CSIRO PUBLISHING

International Journal of Wildland Fire **2013**, *22*, 919–932
http://dx.doi.org/10.1071/WF12215

Post-fire response variability in Mediterranean Basin tree species in Portugal

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Abstract. Fire is the most important natural disturbance driving vegetation dynamics in the Mediterranean Basin. However, studies relating fire-induced tree responses to both fire severity and plant traits are still scarce in this region. We aimed to investigate such relationships further and to develop simple models that could help improve forest management in these fire-prone ecosystems. We compiled data from 16 fire sites in different regions and used models to relate post-fire responses of 4155 trees from 14 species with fire severity indicators and tree characteristics. The influence of several spatiotemporal factors at the site level was also considered. Results showed that pine mortality was usually high and mainly determined by fire severity, whereas plant traits played a minor role. In contrast, mortality of broadleaved trees was usually low, even for high-severity fire, but most trees were top-killed. Stem mortality increased with fire severity and decreased with bark thickness and tree size. The models for predicting individual mortality of pines and stem mortality of broadleaves showed very good performance, including when validated against independent datasets. Our results suggest that it is possible to accurately predict the most common post-fire responses of Mediterranean species based on simple fire and tree characteristics.

Additional keywords: broadleaves, experimental fire, modelling, mortality, pines, top-kill, wildfire.

Received 14 December 2012, accepted 20 March 2013, published online 23 July 2013

Introduction

Fire is the most important natural disturbance driving vegetation dynamics in Mediterranean Basin ecosystems (Pausas and Keeley 2009; Keeley *et al.* 2012), causing important economic and ecological impacts. Wildfires can quickly transform forest landscapes by reducing vegetation biomass and drastically changing forest structure and composition. Therefore, understanding the way trees respond to fire is crucial to understanding forest dynamics and biogeochemical processes in Mediterranean ecosystems, which are among the most fire-prone in the world (Keeley *et al.* 2012).

For a given species, fire severity (i.e. the level of the consumption or degradation of biomass by fire, Keeley 2009) is expected to be a primary factor determining post-fire plant response. For trees, variables indicative of fire-caused injury to the stem and crown (i.e. aboveground fire severity) are the most widely used indicators of fire severity. Char height correlates with flame size or fire intensity (e.g. Finney and Martin 1993) and indirectly provides information on possible injury to cambial tissue or foliage (Regelbrugge and Conard 1993; Pausas *et al.* 2003; Thies *et al.* 2006; Catry *et al.* 2012; Woolley *et al.* 2012). Other measures such as crown scorched, consumed or both crown scorched and consumed have been extensively used, particularly for conifers, linking fire intensity to the loss of photosynthetic material and subsequent tree mortality (e.g. Peterson and Ryan 1986; Sieg *et al.* 2006; Catry *et al.* 2010; Vega *et al.* 2011).

The species characteristics that determine the way trees respond to fire include plant resprouting ability (i.e. resprouter or non-resprouter), tree size and bark thickness. Resprouting refers to the initiation of new shoots from existing meristems after the aboveground parts of a plant have been fully affected by fire (e.g. charred to the top and totally defoliated); this trait allows plant populations and individuals to persist under recurrent fires (Bond and Midgley 2001; Pausas *et al.* 2004). This trait, which is common in all Mediterranean broadleaves and is very rare in conifers (Paula *et al.* 2009; He *et al.* 2012), has often been used to separate species into two functional types: resprouters and non-resprouters (Pausas *et al.* 2004; Vesk and Westoby 2004). However, after a disturbance that affects all aboveground plant parts, not all individuals of resprouting species survive (e.g. Moreira *et al.* 2012).

There are several plant morphological traits conferring resistance to fire, but bark thickness and tree size (height and diameter) have been the most widely used to account for resistance to fire injury in different ecosystems worldwide (Ryan and Reinhardt 1988; Fernandes *et al.* 2008; Catry *et al.* 2009; Brando *et al.* 2012; Woolley *et al.* 2012). These individual characteristics vary among species but also vary through time (tree age and growth) and space (site conditions), and are often correlated (Whelan 1995). Although thick bark has been associated with lower levels of tree injury for many species subjected to surface fire regimes (Keeley and Zedler 1998; van Nieuwstadt and Sheil 2005; Brando *et al.* 2012; He *et al.* 2012), the role of stem survival for resprouters in crown-fire ecosystems remains poorly understood (for important exceptions see e.g. Pausas 1997; Catry *et al.* 2012). Additionally, and adding further complexity, post-fire tree responses can also be affected by temporal and spatial factors such as the physiological condition of the trees when the fire occurs (Whelan 1995; Moreira *et al.* 2012), the site edapho-climatic conditions, or the occurrence and intensity of additional stressing factors, such as drought, insects and diseases (e.g. DeBano *et al.* 1998; Sieg *et al.* 2006; Vega *et al.* 2011).

Knowledge of the factors responsible for fire-resistance and prediction of tree mortality and regeneration is critical to inform pre- and post-fire management decisions, particularly in ecosystems where wildfires are a recurrent disturbance (Thies and Westlind 2012; Woolley *et al.* 2012). Nevertheless, studies relating individual tree post-fire responses to both fire and plant characteristics are still scarce in Mediterranean Basin, being particularly rare for broadleaved species.

In this study we aim to investigate the main factors associated with post-fire tree mortality and vegetative regeneration of several Mediterranean species. Our hypothesis is that variability in post-fire responses can be predicted from simple variables related to fire severity and tree traits conferring resistance and resilience to fire. To test this hypothesis, we assessed the post-fire regeneration status of 4155 trees belonging to 14 species from the western Iberian Peninsula and analysed their relations with fire severity and tree characteristics.

Methods

Study sites

We compiled data from 16 different burned forests in Portugal, western Mediterranean Basin (Fig. 1), including 11 sites that were affected by summer wildfires (July through September, i.e. dry season), and five sites that were burnt by 15 experimental fires under mild fire weather during fall and winter (November through March). The sample covers a range of ecological conditions and forest types from inland to coastal regions, with mean annual temperatures ranging from 10 to 17.5°C and precipitation ranging from 500 to 2000 mm (Instituto do Ambiente 2012).

Sampling and data collection

Data were collected during the first 3 years following fire, but most (98.6%) trees were assessed during the first 2 years (Table A1 in the Appendix). In most (64%) sites affected by wildfires we used a regular grid of points covering the burned area and defined a circular sampling plot (7850 m^2) around each

