

Interactions between southern *Ips* bark beetle outbreaks, prescribed fire, and loblolly pine (*Pinus taeda* L.) mortality

Bailey H. McNichol^{a,*}, Cristián R. Montes^a, Brittany F. Barnes^a, John T. Nowak^b, Caterina Villari^a, Kamal J.K. Gandhi^a

^aD.B. Warnell School of Forestry and Natural Resources, University of Georgia, 180 E. Green Street, Athens, GA 30602, USA

^bUSDA Forest Service, Forest Health Protection, 200 W.T. Weaver Boulevard, Asheville, NC 28804, USA

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ABSTRACT

The southeastern U.S. is considered the “wood-basket” of the world where loblolly pine (*Pinus taeda* L.) plantations provide tremendous ecological and economic benefits to the region. These plantations are susceptible to various natural and anthropogenic abiotic and biotic stressors and disturbances. The southern pine engravers, *Ips avulsus* (Eichhoff), *I. calligraphus* (Germar), and *I. grandicollis* (Eichhoff), are considered secondary colonizers of stressed, damaged, and dying loblolly pines. However, they may undergo outbreaks and colonize live pine hosts if environmental conditions cause physiological stress to trees. In 2016, > 230 concurrent *Ips* infestations > 2 ha in size were documented in Georgia, U.S., reportedly due to severe drought. In these forests, prescribed burning is often conducted every 2–3 years to reduce fuel-loads, improve wildlife habitat, and manage understory vegetation. However, the effects of low-severity prescribed fire on active southern *Ips* infestations are unknown; fire may exacerbate or alleviate beetle outbreaks. Our objectives were to: (1) compare *Ips* infestations between burned and unburned sites to determine the short-term effects of prescribed fire on loblolly pine mortality; and (2) determine which site-level and tree-level variables were the best predictors of short-term levels of tree mortality. We monitored 838 pines on ten sites for eight months following prescribed fire in spring 2017. Overall, 69 (8%) trees died with 3.6 times higher tree mortality on unburned sites, and a higher probability of survival on burned sites. At the site-level, binomial logistic regression models including treatment (unburned versus burned) and time since burn were the best predictors of loblolly pine mortality. At the tree-level, model selection showed that treatment, crown mortality level (1–5), *Ips* activity level (none, low, medium, and high), and tree diameter provided the best predictions of mortality. Prescribed burning may thus help alleviate pest pressure and increase tree resilience in loblolly pine forests in the southeastern U.S.

1. Introduction

The southeastern U.S. pine (*Pinus* spp.) forests extends from Virginia to Florida and Texas and consist of > 10 native and endemic pine species (Prestemon and Abt, 2002; Schowalter, 2012). These forests include intensively managed southern pine plantations that have increased in size from < 809,000 to ~13 million ha during the last 50–60 years (Schultz, 1997; Fox et al., 2007). Loblolly pine (*P. taeda* L.) is the most economically valuable species due to its ability to grow on diverse and poor-quality sites, its rapid regeneration, substantial yields per hectare, and its use in numerous marketable products (Schultz, 1997; Fox et al., 2007). Production forestry operations in the southeastern U.S. significantly contribute to the growth of regional

economies; e.g., there was a \$35 billion economic impact for 2015 alone in Georgia (Georgia Forestry Association, 2018). These pine forests also provide ecological benefits including maintaining watersheds; preventing and reducing erosion; providing critical food resources and habitat for wildlife; allowing for various recreation opportunities; and carbon sequestration (Wahlenberg, 1960; Schultz, 1997; Schowalter, 2012).

Loblolly pine plantations are susceptible to various insects and diseases during their lifetime, complicating management and affecting their resilience. Specifically, the southern pine bark beetle guild that includes three species of pine engraver, the small southern pine engraver, *Ips avulsus* (Eichhoff); the six-spined ips, *I. calligraphus* (Germar); and the eastern five-spined ips, *I. grandicollis* (Eichhoff), as well as the

* Corresponding author.

E-mail addresses: bailey.mcnichol@gmail.com (B.H. McNichol), crmontes@uga.edu (C.R. Montes), jnowak@fs.fed.us (J.T. Nowak), cvillari@uga.edu (C. Villari), kjgandhi@uga.edu (K.J.K. Gandhi).

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southern pine beetle (*Dendroctonus frontalis* Zimmermann) and the black turpentine beetle (*D. terebrans* [Olivier]), can have major impacts on the survivorship of these stands (Stephen, 2011). The three southern *Ips* colonize the phloem of southern pine species for feeding and reproductive activities (Yearian and Wilkinson, 1967; Nebeker, 2011). Unlike the more aggressive *D. frontalis*, which can colonize live trees, the southern *Ips* species are typically secondary colonizers of stressed, damaged, or dying pines (Wilkinson and Foltz, 1982; Nebeker, 2011). While *D. frontalis* infestations are characterized by expanding groups of contiguous live pines (“spots”), *Ips* beetle infestations most often occur in a single host or a few trees, and are much slower in growth (Stone et al., 2007; Clarke, 2012; Eickwort et al., 2015).

Factors including windstorms, wildfires, pathogens, and drought may render pine stands susceptible to *Ips* infestations (Connor and Wilkinson, 1983; Bryant et al., 2006; Coyle et al., 2016). Numerous *Ips* species are reported to colonize host conifers during or following warmer and drier periods [e.g., *I. confusus* (LeConte) and *I. typographus* (L.)] (Bakke, 1983; Breshears et al., 2005; Faccoli, 2009; Floyd et al., 2009; Aakala et al., 2011; Kolb et al., 2016). Widespread, prolonged drought during the growing season is frequently cited as one of the primary factors facilitating high southern *Ips* populations, leading to significant pine mortality in the southeastern U.S. (Wilkinson and Foltz, 1982; Connor and Wilkinson, 1983). However, most of these observations are anecdotal, as no studies have quantified pine mortality resulting from southern *Ips* infestations during drought periods, or used water deficit data to verify these relationships.

Prescribed fire is another factor that can influence bark beetle population dynamics. Prescribed fire is a forest management practice that may reduce the likelihood of bark beetle infestations if the treatment is timed when beetles are not dispersing and minimizes injury to residual standing pines (Geiszler et al., 1984; Lombardero et al., 2006; Fettig et al., 2007; Nowak et al., 2008, Nowak et al., 2015). Regularly prescribing fire in pine-dominant stands limits the risk of damaging wildfires that have the potential to weaken tree defenses and increase the chance of beetle infestations (Wilkinson and Foltz, 1982). However, prescribed fire can still stress healthy pines and make them susceptible to *Ips* bark beetle attacks, particularly if the fire treatment causes bole char and results in heat damage to the phloem tissue (Lombardero et al., 2006; Fettig et al., 2007; Negrón et al., 2016), crown scorch (Wallin et al., 2003; Bryant et al., 2006), or root injury or death (Geiszler et al., 1984; Bryant et al., 2006). Bark beetles may opportunistically colonize individual fire-injured hosts that are releasing attractive, stress-related volatiles, and thus act as a secondary contributor to pine mortality (Manion, 1991; Regelbrugge and Conard, 1993; McHugh and Kolb, 2003; McDowell et al., 2008).

