

Wildfire provides refuge from local extinction but is an unlikely driver of outbreaks by mountain pine beetle

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Abstract. Bark beetle outbreaks and wildfire are important disturbances in conifer ecosystems, yet their interactions are not well understood. We evaluated whether fire injury increased susceptibility of lodgepole pines (*Pinus contorta*) to mountain pine beetle (*Dendroctonus ponderosae* Hopkins), how it influenced beetle reproductive success, and whether beetle population phase altered this interaction. Eight sites that experienced wildfire and eight unburned sites were examined in the Greater Yellowstone Ecosystem (USA). Half were in areas where *D. ponderosae* was undergoing outbreaks, and half were in areas with low populations. We examined 2056 trees one year after fire for burn injury and beetle attack. We quantified beetle reproductive success in a random sample of 106 trees, and measured gallery areas of *D. ponderosae* and competing subcortical herbivores in 79 additional trees. Baited flight traps sampled stand-level populations of subcortical herbivores and predators.

Wildfire predisposed trees to *D. ponderosae* attack, but nonlinearly, with moderately injured trees being most preferred. This tree-level interaction was influenced by stand-level beetle population size, in that both healthy and fire-injured trees of all classes were attacked where populations were high, but no healthy trees, and only low and moderately injured trees were killed where populations were low. The number of adult brood produced per female was likewise curvilinear, being highest in moderately injured trees. This reflected an apparent trade-off, with high intraspecific competition arising from the large number of beetles needed to overcome defenses in healthy trees, vs. high interspecific competition and low substrate quality in more injured trees.

These results suggest that fire-injured trees can provide a reservoir for *D. ponderosae* during periods when populations are too low to overcome defenses of healthy trees, and might otherwise face localized extinction. However, the likelihood of populations increasing from endemic to outbreak levels in response to increased susceptibility is offset by the opposing constraints of lower substrate quality and higher competitor load in severely injured hosts, and the relative scarcity of moderately injured trees. Wildfire may confer some reproductive increases to populations already outbreaking. We present a conceptual model of how these disturbances and inherent feedbacks interact to affect beetle population dynamics.

Key words: Allee effects, forest ecosystems, insect outbreaks; bark beetle; *Dendroctonus ponderosae*; disturbance interactions; fire; Greater Yellowstone Ecosystem; *Pinus contorta*; plant insect interactions; population dynamics; thresholds.

INTRODUCTION

Biotic and abiotic disturbances play important roles in the functioning of natural ecosystems, contributing to community structure (Baker and Veblen 1990), biodiversity (Chapin et al. 1997), and nutrient cycling (Chapin et al. 1996, Smithwick et al. 2005). Disturbances can also interfere with human uses, such as when wildfires threaten habitations or insects compete for resources that provide economic or other values. Knowledge about the roles and functioning of natural disturbances has increased substantially in recent years.

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Among the most important insights is that interactions among different disturbance agents can strongly affect ecosystem responses, with their combined effects ranging from buffering to synergistic (Pain et al. 1998, Bigler et al. 2005). Unfortunately, the underlying mechanisms by which disturbances interact are not well understood (Chesson and Rosenzweig 1991, Veblen et al. 1994).

Conifer ecosystems that dominate large areas of western North America are strongly affected by two major disturbance regimes: wildfire and outbreaks by native bark beetles (Romme and Knight 1982, Veblen et al. 1994). Both have highly heterogeneous impacts in space and time, have lengthy periods between major events, and show variable effects depending on the scale at which they are considered. Likewise, both respond to exogenous factors such as drought (Bessie and Johnson 1995, Schoennagel et al. 2005) and temperature (Re-

gniere and Bentz 2007), and to endogenous features of forest structure such as age and density (Romme and Knight 1981). Strong reciprocal interactions between these disturbance agents have been proposed, including increased frequency of fires in areas experiencing outbreaks (Martin and Mitchell 1980) and increased susceptibility of fire-injured forests to bark beetles (Geiszler et al. 1980). However, the empirical evidence for both relationships is limited and contradictory (Geiszler et al. 1984, Rasmussen et al. 1996, Romme et al. 2006, Jenkins et al. 2008, Simard et al. 2011b).

Bark beetle adults emerge from the trees in which they developed, disperse, locate new trees, and decide whether to enter them based on chemical cues. They tunnel through the bark, mate, and construct ovipositional galleries. The larvae emerge, and feed and develop in galleries as they tunnel through the phloem (Wood 1982). This destruction of transport tissues is fatal to the host. Trees can resist colonization attempts with integrated constitutive and induced defenses, including rapid accumulation of toxic allelochemicals and autonecrosis that confines and kills the insects (Zulak and Bohlmann 2010). Bark beetles produce aggregation pheromones that rapidly attract additional beetles, enabling them to coordinate mass attacks, in which they surpass a critical density needed to overwhelm these defenses (Raffa and Berryman 1983). Physiological stress can weaken trees' defenses against bark beetles, making them more susceptible to attack (Wallin and Raffa 2001, Jones et al. 2004, Kolb et al. 2007). The population dynamics of eruptive tree-killing bark beetles are characterized by lengthy endemic periods, during which beetles reside in stands at very low densities and kill only a few weakened trees, followed by intermittent outbreaks or epidemics, during which they cause high tree mortality on a landscape scale (Kurz et al. 2008). A critical population threshold appears to separate these dynamics (Raffa et al. 2008).

The question of whether fire injury influences susceptibility to bark beetles has important policy implications, with regard to both formulating responses to wildfire and prescribing controlled burns. Non-outbreak species, such as *Dendroctonus valens* LeConte and *Ips pini* (Say), have shown increased attacks of, or attraction to, fire-injured trees in a number of systems (Rasmussen et al. 1996, Bradley and Tueller 2001, Santoro et al. 2001, McHugh et al. 2003, Wallin et al. 2003). However, results with outbreak species are mixed. For example, Elkin and Reid (2004) observed no increase in mountain pine beetle (*Dendroctonus ponderosae* Hopkins) colonization in trees artificially scorched to simulate ground fires, and Rasmussen et al. (1996) did not observe high mortality in post-wildfire surveys. Likewise, *D. ponderosae* and *Dendroctonus brevicornis* LeConte were not attracted to extracts from burned trees (Kelsey and Joseph 2003). However, Rasmussen et al. (1996) and Hood and Bentz (2007) found that

Dendroctonus pseudotsugae Hopkins were more likely to kill *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) showing several measures of wildfire injury, and Six and Skov (2009) observed higher populations of several tree-killing species following prescribed burns. Further, Geiszler et al. (1984) found increased levels of postfire attack by *D. ponderosae* in an area with low populations, and Elkin and Reid (2004) reported that beetles attacking artificially burned trees in low, but not high, numbers were more likely to produce viable eggs. Fire-injured trees are also hosts to a complex of secondary bark and wood-boring beetles (Ryan and Amman 1996, McHugh et al. 2003), including some that are unable to attack healthy trees. Members of this guild have the potential to both predispose trees to bark beetles (Bradley and Tueller 2001, McHugh et al. 2003) and outcompete them for the stressed-host resource (Flamm et al. 1993). Together, these results suggest that beetle responses to fire are complex and that entry behavior, reproductive success, and stand-level population density all need to be considered to evaluate these interactions.

The purpose of our research was to determine (1) whether various levels of natural fire injury influence the likelihood of colonization by *D. ponderosae* at the scale of individual trees; (2) whether stand-level population densities of *D. ponderosae*, and other site- and tree-level variables, influence the above relationships; and (3) whether various levels of fire injury affect reproduction by *D. ponderosae*, the composition of other bark and wood-boring beetles, and their competitive interactions.

MATERIALS AND METHODS

Study sites and experimental design

This study was conducted in the Greater Yellowstone Ecosystem, which consists of 8 million ha within Wyoming, Montana, and Idaho, USA. The area is composed of diverse vegetation types, including multiple forest types. All study sites were in >90% basal area *Pinus contorta* var. *latifolia* Douglas (lodgepole pine) forests, the dominant type in the region and the predominant host of *D. ponderosae* (Kashian et al. 2004, Safranyik and Carroll 2006). In the 1970s and 1980s, and again as recently as 2003, forests in the region were affected by bark beetle eruptions. Stand replacing fires occur in lodgepole pine, on average, every 100–300 years in the region (Simard et al. 2011b).