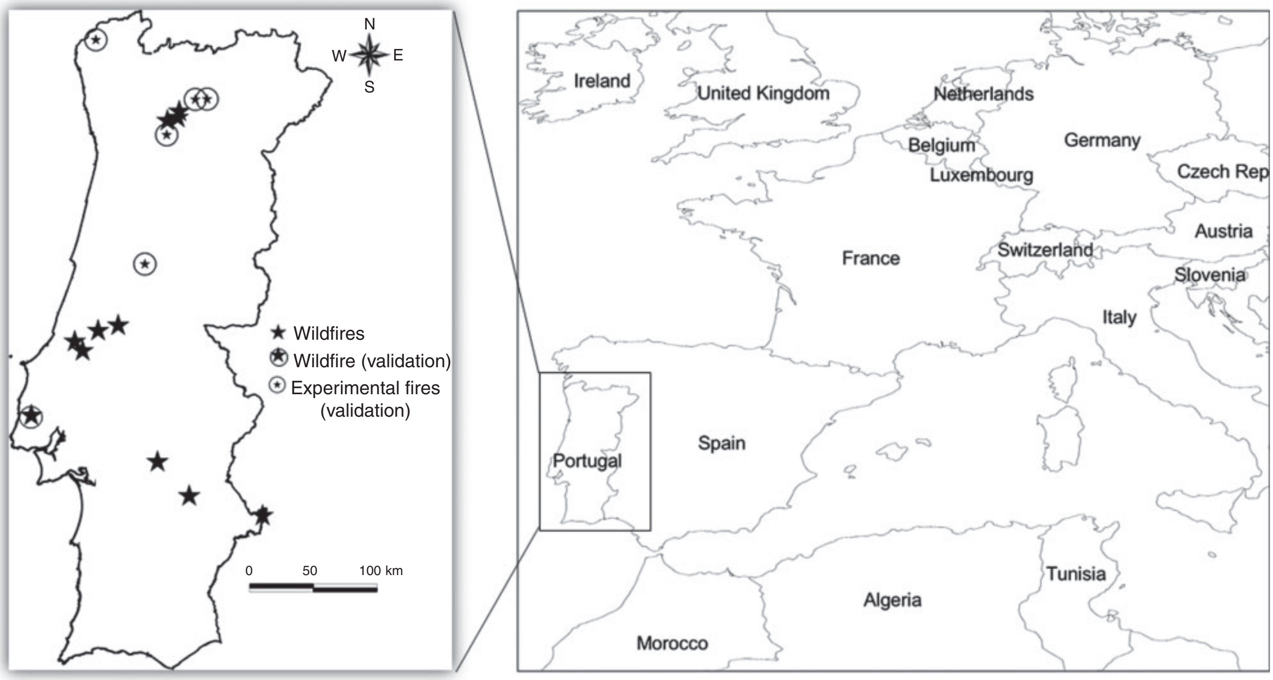

Fig. 1. General location of Portugal within the Mediterranean Basin (right) and location of the 16 study sites (left).

point. In plots with 30 trees or less, all trees inside the plot were assessed. Otherwise, we laid out up to four strip transects and sampled 30 individuals per plot. In the remaining sites, plots were smaller (ranging from 28 to 2000 m^2) and all trees inside each plot were sampled. In total, 192 plots were sampled across the 11 wildfire sites (Table A1). Two sampling schemes were used in the sites subjected to experimental fire: (1) the measurement of all trees within 200–500-m^2 rectangular plots and (2) the measurement of a variable number of trees (representative of variation in size and fire severity) in 1000–2000-m^2 rectangular plots. In all cases, only trees with at least 1-cm diameter at breast height (DBH) were included. The wildfire sites included 2843 individuals belonging to 13 tree species (11 broadleaves and two pines), and the sites subjected to experimental fire included 1312 trees belonging to two pine species (Table 1). Overall we sampled 4155 trees from 14 species belonging to eight genus and six taxonomic families. Species were classified by their resprouting ability (RS; resprouter *v.* non-resprouter) and leaf habit (LH; evergreen *v.* deciduous); all the studied broadleaved species were resprouters and all the studied coniferous species (pines) were non-resprouters (Table A2).

In each site, and for all selected trees, we recorded the species and assessed the tree post-fire vegetative status (dead or alive) and regeneration type. Trees were considered alive whenever green foliage was present, regardless of its location on the tree. The surviving individuals were classified as having: (1) stem mortality (top-kill), i.e. resprouting from belowground organs only (root collar or roots) or (2) stem survival, i.e. resprouting from aboveground organs (crown or stem). We also measured total tree height (H) and DBH in each tree. For *Q. suber* trees, we measured bark thickness (BT) at 1.30 m, as in this species BT is rarely affected by fire. For the other 13 species, BT was not measured directly on burned trees because the bark is often partially consumed by fire and may detach from the stem. For these species we estimate BT for each burned tree from allometric equations derived from nearby unburned trees (Table A3).

We assessed two fire severity indicators at the individual tree level: the proportion of maximum tree height charred (PHC) and the proportion of crown volume damaged (PCD). In all wildfires, the maximum bole char height (the vertical extent of blackening of the outer bark i.e. the lee side of the tree) was measured in each tree. Then, PHC was calculated as maximum char height relative to total tree height. For pines, we estimated PCD visually, because direct indicators of crown damage have been consistently reported to be the best predictors of mortality for conifers (e.g. Woolley *et al.* 2012). PCD included both the crown volume scorched and consumed (McHugh and Kolb 2003), as this combined variable was reported to describe well crown injury, often better than using the two variables separately (Catry *et al.* 2010; Vega *et al.* 2011). In the experimental fires, PCD was the only fire severity indicator assessed.

For wildfire sites, we assessed several environmental variables at the site level. Specifically, the dominant slope (%) and aspect were measured in each plot or transect; then, for each site, slope was averaged, whereas aspect was simplified as the proportion of trees in unfavourable aspects (i.e. S, SE or SW, which have drier conditions in the study area). We also used GIS to locate all the study sites (both wildfire and experimental fire sites) and obtain additional site-level data, namely elevation, mean annual precipitation and mean annual temperature (Instituto do Ambiente 2012). Fires were grouped by month of occurrence: July, August or September, corresponding to early, mid and late summer. The time between the fire date and tree assessment ranged from 1 to 3 years. The Canadian Fire Weather Index was calculated using data from the nearest meteorological station (collected at 1200 hours on fire day) and it was included as a descriptor of potential fire behaviour (Table A1).

Data analysis and model development

To study the relationships between the post-fire tree responses (dead tree, dead stem with basal resprouting, live stem with regenerating crown) and the different explanatory variables that have variability at the tree level, we followed a nested approach. We started by analysing all species together (overall model) to assess the effect of the tree-level (PHC, PCD, BT, DBH, H) and species-level (RS and LH) variables on individual mortality (i.e. whole-plant mortality). Then, we focussed on broadleaves and conifers separately (functional-group models). Broadleaf post-fire responses were investigated following a two-step sequential model (Pausas 1997): the probability of individual tree mortality and the probability of stem mortality for surviving trees (i.e. basal resprouting). For conifers, a single-step model (i.e. whether trees died or survived) was enough to describe their post-fire responses, because the studied pine species do not resprout. For these analyses, we used 1863 trees from eight species recorded in 10 sites (hereafter, the development dataset; see Table A2), corresponding to the wildfire dataset excluding the Mafra fire, which was reserved for model validation (see next section). Finally, we fitted individual models for each species using the entire wildfire dataset, for assessing the potential existence of species-specific trends in post-fire responses.

