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Natural establishment of *Eucalyptus globulus* Labill. in burnt stands in Portugal

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ABSTRACT

Exotic tree species are increasingly common in many regions of the world and at least some species are becoming naturalized in the regions where they were introduced. Disturbances like fire may be at the origin or accelerate the naturalization of these species. Portugal holds one of the largest areas of exotic *Eucalyptus globulus* plantations in the world and is one of the countries most affected by forest fires. These two facts have triggered the present research. This study aimed at characterising medium-term natural establishment of *E. globulus* plants originated from seeds under natural conditions in burnt planted forests (pure *E. globulus* stands, pure *Pinus pinaster* stands, and mixed stands of both species), and at analysing factors associated with this establishment. Occurrence, abundance and height of naturally established *E. globulus* plants were characterized in 284 sites distributed in burnt areas, across Central and Northern Portugal, 5–7 years after wildfire. Generalized linear models were used to assess the influence of stand type, regional productivity potential, and post-fire management practices on occurrence probability, density, and median height of sampled *E. globulus* individuals. The influence of these explanatory variables on the structure (in terms of size class distribution) of naturally established *E. globulus* cohort was examined using analysis of similarity and non-metric multidimensional scaling. Naturally established *E. globulus* plants were present in 93.1%, 19.0% and 98.6% of samples in pure *E. globulus*, pure *P. pinaster* and mixed stands, respectively. Cohort median density was 0.20 plants m^{-2} and maximum density was 4.55 plants m^{-2}. Median height of plants was 2.0 m and 95.3% of them had $h > 1.30$ m and DBH $\leqslant 5$ cm. Establishment probability, density and median height were highest in the most productive regions. Three post-fire management operations had a significant influence on the response variables: (i) salvage logging was associated with a higher density; (ii) tillage was associated with a lower density and a smaller median height; (iii) understorey removal was associated with a lower occurrence probability. Tillage was the only studied factor influencing the size structure of spontaneously established cohort, eliminating larger plants. This study showed that stand type, productivity region and post-fire management operations might have significantly influenced the natural establishment of *E. globulus* in burnt areas, and consequently the species naturalization process in Portugal. The implications of these findings for management are discussed.

1. Introduction

Given the expansion of exotic tree plantations in the world (MCPFE, 2007; FAO, 2010), the study of ecological processes associated with these forests is increasingly important. Some of the most relevant issues are related to naturalization or invasive potential of exotic tree species, since significant interactions with the native ecosystems are possible (Richardson, 1998). Disturbances in general and fire in particular are known to facilitate the recruitment of different exotic species (e.g. Anderson and Brown, 1980; Mandle et al., 2011; Arianoutsou and Vilà, 2012; Vallejo et al., 2012). Therefore, the fire-mediated naturalization of planted exotic trees is a relevant research topic (Silva and Marchante, 2012).

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Eucalyptus globulus Labill. (Tasmanian blue gum) is one of the most widely planted and economically important hardwood species in temperate regions of the world (Potts et al., 2004). This eucalypt is native to SE Australia and it is planted in many regions around the world. Portugal is among the countries that have largest areas of planted *E. globulus* in the world (Potts et al., 2004). This species was introduced in Portugal in the middle of the 19th century (Radich, 2007) and is now the most widespread tree species in Portuguese mainland, representing 26% (812×10^3 ha) of its forest cover (ICNF, 2013).

E. globulus forests in Portugal are planted and mostly managed through a coppice system (10–12 year rotations) (Turnbull and Pryor, 1984; Soares et al., 2007). Their wood is almost exclusively used for pulp production. Water availability and episodic occurrence of temperatures below 0 °C are considered the main limiting climatic factors to *E. globulus* development in Portugal (Almeida et al., 1994; Ribeiro and Tomé, 2000; Alves et al., 2012), where wood yields are very variable due to site conditions and may exceed 30 m^3 ha^{-1} $year^{-1}$ in the very best sites (Tomé, 2000). However, the good adaptation of *E. globulus* to many Portuguese environmental conditions is having other implications, as the species has become naturalized. The species reproduces by seeds and naturally established plants are commonly found within or close to planted stands nowadays (Marchante et al., 2008; Silva and Marchante, 2012). Although the first reference to naturalization of *E. globulus* in Portugal dates from 1943 (Almeida and Freitas, 2006), we found no quantitative assessments of this process in the literature. Naturalization processes are known to have resulted in considerable economic and environmental costs for several alien species (Andreu et al., 2009). Naturally established plants may modify ecosystem/plantation dynamics and changes in forest management may be required to control them, since *E. globulus* grows fast (Silva et al., 2007a). Most of the literature concerning the seed regeneration from *E. globulus* plantations reports qualitative assessments in order to infer about the naturalization or the invasive status of the species (Ritter and Yost, 2009; Gassó et al., 2010; Gordon et al., 2012). The few references that provide quantitative data are not comparable due to differences on methods and on considered factors (Virtue and Melland, 2003; Calviño-Cancela and Rubido-Bará, 2013; Larcombe et al., 2013).

Fire is often related with eucalypt recruitment and establishment (Mount, 1964; Cremer, 1965; Mount, 1969; Ashton, 1981; Gill, 1997). Causes for fire facilitated recruitment/establishment of eucalypts are related with: increased seed shed from canopy (Cremer, 1965; Pryor, 1976; O'Dowd and Gill, 1984; Wellington and Noble, 1985b; Florence, 1996); seed-predator satiation (O'Dowd and Gill, 1984; Wellington and Noble, 1985b; Gill, 1997); increased light availability (Jacobs, 1955; Kirkpatrick, 1975; Gill, 1997); "ash-bed effect" (Pryor, 1976; Chambers and Attiwill, 1994); reduced competition (Wellington and Noble, 1985a; Whelam, 1995; Gill, 1997); removal of allelopathic substances (Pryor, 1976; Stoneman, 1994); and decreased predator activity (Whelam, 1995). Larcombe et al. (2013) demonstrated that fire was associated with higher recruitment levels of *E. globulus*, as it had been suggested earlier by Kirkpatrick (1975).

Portugal has the largest percentage of burnt forest area in Europe and one of the largest in the world (FAO, 2010; JRC, 2012) and the National Forest Strategy (DGRF, 2007) indicates that wildfires are a major threat to sustainable forest management in this country. Moreover, eucalypt stands are highly flammable in comparison to other forest systems in Europe and particularly in Portugal (Nunes et al., 2005; Moreira et al., 2009; Silva et al., 2009; Fernandes et al., 2011; Xanthopoulos et al., 2012).

Effects of post-fire operations on seedling establishment depend on how and when they are performed. Post-fire management of burnt forests often includes: salvage logging; tillage; and shrub removal. Post-fire salvage logging usually occurs before establishment of the next generation of trees and its major effects consist of environmental changes derived from removal of burnt trees. If it occurs after seedling establishment, significant seedling mortality can happen (McIver and Starr, 2000). *In situ* germination of seeds from logging eucalypt slash is common under favourable conditions (Fagg, 2001) and *E. globulus* plants may establish and grow normally or become dominated trees under coppice shoots (Skolmen and Ledig, 1990). Tillage is aimed at improving soil conditions for root development (Madeira et al., 1989), but in burnt areas can largely enhance erosion, if it is not performed with caution (Coelho et al., 1995; Shakesby et al., 1996). Established plants that were born after fire may be destroyed by tillage (Catry et al., 2010). Few years after fire, understorey is well developed in forests. Since *E. globulus* is very sensitive to competition with understorey plants especially in early years of life, and fuel load build up increases fire hazard, periodic understorey removal is performed in this species stands (Pereira, 2007; Soares et al., 2007; Moreira et al., 2009; Alves et al., 2012).

To our knowledge, a quantitative assessment of natural establishment of *E. globulus* in burnt areas has never been carried out in Europe. We chose to study the post-fire seminal regeneration of *E. globulus* because there were recurrent references to fire-induced eucalypt establishment (Jacobs, 1955; Cremer, 1965; Kirkpatrick, 1975; Pryor, 1976; O'Dowd and Gill, 1984; Chambers and Attiwill, 1994; Stoneman, 1994; Florence, 1996; Gill, 1997), as well as frequent observations of *E. globulus* saplings in recently burnt areas in Portugal (Silva et al., 2007a, 2007b; Silva and Marchante, 2012). Stands with *Pinus pinaster* were included in the study because this species is highly represented in Portuguese mainland (23% forest cover) (ICNF, 2013), and it has similarities to *E. globulus* on its ecological requirements and geographical range. Additional grounds were the common coexistence of these species in mixed stands (Silva et al., 2011) and the high fire proneness of *P. pinaster* stands (pure or mixed) (Moreira et al., 2009).