We sampled 16 lodgepole pine sites (Table 1). Eight experienced wildfire, and eight were neighboring unburned sites. Four of the sites burned during the summer of 2006, and four burned during the summer of 2007. Four of the burned sites (two per year) were within areas where *D. ponderosae* was at epidemic population levels, and four (two per year) were in areas where it was at endemic population levels, based on USDA Forest Service aerial detection surveys. Areas having >30 trees/ha killed by *D. ponderosae* were considered outbreaks (USDA Forest Service 2007, 2008a, b). More detailed

TABLE 1. Mountain pine beetle (MPB, *Dendroctonus ponderosae*) population phase, burn history, and MPB measurements in lodgepole pines (*Pinus contorta*) throughout study sites in the Greater Yellowstone Ecosystem, USA.

<i>D. ponderosae</i> phase and site	Burn date	MPB measurements in pines		
		Incidence of colonization	Reproduction	Subcortical galleries
Epidemic				
Purdy	4 Aug 2006	x	x	x
Purdy control	unburned	x		
Battle Mountain	2 Jul 2006	x	x	x
Battle Mountain control	unburned	x		
Salt Lick	11 Jul 2007	x	x	x
Salt Lick control	unburned	x	x	x
Hardscrabble	9 Aug 2007	x	x	x
Hardscrabble control	unburned	x	x	x
Endemic				
Magpie	17 Jul 2006	x		
Magpie control	unburned	x		
Hechtman Creek	19 Aug 2006	x		
Hechtman Creek control	unburned	x		
Owl	20 Sep 2007	x		
Owl control	unburned	x		
Madison Arm	27 Jun 2007	x		
Madison Arm control	unburned	x		
Total trees		2056	106	79

Note: An “x” indicates that the measurement was made. Site locations determined by Universal Transverse Mercator (UTM) are listed in Appendix A and Appendix B. *Dendroctonus ponderosae* population phase was determined by USDA Forest Service aerial surveys.

site data, such as geographic coordinates UTM, burn size (ha), and observed vegetation type, are presented in Appendix A.

The burn sites were separated by 30–159 km in 2006, and 52–217 km in 2007 (Fig. 1), substantially higher than the effective dispersal range of *D. ponderosae* of ~5 km (Safranyik and Carroll 2006), although passive movement in upper air currents can be much higher (Jackson et al. 2008). We performed four types of sampling: (1) incidence of colonization by *D. ponderosae* at all 16 sites the year following each wildfire; (2) brood production per *D. ponderosae* female within colonized trees at four of the eight burn sites and two unburned sites; (3) incidences and gallery areas of *D. ponderosae* and other subcortical insects in the same sites as in point 2; and (4) subcortical insects captured in flight traps baited with semiochemicals at the eight burn sites.

Effects of fire injury and beetle population phase on host colonization by Dendroctonus ponderosae

Four 5 × 100 m belt transects were established in each site, beginning at the edge of tree mortality, and extending away from the burn epicenter in each cardinal direction. Slope, aspect, and elevation were recorded for each transect. Sampling and tabulation of burn category for all trees proceeded along each transect until at least five trees each within the low, moderate, and high fire injury categories were obtained. Four measurements were incorporated into these evaluations: basal injury, bole injury, canopy injury, and cambium kill rating. The first three measurements were based on a percentage

scale, by increments of 10. Basal injury describes the tree trunk–soil interface to estimate potential damage to root tissue. Bole injury describes the trunk of the tree from ground to 1.3 m. Canopy condition includes any branches that contained photosynthetically active needles at the time of the burn, based on visible scorching. Cambium kill rating was measured by removing a 2 cm diameter disk of bark from each cardinal direction, with the number of disks with darkened, dead cambial tissue providing a scale of zero to four as described by Ryan (1982). “Low” injury trees had 0–10% basal and bole injury, 0% canopy injury, and a cambium kill rating of zero or one. “Moderate” trees had 0–50% basal and bole injury, 0–10% canopy injury, and a cambium kill rating of one to three. “Low” and “moderate” trees were all alive postfire. “High” trees had 50–100% basal and bole injury, 10–100% canopy injury, and a cambium kill rating of three to four; these trees were usually killed by the wildfire. We also sampled eight neighboring unburned sites by the same method to obtain completely noninjured trees.

All sampled trees ($N = 2056$) were examined to determine the incidence of *D. ponderosae* and other subcortical insects. Incidence was determined by examining entry holes and peeling small pieces of bark to observe galleries characteristic of each species (Furniss and Carolin 1977).

Biotic stress agents such as pathogens are also known to predispose trees to bark beetle attack. Therefore, we examined each tree for symptoms of dwarf mistletoe (*Arceuthobium americanum* Nuttall Ex. Engelmann)

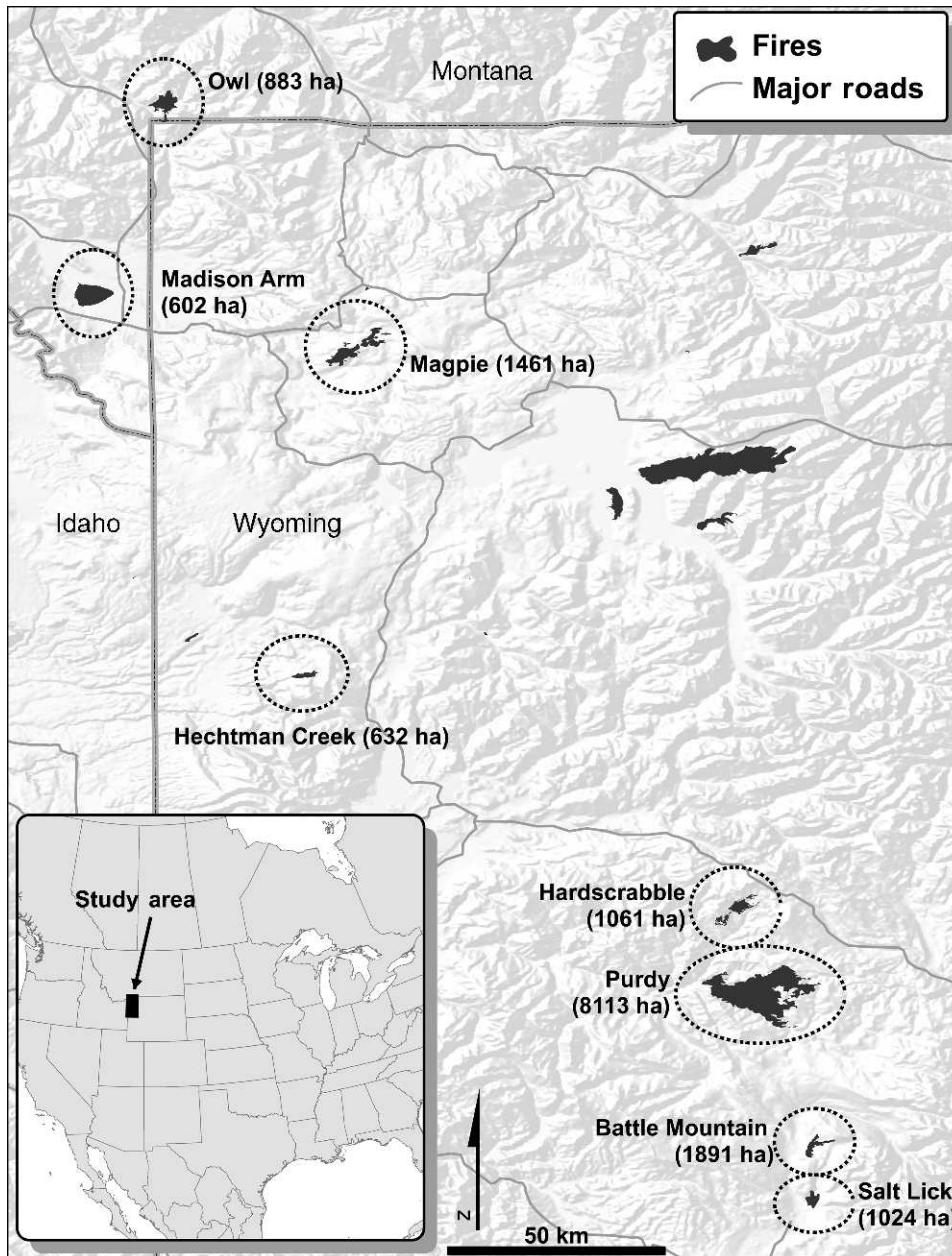


FIG. 1. Spatial scale and location of the eight wildfire sites evaluated throughout the Greater Yellowstone Ecosystem, USA. The numbers in parentheses represent the area of each burn.

using the method of Hawksworth (1979), and *Cronartium* stem rusts using the method of Geils and Jacobi (1984).

