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# Ambrosia Beetle Attacks in Mediterranean Cork Oak Forests Following Fire: Which Factors Drive Host Selection?

**Filipe X. Catry [1,*], Manuela Branco [2], Francisco Moreira [3], Edmundo Sousa [4] and Francisco Rego [1]**

1 Centre for Applied Ecology/Research Network in Biodiversity and Evolutionary Biology (CEABN/InBIO), School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-017 Lisboa, Portugal
2 Forest Research Centre (CEF), School of Agriculture, University of Lisbon (ISA, UL), Tapada da Ajuda, 1349-017 Lisboa, Portugal
3 Research Centre in Biodiversity and Genetic Resources/Research Network in Biodiversity and Evolutionary Biology (CIBIO/InBIO), School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-017 Lisboa, Portugal
4 Forest Research Unit, National Institute of Agricultural and Veterinary Research (INIAV), Avenue da República, Quinta do Marquês, 2780-157 Oeiras, Portugal
* Correspondence: fcatry@isa.ulisboa.pt

**Abstract:** Mediterranean Basin forest ecosystems are recurrently affected by wildfires. The occurrence of insect pests following fire may be a critical factor affecting tree survival and forest recovery. Although ambrosia beetles are viewed with increasing concern, information about the host selection and colonization behavior of these beetles in Mediterranean broadleaf forests is very scarce and inexistent in areas affected by wildfires. After a forest fire in Portugal, we selected 841 burned and unburned cork oak trees and assessed the presence and intensity of ambrosia beetle attacks, as well as other tree characteristics, and used generalized linear models to investigate the factors driving host selection. In contrast with burned oaks, where beetle attacks were frequent, the unburned trees were little affected. Attacks in the burned forest were more frequent in larger trees that suffered higher fire severity, in trees being exploited for cork (but with thicker bark), and in trees that were closer to the unburned area. A contagious effect to neighboring unburned trees was not observed, and cork harvesting in subsequent years following fire also did not increase the probability of beetle attacks. These results help us to understand the risk of ambrosia beetle attacks and improve forest management in cork oak forests.

**Keywords:** *Platypus cylindrus*; Xyleborini; *Xyleborus* spp.; *Xyleborinus saxesenii*; colonization; wildfire; *Quercus suber*; fire severity; cork harvesting

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## 1. Introduction

Mediterranean Basin ecosystems are recurrently affected by wildfires, with an average of nearly 400 thousand hectares burned every year in the last two decades [1]. The occurrence of wood-boring insect attacks following fire may be a critical factor affecting tree survival and forest recovery. Bark beetles and ambrosia beetles are among the most important insects that quickly colonize trees damaged by fire, compromising their survival and regeneration [2–4]. Additionally, the availability of reproduction resources may lead to local outbreaks of the beetle's population, which may then, by its large numbers, be able to massively attack healthy trees, overcome their defences, and kill them. Relatively few bark and ambrosia beetles are able to colonize and kill entire trees, but those that do can have major ecological and economic impacts [5].

Ambrosia beetles are a polyphyletic group comprising several species of the subfamilies Scolytinae and Platypodinae (Coleoptera: Curculionidae), the larvae of which feed primarily on coevolved, symbiotic "ambrosia fungi" which adults cultivate in tunnel systems in woody tissues [5]. Ambrosia beetles in the subfamily Platypodinae always exceed 3 mm in length, whereas the scolytid ambrosia beetles seldom exceed 3 mm [6]. Most of these xylomycetophagous species transport their fungi in mycangia or the gut and colonize the trees by boring a hole in the tree trunk or branches and penetrating the plant tissue. Once in the xylem, the beetles excavate brood galleries, releasing the spores of the fungi, and the females deposit their eggs in these galleries. Ambrosia beetles are known to attack mostly recently dead, dying, and highly physiologically stressed trees [7]. However, there are both older and more recent reports of ambrosia beetle species also attacking and killing healthy trees [5,8]. These beetles can have major ecological and economic impacts, and this is a particular concern during outbreaks. The impacts depend on the fungi species carried by the ambrosia beetles and whether these fungi are weakly or strongly pathogenic to the host tree species. An example of a very destructive insect–disease complex of species is the *Euwallacea fornicatus* Eichhoff (Coleoptera: Curculionidae), responsible for killing the vascular tissue and causing tree death in several host plants [9,10]. In addition, the ambrosia beetle *Platypus quercivorus* Murayama (Coleoptera: Curculionidae) associated with the fungi *Raffaelea quercivora* (Kubono & Ito) was found to be highly destructive, causing oak decline in Japan [11].

In the western Mediterranean, the ambrosia beetle *Platypus cylindrus* Fabricius (Coleoptera: Curculionidae) was also reported as being responsible for causing tree death in live cork oak (*Quercus suber* L.) trees, and it is considered one of the most serious pests associated with oak decline [12–15]. This beetle has become an emergent pest of cork oak forests in the Iberian Peninsula in the last four decades, causing great concern for land managers [12,13].

*Q. suber* is an evergreen oak species distributed along both rims of the western Mediterranean Basin. Cork oak ecosystems cover an area of about 2.1 million hectares, of which 77% are in southern Europe and 23% in North Africa [16]. Cork oaks are managed with the main objective of cork production. This tree has the distinctive particularity of regenerating its bark after each harvest. The cork is usually harvested at nine-year intervals during summer when the tree phellogen is most active. This is carried out manually by making vertical and horizontal incisions on the trunk and branches with an axe (mechanical cutting is still extremely limited) and pulling the cork planks. This operation is a delicate process that should be performed carefully by experienced workers without reaching and damaging the vascular cambium. Cork is the most important forest product of these oak forests, feeding an industry with many industrial applications, including application as world-famous wine cork stoppers [17]. Cork debarking is considered to increase susceptibility to ambrosia beetle attacks [14]. Wounds left by careless cork debarking, which range from thin, linear wounds caused by the incisions to large wounds of different shapes related to the pulling of the planks, can further increase this effect. The combination of cork debarking and the vicinity of fire occurrence can thus be a highly risky management option.

In a previous study [18,19], we reported the presence of large numbers of ambrosia beetles (one Platypodinae and three Scolytinae-Xyleborini species) in a cork oak forest following a wildfire. However, information about the host selection and colonization behavior of these beetles is extremely scarce, and we could not find any study specifically focusing on host selection following fire.