Previous research has found associations between prescribed burning and *Ips* bark beetle activity (Geiszler et al., 1984; Bradley and Tueller, 2001; Campbell et al., 2008). In some instances, *Ips* have been observed to preferentially mass attack dead or dying pines that were moderately to severely fire-damaged during prescribed burns, particularly small diameter pines (Davis et al., 2012; Fettig and McKevey, 2014; Negrón et al., 2016). Conversely, several authors have found no relationships between prescribed fire treatments and the subsequent level of bark beetle attraction and infestation (Sullivan et al., 2003; Elkin and Reid, 2004; Lombardero et al., 2006). For instance, no evidence was found of *I. grandicollis* attraction to burned stands of longleaf pine (*P. palustris* Mill.), although this species is known to colonize recently burned trees (Sullivan et al., 2003). Similarly, fire damage to the boles of red pines (*P. resinosa* Aiton) did not influence the landing rates of *I. pini* and *I. grandicollis* (Lombardero et al., 2006). Prescribed fire injury on lodgepole pine (*P. contorta* Douglas ex Loudon) did not influence landing behavior, which trees were infested, attack rate, or the reproductive success of mountain pine beetle (*D. ponderosae* Hopkins) (Elkin and Reid, 2004), although this finding may be more closely related to changes in the host tree physiology post-burn than the beetle (Jenkins et al., 2014). A lack of consistent relationships between

prescribed fire and bark beetle infestation of recently burned hosts suggests that the degree of fire injury and physiology of individual trees (i.e., defensive response following a burn) may play a significant role in host attractiveness and colonization by bark beetles.

The southeastern U.S. experienced drought conditions in 2016 that accelerated beginning in June and became more severe in September and October (U.S. Drought Monitor, 2017). By November 2016, 60% or more of the land area in Alabama, Georgia, Mississippi, and Tennessee was classified as being in a state of “exceptional drought” or “extreme drought” (U.S. Drought Monitor, 2017). However, it should be noted that the U.S. Drought Monitor classifies drought using the Palmer Drought Severity Index (PDSI), which features a water balance model that does not account for precipitation events occurring over short time scales, differences between potential versus actual evapotranspiration rates, or variation in the depth of soil moisture capacity (Alley, 1984). Additionally, the PDSI features drought severity classes that are arbitrarily defined, and does not have a clear method to demarcate the beginning and end of a drought period (Alley, 1984; Heddinghaus and Sabol, 1991). These limitations make it difficult to determine specifics regarding local soil water balance and water availability, and their relationships to individual tree-level rooting characteristics and physiology. Thus, drought may not indicate availability of water to trees, and we are cautious in assuming that severe drought unequivocally means water-stressed host pines were available.

Beginning in September 2016, over 300 southern *Ips* beetle infestations were recorded in the Oconee Ranger District of the Chattahoochee-Oconee National Forest (Eatonton, Georgia) during the drought period, and hundreds of other infestations were documented throughout other areas in the southeastern U.S. (P. Merten, personal communication, 8 February 2017). Infestations mostly occurred on loblolly pine and resembled *D. frontalis* infestations with respect to intensity and growth, expanding concentrically outwards and in severe cases, killing numerous hectares of pines. Sampling of several trees felled in the Oconee Ranger District revealed colonization by all five members of the southern pine bark beetle guild, with the highest densities of the three southern *Ips* species. Standing, symptomatic trees exhibited reddening and wilting of the needles, and had many entrance and exit holes and frass in the crevices of the bark. Almost none of the characteristic exudation of resin (“pitch tubes”) was observed at beetle entrance holes, suggesting that host tree defense mechanisms may have already been compromised prior to *Ips* colonization due to drought stress or other factors (Allen et al., 2010; Hain et al., 2011; Stephen, 2011).

The management recommendation for winter 2017 was to avoid applying prescribed fire in stands with signs or symptoms of *Ips* beetles to prevent potentially exacerbating their infestations (Georgia Forestry Commission, 2017; P. Merten, personal communication, 8 February 2017; C. Schmidt, personal communication, 21 March 2017). However, because so few infestations of this magnitude have been reported in the Southeast (though such infestations have likely occurred historically), no study in the region has previously investigated the effects of prescribed fire on active *Ips* infestations. Some studies have addressed the risk of southern pine mortality post-burn (Mann and Gunter, 1960; Lilieholm and Hu, 1987; Sullivan et al., 2003; Campbell et al., 2008), but there is no literature on the impacts of prescribed fire on the health of loblolly pines experiencing southern *Ips* beetle infestations.

To assist with forest management, our research objectives were to: (1) compare *Ips* infestations in unburned versus burned sites to determine the short-term effects of low-severity prescribed fire on beetle activity and loblolly pine mortality, and (2) assess which variables were the best overall predictors of loblolly pine mortality at the tree- and site-level. We hypothesized that there would be more loblolly pine mortality in burned than unburned sites in these insect outbreak areas because trees subjected to fire (as based on fire severity) are frequently attacked by bark beetles in the short-term. However, we may observe opposite trends, where pine trees may grow more vigorously due to

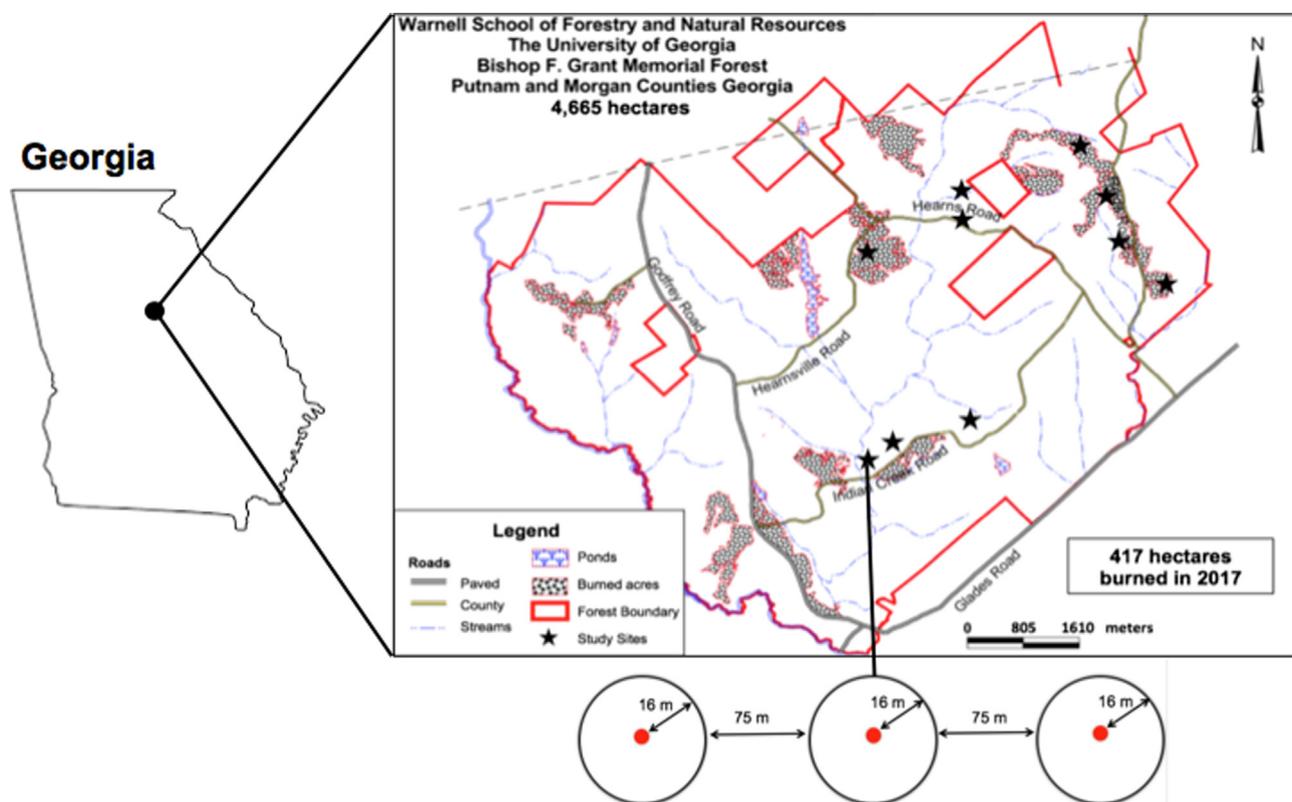


Fig. 1. Map showing the location of Bishop F. Grant Memorial Forest in the state of Georgia, the ten study sites within B.F. Grant Memorial Forest (denoted as stars), 2017 prescribed burn treatments (gray areas), and the site-level experimental design layout. Map credit: Dustin Thompson, Forest Resources Manager, Bishop F. Grant Memorial Forest.

reduction in competition and may be better able to defend themselves after the fire, and hence tree mortality would be lower in the burned sites. At the site-level, we expected basal area, treatment (unburned and burned), and time since burn to be significant predictors of loblolly pine mortality. Further, there may be interactions between treatment, the level of *Ips* activity, and the level of crown mortality, and these variables may influence the probability of mortality at the tree-level. We also expected to see an interaction between tree DBH and the level of *Ips* infestation, with increased beetle activity occurring in smaller-sized pines, as previously shown in other studies (e.g., [Fettig and McKelvey, 2014](#)).

