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Variables associated with the occurrence of *Ips* beetles, red turpentine beetle and wood borers in live and dead ponderosa pines with post-fire injury

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Abstract

1 Recently, wildfires and prescribed burning have become more frequent in conifer forests of western North America.
2 Most studies examining the impacts of insects on trees with post-fire injury have focused on contributions to tree mortality. Few studies have examined fire-caused injuries to estimate the probability of attack by insects. Scant data quantifying insect associations with one another, or with live and dead fire-injured trees, are available.
3 We examined live and dead trees with varying levels of fire injury in wildfires in Colorado, Montana, Arizona and the Black Hills aiming to determine fire injury associated with insect infestation, co-occurrence between insects and insect association with live and dead fire-injured trees.
4 Bole scorch height estimated the likelihood of attack by *Ips* spp. Diameter at breast height, bole scorch height and crown scorch height estimated the likelihood of attack by *Dendroctonus valens* LeConte. Diameter at breast height and bole scorch height estimated the likelihood of attack by wood borers.
5 *Ips* spp., *Dendroctonus valens* and wood borers were associated with one another. *Ips* spp. beetles and wood borers were associated with dead fire-injured trees, whereas *D. valens* was often associated with live fire-injured trees.
6 Focusing on certain fire-caused injuries may identify trees targeted by *Ips* spp. beetles, *Dendroctonus valens* and wood borers.

Keywords *Dendroctonus valens*, fire injury, *Ips* beetles, *Ips* spp., *Pinus ponderosa*, wood borers.

Introduction

Disturbance processes constantly modify and shape forest structure and composition (Oliver, 1981). Agents of change include biotic factors such as insects and diseases, and abiotic influences such as fire, windthrow and drought, amongst others. Although these agents are sometimes considered to work in isolation, the reality is that they constantly interact, exacerbating or negating the effects of one another (Seidl *et al.*, 2011). In the western U.S.A., numerous fires have occurred over the past two decades in coniferous forests, with the years 2000 and 2002 being particularly notable (Graham *et al.*, 2004; Pielke *et al.*, 2005) as a result of extremely dry conditions. Wildfires can burn thousands of hectares of forests, resulting in extensive tree mortality before they dwindle or are suppressed. Extensive efforts on the implementation of fuel reduction and forest restoration projects are currently underway (Underhill *et al.*, 2014) and prescribed fire, which can cause tree mortality, is a key tool (Stephens *et al.*, 2012; Reynolds *et al.*, 2013).

Many studies have examined tree mortality of ponderosa pine *Pinus ponderosa* Douglas. ex P. & C. Lawson. resulting from fire

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injury after prescribed burning or wildland fires (Wyant *et al.*, 1986; Harrington, 1987; Ryan & Reinhardt, 1988; McHugh & Kolb, 2003; Thies *et al.*, 2006; Breece *et al.*, 2008). Tree mortality to fire injury can be influenced by factors, such as crown damage and bole charring (Saveland & Neuenschwander, 1990; McHugh & Kolb, 2003; Wallin *et al.*, 2003), tree diameter (Wyant *et al.*, 1986; Regelbrugge & Conard, 1993; Thies *et al.*, 2005) and surface fire severity (Swezy & Agee, 1991; Stephens & Finney, 2002). A number of studies have also addressed tree mortality caused by sublethal fire damage and subsequent insect infestations (Amman & Ryan, 1991; McHugh *et al.*, 2003; Schwilk *et al.*, 2006; Sieg *et al.*, 2006; Breece *et al.*, 2008; Fettig *et al.*, 2008; Fettig *et al.*, 2010a; Fettig *et al.*, 2010b; Davis *et al.*, 2012). For example, McHugh *et al.* (2003) examined ponderosa pine mortality post-fire and reported that dead trees exhibited more crown scorch, crown consumption, bole scorch, ground char and bark beetle attacks, and concluded that total crown damage and bole char were the best predictors of tree mortality 3 years post-fire. Sieg *et al.* (2006) and Fowler *et al.* (2010) examined predictors of ponderosa pine tree mortality after wildfires in 2000 in Colorado (CO), Arizona (AZ), Montana (MT) and the Black Hills of South Dakota (BH). Their results indicated that percentage crown scorch and percentage consumption volume were the best predictors of tree mortality. Wildfires can vary widely in severity and intensity across landscapes due to weather conditions, fuel characteristics and topography, amongst other factors. Fires, however, more often than not burn with mixed severities and, when this occurs, many trees succumb, others sustain sublethal fire injury, and some escape fire injury.

One motivation for many of these studies is the need for guidelines for post-wildfire salvage projects to aid in the selection of trees for removal (Sieg *et al.*, 2006; Jenkins *et al.*, 2014), particularly those trees that do not die immediately after the fire but may exhibit delayed mortality (Thies *et al.*, 2005). Another concern for forest managers is the need to mitigate insect infestations from augmenting populations that could spread to unburned forests (Rasmussen *et al.*, 1996; McHugh & Kolb, 2003; Keyser *et al.*, 2006; Sieg *et al.*, 2006; Stephens *et al.*, 2012), although other studies have indicated that this may not be the case (Davis *et al.*, 2012; Powell *et al.*, 2012; Jenkins *et al.*, 2014). In addition, there are efforts being made for the re-introduction of fire into many ponderosa pine-dominated forests after many years of fire exclusion to reduce accumulated fuel loads or restore degraded ecosystems, or both (Parsons, 1995; Underhill *et al.*, 2014). Prescribed fires, often in combination with vegetation management to reduce tree density, can cause injury to trees intended for preservation (Breece *et al.*, 2008; Fettig *et al.*, 2008; Youngblood *et al.*, 2009). Understanding the interactions of insect guild activity and fire injury levels may contribute to refining recommendations for managers, discerning the physiological processes influencing insect infestations, and increasing our understanding of how disturbance interactions shape the structure and composition of forests.

Attraction and attack of some bark beetles to fire-injured ponderosa pine has been well documented. For example, western pine beetle (*Dendroctonus brevicomis* LeConte) (WPB), pine engraver beetles (*Ips* spp.), red turpentine beetle (*Dendroctonus valens* LeConte) (RTB), roundheaded pine beetle (*Dendroctonus adjunctus* (Blandford) (RPB) and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (MPB) have all been reported to successfully invade fire-injured trees, although their role in causing tree mortality or being able to reproduce is not always evident (Miller & Patterson, 1927; Miller & Keen, 1960; Peterson & Ryan, 1986; Kelsey & Joseph, 2003; Fettig *et al.*, 2008; Davis *et al.*, 2012; Powell *et al.*, 2012). Insects commonly observed attacking ponderosa pine after fires also include wood borers (WB) belonging to the families Buprestidae (metallic wood borers), Cerambycidae (long-horned beetles) and Siricidae (wood wasps) (Costello *et al.*, 2011).

A question that has received less attention is the identification and levels of tree injury that make a tree a more probable target for specific insects (McHugh *et al.*, 2003; Breece *et al.*, 2008; Youngblood *et al.*, 2009; Davis *et al.*, 2012). Moreover, the association of different insects with one another and with live or recently dead fire-injured trees, although well-documented anecdotally, has not been adequately quantified or characterized. An increased understanding of these interactions will improve our foundation for the examination of the physiological and ecological processes at work among insects, host trees and abiotic factors such as fires.

