

**INTERACTIONS AMONG DISTURBANCE AGENTS IN CONIFER FORESTS:
DOES FIRE INJURY INCREASE SUSCEPTIBILITY OF LODGEPOLE PINE TO
MOUNTAIN PINE BEETLES AND INFLUENCE THEIR POPULATION
DYNAMICS?**

By

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A thesis submitted in partial fulfillment of
the requirements for the degree of

Master of Science

(Entomology and Forest & Wildlife Ecology)

at the

UNIVERSITY OF WISCONSIN – MADISON

2010

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THESIS ACKNOWLEDGEMENTS

I'd like to first thank Ken Raffa for his advisement during my masters program. Not only from him do knowledge, patience, and support abound, but so do colorful anecdotes and witty analogies, offered with such generosity to those of us who need a few imaginative descriptions to aid in the push up the learning curve. Thanks to him for the lessons given with a little chuckle on the side! I'd also like to thank my committee members, Dan Young, Monica Turner, and Phil Townsend for sharing their time and providing direction throughout my masters program.

Many thanks and much indebtedness is owed to my labmates. Aaron Adams, Andy Lerch, Charlie Mason, Celia Boone, Dave Coyle, and Jesse Pfammatter, thanks to them for fruitful discussions (over a wide range of topics!) that have been accompanied by their support and laughter, some good food, and the occasional beer. Thanks to Jake Griffin and Martin Simard who provided invaluable support and companionship during our field seasons in Wyoming. With their infectious optimism, I will always remember that when life hands you snow, build snowmen! Without my field assistants, none of this would be possible! Megan Fork, Kat Molter, Meme Greulich, Chris Foelker, Andy Long, Chris Pennings, and Hillary Thompson, worked tirelessly despite wind, rain, snow, stuck trucks, broken trucks, tourist jams, cowboys with guns, poorly aimed bear spray administration, and less than welcoming wildlife.

The staff of both the Entomology and Forest & Wildlife Ecology Departments was tremendously helpful throughout my masters program. Thanks to Steve Krauth, Insect Research Collection, for his help with insect identifications. Thanks to Helen Thompson, Shelia Timme, Laurie Ballentine, and Sara Rodock for help with administrative paper work.

I would also like to thank Nick Keuler, CALS statistical consulting lab, for his statistical guidance. Hank Harlow was a fantastic host at the UW NPS Research Station in Grand Teton National Park. Thanks to him for providing lodging and lab space that is hard to top!

Lastly, I would like to thank my family and friends. These are the folks with patience that I hope to emulate, one day. They have put up with me and supported me at my least gracious. Thanks to my husband John for laughter when I needed it, cooking when I couldn't do it (even though he detests it), rescuing me from the wild land of Idaho Falls when I really needed help, and tearing me away from my computer screen when my eyes were blurred and my life was teetering off balance. I hope to provide just as much support to him when he gets to this point in his graduate program.

THESIS ABSTRACT

Wildfire and bark beetle outbreaks are important and widespread natural disturbances in North American conifer ecosystems, yet little is known about how and to what extent they interact. We addressed whether fire injury increased the susceptibility of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) trees to colonization by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and whether the beetle's population phase affected this interaction. I also addressed whether fire injury affected the per-capita brood production of *D. ponderosae* and how wildfire affects composition of coleopteran species. Eight sites that experienced wildfire and 8 adjacent paired control sites were examined in the Greater Yellowstone Ecosystem. Half of the sites were in areas in which *D. ponderosae* populations were in an outbreak phase and half were where populations were at low densities. A total of 2056 trees was sampled the following year, with each categorized accordingly to a range of fire injury levels and the presence or absence of *D. ponderosae*. Percent basal injury, percent bole injury, percent canopy injury, and cambium kill rating were used to assign each tree into its fire injury category. I also deployed 72 baited 12-funnel flight traps the year following each fire to sample the flying insects within the 8 burned sites. Nine traps were at each site, 3 each baited with myrcene, *exo*-brevcomin and *trans*-verbenol, (-) ipsdienol and lanierone, and (+) α -pinene and EtOH. One hundred and six trees within the 4 *D. ponderosae* outbreak burn sites and 2 corresponding non-burned sites were noted for level of fire injury and grouped into fire injury categories (unburned, low-, moderate-, and high-severity). I examined these trees for *D. ponderosae* attack density, and the density of exit holes by emerging adult offspring to determine per-capita brood production. Entry holes were counted after beetle flight, one year post-fire, and emergence holes were counted after

beetle flight, at least two years post-fire. Seventy nine different trees within these 6 sites were also noted for level of fire injury and grouped into the previously specified fire injury categories. I measured the total average ovipositional or larval gallery area of *D. ponderosae* and other additional coleopteran subcortical herbivores under the bark of two 8 cm² diameter disk shaped areas on the bole of each of the 79 trees.

My results indicate that fire injury predisposes trees to *D. ponderosae* attack, but the extent to which this occurs varies in a nonlinear fashion with the severity of injury. Moderate-severity trees were the most commonly attacked, both in sites with endemic and outbreak beetle populations. The beetle-host interaction at the tree level was also affected by beetle population density at the stand level. Trees of all fire injury categories, including unburned, were attacked by outbreak populations, whereas only low- and moderate-severity trees were attacked by endemic populations.

Dendroctonus ponderosae is most reproductively successful in moderate-severity trees, and the rates of *D. ponderosae* entry and emergence decrease with fire injury. The total gallery area of *D. ponderosae* is the greatest in trees not injured by fire, while the total gallery area of *Ips pini* (Say), coleopteran wood-borers (Cerambycidae spp.), and *Pityogenes* spp. was larger in fire-injured trees. Funnel traps captured several subcortical herbivores, most of which were *D. ponderosae*, *I. pini*, *Pityogenes* spp., *Pityokteines* spp., and *Pityophthorus* spp.

Several tree- and stand-level factors such as host susceptibility, host substrate quality, and regional beetle dynamics also appeared to affect the potential of *D. ponderosae* populations to initiate or sustain an outbreak.

Key Words: bark beetles, *D. ponderosae*, wildfire, disturbance interactions, population dynamics, reproductive success, Greater Yellowstone Ecosystem

THESIS INTRODUCTION

Disturbances influence forest ecosystems at multiple scales. In the Greater Yellowstone Ecosystem (GYE), fire and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) are two of the most important disturbance agents, and their effects range from the tree to landscape levels (Romme et al., 1986; Turner et al., 1999). Fire and population eruptions by *D. ponderosae* may help to maintain lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) ecosystems, due to various adaptations lodgepole pine has to these disturbances (Perry and Lotan, 1979). Strong reciprocal interactions between these disturbance agents have been proposed, including increased frequency of fires in areas experiencing bark beetle outbreaks (Martin and Mitchell, 1980) and increased susceptibility of fire-injured forests to beetle colonization and subsequent outbreaks (Geiszler et al., 1980). I investigated one direction of interactions between these two important disturbances from a mechanistic perspective of drivers and feedbacks influencing herbivore population dynamics.

Many factors need to be considered when investigating interactions between disturbances, including biotic agents. For example, some bark beetle species appear to behave differently at varying population densities. At endemic levels, they are limited to trees that have decreased defenses (Wood, 1982). In contrast, the pheromone-mediated mass attack behavior of bark beetles permits high populations to overwhelm a healthy tree's defenses, thereby successfully colonizing and killing it during epidemics (Wallin and Raffa, 2004).

Because a broad range of physiological stresses are known to compromise tree defenses against bark beetles (Raffa and Berryman, 1987; Raffa et al., 2005), it seems plausible that fire-injured trees may serve as a reservoir for low-density *D. ponderosae*

populations. Further, the resulting population increases may be sufficient to surpass the threshold at which populations generate positive feedback and eruptions occur. Prescribed burns have been used to examine the response of *D. ponderosae* to fire-injured trees. The incidence of colonization by wood-boring insects, and bark beetles, increased in trees that were burned less than three years prior to colonization, but *D. ponderosae* colonization of non-fire-injured trees was not studied (McHugh et al., 2003). Elkin and Reid (2004) also experimented with prescribed burns and *D. ponderosae* dynamics. Brood sizes and reproductive rates were not observed to increase in fire-injured trees. While this stressed-tree resource was hypothesized to provide potential for the build-up of *D. ponderosae* populations, the impact on *D. ponderosae* by competitors was not addressed.

There are many drivers of potential increase of bark beetle populations in fire-injured trees: host tree resistance and suitability (Lombardero et al., 2006; Parker et al., 2006), reproductive success (McHugh et al., 2003; Elkin and Reid, 2004), population size (Berryman, 1976; Safranyik and Carroll, 2006), and competition (Poland and Borden, 1998; Raffa et al., 2005). Each needs to be examined to fully understand *D. ponderosae* population dynamics within burned lodgepole pine forests. The objective of this work was to focus on the role of fire-injured lodgepole pine both as a reservoir for *D. ponderosae* and as a potential source of population increase. Specifically, I investigated the relative likelihood of fire-injured versus healthy trees being colonized and related per-capita brood production of *D. ponderosae* in colonized fire-injured versus healthy trees.

In chapter 1, I discussed the susceptibility of fire-injured lodgepole pine to the likelihood of colonization by *D. ponderosae*, while also considering the population phase of the beetle. The specific objectives were 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.

In chapter 2, I discussed the per-capita brood production of *D. ponderosae* in successfully attacked trees, and the potential for competition between *D. ponderosae* and other additional subcortical herbivores in fire-injured lodgepole pines. Specifically, I examined attack densities and densities of emerging adult offspring in relation to fire injury. I also evaluated the species composition of other subcortical insects within fire-injured trees, and sampled burn sites for the composition of flying insects using baited 12-funnel flight traps.

The appendix of chapter 1 contains supplemental information on the relationship between colonization of *D. ponderosae* and each of 11 sites, 7 of which were burned by wildfire and 4 of which were not. The appendices of chapter 2 contain supplemental information on the relationship between rates of *D. ponderosae* emergence and ratios of *D. ponderosae* emergence to entrance and fire injury, while also examining the variation caused by one site and the relationship between rates of *D. ponderosae* entry to the average number of beetles captured in multiple baited funnel traps.

The chapters in this thesis are in the format of journals intended for publication.

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CHAPTER 1

**INTERACTIONS AMONG BIOTIC AND ABIOTIC DISTURBANCE AGENTS:
EFFECTS OF FIRE INJURY AND STAND-LEVEL POPULATION DENSITY ON
COLONIZATION OF LODGEPOLE PINE BY MOUNTAIN PINE BEETLES IN
THE GREATER YELLOWSTONE ECOSYSTEM**

Abstract

Wildfire and bark beetle outbreaks are important natural disturbances in North American conifer ecosystems, yet little is known about how and to what extent they interact. We addressed whether fire injury increased the susceptibility of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann) trees to the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and whether the beetle's population phase affected this interaction. Eight sites that experienced wildfire and 8 adjacent paired control sites were examined in the Greater Yellowstone Ecosystem (Wyoming, U.S.A). Half of the sites were in areas in which *D. ponderosae* populations were in an outbreak phase and half were where populations were at low densities. Trees (N=2056) were sampled one year after fire, with each tree categorized by fire injury and the presence or absence of *D. ponderosae*. Percent basal injury, percent bole injury, percent canopy injury, and cambium kill rating were used to assign each tree into its fire injury category. Our results indicate that fire injury predisposes trees to *D. ponderosae* attack, but the extent to which this occurs varies in a nonlinear fashion with the severity of injury. Moderate-severity trees were the most commonly attacked, both in sites with endemic and outbreak beetle populations. The beetle-host interaction at the tree level was also affected by beetle population density at the stand level. Trees of all fire injury categories, including unburned, were attacked by outbreak populations, whereas only low- and moderate-severity trees were attacked by endemic populations. These results suggest fire-injured lodgepole pines can provide a reservoir to *D. ponderosae* during the lengthy periods during which their populations are too low to overcome the resistance of healthy trees. Likewise, wildfire could contribute to high-density populations remaining at outbreak levels, to the extent that they provide a source of moderate-severity trees. However, whether

fire injury could increase beetle populations from nonoutbreak to outbreak levels is uncertain, and could be offset by the unsuitability of severely injured trees due to lower substrate quality, the unsuitability of low-severity trees due to host defenses, and the extent to which the heterogeneity of wildfire disturbance limits the availability of moderate-severity hosts. This heterogeneity among and within sites necessitates the use of multiple rather than single fire injury measurements to assess the susceptibility of fire-injured trees to *D. ponderosae* attack. There is also evidence at some sites of effects of other variables, such as topography and incidence of disease, on *D. ponderosae* colonization. These results further illustrate the importance of cross-scale interactions and thresholds in insect outbreaks, specifically behavioral differences in how *D. ponderosae* select individual hosts during their various stand-level population phases.

Key words: bark beetle, fire, plant defense, population dynamics, disturbance interactions, Greater Yellowstone Ecosystem

1. Introduction

Biotic and abiotic disturbances play important roles in the functioning of natural ecosystems, contributing to community structure and composition (Taylor, 1973; Pickett and White, 1985), biodiversity (Chapin et al., 1997; Hiers et al., 2000), and nutrient cycling (Christensen, 1987; Chapin et al., 1996; Smithwick et al., 2005). Disturbances can also interfere with human objectives, 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 dramatically in recent years. Among the most important insights are that disturbances are highly heterogeneous in space, time, and intensity (Turner et al., 1994; Burton et al., 2008; Schoennagel et al., 2008), and that interactions among different disturbance agents can strongly affect ecosystem responses, with these interactions ranging from buffering to synergistic (Kulakowski et al., 2003; Bigler et al., 2005). Unfortunately, we know little about the mechanisms of how disturbances interact (Chesson and Rosenzweig, 1991).

Conifer ecosystems dominate large areas of western North America. These forests are strongly affected by two major disturbance regimes: wildfire and outbreaks by native insects, especially bark beetles (Romme and Knight, 1982; Attiwill, 1994; Hessburg and Agee, 2003). Both are highly heterogeneous, have lengthy periods between major events, and show variable effects depending on the scale at which they are considered. Likewise, both respond to exogenous weather factors such as drought (Bessie and Johnson, 1995; Schoennagel et al., 2005) and temperature (Regniere and Bentz, 2007), and to endogenous features of forest structure such as stand age and density (Safranyik et al., 1974; Romme and

Knight, 1981). They differ in that bark beetles are strongly associated with particular tree genera, and respond to specific predisposing biotic agents such as defoliators and root pathogens (Klepzig et al., 1991; Wallin and Raffa, 2001). Strong reciprocal interactions between these disturbance agents have been proposed, including increased frequency of fires in areas experiencing bark beetle outbreaks (Martin and Mitchell, 1980) and increased susceptibility of fire-injured forests to beetle colonization and subsequent outbreaks (Geiszler et al., 1980). However, the empirical evidence for both relationships is limited and contradictory (Gara et al., 1984; Geiszler et al., 1984; Rasmussen et al., 1996; Romme et al., 2006; Jenkins et al., 2008; Simard et al., in press).

Conifers exhibit a variety of adaptations to fire (Habeck and Mutch, 1973; Kilgore, 1973). Some, such as ponderosa pine and Douglas-fir, insulate the cambium and phloem tissues with thick bark (Peterson and Arbaugh, 1986; Peterson and Ryan, 1986). Others, such as lodgepole pine, have thin bark that makes it susceptible to fire injury (Ryan and Reinhardt, 1988), but possess serotinous cones that release seeds post-fire and favor rapid reproduction (Tinker et al., 1994; Schoennagel et al., 2003).

Bark beetles (Coleoptera: Curculionidae, Scolytinae) mine ovipositional and larval galleries within phloem, and are a major cause of tree mortality (Wood, 1982). Trees respond to colonization attempts with integrated constitutive and induced defense responses. Resinosis at the site of beetle entry can “pitch-out” or delay the beetle (Safranyik and Carroll, 2006). Induced responses, including rapid accumulation of toxic allelochemicals at the attack site and autonecrosis, can confine and kill the insects (Zulak and Bohlmann, 2010). Bark beetles produce aggregation pheromones that rapidly attract additional beetles in coordinated mass attacks (Wood, 1982), enabling them to surpass a critical threshold needed

to overwhelm those defenses (Raffa and Berryman, 1983). Physiological stress can weaken the trees' defenses against bark beetles making them more susceptible to attack (Lorio, 1993; 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 remain present in stands at very low densities, followed by intermittent outbreaks, during which they cause high tree mortality on a landscape scale (Coulson, 1979; Safranyik and Carroll, 2006). For example, the current mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreak in western North America exceeds any previously recorded forest insect outbreak (Taylor et al., 2006). A critical population threshold appears to separate these dynamics (Berryman, 1976; 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; McHugh et al., 2003; Wallin et al., 2003; Santoro et al., 2001). However, results with outbreak species are mixed. For example, Elkin and Reid (2004) observed no increase in *D. ponderosae* 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 brevicomis* 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 Douglas-firs that had

experienced several measures of wildfire injury. Further, Geiszler et al. (1984) found increased levels of attack by *D. ponderosae* following fire in an area with low populations, and suggested that fire-injured trees could provide a reservoir during endemic periods. Likewise, Elkin and Reid (2004) reported that *D. ponderosae* attacking trees in low numbers were more likely to produce viable eggs if the tree was artificially burned, but there was no relationship with fire when they attacked trees in high numbers. In a nonoutbreak area, Wallin et al. (2003) found that fire injury to ponderosa pine resulted in increased attraction of *D. ponderosae*, but their rate of successful colonization was uniformly low. Together, these results suggest that beetle population phase may be an important factor in understanding how outbreaking bark beetle species respond to fire, both individually and in their numerical trends.