Our main objective in the present work was to assess which are the main factors driving host selection by ambrosia beetles in Mediterranean cork oak forests following fire. With this research, we intended to investigate and, where possible, clarify (i) which are the most important factors influencing ambrosia beetle attacks, (ii) if fires and cork harvesting are major drivers of ambrosia beetle attacks, and (iii) if, after a wildfire, the neighboring forest stands are at higher risk.

In general, we expected that less vigorous trees would be more likely to be colonized by ambrosia beetles. Since wildfires have been shown to severely affect cork oaks, and particularly trees being exploited for cork [20,21], we hypothesized that fire would be the most important factor driving the ambrosia beetle attacks and that exploited trees would be more vulnerable than unexploited ones. Additionally, since debarking is recognized as a stressful activity [22,23] and it was reported that recently debarked cork oaks are particularly susceptible to ambrosia beetle attacks [24], we hypothesized that the sooner the cork harvesting after the fire and the closer to the burned area, the greater the probability of ambrosia beetle attacks. The knowledge acquired about the ecology of ambrosia beetles in forest ecosystems affected by fire can help to improve management decisions.

## 2. Materials and Methods

### 2.1. Study Area

The study area included public land owned by the municipality of Coruche ("Herdade dos Concelhos", central Portugal, western Iberian Peninsula) and neighboring private forest stands. Climate is Mediterranean, with a mean annual precipitation of 500–600 mm, a mean annual temperature of 15–16 °C, and two summer months with a maximum temperature above 30 °C [25].

The vegetation in the area is dominated by mixed Mediterranean forests and shrublands, where the main tree species are *Q. suber*, *Pinus pinaster* Ait. (maritime pine) and *Pinus pinea* L. (stone pine) and the shrub layer is dominated by species such as *Cistus salvifolius* L. (sage-leaved rock-rose), *Calluna vulgaris* L. (heather), *Rosmarinus officinalis* L. (rosemary), *Arbutus unedo* L. (strawberry tree), and *Quercus lusitanica* Lam. (Lusitanian oak), among others.

In the summer of 2013 (4 July), a wildfire affected nearly 166 ha of land in this area (Figure 1), and the observation of abundant ambrosia beetle attacks in the subsequent months motivated the start of the present research. The ambrosia beetle species confirmed to be present in the study area were: *P. cylindrus*, *Xyleborus monographus* Fabricius (Coleoptera: Curculionidae), *Xyleborus dryographus* Ratzeburg (Coleoptera: Curculionidae), and *Xyleborinus saxesenii* Ratzeburg (Coleoptera: Curculionidae) [18].

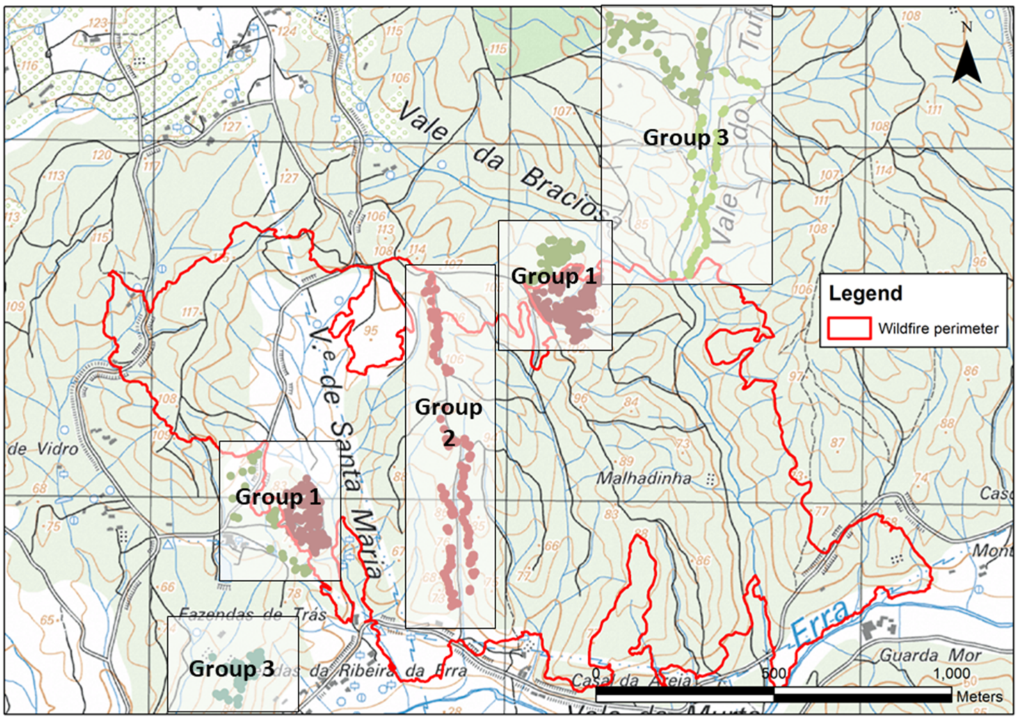


**Figure 1.** Location of the wildfire perimeter (red line) and of the three major groups of trees used in the current study, comprising 841 burned and unburned cork oaks assessed within and surrounding the burned area (burned and unburned trees are represented in a reddish and greenish colour, respectively).

### 2.2. Data Collection

The present study was carried out using three groups of data collected within and in the vicinity of the area burned by the 2013 wildfire. These different groups and locations were selected with the goal of helping to answer our main research questions. In total, 841 cork oaks, burned and not burned, were assessed (Figure 1).

Since we were interested in investigating specifically the ambrosia beetle attacks on cork oaks, in all cases we collected the following two response variables: presence/absence and the number of recent ambrosia beetle holes on the tree trunk. The presence of ambrosia beetle (one Platypodinae species and three species from the Xyleborini tribe) attacks was recognized by the existence of small entrance holes (about 0.5–1.5 mm in diameter) in tree trunks, typically with the presence of fine sawdust (see Figure 2). The fine boring dust expelled from the galleries often collects in crevices of the bark in the trunk and at the base of the tree. Ambrosia beetles use the entrance holes to exit [6]; thus, potential confusion between colonizing beetles and their offspring was not an issue. Entrance holes were considered as a proxy of host selection. The counting of the number of holes in each tree was only performed from the ground level up to 2 m high because of the difficulty of counting at higher parts of the trunk. Several additional details about the location of beetle holes, as well as data concerning potential explanatory variables for host selection, were collected at the tree level, but they were not always the same for the different groups of trees (forest stands) (see details below and a summary in Table 1).

