



Resin ducts and bark thickness influence pine resistance to bark beetles after prescribed fire

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ABSTRACT

After fire, bark beetles pose a significant threat to trees. Resin duct characteristics in trees can increase resistance to bark beetles. However, little is known about how intra- and interspecific variations in resin ducts due to tree characteristics, fire-caused tree injury and life history traits contribute to resistance. In fall 2013, a mixed-stand of *Pinus sylvestris* and *P. nigra* was underburned, with some trees subsequently attacked and killed by bark beetles (*Ips sexdentatus*) during the following two years. We investigated whether inter- or intraspecific differences in constitutive defenses (i.e. bark thickness, tree size and growth, resin ducts) or fire-caused tree injury could explain tree resistance to bark beetles. Beetles preferentially attacked *P. sylvestris* over the more fire-resistant *P. nigra* subsp. *salzmannii*. In *P. nigra*, attacks were limited to smaller trees, whereas the probability of mortality from *I. sexdentatus* increased with diameter in *P. sylvestris*. The decrease in bark thickness along the stem significantly affected the probability of mortality in *P. sylvestris* but not in *P. nigra*. As tree size increased, bark thickness and resin duct area investment were lower in *P. sylvestris* than *P. nigra*, suggesting reduced defences in *P. sylvestris*. For both species, pines that survived had faster growth, higher resin duct area, and fewer but larger ducts than pines that died after the attack. However, resin duct area and density rather than growth or fire-caused injury were better predictors of tree resistance. Moreover, in unattacked trees resin duct area increased with diameter in *P. nigra*. Our study showed that bark beetles attacks were tree species and size specific, but ultimately resin duct characteristics determined host colonization. Our findings suggest managers can expect higher delayed mortality from bark beetles in *P. sylvestris* after burning; however, actions that encourage faster growth may increase resin duct-related defences in both pine species.

1. Introduction

Post-fire delayed tree mortality can occur directly as a function of fire-caused injuries, or in combination with other stressors, such as drought or insects (Kane et al. 2017; Hood et al. 2018). After fire, bark beetles (Coleoptera, Scolytidae) can attack fire-weakened trees (Bradley and Tueller 2001; Wallin et al. 2003; Lombardero and Ayres 2011), potentially increasing the population above pre-burning levels and leading to higher levels of tree mortality (Santoro et al. 2001; McHugh et al. 2003). Fire can cause short-term increases in attacks of burned trees, but little evidence exists for fire causing bark beetle outbreaks (Lerch et al. 2016; Tabacaru et al. 2016; Davis et al. 2012; Powell et al. 2012). *Pinus* species have numerous defences to resist bark beetle attack

(Franceschi et al. 2005; Seybold et al. 2006), some of which are influenced by fire (Hood et al. 2015; Valor et al. 2017a). *Pinus* species also vary in their tolerance of fire, ranging from easily killed to highly resistant (Fernandes et al. 2008). Therefore, a tree's ability to survive fire is likely driven by the combined influence of species traits that provide resistance to both fire and bark beetles.

Prescribed burning is widely used in temperate forests to reduce fire hazard, as well as for forest management (Fernandes et al. 2013; Ryan et al. 2013). For example, in the Mediterranean basin, about 10 000 ha yr⁻¹ are managed using prescribed burning. These burns are typically low to mid-intensity surface fires, although some trees may be weakened depending on the species vulnerability to fire, the degree of fire injury and tree diameter (Valor et al. 2017b). An increased understanding of

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how prescribed burning impacts tree resistance to bark beetles and beetle attack preferences after burning is needed to successfully manage forested lands using fire.

Bark beetles respond to chemical and visual cues when selecting suitable host trees (see review in Gitau et al. 2013; Raffa 2014). After fire, bark beetle attack preferences to fire-injured trees have been widely reported (e.g., McHugh et al. 2003; Wallin et al. 2003), but others have found little evidence for this (Elkin and Reid 2004). These contradictory results can be partially explained by trait differences in both tree and bark beetle species studied. Tree species will influence the type and degree of fire injuries, while bark beetle species have specific host tree preferences (Davis et al. 2012). The net impact of fire on a given tree will be determined, among others, by the interaction between the degree of injury and tree resistance (i.e. tree characteristics, life history traits). For example, tree size is recognized as a significant predictor of bark beetle attack after fire (McHugh et al. 2003; Hood and Bentz 2007), but results show broad bark beetle tree size preferences (see review in Parker et al. 2006) likely because the degree of fire injury varies across tree sizes and species. Ultimately, the potential for successful colonization once bark beetles select a host tree will be first determined by the constitutive defense system of the specific pine species (e.g. mechanical properties of the bark, pre-existing resin ducts, oleoresin characteristics).

Bark is the first barrier bark beetles encounter when a host tree is selected, acting as a physical defence. While bark thickness is recognized as a fire-adapted trait (Jackson et al. 1999; Keeley et al. 2011; Pellegrini et al. 2017) insulating the cambium from heat during surface fires, it may also be an adaptation from biotic aggressions. The relative importance of bark thickness in conferring resistance to beetle attack is, however, debated. Some authors suggest that beetles prefer species with thinner bark (Parker et al. 2006; Breece et al. 2008), others argue that bark beetles select bark thickness depending on its body size (Amezaga and Rodríguez 1998), while some suggest that bark thickness does not influence beetle attack (Wood 1982). Again, these contrasting results may be explained partially by differences in the bark beetle and pine species studied.

Resin ducts synthesize, store, and transport oleoresin, therefore contributing significantly to tree defense against bark beetle attack. Oleoresin is both a physical defense that can trap bark beetles boring through bark (Phillips and Croteau 1999) and a chemical defense, as some oleoresin compounds can be physiologically toxic to bark beetles (Seybold et al. 2006). Resin ducts are plastic, changing with climate, management, and disturbance (see Vázquez-González et al. 2020 for review), but also under genetic control (Westbrook et al. 2015). Importantly, resin ducts are positively related with resin flow (Hood and Sala 2015) and can be retrospectively quantified from secondary xylem samples to allow examination of factors that influence resin duct-related defenses, while resin flow offers only a snapshot in time of defense levels. Several studies, mostly conducted in *Pinus* species of North America, have shown that trees with a higher number of resin ducts per ring year and/or larger resin ducts (i.e. mean resin duct size) are more likely to survive beetle attacks (e.g., Kane and Kolb 2010; Ferrenberg et al. 2014; Hood et al. 2015; Zhao and Erbilgin 2019), but we are aware of no studies that have examined the interaction of fire and resin duct defenses on resistance to bark beetles.

In this study, we analysed tree resistance to *Ips sexdentatus* Boern. (Börner 1776) after prescribed burning in pines with contrasting tolerance to surface fires: the fire resistant *P. nigra* subsp. *salzmannii* (Dunal) Franco and the moderately fire-resistant *Pinus sylvestris* L. *I. sexdentatus* colonizes weakened, dying or recently dead trees (Gil and Pajares 1986) and attacks observed following wildfires in *P. pinaster* in northwest Spain (Fernández-Fernández 2006; Santolamazza-Carbone et al. 2011) indicated a preference for small *P. pinaster* trees (Santolamazza-Carbone et al. 2011) but with mixed attraction to fire-injured trees (Fernández-Fernández 2006; Santolamazza-Carbone et al. 2011). Our objective was to determine to what degree species traits, constitutive defenses, and fire-caused injury can explain why some individuals of *P. nigra* and

P. sylvestris succumbed to beetle attack. Previous research on *I. sexdentatus* attacks after wildfire have focused on tree size and fire injury preferences (Fernández-Fernández 2006; Santolamazza-Carbone et al. 2011) but the relationship between attack and resin duct characteristics has not been quantified.