The study aimed at answering four questions related to medium-term establishment of *E. globulus* plants originated from seeds under natural conditions in burnt forests (pure *E. globulus* stands, pure *P. pinaster* stands, and mixed stands): (a) what is the likelihood of *E. globulus* natural establishment in burnt areas; (b) which are the most important factors related with site characteristics, stand type and post-fire management practices influencing this likelihood; (c) how do these variables affect the density of post-fire naturally established *E. globulus* cohort and the median height of its individuals; and (d) how do these variables influence the size structure (distribution of individuals among size classes) of post-fire naturally established *E. globulus* cohort.

2. Material and methods

2.1. Study areas

Forty areas that had burnt during 2005 and 2006 were selected in Central and Northern Portugal (Fig. 1), regions where *E. globulus* is common. Burnt areas were identified from existing fire maps created through semi-automated classification of remote sensing satellite data (Marques et al., 2011). Selection of burnt areas was based on time-since-fire (5–7 years), size (largest areas were preferred), accessibility and presence of pure or mixed stands of *E. globulus* and *P. pinaster* (pure stands corresponding to cover of target species ⩾75%, and mixed stands to cover of either species <75%) (AFN, 2009). The selected areas ranged in size from 6 to 10924 ha, with an average of 2078 ha. The sampling grid (500 m × 500 m) created for the National Forest Inventory (NFI) (AFN, 2010) was used to define potential study sites within the

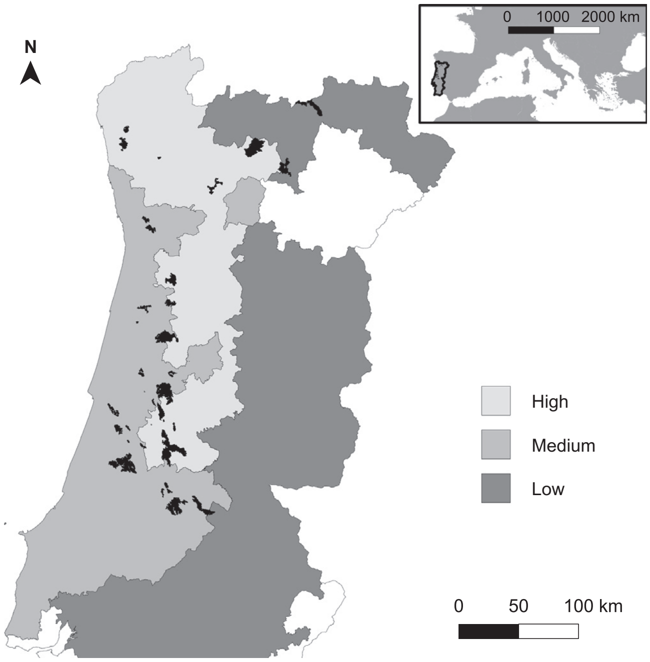

Fig. 1. Location of the 40 studied burnt areas in Portugal (in black). Limits for the three *E. globulus* productivity regions are also shown (in shades of grey). White areas refer to regions where sampling did not occur.

selected areas. From these potential sites, those corresponding to pure or mixed stands of *E. globulus* and *P. pinaster* were selected, based on pre-2005 NFI data. Depending on the size of the selected areas, up to 30 sites were chosen per area. The selected sites were checked in the field for eventual land cover changes after fire, and the ones that had been converted to other land uses after fire were excluded. A total of 321 sites was obtained (range = 1–30 sites per burnt area): 37 for refining sampling method (data not presented), and 284 for definite sampling.

2.2. Field sampling

Sites were sampled between June 2010 and June 2012. The sampling design was an adaptation of the method used in Portuguese National Forest Inventory (AFN, 2009) for minor trees assessment, and consisted of a combination of transect sampling (to allow a more effective detection of eucalypt presence) with area surveys (subplots) to measure plant densities. Each sampling site consisted of a 6.78 m radius circular plot centred on the site coordinates (located using a hand-held GPS – Garmin, e-Trex, Taiwan). Four 5 m × 2 m transects were established at every site, diverging from the plot centre and oriented towards the north, the south, the east and the west. At the end of each transect, a 1.78 m radius subplot was established, with its centre 5-m distant from plot centre. Presence of post-fire naturally established *E. globulus* plants was checked inside the four subplots and along the four transects. In order to distinguish these individuals from pre-fire, artificially sown or planted individuals, we observed cumulatively the following features: absence of charred parts; presence of a conspicuous lignotuber; and location within the plantation inconsistent with spacing. The number of target plants and the height of the median individual were measured *in loco* inside each of the four subplots. Each individual was assigned to one of the four size classes using a combination of height (h) and diameter at breast height (DBH) – size class 1: $h \leqslant 1.3$ m; size class 2: $h > 1.3$ m and DBH $\leqslant 5$ cm; size class 3: $h > 1.3$ m and $5 < \text{DBH} \leqslant 7.5$ cm; size 4: $h > 1.3$ m and DBH > 7.5 cm. At all sampling sites, evidences of several post-fire stand management operations (Table 1) were collected by field observation and, whenever possible, by inquiring land owners. Information about site physiographic position, slope, and aspect was also collected (Table 1). A hypsometer (Haglöf Vertex III, Sweden) was used to measure slope. Aspect was measured using a compass. Additionally, the presence of potential mother trees, either in the plot or in its surroundings (up to 100 m), was registered.

2.3. Data analysis

Considering that there is no accurate and quick method of determining age of *E. globulus* plants, we decided to use a broad

Table 1
Description of assessed explanatory variables.

Variable	Data description	Data type	Data source	Frequency (%)
Pre-fire forest type	Dominant species in the plot	Categorical	Forest inventory data and field evidence	*P. pinaster* (29.6) *E. globulus* (45.8) Mixed (24.6)
Productivity region	*E. globulus* productivity classes, based on annual precipitation and number of frost days per year	Categorical	Ribeiro and Tomé (2000); Tomé et al. (2001)	High (35.6) Medium (53.9) Low (10.6)
Post-fire salvage logging	Cut of *Eucalyptus globulus* poles and/or *Pinus pinaster* trees (all or only dead)	Binary (0/1)	Inquiries and field evidence	69.4
Post-fire tillage	Mechanical disturbance of the forest floor, by harrowing, ploughing or ripping	Binary (0/1)	Inquiries and field evidence	15.8
Post-fire understorey removal	Mechanical removal of understorey shrubs and small trees	Binary (0/1)	Inquiries and field evidence	16.2
Terrain physiography	Plot physiographic position	Categorical	Field evidence	Flat or valley bottom (10.9) Slope (78.5) Ridge (10.6)
Slope	In degrees	Continuous	Field measurement	[0°;15°] (50.0)]15°;30°] (44.0)]30°;45°] (6.0)
Aspect	Aspect classes based on Kutiel and Lavee (1999): unfavourable – SE, S, and SW aspects; favourable – remaining aspects	Categorical	Field evidence	Unfavourable (31.3) Favourable (68.7)

concept of cohort in this study – cohort as a group of individuals of the same species that experienced the same event within the same time interval (Ryder, 1965), using as cohort definer (*sensu* Schaie (1984)) the natural establishment in a burnt stand. Accordingly, we included all *E. globulus* plants that had been naturally established within 5–7 years after fire in a single cohort, which was our study subject.

For simplicity purposes, we will refer to post-fire natural establishment of *E. globulus* as establishment. Similarly, post-fire naturally established *E. globulus* plants/individuals and post-fire naturally established *E. globulus* cohort, will be respectively named as plants/individuals and cohort. Nevertheless, the extensive names will be used whenever the use of short names results in ambiguity.

Three response variables were modelled using generalized linear models (GLM): occurrence of establishment (presence/absence), cohort density (plants m^{-2}), and plant median height (m). A plot was considered as having established plants if they occurred in at least one of its transects or subplots. Plant density was estimated by averaging the densities from the different subplots. Median height was also calculated across subplots. Nine explanatory variables were used (Table 1): stand type; tillage; understorey removal; salvage logging; terrain physiography; slope; aspect (based on Kutiel and Lavee (1999)); and *E. globulus* productivity regions (Fig. 1; adapted from Ribeiro and Tomé (2000) and Tomé et al. (2001)). Productivity region factor was chosen as it could be a surrogate of habitat quality for *E. globulus* and, consequently, for seedling establishment and growth of this species.