**Figure 2.** Ambrosia beetle holes and sawdust in the trunk of a burned cork oak tree: detailed view (**left**) and overview (**right**).

**Table 1.** Summary of the main characteristics and data collected (x indicates data collection) in the three groups of trees surveyed in the current study, including a total of 841 cork oaks sampled (for details, see the subsections from Sections 2.2.1–2.2.3).

| Groups | | Group 1 | Group 2 | Group 3 |
|---|---|---|---|---|
| **Characteristics** | | | | |
| Sampled Trees | n | 491 | 140 | 210 |
| Sampling time after fire | months | 5–8 | 12 | 39 |
| **Variables assessed** | Units | | | |
| Burned/Unburned (B/U) | n | 369B/122U | 140B | 210U |
| Presence of beetles (0–2 m) | holes | x | x | x |
| Density of beetles (0–2 m) | holes/m$^2$ | x | x | x |
| Location of beetles in the trunk | cat. | x | x | x |
| Tree size (DBH, height) | cm/m | x | x | x |
| Exploited/Unexploited (E/U) | n | 391E/100U | 113E/27U | 210E |

**Table 1.** *Cont.*

| Groups | | Group 1 | Group 2 | Group 3 |
|---|---|---|---|---|
| Last debarking year | year | 2008/2012 | 2012 | 2014/2015/2016 |
| Debarking intensity | $m/m^2$ | x | | |
| Bark thickness | mm | x | | |
| Stem wounds | cat./n | x | | x |
| Tree status (live/dead) | cat. | x | x | x |
| Crown status | cat. | x | x | x |
| Tree regeneration (crown/basal) | cat. | x | x | |
| Fire severity (depth/height) | cat./% | x | x | |
| Distance to burned/unburned | m | x | x | x |
| Vegetation cover (trees/shrubs) | % | x | | |
| Basal area (trees/shrubs) | $m^2$/ha | x | | |
| Aspect | cat. | x | | |
| Slope | % | x | | |
| Other pests/diseases | cat./n | x | | |

#### 2.2.1. Assessing Early Ambrosia Beetle Attacks in Burned and Unburned Cork Oaks—Group 1

A few months after the wildfire, we selected two forest stands located at the edge of the burned area, each including both burned and unburned (control) cork oak trees. The two oak stands were about 1000 m from each other and had similar soil and climatic conditions. In total, we randomly selected 491 *Q. suber* trees for monitoring (Figure 1—Group 1).

Between December 2013 and February 2014, we assessed the presence/absence of recent ambrosia beetle activity, as described above. The data collected at the tree level also included: the geographical coordinates of each tree (collected with GPS—global positioning system); the trunk diameter at breast height (DBH; average of two perpendicular measurements at 1.3 m, outside bark); tree height (TH; measured with a hypsometer); bark thickness (BT; estimated as the average of four cork thickness measurements at breast height made with a bark gauge at opposite sides of the trunk); tree bark exploitation status (Ex; classified as either exploited or unexploited based on the presence of harvesting marks on the tree); for exploited trees, the maximum height (m) of debarking and the surface debarked ($m^2$); and presence and characteristics of stem wounding up to 2 m from the ground (usually caused during debarking), namely, number of stem wounds larger than 3 cm and area ($cm^2$) covered by the three larger stem wounds. The vegetative status of each tree (TS) was recorded as dead, live basal resprouts only, live crown and basal resprouts, or live crown only. The crown volume with green leaves, brown/yellow leaves, and with no leaves was also visually estimated (the sum of the three values totalling 100%). Within a radius of 10 m around each cork oak (area of ~114 $m^2$), and based on remaining woody material in the burned area, we also estimated the pre-fire percent tree cover (trees larger than 3 m high existing before the 2013 fire), shrub cover (shrubs and trees smaller than 3 m high), and shrub layer mean height (cm) (the cover was estimated to the nearest 5% and height to the nearest 10 cm). Within a radius of 5 m around each cork oak (area of ~80 $m^2$), we assessed the tree basal area ($m^2$/ha) for each species based on DBH measurements. The dominant aspect (8 directions) and slope (degrees) were assessed for each tree. Using the GPS measurements and the burned area map, we also calculated in GIS the linear distance from each tree to the nearest unburned area.

For burned cork oaks, we assessed two fire severity indicators: the proportion of tree height charred (PHC) and the bole char depth (BCD). Char height (the vertical extent of blackening of the outer bark in the trunk/branches) is extensively used in fire ecology studies, being recognized as a good indicator of fire severity for several Mediterranean tree species, including cork oak [20,21,26]. The minimum and maximum char heights were measured in each tree using a hypsometer. Then, PHC was calculated as the minimum and maximum char height relative to total tree height. Bole char depth was used as an alternative indicator of fire injury. BCD was visually assessed at the base of the trunk in the first 50 cm above ground, because cambial damage is usually greater near ground level than at breast height [27,28]. Char depth was classified in three levels according to the following criteria: superficial (with evidence of light scorching), moderate (the bark is uniformly black, but its character is still discernible), and deep (the bark is deeply charred, and surface characteristics are lost) [28]. The proportion of basal bole with each damage class was then recorded.

In a second phase, at the end of the first winter following the fire (early March 2014), and due to the high number of holes observed in the previous assessment, we registered the number of holes in each tree and a series of other characteristics concerning their location, namely: (1) whether they were located in exploited cork and/or unexploited cork and/or in wounds; (2) in which quadrants (north, east, south, west) of the trunk they were located; and (3) minimum and maximum height (cm) at which they occurred (when higher than 2 m, it was recorded but no counting was carried out).

#### 2.2.2. Assessing Ambrosia Beetle Attacks along a Distance Gradient to the Unburned Area—Group 2

In the first summer after the wildfire occurrence (i.e., one year after fire; early July 2014), we established one transect along a forest path that crosses the burned area to further assess if there was a relationship between beetle attacks and distance to the unburned area. Walking along this transect, we monitored 140 cork oak trees affected by fire, located on both sides of the path (up to 30 m from the path; Figure 1—Group 2). For each tree, we observed and registered the geographic location (with GPS), the presence and number of ambrosia beetle holes (as described above), whether the holes were located in the exploited or unexploited cork, and whether the tree was exploited or not, was alive or dead, and whether it had post-fire basal and/or crown regeneration. We also measured the diameter at breast height (DBH; an average of two perpendicular measurements at 1.3 m), and we visually assessed the fire severity in each tree based on char depth at the base of the trunk (see description in Section 2.1). Finally, using the GPS measurements and the burned area map, we also calculated in GIS the linear distance from each tree to the nearest unburned area.