2. Methods

2.1. Study site and prescribed burn treatments

The study was conducted during 3 April–14 November 2017 in the Bishop F. Grant Memorial Forest, located in Putnam and Morgan Counties in the east-central region of Georgia (33°25'N, 83°27'W), adjacent to the Oconee Ranger District ([Fig. 1](#)). The 4665 ha forest is situated in the Piedmont region, and contains naturally-regenerated pines, pine plantation, mixed pine-hardwood, upland hardwood, and bottomland hardwood stands. Soils within the study site are primarily Davidson clay loam and loams and Vance sandy loam that are eroded as a result of previous agricultural activity ([Soil Survey Staff, USDA NRCS, 2018](#)). In 2017, the local annual mean temperature was 18.4 ± 0.38 °C, and cumulative annual precipitation was 124.54 cm ([PRISM Climate Group, 2018](#)). The D.B. Warnell School of Forestry and Natural Resources manages B.F. Grant Memorial Forest for teaching, outreach, and research in cooperation with the Georgia Department of Natural Resources, which utilizes the forest as a state Wildlife Management Area.

A total of 417 ha were treated with prescribed fire in March 2017 ([Fig. 1](#)). The primary management objectives of the burns were to: (1) control understory growth (primarily sweetgum, *Liquidambar styraciflua* L.); (2) reduce fuel loads; (3) encourage loblolly and shortleaf (*P. echinata* Mill.) pine growth; and (4) improve wildlife habitat for various species. The pine-dominant stands have not been on a regular burn rotation, but the forest managers are currently working to establish uniform three-year burn rotations throughout the forest (see [Table 1](#) for more details regarding the previous management and burn history for study sites). Firebreaks were installed prior to all burns, and primarily backing fires were used in an effort to reduce the heavy fuel loads and minimize rapid movement of fire through stands. The burns were carefully supervised to maintain flame height around a maximum of 1 m when possible, although shifting wind patterns and high ground fuel loads did result in some bole char and needle scorch.

2.2. Experimental design

Ten sites that were actively experiencing *Ips* infestations or had signs of recent infestation were treated with either: (1) prescribed fire in March 2017; or (2) remained unburned that year (five each of burned and unburned sites). A minimum of 500 m was present between each site ([Table 1, Fig. 1](#)). In each site, three 0.08-ha (16 m radius) circular plots were placed along a transect line, with > 75 m between each plot ([Fig. 1](#)). A total of 30 plots were established in early April 2017, and plots were revisited in late May, July, September, and November 2017.

All trees within each plot that had a DBH > 7 cm were measured and recorded, and pine trees were identified to species and marked with a unique tree tag to allow for temporal monitoring. The total number of dead trees in each plot at the initiation of the study was recorded. Pine basal area was calculated at the tree-level using the DBH measurements, summed over the three plots, and divided by total area (0.24 ha)

Table 1
Summary of forest management activities, prescribed fire history, and stand characteristics for the ten study sites in 2017.

Site	Treatment (Date of Burn)	Last Recorded Burn	Prior Management	Pine BA (m ² /ha)	Mean Pine DBH (cm ± SE)	Mean Pine Age (yrs. ± SE)	Mean Pine Height (m ± SE)	Latitude and Longitude
1	Burned (7 March 2017)	2003	N/A	22.64	46 ± 3.3	68 ± 5.4	33 ± 6.0	32°26.1'N, 83°26.4'W
2	Unburned	Before 2003	Thinned in 2016	22.72	21.5 ± 0.47	26 ± 4.5	17 ± 6.8	33°26.0'N, 83°27.8'W
3	Unburned	Before 2003	Thinned in 2016	23.84	21.5 ± 0.47	23 ± 0.9	16 ± 3.1	33°26.1'N, 83°27.8'W
4	Burned (20 March 2017)	Before 1997	Thinned in 2012	21.40	24 ± 0.84	31 ± 1.7	20 ± 5.3	33°25.8'N, 83°28.4'W
5	Unburned	Before 2003	Thinned in 2015	17.54	26.5 ± 1.05	40 ± 3.1	21 ± 3.9	33°23.8'N, 83°28.9'W
6	Unburned	Before 2003	Thinned in 2015	20.14	25 ± 0.82	28 ± 1.2	21 ± 3.0	33°23.9'N, 83°28.3'W
7	Unburned	2012	Thinned in 2008	20.76	24 ± 0.65	29 ± 1.1	16 ± 3.2	33°24.2'N, 83°27.5'W
8	Burned (21 March 2017)	2004	Thinned in 2013	14.92	29 ± 1.22	37 ± 1.0	31 ± 2.1	33°25.7'N, 83°26.0'W
9	Burned (21 March 2017)	2004	N/A	15.19	26 ± 2.08	52 ± 5.0	30 ± 9.5	33°26.1'N, 83°26.2'W
10	Burned (21 March 2017)	2006	N/A	19.51	26 ± 1.89	48 ± 4.4	29 ± 5.5	33°25.5'N, 83°25.8'W

to determine the mean basal area for each site (Table 1). For one each of dominant, co-dominant, and intermediate trees in each plot (nine total per site), cores were taken with an increment borer to estimate mean age within the site (Table 1). The same nine pines were measured with a clinometer to obtain an estimate of mean tree height at the site-level (Table 1). Overall, our 10 sites and 30 plots included 838 study trees (831 loblolly pines and 7 shortleaf pines). Given that the overwhelming majority of the trees were loblolly pines (99%), our analyses and models aimed to predict loblolly pine mortality.

For every tagged pine tree, crown class was recorded as suppressed, intermediate, co-dominant, or dominant. The overall crown mortality was assessed for each tree on a scale from 1 to 5: 1 = 0% mortality; 2 = 25% dieback (red and/or fading needles); 3 = 50% dieback; 4 = 75% dieback; and 5 = dead, 100% mortality. In plots occurring on the five burned sites, for each tree the maximum height of char on the bole was estimated, and needle scorch was marked as present or absent. Signs of southern *Ips* activity on each tree were recorded as presence/absence of entrance and exit holes, frass, and pitch tubes. Based on the number of entrance and exit holes on the lower 2 m of the bole, trees were rated as having either: (1) no *Ips* activity (zero holes); (2) low *Ips* activity (1–10 visible holes); (3) medium *Ips* activity (11–20 visible holes); or (4) high *Ips* activity (> 20 visible holes).

Tree health assessments were performed on the tagged trees every ~6–8 weeks to record the crown mortality rating and to determine the current level of bark beetle activity. To avoid an observer effect, the same observer noted these data throughout the time periods. During each assessment, the total number of dead trees in each plot was counted and recorded, and temporal measurements continued until the fifth visit in November 2017, when no additional *Ips* activity was observed (i.e., infestations were no longer expanding and/or had collapsed).

2.3. Statistical analyses

2.3.1. Survival analysis

To determine whether the unburned and burned treatments showed differences in loblolly pine survival, we performed a Kaplan-Meier survival analysis (Kaplan and Meier, 1958). The Kaplan-Meier estimator is a non-parametric statistic that can be used to estimate the probability of survival at various points in time. A log-rank test was applied to compare the survival curves of the two groups (unburned and burned sites) over time (April, May, July, September, and November 2017). All analyses were performed in R 1.0.136 (R Core Team, 2016), and the following packages were used for analyses and visualization of results: ‘survival’, ‘survminer’, and ‘readxl’ (Therneau, 2015; Wickham and Bryan, 2017; Kassambra and Kosinski, 2018).

