CHAPTER 9.

Woodboring Beetle Colonization of Conifers Killed by Fire and Bark Beetles: Implications for Forest Restoration and Black-backed Woodpecker Conservation

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INTRODUCTION

Woodboring beetles (Cerambycidae and Buprestidae) are common in coniferous forests of the Western United States, where they are considered secondary forest pests because they generally colonize trees killed or weakened by disturbance (Furniss and Carolin 1977), including wildfire and outbreaks of primary forest pests such as bark beetles (Scolytinae). Disturbances caused by wildfire and bark beetle outbreak (BBO) are expected to be increasingly common in the coming decades (Bentz and others 2010, Kitzberger and others 2017), providing more potential habitat for woodboring beetles. Although woodboring beetle activities can reduce timber values (Lowell and Cahill 1996), woodborers also contribute to ecological services such as snag decomposition and nutrient recycling (Kahl and others 2017), and serve as prey for early-seral habitat specialists like the black-backed woodpecker (*Picoides arcticus*), a species of management interest (Siegel and others 2018) that feeds primarily on the larvae of woodboring beetles (Murphy and Lehnhausen 1998). Understanding how woodborers respond to different types of forest disturbance and stand characteristics is important for predicting the response of forest communities to changes in the disturbance regime, and for designing restoration and management efforts that maximize the ecological services provided by woodborers.

Larval woodborers mature in 1 or more years depending on environmental conditions (Kariyanna and others 2017), feeding within the cambium during early development and later tunneling into sapwood and heartwood. Within trees colonized by bark beetles, there is some evidence that bark beetles and woodborers compete for phloem (Coulson and others 1976, Foelker and others 2018) and that woodborers consume bark beetles during the larval stage (Dodds and others 2001). Adults emerge and fly during the warmer months, using chemical cues to seek out recently dead or weakened trees (Kelsey and Joseph 2003, Miller 2006). Some woodborers locate burned trees by sensing heat and/or smoke (Schmitz and others 1997, Schütz and others 1999). Females deposit eggs in bark crevices, under bark scales, or in small cut niches, and have been observed to avoid oviposition where bark beetle activity is high (Gardiner 1957).

Research on woodboring beetles has concentrated primarily on native species that cause damage to wood products (Álvarez and others 2015) or exotic and invasive species that disrupt entire ecosystems (Aukema and others 2010, 2011). Much less is known about how native woodboring beetles colonize and use trees damaged by fire and primary bark beetles, and how woodborers respond to the timing and severity of disturbance, forest composition and structure, host tree attributes, and interspecific competition (Brin and Bouget 2018, Costello 2013, Costello and others 2011). To inform forest management strategies designed to maintain processes dependent on woodborers, we characterized woodborer activity in 16 sites representing 11 wildfires and five BBOs. Project objectives were as follows: (1) trap

adult beetles to identify and quantify the species of woodboring beetles inhabiting post-wildfire stands and bark beetle-impacted stands; (2) sample beetle larvae to identify and quantify the species of woodboring beetles colonizing fire-killed conifers and unburned bark beetle-killed conifers (primarily yellow pine [*Pinus* spp.] and true fir [*Abies* spp.]); (3) in burned areas, determine if the level of woodborer colonization and activity is associated with the severity of fire injury, tree species, tree diameter, stand-level burn severity, seasonal timing of the fire, and the number of years post-fire; (4) in unburned, beetle-killed areas, determine whether black-backed woodpeckers use bark beetle-killed stands in elevated densities compared to surrounding forest; (5) relate woodboring beetle activity to observed patterns of black-backed woodpecker occupancy and foraging habitat selection; and (6) use the above information to help guide the formulation of forest restoration and salvage logging treatments that effectively address the needs of woodpecker prey species.

METHODS

As detailed in Ray and others (2019), during 2015–2016 we surveyed 11 burned and five BBO sites within Sierran mixed conifer and eastside pine forests in the greater Sierra Nevada region, using a plot-within-transect design. Burned sites were selected using U.S. Department of Agriculture Forest Service, Region 5 Vegetation Burn Severity data (USDA Forest Service, Region 5 2018) and represented a range of fire ages (1–8 years post-burn) and ignition dates (July 5–September 13).