P. nigra, with its thicker bark, is considered more resistant to fire-caused injury than *P. sylvestris* (Fernandes et al. 2008; Valor et al. 2017b); thus, we expected a higher vulnerability of *P. sylvestris* to beetle attack than *P. nigra*. Furthermore, bark thickness decreases along the tree stem, at least in small *P. nigra* (Fernandes et al. 2012), and this decrease is likely even greater in *P. sylvestris* given the characteristic thinner bark on the upper stem. Consequently, as *I. sexdentatus* is able to attack bark thinner than its own mean body depth (Amezaga and Rodríguez 1998), we hypothesized that the interspecific differences in bark thickness would favour *P. nigra* resistance to *I. sexdentatus* in comparison with *P. sylvestris*. Additionally, as bark thickness increases linearly with tree size, we expected potential inter- and intra-specific differences in stem bark thickness reduction along the stem among tree sizes. Regarding resin ducts defenses, we hypothesized that non-attacked trees will have larger resin ducts and/or higher number of resin ducts per ring year than attacked trees.

2. Methodology

2.1. Study site

The study was performed in the foothills of the Pyrenees (NE Iberian Peninsula), at an altitude of 715 m.a.s.l. in the forest locality of Lloreda (1.5706 °E, 42.0569 °N). In this area, the Forest Actions Support Group (GRAF) of the Autonomous Catalan Government (Generalitat de Catalunya) has managed a total of 59 ha using prescribed burning within the framework of a strategic wildfire prevention plan. The climate is sub-Mediterranean with milder summers and colder winters than the typical Mediterranean climate. Soils are developed from calcareous colluviums and are classified as Calcaric inceptisols (FAO 2006), between 0.5 m and 1.0 m deep, basic (pH 6.8–7.5), and with a fine texture. The forest overstory is dominated by *P. nigra* subsp. *salzmannii* and *P. sylvestris*; broadleaf trees (i.e. *Quercus pubescens* Willd., *Acer monspessulanum* L., *Sorbus aria* (L.) Crantz) are also common. The understory is composed mainly of the evergreen *Buxus sempervirens* L. and deciduous species (e.g. *Lonicera etrusca* L., *Viburnum lantana* L., *Amelanchier ovalis* Medik.). Other evergreen shrubs are also common in the understory (e.g. *Juniperus oxycedrus* Sibth. and Sm., *Q. coccifera* L.).

In 2012, before prescribed burning, we selected a stand of mixed *P. sylvestris* and *P. nigra*. In the stand, the proportion of *P. nigra* individuals was higher (76.3%) than that of *P. sylvestris* (23.7%), while mean tree age of the two species was rather similar (56 ± 10 years vs. 59 ± 6 years, respectively). Within the stand, we selected two paired units (1 ha each) to burn either in spring or fall. Prescribed burning was conducted in late spring (5 June 2013) and fall (8 November 2013) by the GRAF with the objective of reducing surface and ladder fuels. In general, understory prescribed burns were carried out following a strip headfire ignition pattern under mild meteorological conditions. In 2013, we started studying the effects of burning season on understory and overstory mortality and post-fire growth (Valor et al. 2017b 2020; Casals et al. 2018). In the summer 2014, we first noticed that a number of trees were attacked by *I. sexdentatus* within the site burned during the previous fall (Fig. 1).

2.2. Data collection

We established one plot (30 × 30 m, 0.1 ha) in each unit prior to burning to monitor the effects of fire on pine mortality (Valor et al. 2017b). In the monitoring plots, we tagged all pines with a diameter at 1.30 m height (DBH) larger than 2.5 cm with a metal number and measured DBH. Two weeks after prescribed burning, for each tree, we



Fig. 1. *Pinus sylvestris* attacked by *I. sexdentatus* one year after fall underburning.

characterized the degree of crown and stem injury using several indicators (see details in Valor et al. 2017b). For the current study, we used maximum bole scorch height (BSH_{max}) to characterize stem injury (Wyant et al. 1986). BSH_{max} was measured from the ground level to the highest point on the bole where scorch/charring was evident. It should be noted, that BSH is an indirect assessment of injury, and may not adequately reflect cambium tissue killed if the bark is thick enough.

In summer 2014 and 2015, we surveyed all trees in the 1 ha units burned in 2013 for signs of being attacked by beetles. Infested trees were identified through visual examination of each tree bole by looking for the presence of beetles, galleries and boring dust. No attacks were observed in the unit burned in spring, but bark beetles infested 66 out of 583 pines in the fall burn unit. The attacks occurred throughout the fall burn unit but not in our 0.1 ha established plot; therefore, to examine beetle attack preferences we expanded our sampling to measure DBH and BSH_{max} of all trees larger than 2.5 cm in DBH within the 1 ha fall burn unit independently of whether the trees were infested or not. All infested trees died within 2 years after the first notice of attack.

DBH of all trees measured within the sites burned in spring (0.1 ha plot) and fall (1 ha unit) was used to estimate diameters at 0.20 m (D₂₀) and 0.50 m (D₅₀) and bark thickness at each diameter height (BT₂₀, BT₅₀ and BT₁₃₀) based on the allometric equations developed by Valor et al. (2017b) that related BT to diameter at different heights and between DBH and D₂₀ and D₅₀. For BT₂₀ and BT₁₃₀, we calculated the relative bark thickness of each individual as the ratio of bark thickness to stem radius (rBT₂₀ or rBT₁₃₀). Then, to quantify the reduction in bark thickness with stem height, we computed the relative bark thickness reduction with stem height (rBT_{red}) as the difference between the rBT₂₀ and rBT₁₃₀ expressed as a percentage.

2.3. Tree selection for resin duct measures

Resin duct characteristics were analysed from a subsample of 48 trees by selecting trees from the fall burn unit with different tree status and encompassing a range of DBH. Trees were grouped into two status classes: 'Live' (i.e. pines that avoided beetle attack) and 'Dead' (i.e. pines infested by beetles that died within 2 years of attack). Three DBH classes were defined: the 5 cm DBH class ($2.5 \text{ cm} \leq \text{DBH} < 7.5 \text{ cm}$), the 10 cm

DBH class ($7.5 \text{ cm} \leq \text{DBH} < 12.5 \text{ cm}$) and the 15 cm DBH class ($12.5 \text{ cm} \leq \text{DBH} < 17.5 \text{ cm}$). For each species we selected 2–5 trees per combination of diameter classes (i.e. 5, 10 and 15 cm) and tree status (i.e. 'Live' and 'Dead'), with the exception of dead *P. nigra* pines in the 15 cm class where only one tree was available for sampling. Still, we selected 5 live *P. nigra* trees of the 15 cm DBH class as we aimed to compare resin duct metrics of live individuals between both pine species. To select trees, first, we chose a dead pine and then, the closest live tree with similar DBH, working through the area until all species \times status \times diameter bins were filled. Tree and BSH_{max} characteristics of the 48 sampled trees can be found in Table 1. In *P. nigra* significant differences in DBH and bark thickness between tree status are caused by the fact that only one individual was in the dead, 15 cm DBH class (Table 1).