The objectives of the present study were: (i) to determine types and level of fire injury that influence the probability of attack by *Ips* beetles, RTB and WBs in fire-injured trees that either die or survive the fire; (ii) explore the associations among these insect species or groups in fire-injured trees; and (iii) examine the associations of these insect species or groups in fire-injured live or dead trees. We were interested in examining these objectives 3 years post-fire because fire-injured trees can exhibit delayed mortality. The data originate from four wildfires: one in each in CO, MT, AZ and BH used in the study by Sieg *et al.* (2006) where logistic regression models of tree mortality were presented. This work therefore represents a companion study to Sieg *et al.* (2006) focusing on insect interactions in post-fire injured trees.

Materials and methods

Study sites

The present study was conducted from the summer of 2001 up to the summer of 2003 at four wildland fires in ponderosa pine forests in CO, MT, AZ and BH and follows a previous study conducted by Sieg *et al.* (2006). In north-central CO, we examined the Bobcat fire, which burned approximately 1200 ha in the Arapaho-Roosevelt National Forest in June 2000. Elevation at the site ranges from 1800 to 2500 m a.s.l. The second study location comprised the Stag and Tobin fires in the Custer National Forest in MT, which started in July 2000 and burned approximately 29 000 ha. Elevation at the site ranges from 1000 to 1200 m a.s.l. The third site sampled was the Pumpkin fire in the Kaibab National Forest in northern AZ, which burned in May 2000 and comprised 6000 ha with an elevation ranging from 2200 to 3000 m a.s. l. The last site was the Jasper fire, which was in the BH National Forest of South Dakota and Wyoming in August 2000 and burned approximately 34 000 ha. Elevation at the site ranges from 1500 to 2100 m a.s.l.

Tree measurements

During the summer of 2001, we recorded tree condition (live, dead as a result of fire, insects, or both, or dead as a result of unknown causes), fire injury and insect colonization data for over 900 trees in each fire. Trees were considered live if green foliage was still present in the crown. In the Bobcat, Stag and Tobin, and Pumpkin fires, trees were revisited in 2002 and 2003. Trees in the Jasper fire were initially evaluated in 2002 and revisited in 2003. To include a range of diameter classes and fire injury, we evaluated trees in transects 200 m long and 10 m wide randomly located within each fire. The number of transects varied from 9 to 12 depending on the fire. Measurements were not destructive, with the aim of preventing the disruption of insect colonization patterns, as described below.

Data were recorded for every tree greater or equal to 5.1 cm in diameter at 1.4 m above the ground (DBH) and trees were marked with a numbered tag to facilitate relocation for re-measurements. Tree data recorded included DBH, total tree height and height to the first live branch. Pre-fire live crown ratio was calculated from these data as the ratio of estimated live crown to tree height prior to the fire. Crown fire injury data included an estimate of percentage crown scorch (CSV), which is the part of the pre-fire live crown scorched by the fire but not consumed (Ryan, 1983; Harrington, 1987). We obtained an estimate of percentage crown consumed (CCV), which is the part of the pre-fire live crown where complete foliage consumption occurred as indicated by fascicle remnants (Wyant *et al.*, 1986; McHugh & Kolb, 2003). Both of these estimates were based on visual evaluations of trees from all sides. Total crown damage was the sum of CSV + CCV. We measured crown scorch (CSH) and consumption height. Measures of bole fire injury included maximum (BSH) and minimum bole scorch height, and percentage of basal circumference scorched 30 cm above the ground. These variables are considered to be descriptive of fire injury (Fowler & Sieg, 2004).

Insect data recorded included evidence of infestation by bark beetles such as WPB, MPB, RTB, *Ips* beetles and WBs. The presence of insects was determined by observation of attack signs such as pitch tubes, accumulation of boring dust at the base of the tree or bark crevices, and characteristic gallery patterns examined after tree mortality. Mortality of fire-injured trees and their attack by insect populations can take a number of years; therefore, all trees were revisited the 2 years post-fire (1 year for the BH) and evaluated to determine whether they were alive or dead based on the presence or absence of live foliage and their status and insect activity updated.

Statistical analysis

Analysis focused on insect data from *Ips* beetles, RTB and WBs because these were the most common insect species or groups (hereafter referred to simply as insect or insects) on all sites. A few other species such as MPB and WPB attacked some trees, although their occurrence was rare. We used the Cochran–Mantel–Haenszel statistic to determine whether the proportions of pairwise insect combinations were different among fires and the Breslow–Day Statistic to determine whether the proportions of pairwise insect combinations were different across years. Although trees could have been attacked by more than two insect species or groups, we focused on pairwise occurrence because three-way interactions can become increasingly complex and patterns difficult to determine. Any tree that died to other causes other than fire injury or insect attack was removed from the data set. Because of the significant results from these tests, we conducted all analyses separately for each fire. We compared variables measured between live and dead trees for each fire using Wilcoxon rank sum tests. To examine whether there were fire injury metrics that could be used to estimate the probability of occurrence of different insects, we employed logistic regression modelling using presence or absence 3 years post-fire as a response variable. Using the logistic approach, models take the form:

$$(\mathrm{P})\ \text{infestation} = 1/1 + e^{-b'X'}$$

where $b'X$ represents a linear combination of explanatory variables X with their estimated parameters b, and e is the base of natural logarithms. For regression modelling, we used transects as a random effect in mixed models to account for correlations among transects within each fire (SAS Institute, 2004). Models using different variable combinations were used to identify the best explanatory models. Variables were selected using backward elimination with $P < 0.05$ as the threshold. Because the literature suggests (see Discussion) that WBs primarily infest dead and dying trees, we conducted logistic regression for this group using data from dead trees only. Although insect combinations were influenced by fire and year, which is likely a result of differences in background insect population levels, variables selected in the logistic regressions for each insect were similar among fires. Therefore, we conducted a logistic regression analysis for insects across all fires using fire as a random effect in mixed models to account for correlations among fires. The response of each model was portrayed by graphing the estimated probability of attack across the observed range of the predictor variable(s). To examine the accuracy of the logistic models, we used the 'concordance index' (area under a receiver operating characteristic curve), a standard metric that describes the probability that a positive response has a larger probability of attack than a negative response. We examined the occurrence of pairwise insects (*Ips* with RTB, *Ips* with WB and RTB with WB) independent of tree status (live or dead) and the association of *Ips*, RTB and WB with live or dead trees independent of fire injury levels using cross-tabulations and Fisher's exact test 3 years post-fire. We acknowledge that these interactions are influenced by fire injury levels, although we captured this using the logistic models, and inclusion into examinations of insect association would have considerably increased the complexity of the analysis and the interpretation of the findings. To examine DBH associations with live trees, dead trees and both combined with attacked and not attacked trees by the different insects, we used DBH classes and tested associations using cross-tabulations and Fisher's exact test.

Results

For all fires, significant differences were observed for all variables measured between live and dead trees except for CSH and BSH in CO (Table 1). Of the insects monitored in the study over

Table 1 Means (SEM) for diameter at breast height (DBH), total tree height (THT), pre-fire live crown ratio (LCR), crown scorch volume (CSV), crown consumption volume (CCV), total crown damage (TCD = CSV + CCV), basal circumference scorch (BSC), height to first live branch (LBH), crown scorch height (CSH), crown consumption height (CCH), maximum bole scorch height (BSH) and minimum bole scorch height (BSL) for live and dead trees for fires in Colorado, Montana, Arizona and the Black Hills at the time of initial measurements, 2001–2002