Bark beetle outbreak sites were identified as areas of high tree mortality occurring in the 2–3 years prior to 2016, using the 2015 Region 5 Aerial Detection Survey data layer (USDA Forest Service, Region 5 2015). Within each site, transect placement was stratified by two tree size classes and three levels of burn severity: small (15–28-cm diameter at breast height [d.b.h.]) or large (>28-cm d.b.h.) tree size classes adapted from the California Wildlife Habitat Relationships classification system (California Department of Fish and Game 2005), and low, moderate, or high burn severity classes according to the Relative Differenced Normalized Burn Ratio (RdNBR). Each 100-m transect consisted of three variable-radius plots (VRPs) with centers at 0, 50, and 100 m. We sampled up to 12 transects per site, for a total of 159 transects and 477 VRPs. Each VRP was centered on a panel trap for adult beetles. To avoid attraction bias, traps were unbaited and positioned at least 2 m from the closest tree. Traps were visited every 2 weeks during an 8-week trapping period.

Adult activity per plot was defined as the number of captures per trap visit for each woodboring beetle taxon analyzed. Larval woodborer activity was measured in bark quadrats (15 cm × 15 cm) on the north and south sides of up to six (mean ± standard error [SE] = 5.19 ± 0.09) snags central to each VRP.

Larval activity per quadrat ranged 0–4 and was defined as the number of quarter-quadrats containing signs characteristic of any woodboring beetle larvae (Furniss and Carolin 1977). Bark quadrats were also sampled for

bark beetle presence, bark condition, and char depth class (Ryan 1982). Snags containing bark quadrats were scored for several characteristics including species, char height, d.b.h., percent needles retained, and woodpecker sign.

Woodpecker foraging activity per snag ranged 0–6 and was defined as the number of strata containing excavations or flaked bark characteristic of woodpecker foraging, where strata (n = 6) were the top, middle, and bottom thirds of the north- and south-facing sides of each snag. In each VRP, we also recorded all tree species, live tree basal area (BA), and snag BA.

Each of the three response variables defined above (adult activity, larval activity, or woodpecker foraging activity) was related to potential predictor variables (as suggested in objectives 1–5) using generalized linear mixed-effects models, including nested random effects of site, transect, plot, and snag as appropriate to account for the spatial dependence among samples and (for adult models) repeated measures at each trap. Null models (random effects only) and alternative models of each response were ranked using an information criterion (AIC$_c$ or, for over-dispersed Poisson models of adult activity, QAIC$_c$; Burnham and Anderson 2002). Data from burned sites were modeled separately to assess effects of burn severity and timing not applicable in BBO sites.

RESULTS

We identified 10,412 adult insect captures belonging to six families, including 1,718 Buprestidae and 1,277 Cerambycidae. The most frequently captured buprestids were *Cypriacis aurulenta* (n = 466), *Melanophila consputa* (n = 200), and *Chalcophora angulicollis* (n = 193), while *Xylotrechus longitarsus* (n = 190), *Monochamus obtusus* (n = 89), and *Ortholeptura valida* (n = 88) were most frequent among cerambycids. Larval activity was evident mainly from galleries, frass/boring dust, and exit/transit holes. These indirect signs were sufficient for distinguishing larval woodborers from other taxa but often insufficient for differentiating woodborers by family due to intermingled galleries of unrelated taxa and deterioration of the inner bark and sapwood interface on older snags.