This data analysis approach was performed using binomial generalised linear mixed-effects models (GLMM) with a logit link, using the lme4-package for R (Bates *et al.* 2009; Zuur *et al.* 2009). In the overall and functional-group models we used both site and species as random factors, whereas in the single-species models we used site as random factor. Prior to GLMM, correlation between pairs of variables was checked using the Pearson correlation coefficient (between continuous variables) and the point biserial correlation (between continuous and dichotomous variables); when correlation was greater than 0.60, only one variable was used in order to avoid colinearity problems (Zuur *et al.* 2009). We included a quadratic term for DBH and BT in the models in order to consider more complex post-fire tree responses (McHugh and Kolb 2003). For each response type we started with a GLMM including all variables. Model selection was performed by removing, in each step, the variable that explained less deviance (backward elimination; Zuur *et al.* 2009), until all remaining variables in the model were significant ($P < 0.05$). Finally, to assess the relative contribution of each variable, the selected models were evaluated by adding all significant variables sequentially and tested with a likelihood ratio test. The Nagelkerke pseudo-R^2 (Nagelkerke 1991) was used as an indicator of the proportion of variance explained by the models. Finally, model performance was assessed by

Table 1. Summary of the main tree characteristics for the 14 species in the 16 study sites

Fire type, whether trees were sampled in a wildfire site or a site subjected to experimental fire; Sample, number of trees assessed from each species; Sites, code of the fire sites where trees were assessed (details of each site are given in Table A1); DBH, diameter at breast height (cm); H, tree height (m); BT, bark thickness (cm); PHC, maximum char height expressed as percentage of tree height (%); PCD, percentage of crown volume damaged (%); $\bar{x}$ (s.d.), mean (standard deviation)

Fire type	Sample	Sites	DBH (cm)		H (m)		BT (cm)		PHC (%)		PCD (%)	
Species	(n trees)		$\bar{x}$ (s.d.)	Range	$\bar{x}$ (s.d.)	Range	$\bar{x}$ (s.d.)	Range	$\bar{x}$	Range	$\bar{x}$	Range
Wildfire												
A. unedo	92	AG, AT, BA, PM, VF	11.0 (6.0)	5–41	6.3 (2.5)	3–15	0.6 (0.2)	0.4–1.4	85	15–100	100	100
C. monogyna	133	TM	17.8 (7.1)	5–41	4.0 (1.1)	2–8	0.9 (0.2)	0.4–1.6	95	17–100	100	100
C. sativa	30	TM	21.0 (7.5)	10–38	7.5 (2.1)	4–11	1.2 (0.4)	0.6–2.1	31	6–75	100	90–100
F. angustifolia	82	TM	41.4 (13.7)	10–76	11.3 (3.6)	5–18	2.0 (0.6)	0.6–3.4	59	7–100	99	65–100
O. europaea	159	BA, TM	19.3 (10.0)	3–54	4.6 (1.4)	1–10	1.0 (0.3)	0.4–2.2	97	25–100	100	100
P. lentiscus	113	TM	7.8 (3.8)	3–20	2.4 (0.8)	1–5	0.5 (0.2)	0.2–1.1	97	33–100	100	100
P. pinaster	437	AG, AT, PM, TM, VF	26.3 (14.0)	7–101	14.2 (4.2)	5–25	2.9 (1.4)	0.8–9.2	59	3–100	84	10–100
P. pinea	80	AG, TM	47.5 (16.1)	16–92	12.4 (2.6)	3–17	4.7 (1.5)	1.7–9.0	69	20–100	92	50–100
Q. coccifera	120	TM	12.8 (5.7)	4–30	3.8 (1.3)	1–8	0.6 (0.2)	0.2–1.2	99	42–100	100	60–100
Q. faginea	226	AG, AT, PM, TM, VF	30.1 (15.6)	10–94	8.9 (2.9)	3–19	1.6 (0.5)	0.9–3.1	77	5–100	95	10–100
Q. pyrenaica	528	LO, MA, SI	9.7 (5.4)	2–42	7.3 (2.5)	2–18	0.4 (0.1)	0.1–1.4	71	1–100	–	–
Q. rotundifolia	494	AG, AT, BA, PM, VF	16.5 (9.5)	5–58	5.9 (1.6)	2–11	1.2 (0.4)	0.6–2.8	85	6–100	98	10–100
Q. suber	349	AG, BA, EV, PO, TM, VF	28.1 (18.4)	10–140	7.1 (2.6)	3–16	3.2 (1.7)	0.5–14.3	90	18–100	97	10–100
All	2843	All	20.4 (15.0)	2–140	7.8 (4.2)	1–25	1.6 (1.5)	0.1–14.3	79	1–100	95	10–100
Experimental fire												
P. nigra	259	MO	8.1 (3.0)	2–16	4.5 (1.5)	2–13	0.5 (0.3)	0.1–1.3	–	–	76	30–100
P. pinaster	1053	LA, PA, TI, VC	8.0 (4.3)	1–24	6.1 (2.9)	1–13	1.0 (0.6)	0.1–3.3	–	–	64	10–100
All	1312	All	8.0 (4.0)	1–24	5.8 (2.8)	1–13	0.9 (0.6)	0.1–3.3	–	–	66	10–100

Table 2. Synthesis of the selected combined-species models

Main variables affecting tree post-fire responses and model evaluation results (below are the results of model validation using independent datasets).PHC, maximum char height expressed as percentage of tree height (%); PCD, percentage of crown volume damaged (%); BT, bark thickness (cm); DBH, diameter at breast height (cm); H, tree height (m); RS, resprouter (no *v.* yes); PHC × RS, interaction between PHC and RS; ROC AUC, area under the receiver operating characteristics curve; R^2, Nagelkerke R^2; CC, cross-classification – overall accuracy (%). Variables are significant at: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Response type	Species	Development dataset						Validation dataset			
		Response (%)	Model	n trees	Variables	ROC AUC	R^2	n trees	Fire type	ROC AUC	CC (%)
Individual mortality	All species	23.4	OM	1863	PHC (+)***; RS (–)*; BT (–)***; PHC*RS***	0.91	0.29	980	Wildfire	0.93	96.8
	Pines (non-resprouters)	74.2	PM1	383	PHC (+)***	0.96	0.69	134	Wildfire	0.93	87.3
			PM2	383	PCD (+)***	0.98	0.83	134	Wildfire	0.88	82.8
								1312	Experimental	0.96	87.8
	Broadleaves (resprouters)	10.3	BM	1480	PHC (+)***; BT (–)*	0.79	0.08	846	Wildfire	0.17	98.9
Stem mortality	Broadleaves (resprouters)	54.9	BSM	1328	PHC (+)***; BT (–)***; H (–)***	0.93	0.47	837	Wildfire	0.94	88.1

calculating the area under the receiver operating characteristics (ROC) curve (Hosmer and Lemeshow 2000; Pearce and Ferrier 2000). The ROC method has advantages in assessing model performance in a threshold-independent fashion, being independent of prevalence (Manel *et al.* 2001). Area under the ROC curve (AUC) values of 0.7–0.9 usually indicate useful applications and values above 0.9 indicate high accuracy (Swets 1988).

In order to explore to what extent random (site-level) effects in the GLMM could be related to environmental variables, we extracted the coefficients for each site for the different models and correlated them with the environmental variables in each site (Bates *et al.* 2009). For categorical variables, a non-parametric correlation test was used. For this analysis we used the entire wildfire dataset.

External model validation

Two independent validation datasets were used to further evaluate the performance of the overall and functional-group models: one wildfire subset and the experimental fire dataset. The wildfire validation subset came from the Mafra wildfire, which included 980 trees from 10 species (Tables 1, A1). We selected this wildfire site because it included the largest number of sampled trees and the largest number of species representing both pines and broadleaves. Additionally, we used the pooled data from 15 experimental fires that included 1312 trees belonging to two pine species (Tables 1, A1). This dataset represented an opportunity to assess the performance of pine mortality models under mild fire weather similar to prescribed fire conditions.

Agreement between model predictions and observed responses was evaluated using ROC curve analysis and cross-classification tables. For cross-classification analysis, a 0.5 probability threshold (cut-point) was used to convert event probability (mortality or top-kill) to dichotomous (presence or absence) data (e.g. Hosmer and Lemeshow 2000; Thies and Westlind 2012). If the estimated probability exceeds the cut-point the tree is predicted to die or to have stem mortality.