Table 1

Tree and bole scorch variables by status of *Pinus nigra* and *P. sylvestris* of the subsampled trees (n = 48; fall burn unit only) for the quantification of resin duct metrics. Values are means \pm standard error. Different letters between tree status for each species represent significant differences ($P < 0.05$) as a result of a *t*-test. Diameter at breast height (DBH) range is shown in parentheses.

	<i>P. nigra</i>		<i>P. sylvestris</i>	
	Live (n = 13)	Dead (n = 10)	Live (n = 12)	Dead (n = 13)
DBH (cm)	11.5 \pm 3.45a (5.8–17.1)	7.1 \pm 2.58b (4.4–11.0)	12.5 \pm 4.88a (7.0–20.1)	10.3 \pm 3.62a (4.0–16.0)
D ₅₀ (cm)	13.5 \pm 3.98a	8.6 \pm 2.97b	14.6 \pm 6.00a	12.0 \pm 4.46a
D ₂₀ (cm)	15.4 \pm 4.11a	10.3 \pm 3.08b	16.1 \pm 5.95a	13.5 \pm 4.42a
BT ₁₃₀ (cm)	1.08 \pm 0.34a	0.63 \pm 0.25b	1.18 \pm 0.48a	0.97 \pm 0.36a
BT ₅₀ (cm)	2.11 \pm 0.40a	1.61 \pm 0.29b	2.22 \pm 0.59a	1.96 \pm 0.44a
BT ₂₀ (cm)	2.30 \pm 0.41a	1.78 \pm 0.30b	2.38 \pm 0.65a	2.09 \pm 0.48a
BSH _{max} (cm)	148.5 \pm 89.03a	149.8 \pm 46.64a	74.3 \pm 48.13a	75.5 \pm 34.48a

D₂₀, diameter at 20 cm; D₅₀, diameter at 50 cm

BT, bark thickness; BT₂₀, at 20 cm height; BT₅₀, at 50 cm height; BT₁₃₀, at 130 cm height

BSH_{max}, maximum bole scorch height

2.4. Tree growth and resin ducts measures

In March 2016, we extracted one 4.5-mm-wide increment core from the 48 subsampled trees at breast height for tree growth and resin duct measures. Cores were prepared following standard dendrochronological techniques (Stokes and Smiley 1968). All cores were visually crossdated by comparing characteristic narrow rings present in all trees to detect any false or missing rings. We assigned the correct calendar year to each tree ring. Then, we scanned all cores using an HP Officejet Pro 6830 platform scanner at 1200 d.p.i. and measured ring widths to the nearest 0.001 mm using CooRecorder v9.4 (Cybis Elektronik & Data AB, Salt-sjöbaden, Sweden). We measured resin ducts in ImageJ (version 1.52a, National Institutes of Health, Bethesda, MD, USA) to the nearest $1 \times 10^{-7} \text{ mm}^2$ using the ellipse tool and assigned the calendar year in which each resin duct formed. We measured resin ducts formed from 1983 until 2012, the year before prescribed burning.

For each core, we calculated five resin duct metrics for four-time intervals that included the 5, 10, 20, and 30 last years. Following Hood and Sala (2015), we captured annual absolute investment in resin ducts using metrics unadjusted for ring area: mean resin duct size (i.e. mean size of all resin ducts per annual ring, in $\text{mm}^2 \text{ duct}^{-1}$), resin duct production (i.e. total number of resin ducts per annual ring, in no. duct year^{-1}) and total resin duct area (i.e. sum of duct area per annual ring, $\text{mm}^2 \text{ year}^{-1}$). If resin ducts were not present in a given year, we coded resin duct size as NA (not applicable). Annual investment in resin ducts was standardized to ring area by calculating resin duct density (i.e. total number of ducts per annual ring divided by ring area, in no. $\text{mm}^{-2} \text{ year}^{-1}$) and relative duct area (i.e. total resin duct area divided by ring area, in % annual ring). Ring area was calculated by multiplying ring width by core diameter. For annual growth metrics, we used raw ring width (RW) values and calculated basal area increment (BAI) using the dplR package v. 1.6.0 in R v. 3.0.1 (Bunn 2008).

2.5. Data analysis

2.5.1. Bark beetle attacks

We summarized the proportions of dead and live trees for each species and DBH class. As there were no attacks in the spring unit, in further analysis we used only trees from the fall unit ($n = 263$).

To examine bark beetle attack preferences, we used general linear models to analyse the differences in tree level variables (i.e. DBH and rBT_{red}) or BSH_{max} in relation to tree status, pine species, and their interaction. DBH was not included in the BSH_{max} or rBT_{red} model because sample size among diameter classes and tree status was highly unequal. An additional model was included to analyse the differences in rBT_{red} as a function of DBH and pine species. To account for multiple testing, P values adjusted by the Bonferroni correction are provided, that is the P values are multiplied by the number of comparisons, with $\alpha = 0.05$ used as the significance level.

To test the probability of tree mortality, three general linear models with a binomial error distribution, specified logit link function were used. In the first model, the probability of tree mortality was modelled as a function of DBH and species. After, for each species, we developed a model that included rBT_{red} and BSH_{max} . The reason for splitting the models by pine species are due to the significant differences observed between species in rBT_{red} (t -test (258) = -10.02, $P < 0.001$) and BSH_{max} (t -test (258) = -10.02, $P < 0.001$). We did not include DBH in these models because it was highly correlated with rBT_{red} . Furthermore, in the *P. nigra* model only trees with DBH < 12.5 cm were included because only trees of those sizes were attacked. Model performance was assessed by the computed area under the curve (AUC) which represents the degree or measure of separability; that is, how much the model is capable of distinguishing between dead and live pines.

2.5.2. Resin duct and growth metrics

Resin duct and growth analyses were conducted in the sampled trees

($n = 48$). Before conducting any inferential analysis, we pre-selected each resin duct and growth variable for the time intervals most related with tree mortality (i.e. the 5, 10, 20, and 30 most recent years; Table A1 in Supporting Information, variables selected after the thresholding step) and, then, those that were tightly related with tree mortality regardless of time interval (Table A1, variables selected after the interpretation and prediction step). This analysis was done executing a random forest algorithm implemented in "VSURF" (Genuer et al. 2015). Details of the analyses and variables selected can be found in Supporting Information, Table A1.

To assess if the resin duct metrics tightly related with tree mortality (Table A1, variables after the interpretation step) differed between species and tree status, we used a general linear model for each selected resin duct metric as a function of pine species, tree status and the interaction between them. As we found that *P. sylvestris* had higher resin duct area than *P. nigra*, but a higher probability of mortality with stem diameter, we used a general linear model to analyse the effect of tree size on these resin duct metrics. In living trees, each resin duct metric selected was modelled as function of species and DBH. A set of candidate models including each diameter sampling height (D_{20} , D_{50} and DBH) separately was developed. Then, we selected the best model based on corrected Akaike criterion (AICc). All two-way interactions were included. Residuals of the models developed presented no pattern and highly correlated explanatory variables were avoided. All analyses were conducted with the software R (v. 3.2.1, the R Foundation for Statistical Computing) using the package nlme (Pinheiro et al. 2007) and the package AICcmodavg (Mazerolle 2019) for model selection. In addition, for each species we compared resin duct and growth metrics between live and dead trees using a t -test. Only the most relevant time intervals of each resin and growth measurements were compared (Table A1, variables selected after the thresholding step). Resin duct and growth variables were log-transformed to achieve normality.