Occurrence of establishment (presence/absence) was modelled by setting a binomial distribution for the response variable and a logit link (occurrence model) (Quinn and Keough, 2002). The cohort density (Fig. 2) was modelled using a gamma distribution and a log link (density model). In this case, only sites with plant establishment were considered. The median heights of established plants had a log normal distribution (Fig. 3), so they were log-transformed and modelled through a Gaussian distribution and an identity link (height model) (Quinn and Keough, 2002). The only three sites with regeneration at subplots located in low productivity regions were discarded in density and height models as these regions were not sufficiently represented. Model selection followed Zuur et al. (2009), starting with a model that included all nine explanatory variables and sequentially removing the variables that did not contribute significantly ($\alpha = 0.05$) to the explained deviance (according to analysis of deviance tests). Modelling was performed using R statistical software (R Core Team, 2012).

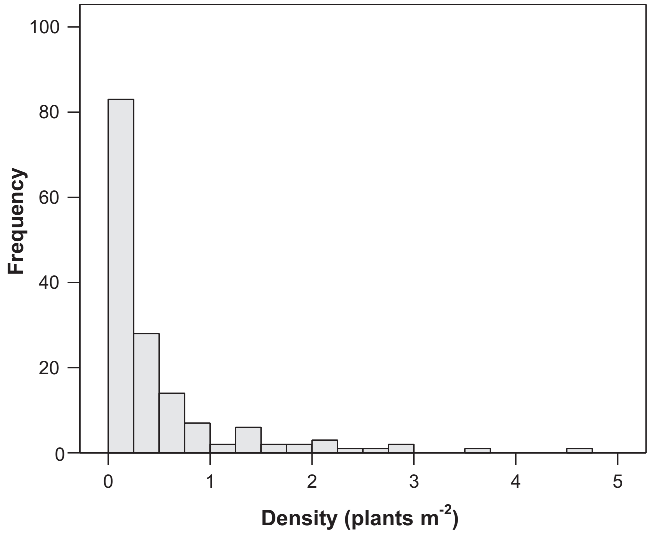

Fig. 2. Observed densities of post-fire naturally established *E. globulus* cohort, in sampled sites where it was present. $n = 153$.

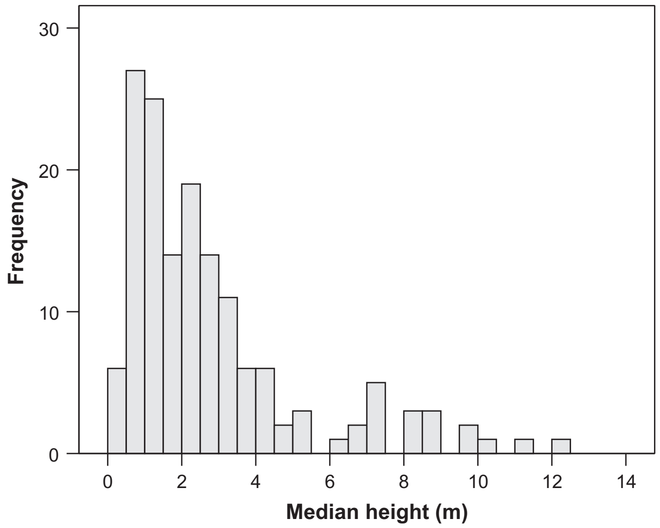

Fig. 3. Median heights of post-fire naturally established *E. globulus* plants in sampled sites. $n = 152$.

Assessment of each model performance was based on the fraction of total deviance explained by the model. Performance of occurrence model was additionally assessed through the area under the receiver operating characteristics curve, commonly known as area under the ROC curve (AUC) (Pearce and Ferrier, 2000). AUC was estimated using package ROCR for R (Sing et al., 2009). The eventual presence of spatial autocorrelation in the model residuals was tested through a spatial correlogram using the Moran's I autocorrelation coefficient (Fortin and Dale, 2005), employing the function correlog of the ncf package for R statistical software (Bjornstad, 2009). Significance was tested using 100 permutations and the progressive Bonferroni correction (Legendre and Legendre, 1998).

Relationship between regeneration occurrence and presence of potential mother trees was analysed through a contingency table, X^2 test, and Φ_2 coefficient (Zar, 1996).

Differences on size structure of the naturally established cohort (given by the distribution of individuals into size classes) among sites were assessed, using analysis of similarity (ANOSIM) and non-metric multidimensional scaling (MDS) (Clarke, 1993). Data on distribution of individuals among sizes classes in different sites were standardized. Then, a similarity matrix of those frequencies was computed using the Bray–Curtis coefficient of similarity (Bray and Curtis, 1957; Clarke, 1993). MDS was performed with 20 restarts and a two-dimension MDS diagram was built. A one-way ANOSIM test was performed for each factor separately. Then, obtained global *R* value was compared with the *R* probability distribution, previously produced with a maximum of 9999 random permutations, considering $\alpha = 0.05$. ANOSIM and MDS were performed using software Primer 5 for Windows (version 5.2.9) (Primer-e, 2002).

3. Results

The 284 sites were unevenly distributed among different stand types, productivity regions and topographic conditions (Table 1).

Post-fire management occurred in 78.5% of sites. Salvage logging was the most common operation (69.4%), while understorey removal (16.2%) and tillage (15.8%) were less common (Table 1).

A total of 3062 naturally established *E. globulus* plants were observed across 72.5% of the 284 sampling sites. Almost every site

(99.5%) with natural regeneration had or had had potential mother trees inside the plot or nearby. At sites with no regeneration, these seed trees were, or had been present in 29.5% of cases. This difference was significant ($\varphi^2 = 0.79$, $p < 0.001$). At the sites where studied plants were present at the subplots, cohort density had its median at 0.20 plants m^{-2} and its maximum at 4.55 plants m^{-2} (mean ± SD = 0.48 ± 0.73 plants m^{-2}). Plant median height was 2.0 m, and the values ranged from 0.2 to 12.1 m (mean ± SD was 2.7 ± 2.4 m). These two variables had positively skewed distributions (Figs. 2 and 3).

The occurrence model showed that establishment was significantly influenced by stand type, productivity region, and understorey removal, together explaining 56.8% of the deviance (Table 2). AUC value for occurrence model was 0.941, revealing its high accuracy (Swets, 1988). Establishment probability was higher in mixed and pure *E. globulus* stands, in medium and high productivity regions, and when understorey vegetation was not removed, although this latter effect was less important and appeared to be overshadowed by other factors (Fig. 4(a)). The main explanatory variables in the density model were productivity region and two post-fire management operations, although altogether they only explained 11.6% of the deviance (Table 2). Density was higher in the high productivity region, and when salvage logging had occurred, while it was lower following tillage (Fig. 4(b)). According to height model, plants were taller in the high productivity region and smaller where the soils were tilled (Fig. 4(c)). However, this model only explained 8.0% of the deviance (Table 2). There was no significant spatial autocorrelation pattern in any of the models' residuals.

The MDS analysis performed to compare the size structure of the spontaneous cohort among different sites had a stress of 0.03, revealing an excellent representation with no prospect of misinterpretation (Clarke, 1993). The 2-dimension MDS diagram (Fig. 5) showed two main groups of sites: one group of 52 sites lacking plants of size 1, located along the vertical axis (group A); and another group of 119 sites lacking of sizes 3 and 4, located along the horizontal axis (group B). The two groups partially overlapped. This overlap involved 38 sites that only had plants of size 2. The far end of group B comprised sites only with plants of size 1 (*C*; $n = 23$). In between groups A and B, there were sites with different proportions of plants belonging to several size classes (1, 2, and 3 or/and 4). Size classes 1 and 2 were prevalent in the study, 95.4% of plants belonged to one of these classes, and they were present in all sites that had natural regeneration at the subplots. Size classes 3 and 4 were the rarest, together they occurred in 20.6% of sites which had natural regeneration at subplots (all but group B) and they represented only 4.5% of plants. ANOSIM showed that tillage was the only explanatory variable that significantly affected cohort size structure ($p = 0.048$) but its influence on relative abundances of different size classes was not very strong (global $R = 0.064$). Plants of sizes 3 and 4 were absent in tilled sites (Fig. 5).

Table 2
Generalized linear models for natural establishment of *E. globulus* – occurrence likelihood, cohort density, and plant median height. For each response variable, explanatory variables kept in the respective final model are indicated through their coefficient ± SE, as well as their significance ($^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$).