Reproduction of Dendroctonus ponderosae, and incidence of competitors, in relation to fire injury

Dendroctonus ponderosae entry holes were tabulated from tree base to 1.3 m, one year after each wildfire, following one flight period of *D. ponderosae*. Emergence holes were counted over the same area, at least one year later and before another flight period. Emergence holes

were distinguished from entry holes by the lack of resin and frass that is present at the site of entry. Emergence holes were distinguished from ventilation holes by their location at right angles from the ovipositional gallery and their alignment with pupal chambers beneath the tree bark, whereas ventilation holes are located along the ovipositional gallery. In cases where there was uncertainty distinguishing between emergence and ventilation holes, we excavated under the tree bark. We also excavated under the tree bark to reveal pupal chambers and thereby account for the possibility of multiple

beetles emerging from the same hole at high attack densities (Reid 1963). Adult brood production per *D. ponderosae* female was estimated from a random selection of all trees as the ratio of emergence to entry holes ($N = 106$ trees). Galleries of *D. ponderosae* and other beetles were examined in 79 additional randomly selected trees. The sampling was conducted in the same sites and transects as the measurements of brood production per *D. ponderosae* female. Galleries of various species were identified based on descriptions in Wood (1982) and Furniss and Carolin (1977). Samples were quantified using the method of Coulson et al. (1976). At each tree, two 14 cm diameter disks of bark were removed at 1.3 m, on the north- and south-facing surfaces, respectively. The disks were photographed, uploaded into Adobe Photoshop (Knoll et al. 2003), and the number of pixels for each bark beetle ovipositional or wood-boring larval gallery, and the entire disk, was counted. The gallery areas were grouped according to beetle taxonomic group, adjusted to per square centimeter total bark disk, and averaged for each tree (Flamm et al. 1993).

Species composition and abundance of subcortical insects in flight traps

At each of the eight burn sites, three 12-funnel flight traps (Lindgren 1983) were baited with myrcene, *exo*-brevicomin, and *trans*-verbenol to capture flying *D. ponderosae* (Borden et al. 1993), three were baited with (–) ipsdienol and lanierone to capture *Ips* spp. (Safrahyik et al. 1996), and three were baited with EtOH and (+) α -pinene to capture various other bark and wood-boring insects (Schroeder and Lindelöw 1989, Brockerhoff et al. 2006, Gandhi et al. 2009). Traps ($N = 72$) were deployed at least 100 m from each transect, so as not to influence colonization patterns in the sampled trees (Sullivan and Mori 2009). Three groups of three traps were arranged 120° apart, deployed in early June prior to beetle flight, and collected one month later. All captured insects were killed with a 2-cm square of Hot Shot No-Pest Strip (Spectrum Brands, Madison, Wisconsin, USA), dried, identified based on descriptions in Wood (1982), Turnbow and Thomas (2002), and Opitz (2002), and counted. Voucher specimens were submitted to the University of Wisconsin-Madison, Department of Entomology, Insect Research Collection, Madison, Wisconsin, USA.

Statistical analyses

We performed two multinomial chi-squared analyses to examine effects of fire, beetle population phase, and their interactions on the binary response of colonized/not colonized by *D. ponderosae*. The first modeled all fire injury categories as separate levels, and the second pooled the various burn categories to compare burned vs. unburned trees. These analyses were performed using R, version 2.7.2 (R Core Development Team 2008). We constructed a single generalized linear mixed-effects

model with a logit transformation (lme4 package in R; Bates and Maechler 2010) to evaluate other potentially important pathogenic and environmental variables on colonization by *D. ponderosae*, while incorporating random effects for site and transects nested within each site. We used Akaike's information criteria (AIC; Akaike 1973) to identify the most parsimonious model for each combination of potential variables, excluding those with $\alpha > 0.05$. The occurrence of trees in each fire injury category per transect were compared using pairwise Wilcoxon rank sum analyses.

The data for *D. ponderosae* entry, emergence, and adult brood production per female were distributed normally and with constant variance, based on quantile–quantile plots and Bartlett tests. We compared beetle entry, emergence, and adult brood production per female among fire injury categories using ANOVA. In addition, entry, emergence, and adult brood production per female were analyzed with separate linear regression models that included diameter at breast height (dbh), height, mistletoe rating, presence of blister rust, presence of other bark and wood-boring insects, individual fire injury measurements, degree of slope, aspect, and elevation. We used AIC to select the most parsimonious set of variables exhibiting $\alpha < 0.05$.

The incidence of galleries of various beetle species was analyzed with the inclusion of the above tree- and stand-level measurements. We constructed separate generalized linear regression models for each species group, *D. ponderosae*, *Ips* sp., *Pityogenes* sp., and Cerambycidae spp., using a logit transformation with the lme4 package in R, version 2.7.2 (Bates and Maechler 2010). Generalized linear regression models for the various galleries were chosen using the same AIC selection approach as the linear regression models for *D. ponderosae* entry, emergence, and productivity.

Beetle gallery areas were distributed in a non-normal fashion, and many trees contained some, but not all, of the study species. Therefore, we assessed differences among beetle gallery areas across the four different fire injury categories with a one-way analysis of similarity (ANOSIM), using Primer (Clarke and Gorley 2006). Likewise, we assessed differences among the gallery areas of different beetle species while including multiple predictor variables with canonical correspondence analysis (CCA). These predictor variables were dbh, height, mistletoe rating, the presence of blister rust, the presence of other bark and wood-boring beetles, the individual fire injury measurements, slope, aspect, and elevation. This analysis was done using PC-ORD (McCune and Mefford 2006).

We separated the effects of host quality and interspecific competition on *D. ponderosae* reproduction by testing for differences between trees that were or were not colonized by other beetles across burn categories. We used Kruskal-Wallis and Wilcoxon rank sum analyses, as these data were not normally distributed.

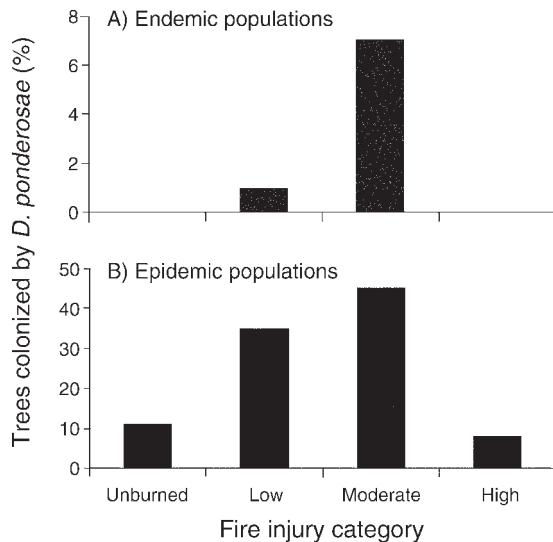
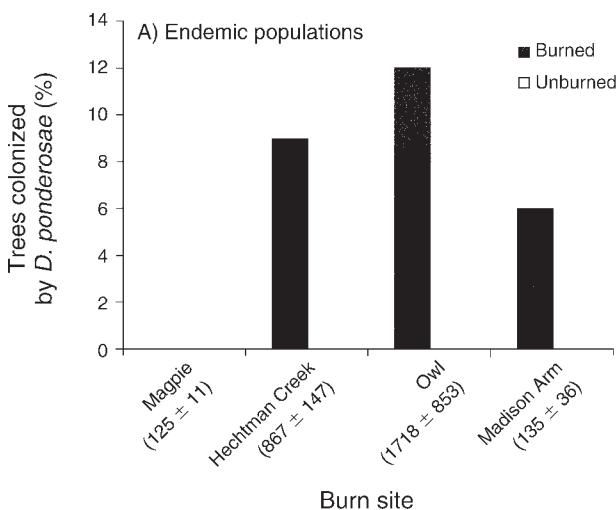


FIG. 2. Effect of wildfire injury on colonization of lodgepole pine (*Pinus contorta*) by the mountain pine beetle *Dendroctonus ponderosae*. Sites were designated as epidemic or endemic based on USDA Forest Service data and criteria: (A) endemic beetle population phase and (B) epidemic beetle population phase. Total number of trees = 2056.