2.3.2. Site-level predictors of loblolly pine mortality

To examine the influence of numerous explanatory variables on pine tree mortality, previous studies have employed binary logistic regression models to predict expected tree mortality (Regelbrugge and Conard, 1993; McHugh and Kolb, 2003). Logistic regression is optimal for modeling probabilities because the model has a Bernoulli distribution (ranges from 0 to 1), and can use continuous or categorical explanatory variables to predict a binary response variable, such as whether a tree is alive or dead (Regelbrugge and Conard, 1993). The full logistic regression model form is:

$$P_m = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_1 + \dots + \beta_n X_n)}} \tag{1}$$

where P_m is the probability of tree mortality, e is the natural logarithm base, β_0 , β_1 , and β_n are the estimated slope parameters (regression coefficients), and X_1 and X_n are the explanatory (independent) variables (Bradley and Tueller, 2001; McHugh and Kolb, 2003; Negrón et al., 2016).

To account for unmeasured variables that may have influenced

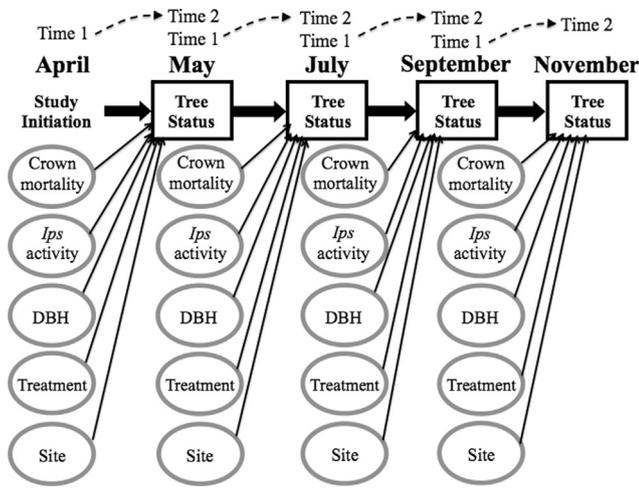


Fig. 2. Conceptual model demonstrating the relationships tested by logistic regression models regarding the best combinations of predictors of tree-level probability of loblolly pine mortality. Variables in gray circles are predictors, while tree status (alive = 0, dead = 1), shown in the black boxes, is the response variable.

overall observed mortality at the site-level ($n = 10$), we summarized the proportion of dead trees on each site during each month, and used binary logistic regression models to determine the effects of the following predictor (independent) variables on loblolly pine mortality at the site-level: (1) treatment (unburned or burned); (2) site-level basal area; and (3) time since burn. The response (dependent) variable in Eq. (1) for all models was tree status (alive = 0, dead = 1), which allowed for comparison among models. Models were developed to test how the levels of each predictor variable at time 1 influenced loblolly pine mortality (status) at time 2 (e.g., how variables in April affected mortality in May, and so on) (Fig. 2). Logistic regression models were estimated using generalized linear models (GLMs) with the logit link function (Tsai and Gill, 2013). We tested GLMs including each predictor variable individually, along with two-way and three-way interactions between variables. If interactions were not significant, they were removed and additive models including the main effects were tested. All analyses were performed in R 1.0.136 (R Core Team, 2016), and the ‘plyr’, ‘readxl’, and ‘stat’ packages were used (Wickham, 2011; R Core Team, 2016; Wickham and Bryan, 2017).

2.3.3. Tree-level predictors of loblolly pine mortality

To determine if variables measured at the individual tree-level ($n = 838$) were important predictors of mortality, GLMs with the logit link function were used to estimate the binary logistic regression models. Models testing our hypotheses included combinations of the following predictor variables: (1) site; (2) treatment (unburned or burned); (3) level of *Ips* activity (none, low, medium, or high); (4) level of crown mortality (1 = 0%, 2 = 25%, 3 = 50%, 4 = 75%, 5 = 100%); and (5) DBH (cm). Similar to the site-level analyses, the response variable for all of our models was tree status (alive = 0, dead = 1), and models were developed to test how the levels of each predictor variable at time 1 influenced loblolly pine mortality (status) at time 2 (Fig. 2). Due to perfect collinearity between site and treatment that resulted in singularities in the GLM regression matrix (as each site had one associated treatment), these two predictors were not included in the same candidate models (Nielsen et al., 2004). The variance inflation factors for each model were examined to quantify correlations present between predictor variables, and no further evidence of collinearity was revealed (Fox and Weisberg, 2011).

We tested GLMs including each predictor variable individually, along with two-way, three-way, and four-way interactions between the predictors (site or treatment, *Ips* activity, crown mortality, and DBH).

Where interactions were not significant, additive models including the main effects were tested. All significant logistic regression models associated with our tree-level hypotheses were evaluated using Akaike’s Information Criterion (AIC), which is an information-theoretic approach to model selection (Burnham and Anderson, 2002). When all included model parameters are known, AIC values are calculated using the maximized log-likelihood:

$$AIC = -2\log(\mathcal{L}(\hat{\theta}|y)) + 2K \tag{2}$$

where $\log(\mathcal{L}(\hat{\theta}|y))$ is the numeric log-likelihood value at its maximum point (corresponding to maximum likelihood estimates), and K is the number of estimable parameters in the model (Akaike, 1973; Burnham and Anderson, 2002). To allow for more clear interpretation of the relative likelihood of each of our candidate models, Akaike weights – which are distributed based on the Δ AIC (each value minus the lowest AIC value) for each model and give the most weight to the best candidate model – were determined using the following expression:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum \exp(-\frac{1}{2}\Delta_i)} \tag{3}$$

where w_i is the Akaike weight and Δ_i is the delta AIC value for that model (Burnham and Anderson, 2002). For the model including the best combination of predictor variables (with the highest Akaike weight derived using Eq. (3)), predicted probabilities of loblolly pine mortality [referred to as P(dead) hereafter] were calculated for different levels of each predictor variable to determine the influence of each variable on mortality. Assessment of the contribution of individual predictor variables to overall P(dead) was important to isolate the relative importance of each variable. As evaluating the model for every observed DBH from 8 to 55 cm would be exhaustive, to summarize the influence of DBH on P(dead), we selected three values to generalize the effect of tree diameter in the model: a low (10 cm), medium (25 cm – the mean for our observed data), and high (50 cm) DBH size-class. Model evaluation and selection was performed in R 1.0.136 (R Core Team, 2016), and the ‘car’, ‘readxl’, and ‘stat’ packages were used (Fox and Weisberg, 2011; R Core Team, 2016; Wickham and Bryan, 2017).

3. Results

3.1. Survival analyses

Of the 838 pines included in our study, 69 (8%) died by the final set of temporal measurements in November 2017, with 15 (22%) of the dead trees occurring on burned and 54 (78%) on unburned sites. The majority of loblolly pine mortality on unburned sites occurred prior to our surveys in May ($n = 36$), and most of the mortality on burned sites occurred preceding measurements in November ($n = 8$) (Fig. 3a). Kaplan-Meier survival analyses showed that there was a lower probability of survival in the unburned than burned sites during all survey months (log-rank $p = 0.02$) (Fig. 3b).

The crown mortality level was 5 (100%) for all 69 trees that died, as they had stopped producing new green needles. Overall, there were a higher proportion of loblolly pines with crown mortality levels 3 and 4 on burned sites (Fig. 4a and b). Seven of the dead trees (10%) had no signs of *Ips* activity, seven (10%) had low *Ips* activity, seven (10%) had medium *Ips* activity, and the remaining 48 (70%) had high *Ips* activity levels. In general, there were higher proportions of loblolly pines with a low level of *Ips* activity on the burned sites (Fig. 5a and b). Interestingly, five out of the seven dead trees with no *Ips* activity died on the burned sites prior to November and had significant crown scorch, suggesting mortality of these trees may have resulted from the prescribed burn. Trees that died during the study had DBH measurements ranging from 8 to 55 cm (mean \pm SE 25 \pm 0.35 cm).