Results

Our sampling captured a wide range of tree species and individual tree characteristics, as well as varying levels of fire severity and site conditions (see Tables 1, A1). From 2843 trees in the wildfire dataset (11 sites, 13 species), most were severely affected (average PHC of 79%; Table 1). This is characteristic of summer wildfires in the Mediterranean region. Overall average individual tree mortality was 19.4%, but it was highly variable, being much higher among pines (75.6%) than among broadleaved species (6.9%). However, despite the relatively low mortality of broadleaves, 59.9% of the surviving individuals were top-killed and resprouted from basal buds only (i.e. stem mortality).

Overall mortality models

The best model for predicting overall tree mortality (model OM) included the interaction between PHC and RS, and BT, by decreasing order of importance (Tables 2, A4). Individual tree mortality increased with increasing PHC, but this variable had a much stronger effect on the mortality of pines than on broadleaves (significant interaction; Fig. 2). Tree mortality also decreased with increasing BT, although this variable was less important and accounted for little additional variation in the model (Table A6).

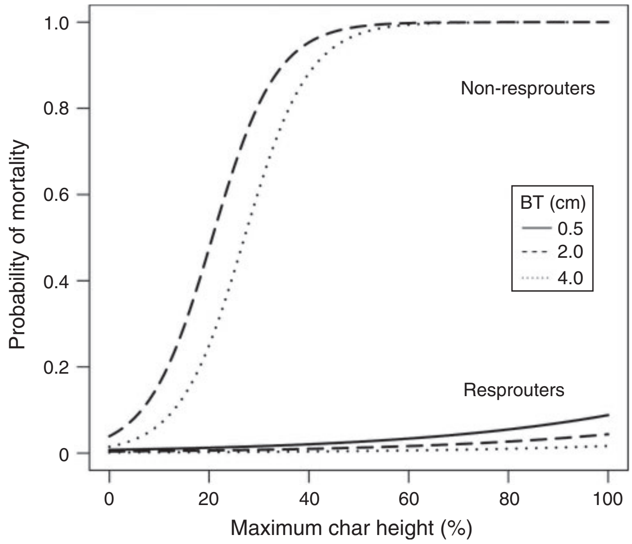

Fig. 2. Predicted probability of post-fire mortality for resprouters (broadleaves) and non-resprouters (pines) as a function of fire severity (expressed by the proportion of maximum tree height charred, PHC) and bark thickness (BT). Model OM based on data from 1863 trees (eight species) sampled in 10 wildfire sites (model AUC = 0.91).

Model performance was very good, even when applied to the independent wildfire validation subset (AUC = 0.93; Table 2). Global accuracy was 96.8% as shown by the cross-classification evaluation; within this subset, 84.0% of the trees predicted to die were in fact dead 1 year following fire and 98.7% of the trees were correctly predicted to survive (Table A7).

Pine mortality models

The best mortality model for pines included a fire severity indicator only. Both PHC and PCD were positively related with tree mortality (models PM1 and PM2; Tables 2, A4). Because PCD and PHC were highly correlated ($r = 0.64$) they were not used together in the same model, but we fitted separate models to compare their performance. Both models performed very well, although a model with PCD (model PM2; Fig. 3) achieved better results (AUC = 0.98 and $R^2 = 0.83$; Table 2).

When applied to the independent wildfire validation subset, the performance of these models decreased but was still good (Table 2). The cross-classification evaluation shows that, using any of the two fire severity indicators, nearly 88% of the trees were correctly predicted to die (Table A7); however, when using the model with PHC more trees were correctly predicted to survive (81.3 *v.* 58.3), resulting in higher global accuracy (87.3% *v.* 82.8%).

In contrast, when applied to the experimental fires the model with PCD globally performed better than when applied to the wildfire validation dataset, but the proportion of trees correctly predicted to die was lower in the former case (68.1 *v.* 88.2%; Tables 3, A7). Because of this considerably poorer ability to

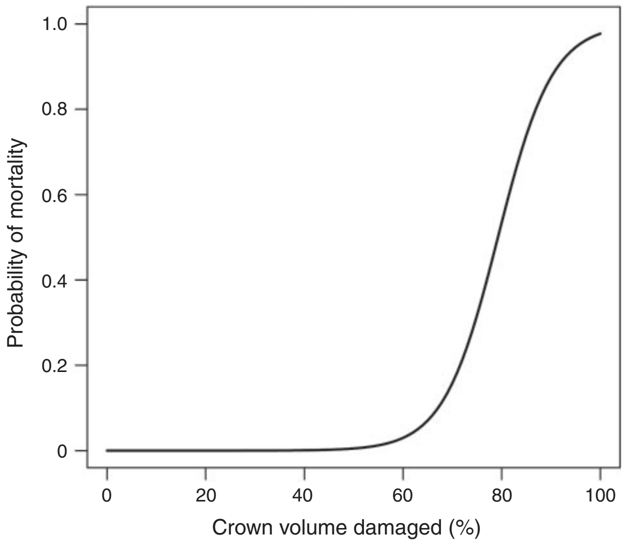

Fig. 3. Predicted probability of post-fire mortality for pines as a function of fire severity (expressed by the proportion of crown volume damaged, PCD). Model PM2 based on data from 383 trees (two species) sampled in four wildfire sites and including trees in the 7–50-cm diameter at breast height (DBH) range (model AUC = 0.98).

predict mortality in experimental fires, we fitted a new model using trees from both wildfire and experimental fire datasets and including fire type as a variable. Because trees had significantly different sizes in each dataset (Table 1), we selected only *P. pinaster* individuals with comparable size (DBH ranging between 7 and 25 cm). Results indicated that, for both types of fire, the probability of mortality increased primarily with PCD; however, wildfires corresponded to much higher mortality, particularly for PCD values above 40% (Fig. 4), which likely overestimated dead trees in the experimental fires derived from the previous model (Table A7). Bark thickness also had a significant negative influence on tree mortality, although its importance was much lower. A model with three variables showed a very good performance (AUC = 0.99, $R^2 = 0.63$). However, this model underestimates mortality for trees with 100% crown damage in experimental fires; indeed, all trees with 100% PCD died, but the low mortality (17%) among trees with 95% PCD was the reason for the mortality predictions remaining relatively low for 100% PCD.

For pines affected by wildfires the mortality trends were similar between single-species models (*P. pinaster* and *P. pinea*) and the combined pine model (Tables 3, A4), although the results suggest that *P. pinaster* was slightly more fire-sensitive than *P. pinea*, particularly for crown damage of 60–80%.

Broadleaf response models

Both PHC and BT had a significant effect on mortality of broadleaved trees (Tables 2, A4). Mortality increased with PHC and decreased with BT; however, model performance was relatively poor when compared with the pine models (model BM; AUC = 0.79, $R^2 = 0.08$) and decreased when applied to the independent validation subset (AUC = 0.17; Tables 3, A7).