#### 2.2.3. Assessing Beetle Attacks in Unburned Oaks Debarked in Different Years Following the Wildfire—Group 3

With the objective of assessing potential ambrosia beetle attacks in unburned cork oak stands and the relation between attacks and the year of cork debarking, we extended the monitoring beyond the wildfire perimeter and assessed the situation of attacks in neighboring areas. In October 2016, we selected three forest stands around the burned area (owned and managed by private landowners) that were debarked in three consecutive years following the 2013 wildfire, i.e., debarked in the summers of 2014, 2015, and 2016 (usually, cork harvesting in this region occurs during June–July), and assessed the condition of 210 randomly selected, unburned adult cork oak trees being exploited for cork production (70 trees in each stand/year; see Figure 1—Group 3).

For each tree, we registered the geographic location (with GPS), the year of cork debarking, the presence and number of ambrosia beetle holes in the trunk, whether there were holes located in debarking wounds, exploited or unexploited cork, the area of the stem affected by debarking wounds (in 4 intensity classes: low, <20 $cm^2$; moderate, 20–500 $cm^2$; high, 500–2500 $cm^2$; very high, >2500 $cm^2$), and the volume of green (live) crown and the volume of brown/yellow (dry) crown (both as percentage of the original/normal crown). We also measured the diameter at breast height (DBH). Finally, using the GPS measurements and the burned area map, we calculated in GIS the linear distance from each tree to the nearest burned area.

### *2.3. Data Analyses*

Data analyses were performed for each of the three groups presented above. We started by performing descriptive analyses and then we fitted several models to investigate the relationship between beetle attacks and the other variables collected in the field. As dependent variables, we used the presence (as binary variable, i.e., yes/no) and the number of ambrosia beetle holes in the tree trunk as indicators of ambrosia beetle attacks. These indicators were examined in relation to the different independent (explanatory) variables that were sampled at the tree level in each group. For modelling purposes, the ordinal variable stem wound intensity (4 classes, following an increasing intensity gradient) was treated as continuous.

We used generalized linear models (GLM) to analyze the presence and intensity of ambrosia beetle attacks (binomial and negative binomial distributions, respectively) in relation to the remaining variables. The models to assess the presence of beetle holes included all trees assessed in a given group, while the models to assess the intensity of attacks included only the trees where beetle presence was confirmed. For the intensity of attacks, we used the number of holes as the dependent variable and considered the area of the trunk assessed (log10) as the offset, because the sampled area varied for each tree as a result of different trunk diameters.

Prior to model building, the correlation between variables was assessed (Pearson's correlation coefficient). When correlation was greater than 0.60, only one variable was used in order to avoid collinearity problems [29]. Finally, we also computed variance inflation factors (VIF) to confirm and select the final set of variables, avoiding multi-collinearity between explanatory variables; since no formal cut-off value or method exists to determine when a VIF is too large, we opted for a conservative approach and selected a final set of variables with VIF < 3 [28] using the usdm R package [30].

Model selection followed [29], starting with a model that included all explanatory variables and sequentially removing the variables that did not contribute significantly to the explained deviance (based on analysis of deviance tests). The Nagelkerke pseudo-$R^2$ (Nagelkerke, 1991) and the explained deviance were used as indicators of the model's performance [29]. All GLM analyses were performed using R [31] and the MASS package [32].

## 3. Results

### *3.1. Drivers of Early Ambrosia Beetle Attacks in Burned and Unburned Cork Oaks—Group 1*

In the first winter following the wildfire, ambrosia beetle holes, indicating tree selection by these insects, were found exclusively in the trunk of burned cork oaks (Table 2). No signs of activity were observed in unburned cork oaks. In total, 47% ($n$ = 174) of the burned cork oaks showed signs of attack; among these trees, 39% were slightly attacked (1–30 holes/m$^2$), 28% moderately (31–60 holes/m$^2$), and 33% highly attacked (>60 holes/m$^2$). Among the trees attacked, 92% had holes in the exploited cork, 43% in unexploited cork, and 52% in wounds with exposed wood. The holes were predominantly located in the lower part of the trunk, with 93% of the trees having holes below 1 m high, 78% having holes between 1 and 2 m, and 45% having holes above 2 m. There was a significantly greater presence of holes in the northern and eastern quadrants of the trunk when compared to the southern and western quadrants ($p < 0.001$).

Since there were no attacks on unburned trees in group one, we continued our analyses focusing exclusively on burned cork oaks. The selected models (Table 3) showed that the presence of ambrosia holes in the first winter was negatively related to the green crown volume and to the distance to the unburned area, while it was positively related to tree diameter, higher fire severity, and presence of debarking. Similarly, the intensity of attacks was negatively related to the distance to the unburned area and the green crown volume and was positively related to debarking height; however, the effect of tree diameter and fire severity was not significant, and there was a positive relationship with bark thickness. These two models performed well, with an $R$-squared of 0.66 and 0.42 and explained deviance of 49% and 27%, respectively (Table 3).

**Table 2.** Characteristics of the 631 cork oak trees sampled in groups 1 and 2.

| Groups | Group 1 | | | | Group 2 | |
|---|---|---|---|---|---|---|
| | Burned | | Unburned | | Burned | |
| **Number of Sampled Trees** | **369** | | **122** | | **140** | |
| **Exploited/Unexploited (E/U)** | **298E/71U** | | **93E/29U** | | **113E/27U** | |
| **Variable** | **Mean (SE)** | **Range** | **Mean (SE)** | **Range** | **Mean (SE)** | **Range** |
| DBH [1] | 23.0 (0.4) | 6–57 | 25.9 (0.9) | 6–50 | 28.6 (3.8) | 9–56 |
| Bark thickness [2] | 17.8 (0.5) | 5–61 | 20.6 (0.7) | 9–46 | - | - |
| Debarking height [3] | 1.7 (0.5) | 0–6 | 1.8 (0.1) | 0–4 | - | - |
| Stem wounds [4] | 0.1 (0.0) | 0–1 | 0.1 (0.0) | 0–1 | - | - |
| Green crown volume [5] | 5.1 (0.5) | 0–60 | 78.4 (1.5) | 20–100 | - | - |
| Maximum char height [6] | 91.2 (0.8) | 21–100 | - | - | - | - |
| Trunk char depth class 1 [7] | 2.2 (0.4) | 0–60 | - | - | 6.4 (1.5) | 0–100 |
| Trunk char depth class 3 [8] | 49.9 (2.0) | 0–100 | - | - | 20.1 (1.6) | 0–80 |
| Number of ambrosia [9] | 9.3 (0.7) | 0–40 | 0.0 (0.0) | 0 | 9.2 (1.2) | 0–89 |
| Density of ambrosia [10] | 40.2 (3.4) | 0–367 | 0.0 (0.0) | 0 | 28.4 (3.8) | 0–285 |