Patterns of adult woodborer activity varied by taxon (Ray and others 2019). The activity of adult buprestids was significantly higher at burned than BBO sites, according to null models fitted for each analysis (fig. 9.1A). Adding a fixed effect of burn severity class showed that buprestid activity also increased significantly with moderate and high RdNBR (fig. 9.1B). The five most highly ranked models of adult buprestid activity in burned sites included significant (α = 0.05, p <0.05) linear and quadratic effects of ignition date indicating a peak in adult activity at fires ignited mid-season, along with a significant decline in activity with fire age, and significant positive effects of snag BA and char height in the VRP. In BBO sites, the top-ranked model of adult buprestid activity included a significant negative effect of live tree BA, suggesting buprestids were most attracted to areas with few surviving trees, a pattern upheld by the second-ranked model, which included a significant positive effect of bark beetle
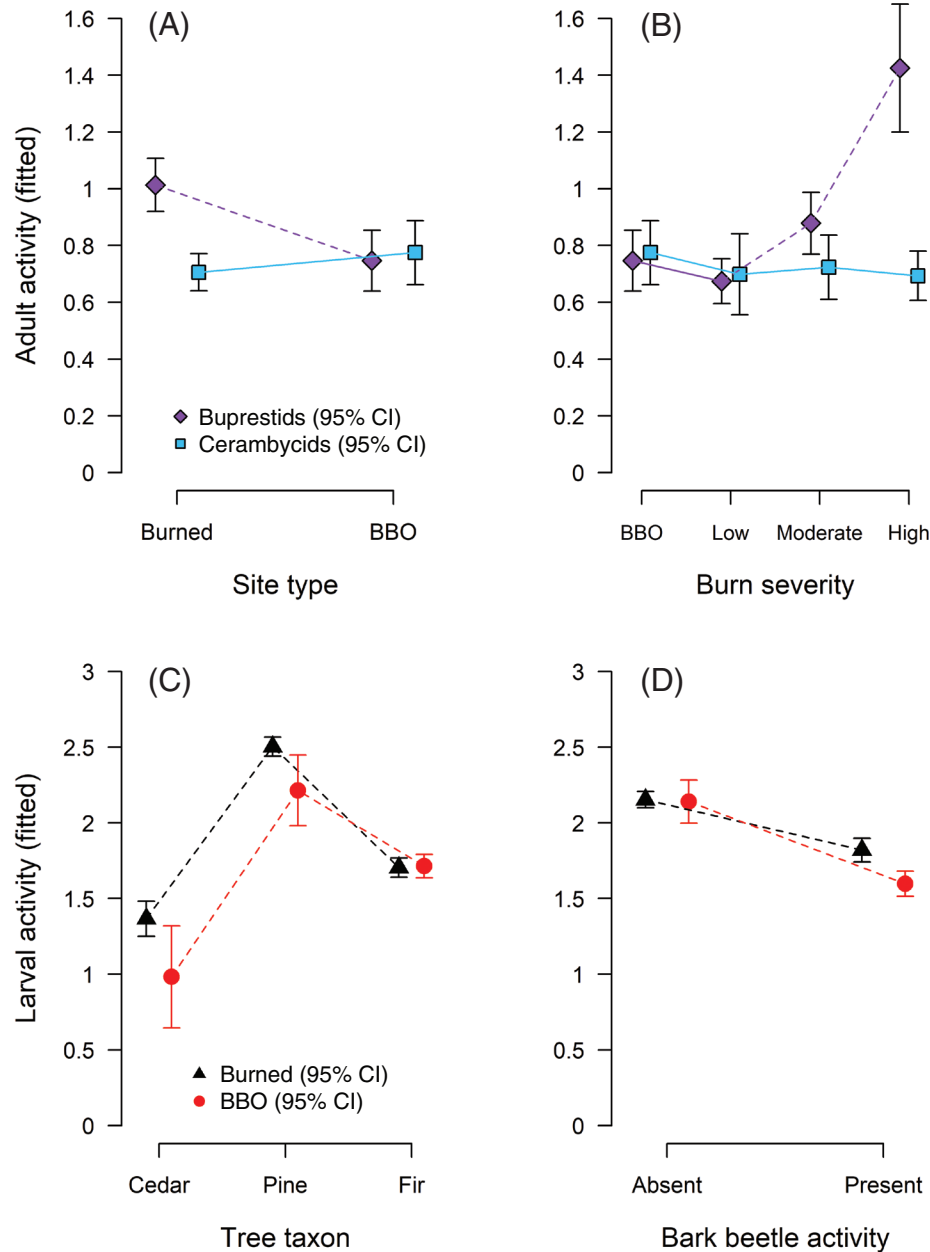
Figure 9.1—Fitted mean woodborer activity and 95-percent confidence interval (CI) from mixed-effects models, showing apparent effects of disturbance type (A) and severity (B) on adult buprestid activity (abundance index), and apparent effects of tree taxon (C) and localized bark beetle sign (D) on larval woodborer activity. Within each panel, lines join results for a given taxon, and solid lines join means that do not differ significantly. In (A), adult datasets from two taxa and two site types were each fit to a null model accounting for nested random effects of site, transect, and plot. In (B), a fixed effect of burn severity was added to the null model of data from burned sites for comparison with unburned (BBO) sites. In (C) and (D), larval data from two site types were each fit to a model with nested random effects of site, transect, and tree plus one fixed effect of host tree taxon (C) or bark beetle activity (D).

