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The novel interaction between *Phytophthora ramorum* and wildfire elicits elevated ambrosia beetle landing rates on tanoak, *Notholithocarpus densiflorus*

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ABSTRACT

The 2008 wildfires in the Big Sur region of California's central coast—the first to occur in forests impacted by *Phytophthora ramorum*, the non-native, invasive pathogen that causes sudden oak death—provided the rare opportunity to study the response of scolytid and other subcortical beetles to this novel disturbance interaction. We used sticky card traps attached to the main stem of tanoak, *Notholithocarpus densiflorus*, the tree species most susceptible to *P. ramorum*, to determine which subcortical beetle species may be using tanoak as a host and to compare insect landing rates on these trees in forest plots impacted by neither disturbance, either wildfire or *P. ramorum* disturbance alone, or both disturbances combined. *Xyleborinus saxesenii* and *Gnathotrichus pilosus*, two species of ambrosia beetles (Coleoptera: Scolytidae), composed the majority (48% and 40%, respectively) of subcortical beetles landing on tanoaks during both years of the study. Adults of two species of a small, branch-feeding flatheaded borer (*Anthaxia* sp.; Coleoptera: Buprestidae) were also captured in relative abundance landing on tanoaks in the combined disturbance plots during the second year of the study. All but two of the 2779 scolytid beetles collected in this study were trapped on tanoaks in forest plots disturbed by *P. ramorum* and/or fire, and 75% of these scolytids were trapped during the fall 2009 season. The majority of scolytids were trapped on tanoaks in plots containing both disturbances (81% in 2009 and 79% in 2010), and, of the two disturbances, more scolytids were trapped on tanoaks in burned plots than in *P. ramorum*-infested plots (92% more in 2009 and 476% more in 2010). Semiochemicals emanating from the tanoaks upon which the sticky cards were attached—either in the form of host volatile compounds or scolytid aggregation pheromones—presumably affected ambrosia beetle landing rates, and greater quantities of moribund and recently-killed trees in the plots disturbed both by *P. ramorum* and fire may have led to greater population densities of ambrosia beetles in these areas. Our findings of elevated ambrosia beetle landing rates in Big Sur forests with mixed disturbances suggest a heightened threat to tanoak in these areas, but additional research is needed to determine the actual frequency of ambrosia beetle gallery initiation in living tanoaks and whether colonization hastens or leads to tree mortality.

1. Introduction

Both biotic and abiotic disturbances shape forest ecosystems by influencing their composition, structure, and functional processes (Pickett and White, 1985). Yet even as disturbances proliferate due to climate and habitat change, biological invasions, and other processes, little is known about the interactions among multiple disturbances (Turner, 2010). Disturbance interactions of any type are important because they may exceed the ecological resilience of a particular ecosystem (Paine et al., 1998), but interactions that involve a novel disturbance and a pre-existing disturbance regime are of particular significance due to their increasing frequency and potential for dramatic and sustained changes to landscape structure and function (Buma and Wessman, 2011).

The feedbacks between invasive forest pests and wildfires are examples of interacting disturbances that are of great relevance in the United States (USA). From 1990 to 2006, there was a nearly threefold increase in the rate of detection of established 'high impact' forest pathogens and insects (those species of regulatory significance or that have caused notable damage to forest trees) compared to the previous 130 yr (Aukema et al., 2010).

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Additionally, the frequency of large wildfires in the western USA has increased significantly since the mid-1980s in association with warming temperatures and lengthened fire seasons (Westerling et al., 2006).

As a specific example of two interacting disturbances in western North America, native bark beetles [Coleoptera: Scolytidae (*sensu* Wood, 2007; Bright, 2014)] frequently attack fire-damaged coniferous trees. They are considered the most significant insects following fires in western North America because they can kill weakened trees that may have otherwise recovered from the burn injury (reviewed in McCullough et al., 1998; Parker et al., 2006; Jenkins et al., 2008). Ambrosia beetles (Coleoptera: Scolytidae) are also associated with burned, coniferous forests; they tend to utilize fire-killed trees, and, in the process, enhance the rate of deterioration in this wood by introducing stain fungi (Lowell et al., 1992; Kelsey and Joseph, 2003). In contrast to coniferous forests, there is little information on the response of scolytid beetles to burned hardwood trees in western North America, even in forests where wildfire is part of an established disturbance regime.