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. We sampled lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelmann), the primary host of *D. ponderosae*, in burned and unburned and outbreak and nonoutbreak, sites throughout the Greater Yellowstone Ecosystem.

2. Methods

2.1. Study Sites

We sampled 16 lodgepole pine sites within the Greater Yellowstone Ecosystem (Table 1). Eight experienced wildfire, and 8 were neighboring unburned sites. Four of the wildfire sites burned during the summer of 2006, and 4 burned during the summer of 2007. Four of the burned sites (two within each year) were within areas where *D. ponderosae* was at epidemic population levels, and 4 (two within each year) were in areas where it was at endemic population levels. The burn sites were separated by 30 - 159km in 2006, and 52 - 217km in 2007. The dispersal range of *D. ponderosae* is approximately 5km (Safranyik and Carroll, 2006). All sampling was conducted during the year following each wildfire, which allowed for one intervening flight period by *D. ponderosae*.

2.2. Transect Establishment, and Sampling of Fire Injury and Colonization by *Dendroctonus ponderosae*

Four, 5m x 100m belt transects were established in each site, beginning at the edge of tree mortality caused by the wildfire, and extending away from the epicenter. Trees within each transect were sampled to determine the degree of fire injury (see below). The origins of these transects were located approximately at the cardinal directions of the burn borders. Sampling along each transect progressed until it contained at least five trees each within the low-, moderate-, and high-severity fire injury categories. We also sampled 8 adjacent paired unburned sites by the same method to obtain fully unburned trees. A total of 2056 trees was sampled.

All sampled lodgepole pines were examined to determine presence or absence of *D. ponderosae* and other subcortical insects. The presence of all subcortical insects was

determined by examining entry holes and peeling small pieces of bark to observe characteristic beetle galleries.

We examined each tree for symptoms of dwarf mistletoe (*Arceuthobium americanum* Nuttall Ex. Engelmann) and comandra blister rust (*Cronartium comandrae* Peck). We recorded slope, aspect, and elevation and population phase at each transect. The presence of symptoms due to described blister rust was noted visually using the method of Geils and Jacobi (1984). The severity of mistletoe was rated as described in Hawksworth (1979). Slope was determined by clinometer, aspect was determined by compass, and elevation was determined by GPS.

2.3. Fire-Injury Classification

All trees were examined to determine their degree of fire injury, and assigned into one of four categories: “unburned”, “low-severity”, “moderate-severity”, and “high-severity”. 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 represent potential damage to root tissue. Bole-injury describes the trunk of the tree from ground to 1.3m in height. 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 2cm diameter disk of bark from each cardinal direction, with the number of disks with darkened, dead cambial tissue providing a scale of 0 to 4 as described by Ryan (1982) .

Trees with no fire injury for any of these parameters were designated as “unburned”. “Low-severity” trees had 0-10% basal- and bole- injury and 0% canopy-injury, and a cambium kill rating of 0 or 1. “Moderate-severity” trees had 0-50% basal- and bole- injury, 0-10% canopy-injury, and a cambium kill rating of 1-3. “Unburned”, “low-severity”, and “moderate-severity” trees were all alive post-fire. “High-severity” trees had 50-100% basal- and bole- injury, 10-100% canopy-injury, and a cambium kill rating of 3-4; these trees were usually killed by the wildfire.

2.4. *Dendroctonus ponderosae* Population Phase

The population phase of *D. ponderosae* was determined for each site based on USDA Forest Service aerial detection surveys from 2007 and 2008. Areas where more than 30 trees per ha killed by *D. ponderosae* were considered outbreak areas (USDA, 2007, 2008a, 2008b).

We sampled beetle populations by deploying three 12-funnel flight traps per burn site. Traps were baited with myrcene, *exo*-brevcomin, and *trans*-verbenol (Borden et al., 1993). Traps were deployed at burn edges and were at least 100m from each transect so as not to influence colonization patterns in the sampled trees. Traps were distributed around each burn by approximately 120°.

2.5. Statistical Analyses

All analyses were performed using the statistical software R v2.7.2. The binary response of colonized / not colonized by *D. ponderosae* was measured in all cases. We performed two Multinomial Chi-Squared analyses to examine effects of fire, beetle population phase, and their interactions. The first modeled all fire injury categories as separate levels, and the second pooled the various burn categories to compare burned versus unburned trees.

We also used a generalized linear model (lme4 package in R v2.7.2, Bates and Maechler, 2010), to incorporate site as a covariate. We modeled fire injury category and population phase with a logit transformation. Five sites did not have trees colonized by *D. ponderosae*, so 11 sites were included in the final model. Four sites were burned and in areas where *D. ponderosae* populations were epidemic; 4 were unburned and in areas where *D. ponderosae* populations were epidemic; 3 were burned and in areas where *D. ponderosae* populations were endemic. We plotted the coefficients for the site variables against the average number of *D. ponderosae* captured in the baited 12-funnel flight traps at each site. We then performed a Wilcox rank sum test to differentiate between the coefficients of epidemic and endemic population sites.

Variation between sites was too high to permit use of one single mixed-effects model to evaluate other potential pathogenic and environmental variables on colonization response. To test effects of these potential variables on colonization, we performed separate analyses for each site using a generalized linear model with a logit transformation. We used a backward elimination procedure with Akaike's information criteria (AIC) (Akaike, 1973), and selection of variables with $\alpha = 0.05$, to identify the best model for each site.

We constructed single variable models for each of the ten measurements, on a per site basis, to identify potentially common variables across all sites while also contending with high site-level variation. The colonization response was predicted for each model. We then compared the predictions for each model with the actual observed values. The predicted values were proportional and fell between 0 and 1, whereas the observed values were binomial. We tallied each predicted value that was at least 50% of the observed value. If 65% or more of the predicted values for each single-variable model were within 50% of the observed value, that variable was compared across each of the sites. Sixty-five percent was chosen because it was the maximum percentage of points with a 50% fit for three sites.

3. Results

Of the 2056 trees that we sampled, there was an average of 28 (\pm 26) unburned, 18 (\pm 31) low-severity, 9 (\pm 9) moderate-severity, and 10 (\pm 6) high-severity trees per transect. There were significantly fewer moderate-severity trees when compared with both low- and high-severity trees at each transect (Wilcoxon rank sum for moderate and low trees, $P < 0.01$; Wilcoxon rank sum for moderate and high trees, $P < 0.01$). There was no significant difference between low- and high-severity trees at each transect (Wilcoxon rank sum, $P = 0.77$). Unburned trees were not compared with other fire injury categories as they were sampled from separate unburned sites, and therefore did not share transects with other fire injury categories.

Fire injury strongly influenced colonization of lodgepole pine by *D. ponderosae* (Fig. 1) ($\chi^2 = 120$, $df = 3$, $P < 0.01$). However, this relationship was non-linear, with the highest

rates of attack on moderate-severity trees. There was no significant interaction between degree of fire injury and beetle population phase (Multinomial $\chi^2 = 8$, $df = 6$, $P = 0.24$). Because the small percentage of colonized trees in endemic sites may have obscured an interaction between degree of fire injury and population phase, we also combined fire-injured trees of varying severities. When all trees are categorized as either burned or unburned (Fig. 2) there is a strong interaction between fire injury and beetle population phase in colonization behavior (Multinomial $\chi^2 = 93$, $df = 1$, $P < 0.01$). In particular, *D. ponderosae* colonized unburned trees in epidemic but not endemic sites. The number of adult beetles caught per flight trap averaged 3419 among epidemic sites and 711 among endemic sites (Fig. 2).

We further explored the *D. ponderosae* – fire relationship using a generalized linear regression model (Table 2). This generalized linear regression model with injury category and site as the only variables was constructed to examine their impact on *D. ponderosae* colonization. Each site coefficient from the model was significant at $\alpha = 0.05$, confirming preliminary results that site variability was very high. Each of the four fire injury category factors in this model was also significant at $\alpha = 0.05$. This confirmed our Multivariate χ^2 result of a significant difference of *D. ponderosae* colonization across the fire injury categories. The coefficients from the epidemic and endemic sites found within Table 2 were plotted against the mean number of beetles captured in flight traps (Fig. 3). The coefficients of the three endemic sites were lower than those of all epidemic sites, whether burned and unburned (Wilcox rank sum, $P = 0.06$). There also appeared to be a step increment once the population phase exceeded approximately 1700 beetles per trap. There was no significant difference between the site coefficients in the burned and unburned epidemic sites (Wilcox rank sum, $P = 0.98$). We found similar trends, of high variability among all sites and

especially large differences between epidemic and endemic sites, when a generalized linear regression model was constructed using site as the only variable (Appendix 1).

Trends within each site varied (Table 3), as expected given the high site-level variation (Table 2). All epidemic site models included fire injury category, though not each category factor was significant at $\alpha = 0.05$, and the colonization pattern for each model differed. For example, the model for Purdy revealed increased colonization with percent basal injury but decreased colonization with increasing fire injury category, and only the factors for unburned and high-severity categories were significant. Battle Mountain displayed a polynomial relationship between colonization and fire injury category, with significance only among factors for unburned, low-severity, and moderate-severity categories, and the highest level of colonization in the moderate-severity category. Salt Lick displayed a polynomial relationship between colonization and fire injury category, though only the factor for unburned category was significant. There is a high standard error for the factor for high-severity category, due to the lack of colonization in that category. Low percentages of colonization in variables results in large standard errors, and consequently a lack of significance at $\alpha = 0.05$. Hardscrabble displayed a bimodal relationship of colonization with fire injury category, with the highest levels of colonization among the low- and high-severity categories, although only the factors for unburned and low-severity categories were significant. This model also revealed increased colonization with cambium kill rating, and slightly decreased colonization with the interaction between percent bole injury and cambium kill rating. The three models for endemic sites did not share common variables. Hechtman Creek displayed an exponential increase of colonization with percent bole injury and a linear increase of colonization with cambium kill rating. Owl displayed an

exponential increase of colonization with percent basal injury. Madison Arm displayed increased colonization with percent bole injury and decreased colonization with the interaction between the percent bole injury and cambium kill rating. Topographic variables were significantly related to colonization in the models for two of seven sites. Purdy displayed increased colonization with increased angle of slope, and Hardscrabble displayed increased colonization with the interaction between angle of slope and elevation.

To identify common variables among all sites, we compared predicted with observed values of *D. ponderosae* colonization among separate models for each variable from each site. These models identified at least one fire injury measurement and at least two environmental variables consistent across all applicable sites, though the variables were not the same across the sites (Table 4). Slope, however, was the only variable that emerged from this analysis that commonly predicted a relationship with colonization with even a 50% level of accuracy. Colonization for 4 sites (3 of which had endemic populations) was predicted within 50% of the observed value for all variables. These models were highly conservative due to the small percentage of colonized trees within most of these sites. Colonization was not predicted within 50% of the observed value for the fire injury category models in three sites, all in outbreaks. Because no single fire injury measurement was consistently predicted among all 7 sites, all fire injury measurements appear necessary to accurately predict *D. ponderosae* colonization across multiple burn sites.

4. Discussion

Our results indicate that fire injury influences colonization rates by *D. ponderosae*, but in a nonlinear manner, and in a manner mediated by stand-level population density. These results have several implications for bark beetle epidemiology, disturbance interactions, and natural resource management. First, fire-injured trees can serve as a reservoir for beetles during their endemic population phase, when they lack sufficient numbers to overwhelm the defense of healthy trees (Geiszler et al., 1984; Wallin et al., 2003). However, this may be tempered by the reduced suitability of severely injured trees (Fig. 1), and the potentially lower beetle productivity in them due to competitors and reduced substrate quality (Jakubas et al., 1994; Elkin and Reid, 2004; Powell, 2010 Chpt 2). Second, population increases in fire-injured trees could conceivably lead to sufficient numbers to develop into subsequent outbreaks, but there are likewise important constraints. For example, unburned and high-severity trees were not susceptible to *D. ponderosae* when their populations were low (Fig. 2), and the availability of the more suitable, moderate-severity trees was relatively low (50% low-, 23% moderate-, 27% high-severity) following these fires. A third possibility, that fire injury could help sustain outbreaks already underway by providing more optimal trees, should also be considered. Additional studies incorporating beetle per-capita brood production, longer time frames, and larger spatial scales are needed to test how these various processes interact. Lastly, these results provide further support for the views that disturbance interactions can play important roles in ecosystem functioning (Pickett and White, 1985; Bigler et al., 2005), and that simultaneous investigations at several scales (e.g. within-tree and within-stand in this system) are needed to identify these relationships (Turner et al., 2003; Raffa et al., 2008).

These results may help clarify the wide range of results reported in the literature on interactions among fire, conifers, and tree-killing bark beetles. For example, Six and Skov (2009) found three bark beetle species preferred trees more severely injured by fire to trees that were unburned or low-severity, but did not in areas with higher beetle population phases. We found high-severity trees were colonized under outbreak but not nonoutbreak conditions. Elkin and Reid (2004) observed an interaction between beetles and fire injury at the higher colonization density at the tree level. Our results indicate the beetle population phase at the stand-level affects colonization of certain fire-injured trees over others. As population levels increase, we observe a potential threshold that beetles overcome to colonize trees both with and without fire injury (Fig. 3).

There was some evidence for involvement of additional tree- and stand- level variables in *D. ponderosae* colonization. However, the importance of these variables was inconsistent. Only two of our single-site models revealed significant stand-level variables, one with a positive relationship between colonization and slope, and one with a slightly negative relationship between colonization and the interaction between elevation and slope at our highest elevation site (Table 3). Slope, aspect and elevation contributed to our predictive ability at the majority of sites (Table 4). The presence of mistletoe and blister rust also predicted colonization at several sites. However, caution is needed in interpreting these relationships. For example, distributions of pathogens such as comandra blister rust and dwarf mistletoe occur in mosaics across the landscape (Kipfmüller and Baker, 1998), which can confound sampling schemes not designed explicitly to test their effects.

Our results support the view that incorporating multiple measurements of fire injury can improve our ability to predict responses by bark beetles (Hood and Bentz, 2007).

Specific fire injury measurements were more important in some sites than others (Table 3). Hence, inclusion of multiple measurements appears useful for contending with high inter-site variability. There was variability among the fire injury measurements in their ability to predict *D. ponderosae* colonization within 50% of the observed values across the sites (Table 4). All fire injury measurements had useful predictive value in sites with low *D. ponderosae* populations, but only one or two injury measurements were useful in outbreak sites. This information can help the design of future studies, specifically logistical decisions regarding trade-offs between sampling multiple fire measurements per tree versus sampling more trees.

These results also have implications to our understanding of the population dynamics of eruptive bark beetles. Specifically, eruptive species such as *D. ponderosae* appear to have flexible host selection strategies, being limited to stressed trees when their populations are low, but attacking almost any tree once their populations are high enough to overwhelm the defenses of vigorous hosts (Wallin and Raffa, 2004; Safranyik and Carroll, 2006). This allows individuals to fully exploit their host resource when there are sufficient conspecifics to overwhelm tree defenses, yet avoid localized extinction due to Allee effects when their populations are below this capability (Raffa et al., 2008). In response to this particular predisposing agent, *D. ponderosae* colonize fire-injured trees differently during different population phases. Investigations of defense physiology, interspecific competition, and substrate quality in fire-injured trees, and mechanisms of intraspecific variation in host selection behavior, should provide some insight into underlying mechanisms driving these transitions.

Acknowledgements

This research was supported by McIntire Stennis WIS0469, the Joint Fire Sciences Program 06-2-1-20, the National Science Foundation DEB-0816541, and the Univ. Wisconsin College of Agricultural and Life Sciences. We thank the National Park Service, especially Cindy Hendrix of Yellowstone National Park and Sue Consolo Murphy of Grand Teton National Park, for permission to conduct research within the park boundaries. Henry Harlow of the University of Wyoming and the crew at the University of Wyoming, National Park Service Research Center provided lodging and support during the field season, and Megan Fork, Katherine Molter, Christopher Foelker, Melissa Greulich, Jake Griffin, and Martin Simard provided valuable assistance in the field. Nicholas Keuler at the Univ. Wisconsin Statistical Consulting Lab provided statistical advice, and William Romme (Colorado State Univ.), Daniel Tinker (Univ. Wyoming), Philip Townsend (Univ. Wisconsin), and Monica Turner (Univ. Wisconsin) assisted with field site selection. The critical reviews of Philip Townsend, Monica Turner, and Daniel Young (Univ. Wisconsin) are greatly appreciated.