Subcortical herbivores and predators captured in flight traps in sufficient numbers (≥ 81 total) were examined for normal distribution at each site with a quantile–quantile plot. Counts were not normally distributed, so they were compared across bait types with chi-squared analysis. Beetles captured from traps baited with the effects of different lures and the effects of population stage were also tested for differences across all eight sites using multinomial chi-squared analyses.



RESULTS

Effects of fire injury and beetle population phase on host colonization by *Dendroctonus ponderosae*

Fire injury strongly influenced colonization of lodgepole pine by *D. ponderosae* ($\chi^2 = 120$, $df = 3$, $P < 0.01$; Fig. 2). However, the colonization response was nonlinear, with the highest rates of attack on trees with moderate fire injury. Trees with low fire injury were also more susceptible than unburned trees. Unburned and severely burned trees were only colonized in sites at which beetles were at epidemic levels. Among all trees tabulated in burned sites ($N = 1260$), 50% had low fire injury, 23% were moderately injured, and 27% were severely injured.

The number of adult *D. ponderosae* captured in flight traps averaged 3419 in epidemic sites and 711 in endemic sites (Fig. 3). When trees were categorized as either burned or unburned (Fig. 3), there was a strong interaction effect between fire injury and site-level beetle population phase on tree-level colonization ($\chi^2 = 93$, $df = 1$, $P < 0.01$). When trees with varying degrees of fire injury and population phase were treated separately, the interaction between fire injury and site-level population phase was obscured by the low numbers of colonized trees in endemic sites ($\chi^2 = 8.0$, $df = 6$, $P = 0.24$).

Three variables (fire injury category, *D. ponderosae* population phase, and to a lesser extent, the degree of slope within transects) explained *D. ponderosae* colonization in the generalized linear mixed model (Table 2) as follows:

$$\ln(\mu_{jkl}/1 - \mu_{jkl}) = \beta_0 + \beta_{jkl}x + g_l + g_{kl}. \quad (1)$$

Each predictor variable is represented by β ; x represents the estimation of each fixed effect; and g_l and g_{kl} are

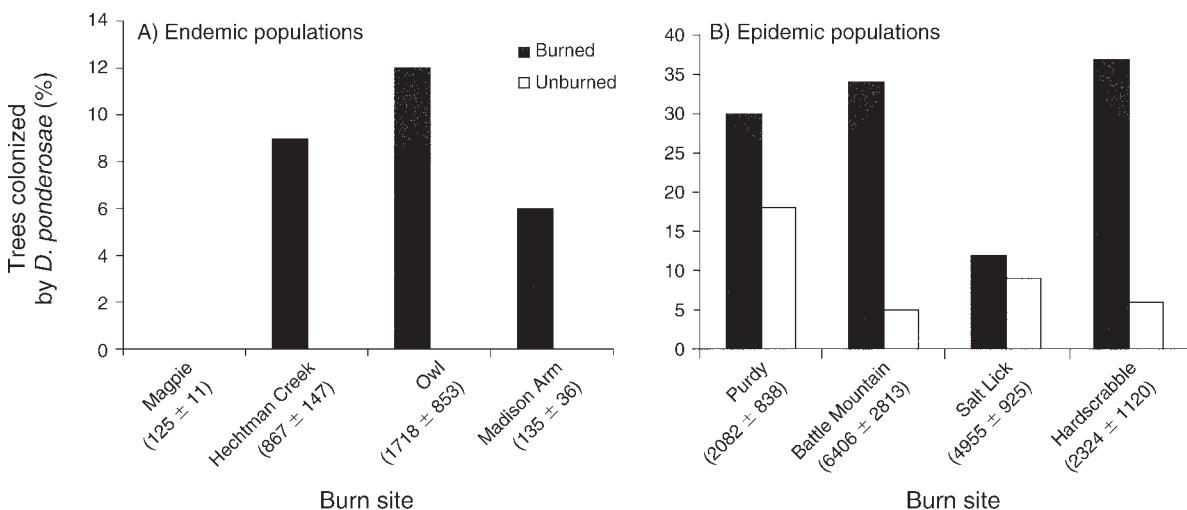


FIG. 3. Percentages of lodgepole pines colonized by *D. ponderosae* in 16 sites (burned and unburned sites in each of eight areas) in the Greater Yellowstone Ecosystem. Colonization varies with both burn injury and beetle population phase: (A) endemic populations and (B) epidemic populations. Names refer to the sites in Table 1; in parentheses are the number of *D. ponderosae* adults obtained in funnel flight traps at each site (mean \pm SE). For the Magpie site, beetles were trapped, but no trees were colonized.

TABLE 2. Generalized linear mixed model, with logit transformation, relating incidence of *D. ponderosae* colonization to fire injury category, *D. ponderosae* population size, and degree of slope of transect.

Fixed effects	Estimate (x)	SE	P
β_0 (intercept; unburned and endemic category)	-7.0	0.80	<0.01
β_1 (low category)	2.2	0.67	<0.01
β_2 (moderate category)	3.1	0.67	<0.01
β_3 (high category)	0.22	0.72	0.76
β_4 (epidemic category)	3.5	0.66	<0.01
β_5 (degree of slope)	0.05	0.02	0.05

Notes: Significance level indicates each variable's estimate of difference from β_0 (unburned category and endemic population category), $N = 2056$. These results are fitted to Eq. 1 (see Results: Effects of fire injury and beetle population phase on host colonization by *Dendroctonus ponderosae*). Each predictor variable is represented by β ; x represents the estimation of each fixed effect; and g_1 and g_{kl} are random effects on the site (l) and transect within site (kl) level. The β variables are as follows: β_0 , intercept and reference level (unburned fire injury category and endemic population size); β_1 , low fire injury category; β_2 , moderate fire injury category; β_3 , high fire injury category; β_4 , epidemic population size; β_5 , degree of slope. There were two random effects in this model. The random effect for site had a standard deviation of 0.85, and the random effect for transect within a site had a standard deviation of 0.81.

random effects on the site (l) and transect within site (kl) level. The β variables are as follows: β_0 , intercept and reference level (unburned fire injury category and endemic population size); β_1 , low fire injury category; β_2 , moderate fire injury category; β_3 , high fire injury category; β_4 , epidemic population size; and β_5 , degree of slope.

Colonization was greater in low- and moderate-injury trees than in unburned and high-injury trees. Colonization was also greater in the low- and moderate-injury categories than the unburned (reference) trees, while colonization did not differ between trees in the high-injury and unburned categories. Colonization was higher in epidemic than endemic population areas. Colonization rates were higher on transects with steep slopes.

Because site-level variation was high, we also developed generalized linear models to predict colonization at each site (Appendix B). All fire injury measurements were significant predictors at sites with low *D. ponderosae* populations, but only one or two were useful in epidemic sites (see Appendix B). The fire injury measurements that proved to be the most useful for predicting colonization at epidemic sites varied among sites. As such, multiple measurements of fire injury are useful to characterize the heterogeneity of fire impacts on this system.