[1] trunk diameter at breast height (cm); [2] bark thickness at breast height (mm); [3] maximum debarking height (m); [4] area of the trunk with exposed wounds ($cm^2$); [5] volume of green (live) crown (%); [6] maximum char height relative to tree height (%); [7] trunk char depth of the lower severity class 1 (%); [8] trunk char depth of the higher severity class 3 (%); [9] number of ambrosia beetle holes up to 2 m high (n); [10] density of ambrosia beetle holes up to 2 m high ($n/m^2$).

**Table 3.** Generalized linear models (GLM) showing the variables influencing the presence and intensity of ambrosia beetle attacks in burned cork oaks in the first winter following fire (variables are ordered by decreasing order of importance; models based on 369 and 174 trees, respectively).

| Model | Variables | Coefficients | *p*-Value | AIC |
|---|---|---|---|---|
| Presence of attacks ($n$ = 369) | $\beta_0$ [1] | $-24.013 \pm 997$ | - | - |
| | Trunk diameter [2] | $0.268 \pm 0.04$ | <0.001 | 342.6 |
| | High fire severity [3] | $0.028 \pm 0.01$ | <0.001 | 309.6 |
| | Green crown volume [4] | $-0.113 \pm 0.03$ | <0.001 | 295.4 |
| | Exploited (yes) [5] | $18.028 \pm 997$ | <0.001 | 290.1 |
| | Distance to unburned [6] | $-0.023 \pm 0.01$ | <0.001 | 284.6 |
| Intensity of attacks ($n$ = 174) | $\beta_0$ [1] | $2.698 \pm 0.24$ | - | - |
| | Distance to unburned [6] | $-0.011 \pm 0.00$ | <0.001 | 1350.8 |
| | Bark thickness [7] | $0.050 \pm 0.01$ | <0.001 | 1349.7 |
| | Debarking height [8] | $0.236 \pm 0.07$ | <0.001 | 1334.5 |
| | Green crown volume [4] | $-0.040 \pm 0.01$ | <0.01 | 1332.8 |

Model coefficients (± standard error): [1] $\beta_0$, intercept; [2] trunk diameter at breast height (cm); [3] high fire severity (char depth class 3) at the trunk base (%; see methods); [4] green crown volume (%); [5] exploited for cork (yes vs. no); [6] distance to the unburned area (m); [7] bark thickness at breast height (mm); [8] maximum debarking height (m). The importance of each variable was evaluated by the significance of $p$-values (*chi-squared test*) and model AIC resulting from removal of that variable. Model fit (presence): Nagelkerke $R^2$ = 0.66; explained deviance = 48.97%. Full model AIC = 279.8. Model fit (intensity): Nagelkerke $R^2$ = 0.42; explained deviance = 26.52%. Full model AIC = 1327.4.

### *3.2. Ambrosia Beetle Attacks along a Distance Gradient to the Unburned Area—Group 2*

Among the 140 cork oaks sampled along the transect that crossed the burned area from north to south, the large majority (81%) was previously exploited for cork production (Table 2). In the first summer after the fire (i.e., one year after fire), 49% of all trees were still alive, while the remaining 51% had no sign of vegetative activity (no green leaves in the crown or at the base). Of the burned cork oaks, 84% initially had post-fire crown regeneration, but, in most cases, they dried out, and, at the time of sampling, only 33% still showed green leaves in the crown, while 29% had live basal regeneration.

Overall, the presence of ambrosia beetles was registered in 56% ($n$ = 78) of the cork oaks sampled, but the attacks were concentrated on exploited trees (75 trees attacked, i.e., 66% of exploited trees), while unexploited oaks were little affected (only three trees, i.e., 11% of unexploited trees). The number of holes in the trunk below 2 m per attacked tree ranged between 1 and 89 (mean 9.2 ± 1.2 SE), and the density (holes/$m^2$) ranged between 3 and 285 (mean 28.4 ± 3.8 SE). Concerning the location of holes in the tree, they were mostly concentrated on the lower part of the main trunk (below 2 m above ground), and, in the exploited cork, only 24% of the trees had holes above 2 m, and only 18% had holes in the unexploited (virgin) cork.

The obtained models showed that tree size was a major factor positively affecting ambrosia beetle attacks one year after fire occurrence. Live crown and low fire severity were both negatively related to the presence of attacks, while the distance to the unburned area had a negative effect on the attack intensity, though its significance was lower. The first model performed better than the second (Table 4).

**Table 4.** Generalized linear models (GLM) showing the variables influencing the presence and intensity of ambrosia beetle attacks in burned cork oaks along a transect crossing the burned area one year following fire (variables are ordered by decreasing order of importance; models based on 140 and 78 trees, respectively).

| Model | Variables | Coefficients | *p*-Value | AIC |
|---|---|---|---|---|
| Presence of attacks ($n$ = 140) | $\beta_0$ [1] | 0.267 ± 0.04 | - | - |
| | Trunk diameter [2] | 0.186 ± 0.04 | <0.001 | 168.0 |
| | Live crown [3] | −1.560 ± 0.51 | <0.01 | 141.9 |
| | Low fire severity [4] | −0.004 ± 0.01 | <0.01 | 141.8 |
| Intensity of attacks ($n$ = 78) | $\beta_0$ [1] | 3.661 ± 0.18 | - | - |
| | Distance to unburned [5] | −0.002 ± 0.00 | 0.01 | 589.0 |

Model coefficients (± standard error): [1] $\beta_0$, intercept; [2] trunk diameter at breast height (cm); [3] presence of live crown (usually post-fire regeneration); [4] low fire severity (char depth class 1) at the trunk base (%; see methods); [5] distance to the unburned area (m). The importance of each variable was evaluated by the significance of *p*-values (*chi-squared test*) and model AIC resulting from removal of that variable. Model fit (presence): Nagelkerke $R^2$ = 0.51; explained deviance = 34.71%. Full model AIC = 133.5. Model fit (intensity): Nagelkerke $R^2$ = 0.12; explained deviance = 7.39%. Full model AIC = 586.4.