	Colorado		Montana		Arizona		Black Hills	
Variable	Live ($n = 567$)	Dead ($n = 376$)	Live ($n = 885$)	Dead ($n = 749$)	Live ($n = 939$)	Dead ($n = 318$)	Live ($n = 812$)	Dead ($n = 432$)
DBH (cm)	21.6 (0.4)*	10.2 (0.3)	20.3 (0.4)*	11.0 (0.2)	25.8 (0.4)*	19.3 (0.5)	25.5 (0.2)*	21.9 (0.3)
THT (m)	10.8 (0.2)*	6.6 (0.1)	12.6 (0.2)*	8.0 (0.1)	12.9 (0.1)*	10.8 (0.2)	14.9 (0.1)*	14.8 (0.2)
LCR (%)	66.3 (0.7)*	60.1 (0.9)	64.1 (0.6)*	57.1 (0.7)	59.6 (0.5)*	56.3 (0.9)	63.4 (0.4)*	55.4 (0.7)
CSV (%)	44.4 (1.2)*	79.4 (1.8)	31.4 (1.1)*	82.0 (1.3)	39.8 (1.1)*	63.4 (2.5)	43.2 (1.0)*	60.7 (2.1)
CCV (%)	1.5 (0.3)*	19.7 (1.8)	0.4 (0.1)*	17.9 (1.3)	1.0 (0.3)*	35.2 (2.5)	0.2 (0.1)*	35.7 (2.1)
TCD (%)	45.9 (1.2)*	99.1 (0.3)	31.9 (1.1)*	99.6 (0.2)	40.8 (1.1)*	97.8 (0.6)	43.4 (1.0)*	96.6 (0.6)
BCS %	94.3 (0.7)*	99.7 (0.1)	92.7 (0.6)*	99.2 (0.2)	90.0 (0.8)*	99.5 (0.3)	95.3 (0.5)*	99.8 (0.1)
LBH (m)	3.6 (0.1)*	2.6 (0.09)	4.8 (0.1)*	3.4 (0.1)	5.2 (0.1)*	4.7 (0.1)	5.5 (0.1)*	6.6 (0.1)
CSH (m)	5.6 (0.1)	5.7 (0.2)	6.2 (0.2)*	6.8 (0.2)	6.7 (0.2)*	7.3 (0.3)	9.1 (0.1)*	11.6 (0.3)
CCH (m)	0.4 (0.1)*	1.7 (0.2)	0.2 (0.04)*	2.0 (0.2)	0.2 (0.05)*	4.5 (0.3)	0.6 (0.1)*	5.6 (0.3)
BSH (m)	4.0 (0.1)	4.0 (0.1)	3.0 (0.1)*	5.3 (0.2)	4.3 (0.1)*	8.9 (0.2)	4.1 (0.1)*	11.0 (0.2)
BSL (m)	1.0 (0.1)*	2.3 (0.1)	0.8 (0.05)*	3.4 (0.2)	1.6 (0.1)*	6.9 (0.3)	1.4 (0.1)*	8.3 (0.3)

Asterisks indicate significant differences between live and dead trees within fires, Wilcoxon rank sum test at $P < 0.05$.

Table 2 Influence of fire (Cochran–Mantel–Haenszle) and year (Breslow–Day) on pairwise insect associations and insect with status association for fires in Colorado, Montana, Arizona and the Black Hills 3 years post-fire, 2001–2003

	Cochran–Mantel–Haenszle			Breslow–Day		
Pairwise association	Value	d.f.	*P*	Chi-squared	d.f.	*P*
RTB versus *Ips*	160.1	1	<0.0001	17.3	3	0.0006
RTB versus WB	121.9	1	<0.0001	48.8	3	<0.0001
Ips versus WB	531.4	1	<0.0001	33.5	3	<0.0001
Ips versus Status	543.0	1	<0.0001	54.2	3	<0.0001
RTB versus Status	21.5	1	<0.0001	156.5	3	<0.0001
WB versus Status	2033.9	1	<0.0001	157.0	3	<0.0001

RTB, red turpentine beetle; WB, wood borer.

the 3 years post-fire, three of them were prevalent in all fires: *Ips* beetles, RTB and WBs. The most common *Ips* in CO, MT and the BH was *Ips pini* (Say), whereas, in AZ, a guild of pine engravers included *Ips lecontei* Swaine, *Ips pini*, *Ips calligraphus* (Germar), *Ips latidens (=Orthotomicus latidens)* (LeConte), *Ips knausi* Swaine and *Ips integer* (Eichhoff). Hereafter, for simplicity, we refer to the guild of *Ips* spp. simply as *Ips* unless referring to a particular species. Wood borers were not identified to species, although the most common ones in the study sites include various species of *Monochamus* and *Acanthocinus*. Western pine beetle was found in AZ, where 56 dead trees and 8 live trees exhibiting fire injury had been infested, and in one dead tree in MT. Fire sites in CO and the BH are outside the geographical distribution of WPB. Mortality caused by WPB has been reported in fire-injured trees in the past (Miller & Patterson, 1927; Miller & Keen, 1960; Fettig *et al.*, 2008; Davis *et al.*, 2012). Mountain pine beetle was observed in 7 live and 12 dead trees in CO, in 1 live and 1 dead tree in AZ, and in 7 live and 13 dead trees in the BH. No further analysis was conducted with these insects as a result of their infrequent occurrence.

Few trees sampled in the study exhibited no fire injury. In CO, one live tree and no dead trees lacked fire injury and the live tree had no insect attack. In MT, nine live trees had no fire injury and no insect attacks; all dead trees had fire injury. In AZ, 26 live trees had no fire damage and no insect attacks and 1 dead tree with no fire injury had WB attacks. In the BH, there were no trees without fire injury.

The Cochran–Mantel–Haenszle and the Breslow–Day tests were significant for all insect pairwise combinations, as well as insect with tree status, indicating the influence of sampling year and fire location (Table 2). This was related to the difference in the abundance of the different insects across years and fires (Table 3). Three years post-fire, a higher percentage of *Ips* beetles-attacked trees occurred in MT and the BH. Red turpentine beetle attacked a higher percentage of trees in the BH and the percentage of trees attacked by WBs was higher in CO. New attacks of *Ips* beetles increased substantially in MT from 2001 to 2002.

Variables associated with insect attack

Logistic regression analysis indicated that the probability of attack by *Ips* beetles could be estimated with the BSH variable in all four fires and across all fires combined, with concordance index (CI) values ranging from 0.58 to 0.72 (Table 4). For RTB, logistic regression models identified combinations of DBH, BSH

Table 3 Attacks per year (2001–2003), total attacks by 2003 and percentage of fire-injured trees attacked by *Ips* spp. beetles, *Dendroctonus valens* (RTB) and wood borers (WB) to *Pinus ponderosa* in fires in Colorado ($n = 943$), Montana ($n = 1630$), Arizona ($n = 1257$) and the Black Hills ($n = 1244$) (sampling in the Black Hills started in 2002), 2001–2003

Wildfire	*Ips* in 2001	New *Ips* in 2002	New *Ips* in 2003	Total *Ips* attacks	Percentage of trees attacked
Colorado	1	42	53	96	10.2
Montana	103	257	33	393	24.1
Arizona	0	54	26	80	6.4
Black Hills	NS	289	36	325	26.1
Wildfire	RTB in 2001	New RTB in 2002	New RTB in 2003	Total RTB attacks	Percentage of trees attacked
Colorado	36	66	38	140	14.8
Montana	21	48	20	89	5.4
Arizona	119	65	15	199	15.8
Black Hills	NS	242	116	358	28.8
Wildfire	WB in 2001	New WB in 2002	New WB in 2003	Total WB attacks	Percentage of trees attacked
Colorado	272	303	117	692	73.4
Montana	222	434	112	768	47.0
Arizona	411	119	91	621	49.4
Black Hills	NS	501	177	678	54.5

NS, not sampled.

and CSH as variables for estimating its presence, with CI values ranging from 0.67 to 0.81. For WB presence in dead trees, the logistic model identified DBH as the best variable in CO, MT, BH and across all fires, whereas, in AZ, BSH was the selected predictor variable. For these models, CI values ranged from 0.57 to 0.78 (Table 4).