Reproduction of Dendroctonus ponderosae, and incidence of competitors, in relation to fire injury

Indices of *D. ponderosae* performance varied with fire injury, but again in a complex pattern (Fig. 4). The density of attacking beetles was highest in uninjured trees, and decreased with severity of fire injury ($F_{3,102} = 110$, $P < 0.01$). We did not observe a relationship between background population size and attack density (Appendix C), suggesting attack densities are determined primarily by tree-level factors. The density of emergence sites also decreased with fire injury ($F_{3,102} =$

34, $P < 0.01$). However, adult brood production per female showed a parabolic relationship ($F_{3,102} = 5.1$, $P < 0.01$), with moderately injured trees yielding the highest brood production per female. Linear regression models supported these results. There was no relationship between brood production and dbh ($F_{1,103} = 0.31$, $P = 0.58$), nor was dbh significant when controlled for in the linear model ($t = 0.35$, $P = 0.73$). Attack density decreased sharply with fire injury category, being three times higher on unburned than severely injured trees

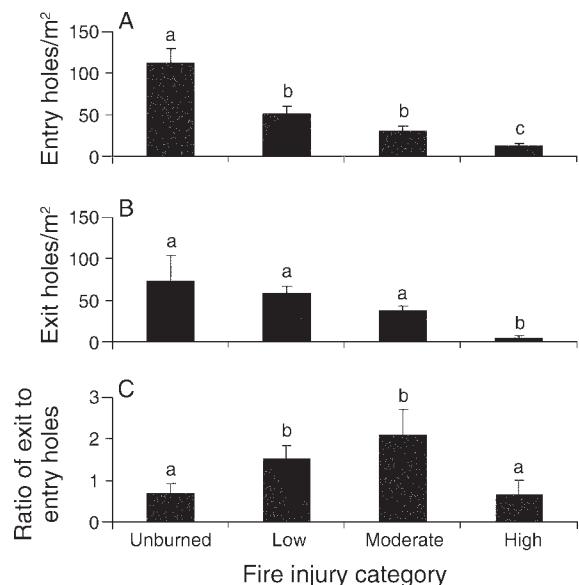


FIG. 4. Performance of *D. ponderosae* in colonized trees across four fire injury categories: unburned ($N = 20$), low severity ($N = 29$), moderate severity ($N = 32$), high severity ($N = 25$): (A) attack density; (B) density of emerging adult offspring; and (C) adult brood production per female, shown as the ratio of emergence to entry holes per tree. Data are shown as mean + SE. Different lowercase letters indicate statistical difference ($\alpha \leq 0.05$) by Student's t test.

TABLE 3. Linear regression models where the response variable is related to several tree- and stand-level variables in lodgepole pines colonized by *D. ponderosae* ($N = 106$).

Variable	Estimate (\bar{x})	SE	P
A) <i>D. ponderosae</i> attack density (entry holes): $R^2 = 0.36$, $F_{3,102} = 20$, $P < 0.01$			
β_0 (intercept; unburned category)	110	10	<0.01
β_1 (low category)	-63	13	<0.01
β_2 (moderate category)	-83	13	<0.01
β_3 (high category)	-100	14	<0.01
B) Emergence of <i>D. ponderosae</i> adult offspring (exit holes): $R^2 = 0.14$, $F_{4,101} = 4.0$, $P < 0.01$			
β_0 (intercept; unburned category)	91	19	<0.01
β_1 (low category)	-26	23	0.27
β_2 (moderate category)	-43	22	0.06
β_3 (high category)	-77	24	<0.01
β_4 (incidence of <i>P. plagiatus</i>)	-44	19	0.02
C) Adult brood production per <i>D. ponderosae</i> female (ratio of exit holes to entry holes): $R^2 = 0.10$, $F_{4,101} = 2.7$, $P = 0.034$			
β_0 (intercept; unburned category)	1.1	0.56	0.06
β_1 (low category)	0.59	0.68	0.39
β_2 (moderate category)	1.3	0.66	0.06
β_3 (high category)	-0.21	0.70	0.76
β_4 (incidence of <i>P. plagiatus</i>)	-0.98	0.55	0.08

Note: Models were selected based on best fit by R^2 .

(Table 3A). Emergence also decreased with fire injury (Table 3B), but the only significant difference was between unburned and highly injured trees.

The number of *D. ponderosae* emergence holes, and adult brood production per female, also decreased with the incidence of the secondary bark beetle *Pityogenes plagiatus knechteli* Swaine (Table 3B, C). Because a large proportion of *P. plagiatus* was captured at one site (370 per trap at Hardscrabble vs. an average of 63 at the others), we analyzed the data both including and excluding the Hardscrabble site. The linear regression model without Hardscrabble showed no effect of *P. plagiatus* in the model with the best fit ($R^2 = 0.19$, $F_{3,74} = 6.1$, $P < 0.01$; Appendix D1). This suggests that the high number of *P. plagiatus* at Hardscrabble (Powell 2010) may account for the differences among the full model (Table 3B), the model that excludes Hardscrabble (Appendix D: Table D1), and the model for only Hardscrabble (Appendix D: Table D2), indicating its

potential competitive influence on *D. ponderosae* brood development.

To identify underlying factors contributing to the bimodal relationship between degree of fire injury and adult brood production per female, we evaluated potential roles of interspecific competition and reduced substrate quality. The composition of subcortical herbivores varied across fire injury categories (global $R = 0.076$, $P = 0.03$). Whereas total ovipositional gallery area of *D. ponderosae* was generally larger in unburned trees, competitor ovipositional and larval gallery areas were larger in fire-injured trees (Table 4A). For example, ovipositional gallery area of *Ips* sp. was highest in high-injury trees, and likewise high in low- and moderate-injury trees. Cerambycidae spp. larval gallery area was highest in high-injury trees, with very few to no galleries in others. *Pityogenes* sp. gallery area was highest in moderately injured trees. Because many disks included galleries of some, but not all species groups, we repeated

TABLE 4. Gallery areas for various subcortical herbivores across four fire injury categories.

Species	Unburned			Low			Moderate			High			χ^2	df	P
	\bar{x}	SE	N	\bar{x}	SE	N	\bar{x}	SE	N	\bar{x}	SE	N			
A) All samples															
<i>D. ponderosae</i>	0.088	0.028	19	0.058	0.012	19	0.039	0.011	22	0.029	0.008	19	2.1	3	0.55
<i>Ips</i> sp.	0.002	0.001	19	0.009	0.004	19	0.006	0.003	22	0.015	0.005	19	8	3	0.05
Cerambycidae spp.	0	0	19	0.004	0.004	19	0	0	22	0.007	0.004	19	9.8	3	0.02
<i>Pityogenes</i> sp.	0.001	0.0003	19	0.003	0.002	19	12	0.006	22	0.004	0.004	19	0.85	3	0.84
B) Samples with species not present															
<i>D. ponderosae</i>	0.19	0.039	9	0.079	0.012	14	0.057	0.013	15	0.049	0.009	11	47	3	<0.01
<i>Ips</i> sp.	0.013	0.006	3	0.028	0.008	6	0.013	0.004	10	0.026	0.007	11	3.5	3	0.32
Cerambycidae spp.	0	0	0	0.008	0	1	0	0	0	0.035	0.013	4	1.5	1	0.68
<i>Pityogenes</i> sp.	0.004	0.002	3	0.017	0.008	3	0.051	0.016	5	0.025	0.022	3	3.2	3	0.37

Notes: Data are shown both for (A) all samples and (B) excluding samples where that particular species was not present. Gallery area was measured as the ratio of cm^2 gallery per cm^2 of tree. Statistical analyses were performed by Kruskal-Wallis tests.