	Occurrence	Density	Height
Intercept	1.002 ± 0.925	−0.812 ± 0.260*	0.889 ± 0.113***
Stand type	–***		
E. globulus	0		
P. pinaster	−4.000 ± 0.521		
Mixed	1.717 ± 1.073		
Productivity region	–**	–*	–*
High	1.732 ± 0.900	0	0
Medium	2.299 ± 0.877	−0.501 ± 0.259	−0.293 ± 0.146
Low	0	–	–
Salvage logging		0.597 ± 0.278*	
Tillage		−0.864 ± 0.333*	−0.436 ± 0.193*
Understorey removal	−1.462 ± 0.624*		
n	284	150	149
Explained deviance	56.8%	11.6%	8.0%
AUC	0.941		

4. Discussion

Considering the wide geographical range of the survey, the diversity of sampled stands and the relatively small size of the sampling plots, it is relevant that 72.0% of plots from all stands had naturally established *E. globulus* plants. The positive association between the occurrence of these plants and the presence of potential mother trees suggested the existence of a widespread establishment in burnt stands where close seed sources were available. The occurrence of progeny restricted to vicinity of these trees is in accordance with the limited dispersal capacity of the species (Cremer, 1977) and occasional occurrence of regeneration some tens of meters away from these trees are compatible with results obtained by Larcombe et al. (2013) and Calviño-Cancela and Rubido-Bará (2013).

The occurrence model revealed high accuracy in predicting the likelihood of establishment, pointing at stand type, productivity region, and understorey removal as main explanatory variables.

Natural establishment was very common in pure *E. globulus* stands (90.9%) and mixed stands (94.9%), while it only existed in 19.1% of pure *P. pinaster* stands. This difference was very significantly reflected in the occurrence model. While this result is not surprising, since the presence of adult *E. globulus* trees (seed sources) naturally increases the likelihood of recruitment, it is noticeable that this type of establishment also occurred often in pure *P. pinaster* stands. However, all but one of concerned sites had adult *E. globulus* trees or its burnt remnants within the plot or had conspicuous potential mother trees in the surrounding area. The presence of sexually mature *E. globulus* trees in pure *P. pinaster* stands is common in Portugal (Godinho-Ferreira et al., 2005).

Likelihood of establishment was higher in better productivity regions, based on classification proposed by Ribeiro and Tomé (2000). The criteria used in this classification to define homogeneous climatic regions for *E. globulus* productivity (~growth) were essentially based on indicators of water availability and frost occurrence. These factors are known to affect not only *E. globulus* growth, but also this species recruitment, establishment, and survival. In fact, water deficit negatively affects: *E. globulus* seed germination (López et al., 2000; Humara et al., 2002); *E. globulus* seedling establishment success (González-Muñoz et al., 2011); and summer survival of young eucalypts (Jacobs, 1955; Whelam and Main, 1979; Wellington and Noble, 1985a; Stoneman et al., 1994; Richards and Lamont, 1996). Additionally, frost may directly kill foliage and buds and sometimes the whole plant (Cremer et al., 1984). T50 for *E. globulus* seedlings leaves is −5.5 °C (Almeida et al., 1994). These facts may explain why higher productivity regions are more likely to have *E. globulus* establishment. Results obtained by Larcombe et al. (2013) point at the same direction, since they found that sites where precipitation seasonality was lower had higher probability to have natural establishment of this species, in Australia, similarly to what happens in areas corresponding to higher productivity regions in Portugal, probably due to reduced water stress in late summer.

Most of the surveyed sites (68.3%) did not show any evidences of management activities, except for salvage logging. Establishment

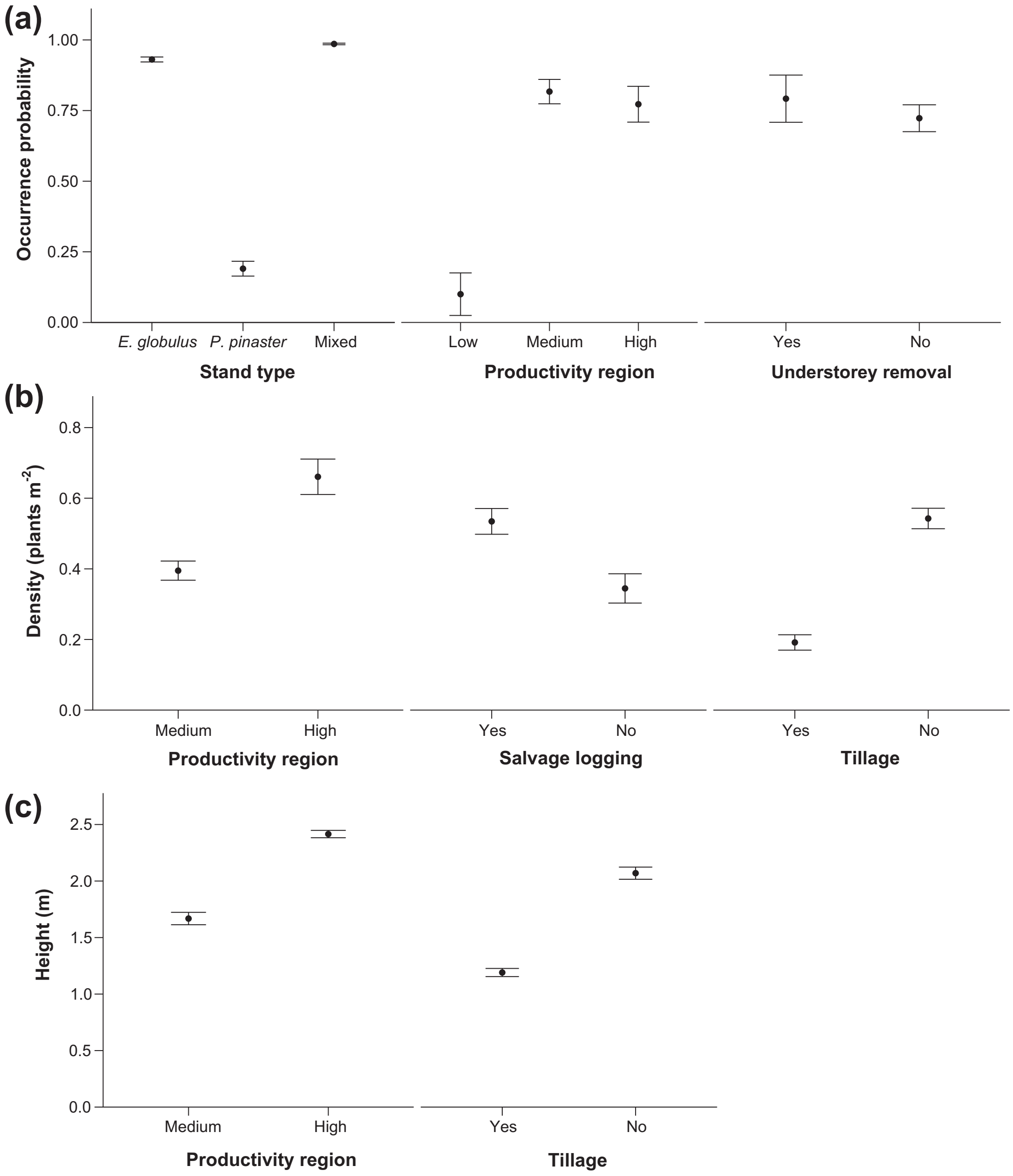

Fig. 4. Predictions of produced models (mean ± 95 CI) for *E. globulus* post-fire natural establishment: (a) occurrence model; (b) density model and (c) median height model.

occurred in all but one of those “unmanaged” sites in pure *E. globulus* stands, and the same happened in mixed stands, while only 15.8% of “unmanaged” pure *P. pinaster* sites had spontaneous *E. globulus* plants. This suggests that poor management or total lack of it favoured establishment both in pure *E. globulus* stands and in mixed stands; while other factors may have major influence on the phenomenon in pure *P. pinaster* stands. However, a more detailed analysis shows that different management operations had different effects.

Sites where understorey removal had occurred were less likely to have naturally established *E. globulus* plants, although this effect was minor. This operation is aimed at destroying understorey vegetation, which may include small *E. globulus* individuals. In some sites where understorey was removed, probably all previously recruited *E. globulus* seedlings/saplings were killed and no subsequent establishment succeeded, resulting in absence of plants at sampling time. This would be compatible with the idea that most post-fire establishment happens shortly after fire (Pryor, 1976; Florence, 1996).