An examination of the logistic model for trees attacked by *Ips* beetles portrays an increasing estimated probability of attack with increasing BSH for all fires and across all fires (Fig. 1). The response curves for MT and BH estimate higher probability levels than for CO and AZ. The range of BSH values was 0–15 m for CO, 0–19 m for AZ, and 0–24 m for MT and the BH. For RTB in CO, the response also shows an increase in estimated probability of attack for trees as DBH and BSH increase (Fig. 2). The estimated probability of RTB attack also increased in MT, AZ and the BH with increasing DBH, BSH and CSH, respectively, and also as CSH increases across all fires. The range of DBH for CO and MT was from 5 to 61 cm. The range of CSH for the BH was from 0 to 25 m. For WBs, the estimated probability of attack on dead trees increased with increasing DBH for CO, MT and BH, and across all fires, and there was also an increase in the estimated probability of WB attack with increasing BSH in AZ. The range in DBH for the BH was from 5 to 51 cm (Fig. 3).

Association between insects and insects with tree status 3 years post-fire

Examination of the occurrence of insect pair combinations in live and dead trees combined, independent of fire injury levels, indicated that the proportion of trees attacked by *Ips* was higher on trees that had attacks by RTB (Table 5) or by WBs in all fires 3 years post-fire. The proportion of trees attacked by WBs was also higher in trees with RTB attacks; for CO, the relationship was significant at the $P < 0.1$. Examination of insect attacks in live or dead trees indicated that the proportion of *Ips* beetle-attacked trees and WB-attacked trees was higher on dead trees compared with live trees in all fires (Table 6). The proportion of trees attacked by RTB was higher on live trees in CO and MT (at the 0.09 level) but higher in dead trees in AZ, with no differences in the BH.

Association between infested trees and tree diameter classes

The proportion of trees attacked by *Ips* was higher in trees with <32 cm DBH for all trees and dead trees in CO and MT; for trees in the 17–32 cm DBH class for all trees in AZ; and in the 17–32 cm class of dead trees in the BH (Table 7). The proportion of trees attacked by RTB was higher in trees <32 cm for all trees and dead trees in CO; for all trees, live trees and dead trees in MT; and in the 17–32 cm DBH class for all trees, live trees and dead trees in AZ and the BH (Table 8). The proportion of trees attacked by WBs was higher in the two smaller DBH classes for all trees and in the 17–32 cm live trees DBH class for CO; for all trees, live trees and dead trees <32 cm in MT; for all trees and live trees in the <32 cm DBH class for AZ; and for all trees, live tress and dead trees in the 17–32 DBH class in BH (Table 9).

Discussion

The most abundant insects that we observed were RTB, *Ips* beetles and WBs, all known to commonly utilize fire-injured trees, and their incidence was variable across fires and years. Types of fire-related injury associated with insect attacks included primarily BSH, CSH or tree DBH. The range of CIs for the logistic regressions suggest that the models should be used as general guidance and caution should be taken if used for estimating specific probabilities of individual cases. The response of

Table 4 Logistic regression parameters for estimating the probability of attack by *Ips* spp beetles, *Dendroctonus valens* and wood borers in fire-injured *Pinus ponderosa* at four different fires and all fires combined with concordance index (CI), 2001–2003

Insect and Location	Predictor	Estimate	SE	Wald χ^2	*P*	CI
***Ips* spp.**						
CO	Intercept	−2.5721	0.2049	157.6	<0.00001	0.58
	BSH	0.0916	0.0381	5.8	0.02	
MT	Intercept	−1.8983	0.0942	405.9	<0.0001	0.64
	BSH	0.1648	0.0150	121.4	<0.0001	
AZ	Intercept	−3.4451	0.2228	239.2	<0.0001	0.65
	BSH	0.1209	0.0263	21.9	<0.0001	
BH	Intercept	−2.0010	0.1224	267.0	<0.0001	0.72
	BSH	0.1348	0.0134	101.4	<0.0001	
All	Intercept	−2.2981	0.0641	1286.0	<0.0001	0.65
	BSH	0.1330	0.0082	263.6	<0.0001	
Dendroctonus valens						
CO	Intercept	−3.3831	0.2390	200.4	<0.0001	0.73
	DBH	0.0444	0.0084	27.8	<0.0001	
	BSH	0.1717	0.0346	24.7	<0.0001	
MT	Intercept	−4.1936	0.2350	317.3	<0.0001	0.78
	DBH	0.0680	0.0088	60.0	<0.0001	
AZ	Intercept	−3.6118	0.1958	340.2	<0.0001	0.81
	BSH	0.2839	0.0217	170.7	<0.0001	
BH	Intercept	−2.2865	0.1706	179.6	<0.0001	0.67
	CSH	0.1492	0.0139	85.9	<0.0001	
All	Intercept	−2.9779	0.0895	1107.8	<0.0001	0.72
	CSH	0.1507	0.008	327.0	<0.0001	
Wood borers						
CO	Intercept	1.6994	0.3811	19.8861	<0.0001	0.70
	DBH	0.0748	0.0329	5.1540	<0.0.0232	
MT	Intercept	−1.1686	0.1807	41.8196	<0.0001	0.77
	DBH	0.1615	0.0168	92.0843	<0.0001	
AZ	Intercept	2.4574	0.4891	25.2470	<0.0001	0.69
	BSH	0.1655	0.0752	4.8412	<0.0278	
BH	Intercept	1.2109	0.7657	2.5011	0.1138	0.57
	DBH	0.0929	0.0372	6.2495	<0.0124	
All	Intercept	−0.3948	0.1275	9.6	<0.0020	0.78
	DBH	0.1547	0.0106	213.8	<0.0001	

BSH, bole scorch height (m); DBH, diameter at breast height (cm); CSH, crown scorch height (m). CO, Colorado; MT, Montana; AZ, Arizona; BH, Black Hills of South Dakota.

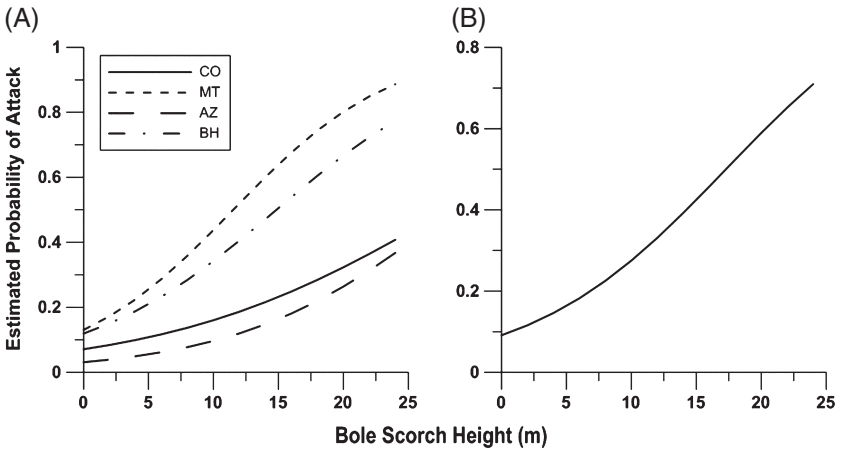

Figure 1 Logistic model response for estimating probability of attack by *Ips* spp. to *Pinus ponderosa* in (A) four fires and (B) across all fires based on bole scorch height (m), 2001–2003. CO, Colorado; MT, Montana; AZ, Arizona; BH, Black Hills of South Dakota.