The probability of pine mortality was modeled using conditional inference trees (Ctree model) using the package Party (Hothorn et al. 2008) in the subsample of 48 trees (paired dead and living pines). Ctree model estimates a regression relationship by binary recursive partitioning in a conditional inference framework that is based on maximally selected rank statistics (Hothorn et al. 2006). For individual and pooled species, a Ctree model was developed using selected resin duct variables (Table A1 in Supporting Information, variables after "prediction step") as well as growth and bark thickness variables and BSH_{max} as an indicator of fire-caused injury. Model performance was assessed by agreement rates between the observed and predicted tree status.

3. Results

3.1. Tree level characteristics and bole scorch height of live and dead pines across pine species

Two years after spring and fall burns, 11.3% of the trees had died by bark beetle attack ($n = 66$), all of which were in the fall burn unit. In *P. sylvestris*, 24.0% of trees died ($n = 32$) whereas only 7.2% of *P. nigra* trees died ($n = 34$). In contrast, *P. nigra* showed higher BSH_{max} than *P. sylvestris* (t -test (258) = -10.02, $P < 0.001$).

Overall, we found a significant interaction between species and tree status for DBH ($P < 0.001$), rBT_{red} ($P = 0.040$) and BSH_{max} ($P = 0.002$). In *P. nigra* dead pines had significantly lower DBH and BSH_{max} than live pines but similar rBT_{red} (Fig. 2). In contrast, in *P. sylvestris* dead pines had significantly higher DBH and rBT_{red} than live pines but similar BSH_{max} (Fig. 2). When modeling rBT_{red} as a function of DBH and pine species, a significant interaction between species and DBH was found ($P = 0.015$). This interaction indicated that rBT_{red} was higher in *P. sylvestris* than in *P. nigra* along all diameters, and that the difference in rBT_{red} between species increases as diameter increased (Fig. 2d).

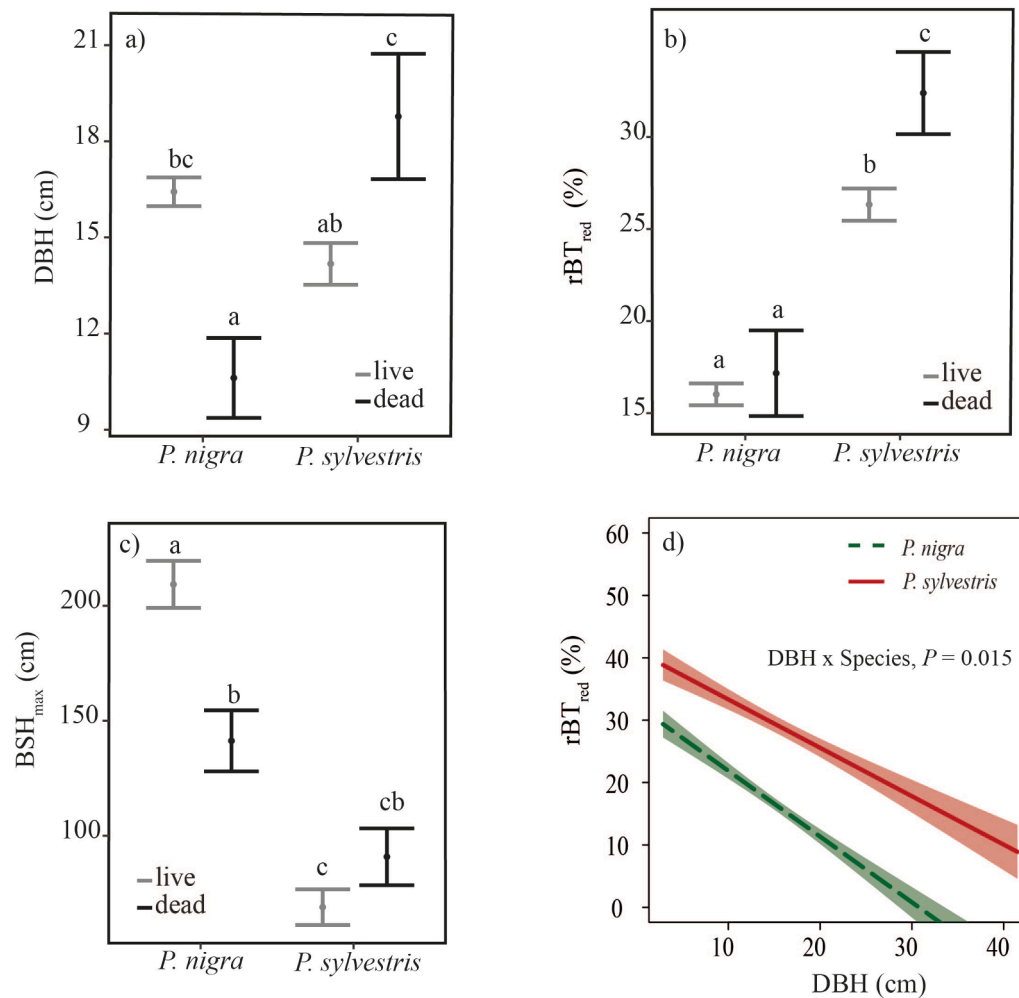


Fig. 2. Mean and standard error diameter at breast height (DBH) (a), relative bark thickness reduction in stem height (rBT_{red}) (b) and maximum bole scorch height (BSH_{max}) (c) by species and tree status. A total of 262 trees were assessed within the fall burn unit. Means followed by the same letter are not significantly different (P greater than 0.05, P values adjusted by the Bonferroni correction). Prediction lines showing the interaction between pine species and DBH to explain rBT_{red} (d).

3.1.1. Mortality models using bole scorch height and tree level characteristics

The model combining both species had the highest accuracy (AUC = 0.77) for predicting tree mortality from *I. sexdentatus*, followed by the *P. sylvestris* model (AUC = 0.70), and then the *P. nigra* model (AUC = 0.66).

The pooled *P. nigra*-*P. sylvestris* model included pine species, DBH and the interaction between them (Table 2). For trees with DBH greater than 10 cm, *P. sylvestris* had a higher probability of dying by bark beetle attack than *P. nigra* (Table 2) and the probability increased with respect to *P. nigra* as DBH increases (Fig. 3a).

The *P. nigra* and *P. sylvestris* models for predicting tree mortality differed in the significance of the variables included and their direction (Table 2). In *P. nigra*, the probability of tree mortality decreased with BSH_{max} , while rBT_{red} had no effect (Table 2 and Fig. 3b). Contrary, in *P. sylvestris*, the probability of mortality increased with BSH_{max} and rBT_{red} (Fig. 3c and d).

3.2. Resin duct metrics of live and dead pines across pine species

For pooled species, the resin duct metrics correlated with pine mortality were total duct area for the 30- and 20- year periods and duct density for the 30-yr and 10-yr periods (Table A1 in Supporting Information). Resin duct area was significantly greater in *P. sylvestris* than in *P. nigra* (Fig. 4a and Table 3). Regardless of species, live trees had higher

Table 2

Parameters estimates (Est.), standard error (S.E.), and P values for the three general linear models of tree mortality by bark beetle (*I. sexdentatus*) attack. In the first model, the intercept and DBH represented the estimate coefficients for *P. nigra*, and the estimated coefficients for *P. sylvestris* resulted from the differences between those and the coefficients Sp. (P_s) or Sp. (P_s) \times DBH. DBH, diameter at breast height; rBT_{red} , relative bark thickness reduction with stem height; BSH_{max} , maximum bole scorch height.