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Table 1. Eight sites burned by wildfire, and 8 corresponding unburned sites, in which individual lodgepole pines (N = 2056) were sampled for degree of fire injury and attacks by *D. ponderosae* throughout the Greater Yellowstone Ecosystem.

<i>D. ponderosae</i> population phase [†]	Site name	UTM*	Burn date	Size (ha)	Observed vegetation type
Epidemic	Purdy	E 578067 N 4822718	8/4/2006	8,113	Lodgepole pine
Epidemic	Purdy (unburned)	E 579432 N 4815124	N/A	N/A	Lodgepole pine
Epidemic	Battle Mountain	E 584084 N 4793634	7/2/2006	1,891	Lodgepole pine
Epidemic	Battle Mountain (unburned)	E 583919 N 479182	N/A	N/A	Lodgepole pine
Epidemic	Salt Lick	E 587219 N 4787509	7/11/2007	1,024	Lodgepole pine, mixed spruce/lodgepole
Epidemic	Salt Lick (unburned)	E 583905 N 4785703	N/A	N/A	Lodgepole pine, mixed spruce/lodgepole
Epidemic	Hardscrabble	E 573833 N 4837943	8/9/2007	1,061	Lodgepole pine, mixed whitebark/spruce/lodgepole
Epidemic	Hardscrabble (unburned)	E 574386 N 4836528	N/A	N/A	Lodgepole pine, mixed whitebark/spruce/lodgepole
Endemic	Magpie	E 522241 N 4940518	7/17/2006	1,461	Lodgepole pine
Endemic	Magpie (unburned)	E 514475 N 4936260	N/A	N/A	Lodgepole pine
Endemic	Hechtman Creek	E 516769 N 4877466	8/19/2006	632	Lodgepole pine, mixed spruce/lodgepole
Endemic	Hechtman Creek (unburned)	E 518775 N 4875209	N/A	N/A	Lodgepole pine, mixed spruce/lodgepole
Endemic	Owl	E 498096 N 4985506	9/20/2007	883	Lodgepole pine, mixed spruce/lodgepole
Endemic	Owl (unburned)	E 494956 N 4985335	N/A	N/A	Lodgepole pine, mixed spruce/lodgepole
Endemic	Madison Arm	E 487478 N 4949514	6/27/2007	602	Lodgepole pine
Endemic	Madison Arm (unburned)	E 488335 N 4944965	N/A	N/A	Lodgepole pine

[†] Determined by USDA Forest Service aerial surveys.

* Universal Transverse Mercator (UTM) points were within zone 12.

Table 2. A generalized linear model in which *D. ponderosae* colonization is related to 4 factors for fire injury category and eleven factors for burned or unburned site.

Variable	Coefficient	Std. Error	<i>P</i>
Category			
Unburned	0.12	†	†
Low	1.9	0.36	< 0.01
Moderate	2.7	0.37	< 0.01
High	N/A*	N/A*	N/A*
Site			
Purdy	-2.5	0.38	< 0.01
Purdy unburned	-1.5	0.25	< 0.01
Battle Mtn.	-2.3	0.37	< 0.01
Battle Mtn. unburned	-2.9	0.73	< 0.01
Salt Lick	-4.0	0.48	< 0.01
Salt Lick unburned	-2.3	0.40	< 0.01
Hardscrabble	-1.8	0.37	< 0.01
Hardscrabble unburned	-2.7	0.52	< 0.01
Hechtman Creek	-4.4	0.48	< 0.01
Owl	-4.4	0.56	< 0.01
Madison Arm	-5.0	0.53	< 0.01

† Coefficient derived from intercept estimate.

* Coefficient missing because of absent response variable.

Table 3. Individual generalized linear models for each burn site in which *D. ponderosae* colonization is related to several tree- and stand-level variables. The variables for each site below were in the model with the lowest AIC value.

<i>D. ponderosae</i> population phase	Site name	Variable	Coefficient	Std. Error	<i>P</i>
Epidemic	Purdy	Category:			
		Unburned	-1.9	0.27	<0.01
		Low	-0.17	0.68	0.80
		Moderate	-2.0	1.6	0.20
		High	-4.8	1.9	0.011
		% Basal	0.029	0.016	0.074
		% Slope	0.070	0.025	<0.01
Epidemic	Battle Mountain	Category:			
		Unburned	-2.9	0.27	<0.01
		Low	2.4	0.82	<0.01
		Moderate	3.4	0.85	<0.01
		High	0.38	0.94	0.69
Epidemic	Salt Lick	Category:			
		Unburned	-2.4	0.40	<0.01
		Low	0.96	0.60	0.11
		Moderate	0.45	0.74	0.54
		High	-16	1200 [†]	0.99
Epidemic	Hardscrabble	Category:			
		Unburned	-0.44	1.3	0.073
		Low	2.0	0.69	<0.01
		Moderate	0.90	1.6	0.57
		High	2.5	2.6	0.33
		CKR	2.0	0.82	0.015
		% Bole:CKR	-0.0029	0.0010	<0.01
		Elevation: Slope	-1.4 x 10 ⁻⁵	7.3 x 10 ⁻⁶	0.052
Endemic	Magpie	N/A*	N/A*	N/A*	N/A*
Endemic	Hechtman Creek	(% Bole) ²	0.00072	0.00027	<0.01
		CKR	1.6	0.46	<0.01
Endemic	Owl	% Basal	0.91	0.37	0.015
		(% Basal) ²	-0.0063	0.0024	0.01
Endemic	Madison Arm	% Bole	0.23	0.070	<0.01
		% Bole:CKR	-0.10	0.041	0.015

[†] High standard errors are due to a lack of mountain pine beetle colonization within the category.

* Magpie had no colonization by the mountain pine beetle to model.

Table 4. Single variable models from each of the 8 burns sites where *D. ponderosae* colonization was predicted within 50% of observed *D. ponderosae* colonization. Commonly predicted values were compared across the sites.

Variable	Epidemic				Endemic			
	Purdy	Battle Mountain	Salt Lick [†]	Hardscrabble	Magpie*	Hechtman Creek [†]	Owl [†]	Madison Arm [†]
Fire Injury								
composite fire injury category			×		N/A	×	×	×
% basal		×	×		N/A	×	×	×
% bole	×		×	×	N/A	×	×	×
% canopy	×		×		N/A	×	×	×
cambium kill rating	×		×	×	N/A	×	×	×
Pathogens								
mistletoe		×	×		N/A	×	×	×
blister rust	×		×		N/A	×	×	×
Topography								
slope	×	×	×	×	N/A	×	×	×
aspect	×	×	×		N/A	×	×	×
elevation	×		×	×	N/A	×	×	×

[†] All predicted variables in endemic sites and Salt Lick were within 50% of observed value due to the conservative nature of the models.

* No possible model for Magpie due to a lack of mountain pine beetle colonization.

× At least 65% of predictions for each site were within 50% of observed value.

Fig. 1. Effect of wildfire injury on colonization of lodgepole pine by mountain pine beetles. Sites were designated as epidemic or endemic based on USDA Forest Service data and criteria. Left) Epidemic beetle population phase; Right) Endemic beetle population phase.

Fig. 2. Percentages of lodgepole pines colonized by mountain pine beetles in 16 sites in the Greater Yellowstone Ecosystem. Colonization varies with both burn injury and beetle population phase. Left) Epidemic populations; Right) Endemic populations. The names refer to the sites in Table 1. The numbers are the means and standard errors of mountain pine beetle adults trapped in flight traps at each site.

Fig. 3. Site variable coefficients from a generalized linear model of mountain pine beetle colonization in fire-injured trees at 11 sites ($\log(D. ponderosae) = \beta_0 + \beta_1 \log(\text{fire injury category}) + \beta_2 \log(\text{site})$) plotted against the average number of mountain pine beetle collected in flight traps from each site. The more negative the coefficient, the lower the percentage of colonized trees. Open points refer to endemic sites and closed figures refer to epidemic sites.

Fig. 1.

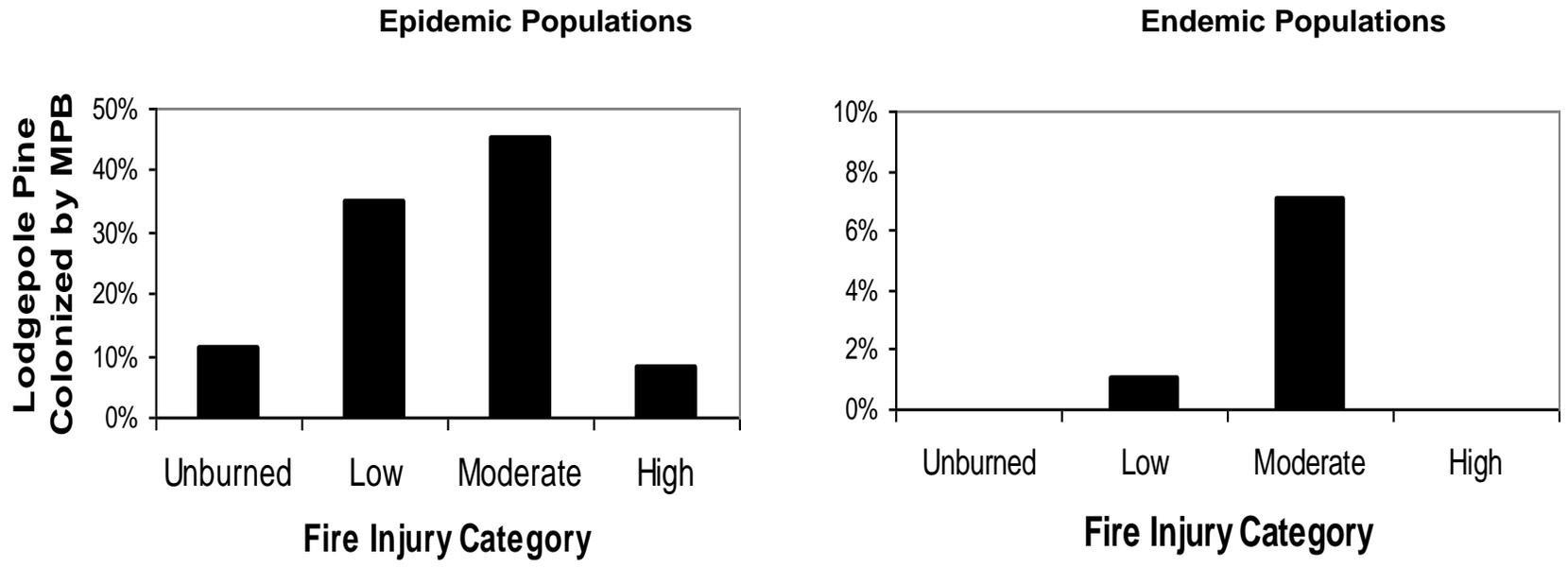


Fig. 2.

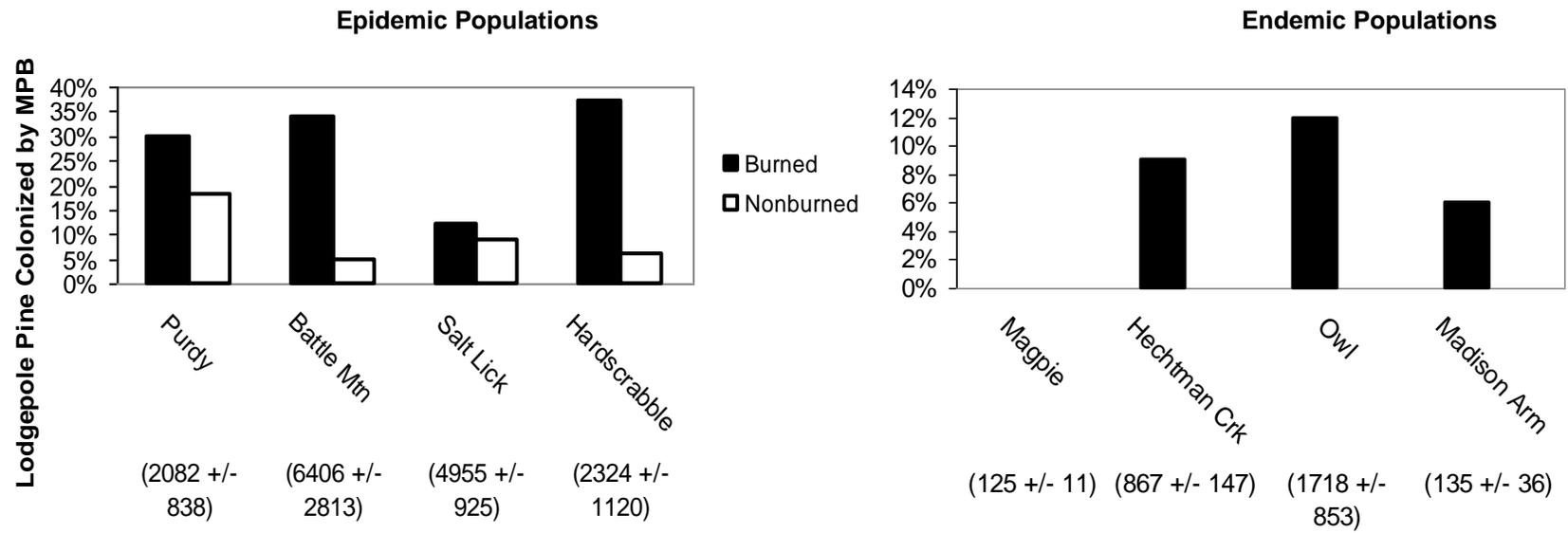
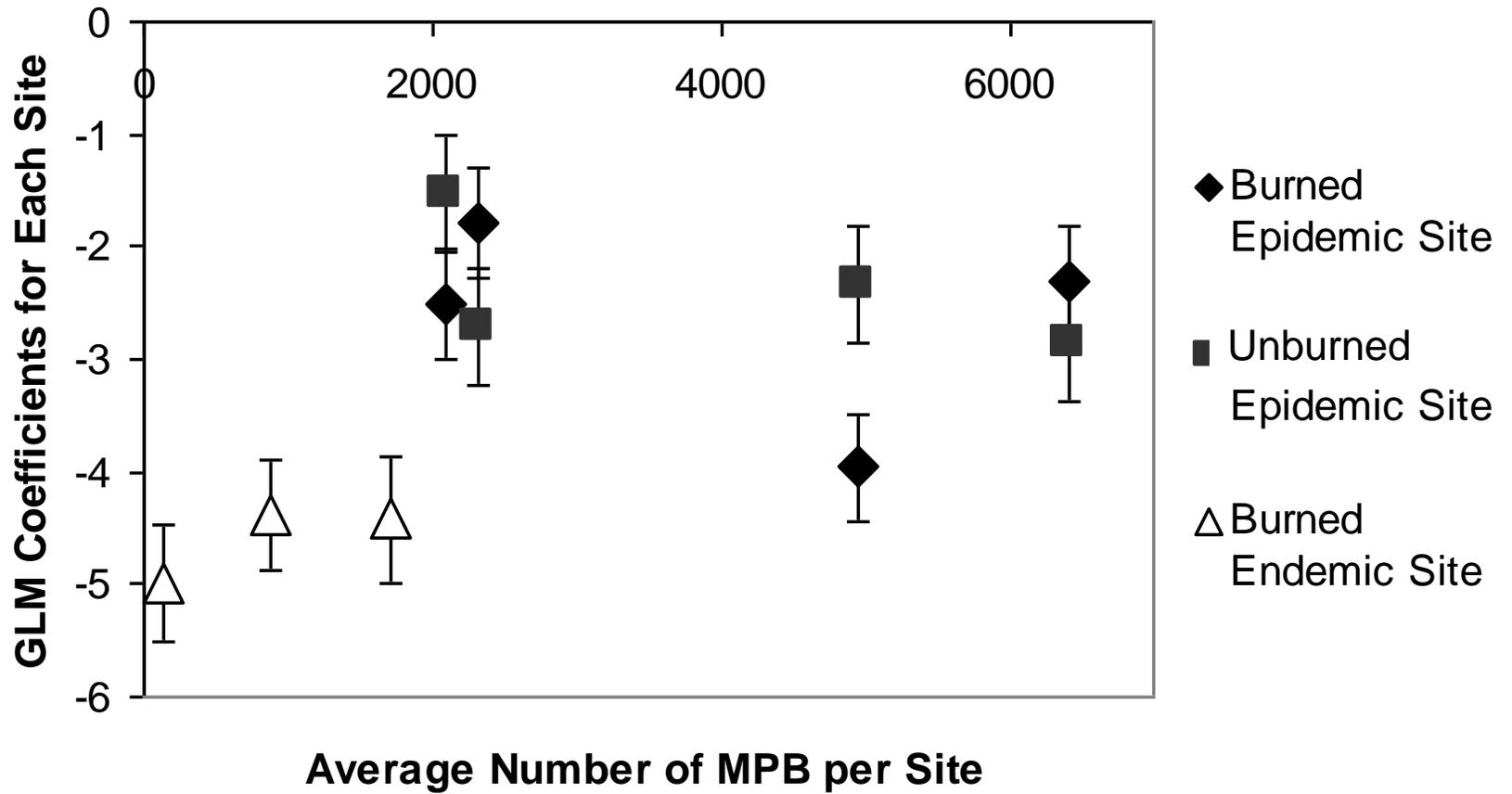


Fig. 3.