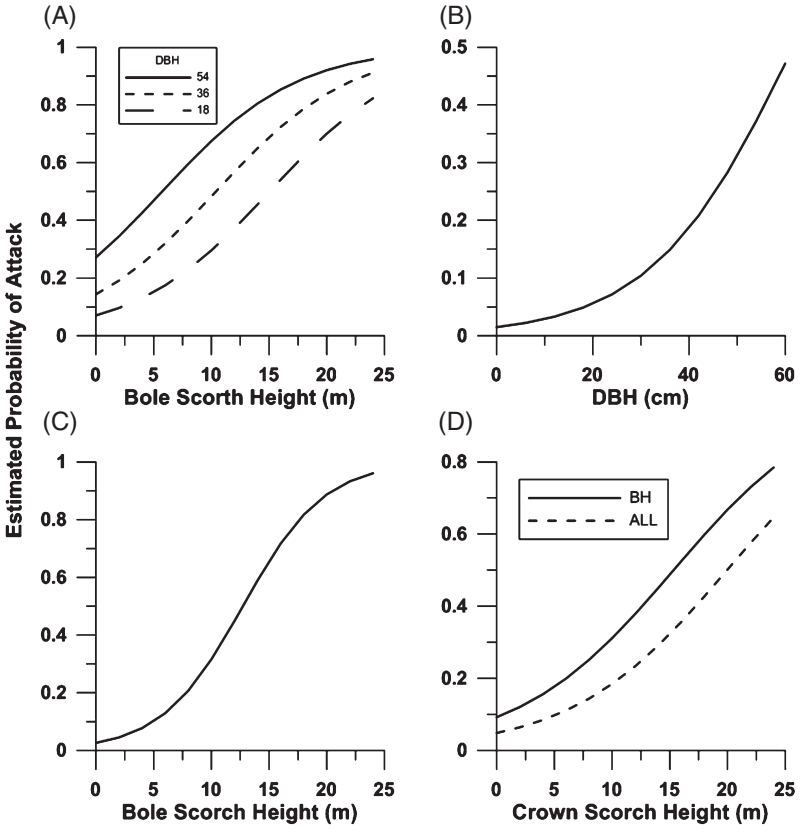

Figure 2 Logistic model response for estimating probability of attack by *Dendroctonus valens* to *Pinus ponderosa* in four fires based on (A) bole scorch height (m) and diameter at breast height (DBH) (cm) for a fire in Colorado; (B) based on DBH for a fire in Montana; (C) based on bole scorch height for a fire in Arizona; and (D) based on crown scorch height (m) for a fire in the Black Hills and across all fires, 2001–2003. BH, Black Hills of South Dakota.

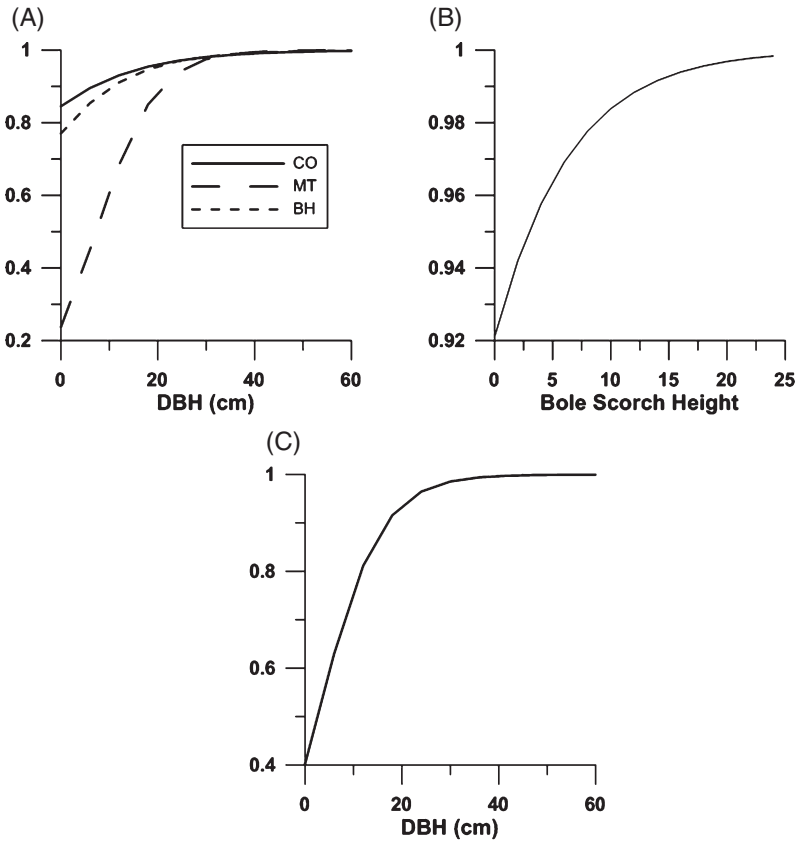

Figure 3 Logistic model response for estimating probability of attack by wood borers to dead *Pinus ponderosa* based on: (A) diameter at breast height (DBH) (cm) for fires in Colorado, Montana, and the Black Hills; (B) on bole scorch height (m) for a fire in Arizona; and (C) on DBH across all fires, 2001–2003. CO, Colorado; MT, Montana; BH, Black Hills of South Dakota.

Table 5 Number (percentage attacked) of trees with co-occurring *Dendroctonus valens* (RTB) with *Ips* spp., *Ips* spp. beetles with wood borers (WB) and *Dendroctonus valens* with wood borers in attacked and not attacked *Pinus ponderosa* in wildfires in Colorado, Montana, Arizona and the Black Hills, 2001–2003 (Fisher's exact test was conducted using the count data but percentages are presented for ease of interpretation)

		Ips 2003		
Wildfire	RTB 2003	No attack	Attack	*P*
Colorado	No attack	735	68	
	Attack	112 (13.2%)	28 (29.2%)	<0.0001
Montana	No attack	1206	339	
	Attack	35 (2.8%)	54 (13.7%)	<0.0001
Arizona	No attack	1007	51	
	Attack	170 (14.4%)	29 (36.3%)	<0.0001
Black Hills	No attack	681	205	
	Attack	238 (26.0%)	120 (36.9%)	<0.0001
		WB 2003		
Wildfire	*Ips* 2003	No attack	Attack	*P*
Colorado	No attack	242	605	
	Attack	9 (3.6%)	87 (12.6%)	<0.0001
Montana	No attack	778	463	
	Attack	88 (10.2%)	305 (39.7%)	<0.0001
Arizona	No attack	630	547	
	Attack	6 (0.01%)	74 (11.9%)	<0.0001
Black Hills	No attack	547	372	
	Attack	19 (3.3%)	306 (45.1%)	<0.0001
		WB 2003		
Wildfire	RTB 2003	No attack	Attack	*P*
Colorado	No attack	222	581	
	Attack	29 (11.6)	111 (16.0%)	<0.1
Montana	No attack	839	706	
	Attack	27 (3.1%)	62 (8.1%)	<0.0001
Arizona	No attack	608	450	
	Attack	28 (4.4%)	171 (27.5%)	<0.0001
Black Hills	No attack	437	449	
	Attack	129 (22.8%)	165 (33.8%)	<0.0001

insect populations to post-fire availability of trees with sublethal fire injury exhibits variability, from modest or no increases in insect-caused mortality (Schwilk *et al.*, 2006; Youngblood *et al.*, 2009; Davis *et al.*, 2012; Powell *et al.*, 2012; Jenkins *et al.*, 2014), to moderate levels (McHugh *et al.*, 2003; Breece *et al.*, 2008), and to higher levels of impact (Bradley & Tueller, 2001; Fettig *et al.*, 2008). If tree mortality is caused by insects, this can result from a single species or by various species utilizing the same tree as a host. Examinations of these interactions necessitate the presence of insect populations that can benefit from an abundance of fire-injured trees (McHugh *et al.*, 2003). Referring to the many factors that influence studies examining post-fire tree injury and insect infestations, Powell *et al.* (2012) provided an elegant summary, stating that 'results suggest that beetle responses to fire are complex and that entry behavior, reproductive success, and stand-level population density all need be considered to evaluate these interactions'. In addition, the size and proximity of insect populations to burned stands and host species will also affect infestation levels and patterns in burned stands. These factors, however, exhibit high variability among studies or are difficult to assess, or both, adding to the complexity of examining insect attacks in burned trees and often making comparisons among studies difficult.