Pooled <i>P. nigra</i> - <i>P. sylvestris</i>	Est.	S.E.	P
Intercept	1.047	0.538	0.051
Sp. (P_s)	-2.626	0.750	<0.001
DBH	-0.190	0.042	<0.001
Sp. (P_s) \times DBH	0.260	0.051	<0.001
<i>P. nigra</i>	Est.	S.E.	P
Intercept	0.593	0.585	0.372
rBT_{red}	-0.020	0.029	0.993
BSH_{max}	-0.009	0.003	0.017
<i>P. sylvestris</i>	Est.	S.E.	P
Intercept	-3.411	0.998	<0.001
rBT_{red}	0.081	0.029	0.006
BSH_{max}	0.007	0.040	0.040

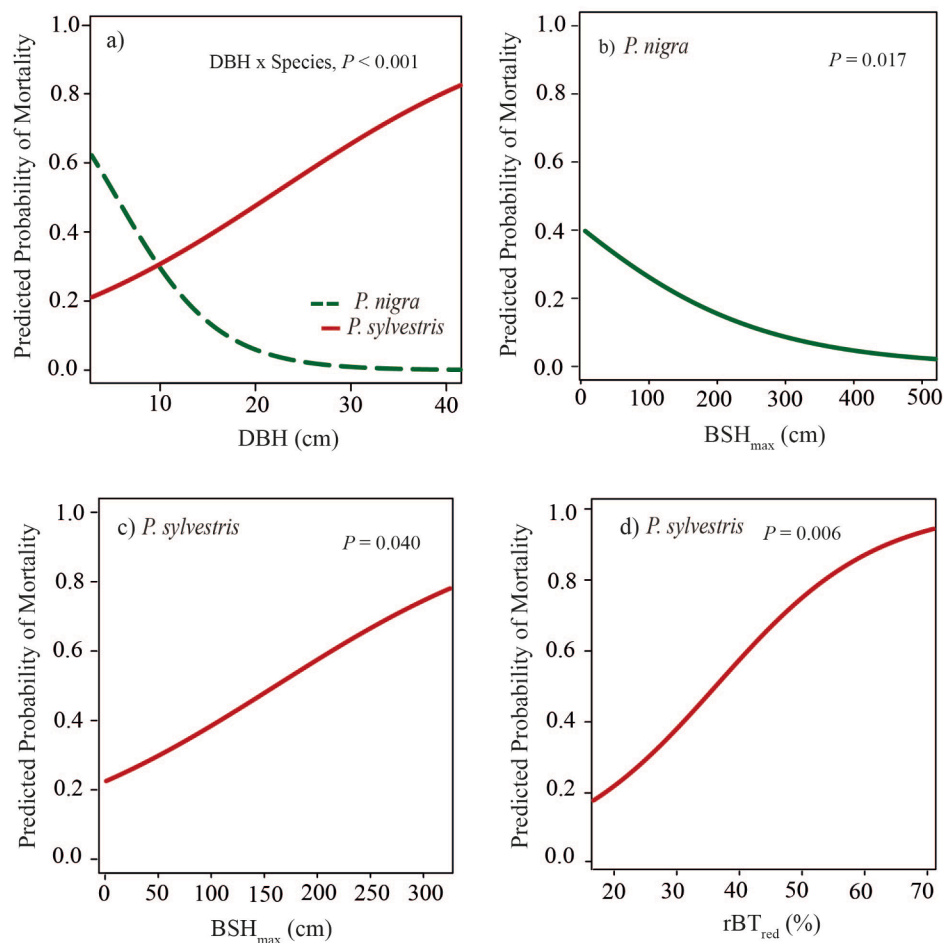


Fig. 3. Predicted mortality by bark beetle attack curves as a function of diameter at breast height (DBH) according to pine species in the pooled *P. nigra*-*P. sylvestris* model (a), maximum bole scorch height (BSH_{max}) in the *P. nigra* model (b) and BSH_{max} (c) and relative bark thickness reduction (rBT_{red}) (d) in the *P. sylvestris* model. Significance is based on the results of the general linear models showed in Table 2.

resin duct area than trees that died for the 30- and 20-year period (Fig. 4a). Regarding resin duct density, we found an interaction between species and tree status for the 30-year period. This interaction indicates that dead *P. nigra* had much higher resin duct densities than live trees, while the difference in resin duct density between tree status was lower in *P. sylvestris* (Fig. 4b).

Using only living trees, we found a significant interaction between species and D₂₀ for the 20-year period to explain resin duct area (Table 3). This interaction indicates that as D₂₀ increases, resin duct area in *P. nigra* trees rises faster in comparison to *P. sylvestris* (Fig. 4c). However, we found no effect of tree size on resin duct density for any period.

For each species, the relevant periods for duct and growth metrics usually comprised longer periods (i.e. 30- and 20 years) rather than shorter ones (i.e. 5 years) (Table A1 in Supporting Information and Table 4). In both species, differences between live and dead trees were encountered in almost all duct resin metrics of the relevant period (Table 4). Moreover, living trees grew significantly faster than trees that died.

3.2.1. Mortality models using resin ducts, bole scorch height and tree level characteristics

None of the fire-caused injury, growth, nor bark thickness variables were included in any of the conditional inference tree models developed. Combining both species, the conditional inference tree model selected resin duct area and density for the 30-year period as the best predictors of tree mortality (Fig. 5a): when resin duct area was higher than 0.63

mm² year⁻¹ most of the trees survived beetle attack; while for trees with lower resin duct area, the probability of dying was related to resin duct density. Complete tree mortality was found in trees with resin duct density higher than 0.5 no. mm⁻² year⁻¹, while at lower resin duct density the probability of dying was reduced to 0.3 (Fig. 5a).

By species, only resin duct density for the 30-year period explained mortality in the *P. nigra* model, while only resin duct area was included in *P. sylvestris* model (Fig. 5b and c). All models had similar accuracy (Table 5). The model combining both species perfectly classified a tree as alive 100% of the time when it was in fact alive (Table 5, specificity). In contrast, the species-specific models were better at classifying a tree as dead. Thus, in *P. nigra* and *P. sylvestris* the models predicted 92% and 91% of the times a tree as dead when it was in fact dead, respectively (Table 5, sensitivity).