CHAPTER 2

EFFECTS OF WILDFIRE INJURY TO LODGEPOLE PINE ON THE REPRODUCTIVE SUCCESS OF MOUNTAIN PINE BEETLES AND EXPLOITATION BY ASSOCIATED SUBCORTICAL HERBIVORES

Abstract

Bark beetle outbreaks cause widespread mortality to conifers across the forests of western North America. Outbreaks of some bark beetle species are known to be prompted by agents that cause physiological stress, thereby reducing tree defenses. We investigated whether injury due to wildfire affects the reproductive success of *Dendroctonus ponderosae* Hopkins in lodgepole pines (*Pinus contorta* Douglas var. *latifolia* Engelman). We sampled healthy and fire-injured lodgepole pine in 4 sites, and 2 corresponding sites not burned by wildfire within the Greater Yellowstone Ecosystem. One hundred and six trees were examined and grouped into fire injury categories based on percent basal injury, percent bole injury, percent canopy injury, and cambium kill rating. We examined these trees for the number of parental entry and adult brood emergence holes to determine reproductive success of *D. ponderosae*. Seventy nine different trees were also examined for level of fire injury, and the gallery areas of *D. ponderosae* and other coleopteran subcortical herbivores, such as other bark beetles and wood-borers (Cerambycidae spp.) within them were sampled. The attack densities and brood emergence of *D. ponderosae* decreased with fire injury. Its reproductive success (per-capita brood production) was highest in moderate-severity trees. The total gallery area of *D. ponderosae* was highest in trees not injured by fire, while the gallery areas of *Ips* spp., coleopteran wood-borers (Cerambycidae spp.), and *Pityogenes* spp. were larger in fire-injured trees. We deployed baited 12-funnel flight traps the year following the fire to capture flying insects in 8 sites burned by wildfire. At each site, three traps each were baited with myrcene, *exo*-brevcomin, and *trans*-verbenol, (-) ipsdienol and lanierone, and (+) α -pinene and EtOH. Funnel traps captured several subcortical herbivores,

of which *Ips pini* (Say), *Pityogenes spp.*, *Pityokteines spp.*, and *Pityophthorus spp.* were predominant. These results suggest that fire injury affects the per-capita brood production of *D. ponderosae*, and therefore may contribute to the population dynamics of the beetle in forests burned by wildfire. However, other subcortical herbivores are also present in these burned forests and establish larger total gallery area within fire-injured trees. These herbivores may act as competitors, thereby limiting the per-capita brood production of *D. ponderosae* in more severely-injured trees. In addition to competition, host suitability, substrate quality, and regional beetle dynamics need to be considered in assessing of *D. ponderosae* population dynamics in forests disturbed by wildfire.

Key Words: *Dendroctonus ponderosae*, reproductive success, population dynamics, fire

Introduction

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are important agents of conifer mortality in North American forests, and their intermittent outbreaks cause significant socioeconomic and environmental challenges. For example, British Columbia is currently experiencing an outbreak by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, which has killed trees across more than 3.25 million ha of lodgepole pine forests, yielding an estimated 435 million cubic meters in timber losses (Walton et al. 2008). Thus, there is increased interest in factors that increase susceptibility to bark beetle colonization, and whether, and the extent to which, outbreak populations will result.

Trees respond to colonization attempts by employing sophisticated constitutive and induced defenses (Berryman 1972, Raffa and Smalley 1995). Upon entering the trees, beetles encounter resin that contains several preformed allelochemicals (Raffa and Berryman 1983) and induce heightened allelochemical biosynthesis and the formation of inconsumable necrotic wound tissue (Lewinsohn et al. 1991). The prevalence of resistant trees restricts bark beetles to defensively weakened trees until beetle populations increase and become sufficient to overwhelm tree resistance mechanisms (Raffa and Berryman 1987).

A variety of biotic and abiotic stress agents have the potential to decrease resistance against bark beetles (Christiansen et al. 1987). Biotic factors, such as below- and above-ground herbivory can predispose trees to an attack (Klepzig et al. 1991). Lightning-injured trees can act as a refuge for bark beetles where their populations are low, and as a source for the build-up of populations into outbreaks (Coulson et al. 1983, Blanche et al. 1985, Flamm et al. 1993).

Stress caused by fire injury can also influence the population dynamics of bark beetles. In particular, fire-injured trees may be more susceptible to colonization, but the population size of the beetles may be an important contributing factor (Wallin et al. 2003, Hood and Bentz 2007, Six and Skov 2009, Powell 2010, Ch.1). Also, the relationship of fire injury to reproductive success in trees can be complex (Elkin and Reid 2004). Thus, we currently cannot predict whether, or the extent to which, wildfire increases the likelihood or magnitude of bark beetles outbreaks.

Fire-injured trees are also hosts to a complex of secondary bark and wood-boring beetles (Coleoptera: Cerambycidae, Buprestidae) (Amman and Ryan 1991, Rasmussen et al. 1996, Ryan and Amman 1996, Werner 2002, McHugh et al. 2003), including those that may be unable to attack live trees of any condition, or unable to attack healthy trees even when their populations are high. Non-eruptive bark beetles and wood-borers found in fire-injured trees have the potential to both predispose trees to bark beetles (Bradley and Tueller 2001, McHugh et al. 2003) and out-compete them for this stressed-host resource (Flamm et al. 1993, Rasmussen et al. 1996).

Our objective for this study was to evaluate the effects of wildfire injury on the per-capita brood production of *D. ponderosae* within lodgepole pines (*Pinus contorta* Douglas var. *latifolia* Engelmann) in the Greater Yellowstone Ecosystem (Wyoming, U.S.A.). We examined the per-capita brood production of *D. ponderosae*, the bark and wood-boring beetle community composition in fire-injured trees, and the insects associated with sites burned by wildfire.

Materials and Methods

Sites and Experimental Design

We sampled 8 sites burned by wildfire, and paired non-burn sites adjacent to 2 of them, throughout the Greater Yellowstone Ecosystem (Fig. 1). Detailed site descriptions are in Powell (2010, Ch.1).

We performed three types of sampling: a) *D. ponderosae* per-capita brood production within colonized trees at 4 of the 8 burn sites and the 2 unburned sites (106 trees); b) incidences and areas of galleries by *D. ponderosae* and other subcortical insects (79 trees, different from above); c) flight traps (N = 72) baited with semiochemicals at the 8 burn sites.

All trees were sampled for four measures of burn injury: basal-injury, bole-injury, canopy-injury, and cambium kill rating. These measures were used to categorize trees as “unburned”, “low-severity”, “moderate-severity”, or “high-severity”, as detailed in Powell (2010, Ch.1). The height and diameter at 1.3m (DBH) were measured at each tree. Colonization by subcortical insects was noted at each tree. Symptoms of dwarf mistletoe (*Arceuthobium americanum* Nuttall Ex. Engelmann), comandra blister rust (*Cronartium comandrae* Peck), slope, aspect, and elevation at each location were also recorded (Powell 2010, Ch.1).

Reproduction of *Dendroctonus ponderosae* within Trees of Various Fire Injury Classes

All sites at which within-tree sampling was performed (4 burned and 2 unburned), were within areas of *D. ponderosae* outbreak, based on USDA Forest Service aerial detection surveys from 2007 and 2008 (USDA 2007, 2008a, 2008b). Trees were sampled along four

5m x 100m belt transects from the burn edge into healthy forest at each site, as described in Powell (2010, Ch.1). At unburned sites, transects crossed each other and extended in the cardinal directions. We evaluated fire categorized trees for colonization by *D. ponderosae*. We continued along transects that were accessible by road or trail until each fire injury category had 20 colonized trees. Due to some miscounts, this value sometimes deviated from 20.

Dendroctonus ponderosae entry holes were identified and counted from tree base to 1.3m on each tree, one year after each wildfire. The emergence holes were counted after at least one more year, but before another flight period. *Dendroctonus ponderosae* entry holes are usually easy to identify by the accumulation of resin that surrounds them (Safranyik and Carroll 2006). On the occasions that an entry hole was not surrounded by resin, a small amount of bark was removed to identify the beginning of the “J-shaped” gallery characteristic of *D. ponderosae* (Safranyik and Carroll 2006). Great care was taken not to disturb eggs that were deposited along the gallery.

Dendroctonus ponderosae emergence holes were also counted on each tree to a height of 1.3m. Emergence holes can be distinguished from entry holes by their smaller size (2mm in diameter) and lack of resin surrounding the hole (Safranyik and Carroll 2006). If there was any uncertainty in our identification, or if only one or two emergence holes were found near a pitch-tube, leading us to suspect multiple adults emerging from the same emergence hole, bark was peeled away and the pupal chambers beneath the bark were counted. The per-capita brood production of *D. ponderosae* was estimated as the ratio of emergence holes to entry holes.

Species Assemblage and Gallery Areas within Trees of Various Fire Injury Classes

Galleries of *D. ponderosae* and other beetles were examined within 79 lodgepole pines that had experienced various degrees of fire injury. Sampling was conducted one year after the wildfire, following the flight of *D. ponderosae* and before another flight. Sampling was conducted in the same sites and transects, but in different trees, as the measurements of *D. ponderosae* per-capita brood production.

Ovipositional galleries of various bark beetles were identified based on descriptions in Wood (1982). Galleries of wood-boring larvae were identified based on descriptions in Furniss and Carolin (1977). Wood-boring beetle adults oviposit on the bark so we could not measure their ovipositional galleries. Samples were quantified using the method of Coulson et al. (1976). At each tree, two 14cm diameter disks of bark were removed at 1.3m on the north and south facing portions respectively. The disks were photographed, uploaded into Adobe Photoshop®, and the number of pixels for each bark beetle adult ovipositional or wood-boring larval gallery was counted. The pixels for the total area of the bark disk were also counted. The gallery areas were grouped according to beetle taxonomic group and averaged for each tree. Galleries were adjusted to a per cm² basis by determining the proportion of total gallery area of all bark or wood-boring beetles to the total area of the bark disk that was removed for the sample (Flamm et al. 1993).

Insects Associated with *Dendroctonus ponderosae* in Sites Burned by Wildfire in the Greater Yellowstone Ecosystem

Baited 12-funnel flight traps were used to capture flying insects in the 8 burn sites. At each site, three traps were baited with myrcene, *exo*-brevcomin, and *trans*-verbenol to

capture *D. ponderosae* (Borden 1993), three were baited with (-) ipsdienol and lanierone to capture *Ips spp.* (Safranyik et al. 1996), and three were baited with EtOH and (+) α -pinene to capture various other bark and wood-boring insects (Schroeder and Lindelow 1989, Brockerhoff et al. 2006, Ganhdi et al. 2009).

The locations for trap deployment at each burn were selected to be at least 100m from the location of each transect, so as not to influence colonization patterns in the sampled trees. Three groups of three traps each surrounded each of the 8 burns and were 120° apart. The traps were deployed in early June prior to beetle flight, and were collected one month later, post-beetle flight. All captured insects were killed with a 2cm square of Hot Shot ® No Pest Strip, dried to preserve them, 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.

Statistical Analyses

Per-Capita Brood Production of Dendroctonus ponderosae within Trees of Various Fire Injury Classes. The data for *D. ponderosae* entry, emergence, and per-capita brood production were distributed normally. Normality was tested using quantile-quantile plots and constant variance was examined using Bartlett tests. We examined beetle entry, emergence, and per-capita brood production across the four fire injury categories with one-way ANOVAs in R v.2.7.2.

Dendroctonus ponderosae entry, emergence, and per-capita brood production were also analyzed with linear regression models that included DBH, height, mistletoe rating, the presence of blister rust, the presence of other bark and wood-boring insects, the individual

fire injury measurements, slope, aspect, and elevation with linear regression models. We constructed three separate linear regression models for beetle entry, emergence, and per-capita brood production. Models were selected using a backward elimination procedure with Akaike's information criteria (AIC) (Akaike 1973), and selection of variables with $\alpha = 0.05$, to identify the best model for each site.

To examine *D. ponderosae* productivity in fire-injured trees without the influence of competition, we tested for difference between trees that were colonized by beetles of other taxonomic groups and trees that were not colonized using a Kruskal-Wallis analysis. These data were not normally distributed, so a Kruskal-Wallis analysis was appropriate.

Species Assemblage and Gallery Areas within Trees of Various Fire Injury Classes. The presence of different beetle galleries was analyzed with the inclusion of the above tree- and stand-level measurements. We constructed generalized linear regression models for the presence of galleries per tree for each species group using a logit transformation with lme4 package in R v2.7.2 (Bates and Maechler 2010). We constructed four separate generalized linear regression models, one for each major species group obtained: *D. ponderosae*, *Ips* spp., *Pityogenes* spp., and wood-boring beetle (Cerambycidae spp.) galleries. The generalized linear regression models for the presence of beetle galleries were chosen using the same method of backward elimination with AIC as for choosing the linear regression models for *D. ponderosae* entry, emergence, and productivity.

Beetle gallery areas were distributed in a non-normal fashion, and in many of the trees, some species were present but others were absent. Therefore, we employed nonparametric statistical analyses that did not necessitate normally distributed data. 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). We similarly assessed differences among beetle gallery areas while including multiple variables: 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, with canonical correspondence analysis (CCA). This analysis was done using PCORD (McCune and Mefford 2006).

Insects Associated with Dendroctonus ponderosae in Sites Burned by Wildfire in the Greater Yellowstone Ecosystem. Predators and subcortical herbivores captured in flight traps in sufficient numbers (≥ 81 from all sites) were tested for normal distribution at each site with a quantile-quantile plot. Because the numbers were not normally distributed, they were compared across the three bait types with Chi square analysis in R v2.7.2. The numbers of bark and wood-boring beetles captured from traps baited with (-) ipsdienol and lanierone were tested for differences across all 8 sites with Chi squared analyses.

Results

Reproduction of *Dendroctonus ponderosae* within Trees of Various Fire Injury Classes

The number of *D. ponderosae* entry sites per attacked tree decreased with fire injury (Fig. 2A, One-way ANOVA, $F_{(3,102)} = 110$, $P < 0.01$). The average numbers of holes/m² were: 110 ± 78 , 51 ± 47 , 30 ± 31 , 13 ± 14 for unburned, low-, moderate-, and high-severity categories, respectively. Likewise, the number of *D. ponderosae* emergence sites decreased with fire injury (Fig. 2B, One-way ANOVA, $F_{(3,102)} = 34$, $P < 0.01$). The average numbers of holes/m² were: 73 ± 140 , 59 ± 82 , 38 ± 52 , 4.8 ± 12 for unburned, low-, moderate-, and

high-severity categories, respectively. Per-capita brood production varied among the fire injury categories, with the moderate-severity category yielding the highest ratio of emergence to entry holes (Fig. 2C, One-way ANOVA, $F_{(3,102)} = 5.1$, $P < 0.01$). Average entry holes/emergence holes ratios were: 0.68 ± 1.1 , 1.5 ± 1.7 , 2.1 ± 3.5 , 0.67 ± 1.7 for unburned, low-, moderate-, and high-severity categories, respectively.

Using linear regressions, we identified several variables relating to *D. ponderosae* entry, brood emergence, and per-capita brood production. *Dendroctonus ponderosae* entry decreased dramatically with fire injury category (Table 1A), at a more than three-fold increase in unburned compared with highly injured trees. *Dendroctonus ponderosae* emergence also decreased with fire injury (Table 1B) category, but the strongest decrease occurred between moderate-severity and high-severity trees. This suggests that trees with high fire injury do not yield very successful broods of *D. ponderosae*. The number of *D. ponderosae* emergence holes also decreased with the interaction between site and the presence of the bark beetle *Pityogenes spp.* The ratio of emergence holes to entry holes followed a non-linear trend across fire injury categories, with the moderate-severity fire injury category having the highest level of productivity, and a negative trend with the interaction between site and the presence of *Pityogenes spp.* (Table 1C, $R^2 = 0.56$, $F_{(6,100)} = 24$, $P < 0.01$).