### *3.3. Ambrosia Beetle Attacks in Unburned Oaks Debarked in Different Years after Fire—Group 3*

The three forest stands studied in group 3 were within 700 m of the wildfire perimeter, and the 210 cork oaks assessed (70 trees per stand) were debarked in the three subsequent years (see Table 5). The stand debarked in the first summer after the wildfire (2014) had, on average, larger trees and trees located closer to the burned area; in spite of this proximity, only one cork oak had signs of ambrosia beetle attack (17 holes, all located in debarking wounds). The stand debarked in the second summer after the fire (2015) had, on average, the trees located further away to the burned area. In this stand, 14 trees (20%) had presence of ambrosia beetle holes (located in debarking wounds in six trees); additionally, this was the only stand where a few trees ($n$ = 3) had recently died. The stand debarked in the third summer after the fire (2016) was in an intermediate situation concerning the distance to the burned area, and no ambrosia beetle attacks were observed (Table 5).

The model developed showed that the area of debarking wounds in the stem (resulting either from the last or older debarking) was the main factor explaining ambrosia beetle attacks, with a significant positive relationship between them (Table 6). The green crown volume was also negatively related to the presence of beetles. The model for presence performed relatively well despite the low number of trees attacked ($n$ = 15). Because of this small number, a model for attack intensity was not fitted.

**Table 5.** Characteristics of the 210 unburned cork oak trees sampled in three private forest stands debarked in different years after the wildfire.

| | Cork Oak Stand Debarking Year | | | | | |
|---|---|---|---|---|---|---|
| | 2014 | | 2015 | | 2016 | |
| Sampled trees [1] | 70 | | 70 | | 70 | |
| Attacked trees [2] | 1 | | 14 | | 0 | |
| Variable | Mean (SE) | Range | Mean (SE) | Range | Mean (SE) | Range |
| DBH [3] | 35.2 (1.0) | 20–60 | 30.0 (0.9) | 15–51 | 28.5 (1.1) | 14–60 |
| Green crown [4] | 83.5 (1.5) | 30–95 | 77.4 (2.3) | 0–95 | 86.6 (1.1) | 40–95 |
| Dry crown [5] | 0.7 (0.0) | 0–2 | 1.7 (1.1) | 0–60 | 0.7 (0.0) | 0–0 |
| Stem wounds [6] | 1.5 (0.1) | 0–3 | 1.7 (0.1) | 0–3 | 1.0 (0.1) | 0–3 |
| Distance to burned [7] | 214 (18) | 7–527 | 591 (8) | 440–696 | 322 (6) | 237–413 |
| Number of ambrosia [8] | 0.2 (0.2) | 0–17 | 3.6 (1.6) | 0–84 | 0.0 (0.0) | 0–0 |
| Density of ambrosia [9] | 1.0 (1.0) | 0–69 | 11.5 (5.1) | 0–283 | 0.0 (0.0) | 0–0 |

[1] number of sampled trees in each site; [2] number of trees attacked by ambrosia beetles; [3] diameter at breast height (cm); [4] volume of green (live) crown (%); [5] volume of brown/yellow (dry) crown (%); [6] area of the trunk with exposed wounds (4 intensity classes, from 0 to 3); [7] distance to the burned area (m); [8] number of ambrosia beetle holes up to 2 m high (n); [9] density of ambrosia beetle holes up to 2 m high (n/m$^2$).

**Table 6.** Generalized linear model (GLM) showing the variables influencing the presence of ambrosia beetle attacks in unburned cork oaks in three forest stands (variables are ordered by decreasing order of importance; model based on 210 trees).

| | Coefficients | *p*-Value | AIC |
|---|---|---|---|
| $\beta_0$ [1] | $-2.258 \pm 1.766$ | - | - |
| Stem wounds [2] | $1.487 \pm 0.498$ | <0.001 | 88.55 |
| Green crown [3] | $-0.048 \pm 0.016$ | <0.01 | 83.37 |

Model coefficients (± standard error): [1] $\beta_0$, intercept; [2] stem wounds, area of the three major stem wounds (see methods); [3] volume of green (live) crown (%). The importance of each variable was evaluated by the significance of *p*-values (*chi-squared test*) and model AIC resulting from removal of that variable. Model fit: Nagelkerke $R^2$ = 0.43; explained deviance = 36.54%. Full model AIC = 74.59.

## 4. Discussion

### *4.1. Major Drivers of Ambrosia Beetle Attacks in Mediterranean Oak Forests Following Fire*

Ambrosia beetles are recognized as playing a very important role in forest ecosystems but, in several cases, they are also seen as a serious concern and a potential cause of major economic impacts [33,34]. For these reasons, they have been receiving increasing attention to determine the mechanisms leading these beetles to select and colonize some trees and not others.

Here, we analyzed the factors that most contributed to tree colonization following fire occurrence. This is most relevant for post-fire management as infested trees likely have lower productivity and a higher probability of mortality, and neighboring forest stands may also be at higher risk.

### *4.2. Wildfire and Fire-Related Factors*

We found that the wildfire that occurred in July 2013 in the study area was the most important driver triggering the ambrosia beetle attacks. In the first five to eight months after the fire, nearly half of the burned oaks were colonized, while none of the unburned oaks located in their close vicinity ($n$ = 122; control) was affected. Additionally, our models showed that, among the burned trees, fire severity indicators related to trunk and crown damage are significant predictors of the presence and intensity of ambrosia beetle attacks, as well as the distance to the nearest unburned area. To our knowledge, this is the first time that such relationships have been clearly shown in broadleaf forest ecosystems in Europe and in the Mediterranean Basin.

Our models showed that the presence of ambrosia beetle attacks increases with increasing fire severity. These findings agree with previous results obtained in the same area using only a few flight interception traps, in which more beetles were captured in severely burned trees with no resprouting [18]. Fire severity is directly linked with post-fire responses of Mediterranean trees, namely with mortality and vegetative regeneration [20,21]. Carbon starvation and hydraulic dysfunction resulting from fire-induced leaf/cambium/phloem necrosis and xylem damage are the main fire effects on trees and are linked with drought and insect impacts [2].