4. Discussion

4.1. Susceptibility of pine species to *I. sexdentatus* attack

I. sexdentatus killed a similar number of *P. sylvestris* and *P. nigra* individuals despite *P. sylvestris* being less frequent in the units. Some bark beetle species can be, among other factors, visually attracted to black tree boles (Strom et al. 1999) and chemically attracted to ethanol released from heat damaged stems (Kelsey and Westlind 2017). Bole scorch height (BSH), which can be used as a proxy of both attraction mechanisms, did not explain species differences in *I. sexdentatus* attack. *P. nigra*, which was less frequently attacked by *I. sexdentatus*, had higher

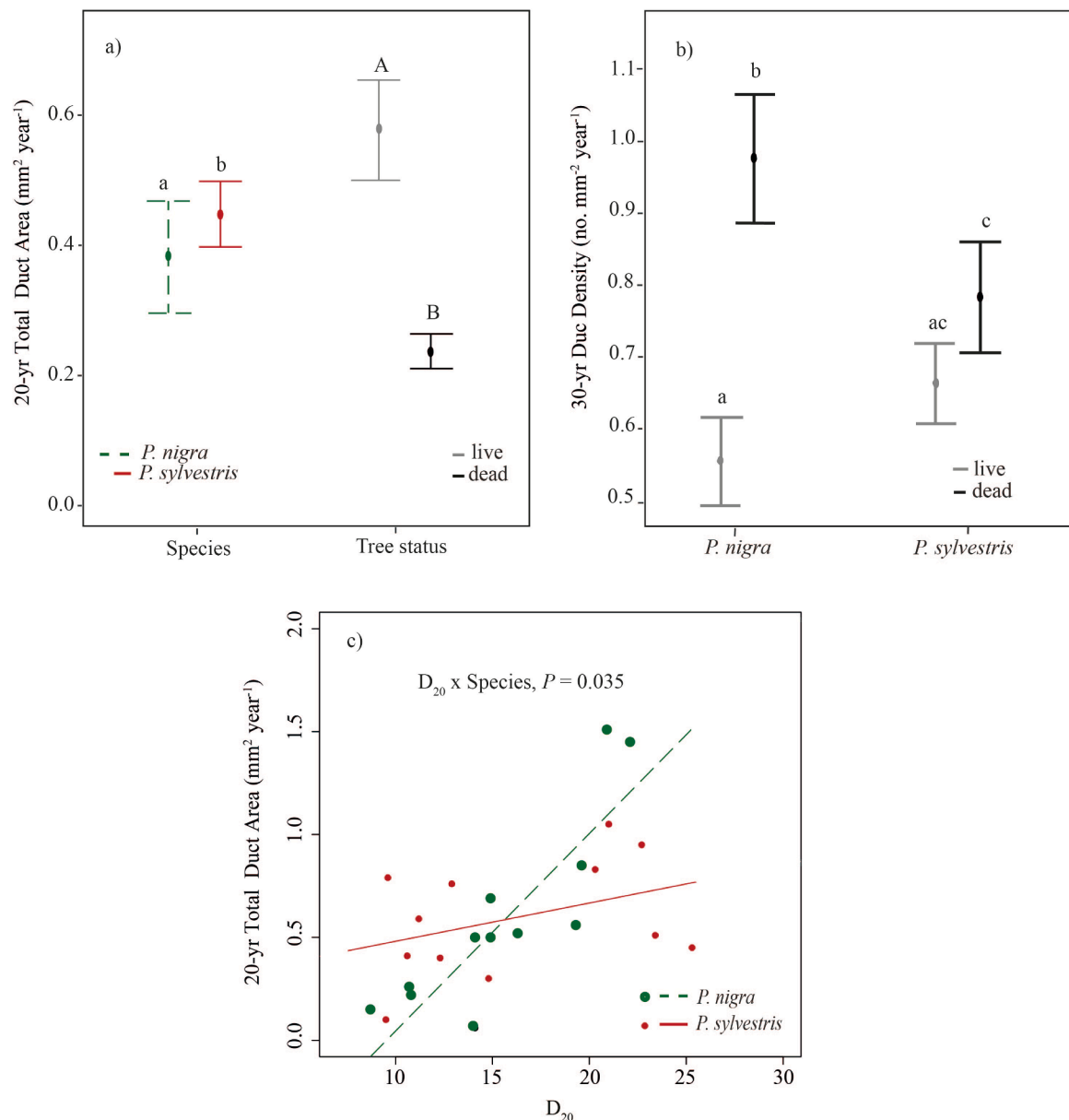


Fig. 4. Total duct area in the last 20 years (a) and resin duct density in the last 30 years (b) of dead and live trees for both pine species (mean \pm SE); and total duct area of living pines in the last 20 years against diameter at 20 cm base height (D₂₀) (c). Significance is based on the results of the general linear models showed in Table 3, where different letters indicate significance differences ($\alpha = 0.05$). In (a), lower letters indicate the comparison results between pine species and capital letters between tree status. Resin duct area and density were log-transformed to stabilize the normality and homogeneity of variance of model residuals.

bole scorch heights than *P. sylvestris* (Fig. 2c). Furthermore, bole scorch height was higher on live *P. nigra* than dead *P. nigra*, and the likelihood of bark beetle attack (i.e. probability of mortality) decreased with bole scorch height (Fig. 3b). If maximum BSH adequately reflects cambium tissue killed by the fire, then, these results suggest that fire injury did not determine beetle attack in *P. nigra*. It is likely that bark in this species was thick enough to prevent cambium kill by fire. Thus, one possible explanation is that in *P. nigra* thermal stress increased resin flow as reported in Cannac et al. (2009) and/or induced traumatic resin ducts or terpene concentrations in those trees in which bole scorch height was higher, thereby preventing bark beetle colonization. For instance, low severity fires can induce traumatic resin ducts, increasing tree survival from subsequent attacks (Hood et al. 2015). However, this deserves future exploration as we did not study resin flow or chemistry after the burns nor induced resin ducts. Our results on *P. sylvestris* are consistent with other studies on *I. sexdentatus* attack after fire (Fernández-

Fernández 2006; Santolamazza-Carbone et al. 2011) and suggest that other factors besides fire-caused tree injury play a major role in host selection. For instance, after a wildfire *I. sexdentatus* first attacked *P. pinaster* trees with 25–50% scorched crowns, but as population levels increased two years after the fire, *I. sexdentatus* attacked healthy unscorched individuals (Fernández-Fernández 2006). However, the influence of tree injury from fire on *P. sylvestris* resistance to beetle attack cannot be totally ruled out, as even though there were no differences between live and dead pines in bole scorch height (Fig. 2c), bole scorch height increased the probability of beetle attack (Fig. 3c). At the same site, we found that *P. sylvestris* was less resistant to fire than *P. nigra* (i.e. higher dying probability after burning), even though *P. sylvestris* had lower values for crown and stem injury indicators than *P. nigra* (Valor et al. 2017b) and hence, likely, was more predisposed to beetle attack.

Previous research has found little evidence for differences in the probability of bark beetle attack between early and late season burns

Table 3

Parameters estimates (Est.), standard error (S.E.), *P* values, and R^2 of the general linear models testing for differences in selected resin duct metrics between species and tree status ($n = 48$) and for the effect of diameter at 20 cm height (D_{20}) ($n = 25$, using only living trees). See Table A1 in [Supporting Information](#) for variable selection. General linear models were conducted on log-transformed data. *Ps*, *Pinus sylvestris*. The Intercept represents the estimate coefficient for the living *P. nigra* while the estimated coefficients for Tree status (Dead), Sp. (*Ps*) and Status(Dead) \times Sp. (*Ps*) interaction, represent the differences between the intercept and dead *P. nigra*, living *P. sylvestris* and the dead *P. sylvestris* respectively.