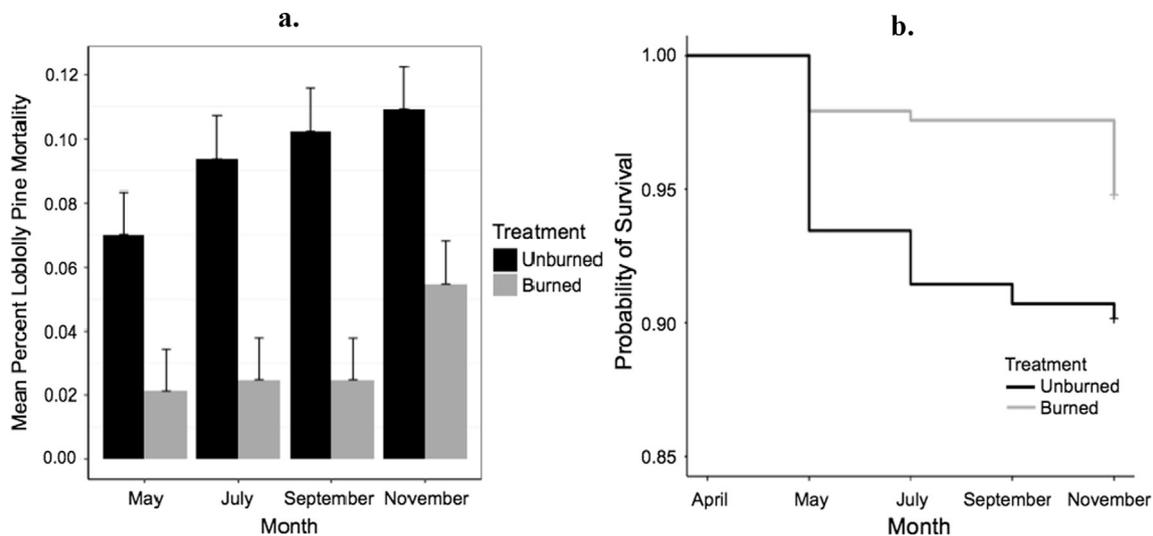


Fig. 3. (a) Mean (± SE) percent loblolly pine mortality that occurred during temporal monitoring on unburned and burned sites; (b) Kaplan-Meier estimation curves for the probability of loblolly pine survival in unburned and burned stands.

3.2. Site-level predictors of loblolly pine mortality

We did not find any significant interactions between treatment, basal area, and time since burn (all p -values > 0.05). GLMs including only site-level basal area and only time since burn were not found to be good predictors of loblolly pine mortality ($p > 0.10$). However, the model including only the effect of treatment (unburned versus burned) on loblolly pine mortality was significant ($F_{1,38} = 37.53, p < 0.001$), with higher mortality occurring on unburned sites (Fig. 3a and b). Additionally, a model including the main (additive) effects of treatment and time since burn was found to be significant ($F_{4, 35} = 10.99, p < 0.001$), indicating temporal differences in mortality between the unburned versus burned treatments. Specifically, there was higher mortality in May on unburned sites, and higher mortality in November on burned sites (Fig. 3a).

3.3. Model selection and influence of predictors on tree-level probability of loblolly pine mortality

None of the hypothesized interactions between tree-level predictor

variables were significant; accordingly, logistic regression models selected for comparison included only the main effects (Table 2). Of all models tested, 14 models including individual predictor variables and the main effects between predictors were found to be significant, and were included in the model selection. Based on the Δ AIC values and associated Akaike weights (w_i), the best candidate model for our data included DBH, treatment, level of *Ips* activity, and level of crown mortality as predictors of loblolly pine mortality (AIC value = 202.25) (Table 2). The best model was given substantially more support than the other 13 candidate models ($w_i = 0.99$), despite having the largest number of parameters ($K = 6$).

For every combination of crown mortality level, *Ips* activity level, and DBH, the $P(\text{dead})$ was higher for unburned than burned sites (Table 3, Fig. 6). Increasing the value for DBH resulted in a higher overall $P(\text{dead})$, regardless of the crown mortality level, *Ips* activity level, or treatment (Table 3). However, the overall influence of DBH as a predictor of $P(\text{dead})$ was not very strong, indicated by the slope of the curves (Fig. 7) (parameter estimates for the effect of DBH). The highest $P(\text{dead})$ occurred when crown mortality level was 5 and *Ips* activity was medium or high, regardless of DBH and treatment [all $P(\text{dead}) \geq 0.89$]

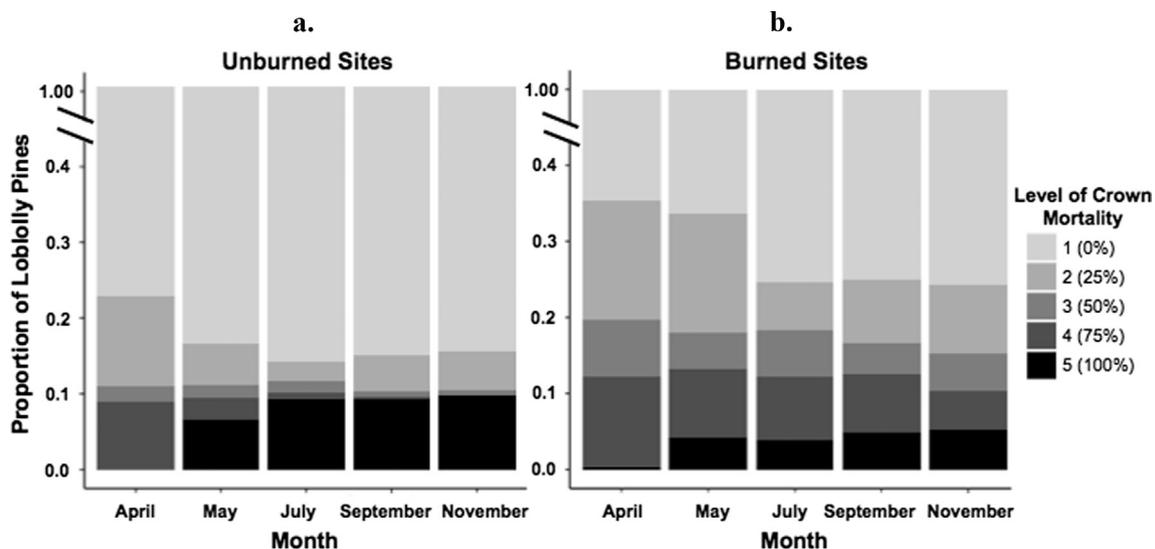


Fig. 4. Temporal changes in the proportions of loblolly pine trees with each level of crown mortality (1 = 0%, 2 = 25%, 3 = 50%, 4 = 75%, and 5 = 100%) for: (a) unburned; and (b) burned sites (note scale break on y-axis to show variation between months).