Despite the lack of data concerning the Mediterranean forest ecosystems, fire has been related to ambrosia beetle attacks in several other ecosystems worldwide. Studies reporting ambrosia beetle attacks in broadleaved trees affected by fire seem to be quite rare. These include, for example, studies on attacks by *X. saxesenii* and *Gnathotrichus pilosus* LeConte (Coleoptera: Curculionidae) in tanoak trees in California [35], attacks by *Platypus*-like and *Xyleborus*-like scolytids on dead and severely damaged trees after fire in the Galapagos Islands [36], and attacks by *Xyleborus perforans* Wollaston (Coleoptera: Curculionidae) and other species in burned *Eucalyptus* and *Araucaria* trees after fire in Papua New Guinea [37]. On the other hand, we found several studies reporting ambrosia beetle attacks in conifers. In Australia, Wylie et al. [4] reported attacks of *X. perforans* two months after a wildfire in standing pine burned trees and observed that beetles are most common in trees that have been severely burned. These authors reported that the attacks did not become a serious problem during the six-month salvage period, though heavy infestations occurred after that in trees left unharvested. In Mexico, Fonseca-González et al. [38] reported that the ambrosia beetle *Gnathotrichus* sp. was colonizing pine trees killed by fire and found a strong relationship between fire damage and the subsequent presence of insects. In the USA, Hanula et al. [39] reported significantly higher trap caches of *Xyleborus* spp. in burned pine stands with moderate and high fire severity than in low severity and unburned stands, while the numbers of four other species, including *X. saxesenii* and *Platypus flavicornis* Fabricius (Coleoptera: Curculionidae), were not significantly different between stands. Also in the USA, Hood et al. [40] reported that the presence of ambrosia beetles (*Trypodendron* and *Gnathotrichus* spp.) is a significant predictor for post-fire mortality of white fir (*Abies concolor* (Gordon) Lindl. ex Hildebr.). In North America, there have also been similar reports concerning prescribed fires in pine forests; Tabacaru et al. [41] reported the presence of *Xyleborus xylographus* Say (Coleoptera: Curculionidae) in burned pine stands after prescribed fires, though beetles were not present in nearby unburned pines, and Sullivan et al. [42] reported that *Xyleborus pubescens* Zimmermann (Coleoptera: Curculionidae) was attracted to burned pines in numbers that correlated positively with burn severity.

Ethanol is considered the most attractive semiochemical for several ambrosia beetles, and its emission from trees represents a primary host-selection cue. Although low amounts of ethanol can be found in the vascular tissue of healthy trees, ethanol production can be induced by a large variety of abiotic and biotic stressors, including flood, drought, and pathogens [43,44]. Fire-injured trees are also known to release high amounts of ethanol and volatile terpenes, which attract ambrosia beetles and other insects, and, as fire injury increases in tree stems and crown, there is an accompanying rise in tissue ethanol concentrations [2,44,45]. Additionally, in the year before the wildfire (2012), the total precipitation was extremely low (132 mm; IPMA), being the driest in a 20-year period. This could have increased the trees' susceptibly to beetle attacks, as drought is also a powerful stressing factor. However, in this case, all the trees were subjected to similar conditions, and the unburned trees were not attacked.

Of the ambrosia beetle species present in our study area, *X. saxesenii* has been reported to positively respond to ethanol concentrations [46,47]. The other species are also likely attracted to ethanol. Several authors reported that primary attraction in the genus *Platypus* is associated with host odors, particularly ethanol and/or monoterpenes [48].

### *4.3. Distance to the Unburned Area*

The distance of the burned cork oak trees to the unburned stands was also an important factor affecting the presence and intensity of ambrosia beetle attacks. Beetle attacks decreased with increasing distance in spite of the sampled burned trees being located quite close to the unburned area (<360 m). These results are consistent with those previously reported by Catry et al. [18] in the same area, in which the number of *P. cylindrus* catches in pheromone traps (installed up to 330 m from the fire perimeter) was strongly and negatively affected by the distance to the unburned area, though this effect disappeared by the end of the first spring following fire.

Ambrosia beetles spend most of their life within their host wood and are only present in the external environment for a short period of time when they are searching for a new host. Very little is known about the flight capacity of the four ambrosia beetles present in the study area. However, both of the above-mentioned results suggest that the flight distance of these species is not large, at least when there are suitable hosts nearby. The flight capacity of ambrosia beetles varies between species and can be influenced by several factors, including temperature and wind [49]. Seo et al. [50] compared the flight capacity and patterns of two ambrosia beetle species in laboratory conditions and found significant differences between them. Over a 24 h period, the flight distance of one species was limited to 20 m, while the other was capable of routinely flying more than 100 m, though only 5% of the individuals were able to fly distances over 1 km. Although these distances seem quite short, it is known that under field conditions and with wind, insect flight distances can be much larger than in the laboratory [51]. In contrast, Okada et al. [52], by conducting experiments using a flight mill, found that *P. quercivorus* can fly at least 27 km.

### *4.4. Crown Physiological Condition (Volume of Green Crown)*

The variable 'volume of green crown', used as an indicator of the tree's physiological condition, was found to be negatively associated with the presence and intensity of ambrosia beetle attacks in both burned and unburned trees, meaning that the attacks decreased with increasing volume of green crown. This result was not surprising since host selection by ambrosia beetles is also mediated by green leaf volatiles, some of which might be deterrent. In an experimental study in Canada, Borden et al. [53] showed that the ambrosia beetle *Trypodendron lineatum* Olivier (Coleoptera: Curculionidae), typically attacking dead or dying coniferous trees, responds negatively to green leaf volatiles. They showed that four green leaf alcohols, released alone or in a blend, caused a reduction in trap caches, baited with aggregation pheromones, of up to 78%. In another study, Pham et al. [54] also showed that the ambrosia beetle *P. quercivorus* uses leaf volatiles in host selection.

