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Fire-mediated interactions between a tree-killing bark beetle and its competitors

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ABSTRACT

In forest ecosystems, biotic interactions such as competition or predation may be mediated by abiotic disturbances such as fire. Bark and ambrosia beetles are important biotic factors regulating forest ecosystems, especially tree-killing species that can reach outbreak levels. In a recent study we found that although endemic-level *Dendroctonus ponderosae*, a tree-killing bark beetle, preferentially colonized fire-injured *Pinus contorta* (lodgepole pine) after prescribed fire, colonization rates decreased consistently over a 3-year period after an initial pulse. This decline may be due in part to an increase in the abundance of the subcortical community, especially competitors such as other bark beetles and ambrosia beetles. Additionally, while bark and ambrosia beetles can be attracted to fire-injured trees, we do not yet fully understand the temporal progression of the insect community in burned forest stands, and whether other species can outbreak after fire. Thus, our main objective was to characterize the bark and ambrosia beetle community and to examine if a disturbance (fire) can mediate the regulation of a tree-killing bark beetle by intensifying competition. We divided beetles into four groups: lower-, main-, and upper-stem bark beetles, and ambrosia beetles. We found that all groups generally increased in abundance after fire, and we observed a time-lag of approximately 1 year in the overall abundance of all species, wherein beetles increased in burned stands more rapidly than in non-burned stands. All groups were present in burned pine stands 1 year after fire, albeit at varying abundances relative to subsequent years. Finally, we found differences in the bark and ambrosia beetle community between areas with and without *D. ponderosae*: areas with *D. ponderosae* contained more bark and ambrosia beetles. Thus, fire likely increases competition, explaining why an initial increase in *D. ponderosae* colonization did not result in a long-term population increase after prescribed fire.

1. Introduction

Forest ecosystems are regulated by various abiotic and biotic disturbances, including fire and insect outbreaks (McCullough et al., 1998; Kurz et al., 2008). Although the direct effects of many of these factors have been evaluated, their interactions can be just as important. For example, insects may increase forest susceptibility to fire by rapidly killing many trees (e.g., Jenkins et al., 2008) and, conversely, fires provide weakened trees for colonization by subcortical insects and pathogens (e.g., Six and Skov, 2009), producing cascading and unpredictable changes in forest ecosystems. Further, biotic interactions such as competition or predation may be mediated by abiotic disturbances such as fire, drought, or flooding (e.g., Elderd, 2006). This is especially noteworthy for ecologically important species whose populations are regulated by interactions with natural enemies and competitors.

Bark beetle (Coleoptera: Curculionidae: Scolytinae) disturbance is an important biotic factor regulating forest ecosystems, and affects forest structure and tree species composition (Kurz et al., 2008; Bentz et al., 2010). *Dendroctonus ponderosae* Hopkins (mountain pine beetle) can cause extensive tree mortality during periodic outbreaks (Safranyik et al., 2010); for example, during the current outbreak, 50% of commercial *Pinus contorta* (lodgepole pine) has been killed in British Columbia, Canada over the last decade (Natural Resources Canada, 2014). Prescribed fires have recently been used in western Canada to reduce pine forest susceptibility to *D. ponderosae* by breaking up even-aged stands. Outbreaks occur after an "incipient-epidemic" stage, during which a population rises enough to successfully attack average large-diameter trees, which would be too well defended to be attacked by a low-density population (Carroll et al., 2006). If conditions remain conducive to population increase, the incipient-epidemic stage

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gives way to the outbreak stage, wherein beetles increase at a high rate and spread across the landscape. Thus, understanding the effects of fire on *D. ponderosae* populations is extremely important to forest management. In a recent study, we found that although *D. ponderosae* always attacked proportionally more trees in burned than in non-burned *P. contorta* stands, the rate of colonization declined over 3 years after a pulse in the year of the fire (Tabacaru, 2015). Since *D. ponderosae* is regulated by a diverse community of subcortical insects at low-density populations (Boone et al., 2008), this decline may be partly due to fire-mediated interactions with the subcortical community, members of which are attracted to burned areas (Tabacaru and Erbilgin, 2015). Specifically, *D. ponderosae* is a poor competitor with other bark beetles (Rankin and Borden, 1991; Safranyik and Carroll, 2006). The bark and ambrosia community is diverse and made up of a variety of feeding guilds, including lower-, main-, and upper-stem feeders, as well as ambrosia beetles (Wood, 1982). Some directly compete with *D. ponderosae* for resources, and others indirectly affect *D. ponderosae* by interacting with the host tree and/or adding to predator and parasitoid loads, resulting in apparent competition (Morris et al., 2005). Thus, examining the responses of the bark and ambrosia beetle community to fire will aid in describing *D. ponderosae* colonization trends and improve our understanding of low-density population dynamics of tree-killing bark beetles in North America.