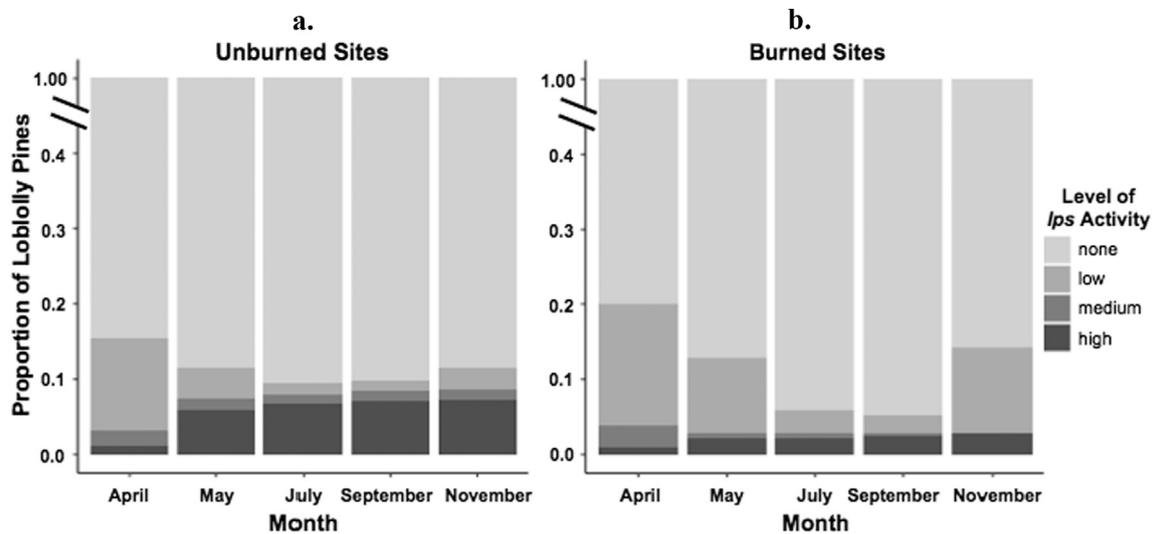


Fig. 5. Temporal changes in the proportions of loblolly pine trees with each level of *Ips* bark beetle activity (none, low, medium, or high) for: (a) unburned; and (b) burned sites (note scale break on y-axis to show variation between months).

Table 2

List of all significant candidate models predicting individual loblolly pine mortality during active *Ips* beetle infestations, ranked by their AIC value.

Model ^a	K	AIC	Δ AIC	w _i
Status _{T2} ~ DBH + treatment + Ips _{T1} + CM _{T1}	6	202.25	0.00	0.99
Status _{T2} ~ treatment + Ips _{T1} + CM _{T1}	5	211.22	8.98	0.01
Status _{T2} ~ DBH + Ips _{T1} + CM _{T1}	5	215.86	13.61	0.00
Status _{T2} ~ Ips _{T1} + CM _{T1}	4	240.23	37.98	0.00
Status _{T2} ~ DBH + CM _{T1} + treatment	5	285.85	83.60	0.00
Status _{T2} ~ CM _{T1} + treatment	4	315.93	113.68	0.00
Status _{T2} ~ DBH + CM _{T1}	4	338.91	136.67	0.00
Status _{T2} ~ CM _{T1}	3	415.01	212.76	0.00
Status _{T2} ~ Site + Ips _{T1}	4	513.18	310.94	0.00
Status _{T2} ~ treatment + Ips _{T1}	4	540.43	338.18	0.00
Status _{T2} ~ DBH + Ips _{T1}	4	555.45	353.20	0.00
Status _{T2} ~ Ips _{T1}	3	564.71	362.46	0.00
Status _{T2} ~ Site	3	1520.93	1318.68	0.00
Status _{T2} ~ treatment	3	1603.36	1401.11	0.00

^a T1 = time 1; T2 = time 2; Status = tree alive (0) or dead (1); Ips = level of Ips activity; CM = crown mortality level; Treatment = unburned or burned; Site = ten total, five unburned/five burned. K is the number of parameters for each model. All significant models were included in model selection, and are ranked above by their Akaike's Information Criteria (AIC) and Δ AIC scores. The best candidate model has the smallest AIC and the highest Akaike weight (w_i). No significant interactions were found; all models included only the main effects between predictor variables (additive).

(Table 3). In general, increasing the level of Ips activity resulted in a higher P(dead) (Table 3, Fig. 8). For burned sites, when crown mortality level was 5 and Ips activity was low or none, P(dead) decreased considerably, particularly when DBH was low [e.g., P(dead) = 0.24 with no Ips activity and P(dead) = 0.63 with low Ips when DBH = 10 cm]. For unburned sites with crown mortality level 5 and low to no Ips activity, all P(dead) were ≥ 0.84 [with the exception of P(dead) = 0.61 for no Ips activity and DBH = 10 cm] (Table 3).

When the crown mortality level was 4, for high levels of Ips activity, all P(dead) were ≥ 0.94, irrespective of treatment or DBH. However, decreases in Ips activity were associated with corresponding decreases in P(dead) for both treatments and there was an influence of DBH [e.g., for burned sites with medium Ips activity, P(dead) = 0.46 for DBH = 10 cm, and P(dead) = 0.95 for DBH = 50 cm]. A significant drop was observed in P(dead) for unburned sites when there was no Ips activity, but only for low and medium DBH [P(dead) = 0.14 when DBH = 10 cm, 0.35 when DBH = 25 cm, but 0.80 at DBH = 50 cm]. Similar trends were observed for P(dead) for unburned and burned sites

when the crown mortality level was 3. When Ips activity level was medium or low, the predictive model showed a significant decrease in P (dead) from crown mortality levels 4 to 3 [at level 3, all P (dead) ≤ 0.50] (Table 3). However, this threshold between crown mortality levels 3 and 4 is not as apparent when the level of Ips activity is high, suggesting Ips activity also has a substantial predictive influence on P(dead). Additionally, we observed that increasing the DBH at crown mortality level 3 when the Ips activity level was none only slightly influenced P(dead), suggesting the importance of DBH as a predictor of loblolly pine mortality is dependent on the levels of other predictors.

When the crown mortality level was 2, P(dead) < 0.001 for both treatments and all levels of DBH, indicating a threshold between crown mortality levels 3 and 2 [i.e., P(dead) is much lower when crown mortality is < 3 (50%)]. However, very large confidence intervals surrounding predicted probability estimates at this level of crown mortality indicate there is a lot of uncertainty associated with P(dead) when the crown mortality level is 2 (Table 3). Interestingly, P(dead) increased slightly when the crown mortality level was decreased to 1 and Ips activity level was high in the unburned sites, suggesting some pine mortality may have primarily been associated with Ips activity [P (dead) = 0.25 at DBH = 25 cm and 0.71 at DBH = 50 cm]. Altering the values of each predictor variable showed that for our study, crown mortality was the overall most important predictor of the probability of loblolly pine mortality (despite uncertainty at crown mortality level 2 indicated by the large confidence intervals).

4. Discussion

The three southern Ips species typically infest hosts in a dispersed pattern, attacking the most stressed and compromised trees in a given stand (Bryant et al., 2006; Stone et al., 2007; Eickwort et al., 2015). Accordingly, large-scale southern Ips outbreaks are relatively uncommon, and there are currently no published studies that provide data on the interactions between Ips bark beetle activity, prescribed fire, and loblolly pine mortality. We found that the majority of loblolly pine mortality during our study occurred on unburned sites (similar to Fetting et al., 2010), and in general, trees that succumbed had higher levels of Ips activity (evidenced by ≥ 20 entrance/exit holes and lots of visible frass) and ~100% crown mortality. Unfortunately, given the occurrence of drought conditions prior to the initiation of southern Ips infestations (and subsequent monitoring), we were unable to quantify the severity of the drought or its potential effects on these infestations.

Table 3

Predicted probabilities of loblolly pine mortality for burned versus unburned sites with 95% confidence intervals, based on the best predictive model including crown mortality level, *Ips* activity level, DBH, and treatment as independent variables.