A large proportion of the *Pityogenes spp.* was captured at one site (370 *Pityogenes* per funnel trap on average at Hardscrabble versus 81, 59, and 50 at other sites), so we analyzed them separately. The linear regression model with Hardscrabble excluded indicated that the presence of *Pityogenes spp.* was not significant in the model with the best fit, $R^2 = 0.68$, $F_{(5,75)} = 32$, $P < 0.01$. This model revealed a significant decrease of *D. ponderosae*

emergence holes with fire injury and a decrease of *D. ponderosae* emergence holes with tree height (Appendix 2A). The linear regression model for only Hardscrabble indicated relationships between *D. ponderosae* emergence holes and several variables not included in the full model (Appendix 2B). Fire injury category was included in this model, though only the unburned category was significant. The percentage of bole injury was also included in this model, but was not significant. Increases in mistletoe rating and the incidence of *Pityogenes spp.*, resulted in significant increases in *D. ponderosae* emergence hole density.

The ratios of *D. ponderosae* emergence to entry holes were examined in the sampled trees where competitors were not present to test for direct effects substrate quality on brood production in fire-injured trees. The lack of difference between trees with competitors present versus absent (Kruskal-Wallis $\chi^2 = 3$, $df = 3$, $P = 0.39$) suggests that substrate quality had a stronger effect than competition on *D. ponderosae* pre-capita brood production, but further investigation is necessary.

Species Assemblage and Gallery Area within Trees of Various Fire Injury Classes

Dendroctonus ponderosae total ovipositional gallery area was generally larger in unburned lodgepole pines (Fig. 3A). In contrast, competitor ovipositional and larval gallery areas were larger in fire-injured trees. For example, *Ips spp.* total ovipositional gallery area was largest in high-severity trees, and total gallery area was also large in low- and moderate-severity trees (Fig. 3B). Wood-borer (Cerambycidae *spp.*) total larval gallery area was largest in high-severity trees, and very few to no galleries were present in trees of the other fire injury categories (Fig. 3C). *Pityogenes spp.* total gallery area was highest in moderate-

severity trees (Fig. 3D). The composition of beetle taxonomic groups is significantly different across fire injury categories (one-way ANOSIM $R = 0.076$, $P = 0.03$).

Many of our sampled disks included galleries of some but not all of the species groups. Therefore we examined the trends across fire injury categories for each species group with zeros removed from the analysis. Similar trends occurred for all species groups (Fig. 4). However, *Pityogenes spp.* total gallery area increased somewhat in low- and high-severity trees when zeros were excluded from when they were included. Overall, there was a decrease in the ratio of *D. ponderosae* total gallery area to the total gallery area of all competitors with fire injury (Fig. 5).

The inclusion of other environmental variables, fire injury category, tree size (DBH, height), and pathogens (mistletoe rating, presence of blister rust), also revealed differences between total gallery area of competitors across the fire injury categories when we performed CCA. The species-environment correlation was 0.57, $P < 0.01$ for axis 1, which denoted fire injury category (Fig. 6). The vector for fire injury category was highly correlated with the sampled trees, as represented by triangles on the graph. Correlations were very low for mistletoe rating and the presence of lesions symptomatic of blister rust. Correlations for DBH (0.38) and height (0.20) were not statistically significant. Despite the level of fire injury, gallery area was larger on average for *D. ponderosae* than all other species, $0.00066\text{cm}^2 \pm 0.0094$ per cm^2 .

The four beetle taxonomic groups (Fig. 7) showed different relationships between their gallery areas and fire injury categories. Larger gallery areas are represented by increasingly larger triangles. Wood-borers and *Pityogenes spp.* gallery area sizes were strongly correlated with higher fire injury categories, and these gallery areas were larger in

high-severity trees than trees of other categories. *Ips spp.* total gallery area was slightly correlated with higher-severity fire injury categories, and the total gallery area was slightly larger in these trees. *Dendroctonus ponderosae* total gallery area was strongly correlated with low-severity categories, and the galleries were larger in these trees. These CCA results agree with the means of gallery areas depicted in Fig. 3, 4, 5.

Generalized linear regression models for each species that colonized fire-injured trees revealed that different variables relate differently to the presence of the galleries of the various beetle taxonomic groups (Table 2). The presence of *D. ponderosae* galleries decreased with fire injury category. However, the coefficients for low-severity and unburned categories are very similar; this may indicate that beetle galleries occur in similar numbers in these trees. The presence of *D. ponderosae* galleries also increased with percent bole injury and DBH, and decreased with their interaction. There was also a high degree of association between the presence of *Pityogenes spp.* and *D. ponderosae* galleries. The presence of *I. pini* galleries increased with percent bole injury. The presence of wood-borer galleries increased with tree height. The presence of *Pityogenes spp.* increased exponentially with both percent bole and basal injury.

Insects Associated with *Dendroctonus ponderosae* in the Greater Yellowstone Ecosystem

A high diversity of insects was obtained in the flight traps. We tabulated only the species considered to be members of the bark and wood-boring beetle subcortical feeding guild, or ecologically associated with *D. ponderosae* such as predators and parasitoids.

Species that occur within dead and dying trees but are not usually considered competitors of

bark beetles were not counted, but their presence was noted. The remaining insects were considered to be incidental occupants of the traps and ignored.

Many of the subcortical herbivores that are likely competitors of *D. ponderosae*, e.g. *I. pini*, *Pityogenes spp.*, *Pityokteines spp.*, *Pityophthorus spp.*, and various Cerambycidae *spp.*, were consistently obtained at all 8 sites (Table 3). The hymenopteran, *Xeris sp.* was found at seven sites. Though *Pityokteines spp.*, *Pityophthorus spp.*, and *Xeris sp.* were commonly found in flight traps at most sites, we did not find their galleries intermingled with those of *D. ponderosae*. We found only one *Dendroctonus valens* (LeConte), a lower stem feeding bark beetle that is commonly associated with stressed trees, including those injured by fire, at one endemic burn site. Other coleopteran families obtained were Elateridae, Eucnemidae, Tenebrionidae, and Bostrichidae; species of Lepturinae (Cerambycidae) were found consistently across sites. Some species within these families are known to be colonizers of dead or dying conifers in western North America but we did not find them within the trees we sampled. We found only one Buprestidae, in a trap at an endemic burn site.

Among the subcortical herbivores, *D. ponderosae* was the most abundance at all 8 burn sites. As expected, there were many more *D. ponderosae* in outbreak than endemic sites. Other Scolytinae were likewise present in larger quantities at the outbreak than endemic sites: *I. pini*, *Pityogenes spp.*, *Pityophthorus spp.*, and *Pityokteines spp.* across the 8 sites (*I. pini*: Multinomial $\chi^2 = 820$, $df = 7$, $P < 0.01$, *Pityogenes spp.*: Multinomial $\chi^2 = 1500$, $df = 7$, $P < 0.01$, *Pityophthorus spp.*: Multinomial $\chi^2 = 4900$, $df = 7$, $P < 0.01$, *Pityokteines spp.*: Multinomial $\chi^2 = 30$, $df = 7$, $P < 0.01$). Numbers of wood-boring

Coleoptera and wood-boring Hymenoptera did not differ between sites with outbreak versus endemic *D. ponderosae* population levels.

Bark beetle natural enemies, such as *Medetera* spp. (Diptura: Dolichopodidae) and hymenopteran parasitoids, were also present in the traps. *Medetera* spp. were found consistently across the 8 burn sites, but at very low numbers. Parasitoid wasps were found inconsistently across the 8 burn sites, with certain sites (e.g. Hardscrabble) having many more than others. More parasitoid wasps were found at outbreak than endemic burn sites. We found two clerid (Coleoptera: Cleridae) genera of bark beetle predators, *Thanasimus* and *Enoclerus*, though not consistently across the sites. The numbers of these predators did not differ in sites where *D. ponderosae* was at outbreak versus endemic 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-brevcomin*, and *trans-verbenol* (Table 3). It was rarely found in other traps, but those individuals were not counted. Also as expected, *I. pini* was predominantly found in traps baited with (-) ipsdienol and lanierone (Multinomial $\chi^2 = 940$, $df = 2$, $P < 0.01$). Also obtained predominantly in trees baited with (-) ipsdienol and lanierone were *Pityogenes* spp. (Multinomial $\chi^2 = 600$, $df = 2$, $P < 0.01$), *Pityophthorus* spp. (Multinomial $\chi^2 = 980$, $df = 2$, $P < 0.01$), and *Pityokteines* spp. (Multinomial $\chi^2 = 36$, $df = 2$, $P < 0.01$). The only predators obtained in relatively large numbers were species of Cleridae. Of these *Enoclerus sphegeus* (Fabricius) were most common. Clerids were found in traps of all three baits, but *Thanasimus* sp. (Multinomial $\chi^2 = 9.1$, $df = 2$, $P = 0.011$) and *Enoclerus lecontei* (Wolcott) (Multinomial $\chi^2 = 6.9$, $df = 2$, $P = 0.032$) were both 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*-brevcomin, and *trans*-verbenol, and EtOH and (+) α -pinene (Multinomial $\chi^2 = 30$, $df = 2$, $P < 0.01$).

Discussion

Per-Capita Brood Production of *Dendroctonus ponderosae* in Fire-Injured Lodgepole Pine

Although fire injury may increase the likelihood of *D. ponderosae* successfully attacking trees (Powell 2010, Ch.1), the attack density and number of emerging adult offspring decreased with increasing degree of fire injury (Fig. 2A and 2B). The relationship between beetle per-capita brood production and degree of fire injury is non-linear, with moderate-severity trees having the highest ratio of emergence to entry holes (Fig. 2C).

There is some discrepancy between these results and a previous study of *D. ponderosae* productivity in fire-injured lodgepole pine. Elkin and Reid (2004) found reproductively successful *D. ponderosae* in fire-injured trees, but only in trees where beetles exhibited low attack densities. These were primarily sites with low background populations. In the Greater Yellowstone Ecosystem, fire injury also influenced *D. ponderosae* reproduction in outbreak sites. Interestingly, we did not observe any relationship between background population size and attack density (Appendix 3), suggesting attack densities are determined primarily by tree-level factors.

Moderate-severity lodgepole pines yield the highest levels of per-capita brood production among fire-injured lodgepole pines, followed by low-, unburned, and high-severity trees (Fig. 2C). This non-linear trend may be attributed to the combined effects of

both increased susceptibility and decreased substrate quality in fire-injured lodgepole pines, and the higher number of entering beetle needed to overcome the defenses of healthy trees. The reproductive success seen in other subcortical herbivores influenced by fire-injury, and can reduce the reproductive success of *D. ponderosae* (Rankin and Borden 1991).

A Conceptual Framework of Fire Injury Effects on Bark Beetle Reproduction

We propose a conceptual framework for the relationship of fire injury to the reproduction and potential for population eruption of *D. ponderosae* (Fig. 8). This incorporates both positive and negative feedbacks arising from endogenous and exogenous drivers affecting the likelihood of colonization and subsequent reproduction. We propose that fire injury both increases host susceptibility and decreases host substrate quality. Fire injury also increases susceptibility to competitors, which negatively affects *D. ponderosae* reproductive success. Stand-level processes, such as the number of vigorous hosts colonized and the regional beetle dynamics, feedback into this system as well.

Host susceptibility to *D. ponderosae* increases with fire injury (Fig. 8(a)), but this is limited to moderate-severity trees when beetle populations are low. When beetle populations are high-, unburned and low-severity trees may also be killed, but high-severity trees are always poor hosts (Powell 2010, Ch.1). *Dendroctonus ponderosae* per-capita brood production also relates to fire injury non-linearly, with moderate-severity trees yielding the highest replacement rates, and the more severely injured trees being the least productive (Fig. 2C, Fig. 8(b)). Poor brood production in trees severely injured by both fire and lightning suggests that the quality of substrate decreases, in part due to tissue desiccation (Fig. 8(c), Anderson and Anderson 1968). Moderate-severity trees also have lower substrate quality,

but it is still adequate for some reproduction, and the defense response is also lessened (Wallin et al. 2003, Elkin and Reid 2004). Thus, the combination of the relationships in this framework results in a non-linear relationship between substrate quality and reproduction.

Dendroctonus ponderosae reproduction is also affected by the relationship between host susceptibility and the incidence of competitors (Fig. 8(e-f)), such as *Ips spp.*, *Pityogenes spp.*, and wood-borers (Cerambycidae *spp.*) (Fig. 3, Fig. 5, Fig. 6, and Fig. 7). Associated subcortical insects in windblown trees can partition the host resource such that interspecific competition is reduced (Poland and Borden 1994), however, all of our measurements were sampled within the same sections of phloem, so we evaluated spatial partitioning.

Because *D. ponderosae* reproduction is affected by competition, host susceptibility, and host substrate quality (Fig. 8(b), (d), (f)), we attempted to partition these effects. We found no significant difference of *D. ponderosae* per-capita brood production in trees colonized by other bark and wood-boring insects versus trees not colonized (Kruskal-Wallis $\chi^2 = 3$, $df = 3$, $P = 0.3916$). This concurs with Poland and Borden (1994), and suggests that the insects we found in fire-injured trees were not necessarily competing for a common resource, but rather may at least partially partition it based on extent of physiological damage.

If this framework is expanded to include the influence of predators and parasitoids on *D. ponderosae* reproduction, an additional negative relationship may emerge (Amman and Cole 1983, Boone et al. 2008). However, our funnel trap catch data revealed very few predators and parasitoids (Table 3). Sampling for coleopteran predators with multiple baited funnel traps is highly efficient, suggesting their populations were low, but additional methods are needed for soft-bodied predators and parasitoids (Aukema et al. 2000, Boone et al. 2008).

Factors affecting the potential for *D. ponderosae* population increase in fire-injured trees arise not only at the tree-level (Fig. 8(a-f)), but also at the stand-level (Fig. 8(g-h)). There is positive feedback between an increase in *D. ponderosae* reproduction and the number of vigorous hosts colonized (Fig. 8(g)). Vigorous hosts were colonized only in sites where beetle populations were at outbreak levels (Powell 2010, Ch.1). This likely explains why after the Yellowstone fires of 1988, neither population build-up (Rasmussen et al. 1996) nor increase in colonization (Amman and Ryan 1991) of *D. ponderosae* in fire-injured trees was found when sampling was performed at endemic population levels.

Overall, the conditions under which the combined relationships affecting *D. ponderosae* reproduction can favor an outbreak may be relatively narrow. In order to fully understand the potential for the build-up of *D. ponderosae* populations in trees that have been injured by fire, regional beetle dynamics need also to be considered. In particular, beetle mortality during the search for new hosts has always been the most difficult component to estimate (Berryman 1976). Because beetles that fail to locate a stressed host are eliminated from the population and do not reproduce, the total amount of reproduction (Fig. 2B) should be considered as an important complementary measure to the within-tree per-capita brood production (Fig. 2C). Additionally, long-term studies are needed to evaluate these processes. For example, population increases of predators and competitors likely include time lags, and it is uncertain how disturbances such as fire would interact with other factors that favor beetle reproduction, such as drought, elevated temperature, and less heterogeneous stands.

Acknowledgements

This research was supported by the National Science Foundation DEB-0816541, McIntire Stennis WIS0469, the Joint Fire Sciences Program 06-2-1-20, and the Univ. Wisconsin College of Agricultural and Life Sciences. We thank the National Park Service, especially Cindy Hendrix of Yellowstone National Park and Sue Consolo Murphy of Grand Teton National Park, for permission to conduct research within the park boundaries. Henry Harlow of the University of Wyoming and the crew at the University of Wyoming, National Park Service Research Center provided lodging and support during the field season, and Megan Fork, Katherine Molter, Christopher Foelker, Melissa Greulich, Christopher Pennings, Andrew Long, Hillary Thompson, Jake Griffin, and Martin Simard provided valuable assistance in the field. Steven Krauth at the Univ. Wisconsin, Entomology Dept. provided help with insect identification, and William Romme (Colorado State Univ.), Daniel Tinker (Univ. Wyoming), Philip Townsend (Univ. Wisconsin), and Monica Turner (Univ. Wisconsin) assisted with field site selection. The critical reviews of Philip Townsend, Monica Turner, and Daniel Young (Univ. Wisconsin) are greatly appreciated.

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Table 1. Linear regression models where the response variable is related to several tree- and stand-level variables in lodgepole pines colonized by *D. ponderosae*.

Intercepts were forced through zero, and models were selected based on best fit by R^2 .

A) Linear regression model of *D. ponderosae* attack density (entry holes). $R^2 = 0.81$,

$F_{(3,102)} = 110, P < 0.01$.

Variable	Coefficient	Std. Error	<i>P</i>
Fire Injury Category			
Category - High	3.0	0.60	<0.01
Category - Moderate	4.9	0.53	<0.01
Category - Low	6.3	0.56	<0.01
Category - Unburned	9.9	0.67	<0.01

B) Linear regression model of emergence *D. ponderosae* adult offspring (emergence holes). $R^2 = 0.57, F_{(6,100)} = 24, P < 0.01$.

Variable	Coefficient	Std. Error	<i>P</i>
Fire Injury Category			
Category - High	1.7	0.88	0.056
Category - Moderate	5.3	0.80	<0.01
Category - Low	6.5	0.81	<0.01
Category - Unburned	7.0	1.0	<0.01
Site*Presence of <i>Pityogenes spp.</i>			
Battle Mtn* <i>Pityogenes</i>	N/A [†]	N/A [†]	N/A [†]
Hardscrabble* <i>Pityogenes</i>	-3.2	1.1	<0.01
Purdy* <i>Pityogenes</i>	N/A [†]	N/A [†]	N/A [†]
Salt Lick* <i>Pityogenes</i>	-1.1	1.9	<0.01

[†] Coefficient missing because *Pityogenes spp.* galleries were not present at these sites.