### *4.5. Tree Size, Bark Thickness, and Cork Exploitation*

In our models for burned trees, and regardless of whether the trees were assessed 5 or 12 months following fire, trunk diameter was the most important variable explaining the presence of ambrosia beetle boring activity. In our study, the smaller burned cork oak being attacked had 15 cm DBH. The presence of beetle attacks increased with increasing tree size, which is in accordance with other studies concerning unburned trees. Bellahirech et al. [55] found that the presence of ambrosia beetle holes in unburned exploited cork oaks in Tunisia is positively related to tree DBH, and Sousa and Debouzie [24] also found that cork oaks attacked by *P. cylindrus* in Portugal are, on average, larger than the trees not attacked. One possible and likely reason explaining this effect is that beetles need a sufficiently large volume of wood to construct the gallery system in the xylem, which is necessary for growing symbiotic fungi to feed the adults and their brood. Larger trunks also likely retain moisture easier, which is crucial for fungi development. If the tree is large enough, several generations may continue to extend the galleries as long as the tree retains sufficient moisture [6]. Maner et al. [56] studied *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae) ambrosia beetle attacks on the broadleaf *Persea borbonia* L. in the southeastern USA and found that beetles that attack larger-diameter trees are more likely to successfully establish a gallery and produce more brood, suggesting that this is the reason for beetles being visually attracted to larger-diameter silhouettes of bigger trees. Another possible and complementary reason could be related to tree age, which is strongly correlated to tree size. Indeed, older cork oaks are usually debarked more times during their life and possibly suffer more from poor management practices, making these trees less vigorous than younger trees [22,23]. However, our models also show that tree diameter does not affect the intensity of the attacks. These results seem to suggest that once the tree is first colonized, the number of subsequent beetles attacking that tree no longer select for diameter. However, this could be also a consequence of the relatively small variation in tree diameter among initially selected trees.

The tree exploitation status was a significant factor affecting beetle presence on burned trees sooner after fire (group 1) but not later (after one year; group 2). The burned trees that were never exploited for cork and that were likely more vigorous were not attacked during the first months following fire, possibly as there were more suitable hosts available, but, after one year, there had already been some attacks also on unexploited trees. The debarking height and the bark thickness were only tested in group 1 and were both found to positively affect the intensity of attacks. Debarking height is a proxy for debarking intensity and was expected to point out trees that were more stressed. Sousa and Debouzie [24] also reported that unburned trees being exploited for cork and with higher debarking height are more likely to be attacked by *P. cylindrus*. Concerning the positive effect of bark thickness, we hypothesize that it could be related to wood moisture, as cork is a very good insulator; indeed, trunks with a very thin layer of cork could dehydrate faster than those with a thicker layer, which is an important characteristic for beetle selection. The importance of wood moisture is emphasized by some authors who mention that cut logs placed in sunny places where the wood dries faster attract fewer ambrosia beetle attacks than those in shaded areas [6,57]. However, this possible explanation for bark thickness needs to be further investigated.

Finally, the surface of the stem that was wounded, which is usually associated with the cork harvesting activity, was the most important variable in the model for unburned trees in group 3, but not for burned oaks in the other groups, which was probably because of the existence of extended fire damages on these trees that masked the debarking wound effect. The presence of tree trunk cavities associated with debarking wounds was found to be the most important factor affecting beetle presence on unburned, exploited cork oaks in Tunisia [55]. Maner et al. [56] also reported that scraping of the tree outer bark results in some small areas of phloem and xylem being exposed that are attractive to *X. glabratus*, and that these areas are usually quickly attacked.

### *4.6. Are Neighboring Unburned Forests at Higher Risk from Ambrosia Beetle Attacks Following Wildfire?*

Some studies reported that beetles developing on fire-injured trees may then affect healthy trees and cause delayed tree mortality [58,59]. In the current study, we wanted to know if, after the wildfire, the neighboring unburned cork oak forest stands were at higher risk, and we hypothesized that the very high number of ambrosia beetles in the burned area [18,19] could cause a spill-over effect to adjacent areas. However, our expectations did not materialize. In the stand debarked in the first summer after the wildfire (2014), which was also the nearest one, only one cork oak tree had signs of the presence of ambrosia beetles, and, in the stand debarked in the third summer after the fire (2016), no ambrosia beetle attacks were registered. Only in the stand more distant from the burned area, debarked in the second year after the fire (2015), could we observe a significant number of trees with ambrosia beetle attacks (20%). However, there was no evidence that these attacks were directly related to the fire event. A more likely explanation for these attacks is the fact that 2015 was a very dry year with a total precipitation well below the average (309 mm; annual average was 553 mm in the 20-year period 1999–2018; IPMA), while 2014 and 2016 were above the average (597 mm and 638 mm, respectively). Higher susceptibility to ambrosia beetles of the trees in this stand could also be due to other stressors resulting from micro-environmental conditions, such as soil quality or pathogens favouring ambrosia beetle attacks [43,46,60,61]. This was also the only stand where a few trees had recently died, further indicating the presence of other stress factors. Thus, our results suggest that ambrosia beetles after fire do not show spread behavior into nearby unburned forest, which is consistent with observations in other studies [39,62]. Nevertheless, we may still hypothesize that ambrosia beetles whose population had built up on the burnt area can fly to new areas and then easily colonize trees if the trees are weakened by other stressors.

The model developed here further shows that debarking wounds in the stem is a main driver for ambrosia beetle attacks in unburned areas. This reinforces the need to carefully conduct debarking during cork harvest to avoid ambrosia beetle attacks. Our model also suggests a negative association between green crown volume and the presence of ambrosia beetles. However, we cannot separate if this was a consequence of the attack or an indicator of previous stress.

## 5. Conclusions

We showed that wildfire occurrence was the most important trigger of ambrosia beetle attacks in the studied cork oak forests. Up to eight months after the fire, nearly half of the burned oaks were attacked, while none of the nearby unburned trees was affected. Up to one year after the fire, the trees with a higher probability of being attacked were those that were most severely affected by fire, located closer to the unburned area, with a larger diameter, with thicker bark, and being exploited for cork. Among the unburned trees attacked in the subsequent years, those with stem wounds and with lower crown vigor were more often attacked.

This study contributes and extends the knowledge about the host-selection habits of ambrosia beetles in the Mediterranean Basin and provides useful information to support pre- and post-fire management decisions. To minimize the probability of ambrosia beetle attacks, the priority should be to implement measures to reduce fire hazard and severity and to reduce to a minimum all the management activities that are known to cause stress to trees. Examples include reducing debarking intensity and avoiding debarking wounds, branch pruning, or soil ploughing as much as possible. Preventing beetle attacks also limits introduction of fungi into trees, increasing the resistance mechanisms against other stress factors. These issues are particularly relevant in the context of climate change, because not only wildfires but other abiotic stressors such as droughts are expected to become more frequent and severe in the future.

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