Crown mortality level ^a	<i>Ips</i> activity level	DBH ^b (cm)	P(dead) ^c , burned	Lower bound, burned	Upper bound, burned	P(dead) ^c , unburned	Lower bound, unburned	Upper bound, unburned
5	high	10	0.993	0.909	1.000	0.999	0.979	1.000
5	high	25	0.998	0.971	1.000	1.000	0.994	1.000
5	high	50	1.000	0.994	1.000	1.000	0.999	1.000
5	medium	10	0.892	0.638	0.975	0.977	0.893	0.995
5	medium	25	0.964	0.832	0.993	0.993	0.962	0.999
5	medium	50	0.995	0.949	1.000	0.999	0.990	1.000
5	low	10	0.635	0.320	0.866	0.899	0.682	0.974
5	low	25	0.851	0.607	0.955	0.967	0.884	0.991
5	low	50	0.976	0.862	0.996	0.995	0.972	0.999
5	none	10	0.238	0.111	0.438	0.615	0.348	0.827
5	none	25	0.505	0.262	0.746	0.840	0.630	0.942
5	none	50	0.881	0.535	0.979	0.974	0.863	0.996
4	high	10	0.940	0.506	0.996	0.988	0.836	0.999
4	high	25	0.981	0.785	0.999	0.996	0.950	1.000
4	high	50	0.997	0.956	1.000	0.999	0.992	1.000
4	medium	10	0.462	0.165	0.789	0.815	0.521	0.947
4	medium	25	0.738	0.381	0.928	0.935	0.784	0.983
4	medium	50	0.953	0.711	0.994	0.990	0.939	0.999
4	low	10	0.153	0.048	0.392	0.481	0.215	0.759
4	low	25	0.372	0.161	0.647	0.752	0.536	0.889
4	low	50	0.811	0.462	0.955	0.956	0.848	0.989
4	none	10	0.031	0.013	0.072	0.142	0.068	0.276
4	none	25	0.096	0.044	0.197	0.352	0.223	0.508
4	none	50	0.434	0.137	0.788	0.797	0.504	0.938
3	high	10	0.410	0.038	0.925	0.781	0.163	0.985
3	high	25	0.695	0.126	0.973	0.921	0.427	0.995
3	high	50	0.943	0.476	0.997	0.988	0.833	0.999
3	medium	10	0.037	0.007	0.184	0.165	0.034	0.525
3	medium	25	0.112	0.021	0.423	0.393	0.111	0.771
3	medium	50	0.477	0.090	0.893	0.824	0.377	0.973
3	low	10	0.008	0.001	0.050	0.040	0.006	0.209
3	low	25	0.026	0.005	0.130	0.120	0.026	0.411
3	low	50	0.161	0.025	0.584	0.495	0.138	0.858
3	none	10	0.001	< 0.001	0.008	0.007	0.001	0.038
3	none	25	0.005	0.001	0.023	0.024	0.005	0.100
3	none	50	0.033	0.005	0.204	0.150	0.027	0.527
2	high	10	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	high	25	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	high	50	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	medium	10	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	medium	25	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	medium	50	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	low	10	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	low	25	< < 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	low	50	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	none	10	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	none	25	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
2	none	50	< 0.001	< 0.001	1.000	< 0.001	< 0.001	1.000
1	high	10	0.020	0.001	0.282	0.094	0.005	0.684
1	high	25	0.062	0.004	0.506	0.254	0.021	0.845
1	high	50	0.324	0.032	0.876	0.711	0.147	0.972
1	medium	10	0.001	< 0.001	0.008	0.006	0.001	0.041
1	medium	25	0.004	0.001	0.022	0.018	0.003	0.098
1	medium	50	0.026	0.004	0.164	0.120	0.021	0.467
1	low	10	< 0.001	< 0.001	0.002	0.001	< 0.001	0.009
1	low	25	< 0.001	< 0.001	0.004	0.004	0.001	0.019
1	low	50	0.006	0.001	0.027	0.028	0.007	0.108
1	none	10	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.001
1	none	25	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.003
1	none	50	0.001	< 0.001	0.005	0.005	0.001	0.020

^a Crown mortality levels: 1 = 0%, 2 = 25%, 3 = 50%, 4 = 75%, 5 = 100%.

^b DBH: mean = 25 cm, 10 and 50 cm selected to show changes in P (dead) with a low and high DBH relative to the mean (DBH range = 8–55 cm).

^c P(dead) = predicted probability of loblolly pine mortality, rounded to three decimal places. Upper and lower bounds are 95% confidence intervals around probabilities, and are asymmetric due to inverse logit transformation (i.e., for error associated with binomial logistic regression to follow a normal distribution).

Previously, *Ips* beetles have been observed to preferentially mass attack pines with moderate to severe crown scorch and bole char that are dead or dying (Geiszler et al., 1984; Hanula et al., 2002; Wallin et al., 2003; Fettig et al., 2008; Negrón et al., 2016). We found that the probability of survival was higher on burned sites during all months

following the initiation of our study, and no support was found for increased *Ips* infestation of hosts on burned sites, which has also been reported in other studies (Sullivan et al., 2003; Lombardero et al., 2006). We recorded a higher proportion of loblolly pines with crown mortality levels 3 and 4 on burned sites. We also found higher

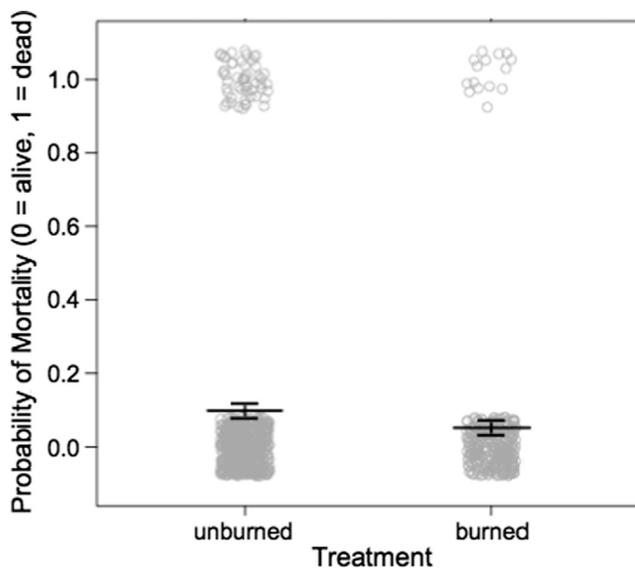


Fig. 6. Probability of mortality (0 = alive, 1 = dead) of individual loblolly pines ($n = 838$) on unburned versus burned sites in November (end of study), including the mean (\pm SE) probability of tree mortality for each treatment.

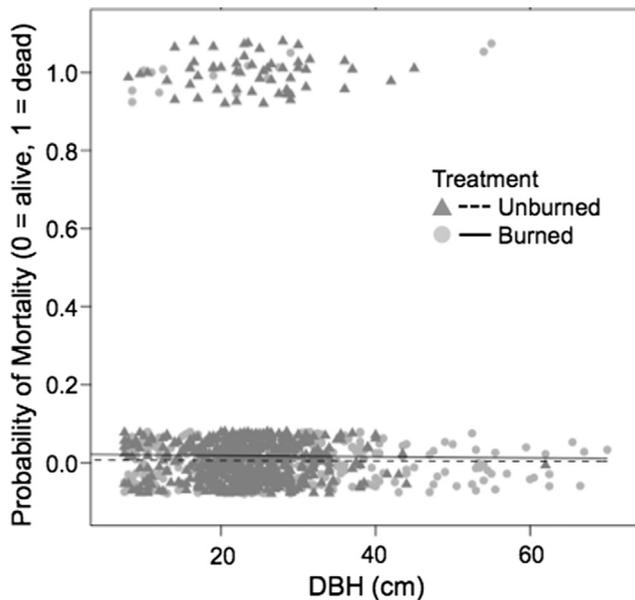


Fig. 7. Probability of mortality (0 = alive, 1 = dead) of individual loblolly pines ($n = 838$) in November (end of study) as compared to diameter at breast height (DBH), labeled by treatment (unburned versus burned). Curves show the parameter estimates associated with DBH for the unburned (dashed line) and burned (solid line) treatments provided by the model.

proportions of loblolly pines with low levels of *Ips* activity on the burned sites, indicating that *Ips* beetles may have been unsuccessful in attacking some of the trees in burned sites, or that prescribed fire may have increased host resilience by reducing competition and/or increasing defensive compounds (Wallin et al., 2003; Hood et al., 2015). Interestingly, Nowak et al. (2015) found similar results for the level of southern pine beetle infestation; stands that had recently been treated with prescribed fire had a lower infestation rate of beetles as compared to unburned stands.