Table 1. (continued)

C) Linear regression model of *D. ponderosae* per-capita brood production (ratio of emergence holes to entry holes). $R^2 = 0.56$, $F_{(6,100)} = 24$, $P < 0.01$.

Variable	Coefficient	Std. Error	<i>P</i>
Fire Injury Category			
Category - High	0.50	0.16	<0.01
Category - Moderate	1.2	0.14	<0.01
Category - Low	1.1	0.14	<0.01
Category - Unburned	0.73	0.19	<0.01
Site*Presence of <i>Pityogenes spp.</i>			
Battle Mtn* <i>Pityogenes</i>	N/A [†]	N/A [†]	N/A [†]
Hardscrabble* <i>Pityogenes</i>	-0.43	0.20	0.039
Purdy* <i>Pityogenes</i>	N/A [†]	N/A [†]	N/A [†]
Salt Lick* <i>Pityogenes</i>	-0.18	0.33	0.58

[†] Coefficient missing because *Pityogenes spp.* galleries were not present at these sites.

Table 2. Generalized linear models for each of the four beetle taxonomic groups in which the presence of the modeled beetle's gallery area is related to several tree- and stand-level variables. The variables for each site below were in the model with the lowest AIC value.

Beetle Taxonomic Group	Variable	Coefficient	Std. Error	<i>P</i>
<i>D. ponderosae</i>	Fire Injury Category			
	Category - High	-7.9	2.6	<0.01
	Category - Moderate	-6.0	2.0	0.011
	Category - Low	-2.9	1.0	0.064
	Category - Unburned	-2.9	2.1	0.015
	% Bole Injury	0.11	0.038	<0.01
	DBH	0.14	0.059	0.016
	% Bole Injury * DBH	-0.0018	0.00092	0.058
<i>Pityogenes</i>	1.9	0.80	0.019	
<i>Ips spp.</i>	% Bole Injury	0.021	0.0074	<0.01
Wood-borers	Height	0.15	0.070	0.033
<i>Pityogenes spp.</i>	(% Bole Injury) ²	-0.00075	0.00033	0.023
	(% Basal Injury) ²	0.00044	0.00018	0.015

Table 3. Average numbers of flying insects captured from three funnel traps of each bait type per burn site.

	Ecol. Role [†]	Totals from all Sites			Purdy			Battle Mountain		
		MPB*	<i>Ips</i> [‡]	HV ⁺	MPB*	<i>Ips</i> [‡]	HV ⁺	MPB*	<i>Ips</i> [‡]	HV ⁺
Coleoptera:										
Curculionidae Scolytinae:										
<i>Dendroctonus ponderosae</i>	SH	18612	rare	rare	2082	rare	rare	6406	rare	rare
<i>Ips pini</i>	SH	6.34	551	37.67	0.67	48	3	0.33	3.33	
<i>Dendroctonus valens</i>	SH	0	0.67	0						
<i>Pityogenes spp.</i>	SH	37.33	448.9	53.33	19.67	29	10	0.33	7	
<i>Pityophthorus spp.</i>	SH	61.34	878.7	218	26	10	12.33	3	4.67	0.67
<i>Pityokteines spp.</i>	SH	10.67	17.99	51.67	7	1	4.33			2.67
Cerambycidae:										
Lepturinae <i>spp.</i>	SH	3.66	27.34	49.66		1	2.33		10	
<i>Megacylene spp.</i>	SH	0	0	2.66						0.33
<i>Rhagium spp.</i>	SH	0	2.33	2.67		0.33	0.33			
<i>Monochamus spp.</i>	SH	1.67	2	13						
Cleridae:										
<i>Thanasimus sp.</i>	PR	7	21.01	9.34			0.33		0.67	
<i>Enoclerus lecontei</i>	PR	0	8.01	4.67						
<i>Enoclerus speigeus</i>	PR	16.67	3.34	38.34						
Buprestidae	SH	0	0	0.33						
Bostrichidae	SH	yes	yes	yes	yes	yes	yes			
Elateridae	O	yes	yes	yes						
Eucnemidae	O	yes	yes	yes			yes			
Tenebrionidae	O	yes	yes	yes				yes		yes
Coccineilidae	O	yes	yes	yes	yes		yes			
Scarabaeidae	D	yes	yes	yes						
Chrysomelidae	F	yes	yes	yes						
Hymenoptera:										
Parasitoids	PA	13.33	56.33	42.66						
Siricidae:										
<i>Xeris sp.</i>	SH	0.33	7.33	25.34		0.67	4.67		2.33	2.67
Diptera:										
Dolichopodidae:										
<i>Medetera spp.</i>	PR	0.33	2.67	2.33			0.33			

Table 3. (continued)

	Ecol. Role [†]	Hardscrabble			Salt Lick			Owl		
		MPB*	<i>Ips</i> [‡]	HV ⁺	MPB*	<i>Ips</i> [‡]	HV ⁺	MPB*	<i>Ips</i> [‡]	HV ⁺
Coleoptera:										
Curculionidae Scolytinae:										
<i>Dendroctonus ponderosae</i>	SH	2324	rare	rare	4955	rare	rare	1718	rare	rare
<i>Ips pini</i>	SH	1.67	265.7	32.67	3.67	73.7	2		3	
<i>Dendroctonus valens</i>	SH								0.67	
<i>Pityogenes spp.</i>	SH	8.33	321.3	39	8.33	37.7	3.67		1.67	0.33
<i>Pityophthorus spp.</i>	SH	19.67	794.3	201.3	12.67	30	3.67		1	
<i>Pityokteines spp.</i>	SH	0.67	2.33	29.33	0.33	2	2.67	2	9.33	2.67
Cerambycidae:										
Lepturinae spp.	SH	0.33	0.67	1		5	15		1.67	0.67
<i>Megacylene spp.</i>	SH									
<i>Rhagium spp.</i>	SH						0.33		0.33	0.67
<i>Monochamus spp.</i>	SH					0.33			0.67	
Cleridae:										
<i>Thanasimus sp.</i>	PR			2.33	4.67	0.67		0.33	10	0.67
<i>Enoclerus lecontei</i>	PR									
<i>Enoclerus sphegeus</i>	PR						1		1	4.67
Buprestidae										
Bostrichidae										
Elateridae	O	yes	yes	yes				yes	yes	yes
Eucnemidae	O					yes		yes	yes	yes
Tenebrionidae	O							yes	yes	yes
Coccineilidae	O									
Scarabaeidae	D									
Chrysomelidae	F									
Hymenoptera:										
Parasitoids	PA	9	49	34	4	7	8.33			
Siricidae:										
<i>Xeris sp.</i>	SH		0.33	1		0.67	1.67		1	2
Diptera:										
Dolichopodidae:										
<i>Medetera</i>	PR	0.33	0.33	1			0.67		1.67	0.33

Table 3. (continued)

	Ecol. Role [†]	Madison Arm			Magpie			Hechtman Creek		
		MPB*	<i>Ips</i> [‡]	HV ⁺	MPB*	<i>Ips</i> [‡]	HV ⁺	MPB*	<i>Ips</i> [‡]	HV ⁺
Coleoptera:										
Curculionidae Scolytinae:										
<i>Dendroctonus ponderosae</i>	SH	135	rare	rare	125	rare	rare	867	rare	rare
<i>Ips pini</i>	SH		31.67			122			3.67	
<i>Dendroctonus valens</i>	SH									
<i>Pityogenes spp.</i>	SH		0.67		0.67	51.6	0.33			
<i>Pityophthorus spp.</i>	SH		0.33			37.7			0.67	
<i>Pityokteines spp.</i>	SH				0.67	3.33	10			
Cerambycidae:										
Lepturinae spp.	SH	2.33	1.67	6	1	2	13.33		5.33	11.33
<i>Megacylene spp.</i>	SH						1			1.33
<i>Rhagium spp.</i>	SH			0.67		0.67	0.67		1	
<i>Monochamus spp.</i>	SH	1		12.67	0.67	0.67	0.33		0.33	
Cleridae:										
<i>Thanasimus sp.</i>	PR				6.67	4.67	4.67		1	0.67
<i>Enoclerus lecontei</i>	PR		6.67	4.67		0.67				
<i>Enoclerus spehegeus</i>	PR	5	1	31.33	11.67	1.67				0.67
Buprestidae	SH						0.33			
Bostrichidae	SH	yes					yes		yes	
Elateridae	O		yes	yes				yes	yes	yes
Eucnemidae	O							yes	yes	yes
Tenebrionidae	O		yes	yes				yes	yes	yes
Coccineilidae	O		yes	yes						
Scarabaeidae	D	yes	yes	yes						
Chrysomelidae	F	yes	yes	yes						
Hymenoptera:										
Parasitoids	PA				0.33	0.33				0.33
Siricidae:										
<i>Xeris</i>	SH				0.33				2.33	13.33
Diptera:										
Dolichopodidae:										
<i>Medetera</i>	PR		0.67							

[†] Common ecological role in western conifer forests:

SH – subcortical herbivore, PR – predator of bark beetles, O – other, D – detritivore,
F – folivore, PA – Parasitoid

* MPB: lure with myrcene, *exo*-brevcomin, and *trans*-verbenol

[‡] *Ips*: lure with (-) ipsdienol and lanierone

⁺ HV: host volatile lure, EtOH and (+) α -pinene

Figure Captions

Fig. 1. Eight wildfire sites throughout the GYE. The numbers represent the size of each burn. Four burns (Magpie, Hechtman Creek, Purdy, and Battle Mountain) occurred in the summer of 2006; 4 (Owl, Madison Arm, Hardscrabble, and Salt Lick) occurred in the summer of 2007. Flying insect assemblages were sampled using baited 12-funnel flight traps at all 8 sites. Reproduction by *D. ponderosae* and the gallery areas of subcortical beetles were sampled at the 4 burn sites indicated in squares. For 2 burned sites (Hardscrabble, Salt Lick) adjacent non-burn sites were also sampled for *D. ponderosae* reproduction and subcortical galleries.

Fig. 2. Measurements of *D. ponderosae* performance in colonized trees across four fire injury categories: unburned (N=20), low-severity (N=29), moderate-severity (N=32), high-severity (N=25). Error bars represent two standard deviations from the mean. A) Attack density. B) Density of emerging adult offspring. C) Per-capita brood production: Ratio of emergence to entry holes per tree.

Fig. 3. Average gallery areas for each beetle taxonomic group per cm² with all samples included, across four fire injury categories: unburned (N=19), low-severity (N=21), moderate-severity (N=20), high-severity (N=19). Error bars represent two standard deviations from the mean. A) *D. ponderosae* (Kruskal Wallace $\chi^2 = 2.1$, df = 3, $P = 0.55$); B) *Ips spp.* (Kruskal Wallace $\chi^2 = 8.0$, df = 3, $P = 0.046$); C) wood-borer (Kruskal Wallace χ^2

= 9.8, df = 3, $P = 0.020$); D) and *Pityogenes spp.* (Kruskal Wallace $\chi^2 = 0.85$, df = 3, $P = 0.84$).

Fig. 4. Average gallery areas for each beetle taxonomic group per cm², with samples lacking galleries excluded, across four fire injury categories: unburned (N=19), low-severity (N=21), moderate-severity (N=20), high-severity (N=19). Error bars represent two standard deviations from the mean. A) *D. ponderosae* (Kruskal Wallace $\chi^2 = 47$, df = 3, $P < 0.01$); B) *Ips spp.* (Kruskal Wallace $\chi^2 = 20$, df = 3, $P < 0.01$); C) wood-borer (Kruskal Wallace $\chi^2 = 1.5$, df = 1, $P = 0.68$); D) and *Pityogenes spp.* (Kruskal Wallace $\chi^2 = 11$, df = 3, $P = 0.01$).

Fig. 5. Average ratio of *D. ponderosae* total gallery area to competitor total gallery area, with samples lacking galleries excluded, across four fire injury categories: unburned (N=19), low-severity (N=21), moderate-severity (N=20), high-severity (N=19). (Kruskal Wallace $\chi^2 = 25$, df = 3, $P < 0.01$).

Fig. 6. Canonical correspondence analysis reveals fire injury category as the environmental factor that is correlated with taxonomic group composition within the trees sampled. The triangles in both graphs represent a tree where gallery averages were measured (N = 79). On graph to the left, the cluster of triangles is nearest to *D. ponderosae* (MPB), which illustrate that the trees have larger *D. ponderosae* gallery area on average than the other taxonomic groups. On the graph to the right, triangles are fitted to the vector for fire injury category. CCA analysis gives a species-environmental correlation for axis 1 as 0.57, $p = 0.0067$, which is correlated with fire injury category. Eigenvalue is 0.032, $p = 0.0044$.

Fig. 7. Canonical correspondence analysis for each taxonomic group reveals each group's relationship to fire injury. These graphs illustrate the species correlation with fire injury category. Each triangle represents a tree where gallery areas were measured. The 4 pertinent competitors are correlated to axis 1, $p = 0.0067$. Axis 1 is correlated with fire injury category. Fire injury category increases as we move to the right of the vector. Large triangles in all graphs indicate larger gallery area. Larger *D. ponderosae* total gallery area is correlated with lower fire injury category. Larger *Ips spp.* total gallery area is somewhat correlated with higher fire injury category. Larger wood-borer total gallery area is correlated with higher fire injury category. Larger *Pityogenes spp.* total gallery area is correlated with higher fire injury category.

Fig. 8. Conceptual framework of potential positive and negative feedbacks of fire injury on bark beetle reproduction. Lower case letters in parentheses represent each relationship in the framework. For each relationship, an increase in the preceding variable can cause an increase (+) or decrease (-) in the recipient variable. Processes on the left are tree-level processes, and those on the right are stand-level. Additional relationships are omitted for simplicity (see Raffa et al., 2008). Population eruptions may affect forest structure and fire, which feed back into the likelihood of subsequent beetle outbreaks, but are likewise omitted for simplicity.

Fig. 1

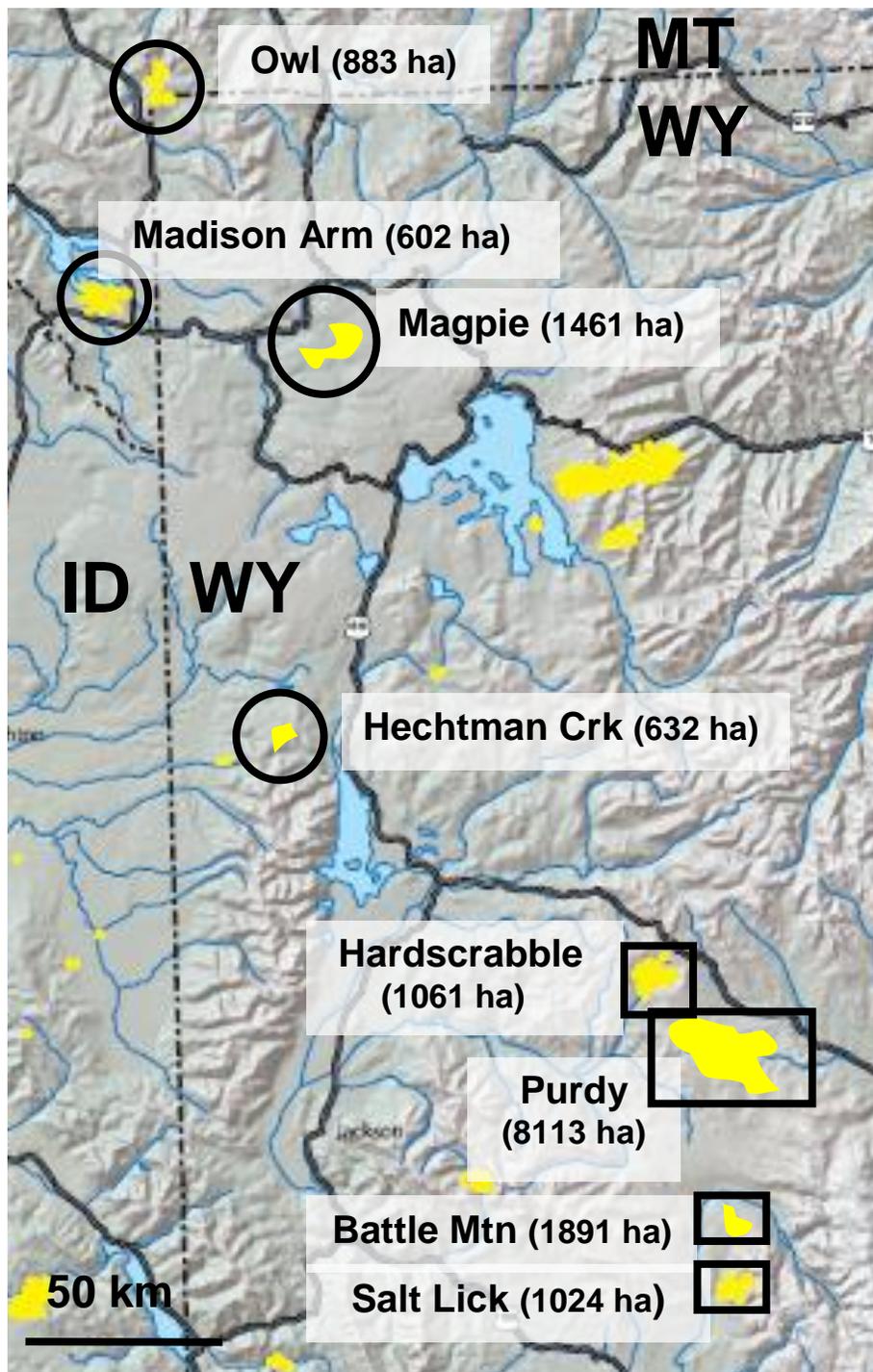
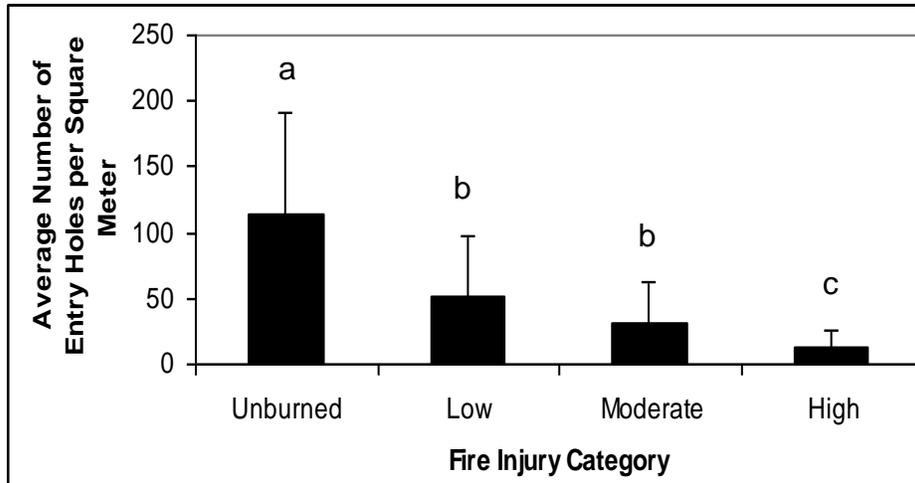