Table 3. Synthesis of the selected single-species models

Main variables affecting tree post-fire responses in wildfire sites and model evaluation results; for pine species (*P. pinaster* and *P. pinea*) individual mortality is equivalent to stem mortality, thus only the former models are presented. PHC, maximum char height expressed as percentage of tree height (%); PCD, percentage of crown volume damaged (%); BT, bark thickness (cm); DBH, diameter at breast height (cm); H, tree height (m); R^2, Nagelkerke R^2; ROC AUC, area under the receiver operating characteristics curve; CC, cross-classification – overall accuracy (%); (V) corresponds to the application of the combined species models (BM, PM2 and BSM) to each species. Variables are significant at: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Species	n trees	n sites	All trees: Tree mortality (%)	Variables	ROC AUC	R^2	ROC AUC (V)	CC (V)	Live trees: Stem mortality (%)	Variables	ROC AUC	R^2	ROC AUC (V)	CC (%, V)
A. unedo	92	5	0.0	–	1.00	1.00	–	100.0	98.9	–	–	–	0.75	83.7
C. monogyna	133	1	0.0	–	1.00	1.00	–	100.0	89.5	PHC (+)**; H (–)*	0.76	0.28	0.77	91.7
C. sativa	30	1	20.0	–	–	–	0.29	80.0	37.5	–	–	–	0.62	58.3
F. angustifolia	82	1	0.0	–	1.00	1.00	–	100.0	8.5	PHC (+)*	0.91	0.53	0.91	90.2
O. europaea	159	2	1.3	–	–	–	0.36	98.7	94.3	H (–)**	0.88	0.15	0.68	93.6
P. lentiscus	113	1	0.0	–	1.00	1.00	–	100.0	100	–	1.00	1.00	–	99.1
Q. coccifera	120	1	0.0	–	1.00	1.00	–	100.0	94.2	–	–	–	0.64	93.3
Q. faginea	226	5	1.3	–	–	–	0.50	98.7	54.7	PHC (+)***; BT (–)***	0.92	0.44	0.79	67.7
Q. pyrenaica	528	3	16.9	PHC (+)***; H (–)**	0.72	0.13	0.70	83.1	63.1	PHC (+)***; H (–)***; BT (–)**	0.96	0.72	0.96	90.2
Q. rotundifolia	494	5	8.7	PHC (+)**	0.78	0.06	0.57	91.3	62.5	PHC (+)***; BT (–)***	0.82	0.38	0.79	79.4
Q. suber	349	6	5.2	BT (–)***	0.78	0.17	0.79	94.8	4.5	BT (–)***	0.91	0.27	0.86	84.6
P. pinaster	437	5	75.3	PCD (+)***	0.97	0.74	0.97	92.4	–	–	–	–	–	–
P. pinea	80	2	77.5	PHC (+)***	0.95	0.68	0.92	88.8	–	–	–	–	–	–

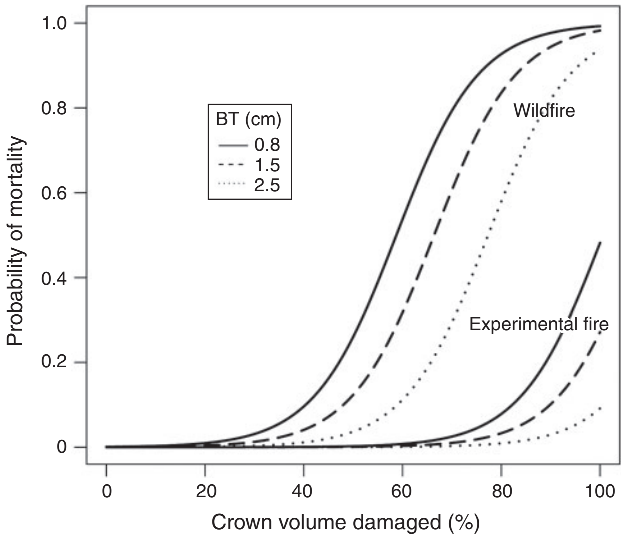

Fig. 4. Predicted probability of post-fire mortality for *P. pinaster* as a function of fire severity (expressed by the proportion of crown volume damaged, PCD), fire type (wildfire or experimental fire) and bark thickness (BT, cm). Model based on data from 868 trees sampled in four wildfires and five experimental fires (247 and 621 trees, respectively). For comparison purposes only trees in the 7–24-cm diameter at breast height (DBH) range were included (model AUC = 0.99). The model underestimates mortality for trees with 100% crown damage in experimental fires (see text).

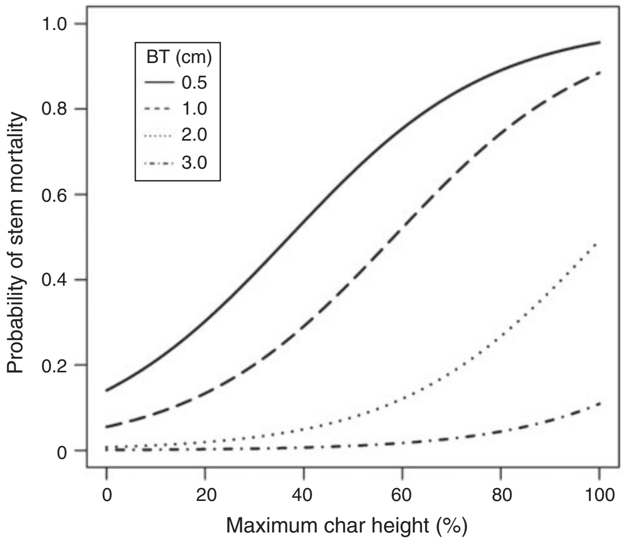

Fig. 5. Predicted probability of post-fire stem mortality (top-kill) for surviving broadleaved trees as a function of fire severity (expressed by the proportion of maximum tree height charred, PHC) and bark thickness (BT) (tree height is held constant at 6 m, representing the average H). Model BSM based on data from 1328 trees (six species) sampled in 10 wildfire sites (model AUC = 0.93).

In contrast, a model with PHC, BT and H was very successful in predicting stem mortality (top-kill) for the surviving trees (model BSM, Tables 3, A5). The probability of stem mortality increased with PHC and decreased with BT and H (Fig. 5), although the contribution of H to model improvement was small (Table A6). The ROC curve indicates that the stem-mortality model with these three variables performed very well (AUC = 0.93), including when applied to the wildfire validation subset (AUC = 0.94; Table 2). The cross-classification evaluation showed a global accuracy of 88.1% and a correct stem mortality prediction rate of 93.5% (Tables 2, A7).

In general, the relationship between broadleaved tree responses and the explanatory variables in the individual species models followed the same major trends found for the combined species models. However, in several cases no relationships were found due to the low variability in the tree responses to fire; for example, nearly 100% of individuals from *A. unedo* and *P. lentiscus* were top-killed, preventing model fitting (Tables 3, A4, A5).

Environmental correlates of between-site variations

Although there was substantial variation in environmental conditions among sites (Table A1), the random (site-level) effects in post-fire tree mortality and top-kill were found to be unrelated to the environmental variables assessed (i.e. no significant correlations were found).

Discussion

The present study showed that the variability in post-fire tree responses was mainly driven by fire severity, but plant traits also played a significant role. Generally, in high-severity fires, non-resprouters (pines) died but most resprouters (broadleaves) survived. Despite the low mortality of broadleaved trees, most were top-killed, particularly when charred to high levels. In such severe conditions, bark thickness and plant size increased fire resistance and were determinant characteristics to avoid top-kill. When subjected to lower fire severity, plant morphological traits were still important for broadleaves, but had a minor effect on pine resistance to fire.

