the seed bank. The present study draws evidence in the same direction, as the litter and the topsoil seed bank of this community were clearly dominated by *E. australis* and *E. umbellata*, even though *P. tridentatum* was the dominant species in the aboveground vegetation. Moreover, seed densities of the two Ericaceae were more abundant under their conspecific shrubs, which was statistically significant at least in the case of *E. australis*. This implies that future studies of soil seed bank sampling should take into consideration the spatial distribution of the main shrubs of the vegetation.

Variability in seedling density was much higher in the litter than in the soil, amounting to twice as high mean values. This higher variability found in the litter seed bank was probably the reflection of the higher seed input of seeds to the litter and, on the other hand, of the higher mortality rates in the litter than in the soil (Facelli and Pickett 1991; Nathan and Muller-landau 2000; Denham et al. 2009; Chambers and MacMahon 2011). Fire occurrence promoted a remarkable decrease in germination density in the litter, likely due to litter consumption. However, due to the high

Table 5 Comparison between pre-fire and post-fire seedling density from the litter and soil samples, for all sampling points, and for the target species collected under the conspecific shrubs. Symbols: ↓ overall decrease, ↔ no overall significant changes

Target species	Seed bank density (seedlings m^{-2})	Litter/ash N	Pre-fire Median	Pre-fire Range	Post-fire Median	Post-fire Range	Overall change (p)	Soil N	Pre-fire Median	Pre-fire Range	Post-fire Median	Post-fire Range	Overall change (p)
All	*E. australis*	23/26	28	1216	0	112	↓ (0.035)	23/24	387	1504	259	3303	↔
	E. umbellata	23/26	62	2768	0	96	↓ (0.002)	23/24	223	1440	292	1559	↔
	P. tridentatum	26/28	0	32	0	16	↔	25/27	0	48	0	80	↔
	Total	26/28	296	2800	24	160	↓(≪0.001)	24/27	912	1936	1112	4208	↔
EAU	*E. australis*	9/8	48	1216	16	64	↓ ns	9/10	1008	1202	499	3176	↔
EUM	*E. umbellata*	4/7	304	2768	0	96	↓ (0.029)	5/7	588	1068	304	1559	↔
PTR	*P. tridentatum*	10/11	0	32	0	16	↔	9/11	0	32	0	80	↔

potential for seedling mortality in the litter layer (Facelli and Pickett 1991; Denham et al. 2009), this decrease may carry limited consequences for the post-fire community regeneration.

A study conducted in a heathland dominated by *E. australis*, in the north of Spain (Valbuena and Trabaud 2001), showed extremely similar overall seed bank density to the present study (unburnt = 1050 seeds m^{-2}). Like this study, the dominant species in the standing vegetation were not proportionally represented in the germination from the seed bank—*Pterospartum tridentatum* in our study and *Erica australis* in their study. They have attributed the lack of correspondence between the seed bank and standing vegetation to low seed viability or high dormancy levels, which can partially explain the lack of *P. tridentatum* seedlings germinating from the seed bank samples.

This study did not detect net fire effects on the germination from the soil seed bank at the slope scale. However, there was evidence that heterogeneity in temperature achieved by fire could promote germination at some locations while inhibiting it at other locations. Maximum temperature was related to changes in germination density of *Erica australis*, even if the relation with the other severity estimations was not clear. Fernández et al. (2013) did not find such relation between fire temperature and *Erica australis* germination, but inter-population variability in fire-related response may explain differences in post-fire germination (Cruz et al. 2003; Vasques et al. 2012). A differential role of fire severity was also observed in the soil seed bank of a maritime pine stand, in which the small net changes in germination of *Erica* spp. were attributed to germination stimulation after low-severity fire, counterbalanced by seed mortality in high-fire severity patches (Maia et al. 2012).