Dead and living trees	30-yr total duct area			20-yr total duct area			30-yr density			10-yr density		
	Est.	S.E.	<i>P</i>	Est.	S.E.	<i>P</i>	Est.	S.E.	<i>P</i>	Est.	S.E.	<i>P</i>
Intercept	−0.16	0.07	0.043	−0.48	0.07	0.000	−0.28	0.04	0.000	−0.17	0.05	0.001
Tree status (Dead)	−0.38	0.09	0.000	−0.368	0.09	0.000	0.25	0.06	0.000	0.29	0.07	0.000
Sp. (<i>Ps</i>)	0.18	0.09	0.057	0.257	0.09	0.009	0.08	0.05	0.143	0.03	0.07	0.648
Status (Dead) X Sp. (<i>Ps</i>)	0.03	0.19	0.855	0.267	0.18	0.159	−0.20	0.08	0.026	−0.14	0.15	0.348
R^2	0.28			0.30			0.29			0.24		

Living trees- D_{20}	30-yr total duct area			20-yr total duct area			30-yr density			10-yr density		
	Est.	S.E.	<i>P</i>	Est.	S.E.	<i>P</i>	Est.	S.E.	<i>P</i>	Est.	S.E.	<i>P</i>
Intercept	−0.69	0.23	0.006	−1.61	0.32	0.000	−0.28	0.04	0.000	−0.21	0.20	0.307
Sp. (<i>Ps</i>)	0.13	0.13	0.317	1.01	0.42	0.025	0.08	0.05	0.155	0.22	0.26	0.409
D_{20}	0.03	0.01	0.009	0.07	0.02	0.001	0.00	0.00	0.649	−0.00	0.01	0.973
Sp. (<i>Ps</i>) X D_{20}	−0.04	0.02	0.118	−0.05	0.02	0.035	−0.01	0.01	0.153	−0.00	0.01	0.652
R^2	0.24			0.40			0.00			0.00		

Table 4

Resin duct and growth variables of live and dead pines of *P. nigra* (*Pn*) and *P. sylvestris* (*Ps*) by time period. Measures are based on a 4.5 mm core diameter. *P* values of resin duct and growth variables are shown as a result of a *t*-test on log-transformed data for the most relevant time periods selected by the random forest algorithm (see Table A1 in [Supporting Information](#) for variable selection). Values are mean and standard error (S.E.) of untransformed data. For significant ($P < 0.05$) and marginal significant ($0.1 > P$ greater than 0.05) differences, the higher value of each pair is highlighted in bold to ease viewing patterns.

Period (years)			<i>P. nigra</i>					<i>P. sylvestris</i>				
<i>Pn</i>	<i>Ps</i>	Resin Duct Metric	Live ($n = 13$)		Dead ($n = 10$)		<i>P</i>	Live ($n = 12$)		Dead ($n = 13$)		<i>P</i>
			Mean	S.E.	Mean	S.E.		Mean	S.E.	Mean	S.E.	
30	20	duct size (mm^2)	0.030	0.002	0.018	0.002	<0.0001	0.023	0.001	0.015	0.001	<0.0001
30	30	duct production (no. year^{-1})	1.138	0.263	0.566	0.101	0.060	1.830	0.214	1.023	0.099	0.003
30	30	duct area ($\text{mm}^2 \text{ year}^{-1}$)	1.007	0.221	0.326	0.054	0.020	1.196	0.158	0.480	0.055	0.002
30	5	duct density ($\text{no. mm}^{-2} \text{ year}^{-1}$)	0.552	0.062	0.977	0.090	<0.0001	0.903	0.277	2.043	0.402	0.015
5	20	rel. duct area (% annual ring)	1.887	0.321	1.136	0.246	0.051	1.512	0.119	1.352	0.128	0.270
20	5	mean BAI ($\text{cm}^2 \text{ year}^{-1}$)	1.441	0.249	0.432	0.070	<0.0001	1.940	0.368	1.165	0.327	0.520
30	30	mean growth (mm year^{-1})	0.745	0.201	0.330	0.101	<0.001	0.790	0.230	0.521	0.141	0.002

(Schwilke et al. 2006; Fettig et al. 2010). The fact that we found no attacks in the spring burn could suggest that burning season can affect a tree's vulnerability to bark beetle attack. However, as fire severity was higher in the fall than in spring burns, we cannot separate the effects of fire severity from seasonal effects (Valor et al. 2017b).

Some bark-beetle species preferentially attack trees with small diameter and thin bark, likely because boring through thin bark requires less energy to successfully attack a tree (Santolamazza-Carbone et al. 2011; Parker et al. 2006; Breece et al. 2008). Similarly to Santolamazza-Carbone et al. 2011, we found that *I. sexdentatus* preferentially attacked small *P. nigra* but this pattern was not found for *P. sylvestris* (Fig. 2a). There are several possible explanations for this result related to inter- and intra-specific differences in bark thickness and resin duct defenses. First, in *P. sylvestris*, the reduction in bark thickness with stem height was a significant predictor of tree mortality (Fig. 3d) but not in *P. nigra*, suggesting that *I. sexdentatus* may find lower resistance to bore *P. sylvestris*. Furthermore, as diameter increased *P. sylvestris* showed a higher reduction in bark thickness along the stem than *P. nigra* (Fig. 2d), possibly facilitating *I. sexdentatus* attack even in bigger *P. sylvestris* trees. Thus, lower mortality in *P. nigra* than in *P. sylvestris* may be explained by the lower reduction in bark thickness with stem height in the former than in the latter as diameter increases. Amezcaga and Rodriguez et al. (1998) found that the range of bark thickness exploited by *I. sexdentatus* seems not to fit with its body size, as this bark beetle attacked bark that was thinner than its own mean body depth. Second, as DBH increased, total resin duct area was higher in *P. nigra* than in *P. sylvestris* (Fig. 4c), indicating that larger *P. nigra* trees allocated more resources to defenses and are less susceptible to beetle attack.

Although our study did not focus on resin chemistry, in a nearby stand that was burned in spring, Valor et al. (2017b) found that *P. sylvestris* foliage had higher amounts of α -pinene, camphene and myrcene than *P. nigra*. These terpenes are positively related to bark beetle behavior and attack success in some species (Seybold et al. 2006), with *I. sexdentatus* being especially attracted to α -pinene (Rudinsky et al. 1971). While chemical traits have less influence on plant resistance than physical traits across a broad range of plant families (Carmona et al. 2011), oleoresin and associated chemical defenses are considered critical in resistance to bark beetles for their conifer hosts (Gitau et al. 2013; Seybold et al. 2006; Raffa 2014). Chemical composition in plant tissue is not always correlative (Manninen et al. 2002; Pureswaran et al. 2004; Latta et al. 2000), and very few studies have examined the effects of fire on resin composition, making additional research on these topics much needed to more fully understand the influence of fire on tree defense traits.