Fire severity and post-fire tree responses

Most trees in the wildfire sites were severely burned, which is characteristic of summer wildfires in the Mediterranean region. Fire severity (expressed by PHC or PCD) was the most important factor influencing tree responses, increasing both tree mortality and top-kill. PHC was a good predictor of both pine and broadleaf post-fire responses (Tables A4, A5), which is in agreement with previous findings (e.g. Regelbrugge and Conard 1993; Woolley *et al.* 2012). For pines, both PHC and PCD were useful for predicting tree mortality with more than acceptable accuracy. PCD is a direct measure of fire-caused injury to tree crown, whereas PHC indirectly provides information on possible injury to cambial tissue or foliage (Woolley *et al.* 2012). Both variables have been previously tied to tree responses, although PCD, directly associated with loss of photosynthetic capacity, is usually considered to be the most useful predictor of conifers post-fire mortality (McHugh and Kolb 2003; Fernandes *et al.* 2008; Vega *et al.* 2011).

Pine mortality was more predictable than the mortality of broadleaved trees and one single descriptor of fire severity explained most of the observed variability. Our pine model based on PCD (Fig. 3) indicates that the predicted threshold ($P > 0.5$) of crown damage to cause pine mortality was 79%

(31% in the model using PHC instead of PCD). The mortality trend in relation to PCD was similar in the two pine species considered, although the individual species models suggest somewhat higher resistance of *P. pinea* in relation to *P. pinaster*, which is consistent with previous studies (Fernandes *et al.* 2008; Catry *et al.* 2010). This mortality threshold is in the upper range of the values reported by Vega *et al.* (2011) for different *P. pinaster* ecotypes in Spain (23–78%). The threshold level at which pine mortality begins seems to vary among studies (McHugh and Kolb 2003), and such differences may be related to several factors such as variations in plant, site, time since fire and fire characteristics. Some of these differences can be perceived when comparing the probability thresholds of *P. pinaster* under wildfire and experimental fire conditions (Fig. 4). Our results suggest that if crown damage is above 40%, trees are more likely to die after wildfires than after experimental fires. Because trees in both types of fire belong to the same size range, different tree responses between wildfires and experimental fires are more likely a consequence of differences in total heat released, tree phenology or in the post-fire stress conditions. In fact, experimental fires were conducted from late autumn to late winter when the forest floor was moist, whereas the wildfires occurred during the summer months under severe fire weather (Table A1) and also when the trees are physiologically more active (Jordy 2004). Higher susceptibility to summer wildfires may have been caused by: (1) higher crown kill (as opposed to crown scorch) due to higher air temperature and longer exposure to convective heat; (2) basal girdling caused by smouldering duff consumption inherent to summer drought; (3) higher physiological activity and tissue moisture content (growing season) and (4) presence of bark beetles (absent from the experimental fire sites).

Plant traits and post-fire tree responses

Although our results generally show that fire severity was the primary factor influencing tree responses, they also show that, for a given level of fire severity, the variability in post-fire tree responses was largely driven by plant traits.

When considering all species together (overall model), the resprouter *v.* non-resprouter dichotomy, corresponding in our case respectively to broadleaves and pines, was an important variable for predicting tree mortality. According to our model, mean probability of mortality is much higher in non-resprouters, particularly if PHC is above 20%, whereas it is usually low in resprouters (<10%) even for trees facing high-severity fires (Fig. 2). The usually-low mortality of Mediterranean broadleaves can be mainly explained by the presence of underground dormant buds protected by the soil from lethal temperatures during fire (Whelan 1995).

Among the tree morphological traits assessed, BT was the most important. In general, BT had a negative effect on both whole-plant mortality and stem mortality; however, this trait was mainly important for top-kill avoidance. For broadleaves, the probability of stem mortality sharply decreased with increasing BT, reaching the lowest level (zero) when tree bark depth exceeded 4 cm. Indeed, most broadleaved trees possessing a thick bark (BT > 1.5 cm) had stem survival, even when charred to the top of their canopies. Bark thickness has been shown to have an important influence on fire-induced responses of several tree species worldwide (Ryan and Reinhardt 1988; Lawes *et al.* 2011; Brando *et al.* 2012). Bark can protect the vascular cambium and buds from lethal temperatures during a fire, and small differences in BT have been reported to produce large differences in fire resistance and resilience (Bond and Van Wilgen 1996; Catry *et al.* 2012). Although there are interspecific differences concerning the characteristics of bark, such as density and moisture which may have some influence on insulation capacity, BT has been reported to exert an overwhelming influence on tree resistance to fire (Pinard and Huffman 1997; Bauer *et al.* 2010; Brando *et al.* 2012).

Tree diameter (DBH) also had a negative effect on tree vulnerability to fire. However, it is not obvious if this relationship is solely a result of the strong positive correlation between DBH and BT ($r = 0.77$), or if it can also be a consequence of the lower probability that larger stems have of being lethally damaged around the entire circumference (Gutsell and Johnson 1996). We found that DBH is a possible alternative variable (instead of BT) for predicting tree responses, often leading to similar model performance; however, in several models BT was clearly a better predictor, and in others DBH was not even significant (Tables A4, A5). This suggests that BT is the main morphological trait conferring resistance to fire in Mediterranean Basin trees. Similarly, H also influenced broadleaf responses. Taller trees may be less vulnerable to fire because their crowns are more distant from surface fuels and are less likely to be heat-damaged, because peak temperature declines with height (e.g. Whelan 1995). Furthermore, there could be some indirect effect of tree diameter, as H in broadleaves had a positive correlation with DBH ($r = 0.54$; but not with BT, $r = 0.36$). In pines, H was highly correlated with DBH ($r = 0.77$) and BT ($r = 0.82$).

The morphological traits assessed played an important role for broadleaves, but pine resistance to fire was weakly or not affected by these traits. Although many studies reported a negative relationship between tree size or BT and pine mortality (Ryan and Reinhardt 1988; Regelbrugge and Conard 1993; Rigolot 2004; Sieg *et al.* 2006), several others found no significant relationship (Thies *et al.* 2006) or reported either significant and non-significant relationships depending on sampling location or species (Stephens and Finney 2002; Hood *et al.* 2010; Vega *et al.* 2011). Such differences may be related to variation in fire severity (as trees with high crown damage will be vulnerable irrespective of other factors) but also to variation in plant traits. In a review about fire resistance of European pines, Fernandes *et al.* (2008) concluded that mortality caused by bole injury is unlikely in thick barked pines such as *P. pinaster* unless trees have DBH < 20 cm or heat from extended smouldering girdles the stem base. In our case, most sampled pines were relatively large and had thick bark (Table 1), which likely explains the nil or small contribution of tree size and BT for the explained variance in the mortality models. Our model centred on smaller pine trees (Fig. 4), as well as reports from other authors (Botelho *et al.* 1998; Vega *et al.* 2011), seem to corroborate this hypothesis.

Models' performance and applications

Most models developed in the present study, particularly those for predicting individual mortality of pines and stem mortality of broadleaves, showed very good performance, including when validated against independent datasets. External validation of the selected models, with data not used in model development, provided insights on their generality. Our results suggest that the pine mortality model based on crown damage only can achieve good results in predicting wildfire-caused mortality of thick barked species, although it may overestimate mortality under prescribed fire conditions. In contrast, individual mortality of broadleaves was difficult to predict due to low mortality (see also, Stephens and Finney 2002; Franklin *et al.* 2006). In contrast, it was possible to accurately predict stem mortality (top-kill), which is the most frequent fire effect on broadleaved trees.