While our study used low-severity prescribed fire treatments that were carefully monitored, some mature pines had significant bole char (4–6 m high) and needle scorch in the lower portions of their crowns post-burn. Additionally, there were a few (4–5) suppressed, low-DBH

pinus with no observable southern *Ips* activity that may have died as a result of the prescribed fire. Nonetheless, we observed 78% of loblolly pine mortality on unburned rather than burned sites. This result is particularly compelling because the burned sites have not been on a regular 2–3 year burn rotation and had increased build-up of surface fuels, which may have resulted in more intense burns and basal cambial damage (e.g., one site had not been burned in the last 20 years, and the other four sites were burned between 2003 and 2006) (McNab, 1977; Varner et al., 2005; O'Brien et al. (2010)).

Our finding that site-level basal area (which encompassed a wide range from 14.9–23.8 m²/ha) was not a good predictor of tree mortality is supported by a previous study that found no clear relationship between basal area and the susceptibility of Jeffrey pines (*P. jeffreyi* Grev. & Balf.) to *Ips* infestations and resulting increases in mortality (Bradley and Tueller, 2001). We found no interactions between any of our tree-level predictors of loblolly pine mortality, but perhaps the most surprising finding was the lack of an interaction between the level of *Ips* activity and host tree DBH. In thinned and prescribed burned ponderosa pine (*P. ponderosa* Douglas ex C. Lawson) stands, almost all tree mortality caused by *I. pini* (Say) occurred on burned sites in the smallest DBH class (19–29 cm) (Fettig and McKelvey, 2014). Various *Ips* spp. occurred at higher proportions in *P. ponderosa* hosts with DBH < 32 cm as compared to larger DBH pines following wildfires (Negrón et al., 2016). Both findings suggest some *Ips* spp. may preferentially select hosts in smaller DBH classes post-burn, perhaps to avoid competition with other insects, or because these trees may be more stressed following fire (smaller pines have thinner bark and are less well-protected from fire). However, for *I. calligraphus*, new progeny adults have been observed to emerge 3–5 days earlier when they developed in thicker phloem at various temperatures (Haack et al., 1987), suggesting that *Ips* colonization in larger DBH hosts with thicker phloem may be advantageous to accelerate brood development. For our study, the best candidate model predicted higher probabilities of loblolly pine mortality with increasing DBH on both unburned and burned sites. It is also likely that these trees may have either been over-mature, or more vulnerable due to disease or another unmeasured physiological stressor (e.g., drought).

While 70% of the dead trees in our study had high levels of *Ips* activity, indicating that the degree of tree-level *Ips* infestation is a contributor to observed mortality, there may have been other factors contributing to tree mortality that were unmeasured in this study. For example, virulent blue-staining fungi (Ascomycetes: Ophiostomatales) assist many bark beetle species with colonization by helping to overwhelm the defenses of conifer hosts (Lieutier et al., 2009). The three southern *Ips* species can carry the blue-stain fungus species *Ophiostoma ips* (Rumbold) Nannfeldt on their exoskeletons, as well as on phoretic mites (Gouger et al., 1975; Klepzig et al., 2001; Stephen, 2011). Additionally, there may have been other pathogens (e.g., *Phytophthora* spp.) present in these clayey, poorly drained soils that could have increased the physiological stress of pines and their susceptibility to infestation by the southern *Ips* beetles (Mistretta, 1984).

Our model selection results show that tree DBH, treatment, level of *Ips* activity, and level of crown mortality were all important predictors of the probability of mortality for an individual loblolly pine. We decided to use categorical (rather than continuous) predictor variables in the models because: (1) categorical measurements are easier to visually assess; (2) categories are more intuitive (e.g., ranking crown mortality levels from 1 to 5, rather than trying to estimate 45% dieback, for example); and (3) categorical rankings do not require specialized training for personnel or expensive equipment (e.g., a laser rangefinder or hyperspectral imaging camera to quantify crown mortality). The tradeoffs of our decision to use categorical variables are that they are somewhat subjective (e.g., two users may interpret the cutoff between level 2 versus level 3 crown mortality differently), and the levels of *Ips* activity were determined using visual assessments primarily in the basal two meters of the tree (i.e., additional *Ips* activity in the crown

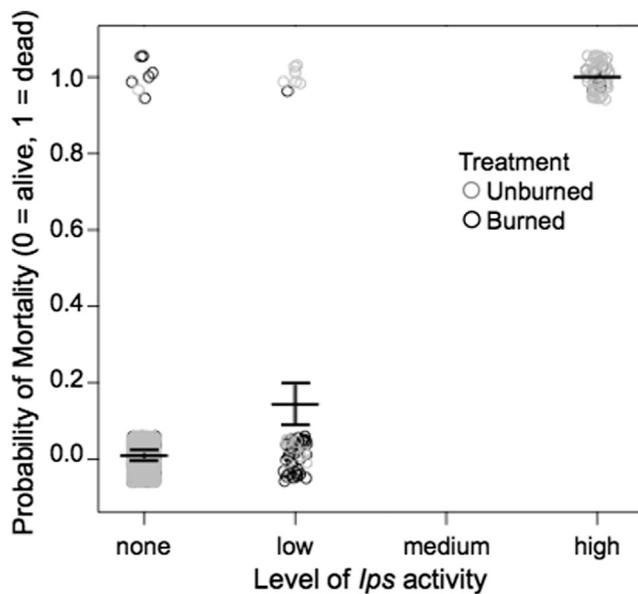


Fig. 8. Probability of mortality (0 = alive, 1 = dead) of individual loblolly pines ($n = 838$) in November as compared to *Ips* activity level, labeled by treatment (unburned versus burned) and including the mean (\pm SE) probability of mortality for each *Ips* activity level. No loblolly pines had a medium level of activity at the end of the study.

may have been unobservable). We took these crown mortality measurements over time to enhance our ability to account for the gradual fading of foliage over time and to ensure that we recorded the most accurate levels of tree mortality.

While our experimental design was limited in that we were not able to collect any pre-fire data on individual tree condition and the level of *Ips* infestation, we began monitoring 2–3 weeks post-burn to capture any sizeable growth in *Ips* activity and expansion of infested host pines. Prescribed burning is conducted differentially as based on the forest manager, and if conducted incorrectly (e.g., at a higher severity than intended), it can cause significant damage to pine trees. Thus, while we cannot conclude that prescribed fire does not contribute to loblolly pine mortality, these low-severity prescribed burns did not cause significant additional mortality within the active southern *Ips* infestations. Another caveat is that we did not fell *Ips*-infested trees to verify which species were present, and our sampling technique did not account for additional *Ips* activity in the upper bole and crown of infested trees. However, all three southern *Ips* species were present in pines felled during preliminary surveys in these sites, though their individual impacts may be variable based on host and stand conditions.

5. Conclusions

Based on our findings, in particular the evident thresholds in the probabilities of loblolly pine mortality predicted by the best candidate model, low-severity prescribed fire may be a viable forest management tool in stands experiencing active southern *Ips* infestations, unless: (A) $\geq 50\%$ of the crowns of numerous loblolly pines have fading or red needles; or (B) there is a medium to high level of *Ips* activity, observable via the presence of frass and many entrance/exit holes (~ 10 holes per 0.1 m^2) on the basal 2 m. As an additional precautionary measure, the use of prescribed fire may be avoided in *Ips*-infested stands that have older, higher-DBH (≥ 50 cm) loblolly pines, as these trees may be more susceptible to other stressors or damage due to their age.

Future research may assess the effects of common management techniques in southeastern pine-dominant forests (e.g., fertilization, herbicide, and thinning) during active southern *Ips* infestations, especially those that produce slash and logging debris, to determine their

impact on beetle population levels. Measurements to quantify tree water use and defenses (e.g., hydraulic conductivity, and resin flow rate and volume), and characterize potential differences in defensive responses between individual loblolly pines, may improve our understanding of why specific host trees may be more susceptible to *Ips* beetles. As climatic conditions continue to be highly variable, interactions between bark beetles and host trees may significantly affect the long-term sustainability of forest resources in the southeastern U.S.

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