Ips beetles

In the present study, BSH was the best predictor variable identified in the logistic modelling for all fires and across all fires for estimating the probability of the presence of *Ips*. These results are consistent with the work of Bradley & Tueller (2001) who estimated the likelihood of *Ips* beetle attacks to Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) after prescribed burning using a logistic regression that included bole char height (similar to our BSH) among the best variables. Ganz *et al.* (2003) examined the susceptibility of attack by RTB and *I. pini* to ponderosa and Jeffrey pine after prescribed burns in California, and concluded that percentage live crown and bark char injury were good predictors of tree mortality from fire injury and subsequent attacks by these species. Bole blackening or charring is considered an indication of cambium damage (McHugh & Kolb, 2003; Fowler & Sieg, 2004; Thies *et al.*, 2006). Trees with cambium injury would be weakened and stressed, making them candidates for *Ips* beetle attack.

The presence of *Ips* beetles was associated with presence of RTB in all fires in the present study. Although these species often occur together, scant data are available quantifying their joint occurrence. Ganz *et al.* (2003) indicated that the year

Table 6 Number (percentage of attacked) of *Ips* spp.-attacked, *Dendroctonus valens* (RTB)-attacked and wood borer (WB)-attacked and not attacked in live and dead *Pinus ponderosa* in wildfires in Colorado, Montana, Arizona and the Black Hills, 2001–2003 (Fisher's exact test was conducted using the count data but percentages are presented for ease of interpretation)

		Status		
Wildfire	*Ips* 2003	Live	Dead	*P*
Colorado	No attack	329	518	
	Attack	16 (4.6%)	80 (13.4%)	<0.0001
Montana	No attack	556	685	
	Attack	52 (8.5%)	341 (33.2%)	<0.0001
Arizona	No attack	792	385	
	Attack	4 (0.05%)	76 (16.5%)	<0.0001
Black Hills	No attack	620	299	
	Attack	28 (4.3%)	297 (49.8%)	<0.0001
		Status		
Wildfire	RTB 2003	Live	Dead	*P*
Colorado	No attack	277	526	
	Attack	68 (19.7%)	72 (12.0%)	<0.002
Montana	No attack	567	978	
	Attack	41 (6.7%)	48 (4.7%)	0.09
Arizona	No attack	751	307	
	Attack	45 (5.7%)	154 (33.4%)	<0.0001
Black Hills	No attack	462	424	
	Attack	186 (28.7%)	172 (28.9%)	1.0
		Status		
Wildfire	WB 2003	Live	Dead	*P*
Colorado	No attack	208	43	
	Attack	137 (39.7%)	555 (92.8%)	<0.0001
Montana	No attack	504	362	
	Attack	104 (17.1%)	664 (64.7%)	<0.0001
Arizona	No attack	623	13	
	Attack	173 (21.7%)	448 (97.2%)	<0.0001
Black Hills	No attack	542	24	
	Attack	106 (16.4%)	572 (96.0)	<0.0001

after an autmn prescribed burn, 59% of trees attacked by RTB were also attacked by *Ips*, which is consistent with our findings.

Ips beetles were associated with dead trees in all fires, which is consistent with available literature. For example, Fettig *et al.* (2008), working with prescribed burns, reported an increase in *Ips*-caused tree mortality in burned plots. The response of *Ips* was limited to the first 2 years after prescribed burns (Fettig & McKelvey, 2014). Consistent with that study, we observed an increase in the number of trees attacked by *Ips* beetles the second year of sampling in CO, MT and AZ (Table 3) (the BH fire was first sampled 2 years after the fire). McHugh *et al.* (2003) examined bark beetle attacks on two prescribed fires and one wildfire in AZ and developed logistic models to estimate the probability of tree survival based on crown damage and combined attacks of *Ips* and *Dendroctonus* beetles. Although *Ips* populations were low in their study, McHugh *et al.* (2003) concluded that the combined attacks of *Ips* and *Dendroctonus* beetles are important in killing ponderosa pines with moderate to heavy crown damage (>50%), whereas the attack of live trees may be limited to those declining in health from sublethal fire injury.

In all of our study sites, *Ips* attacks occurred primarily in trees <35 cm DBH, although mortality was less in the 5-cm DBH class except in AZ. Most commonly, *Ips* beetles utilize smaller trees <20 cm and the tops of larger diameter trees (Kegley *et al.*, 1997). Some larger trees may have been attacked in their tops where we were not able to sample. *Ips* beetles are frequently associated with weakened trees by factors such as drought, slash residues after logging operations, trees attacked previously by other insects, and windthrown and burned trees (Kegley *et al.*, 1997; Steed & Wagner, 2004; Negrón *et al.*, 2009). Consistent with our findings, Fettig *et al.* (2008, 2010b), indicated that most *Ips* killed trees were <15 cm DBH with no trees >35 cm being killed. Previous studies have also portrayed an inverse relationship between tree size and infestation in ponderosa pine with no fire injury (Kolb *et al.*, 2006; Negrón *et al.*, 2009).

Ponderosa pine is a fire-adapted species less susceptible to fire injury as the tree matures because of thick bark (Wyant *et al.*, 1986). Younger or smaller tress do not have such protection, which may explain why smaller trees are more prone to fire injury and therefore more susceptible to *Ips* beetles attacks. For the most part, our data indicate that trees with *Ips* beetles attacks

Table 7 Number (percentage) of all trees, live trees and dead trees attacked and not attacked by *Ips* spp. beetles per diameter classes (cm) in fires in Colorado, Montana, Arizona and the Black Hills, 2001–2003 (Fisher's exact test)

Colorado	DBH Class	All trees Attacked	$P < 0.0007$ Not attacked	Live trees Attacked	$P = 0.5259$ Not attacked	Dead trees Attacked	$P < 0.0001$ Not attacked
	5.1–17.5	42 (4.5)	547 (58.0)	6 (1.7)	96 (27.8)	36 (6.0)	451 (75.4)
	17.6–32.5	43 (4.6)	230 (24.4)	6 (1.7)	168 (48.7)	37 (6.2)	62 (10.4)
	32.6–47.5	9 (1.0)	56 (5.9)	3 (0.9)	51 (14.8)	6 (1.0)	5 (0.8)
	47.6+	2 (0.2)	14 (1.5)	1 (0.3)	14 (4.1)	1 (0.2)	0 (0.0)
Montana	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P = 0.2129$ Not attacked	Dead trees Attacked	$P < 0.0001$ Not attacked
	5.1–17.5	220 (13.5)	873 (53.4)	17 (2.8)	223 (36.7)	203 (19.8)	650 (63.4)
	17.6–32.5	134 (8.2)	268 (16.4)	24 (4.0)	236 (38.8)	110 (10.7)	32 (3.1)
	32.6–47.5	34 (2.1)	90 (5.5)	8 (1.3)	87 (14.3)	26 (2.5)	3 (0.3)
	47.6+	5 (0.3)	10 (0.6)	3 (0.5)	10 (1.6)	2 (0.2)	0 (0.0)
Arizona	DBH Class	All trees Attacked	$P < 0.0162$ Not attacked	Live trees Attacked	$P = 1.0$ Not attacked	Dead trees Attacked	$P = 0.8842$ Not attacked
	5.1–17.5	34 (2.7)	318 (25.3)	1 (0.1)	153 (19.3)	33 (7.2)	165 (35.8)
	17.6–32.5	38 (3.0)	620 (49.4)	2 (0.3)	432 (54.4)	36 (7.8)	188 (40.8)
	32.6–47.5	7 (0.6)	205 (16.3)	1 (0.1)	176 (22.2)	6 (1.3)	29 (6.3)
	47.6+	1 (0.1)	32 (2.6)	0 (0.0)	29 (3.7)	1 (0.2)	3 (0.7)
Black Hills	DBH Class	All trees Attacked	$P = 0.3017$ Not attacked	Live trees Attacked	$P = 0.2124$ Not attacked	Dead trees Attacked	$P < 0.0111$ Not attacked
	5.1–17.5	35 (2.8)	85 (6.8)	0 (0.0)	23 (3.6)	35 (5.9)	62 (10.4)
	17.6–32.5	273 (22.0)	763 (61.4)	28 (4.3)	540 (83.6)	245 (41.1)	223 (37.4)
	32.6–47.5	17 (1.4)	69 (5.6)	0 (0.0)	55 (8.5)	17 (2.3)	14 (2.4)