The present study found no relationship between pre-fire fuel load (estimated by shrub size or litter volume) and fire temperature recorded in the soil. In fact, the litter layer remained unburned in the vast majority of the plot, indicating that the experimental fire that caused a nearly complete combustion of the aerial biomass did not achieve corresponding high severity at the soil level (Keeley 2009). The maximum temperatures recorded in the present study, at 1.5 cm (44 ± 17 °C), were probably not enough to stimulate germination of *P. tridentatum* seeds; germination from

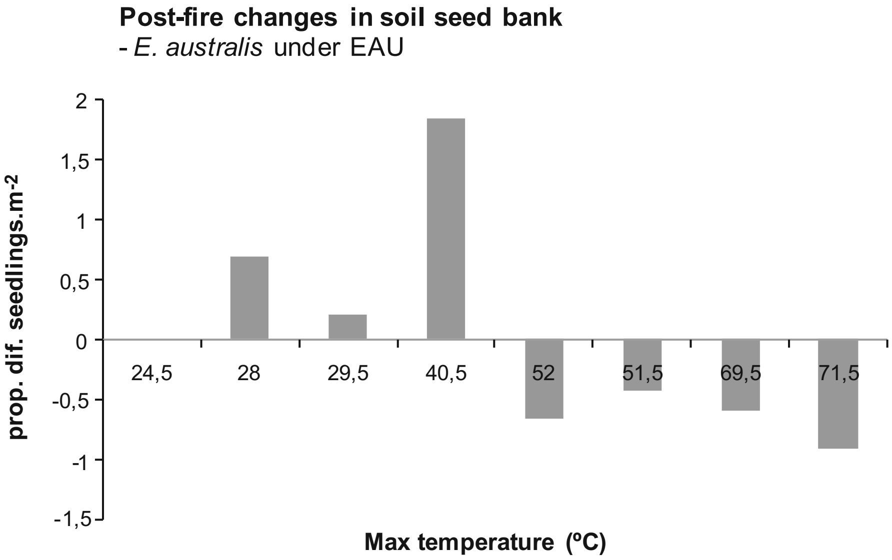

Fig. 4 Proportional changes in germination density, along a gradient of maximum temperature recorded by the thermocouples installed at 1.5 cm depth. The values correspond to proportional density differences (post–pre-fire)/pre-fire, for *Erica australis*, considering the samples collected under EAU shrubs

seeds of a neighboring population was reported to be stimulated after heating at 80 and 100 °C (Vasques et al. 2012). This may imply that the indirect method for evaluating the seed bank was not effective for *P. tridentatum*, since it remained unclear whether low germination densities could be attributed to low seed bank density caused by seed predation (e.g., granivorous ants; Clarke and Campbell 2006; Fox and Deveny 2006) or low seed production (e.g., legume predation by weevils—Podlussány et al. 2001; Rodriguez et al. 2011), or simply due to lack of stimulation by fire. The use of the direct method for evaluating *P. tridentatum* seed bank might be proven more helpful in future studies.

Studies in the Mediterranean report that post-fire cover values of *Erica australis* and *Pterospartum tridentatum* are likely to increase in relation to the pre-fire situation, while those of *E. umbellata* are likely to decrease (Céspedes et al. 2014; Fernandes et al. 2013; Fernández-Abascal et al. 2004; Rego et al. 1991). This highlights the vulnerability of *Erica umbellata,* being an obligate seeder in a community where it is clearly dominated by resprouters, which in addition is known to have potential low mid-term seedling survival (Quintana et al. 2004; Fernández and Vega 2014). Nevertheless, at the present time there is no evidence of decline of the *Erica umbellata* population, since its seed bank is abundant despite the scarcity of adult shrubs and moreover does not seem to be strongly related with the distribution of adult shrubs.

Conclusions

- *E. australis* and *E. umbellata* were well represented in the soil seed bank, being the dominant *taxa*. The density of *P. tridentatum* seeds in the soil seed bank was very low, despite being the dominant species in the standing vegetation.
- The density of *E. australis* seeds in the soil was significantly higher under its canopy, and the same was suggested for *E. umbellata*.
- There were no significant overall effects of fire on germination from the soil seed bank; however, the heterogeneous temperatures attained in the soil caused divergent effects over the plot—in some sampling points germination was increased, while in others it was decreased. In particular, the differences of *E. australis* germination density were significantly related with maximum temperature.
- *E. umbellata* soil seed bank was more abundant, but not limited to the area under its canopy. In this sense, the use of prescribed burning, as a tool for the reduction of fire hazard and severity, should not imply an imminent risk of decline for this species in the community, as long as fire intervals permit plants to mature and replenish the seed bank.