Fig. 2

A)



B)

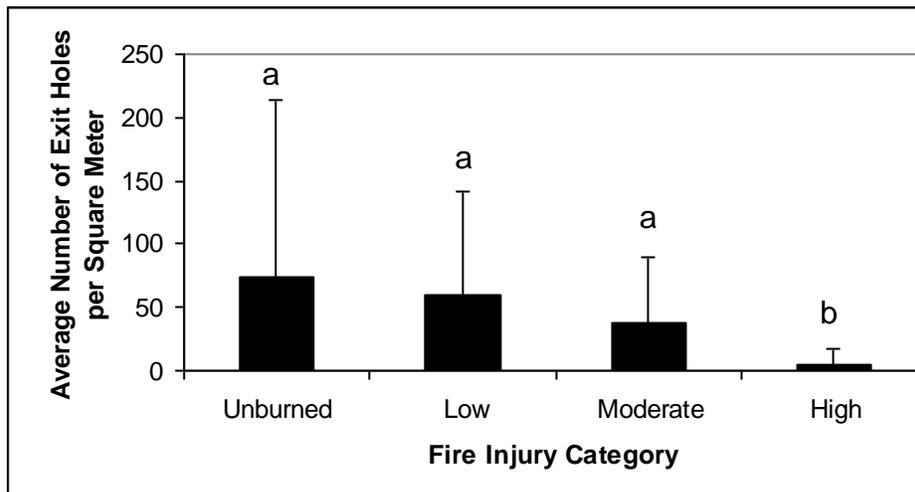


Fig. 2 (continued)

C)