activity. In contrast, cerambycid activity was not explained by metrics of disturbance intensity. The top-ranked model of adult cerambycid activity in burned sites was the null model, and the top three models in BBO sites (only weakly supported relative to the null model) included significant negative effects of incense-cedar dominance, number of broken-topped trees, and mean d.b.h. across the VRP.

Larval woodborer activity also responded less to disturbance type and severity than to stand and tree characteristics. Significant differences in larval activity by host tree taxon were much greater than any differences by disturbance type (fig. 9.1C). We also found evidence for negative effects of bark beetle activity on larval woodborer activity in both burned and BBO sites (fig. 9.1D). The top-ranked models of larval activity in both burned and BBO sites included significant negative effects of bark beetle sign presence within the bark quadrat. Other significant effects in supported models of larval activity in burned sites included positive effects of smaller trees, southern bark aspects, and yellow pine species as the host tree taxon, and (like adult buprestids in burned sites) negative effects of linear and quadratic ignition date. In BBO sites, other significant effects in supported models suggested higher larval activity in more advanced stages of an outbreak, such as negative effects of percent needles retained (Ray and others 2019).

Woodpecker foraging activity was found on a greater proportion of snags in burned sites (95 percent confidence interval = 0.63–0.71)

than BBO sites (0.50–0.62), and on a greater proportion of the sampling strata within each snag in burned sites (0.43–0.51) than in BBO sites (0.29–0.41). Regardless of disturbance type—but especially in burned sites—models of woodpecker foraging activity that included a fixed effect of larval woodborer activity ranked higher than null models of woodpecker foraging activity ($\Delta AIC_c > 2$), and the fitted effect of larval activity was significantly positive in these models.

DISCUSSION

Given the potential for ecological and economic impacts of many woodborer species, characterizing woodborer responses to stand conditions could help guide the management of disturbed forests. Post-disturbance forest management often involves multiple objectives, such as recovering the economic value of dead trees (Eklund and others 2009), mitigating hazards associated with disturbance, facilitating reforestation (Bohlman and others 2016, Collins and Roller 2013), reducing fuel levels and the risk of type conversion (Coppoletta and others 2016), and providing a diversity of wildlife habitats (White and others 2016). Achieving these objectives might be facilitated by manipulating woodborer impacts on woody fuel decomposition, nutrient cycling, and succession as well as the availability of woodboring larvae as prey for other species. The range of woodborer responses we observed suggests that managing for a diversity of disturbance types and severity will support a diverse woodborer community.

The relationships we found broadly support results or hypotheses from previous research on these taxa, such as taxon-specific differences in woodborer response to burn severity, apparent competition between woodborer and bark beetle larvae, and woodpecker response to larval woodborers as a prey resource. We also found preliminary evidence that diurnal warming of the cambium might enhance larval growth and activity on the south sides of smaller diameter trees, and that woodborer dispersal might coincide with the middle of the fire season, such that fires ignited early or late in the season will be colonized by fewer woodborers. If the latter result proves to be general, the current trend toward a longer fire season (Balch and others 2017) might not translate into larger populations of woodboring beetles. However, the relationships we found should be investigated for generality in other regions and across a diversity of fire ages and outbreak sites, to facilitate inferences currently constrained by the naturally high covariance and spatial clustering in values of key predictor variables.

CONCLUSIONS

Our results suggest a dynamic process of local initiation and accumulation of woodborer activity that likely leads to temporal trends in the faunal communities supported by larvae and adults as prey and agents of tree decomposition. Woodboring beetle activity at our study sites was often similar between burned stands and unburned stands damaged by bark beetles but varied dramatically with stand composition, burn severity, and bark beetle

activity in each type of disturbance, suggesting management interventions that might effectively promote successional processes and provide prey for wildlife species like the black-backed woodpecker. Effects of these processes on snag longevity and woodpecker activity should be further explored to inform management of disturbed forest stands.

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