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References

Aguiar C, Capelo J (2000) Plano Sectorial da Rede Natura 2000—Habitats Naturais

Bossuyt B, Honnay O (2008) Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. J Veg Sci 19:875–884

Calvo L, Baeza J, Marcos E, Santana V, Papanastasis VP (2012a) Post-fire management of shrublands. In: Moreira F, Arianoutsou M, Corona P, De las Heras J (eds) Post-fire management and restoration of Southern European Forests. Springer, Netherlands, pp 293–319

Calvo L, Tárrega R, Luis E (2012b) Changes of species richness in heathland communities over 15 years following disturbances. Int J For Res 2012:1–12

Céspedes B, Luna B, Pérez B, Urbieta IR, Moreno JM (2014) Burning season effects on the short-term post-fire vegetation dynamics of a Mediterranean heathland. Appl Veg Sci 17:86–96

Chambers JC, MacMahon JA (2011) A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annu Rev Ecol Syst 25:263–292

Clarke PJ, Campbell ML (2006) Seed dynamics of resprouting shrubs in grassy woodlands: seed rain, predators and seed loss constrain recruitment potential. Austral Ecol 31:1016–1026

Cruz A, Pérez B, Velasco A, Moreno JM (2003) Variability in seed germination at the interpopulation, intrapopulation and intraindividual levels of the shrub *Erica australis* in response to fire-related cues. Plant Ecol 169:93–103

Denham AJ, Whelan RJ, Auld TD (2009) Characterizing the litter in postfire environments: implications for seedling recruitment. Int J Plant Sci 170:53–60

Eshel A, Henig-Sever N, Ne'eman G (2000) Spatial variation of seedling distribution in an east Mediterranean pine woodland at the beginning of post-fire succession. Plant Ecol 148:175–182

Facelli JM, Pickett ST (1991) Plant litter: its dynamics and effects on plant community structure. Bot Rev 57:1–32

Fernandes PM, Davies GM, Ascoli D, Fernández C, Moreira F, Rigolot E, Stoof CR, Vega JA, Molina D (2013) Prescribed burning in southern Europe: developing fire management in a dynamic landscape. Front Ecol Environ 11:e4–e14

Fernández C, Vega JA (2014) Shrub recovery after fuel reduction treatments and a subsequent fire in a Spanish heathland. Plant Ecol 215:1233–1243

Fernández C, Vega JA, Fonturbel T (2013) Fuel reduction at a Spanish heathland by prescribed fire and mechanical shredding: effects on seedling emergence. J Environ Manage 129:621–627

Fernández-Abascal I, Tárrega R, Luis-Calabuig E (2004) Ten years of recovery after experimental fire in a heathland: effects of sowing native species. For Ecol Manage 203:147–156. doi:10.1016/j.foreco.2004.07.058

Ferrandis P, Herranz JM, Martinez-Sanchez JJ (1999) Fire impact on a maquis soil seed bank in Cabaneros National Park (central Spain). Isr J Plant Sci 47:17–26

Fox LR, Deveny AJ (2006) Indirect interactions between browsers and seed predators affect the seed bank dynamics of a chaparral shrub. Oecologia 150:69–77

Gimingham CH (1972) Ecology of heathlands. Chapman and Hall, London

Gross KL (1990) A comparison of methods for estimating seed numbers in the soil. J Ecol 78:1079–1093

Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6(2):65–70

ICNF (2013) Instituto da Conservação da Natureza e das Florestas. http://www.icnf.pt/portal/florestas

Keeley J (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. Int J Wildl Fire 18:116. doi:10.1071/WF07049