Accurate predictions of tree mortality and regeneration following fire are crucial to assist managers making decisions related to prescribed burns, post-fire salvage logging, reforestation, wildlife habitat, carbon stocks and water quality, among many others (e.g. Thies *et al.* 2006; Woolley *et al.* 2012). Such predictions also facilitate understanding of the effects of fire on the composition and structure of plant communities. Therefore post-fire tree response models can be an important component in ecosystem process and succession models (Regelbrugge and Conard 1993). In this paper we show that a large intra- and inter-specific variability in post-fire tree responses of Mediterranean forests can be accurately predicted from simple variables related to fire severity and to tree characteristics. This information could feed simulation models for predicting the consequences of alternative fire and management scenarios.

Acknowledgements

The present study was funded by the Portuguese government, FCT (PhD grant SFRH/BD/65991/2009 and project POCI/AGR/61407/2004), FFP (project Recuperação de Áreas Ardidas), EU (COST FP0701). JGP thanks the TREVOL (CGL2012–39938-C02–00/01) project from the Spanish government. Special thanks to all people involved in the field work.

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Appendix

Table A1. Main characteristics of the 16 study sites

n trees, number of trees sampled in each site; *n* plots, number of plots (in the experimental fires it corresponds to the number of fires); Fire date, date of fire occurrence; Years since fire, years between fire and tree assessment; FWI, Fire Weather Index

Fire type / Fire site	Site code	Natural region	*n* trees	*n* plots	Fire date (month and year)	Years since fire	Mean annual precipitation (mm)	Mean annual temperature (°C)	Mean elevation (m)	FWI
Wildfire										
Agroal	AG	Estremadura	361	15	Sept. 2006	1	700–800	16.0–17.5	146	37.8
Atouguia	AT	Estremadura	56	6	July 2006	1	1200–1400	16.0–17.5	237	32.7
Barrancos	BA	Alentejo	320	19	July 2006	2	500–600	16.0–17.5	300	26.8
Evora	EV	Alentejo	67	4	Sept. 2006	1	700–800	15.0–16.0	323	44.5
Lamas Olo	LO	Alto Portugal	101	15	Aug. 2005	2	1000–1200	10.0–12.5	1050	41.1
Marao	MA	Alto Portugal	352	61	July 2006	2	1400–1600	10.0–12.5	940	32.4
Portel	PO	Alentejo	101	10	Aug. 2005	2	600–700	16.0–17.5	314	56.3
Porto Mos	PM	Estremadura	354	20	Aug. 2006	1	1200–1400	15.0–16.0	357	35.4
Mafra[A]	TM	Estremadura	980	19	Sept. 2003	1	700–800	12.5–15.0	146	46.9
Sirarelhos	SI	Alto Portugal	75	15	Aug. 2005	2	1000–1200	10.0–12.5	640	35.6
Vale Florido	VF	Estremadura	76	8	Aug. 2006	1	1000–1200	16.0–17.5	326	46.5
Experimental fire										
Montes[A]	MO	Alto Portugal	259	1	Dec. 2005	1	1200–1400	10.0–12.5	1160	1.0
Lousa[A]	LA	Beira Serra	387	3	Nov. 1988	2	1200–1400	10.0–12.5	420	5.9
Padrela[A]	PA	Alto Portugal	499	7	Feb. 1990	2	800–1000	10.0–12.5	970	7.6
			30	1	Feb. 1995	3				0.7
Tinhela[A]	TI	Alto Portugal	30	1	Jan. 1995	3	1000–1200	10.0–12.5	920	13.0
V. N. Cerveira[A]	VC	N. Cismontano	107	2	Mar. 1990	2	1600–2000	10.0–12.5	510	3.2

[A]Fire sites used for model validation.

Table A2. List of the sampled tree species

Functional groups: RB, resprouting broadleaf; NRC, non-resprouting conifer. *n*, total number of sampled trees and number of trees in the development dataset (in parentheses)

Scientific name and author	Common name	Family	Functional group	Leaf habit	*n* trees
Arbutus unedo L.	Strawberry tree	Ericaceae	RB	Evergreen	92 (92)
Castanea sativa Mill.	Chestnut	Fagaceae	RB	Deciduous	30 (0)
Crataegus monogyna Jacq.	Weissdorn	Rosaceae	RB	Deciduous	133 (0)
Fraxinus angustifolia Vahl.	Narrowleaf ash	Oleaceae	RB	Deciduous	82 (0)
Olea europaea var. *sylvestris* Brot.	Wild olive	Oleaceae	RB	Evergreen	159 (32)
Pinus nigra Arn.	European black pine	Pinaceae	NRC	Evergreen	259 (0)
Pinus pinaster Ait.	Maritime pine	Pinaceae	NRC	Evergreen	1490 (381)
Pinus pinea L.	Umbrella pine	Pinaceae	NRC	Evergreen	80 (2)
Pistacia lentiscus L.	Evergreen pistache	Anacardiaceae	RB	Evergreen	113 (0)
Quercus coccifera L.	Kermes oak	Fagaceae	RB	Evergreen	120 (0)
Quercus faginea Lam. ssp. *broteroi*	Portuguese oak	Fagaceae	RB	Deciduous	226 (97)
Quercus pyrenaica Willd.	Pyrenean oak	Fagaceae	RB	Deciduous	528 (528)
Quercus rotundifolia Lam.	Holm oak	Fagaceae	RB	Evergreen	494 (494)
Quercus suber L.	Cork oak	Fagaceae	RB	Evergreen	349 (237)

Table A3. Bark thickness (BT, cm) as a function of diameter at breast height (DBH, cm)

Equations obtained for 13 tree species from field measurements taken on 666 unburned trees; all regressions are significant ($P < 0.001$). Equations have the form $BT = b_0\ DBH^{b_1}$. R^2, number of sampled trees. DBH range and site are also shown

Species	Coefficients		R^2	*n*	DBH range (cm)	Site code
	b_0	b_1				
Arbutus unedo	0.131	0.642	0.92	54	4–29	PM
Castanea sativa	0.061	0.970	0.76	41	11–49	TM
Crataegus monogyna	0.072	0.874	0.77	40	3–42	TM
Fraxinus angustifolia	0.062	0.934	0.93	40	3–97	TM
Olea europaea sylv.	0.196	0.539	0.57	42	5–56	TM
Olea europaea sylv.	0.062	0.966	0.75	38	5–46	BA
Pinus pinaster	0.103	1.023	0.90	44	2–105	TM
Pinus pinea	0.133	0.920	0.83	42	11–96	TM
Pinus nigra	0.037	1.274	0.82	80	2–17	CA
Pistacia lentiscus	0.022	1.410	0.69	42	3–23	TM
Quercus coccifera	0.024	1.193	0.73	41	5–35	TM
Quercus faginea	0.241	0.567	0.84	42	4–108	TM
Quercus pyrenaica	0.110	0.507	0.42	30	8–35	SI
Quercus pyrenaica	0.076	0.784	0.63	26	6–41	LO
Quercus pyrenaica	0.176	0.350	0.48	20	6–34	MA
Quercus rotundifolia	0.204	0.644	0.89	44	5–96	BA

Table A4. Coefficients of the selected models for predicting individual tree mortality following fire

β_0, intercept; PHC, maximum char height expressed as percentage of tree height (%); PCD, percentage of crown volume damaged (%); BT, bark thickness (cm); DBH, diameter at breast height (cm); H, tree height (m); RS, resprouter (no *v.* yes); PHC × R, interaction between PHC and resprouter; AIC, Akaike information criteria; R^2, Nagelkerke R^2; ROC AUC, area under the receiver operating characteristics curve. Probabilities are significant at: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ (for categorical variables significance refers to the comparison with the first category); ns, not significant