Densities of naturally established *E. globulus* cohort observed in our study were not easy to compare with other quantitative references on this subject because of differences in methodology and considered factors (Virtue and Melland, 2003; Calviño-Cancela and Rubido-Bará, 2013; Larcombe et al., 2013). In order to compare our data to those from other studies, we needed to consider only pure *E. globulus* stands. Densities observed in our study (maximum = 4.55 plants m^{-2}; mean = 0.48 plants m^{-2}) were largely higher than those registered by Larcombe et al. (2013) (maximum = 1.98×10^{-3} plants m^{-2}; mean = 8.52×10^{-4} plants m^{-2}) within 10 m from plantation borders, including both burnt and unburnt areas. Meanwhile, the absolute values of maximum density mentioned in the other two references had the same order of magnitude that we observed: 1–2 plants m^{-2} (Virtue and Melland, 2003) and about 2 plants m^{-2} (Calviño-Cancela and Rubido-Bará, 2013), both located next to unburnt plantations edges. However, we cannot evaluate if these values are lower or higher than ours because they might result from potential periods of recruitment with very different time lengths.

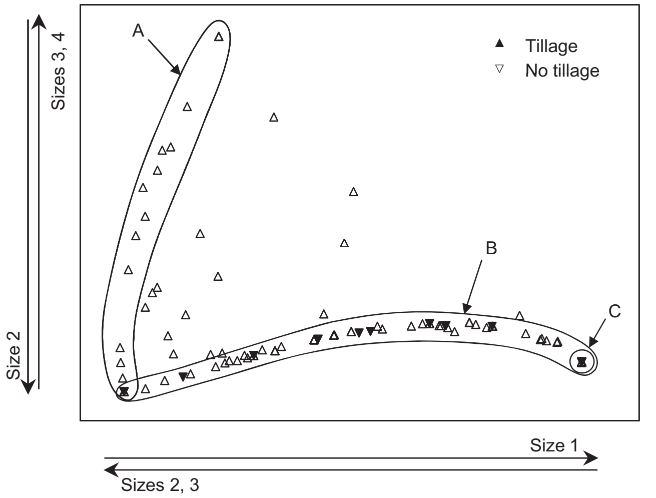

Fig. 5. Ordination diagram of size structure of post-fire naturally established *E. globulus* cohort in sampled sites, obtained from a non-metric multidimensional scaling analysis. Size classes of plants: size 1 – height $\leqslant$ 1.3 m; size 2 – height > 1.3 m and DBH $\leqslant$ 5 cm; size 3 – height > 1.3 m and 5 < DBH $\leqslant$ 7.5 cm. n = 153.

The density model pointed at productivity region and two management operations as the most important studied variables for explaining young cohort density.

Like occurrence, cohort density was higher in the most productive region. Since water deficit can negatively affect eucalypt recruitment, establishment and survival, as discussed before, it may explain this density difference. Our results on density also agreed with those reported by Larcombe et al. (2013) for Australia, with respect to annual precipitation and precipitation seasonality.

Salvage logging had a positive effect on cohort density. Although logging can destroy post-fire established plants (McIver and Starr, 2000), it is not likely because it is recommended to harvest burnt *E. globulus* trees shortly after fire (Shakesby et al., 1996). In fact, logging has been associated with plant recruitment in *E. globulus* stands and in other eucalypt stands (Skolmen and Ledig, 1990; Fagg, 2001), since seedlings may originate from the so-called "slash seed" (Fagg, 2001), which in the specific case of salvage logging may be enhanced by the seed shed caused by fire (Cremer, 1965). Additionally, reduction of competition caused by salvage logging might have improved establishment success of youngsters, resulting in higher densities of their cohort in fallen stands. Eucalypts are not able to become established and develop normally under a complete overstorey canopy (Florence, 1996). *E. globulus* usually regenerates only when the overstorey is removed (Stoneman, 1994). Asymmetrical competition was observed in *E. globulus* by Tomé et al. (1994). Several Australian studies under temperate and Mediterranean climates have shown that water deficits are stronger in eucalypt seedlings in sites with overstorey than in sites where it did not exist, resulting in higher mortality rates in the former (Bowman and Kirkpatrick, 1986; Battaglia and Wilson, 1990; Stoneman et al., 1994). Negative effects of water stress on *E. globulus* recruitment and establishment were already discussed.

Tillage had a negative effect on cohort density. This operation can destroy post-fire regeneration from seeds (Catry et al., 2010). Direct killing of most of naturally established *E. globulus* plants was probably the major cause of low density of their cohort in tilled sites. Harrowing reduces the development of understorey biomass in *E. globulus* plantations (Carneiro et al., 2008) and this may be related to a reduction of nutrients in soil caused by tillage (Madeira et al., 1989; Carneiro et al., 2008). Increased soil erosion due to tillage probably resulted in harsher soil conditions that might have hindered plant establishment (Shakesby et al., 1996) and increased mortality since then, contributing to an even lower density of the cohort in those sites.

Median height of spontaneous *E. globulus* plants in surveyed plots had a broad variation across sites (0.2–12.1 m). This fact could be related either with different times of recruitment or with differences among the sites where these plants were growing. As *E. globulus* age is difficult to determine (Williams and Brooker, 1997; Leal et al., 2004), the relationship between size and age of observed plants is partially speculative. Even so, plant size can be used for demographic interpretations in eucalypt communities (Florence, 1996). Therefore, the existence of continuous recruitment or occurrence of several recruitment episodes might explain the diversity of plant sizes observed in many sites and especially the abundance of smaller plants. Nevertheless, according to literature, it is probable that most of these plants have been recruited in the first year after fire, since: fire improves conditions for eucalypt recruitment (Cremer, 1965; Kirkpatrick, 1975; O'Dowd and Gill, 1984; Chambers and Attiwill, 1994; Stoneman, 1994; Gill, 1997); eucalypt seeds are short lived in soil (Jacobs, 1955; Cremer et al., 1984; Wellington and Noble, 1985b) and germinate as soon as they have favourable conditions to do so in nature (Penfold and Willis, 1961); and *E. globulus* plants take 4–7 years to produce their first seeds (Kirkpatrick, 1975; Turnbull and Pryor, 1984; Jordan et al., 1999) and 7 years to produce seeds after canopy burn (Kirkpatrick, 1975).

More than 95% of sampled individuals were of sizes 1 or 2, and were at most 6.77 m tall (height estimate based in Marques et al. (2011)). If we presume a major event of recruitment in the first year after fire, these plants were shorter than it would be expected (data from WebGlobulus 2.1 simulator (Palma, 2009)). Additionally, they were also much shorter than the resprouts of most of the coexisting burnt trees. Therefore, we may think about the former as dominated, suppressed or growth restricted trees (Skolmen and Ledig, 1990; Florence, 1996). Eucalypt lignotuberous seedlings/saplings are very resistant, therefore they can survive for long years in the understorey, and may be considered as a 'regeneration pool' in eucalypt forests (Florence, 1996; Ashton, 2000), since they can speed up growth after release from overstorey competition (Florence, 1996). If we consider the observed persistence of growth restricted *E. globulus* trees, their latent growth capacity, and their ability to attain reproductive state (pers. observ.); we may say that conditions might exist for natural perpetuation of this species in many surveyed sites. This means that the naturalization process (*sensu* Richardson et al. (2000)) is undergoing.

Plants with the above features are often used in forestry as advance growth (Jacobs, 1955; Florence, 1996; Alves et al., 2012), being a most important aspect of eucalypt forest regeneration cycle in Australia (Ashton, 2000). Although this practice is possible with *E. globulus* in Portugal, the species invasive potential in this territory (Marchante et al., 2008; Silva and Marchante, 2012) must be taken into account.

The height model indicated that productivity region and tillage were significant explanatory variables. Tillage also affected the size structure of the regenerating population. However, other non-studied variables might have significantly influenced the observed plant height.

Plants were taller in the highest productivity region. Climate factors (frost and water availability) that influence *E. globulus* growth, and consequently height, are the basis of this classification. Negative effect of water stress on *E. globulus* growth is broadly known (Wang et al., 1988; Tomé et al., 1994; Osório et al., 1998; Pita and Pardos, 2001; Humara et al., 2002). Actually, lack of water is the main limiting factor to *E. globulus* growth in Mediterranean type ecosystems (Alves et al., 2012), even though this species can deal with more severe water stress in Portugal and Spain than in its native range (Turnbull and Pryor, 1984; Alves et al., 2012). Cold is also an important limiting factor to *E. globulus* growth. Temperatures around 0 ± 2 °C inhibit water uptake and growth of *E. globulus* seedlings (Almeida et al., 1994; Costa-e-Silva et al., 2008). Our results on relative height of plants among productivity regions were obviously consistent with the rationale underlying classification produced by Ribeiro and Tomé (2000). They also coincide with the trends predicted by model Globulus 2.1 (Tomé et al., 2001).