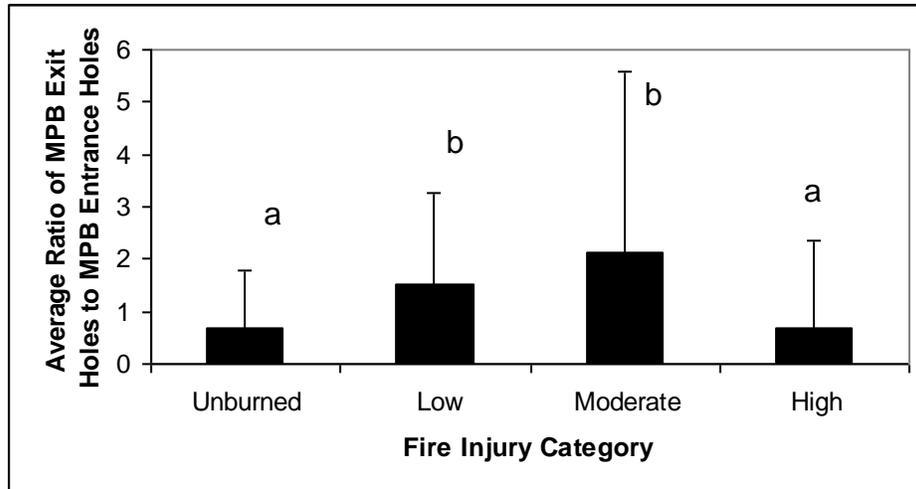


Fig. 3

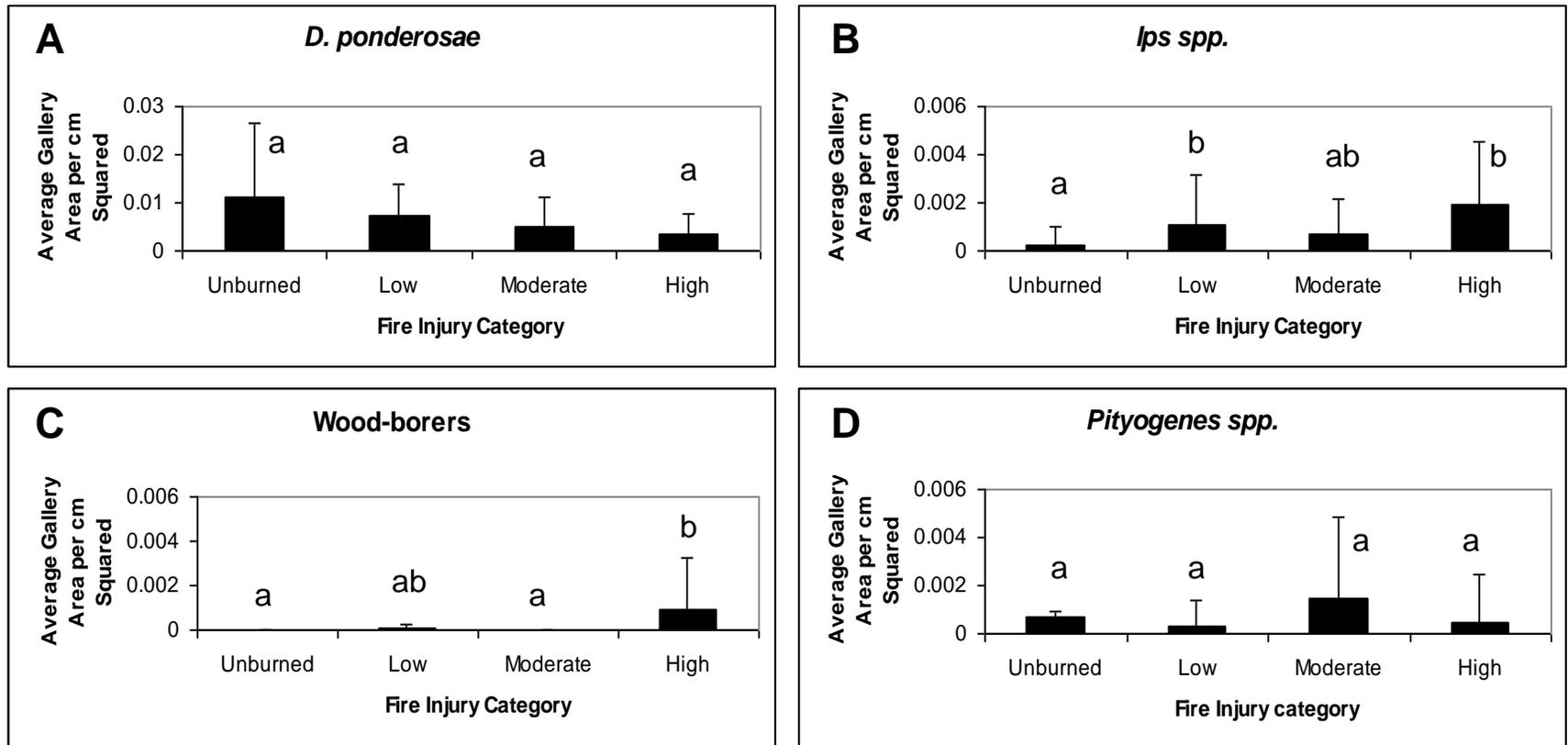


Fig. 4

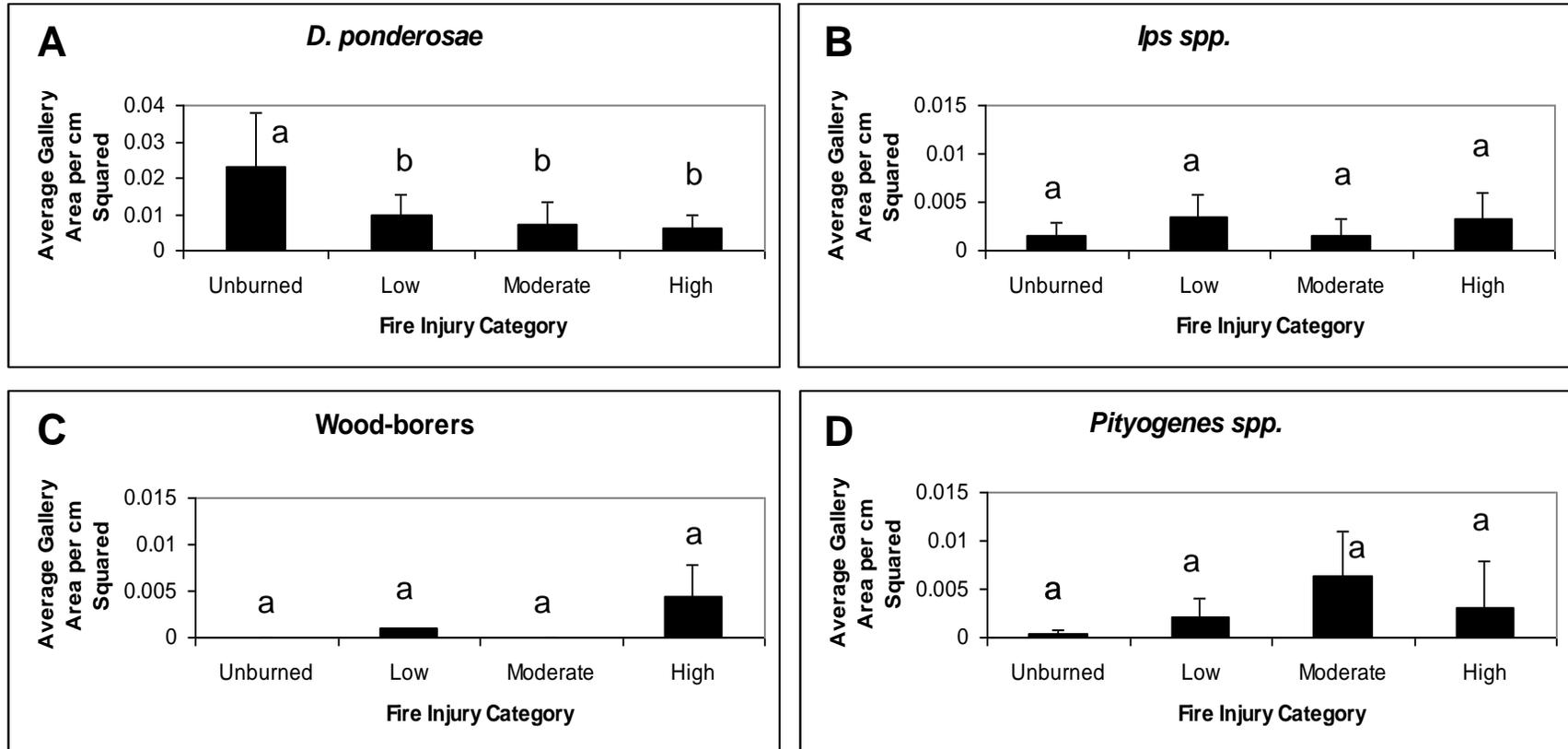


Fig. 5

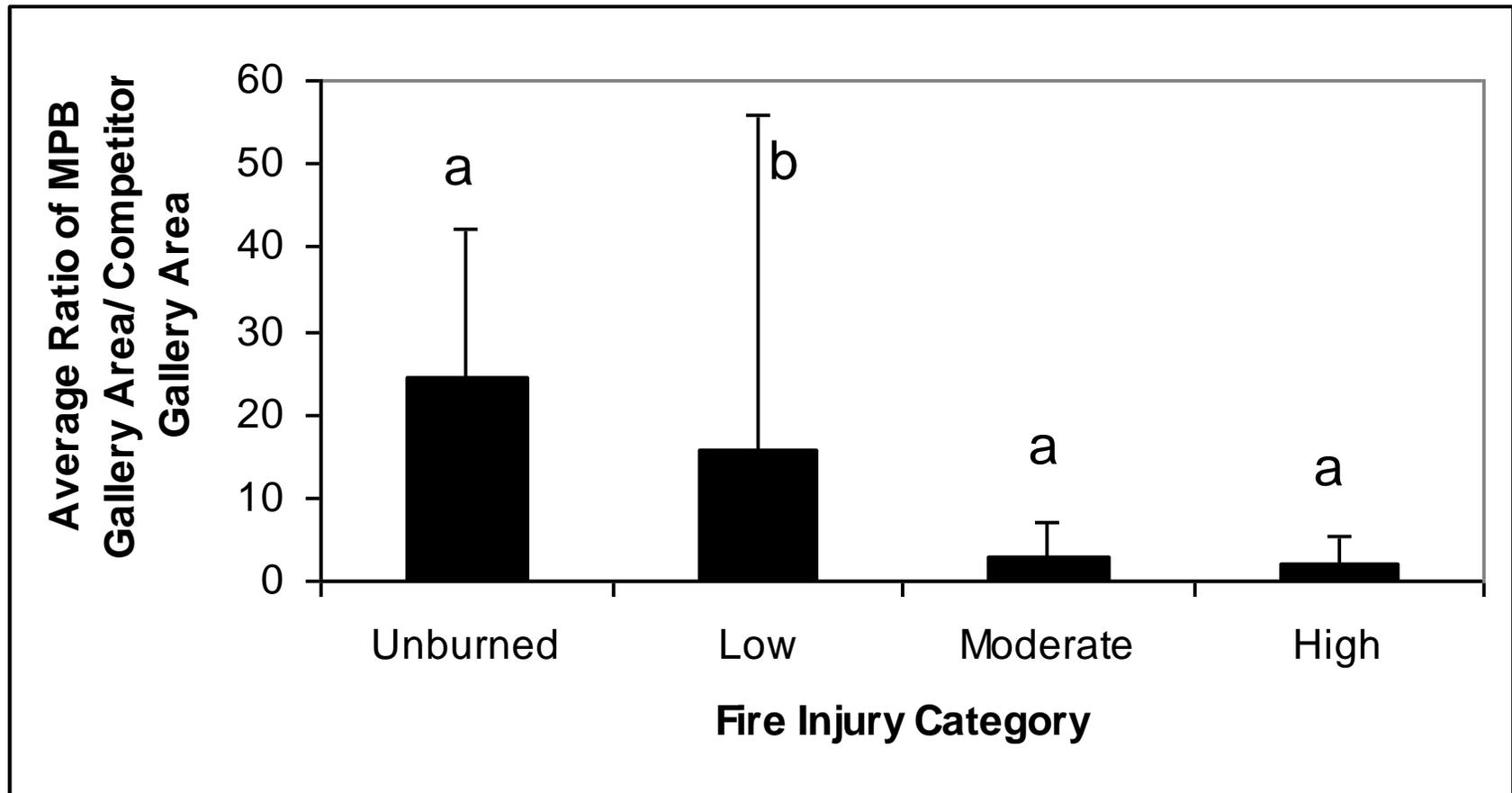


Fig. 6

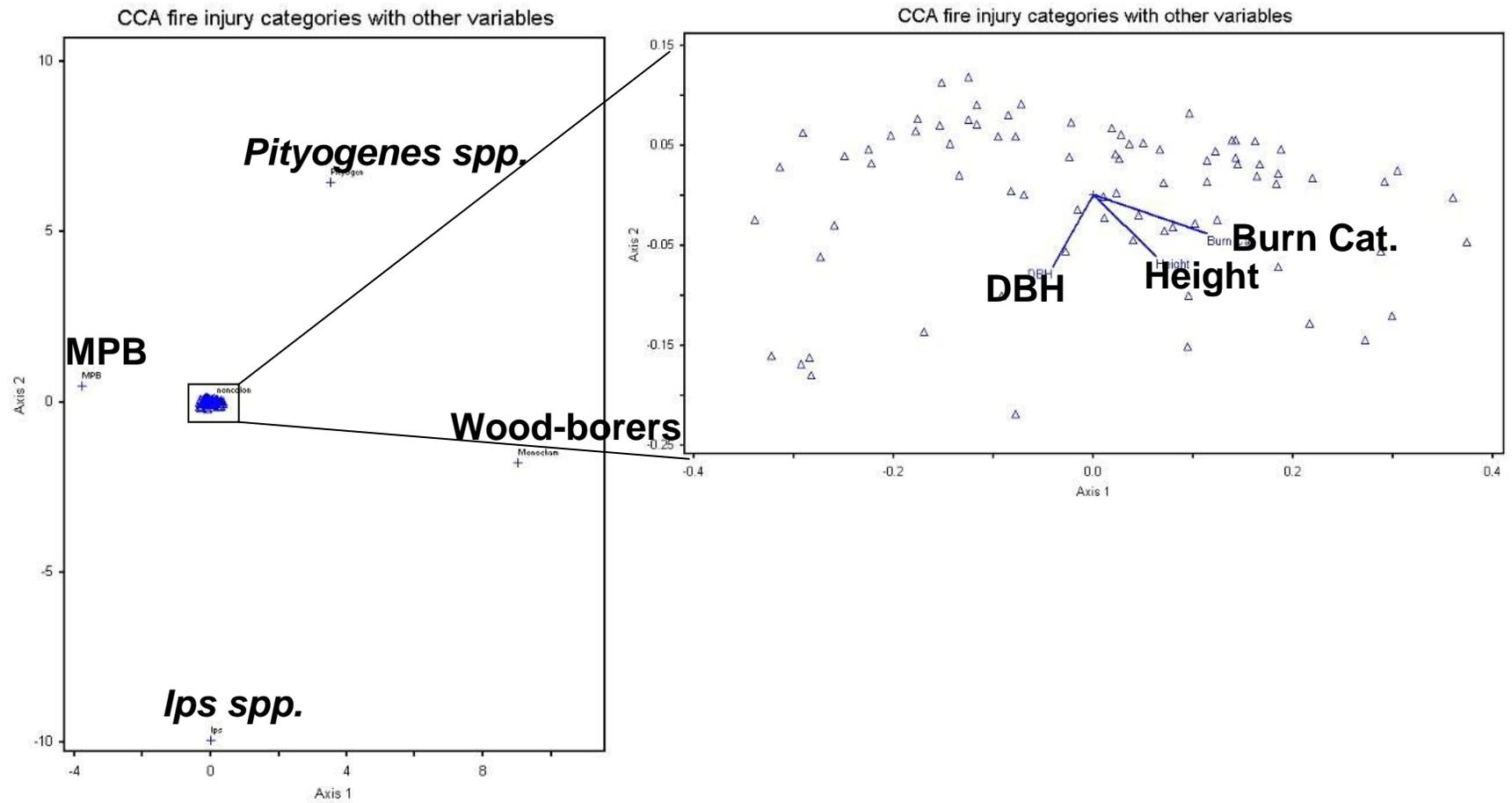
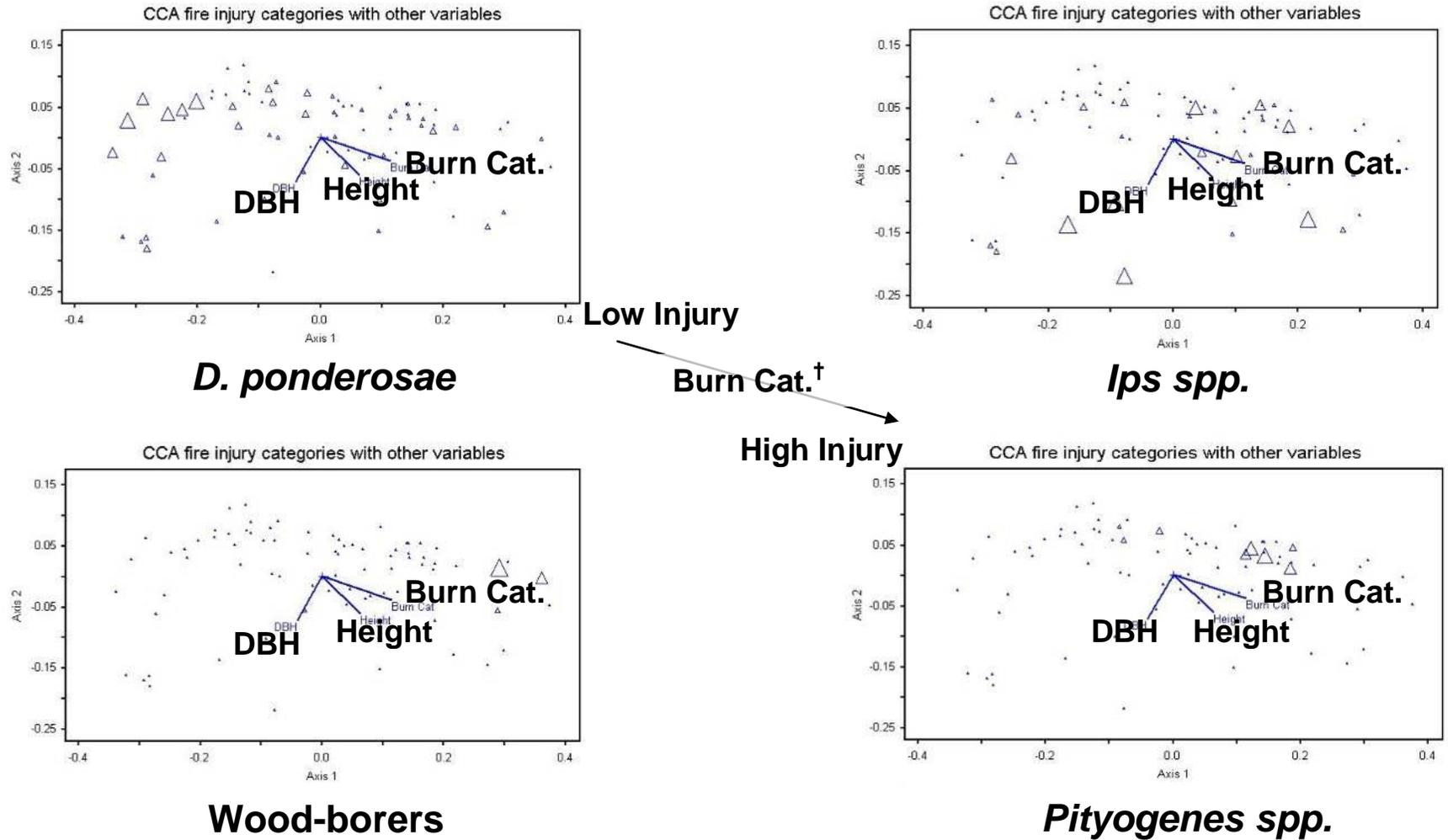
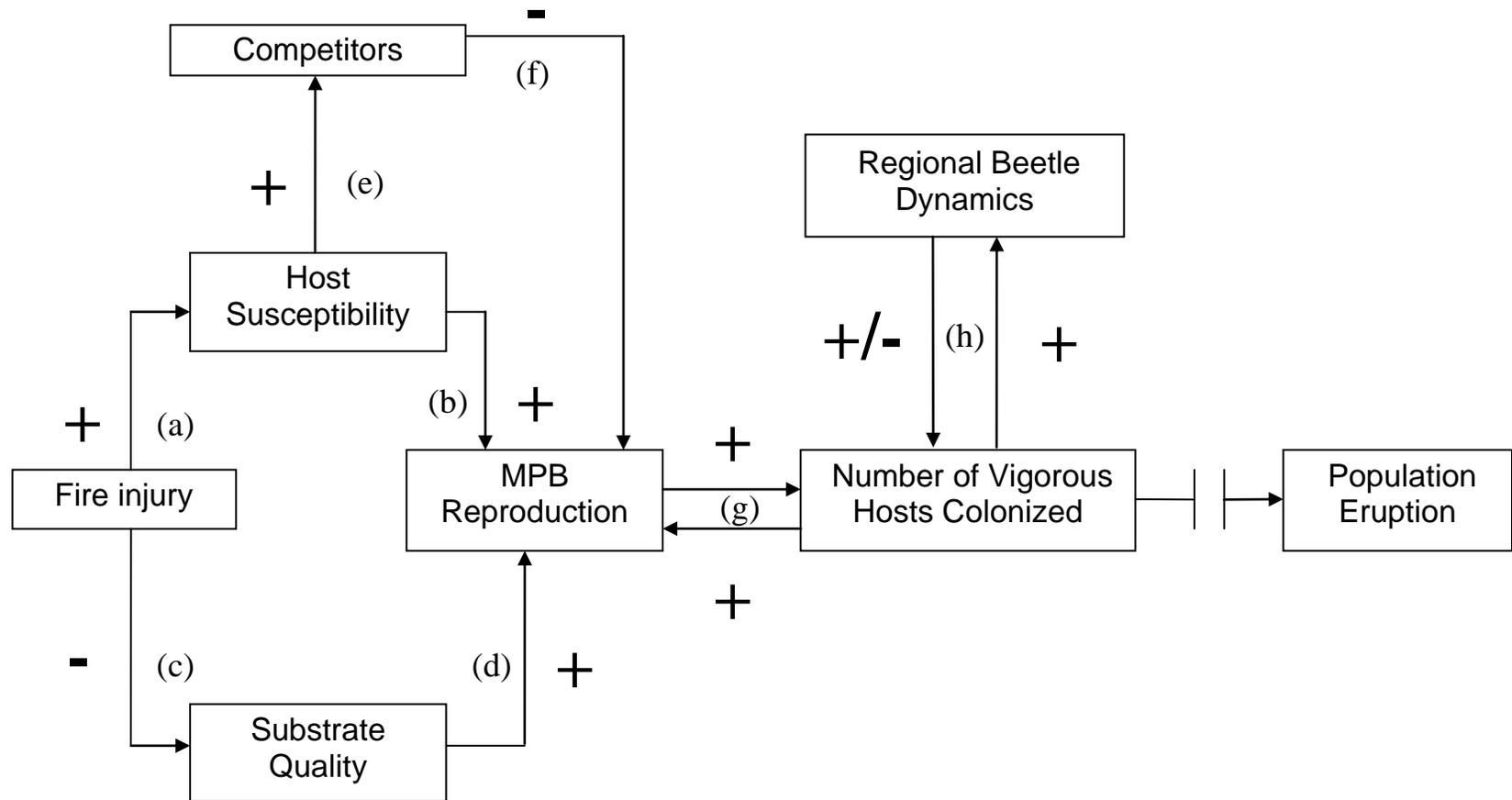


Fig. 7



[†] The vector for burn category represents an increase in fire injury severity from the upper left corner of each graph to the lower right corner.

Fig. 8



THESIS CONCLUSIONS

1. Fire injury predisposes trees to *Dendroctonus ponderosae* Hopkins colonization.

The manner by which this occurs is non-linear: moderate-severity trees were most frequently colonized; non-injured and severely injured trees were least commonly colonized.

2. The beetle-host interaction at the tree level is strongly affected by beetle population density at the stand level. At outbreak population levels, *D. ponderosae* colonized trees of all fire injury levels, whereas at endemic population levels, *D. ponderosae* colonized only low- and moderate-severity trees.

3. Per-capita brood production of *D. ponderosae* was affected by fire injury, but in a non-linear manner. *D. ponderosae* had the highest per-capita brood production in moderate-severity trees, followed by low-, unburned, and high-severity trees respectively. The rates of *D. ponderosae* attack density and emergence of adult offspring decreased with fire injury.

4. The total gallery area of subcortical herbivores varies with fire injury. The total gallery area of *D. ponderosae* is greatest in trees not injured by fire, while the total gallery area of *Ips spp.*, coleopteran wood-borers (*Cerambycidae spp.*), and *Pityogenes spp.* are larger in fire-injured trees.

5. Multiple measurements of fire injury can improve our ability to predict responses by bark beetles. There was high variability among the 8 sites where measurements of *D. ponderosae* colonization took place. Therefore, multiple measurements are useful for detecting relationships.

- 6. Baited 12-funnel flight traps captured several subcortical herbivores, most of which were *D. ponderosae*, *Ips pini* (Say), *Pityogenes spp.*, *Pityokteines spp.*, and *Pityophthorus spp.*** The numbers of *D. ponderosae* collected from traps varied according to the beetle population level at each site. *I. pini*, *Pityogenes spp.*, *Pityokteines spp.*, and *Pityophthorus spp.* were found more frequently in traps baited with (-) ipsdienol and lanierone.
- 7. Collectively, these results identify significant constraints that reduce the likelihood of wildfire releasing *D. ponderosae* populations from endemic to outbreak levels.** Specifically, severe fire injury reduces tree defenses against attack, but also reduces substrate quality for brood development and increases interspecific competition. In contrast, unburned trees are too well defended for beetles to overcome them when their stand-level populations are low, and beetles that overcome such trees during outbreaks incur substantial intraspecific competition. The optimal hosts appear to be those that are moderately injured, but this resource is relatively rare. Thus, additional factors, such as warm temperatures or drought, seem necessary to accompany stresses associated with wildfire, to initiate outbreaks.

Appendix 1. A generalized linear model in which *D. ponderosae* colonization is related to eleven factors of burned or unburned site.

Variable	Coefficient	Std. Error	<i>P</i>
Site			
Purdy	-0.98	0.24	<0.01
Purdy unburned	-1.5	0.25	<0.01
Battle Mtn.	-0.78	0.22	<0.01
Battle Mtn. unburned	-2.9	0.73	<0.01
Salt Lick	-2.1	0.35	<0.01
Salt Lick unburned	-2.3	0.40	<0.01
Hardscrabble	-0.23	0.23	0.31
Hardscrabble unburned	-2.7	0.52	<0.01
Hechtman Creek	-2.3	0.35	<0.01
Owl	-2.7	0.46	<0.01
Madison Arm	-3.2	0.42	<0.01

Appendix 2. Linear regression models with *D. ponderosae* emergence (A and B) and ratio of emergence/ entry (C and D) related to several tree- and stand-level variables. Intercepts were forced through zero, and models were selected based on best fit by R^2 and P value at $\alpha < 0.05$. A) All sites included in model of emergence but Hardscrabble ($R^2 = 0.68$, $F_{(5,75)} = 32$, $P < 0.01$). B) Only Hardscrabble included in model of emergence ($R^2 = 0.72$, $F_{(7,19)} = 7.0$, $P < 0.01$). C) All sites included in model of emergence/ entry but Hardscrabble ($R^2 = 0.65$, $F_{(4,76)} = 35$, $P < 0.01$). D) Only Hardscrabble included in the model of emergence/ entry ($R^2 = 0.38$, $F_{(4,22)} = 5.0$, $P = 0.01$).

A)

Variable	Coefficient	Std. Error	P
Fire Injury Category			
Category - High	4.2	1.8	0.026
Category - Moderate	8.2	1.7	<0.01
Category - Low	11	2.0	<0.01
Category - Unburned	13	2.1	<0.01
Height	-0.20	0.11	0.055

B)

Variable	Coefficient	Std. Error	P
Fire Injury Category			
Category - High	2.8	4.0	0.49
Category - Moderate	2.5	2.5	0.33
Category - Low	0.37	0.83	0.66
Category - Unburned	1.4	0.71	0.059
% Bole Injury	-0.050	0.060	0.43
Mistletoe	0.55	0.18	0.0071
<i>Pityogenes spp.</i>	1.3	0.70	0.089

C)

Variable	Coefficient	Std. Error	P
Fire Injury Category			
Category - High	0.40	0.18	0.027
Category - Moderate	1.3	0.15	<0.01
Category - Low	1.2	0.15	<0.01
Category - Unburned	0.95	0.25	<0.01

Appendix 2. *(continued)***D)**

Variable	Coefficient	Std. Error	<i>P</i>
Fire Injury Category			
Category - High	0.53	0.18	<0.01
Category - Moderate	0.29	0.18	0.12
Category - Low	0.40	0.16	0.022
Category - Unburned	0.19	0.13	0.15

Appendix 3. Attack density of *D. ponderosae* by Average Number of Beetle Captured per Burn Site.