Species	*n* trees	*n* sites	*n* species	Random effects	Model	β_0	PHC	PCD	BT	DBH	H	RS (yes)	PHC × RS	AIC	R^2	ROC AUC
All species	1863	10	8	Site; Species	OM	–2.204*	0.155***	–	–0.500***	–	–	–2.437*	–0.130***	1064	0.29	0.91
					OM[A]	1.670	0.052***	–	–0.455***	–	–	–8.989***	–	1140	0.22	0.90
					OM[A]	0.246	0.055***	–	–	ns	–	–8.387***	–	1151	0.21	0.90
Broadleaves	1480	10	6	Site; Species	BM	–4.539***	0.026***	–	–0.745**	–	ns	–	–	875	0.79	0.08
(resprouters)					BM[A]	–3.899***	0.023***	–	–	ns	–0.113*	–	–	887	0.77	0.06
Pines	383	4	2	Site; Species	PM2	–14.343***	–	0.181***	ns	ns	–	–	–	116	0.83	0.98
(non-resprouters)					PM1	–4.533 ***	0.147***	–	ns	ns	–	–	–	186	0.69	0.96
Q. pyrenaica	528	3	1	Site	QP	–1.407	0.017***	–	–	–	–0.227**	–	–	445	0.12	0.72
					QP[A]	–1.724*	0.020***	–	–4.029**	–	–	–	–	448	0.12	0.70
Q. rotundifolia	494	5	1	Site	QR	–5.594***	0.027**	–	ns	–	ns	–	–	–	0.06	0.78
Q. suber	349	6	1	Site	QS	–0.373	ns	–	–1.151***	–	ns	–	–	–	0.17	0.78
P. pinaster	437	5	1	Site	PP	–9.634***	–	0.133***	ns	ns	–	–	–	177	0.74	0.97
					PP[A]	–2.545***	0.126***	–	–	–0.054***	–	–	–	221	0.66	0.95
					PP[A]	–2.404***	0.124***	–	–0.526***	–	–	–	–	222	0.66	0.95
P. pinea	80	2	1	Site	PI	–4.427**	0.121***	–	ns	ns	–	–	–	44	0.68	0.95
					PI[A]	–13.284	–	0.163***	ns	ns	–	–	–	51	0.60	0.92

[A]The best alternative models, when existing, are also shown for comparison.

Table A5. Coefficients of the selected models for predicting stem mortality of surviving broadleaves following fire

β_0, intercept; PHC, maximum char height expressed as percentage of tree height (%); BT, bark thickness (cm); DBH, diameter at breast height (cm); H, tree height (m); AIC, *Akaike information criteria*; R^2, Nagelkerke R^2; ROC AUC, area under the receiver operating characteristics curve. Probabilities are significant at: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ (for categorical variables significance refers to the comparison with the first category); ns, not significant

Species	*n* trees	*n* sites	*n* species	Random effects	Model	β_0	PHC	BT	DBH	H	AIC	R^2	ROC AUC
Broadleaves (resprouters)	1328	10	6	Site; Species	BSM	0.555	0.049***	−2.159***	–	−0.210***	916	0.47	0.93
					BSM[A]	−0.076	0.050***	–	−0.121***	ns	925	0.46	0.93
					BSM[A]	−0.567	0.052***	−2.754***	–	–	929	0.45	0.93
C. monogyna	133	1	1	–	CM	0.908	0.043**	ns	–	−0.615*	–	0.28	0.76
F. angustifolia	82	1	1	–	FA	−195.309	1.947	ns	–	ns	–	0.53	0.91
O. europaea	157	2	1	Site	OE	6.508***	ns	ns	–	−0.736**	–	0.15	0.88
Q. faginea	223	5	1	Site	QF	2.271	0.023*	−2.903***	–	ns	231	0.21	0.85
					QF[A]	−0.098	0.024**	–	−0.074***	ns	233	0.20	0.84
Q. pyrenaica	439	3	1	Site	QP	−1.529*	0.084***	–	−0.286***	ns	213	0.73	0.96
					QP[A]	0.829	0.085***	−6.197**	–	−0.363***	218	0.72	0.96
Q. rotundifolia	451	5	1	Site	QR	0.358	0.034***	−2.221***	–	ns	437	0.38	0.82
					QR[A]	−0.635	0.034***	–	−0.102***	ns	438	0.37	0.81
Q. suber	331	6	1	Site	QS	1.216	ns	−2.188***	–	ns	96	0.27	0.91
					QS[A]	−0.486	ns	–	−0.128**	ns	114	0.10	0.77

[A]The best alternative models, when existing, are also shown for comparison.

Table A6. Summary of the sequential ANOVA

Results from the sequential ANOVA for each post-fire response model, applied to the variables previously selected by the stepwise procedure (variables are added sequentially in the order of their contribution to the remaining explained deviance). For each post-fire response model: PHC, maximum char height expressed as percentage of tree height (%); PCD, percentage of crown volume damaged (%); BT, bark thickness (cm); RS, resprouter (yes *v.* no); PHC × RS, interaction between PHC and RS; d.f., degrees of freedom; AIC, Akaike information criteria; logLik, log-likelihood; χ^2, Chi-square; *P*-value, significance level

Post-fire response Species	Models		d.f.	AIC	logLik	χ^2	*P*-value
Individual mortality							
All species	OM	Null model	3	1358.0	−676.0	–	–
		+PHC	4	1250.3	−621.2	109.6	<0.0001
		+RS	5	1151.1	−570.5	101.3	<0.0001
		+PHC × R	6	1073.5	−530.8	79.5	<0.0001
		+BT	7	1064.4	−525.2	11.1	0.0008
Pines (non-resprouters)	PM1	Null model	3	411.4	−202.7	–	–
		+PHC	4	185.8	−88.9	227.7	<0.0001
	PM2	Null model	3	411.4	−202.7	–	–
		+PCD	4	115.7	−53.8	297.8	<0.0001
Broadleaves (resprouters)	BM	Null model	3	925.5	−459.8	–	–
		+PHC	4	889.2	−440.6	38.3	<0.0001
		+BT	5	875.0	−432.5	16.2	<0.0001
Stem mortality (top-kill)							
Broadleaves (resprouters)	BSM	Null model	3	1386.9	−690.5	–	–
		+PHC	4	1036.7	−514.3	352.2	<0.0001
		+BT	5	929.2	−459.6	109.5	<0.0001
		+Height	6	916.2	−452.1	15.0	0.0001

Table A7. Comparison between observed and predicted post-fire tree responses

Summary of cross-classification tables resulting from the application of each selected model to the validation datasets; a probability threshold of 0.5 was used in all cases

Model	Validation dataset	Trees	Number trees	Predicted status	Observed status		Correct predictions (%)	Global accuracy (%)
					Dead	Live		
OM	Wildfire	All	980	Dead	105	20	84.0	96.8
				Live	11	844	98.7	
PM1	Wildfire	Pines	134	Dead	104	14	88.1	87.3
				Live	3	13	81.3	
PM2	Wildfire	Pines	134	Dead	97	13	88.2	82.8
				Live	10	14	58.3	
PM2	Experimental fires	Pines	1312	Dead	293	137	68.1	87.8
				Live	23	859	97.4	
BM	Wildfire	Broadleaves	846	Dead	0	0	–	98.9
				Live	9	837	98.9	
BSM	Wildfire	Broadleaves	837	Dead	502	35	93.5	88.1
				Live	65	235	78.3	