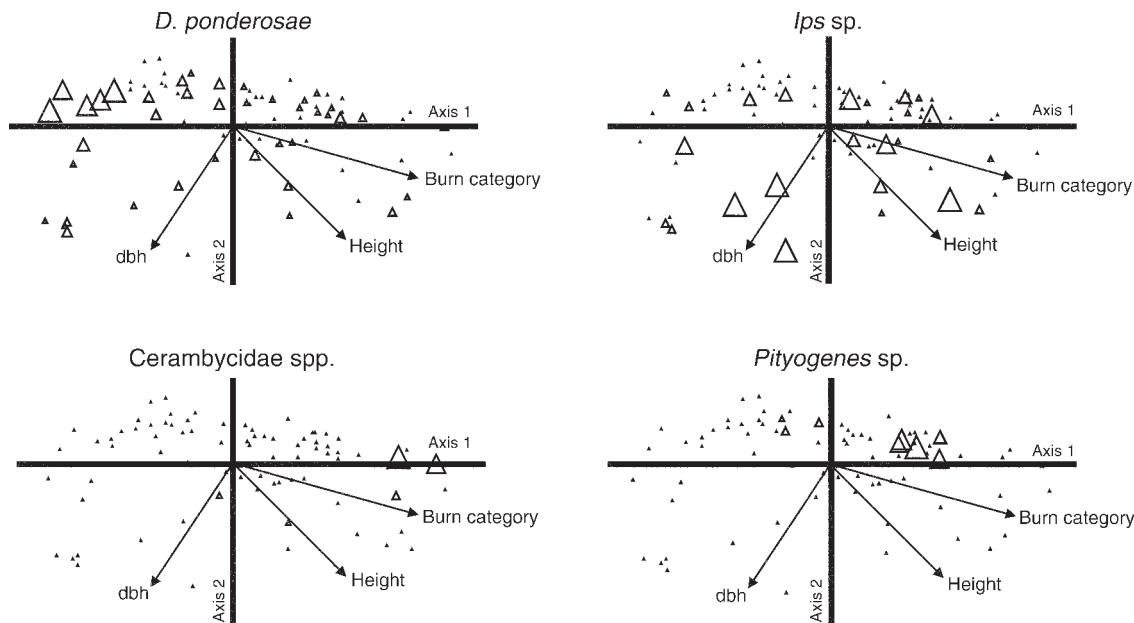


FIG. 5. Canonical correspondence analysis (CCA) for the relationship of subcortical insects to degree of fire injury in lodgepole pines. Each triangle represents a tree in which gallery areas of subcortical insects were measured. The four pertinent species groups are correlated with axis 1, $P < 0.01$. Axis 1 is correlated with fire injury category. Fire injury category increases to the right of the vector. The size of triangles indicates gallery area. Larger *D. ponderosae* total gallery area is correlated with lower fire injury category. Larger *Ips sp.* gallery area is partially correlated with higher fire injury category. Larger Cerambycidae spp. and *Pityogenes sp.* gallery areas are correlated with higher fire injury category. The vector for burn category represents increasing fire injury severity from the upper left corner of each graph to the lower right corner. The vector for dbh represents increasing diameter size from the upper right corner of each graph to the lower left corner. The vector for height represents increasing height from the upper left corner of each graph to the lower right corner.

our analysis with zeros removed. The trends remained similar (Table 4B). Canonical correspondence analysis also showed different relationships between gallery areas of the four beetle groups and fire injury categories (Fig. 5). *Dendroctonus ponderosae* total gallery area was strongly correlated with low-severity categories. *Ips sp.* total gallery area was slightly correlated with higher severity fire injury categories. Cerambycidae spp. and *Pityogenes sp.* gallery areas were strongly correlated with higher fire injury categories. Fire injury category was the only significant variable to explain the difference of gallery area size for all species, despite examination of the potential role other variables, such as tree size and presence of pathogens, may have played (Appendix E).

We constructed four binomial generalized linear regression models for each beetle taxonomic group to relate the incidence of its galleries to tree- and stand-level variables (see Table 5):

$$\ln(\mu_j/1 - \mu_j) = \beta_0 + \beta_j x. \quad (2)$$

The incidence of *D. ponderosae* galleries generally decreased with the aggregate fire injury category, but increased with percentage of bole injury and also dbh. There was a high degree of association between *Pityogenes sp.* and *D. ponderosae*. The incidence of *Ips sp.* galleries slightly increased with percentage of bole injury. The incidence of Cerambycidae spp. galleries

increased with tree height. The incidence of *Pityogenes sp.* increased exponentially with both percentage of bole and basal injury.

Overall, the percentage of *D. ponderosae*'s total gallery area relative to total beetle gallery area decreased with fire injury (Kruskal-Wallis $\chi^2 = 11$, $df = 3$, $P = 0.01$; Fig. 6). We attempted to separate the extent to which decreased gallery area is due to direct competition, vs. the extent to which it may reflect reduced substrate quality for *D. ponderosae* in tissue conditions preferred by other species. We compared adult brood production per female in disk samples in which potential competitors were present or absent, using several types of analyses. Linear regression models indicated a relationship between fire injury categories when competitors were present (Table 6A), but not when they were absent, suggesting a possible role. However, there were no differences within most fire injury classes (Kruskal-Wallis $\chi^2 = 2.0$, $df = 1$, $P = 0.16$), total emergence of *D. ponderosae* did not differ between trees with competitors present or absent within injury classes (Kruskal-Wallis $\chi^2 = 3.0 \times 10^{-4}$, $df = 1$, $P = 0.99$), and adult brood production per female was greater with competitors present than absent in low injury trees (Wilcoxon rank sum $P = 0.01$), suggesting resource partitioning by host physiological condition may dampen direct competition.

TABLE 5. Generalized linear models for subcortical herbivores in which the incidence of each beetle's gallery area is related to several tree- and stand-level variables.

Beetle taxonomic group and variable	Estimate (x)	SE	P
<i>D. ponderosae</i>			
β_0 (intercept; unburned category)	-1.5	0.73	0.05
β_1 (low category)	0.44	0.78	0.57
β_2 (moderate category)	-2.2	1.4	0.11
β_3 (high category)	-4.2	2.0	0.03
β_4 (percentage of bole injury)	0.05	0.03	0.03
β_5 (dbh)	0.06	0.03	0.03
β_6 (incidence of <i>Pityogenes</i> sp.)	1.8	0.78	0.02
<i>Ips</i> sp.			
β_0 (intercept)	-1.2	0.36	<0.01
β_1 (percentage of bole injury)	0.02	0.01	<0.01
Cerambycidae spp.			
β_0 (intercept)	-5.2	1.5	<0.01
β_1 (height)	0.15	0.07	0.03
<i>Pityogenes</i> sp.			
β_0 (intercept)	-1.6	0.40	<0.01
β_1 [percentage of bole injury] ²	-7.5×10^{-4}	3.3×10^{-4}	0.02
β_2 [percentage of basal injury] ²	4.4×10^{-4}	1.8×10^{-4}	0.02

Notes: The variables for each site were in the model with the lowest AIC value. Significance levels indicate the respective parameter's estimate being different from β_0 or the reference level (unburned), $N = 79$. These results are fitted to Eq. 2 (see Results: Reproduction of *Dendroctonus ponderosae*, and incidence of competitors, in relation to fire injury). Each predictor variable is represented by β , and x represents the estimation of each variable. Low, moderate, and high categories refer to the level of fire injury.

Species composition and abundance of subcortical insects in flight traps

The bark beetles, *I. pini*, *P. plagiatus*, *Orthotomicus latidens* (LeConte), *Pityophthorus* spp., and various wood-boring Cerambycidae spp., were consistently obtained in flight traps at all eight sites (Table 7). The wood-boring hymenopteran *Xeris spectrum* Linnaeus was found at seven sites. Surprisingly, only one *D. valens*, a lower stem-feeding bark beetle commonly

associated with stressed trees including those injured by fire, and one Buprestidae, a family of wood-boring insects containing some genera commonly associated with fire, were captured. Both were at a site with endemic *D. ponderosae* populations.

In addition to *D. ponderosae*, other bark beetles more abundant in epidemic than endemic sites were: *Ips pini* ($\chi^2 = 820$, $df = 7$, $P < 0.01$), *P. plagiatus* ($\chi^2 = 1500$, $df = 7$, $P < 0.01$), *Pityophthorus* spp. ($\chi^2 = 4900$, $df = 7$, $P < 0.01$), and *O. latidens* ($\chi^2 = 30$, $df = 7$, $P < 0.01$). Numbers of wood-boring Coleoptera and wood-boring Hymenoptera did not differ between sites with epidemic vs. endemic *D. ponderosae* populations.

A dipteran predator of bark beetles, *Medetera* sp., was found consistently across the eight burn sites, but at very low numbers. Parasitic wasps varied substantially

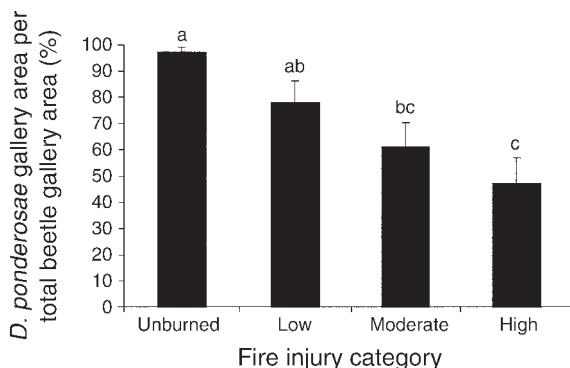


FIG. 6. Percentage (mean + SE) of *D. ponderosae* gallery area out of the total beetle gallery area, across four fire injury categories: unburned ($N = 9$), low severity ($N = 16$), moderate severity ($N = 19$), high severity ($N = 17$). Samples lacking any galleries were excluded. Differences between categories were determined by Kruskal-Wallis, $\chi^2 = 11$, $df = 3$, $P = 0.01$. Pairwise differences were determined by Wilcoxon rank sum ($P \leq 0.05$) and are indicated by lowercase letters above the bars.