Tillage had a negative effect on median height of plants. Wherever performed, this management operation also slightly affected the size structure of the cohort; it completely eliminated plants of sizes 3 and 4 and tended to favour the presence of size 1 plants. If we admit the existence of recruitment along time, since fire until sampling, many of the observed smaller plants might have established after tillage, while all or part of pre-existing plants was destroyed by tillage, both contributing to reduced median height of plants at sampling time at tilled sites. Tillage reduces nutrient availability in soil (Madeira et al., 1989). The synergetic effects of fire and tillage risk aggravating erosion even more (Coelho et al., 1995; Shakesby et al., 1996). Carneiro et al. (2008), found that harrowing reduced understorey development in *E. globulus* plantations and related it with reduction of nutrients in soil. The indirect effect of tillage hampering plant growth can be an additional explanation for lower plant median height at tilled sites.

Aspect, slope and topographic position influence incident solar radiation, water flow and soil erosion; whose effects on temperature, radiation, water and nutrients availability to plants may be determinants of their successful establishment and development (Jacobs, 1955; Moore et al., 1988; Shakesby et al., 1996; Kutiel and Lavee, 1999; Taiz and Zeiger, 2002; Pereira, 2007). Notably, none of topographical explaining variables was considered significant in any of the analyses. Similarly, Larcombe et al. (2013) found no significant influence of slope and aspect either on occurrence of natural establishment of *E. globulus* or on its density. This probably means that potential effects of topography on our response variables were overwhelmed by other factors effects, or even hidden by background noise of data.

The built models did not explain all the observed variability. Some other factors, like fire severity and intensity, might have affected observed establishment (Mount, 1969; Pryor, 1976; Florence, 1996; Gill, 1997; Martínez et al., 2002; Bailey et al., 2012), but they were not considered in this study because accurate evaluation of these features is not feasible 5–7 years after fire, when the study was done.

5. Conclusions

This study showed that the natural establishment of *E. globulus* was widespread in two types of burnt stands (pure *E. globulus* and mixed) and that this establishment was favoured by climatic conditions that enhance the productivity of this species. Considering the frequency of occurrence and the characteristics (presumable age, size, lignotuber) of observed plants, we can say that conditions for natural persistence of *E. globulus* were probably met in those types of stands in the studied regions. However, further studies are needed to assess the capacity that this type of plants has to complete the life cycle under the conditions they are growing at, in order to better understand the naturalization process of this species in Portuguese territory.

The use of a naturally regenerating cohort as advance growth for production purposes seems possible. Nevertheless, whenever this possibility is considered, the fact that *E. globulus* is an exotic species with some invasive potential in Portugal must be kept in mind.

On the other hand, the increased stand density that results from the existence of spontaneously established plants may have detrimental consequences in terms of forest management and may lead to a higher fire hazard. Attention should be paid to the very high prevalence of these plants in two of the studied stand types, regarding the wide distribution of *E. globulus* and the high incidence of forest fires in Portugal. Our results suggested that both the lack and the type of post-fire management operations strongly influenced seminal regeneration of *E. globulus* in burnt stands. Tillage has detrimental effects on this regeneration and may be considered in management programs for its control, in the geographical range of this study.

Mechanisms responsible for this species establishment are still poorly understood. It is not clear yet if post-fire recruitment of plants occurs mainly in a single initial recruitment event or in successive minor events or even if it is continuous along time. Comparative studies on this subject, either in burnt and unburnt areas, are needed to clarify the role of fire on this species recruitment and establishment. For instance: effects of fire severity and intensity on natural regeneration of the species are still unknown; and there is no quantitative evidence on the importance of fire-stimulated seed shed and how it interacts with post-fire management. Considering the wide expansion of *E. globulus* in the world, the study of such mechanisms is undoubtedly a fertile field for future research initiatives.

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References

AFN, 2009. Instruções para o Trabalho de Campo do Inventário Florestal Nacional – IFN 2005/2006. Autoridade Florestal Nacional, Lisbon.

AFN, 2010. Relatório Final do 5º Inventário Florestal Nacional. Autoridade Florestal Nacional, Lisbon.

Almeida, J.D., Freitas, H., 2006. Exotic flora of continental Portugal – a reassesment. Botanica Complutensis 30, 117–130.

Almeida, M.H., Chaves, M.M., Silva, J.C., 1994. Cold acclimation in eucalypt hybrids. Tree Phys. 14, 921–932.

Alves, A.M., Pereira, J.S., Correia, A.V., 2012. Silvicultura – A Gestão dos Ecossistemas Florestais. Fundação Calouste Gulbenkian, Lisbon.

Anderson, R.C., Brown, L.E., 1980. Influence of a prescribed burn on colonizing black locust. In: Garrett, H.E.C., G.S., (Ed.), Proc. Central Hardwood Forest Conference III. University MO, Columbus, pp. 330–336.

Andreu, J., Vila, M., Hulme, P.E., 2009. An assessment of stakeholder perceptions and management of noxious alien plants in Spain. Environ. Manage. 43, 1244–1255.

Arianoutsou, M., Vilà, M., 2012. Fire and invasive plant species in the Mediterranean basin. Israel J. Ecol. Evol. 58, 195–203.

Ashton, D., 1981. Fire in tall open-forests (wet sclerophyll forests). In: Gill, A.M., Groves, R.H., Noble, I.R. (Eds.), Fire and the Australian Biota. The Australian Academy of Science, Camberra, pp. 339–366.

Ashton, D.H., 2000. Ecology of eucalypt regeneration. In: Keane, P.J., Kile, G.A., Podger, F.D., Brown, B.N. (Eds.), Diseases and Pathogens of Eucalypts. CSIRO, Collingwood, pp. 47–60.

Bailey, T.G., Davidson, N.J., Close, D.C., 2012. Understanding the regeneration niche: microsite attributes and recruitment of eucalypts in dry forests. Forest Ecol. Manage. 269, 229–238.

Battaglia, M., Wilson, L.P., 1990. Effect of shelterwoods on stocking and growth of regeneration in dry high altitude *Eucalyptus delegatensis* forests. Aust. Forest. 53, 259–265.

Bjornstad, O.N., 2009. ncf: spatial nonparametric covariance functions. R package version 1.1-3.

Bowman, D.M.J.S., Kirkpatrick, J.B., 1986. Establishment, suppression and growth of *Eucalyptus delegatensis* R.T. Baker in multiaged forests. III. Intraspecific allelopathy, competition between adult and juvenile for moisture and nutrients, and frost damage to seedlings. Aust. J. Botany 34, 81–94.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Monographs 27, 325–349.

Calviño-Cancela, M., Rubido-Bará, M., 2013. Invasive potential of *Eucalyptus globulus*: seed dispersal, seedling recruitment and survival in habitats surrounding plantations. Forest Ecol. Manage. 305, 129–137.

Carneiro, M., Fabião, A., Martins, M., Fabião, A., Abrantes da Silva, M., Hilário, L., Lousã, M., Madeira, M., 2008. Effects of harrowing and fertilisation on understory vegetation and timber production of a *Eucalyptus globulus* Labill. plantation in Central Portugal. Forest Ecol. Manage. 255, 591–597.

Catry, F.X., Bugalho, M., Silva, J.S., Fernandes, P., 2010. Gestão da vegetação pós-fogo. In: Moreira, F., Catry, F.X., Silva, J.S., Rego, F. (Eds.), Ecologia do Fogo e Gestão de Áreas Ardidas. ISAPress, Lisbon.

Chambers, D.P., Attiwill, P.M., 1994. The ash-bed effect in *Eucalyptus regnans* forest: chemical, physical and microbiological changes in soil after heating or partial sterilisation. Aust. J. Botany 42, 739–749.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Coelho, C.O.A., Shakesby, R.A., Walsh, R.P.D., 1995. Effects of forest fires and post-fire land management practice on soil erosion and stream dynamics, Águeda basin, Portugal, Soil and groundwater research report V. In, Environment and quality of life. European Commission, Office for Official Publications of the European Communities, Luxembourg.