4.2. Resin duct metrics and tree resistance

Our study indicates that resin duct metrics more strongly influenced tree resistance to *I. sexdentatus* compared to tree injury from fire and bark thickness variables. This study also confirms that resin ducts may remain functional for years after forming (Lewinsohn et al. 1991), as relevant time periods for duct metrics usually compromised longer rather than shorter periods (Fig. 5). Consistent with the literature, trees of both pine species that resisted *I. sexdentatus* attack had greater resin duct size (Gaylord et al. 2013; Ferrenberg et al. 2014; Hood et al. 2015; Kichas et al. 2020), area (Kane and Kolb 2010; Hood et al. 2015; Kichas

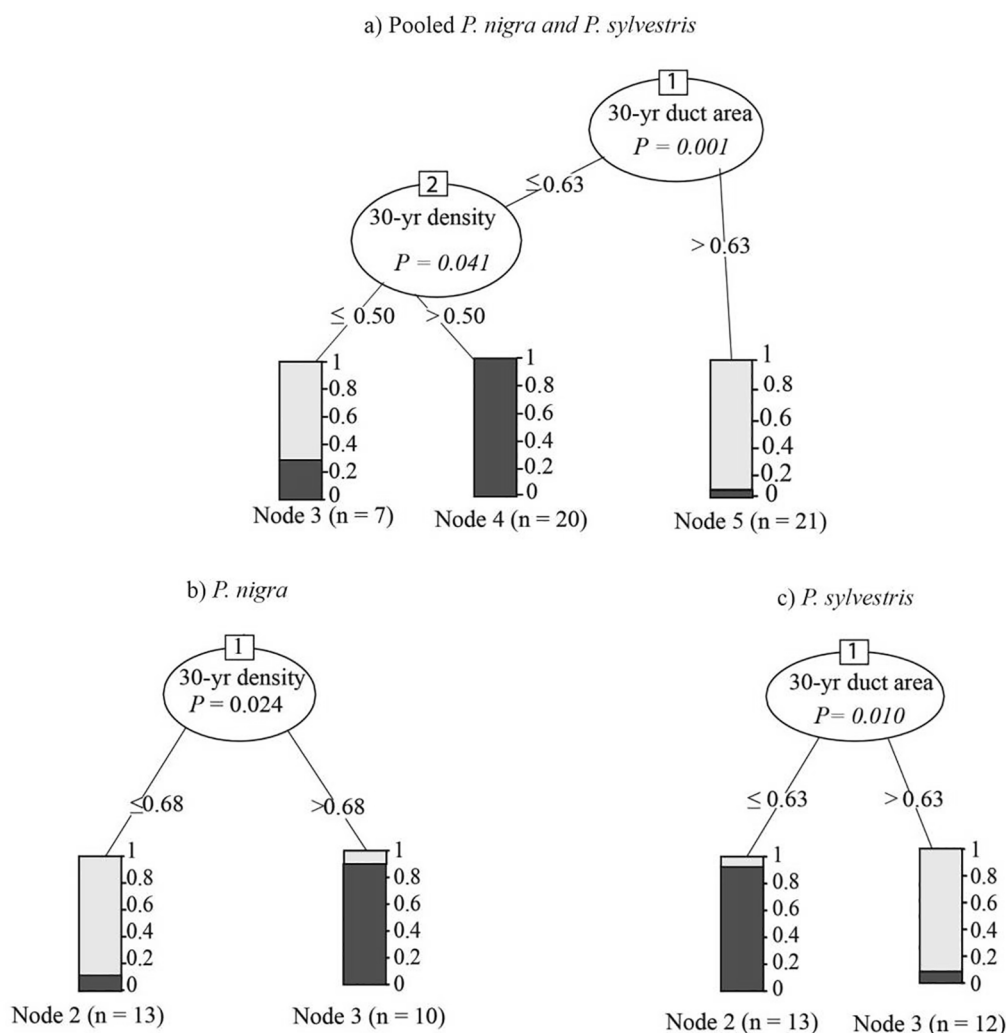


Fig. 5. Conditional inference tree models for bark beetle-caused tree mortality (dark grey = dead trees; light grey = live trees). The numbers inside the squares identify the nodes and the order of variable/partition entrances, starting with 1 in the root node. The predicted probability of mortality for each node is specified by the black proportion of 0–1 bars in the lower part of the diagrams.

Table 5
Measures of model performance for bark beetle-caused tree mortality.

	<i>P. nigra</i> - <i>P. sylvestris</i>	<i>P. nigra</i>	<i>P. sylvestris</i>
Accuracy	0.93	0.91	0.92
Error rate	0.07	0.09	0.08
Sensitivity (TPR)	0.89	0.92	0.91
Specificity (TNR)	1.0	0.90	0.92
Prevalence	0.58	0.56	0.48

TPR = true positive rate; TNR = true negative rate

et al. 2020) and production (Kane and Kolb 2010; Ferrenberg et al. 2014); however, in *P. nigra* the positive association between resin duct production and resistance was not clear (Gaylord et al. 2013; Hood et al. 2015) (Table 4). Regarding standardized metrics of resin duct characteristics, we detected some evidence in *P. nigra* of greater relative resin duct area in resistant pines compared to susceptible trees but not in *P. sylvestris*. Interestingly, in both species, dead trees had greater resin duct density than resistant pines, although only in the last 5 years in the case of *P. sylvestris*. These results are consistent with findings of Kichas et al. (2020) for *P. albicaulis* and those of Zhao and Erbilgin (2019) in *P. contorta*. However, our results are not supported by those of Hood et al. (2015), who found differences in relative resin duct area but not in resin duct density between resistant and susceptible *P. ponderosa* pines,

as well as those for *P. edulis* (Gaylord et al. 2013). Ferrenberg et al. (2014), Kane and Kolb (2010), and Reed and Hood (2021) report mixed support for the importance of resin duct density on tree resistance, with both non-significant and positive effects depending on tree species. Taken together, although the influence of individual resin duct metrics may vary, the literature consistently shows that resin ducts are important defense traits for *Pinus* spp. against bark beetles (Vázquez-González et al. 2020). Resin flow is proportional to the fourth power of the resin duct diameter following Hagen–Poiseuille’s law for liquid laminar flow within a tube (Schopmeyer et al. 1954). Thus, overall, our results suggest that for a given total resin duct area, fewer but larger resin ducts, as observed in resistant pines of both species, relative to more but smaller resin ducts, such as those of susceptible trees, should result in higher resin flow and, hence, higher resistance to *I. sexdentatus* attack.

4.3. Management implications

Prescribed burning in this forest type aims to reduce surface fuel load and decrease ladder fuels by clearing small trees and retaining larger trees. Immediate mortality from fire tended to be similar in fall burns than in the spring burns (Valor et al. 2017b). In fall burns, delayed mortality occurred as a consequence of basal stem girdling (Valor et al. 2017b) due to the lower forest floor moisture content and longer combustion times registered in fall burns, but also, as reported here, as a

result of *I. sexdentatus* attack. In this study, we showed that *P. sylvestris* is less resistant than *P. nigra* to *I. sexdentatus* and that attacks were restricted to small *P. nigra* trees, whereas the probability of *I. sexdentatus* infesting *P. sylvestris* trees increased with tree size. Although the results of the study are clear, additional research on the effects of prescribed burning on bark beetle responses, especially for other beetle species, is needed. Our results suggest that in *P. nigra* stands, more intense prescribed burns that cause higher bole scorch can be used to kill smaller trees and that, even in the case of an *I. sexdentatus* outbreak, tree mortality caused by bark beetles would be concentrated in the smaller tree sizes classes. In contrast, planning intense burns in *P. sylvestris* may kill smaller trees, but may also have the unintended consequence of causing increased mortality of larger trees from bark beetles.

Our study further confirms the importance of intraspecific variation in resin duct and growth metrics for tree defense. We found that resistant pines of both species grew faster, had higher resin duct area, and fewer but larger resin ducts than susceptible trees, which likely results in higher resin flow. An implication of these results is the possibility that resistant pines of both species could be used for seed tree selection to be used in breeding and planting programs. These findings also provide a basis for promoting actions that encourage faster growth, which may increase resin duct-related defenses of both species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119322>.

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