TABLE 6. Linear regression models for adult brood per *D. ponderosae* female productivity across four fire injury categories for trees where competitors of *D. ponderosae* were (A) present and (B) not present ($N = 106$).

Variable	Estimate (x)	SE	P
A) With competitors ($R^2 = 0.21$, $F_{3,69} = 6.2$, $P < 0.01$)			
β_0 (intercept; unburned category)	0.18	0.20	0.72
β_1 (low category)	0.77	0.24	<0.01
β_2 (moderate category)	0.60	0.23	0.01
β_3 (high category)	0.16	0.23	0.51
B) Without competitors ($R^2 = 0.14$, $F_{3,29} = 1.5$, $P = 0.23$)			
β_0 (intercept; unburned category)	0.51	0.20	0.02
β_1 (low category)	-0.12	0.29	0.68
β_2 (moderate category)	0.42	0.32	0.20
β_3 (high category)	-0.43	0.39	0.28

TABLE 7. Average number of flying insects captured from three funnel traps of each lure type for all eight sites, with statistical comparisons.

Species	Ecological role	Insects captured, by lure type			Epidemic > endemic	Lure comparison		
		MPB	Ips	HV		MPB	Ips	HV
Coleoptera								
Curculionidae, Scolytinae								
<i>Dendroctonus ponderosae</i>	SH	18 612	rare	rare	**	**	ns	ns
<i>Ips pini</i>	SH	6.34	551	37.67	**	ns	**	ns
<i>Dendroctonus valens</i>	SH	0	0.67	0	ns	ns	ns	ns
<i>Pityogenes plagiatus</i>	SH	37.33	448.9	53.33	**	ns	**	ns
<i>Pityophthorus</i> spp.	SH	61.34	878.7	218	**	ns	**	ns
<i>Orthotomicus latidens</i>	SH	10.67	17.99	51.67	**	ns	**	ns
Cerambycidae								
<i>Megacylene</i> spp.	SH	0	0	2.66	ns	ns	ns	ns
<i>Rhagium inquisitor</i>	SH	0	2.33	2.67	ns	ns	ns	ns
<i>Monochamus</i> spp.	SH	1.67	2	13	ns	ns	ns	ns
Cleridae								
<i>Thanasimus undatulus</i>	PR	7	21.01	9.34	ns	ns	*	ns
<i>Enoclerus lecontei</i>	PR	0	8.01	4.67	ns	ns	*	ns
<i>Enoclerus sphegeus</i>	PR	16.67	3.34	38.34	ns	**	ns	**
Hymenoptera								
Parasitoids	PA	13.33	56.33	42.66	**	ns	ns	ns
Siricidae								
<i>Xeris spectrum</i>	SH	0.33	7.33	25.34	ns	ns	ns	ns
Diptera								
Dolichopodidae								
<i>Medetera</i> spp.	PR	0.33	2.67	2.33	ns	ns	ns	ns

Notes: Statistical tests (chi-square tests) refer to higher trap catches at epidemic then endemic sites, and higher trap catches with a particular lure. Abbreviations for lures: MPB, myrcene, *exo*-brevicomin, plus *trans*-verbenol; Ips, (-)ipsdienol plus lanierone; HV, EtOH plus (+) α -pinene. Data from each burn site are from Powell (2010). Abbreviations for ecological role are: SH, subcortical herbivore; PR, predator of bark beetles; PA, parasitoid.

* $P < 0.05$; ** $P < 0.01$; ns, not significant.

among sites, with some such as Hardscrabble, having particularly high populations. More parasitic wasps were found at epidemic than endemic sites. Three beetle predators (Cleridae) of bark beetles, *Thanasimus undatulus* (Klug), *Enoclerus lecontei* (Wolcott), and *Enoclerus sphegeus* (Fabricius), were occasionally present, but not consistently across sites. Their numbers did not vary with *D. ponderosae* population levels.

Some species were more associated with certain volatile lures than others. As expected, *D. ponderosae* was consistently found in traps baited with myrcene, *exo*-brevicomin, and *trans*-verbenol, and *I. pini* was predominantly found in traps baited with (-) ipsdienol and lanierone ($\chi^2 = 940$, $df = 2$, $P < 0.01$). *Pityogenes plagiatus* ($\chi^2 = 600$, $df = 2$, $P < 0.01$), *Pityophthorus* spp. ($\chi^2 = 980$, $df = 2$, $P < 0.01$), and *O. latidens* ($\chi^2 = 36$, $df = 2$, $P < 0.01$) were obtained predominantly in trees baited with (-) ipsdienol and lanierone. Clerids were found in traps of all three baits, but *T. undatulus* ($\chi^2 = 9.1$, $df = 2$, $P = 0.011$) and *E. lecontei* ($\chi^2 = 6.9$, $df = 2$, $P = 0.032$) were most commonly found in traps baited with (-) ipsdienol and lanierone, and *E. sphegeus* was most commonly found in traps baited with two types of lures, myrcene, *exo*-brevicomin, plus *trans*-verbenol, and EtOH plus (+) α -pinene ($\chi^2 = 30$, $df = 2$, $P < 0.01$).

DISCUSSION

Our results demonstrate that fire injury influences colonization by *D. ponderosae*, but nonlinearly, and in a manner that is mediated by stand-level population density. Beetles preferred moderately injured trees under all conditions, but only epidemic populations exploited unburned and severely burned trees. Similarly, beetle per capita replacement rates are highest in moderately injured trees. This relationship appears to arise from three processes. First, higher attack densities are required to overcome the defenses of healthy trees, and beetles adjust their aggregation behavior accordingly (Fig. 4A; Raffa and Berryman 1983). Higher attack densities result in higher intraspecific competition (Amman and Cole 1983, Raffa and Berryman 1983). Second, and opposing this trend, injured trees harbor more interspecific competitors (Fig. 6). Third, fire-injured trees have lower substrate quality, as brood production declined with the degree of fire injury, even in samples lacking competitors. This also suggests that the patterns of host association among the various subcortical species are at least partially a consequence of resource partitioning (Fig. 5).

These results have several implications to bark beetle epidemiology, disturbance interactions, and natural

resource management. First, fire-injured trees appear to serve as a reservoir for beetles during their endemic population phase, when they lack sufficient numbers to overwhelm the defenses of healthy trees (Geiszler et al. 1984, Wallin et al. 2003). In contrast, unburned trees were not available to *D. ponderosae* when stand-level populations were low, even though their presence was validated by trapping (Fig. 3). In the absence of fire, other disturbances such as lightning, wind, root herbivory, or root disease would be needed to prevent localized extinction (Lewis and Lindgren 2002, Smith et al. 2011).

Second, the likelihood that population increases in fire-injured trees could trigger outbreaks is reduced by several important constraints. These include increased competition and reduced substrate quality in severely injured hosts at the tree level (Fig. 6; Jakubas et al. 1994, Elkin and Reid 2004), as well as low availability of the optimal, moderately injured trees at the stand level. Trees are available for only one generation, so adults must locate new susceptible hosts, a process that incurs high mortality (Berryman 1979, Safranyik and Carroll 2006). Dispersal losses have been estimated at 57% for a related beetle, *Dendroctonus frontalis* Zimmermann, even in outbreak-level infestations (Pope et al. 1980), and they likely are higher in stands with low populations given the low rates of attack success there (Safranyik and Carroll 2006, Boone et al. 2011). Although we cannot calculate total beetle reproduction on a stand-wide basis, we can estimate a stand-level index by summing the proportion of trees in each injury category that was colonized times emergence density in that category, weighted by the proportion of trees in that fire injury category. This value was zero in unburned endemic stands, because no trees were colonized. The index value was only 0.94 in burned endemic stands, because only 2% of trees in such stands were colonized, and only 23% of burned trees are in the favored moderately injured category. The actual stand-level resource for the beetle is even lower than that estimate, because our transects were located along burn edges, thereby inflating the number of moderately injured trees relative to the landscape as a whole. The burn centers include mostly severely damaged trees and, at a regional scale, burns are surrounded by large areas of unaffected trees. If an increase in population density following wildfire were accompanied by additional factors such as warm temperatures, drought, or steeper slopes, however, their combined effects would be more likely to favor transition to outbreak dynamics. A compounding factor is that some of these conditions can favor both wildfire and bark beetle outbreaks directly (Veblen et al. 1994, Bigler et al. 2005).