Costa-e-Silva, F., Shvaleva, A., Broetto, F., Ortuñuo, M.F., Rodrigues, M.L., Almeida, M.H., Chaves, M.M., Pereira, J.S., 2008. Acclimation to short-term low temperatures in two *Eucalyptus globulus* clones with contrasting drought resistance. Tree Physiol. 29, 77–86.

Cremer, K.W., 1965. Effects of fire of seedshed from *Eucalyptus regnans*. Aust. Forestry 29, 252–262.

Cremer, K.W., 1977. Distance of seed dispersal in eucalypts estimated from seed weights. Aust. Forest Res. 7, 225–228.

Cremer, K.W., Cromer, R.N., Florence, R.G., 1984. Stand establishment. In: Hillis, W.E., Brown, A.G. (Eds.), Eucalypts for Wood Production. CSIRO Academic Press, Melbourne, pp. 82–135.

DGRF, 2007. Estratégia Nacional para as Florestas. Imprensa Nacional-Casa da Moeda, Lisbon.

Fagg, P.C., 2001. Eucalypt Sowing and Seedfall. Native Forest Silviculture Guideline no. 8. Department of Natural Resources and Environment, Victoria, Melbourne.

FAO, 2010. Global forest resources assessment 2010. In: FAO Forestry Paper. Food and Agriculture Organization of the United Nations, Rome, pp. 340.

Fernandes, P.M., Loureiro, C., Palheiro, P., Vale-Gonçalves, H., Fernandes, M.M., Cruz, M.G., 2011. Fuels and fire hazard in blue gum (*Eucalyptus globulus*) stands in Portugal. Boletín del CIDEU, 53–61.

Florence, R.G., 1996. Ecology and Silviculture of Eucalypt Forests. CSIRO, Collingwood.

Fortin, M.-J., Dale, M.R.M.R.T., 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge.

Gassó, N., Basnou, C., Vilà, M., 2010. Predicting plant invaders in the Mediterranean through a weed risk assessment system. Biol. Invasions 12, 463–476.

Gill, A.M., 1997. Eucalypts and fires: interdependent or independent? In: Williams, J.E., Woinarski, J.C.Z. (Eds.), Eucalypt Ecology: Individuals to Ecosystems. Cambridge University Press, Cambridge, pp. 151–167.

Godinho-Ferreira, P., Azevedo, A., Rego, F., 2005. Carta da tipologia florestal de Portugal Continental. Silva Lusitana 13, 1–34.

González-Muñoz, N., Castro-Díez, P., Fierro-Brunnenmeister, N., 2011. Establishment success of coexisting native and exotic trees under an experimental gradient of irradiance and soil moisture. Environ. Manage. 48, 764–773.

Gordon, D.R., Flory, S.L., Cooper, A.L., Morris, S.K., 2012. Assessing the invasion risk of *Eucalyptus* in the United States using the Australian weed risk assessment. Int. J. Forest. Res. 2012, 1–7.

Humara, J.M., Casares, A., Majada, J., 2002. Effect of seed size and growing media water availability on early seedling growth in *Eucalyptus globulus*. Forest Ecol. Manage. 167, 1–11.

ICNF, 2013. IFN6 – Áreas dos usos do solo e das espécies florestais de Portugal Continental. Resultados preliminares. In: Instituto da Conservação da Natureza e das Florestas, Lisbon, pp. 33.

Jacobs, M.R., 1955. Growth Habits of the Eucalypts. Forest and Timber Bureau, Canberra.

Jordan, G.J., Potts, B.M., Wiltshire, R.J.E., 1999. Strong, independent, quantitative genetic control of the timing of vegetative phase change and first flowering in *Eucalyptus globulus* ssp. *globulus* (Tasmanian blue gum). Heredity 83, 179–187.

JRC, 2012. Forest fires in Europe Middle East and North Africa 2011. In: Joint Research Centre Sientific and Technical Reports. Joint Research Centre, Ispra, p. 108.

Kirkpatrick, J.B., 1975. Natural distribution of *Eucalyptus globulus* Labill. Aust. Geograph. 13, 22–35.

Kutiel, P., Lavee, H., 1999. Effect of slope aspect on soil and vegetation properties along an aridity transect. Israel J. Plant Sci. 47, 169–178.

Larcombe, M., Silva, J.S., Vaillancourt, R., Potts, B., 2013. Assessing the invasive potential of *Eucalyptus globulus* in Australia: quantification of wildling establishment from plantations. Biol. Invasions, 1–19.

Leal, S., Pereira, H., Grabnerz, M., Wimmert, R., 2004. Tree-ring structure and climatic effects in young *Eucalyptus globulus* Labill. grown at two Portuguese sites: preliminary results. Dendrochronologia 21, 139–146.

Legendre, P., Legendre, L., 1998. Numerical Ecology. Elsevier, Amsterdam.

López, M., Humara, J.M., Casares, A., Majada, J., 2000. The effect of temperature and water stress on laboratory germination of *Eucalyptus globulus* Labill. seeds of different sizes. Annal. Forest Sci. 57, 245–250.

Madeira, M., Melo, M., Alexandre, C., Steen, E., 1989. Effects of deep ploughing and superficial disc harrowing on physical and chemical soil properties and biomass in a new plantation of *Eucalyptus globulus*. Soil Tillage Res. 14, 163–175.

Mandle, L., Bufford, J., Schmidt, I., Daehler, C., 2011. Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. Biol. Invasions 13, 1815–1827.

Marchante, E., Freitas, H., Marchante, H., 2008. Guia Prático para a Identificação de Plantas Invasoras de Portugal Continental. Imprensa da Universidade de Coimbra, Coimbra.

Marques, S., Borges, J.G., Garcia-Gonzalo, J., Moreira, F., Carreiras, J.M.B., Oliveira, M., Cantarinha, A., Botequim, B., Pereira, J.M.C., 2011. Characterization of wildfires in Portugal. Euro. J. Forest Res. 130, 775–784.

Martínez, E., Madrigal, J., Hernando, C., Guijarro, M., Vega, J., Pérez-Gorostiaga, P., Fonturbel, M., Cuiñas, P., Alonso, M., Beloso, M., 2002. Effect of fire intensity on seed dispersal and early regeneration in a *Pinus pinaster* forest. In: Viegas, D.X. (Ed.), Forest Fire Research and Wildland Fire Safety: IV International Conference on Forest Fire Research 2002. Wildland Fire Safety Summit, Luso, Coimbra.

McIver, J.D., Starr, L.L., 2000. Environmental effects of post-fire logging: literature review and annotated bibliography. In: General Technical Report. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland.

MCPFE, 2007. State of Europe's Forests 2007 – the MCPFE report on sustainable forest management in Europe. In: Ministerial Conference on the Protection of Forests in Europe. UNECE, FAO, Warsaw.

Moore, I., O'Loughlin, E., Burch, G., 1988. A contour-based topographic model for hydrological and ecological applications. Earth Surf. Proc. Landforms 13, 305–320.

Moreira, F., Vaz, P., Catry, F., Silva, J.S., 2009. Regional variations in wildfire preference for land cover types in Portugal: implications for landscape management to minimize fire hazard. Int. J. Wildland Fire 18, 563–574.

Mount, A., 1964. The interdependence of the eucalypts and forest fires in southern Australia. Aust. Forest. 28, 166–172.

Mount, A., 1969. Eucalypt ecology as related to fire. In: Proceedings of Tall Timbers Fire Ecolology Conference, pp. 75–108.

Nunes, M.C.S., Vasconcelos, M.J., Pereira, J.M.C., Dasgupta, N., Alldredge, R.J., 2005. Land cover type and fire in Portugal: do fires burn land cover selectively? Landscape Ecol. 20, 661–673.

O'Dowd, D.J., Gill, A.M., 1984. Predator satiation and site alteration following fire: mass reproduction of alpine ash (*Eucalyptus delegatensis*) in southeastern Australia. Ecology 64, 1052–1066.

Osório, J., Osório, M., Chaves, M., Pereira, J., 1998. Water deficits are more important in delaying growth than in changing patterns of carbon allocation in *Eucalyptus globulus*. Tree Physiol. 18, 363–373.

Palma, J.H.N., 2009. WebGlobulus 2.1: a web-based interface to project *Eucalyptus globulus* stands in Portugal. In: <http://home.isa.utl.pt/~joaopalma/modelos/globulus/> (retrieved in 10.10.13).

Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Model. 133, 225–245.

Penfold, A.R., Willis, J.L., 1961. The Eucalypts – Botany, Cultivation, Chemistry and Utilization. Leonard Hill [Books] Limited, London.