are certain to succumb whether from the delayed effects of fire injury or the activity of the beetles.

Red turpentine beetle

The logistic regression model for RTB attacks, similar to *Ips* beetles, identified BSH as a good predictor of its presence in CO and AZ, and was the second most important variable in MT, suggesting attraction to trees with cambium injury. CSH, identified for the BH, is also indicative of trees exhibiting increased stress. Bradley & Tueller (2001) examined attacks of RTB in burned and unburned plots in Lake Tahoe and, from a logistic regression analysis, indicated that the best models for estimating the probability of attack included crown scorch percent, bole char, bole char height squared, DBH and a soil burn index, with bole char height being the second most important. Our findings are consistent with those of Bradley & Tueller (2001) because our models identified variables included in their models (CSH and BSH) as factors having a positive relationship with the likelihood of attack.

The presence of RTB was associated with the presence of *Ips* in all fires and with live trees in CO and AZ. Red turpentine beetle can also invade trees in conjunction with other bark beetles (Herman, 1954; Wagener, 1961; Ganz *et al.*, 2003; Parker *et al.*, 2006; Fettig *et al.*, 2008; Fettig *et al.*, 2010a; Fettig *et al.*, 2010b). The occurrence of RTB in trees after prescribed or wildfires is well documented, although the insect is usually not considered as a mortality agent on its own (Herman, 1954; Wagener, 1961; Fischer, 1980; Parker *et al.*, 2006). Fettig *et al.* (2008, 2010a,b) reported increased attacks by RTB to ponderosa and Jeffrey pine after prescribed burns in California but did not attribute any mortality to the insect and, instead, attributed tree mortality to fire effects or to attacks of other bark beetles. McHugh *et al.* (2003) indicated that RTB was the most abundant *Dendroctonus* in their study and second only to WBs as a group. The insect was significantly associated with live trees compared with dead trees in the autumn and summer fires, although no differences were observed during the spring fire. It was concluded that their autumn and summer results are consistent with other studies that have not attributed mortality to RTB and that the insect is often found in live trees. However, their spring fire results may suggest that the insect is interacting with other beetles in causing tree mortality. Ganz *et al.* (2003) also did not attribute tree mortality to RTB attacks but suggested that, in combination with *Ips*, it caused extensive mortality. Interestingly, Youngblood *et al.* (2009) attributed tree mortality to RTB in burned plots, as well as burned and thining plots, in trees exhibiting fire damage. It is difficult to separate the role of each insect in tree killing when various insects attack trees; however, our data, consistent with the plurality of previous studies, suggest that RTB is often associated with live trees, although the relationship exhibits variability.

In the present study, RTB attacked trees in all diameter classes but with more trees than expected in the larger diameter classes. Red turpentine beetle attacks in all diameter classes have been reported (McHugh *et al.*, 2003; Schwilk *et al.*, 2006; Fettig *et al.*,

Table 8 Number (percentage) of all trees, live trees and dead trees attacked and not attacked by *Dendroctonus valens* per diameter classes (cm) in fires in Colorado, Montana, Arizona and the Black Hills, 2001–2003 (Fisher's exact test)

Colorado	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P = 0.7607$ Not attacked	Dead trees Attacked	$P < 0.0001$ Not attacked
	5.1–17.5	49 (5.2)	540 (57.3)	17 (4.9)	85 (24.6)	32 (5.4)	455 (76.1)
	17.6–32.5	70 (7.4)	203 (21.5)	38 (11.0)	136 (39.4)	32 (5.4)	67 (11.2)
	32.6–47.5	17 (1.8)	48 (5.1)	10 (2.9)	44 (12.8)	7 (1.2)	4 (0.7)
	47.6+	4 (0.4)	12 (1.3)	3 (0.9)	12 (3.5)	1 (0.2)	0 (0.0)
Montana	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P < 0.0083$ Not attacked	Dead trees Attacked	$P < 0.0001$ Not attacked
	5.1–17.5	22 (1.4)	1071 (65.5)	7 (1.2)	233 (38.3)	15 (1.5)	838 (81.7)
	17.6–32.5	51 (3.1)	351 (21.5)	22 (3.6)	238 (39.1)	29 (2.8)	113 (11.0)
	32.6–47.5	15 (0.9)	109 (6.7)	11 (1.8)	84 (13.8)	4 (0.4)	25 (2.4)
	47.6+	1 (0.1)	14 (0.9)	1 (0.2)	12 (2.0)	0 (0.0)	2 (0.2)
Arizona	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P < 0.0009$ Not attacked	Dead trees Attacked	$P < 0.0001$ Not attacked
	5.1–17.5	30 (2.4)	322 (25.7)	2 (0.3)	152 (19.1)	28 (6.1)	170 (36.7)
	17.6–32.5	125 (10.0)	533 (42.5)	25 (3.2)	409 (51.5)	100 (21.7)	124 (26.9)
	32.6–47.5	36 (2.9)	176 (14.0)	12 (1.5)	165 (20.8)	24 (5.2)	11 (2.4)
	47.6+	8 (0.6)	25 (2.0)	6 (0.8)	23 (2.9)	2 (0.4)	2 (0.4)
Black Hills	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P < 0.0083$ Not attacked	Dead trees Attacked	$P < 0.0001$ Not attacked
	5.1–17.5	6 (0.5)	114 (9.2)	1 (0.2)	22 (3.4)	5 (0.8)	92 (15.4)
	17.6–32.5	313 (25.2)	723 (58.2)	165 (25.5)	403 (62.4)	148 (24.8)	320 (53.7)
	32.6–47.5	39 (3.1)	47 (3.8)	20 (3.1)	35 (5.4)	19 (3.2)	12 (2.0)

2010b). This is consistent with the present study, except that we observed more trees in the 20–25 cm DBH range in the BH, and not the larger trees. Models presented by Bradley & Tueller indicated a preference for smaller diameters in contrast to our findings. We observed an increase in the estimated probability of attack with increasing DBH. The contrast on this topic with Bradley & Tueller (2001) is interesting. Reproduction of *Dendroctonus* bark beetles requires killing of the tree or at least the portion of the tree infested (Raffa & Berryman, 1983), which, in the case of RTB, would be the portion of the base of the tree colonized. Paine *et al.* (1997) describe RTB as a near obligate parasite that does not usually kill the host, consistent with our findings and the literature. Red turpentine beetle is the largest species of *Dendroctonus* in North America (Wood, 1982); therefore, the size of beetles and a requirement for sufficient phloem to be able to develop successfully would suggest the need for larger trees as hosts.