Finally, wildfire could potentially increase total beetle reproduction in stands already experiencing outbreaks. The above index is 44% higher in burned than unburned epidemic stands. However, the possibility that unburned

epidemic stands would ultimately reach these levels anyway cannot be excluded.

Based on these data, we propose a conceptual framework for the relationship between fire injury and beetle population dynamics that incorporates both positive and negative feedbacks (Fig. 7). At the tree level, fire injury (a) increases host susceptibility (Powell and Raffa 2012), (b) decreases host substrate quality, and (c) increases susceptibility to competitors. (d) Host susceptibility and (e) substrate quality improve beetle reproduction, and (f) competitors decrease it. Predators and parasitoids can exert additional negative feedbacks (Amman and Cole 1983), although their numbers appear to be lower in this system (Table 7) than elsewhere for *D. ponderosae* (Boone et al. 2008) or other bark beetles (Aukema et al. 2000). Overall, one feedback from fire to beetle reproduction is positive, and two are negative. Stand-level processes, such as (g) the number of vigorous hosts colonized, and (h) regional beetle population dynamics affected by net migration, population densities in neighboring stands, forest structure, exogenous stresses on trees, and weather (Hicke et al. 2006, Hicke and Jenkins 2008, Bentz et al. 2010, Simard et al. 2011a) exert additional important positive and negative feedbacks. A major source of positive feedback at this level is the flexible host selection strategy of eruptive species such as *D. ponderosae*. Specifically, limiting their attacks to stressed trees when populations are low, but attacking almost any tree once populations are high, allows beetles to fully exploit their available resources when they are capable of overwhelming tree defenses, while avoiding localized extinction when they lack this capability (Lewis and Lindgren 2002, Wallin and Raffa 2004, Boone et al. 2011). If the initial population pulse following a disturbance is very high, this can foster transitions to self-driving dynamics. However, there are significant negative feedbacks, including both those identified in Fig. 7, and a potential satiation effect (i.e., too few beetles to exploit the new and ephemeral resource), the dynamics of wildfire yielding relatively few moderately injured trees, and stochastic processes such as unsuitable weather. Two elements needed to more fully test the relative strengths of this proposed feedback processes model include better estimates of absolute changes in beetle numbers at the stand level and analysis of population trends across longer temporal and spatial scales. For example, population increases of predators and competitors likely include time lags, and physical factors correlated with beetle attack, such as slope, could contribute to other predisposing factors such as drought stress (Dobbertin et al. 2007, Klos et al. 2009).

The general processes depicted in Fig. 7 seem likely to apply to other tree-killing bark beetles, and so may be of broader use for both conceptual and management purposes. However, the strengths of the various mechanisms will vary with system. For example, thick-barked tree species will likely require more severe fire

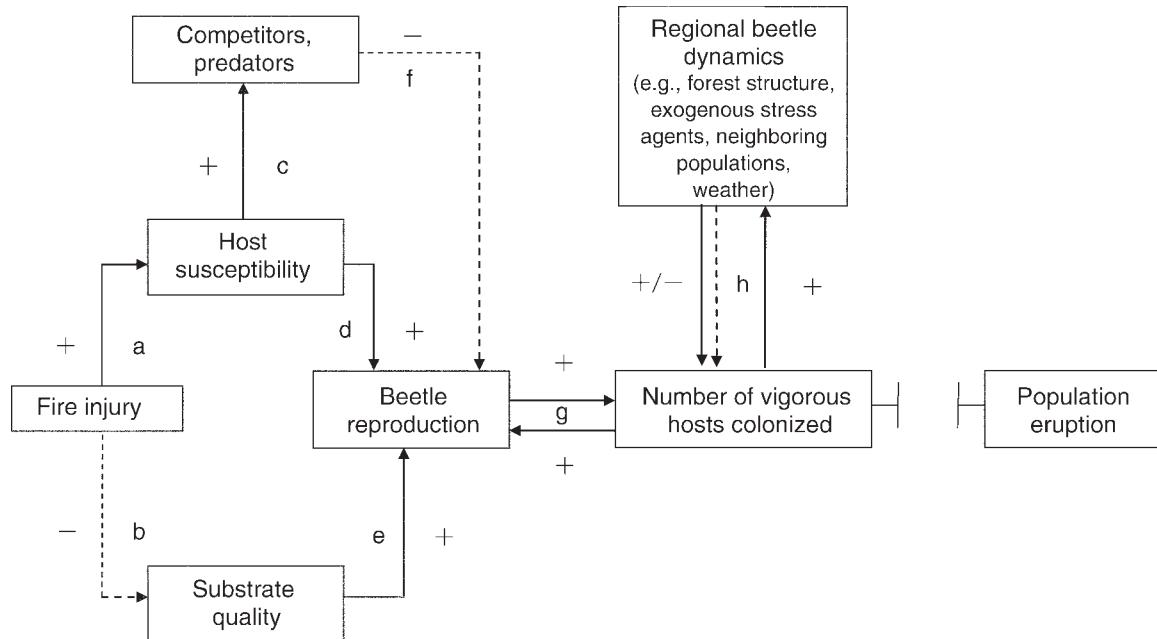


FIG. 7. Conceptual framework of potential positive and negative feedbacks of fire injury on bark beetle reproduction. Lowercase letters represent each relationship in the framework. For each relationship, an increase in the preceding variable can cause an increase (+; solid lines) or decrease (-; dashed lines) in the recipient variable. Processes on the left are tree-level processes, and those on the right are stand-level processes. The gap between “Number of vigorous hosts colonized” and “Population eruption” indicates that, because of the relationships described within the figure, there would have to be a very large initial population increase for a transition to a self-driving outbreak. Additional relationships are omitted for simplicity (see Raffa et al. 2008). Population eruptions affect forest structure, which feeds back into the likelihood of subsequent beetle outbreaks over a longer time frame, but is likewise omitted for simplicity.

injury to affect host defense and substrate quality, competitors and predators exert stronger effects on some beetle species and in some regions than others, and the strengths of different exogenous factors likewise vary with system. Similarly, the amount of initial population increase needed to transition from endemic to eruptive dynamics differs among bark beetle species (Raffa et al. 2008), which will affect the length of gap in Fig. 7.

Overall, the conditions under which wildfire can cause an outbreak appear to be relatively narrow. This likely explains why neither population build-up from endemic levels (Rasmussen et al. 1996) nor increased colonization (Amman and Ryan 1991) of *D. ponderosae* in fire-injured trees was observed after the 1988 Yellowstone fires. Thus, region-wide events such as drought seem more likely to release large-scale outbreaks than more heterogeneous or localized stresses such as root pathogens or fire injury (Raffa et al. 2005). Additional information is needed on how disturbances such as fire interact with other factors that favor beetle reproduction, such as drought, elevated temperature, and management practices that reduce stand heterogeneity.

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SUPPLEMENTAL MATERIAL

Appendix A

A table of location, size, and observed vegetation type for eight sites burned by wildfire, and eight corresponding non-burned sites, in which individual lodgepole pines ($N = 2056$) were sampled for degree of fire injury and attacks by *Dendroctonus ponderosae* throughout the Greater Yellowstone Ecosystem, USA (*Ecological Archives* M082-002-A1).

Appendix B

A table of the individual generalized linear models with logit transformations for each burn site in which *D. ponderosae* colonization was related to several tree- and stand-level variables (*Ecological Archives* M082-002-A2).

Appendix C

A figure of the average attack density of *D. ponderosae* in relation to the average number of beetles captured in pheromone-baited traps at each burn site (*Ecological Archives* M082-002-A3).

Appendix D

Four tables showing the linear regression models with *D. ponderosae* emergence and ratio of emergence/entry related to several tree- and stand-level variables (*Ecological Archives* M082-002-A4).

Appendix E

A figure revealing that, by canonical correspondence analysis (CCA), fire injury category is the factor that is most strongly correlated with taxonomic group composition within the trees sampled (*Ecological Archives* M082-002-A5).

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.vk7sr8tr>