Pereira, J.S., 2007. Uma espécie altamente produtiva. In: Silva, J.S. (Ed.), Pinhais e Eucaliptais, a Floresta Cultivada. Público, FLAD, LPN, Lisbon, pp. 167–183.

Pita, P., Pardos, J.A., 2001. Growth, leaf morphology, water use and tissue water relations of *Eucalyptus globulus* clones in response to water deficit. Tree Physiol. 21, 599–607.

Potts, B.M., Vaillancourt, R.E., Jordan, G.J., Dutkowski, G.W., Costa e Silva, J., McKinnon, G.E., Steane, D.A., Volker, P.W., Lopez, G.A., Apiolaza, L.A., Li, Y., Marques, C., Borralho, N.M.G., 2004. Exploration of the *Eucalyptus globulus* gene pool. In: Borralho, N.M.G., Pereira, J.S., Marques, C., Coutinho, J., Madeira, M., Tomé, M. (Eds.), *Eucalyptus* in a Changing World – IUFRO Conference. RAIZ, Instituto Investigação de Floresta e Papel, Aveiro, pp. 46–61.

Primer-e, 2002. Primer 5 for Windows, version 5.2.9. In: Primer-e.

Pryor, L.D., 1976. The Biology of Eucalypts. Edward Arnold, London.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Radich, M.C., 2007. Introdução e expansão do eucalipto em Portugal. In: Silva, J.S. (Ed.), Pinhais e Eucaliptais, a Floresta Cultivada. Público, FLAD, LPN, Lisbon, pp. 151–165.

Core Team R, 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Ribeiro, F., Tomé, M., 2000. Classificação climática de Portugal Continental, baseada em informação do Atlas do Ambiente. Revista de Ciências Agrárias 23, 39–50.

Richards, M.B., Lamont, B.B., 1996. Post-fire mortality and water relations of three congeneric shrub species under extreme water stress – a trade-off with fecundity? Oecologia 107, 53–60.

Richardson, D.M., 1998. Forestry trees as invasive aliens. Conser. Biol. 12, 18–26.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Diver. Distribut. 6, 93–107.

Ritter, M., Yost, J., 2009. Diversity, reproduction, and potential for invasiveness of *Eucalyptus* in California. Madroño 56, 155–167.

Ryder, N.B., 1965. The cohort as a concept in the study of social change. Am. Sociol. Rev. 30, 843–861.

Schaie, K.W., 1984. Historical time and cohort effects. In: McCluskey-Fawcett, K.A., Reese, H.W. (Eds.), Life-span developmental psychology: historical and generational effects. Academic Press, New York, pp. 1–15.

Shakesby, R.A., Boakes, D.J., Coelho, C.D.O., Gonçalves, A.J., Walsh, R.P., 1996. Limiting the soil degradational impacts of wildfire in pine and eucalyptus forests in Portugal: a comparison of alternative post-fire management practices. Appl. Geogr. 16, 337–355.

Silva, J.S., Marchante, H., 2012. Post-fire management of exotic forests. In: Moreira, F., Heras, J., Corona, P., Arianoutsou, M. (Eds.), Post-Fire Management and Restoration of Southern European Forests. Springer, Dordrecht, pp. 223–255.

Silva, J.N., Feith, H., Pereira, J.C., 2007a. Exploração e silvicultura pós-fogo em eucaliptais. In: Alves, A.M., Pereira, J.S., Silva, J.N. (Eds.), O Eucaliptal em Portugal – Impactes Ambientais e Investigação Científica. ISAPress, Lisbon, pp. 285–312.

Silva, J.S., Sequeira, E., Catry, F., Aguiar, C., 2007b. Os contras. In: Silva, J.S. (Ed.), Pinhais e Eucaliptais, a Floresta Cultivada. Público, FLAD, LPN, Lisbon, pp. 221–259.

Silva, J.S., Moreira, F., Vaz, P., Catry, F., Godinho-Ferreira, P., 2009. Assessing the relative fire proneness of different fores types in Portugal. Plant Biosyst. 143, 597–608.

Silva, J.S., Vaz, P., Moreira, F., Catry, F., Rego, F.C., 2011. Wildfires as a major driver of landscape dynamics in three fire-prone areas of Portugal. Landscape Urban Plan. 101, 349–358.

Sing, T., Sander, O., Beerenwinkel, N., Lengauer, T., 2009. ROCR: visualizing the performance of scoring classifiers. R package version 1.0-4.

Skolmen, R.G., Ledig, T., 1990. *Eucalyptus globulus* Labill. bluegum eucalyptus. In: Burns, R.H., B. (Ed.), Silvics of North America – Hardwoods. United States Department of Agriculture, Washington, DC, pp. 299–304.

Soares, P., Tomé, M., Pereira, J.S., 2007. A produtividade do eucaliptal. In: Alves, A.M., Pereira, J.S., Silva, J.M.N. (Eds.), O Eucaliptal em Portugal – Impactes Ambientais e Investigação Científica. ISAPress, Lisbon, pp. 27–60.

Stoneman, G.L., 1994. Ecology and physiology of establishment of eucalypt seedlings from seed: a review. Aust. Forest. 57, 11–29.

Stoneman, G.L., Dell, B., Turner, N.C., 1994. Mortality of *Eucalyptus marginata* (jarrah) seedlings in Mediterranean-climate forest in response to overstorey, site, seedbed, fertilizer application and grazing. Aust. J. Ecol. 19, 103–109.

Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science 240, 1285–1293.

Taiz, L., Zeiger, E., 2002. Plant Physiology. Sinauer, Sunderland.

Tomé, M., 2000. Wood and non-wood production from plantation forests. In: Greene, T. (Ed.), Ecological and Socio-Economic Impacts of Close-to-Nature Forestry and Plantation Forestry: A Comparative Analysis. Scientific Seminar of the 7th Annual EFI Conference. European Forest Institute, Lisbon, pp. 37–55.

Tomé, M., Tomé, J.A., Araújo, M.C., Pereira, J.S., 1994. Intraspecific competition in irrigated and fertilized eucalypt plantations. Forest Ecol. Manage. 69, 211–218.

Tomé, M., Ribeiro, F., Soares, P., 2001. Modelo Globulus 2.1. In: Relatórios técnico-científicos do GIMREF. Departamento Engenharia Florestal, Instituto Superior de Agronomia, Lisboa, pp. 96.

Turnbull, J.W., Pryor, L.D., 1984. Choice of species and seed sources. In: Hillis, W.E., Brown, A.G. (Eds.), Eucalypts for Wood Production. CSIRO Academic Press, Melbourne, pp. 6–65.

Vallejo, V.R., Arianoutsou, M., Moreira, F., 2012. Fire ecology and post-fire restoration approaches in Southern European forest types. In: Moreira, F., Arianoutsou, M., Corona, P., Heras, J. (Eds.), Post-Fire Management and Restoration of Southern European Forests. Springer Verlag, Dordrecht, pp. 93–119.

Virtue, J.G., Melland, R.L., 2003. The Environmental Weed Risk of Revegetation and Forestry Plants. Department of Water Land and Biodiversity Conservation, Adelaide.

Wang, D., Bachelard, E.P., Banks, J.C.G., 1988. Growth and water relations of seedlings of two subspecies of *Eucalyptus globulus*. Tree Physiol. 4, 129–138.

Wellington, A.B., Noble, I.R., 1985a. Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. J. Ecol., 645–656.

Wellington, A.B., Noble, I.R., 1985b. Seed dynamics and factors limiting recruitment of the mallee *Eucalyptus incrassata* in semi-arid, south-eastern Australia. J. Ecol., 657–666.

Whelam, R.J., 1995. The Ecology of Fire. Cambridge University Press, Cambridge.

Whelam, R.J., Main, A.R., 1979. Insect grazing and post-fire plant succession in south-west Australian woodland. Aust. J. Ecol. 9, 387–398.

Williams, J.E., Brooker, M.I.H., 1997. Eucalypts: an introduction. In: Williams, J.E., Woinarski, J.C.Z. (Eds.), Eucalypt Ecology: Individuals to Ecosystems. Cambridge University Press, Cambridge, pp. 1–15.

Xanthopoulos, G., Calfapietra, C., Fernandes, P., 2012. Fire hazard and flammability of European forest types. In: Moreira, F., Heras, J., Corona, P., Arianoutsou, M. (Eds.), Post-Fire Management and Restoration of Southern European Forests, pp. 79–92.

Zar, J., 1996. Bistatistical Analysis. Prentice Hall, Upper Saddle River.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Verlag, New York.