Wood borers

Logistic regression models indicated DBH as the best variable for estimating likelihood of presence of WBs in dead trees in CO, MT and the BH. The utilization of larger diameter trees by WBs has been documented in various studies (Rose, 1957; Saint-Germain *et al.*, 2004a; Saint-Germain *et al.*, 2004b). This may be a function of thicker bark providing a better niche for oviposition and larval development (Saint-Germain *et al.*, 2004b). Bole Scorch Height identified in AZ may be a function of declining tree vigor or mortality. Although the logistic models for three fires and the model across all fires indicated an increased likelihood of attack with increasing DBH, WB attacks occurred primarily in trees <30 cm DBH in all of our study sites. As with *Ips* beetles, it should be noted that some larger trees were likely attacked higher in the bole where we were not able to sample.

Wood borers have consistently been associated with dead or dying trees (Coulson & Witter, 1984; Barbosa & Wagner, 1988; DeNitto *et al.*, 2000; Saint-Germain *et al.*, 2004a; Parker *et al.*, 2006) and specifically in ponderosa pine (Stevens *et al.*, 1982). It has been demonstrated that some WBs are attracted to fire (Evans, 1966), smoke (Wickman, 1964) and fire-injured trees (Rasmussen *et al.*, 1996), although how much mortality may be directly attributed to these insects in conifers is not well understood (Rasmussen *et al.*, 1996; Fettig *et al.*, 2008).

In agreement with previous studies, WBs, were associated with the presence of both *Ips* and RTB in all fires (Parker *et al.*, 2006; Costello *et al.*, 2011; Costello *et al.*, 2013) and with dead trees (Coulson & Witter, 1984; Barbosa & Wagner, 1988; DeNitto *et al.*, 2000; Saint-Germain *et al.*, 2004a; Parker *et al.*, 2006). Whether wood borers can cause tree mortality on their own is not well understood. McHugh *et al.* (2003) indicated that WB attacks in live trees were primarily in dead portions of the cambium and did not consider them as a source of tree mortality. Fettig *et al.* (2008) reported that 39% of trees infested with WBs in burned plots did not exhibit attacks by primary bark beetles and attributed mortality to WBs; however, this was not the case in another study (Fettig *et al.*, 2010a).

Table 9 Number (percentage) of all trees, live trees and dead trees attacked and not attacked by wood borers (WB) per diameter classes (cm) in fires in Colorado, Montana, Arizona and the Black Hills, 2001–2003 (Fisher's exact test)

Colorado	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P < 0.0001$ Not attacked	Dead trees Attacked	$P = 0.8075$ Not attacked
	5.1–17.5	505 (53.5)	84 (8.9)	53 (15.4)	49 (14.2)	452 (75.6)	35 (5.9)
	17.6–32.5	164 (17.4)	109 (11.6)	72 (20.9)	102 (29.6)	92 (15.4)	7 (1.2)
	32.6–47.5	19 (2.0)	46 (4.9)	9 (2.6)	45 (13.0)	10 (1.7)	1 (0.2)
	47.6+	4 (0.4)	12 (1.3)	3 (0.9)	12 (3.5)	1 (0.2)	0 (0.0)
Montana	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P < 0.0113$ Not attacked	Dead trees Attacked	$P < 0.0001$ Not attacked
	5.1–17.5	567 (34.7)	526 (32.2)	54 (8.9)	186 (30.6)	513 (50.0)	340 (33.1)
	17.6–32.5	165 (10.1)	237 (14.5)	40 (6.6)	220 (36.2)	125 (12.2)	17 (1.7)
	32.6–47.5	32 (2.0)	92 (5.6)	8 (1.3)	87 (14.3)	24 (2.3)	5 (0.5)
	47.6+	4 (0.2)	11 (0.7)	2 (0.3)	11 (1.8)	2 (0.2)	0 (0.0)
Arizona	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P < 0.0002$ Not attacked	Dead trees Attacked	$P < 0.9296$ Not attacked
	5.1–17.5	241 (19.2)	111 (8.8)	48 (6.1)	106 (13.4)	193 (41.9)	5 (1.1)
	17.6–32.5	314 (27.4)	344 (27.4)	97 (12.2)	337 (42.4)	217 (47.1)	7 (1.5)
	32.6–47.5	55 (4.4)	157 (12.5)	21 (2.6)	156 (19.7)	34 (7.4)	1 (0.2)
	47.6+	10 (0.8)	23 (1.8)	6 (0.8)	23 (2.9)	4 (0.9)	0 (0.0)
Black Hills	DBH Class	All trees Attacked	$P < 0.0001$ Not attacked	Live trees Attacked	$P < 0.0082$ Not attacked	Dead trees Attacked	$P < 0.0001$ Not attacked
	5.1–17.5	99 (8.0)	21 (1.7)	12 (1.9)	11 (1.7)	87 (14.6)	10 (1.7)
	17.6–32.5	541 (43.6)	495 (39.9)	86 (13.3)	482 (74.6)	455 (76.3)	13 (2.2)
	32.6–47.5	38 (3.1)	48 (3.9)	8 (1.2)	47 (7.3)	30 (5.0)	1 (0.2)

Conclusions

The topic of ponderosa pine mortality after either prescribed or wildland fire has received considerable attention with crown damage as a good predictor of tree mortality (McHugh & Kolb, 2003; Sieg *et al.*, 2006; Fowler *et al.*, 2010). Some general statements can be made after examining the variables that increase the likelihood of insect attack and the co-occurrence of common insects, as well as their preference of live or dead trees and the available literature. For example, a tree that is attacked by *Ips* beetles post-fire may have initially survived the fire, although our data suggest that its death can be considered imminent, especially if its DBH is <35 cm and exhibits significant blackening to the bole, which may suggest substantial phloem injury has occurred. From our data, trees with RTB attacks often survive and they span a wide range of diameter classes. However, as indicated above, trees with RTB attacks will likely succumb when *Ips* beetles are also present. Wood borers were associated with dead trees at all locations but attacks to live trees were also observed. Studies have ascribed tree mortality to WBs alone and attacks to live trees may be more prevalent than previously considered (Fettig *et al.*, 2008; Youngblood *et al.*, 2009; Costello *et al.*, 2011). This is a topic that needs clarification (Fettig *et al.*, 2008). The body of literature examining insect attacks or mortality, or both, to fire-injury trees suggests that increased insect populations and movement into green stands may or may not occur or may only last for a short time (<5 years) (Rasmussen *et al.*, 1996; Schwilk *et al.*, 2006; Breece *et al.*, 2008; Youngblood *et al.*, 2009; Davis *et al.*, 2012; Powell *et al.*, 2012; Fettig & McKelvey, 2014; Jenkins *et al.*, 2014) depending on many factors, such as the timing of the fire as it relates to insect life cycle and the ability of an existing insect population in the area able to exploit the resource and increase populations levels (McHugh & Kolb, 2003), amongst others. The present study and others have identified variables consistently associated with attacks of certain insects. Considering that many ponderosa pine forests are generally considered to be denser than historically (Cooper, 1960; Johnson, 1994; Fulé *et al.*, 1997; Kaufmann *et al.*, 2000), additional mortality caused by insects post-fire may be of benefit (Negrón *et al.*, 2009). However, when salvage is planned, or a concern for expanding insect population exists, evaluation of the level of fire-caused injury with targeted monitoring of insect populations may provide adequate information for planning purposes.

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