Bark and ambrosia beetles can be attracted to fire-injured trees, which are most suitable to insects that require stressed or weakened hosts (Rasmussen et al., 1996; McHugh et al., 2003). These beetles are responsible for most post-fire mortality and, although most species do not generally outbreak, there is evidence that even so-called secondary bark beetles can significantly increase after fire and cause extensive tree mortality (Amman and Ryan, 1991; Santoro et al., 2001). North American forests provide habitats for a plethora of bark and ambrosia beetles. For example, western *P. contorta* forests can support ∼30 known species (Safranyik et al., 2004), which likely interact extensively through competition and facilitation, or indirectly via natural enemies, and these interactions may alter the beetles' population growth trajectories (Rankin and Borden, 1991; Safranyik and Carroll, 2006; Wallin et al., 2008). Additionally, bark and ambrosia beetle species differ significantly in their life histories, and possibly in their responses to disturbance (Kirkendall, 1983). Thus, a whole-community approach is necessary to understanding the complex effects of fire. For example, although certain bark and ambrosia beetle species are attracted to fire-injured trees, we do not yet understand the temporal changes in the community in burned forest stands, a factor which may ultimately help to characterize differences in the long-term responses of these biotic agents to fire.

Therefore, we sought to characterize the bark and ambrosia beetle community in burned and non-burned *P. contorta* forests and to examine if a disturbance (fire) can mediate the regulation of a tree-killing bark beetle by potentially intensifying competition. We approached this objective by asking three questions: (1) is fire associated with increasing abundances of bark and ambrosia beetles; (2) what is the pattern of bark and ambrosia beetle community progression into burned areas after fire; and (3) can bark and ambrosia beetles affect *D. ponderosae* colonization of burned areas?

2. Materials and methods

2.1. Study sites and fire injury classes

We worked in three prescribed fire sites in ∼90% mature (>120 years old) *P. contorta* forests within the Alberta Rocky Mountains, all burned in spring 2009. The Mt. Nestor fire (115°22′55.617″W, 50°54′25.073″N) was the smallest (618 ha) and was used to improve habitat for grizzly bears (*Ursus arctos*), bighorn sheep (*Ovis canadensis*), and whitebark pine (*Pinus albicaulis*). Most of the fire occurred in areas with a 200–250-year fire cycle (Rogeau et al., 2004). The Mt. Nestor fire was implemented under the following conditions: temperature, 10–20 °C; relative humidity, 30–40%; wind speed 5–10 km/h; fire weather index, <10–30. The Upper Saskatchewan fire (116°37′2.310″W, 52°1′17.964″N) was the largest (4623 ha) and was used to reduce stand susceptibility to *D. ponderosae* and to restore natural fire regime vegetation types. The majority of this fire occurred in areas with a 100–150-year fire cycle, although some areas had 201–250- and 251–300-year fire cycles (Rogeau et al., 2004). The Upper Saskatchewan fire was implemented under the following conditions: temperature, 15–23 °C; relative humidity, 17–63%; wind speed, 2–40 km/h; fire weather index, 21–57. The Ya Ha Tinda fire (115°36′35.079″W, 51°44′07.784″N) was moderately sized (1264 ha) and was primarily used to reduce stand susceptibility to *D. ponderosae*. It occurred in areas with a 64–98-year fire cycle (Rogeau, 2009). The Ya Ha Tinda fire was implemented under the following conditions: temperature, 25 °C; relative humidity, 22%; wind speed, 10 km/h; fire weather index, 25. All three fires were of mixed-severity, and all forests contained low-density populations of *D. ponderosae*. Sites were separated by >100 km.

We divided fire injury into three classes: non-burned, low, and moderate. These were defined using Parks Canada fire severity classifications, which are based on US Geological Survey techniques (Soverel et al., 2010). We used ArcGIS 9.2 (ESRI, Redlands, CA, U.S.A.) to randomly locate at least 15 10 × 10-m plots, placed a minimum of 200 m apart, within each fire injury class at each site. After plot establishment, we visually estimated the bole (trunk) char of each tree and averaged these per plot as a general measure of fire injury. We used bole char because it can be easily estimated across hundreds of trees, although it may not strictly reflect true injury of the phloem or cambium. Parks Canada's non-burned, low, and moderate classes generally corresponded to 0% bole char, 1–15% bole char (mean for all sites 10.86%), and ⩾16% bole char (mean 31.42%), respectively. Rarely, we found areas of low fire injury in Parks Canada's moderate class and vice versa; we categorized plots in these areas according to bole char. Table 1 summarizes plot characteristics.

2.2. D. ponderosae attacks and beetle collection

We quantified annual *D. ponderosae* attacks in each plot for 4 consecutive years (2009–2012), using characteristic *D. ponderosae*

Table 1
Summaries of plot characteristics, including bole char (the percentage of each trunk that was charred), at Mt. Nestor, Upper Saskatchewan, and the Ya Ha Tinda Ranch, divided among fire injury classes. Information regarding classes is provided in materials and methods. All means are ± SE, where SE was determined using the number of plots as the sample size. n/a = not applicable.

	Nr. plots	Nr. trees	Mean DBH (cm)	Mean bole char (%)
Mt. Nestor				
Non-burned	15	158	22.96 ± 1.52	n/a
Low	16	162	25.03 ± 1.53	8.65 ± 1.04
Moderate	14	107	25.17 ± 1.69	28.89 ± 2.17
Upper Saskatchewan				
Non-burned	16	175	24.12 ± 1.55	n/a
Low	19	210	22.32 ± 1.16	8.19 ± 0.99
Moderate	15	96	23.03 ± 1.30	36.14 ± 5.12
Ya Ha Tinda				
Non-burned	15	134	27.76 ± 1.72	n/a
Low	7	63	23.78 ± 1.85	11.33 ± 1.13
Moderate	23	180	26.02 ± 0.95	29.22 ± 1.95