Maia P, Pausas JG, Arcenegui V, Guerrero C, Pérez-Bejarano A, Mataix-Solera J, Varela MET, Fernandes I, Pedrosa ET, Keizer JJ (2012a) Wildfire effects on the soil seed bank of a maritime pine stand—the importance of fire severity. Geoderma 191:80–88

Maia P, Pausas JG, Vasques A, Keizer JJ (2012b) Fire severity as a key factor in post-fire regeneration of *Pinus pinaster* (Ait.) in Central Portugal. Ann For Sci 69:489–498

Moreira B, Pausas JG, Tormo J, Estrelles E (2010) Disentangling the role of heat and smoke as germination cues in Mediterranean basin flora. Ann Bot 105:627–635

Nathan R, Muller-landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Tree 15:278–285

Ottewell KM, Ayre DJ, Krauss SL, Whelan RJ (2009) Genetic structure of seedling cohorts following repeated wildfires in the fire-sensitive shrub *Persoonia mollis* spp. *nectens*. J Ecol 97:752–760

Paula S, Pausas JG (2008) Burning seeds: germinative response to heat treatments in relation to resprouting ability. J Ecol 96:543–552

Paula S, Arianoutsou M, Kazanis D, Tavsanoglu C, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A, Espelta JM, Palacio S, Fernandez-Santos B, Fernandes PM, Pausas JG (2009) Fire-related traits for plant species of the Mediterranean Basin. Ecology 90:1420

Podlussány A, Jermy T, Szentesi Á (2001) On the leguminous host plants of seed predator weevils (Coleoptera: Apionidae, Curculionidae) in Hungary. Acta Zool Acad Sci Hungaricae 47:285–299

Price JN, Wright BR, Gross CL, Whalley WRDB (2010) Comparison of seedling emergence and seed extraction techniques for estimating the composition of soil seed banks. Methods Ecol Evol 1:151–157

Quintana R, Cruz A, Fernández-González F, Moreno JM (2004) Time of germination and establishment success after fire of three obligate seeders in a Mediterranean shrub land of central Spain. J Biogeogr 31:241–249

Rego FC, Bunting SC, Silva JM (1991) Changes in understory vegetation following prescribed fire in maritime pine forests. Forest Ecol Manag 41:21–31

Rivas M, Rivas O, Casal M (2006) Influence of heat and smoke treatments on the germination of six leguminous shrubby species. Int J Wildl Fire 15:73–80

Rodriguez E, Peco B, Gurrea P (2011) Effect of Scotch broom, *Cytisus scoparius*, pod size and patch density on *Exapion fuscirostre* (Coleoptera, Apionidae) seed weevil oviposition. Aust Entomol Soc 51:127–132

Silva J, Moreira F, Vaz P, Catry F, Ferreira P (2009) Assessing the relative fire proneness of different forest types in Portugal. Plant Biosyst 143:597–608

Thompson K, Band SR (1997) Survival of a lowland heathland seed bank after a 33-year burial. Seed Sci Res 7:409–411

Torres I, Céspedes B, Pérez B, Moreno J (2013) Spatial relationships between the standing vegetation and the soil seed bank in a fire-prone encroached dehesa in Central Spain. Plant Ecol 214:195–206

Traba J, Azcárate FM, Peco B (2004) From what depth do seeds emerge? A soil seed bank experiment with Mediterranean grassland species. Seed Sci Res 14:297–303

Valbuena L, Trabaud L (2001) Contribution of the soil seed bank to post-fire recovery of a heathland. Plant Ecol 152:175–183

Valbuena L, Vera ML (2002) The effects of thermal scarification and seed storage on germination of four heathland species. Plant Ecol 161:137–144

Valbuena L, Nuñez R, Calvo L (2001) The seed bank in Pinus stand regeneration in NW Spain after wildfire Web Ecol 2:22–31

Vasques A, Maia P, Pedro M, Santos C, Vallejo VR, Keizer JJ (2012) Germination in five shrub species of Maritime Pine understory—does seed provenance matter? Ann For Sci 69:499–507

Vera DT, Martín RP, Oliva SR (2010) Effect of chemical and physical treatments on seed germination of *Erica australis*. Ann Bot Fenn 3847:353–360