Interactions among insects, wildfire, and forest pathogens also occur but have been rarely studied (Parker et al., 2006), and research on three-way disturbance interactions involving a non-native forest pest has been even scarcer. An opportunity to study such a disturbance interaction occurred in the Big Sur region of California's central coast during the summer of 2008 when wildfires occurred for the first time in forests impacted by *Phytophthora ramorum* S. Werres & A.W.A.M. de Cock, a non-native, invasive pathogen (Metz et al., 2011). This destructive oomycete pathogen causes sudden oak death, an emerging forest disease, which, since the mid-1990s, has killed millions of tanoaks, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon, & Oh [syn. *Lithocarpus densiflorus* (Hook. & Arn.) Rehd.], and oaks, *Quercus* spp., in California's coastal forests (Rizzo et al., 2002, 2005; Meentemeyer et al., 2011). *P. ramorum* causes mortality in these susceptible tree species through the formation of bole cankers, which ultimately lead to cambium death and xylem plugging, but the pathogen can also cause non-lethal foliar and twig infections on a wide variety of host plants (Rizzo et al., 2005; Parke et al., 2007). Of the tree species killed by *P. ramorum*, tanoak is the most susceptible to the pathogen and at-risk of extensive areawide mortality from sudden oak death (Hayden et al., 2011; Cobb et al., 2012). In the Big Sur region, one of the most ecologically diverse areas in California but also one of the earliest infested and most impacted by *P. ramorum* (Maschereti et al., 2008; Meentemeyer et al., 2008), tanoak mortality levels are especially high (Maloney et al., 2005; Davis et al., 2010; Metz et al., 2012).

Several species of scolytids, most of which are ambrosia beetles, are associated with *P. ramorum*-infected oaks and tanoaks (Rizzo et al., 2002; McPherson et al., 2005) and have been shown to be preferentially attracted to *P. ramorum*-infected coast live oak, *Q. agrifolia* Née (McPherson et al., 2008). Scolytid entrance holes on *P. ramorum*-infected trees are aggregated in the cankered region of the bole and frequently occur before there are any symptoms of disease in the crown of the tree (McPherson et al., 2000). This targeted colonization of live trees is an unusual behavior for ambrosia beetles of temperate forests (McPherson et al., 2008), as these scolytids are known primarily as opportunistic pests that bore into the sapwood and heartwood of nearly or recently dead trees in order to inoculate the symbiotic ambrosia fungi upon which they feed (Furniss and Carolin, 1977). *P. ramorum*-infected coast live oaks and tanoaks that are colonized by ambrosia beetles display a 65–80% reduction in survival time compared to *P. ramorum*-infected oaks *not* colonized by these beetles (McPherson et al., 2010). This hastened mortality may be due to wood decay fungi that gain entry into the trees on the beetles as they bore through the bark to the xylem, or to the weakened structural integrity of the tree bole caused by the beetle galleries (McPherson et al., 2008, 2010, 2013).

Despite the susceptibility of tanoak to *P. ramorum*, the impacts of scolytid colonization of *P. ramorum*-infected tanoak have received little attention compared to those on coast live oak. Tanoak has been recorded as a host for western oak bark beetles, *Pseudopityophthorus pubipennis* (LeConte) (Bright and Stark, 1973; Furniss and Carolin, 1977; Swiecki and Bernhardt, 2006) and several ambrosia beetles, *Monarthrum scutellare* (LeConte) (Wood and Bright, 1992; Swiecki and Bernhardt, 2006) and *Xyleborinus saxesenii* (Ratzeburg) (Bright and Stark, 1973). No additional host records for scolytids on tanoak were reported in supplements to the world catalog for this family (Bright and Skidmore, 1997, 2002; Bright, 2014).

In 2008, two major wildfires in the Big Sur region created the unique circumstances in which to investigate the response of scolytids to the novel interaction between wildfire and a non-native, destructive pathogen in the coastal forests of California. Specifically, we were interested in the scolytids and other opportunistic subcortical beetles associated with tanoak in this region. If opportunistic subcortical beetles are attracted to tanoaks in Big Sur forests disturbed by wildfire or *P. ramorum*, then compromised trees will have to contend with the additional stress of attempted colonization by these beetles. Opportunistic beetles may react unpredictably to trees in forests that are both burned and *P. ramorum*-infested. For example, beetles may demonstrate a compounded or multiplicative attraction to tanoak in forests with both disturbances, potentially causing damaging levels of beetle colonization and secondary disturbance to this vulnerable tree species.

In this study, we assessed whether *P. ramorum* infestation, wildfire, or the combination of both disturbances affected the landing rates of scolytids on tanoak trees in the Big Sur region. The specific objectives of our research were to determine: (1) Which scolytid species and/or other subcortical beetles landed on sticky cards positioned on the main stems of tanoaks in the Big Sur region; (2) Whether scolytid abundance was influenced by seasonality and/or forest disturbance; and (3) Whether two forest disturbances, *P. ramorum* and fire, interacted to elicit an elevated scolytid landing response on tanoaks.

2. Methods

2.1. Study region

The Big Sur ecoregion (Monterey Co., CA), situated on the western flank of the Santa Lucia Mountains, is a rugged landscape crisscrossed by numerous steep slopes and drainages (Fig. 1). The elevation in the region ranges from sea level to 1571 m within 5 km of the Pacific Coast, facilitating the wide variety of climatic zones and plant communities that contribute to Big Sur's ecological richness (Davis and Borchert, 2006; Meentemeyer et al., 2008; Davis et al., 2010). Redwood-tanoak forests, in which *P. ramorum* is most destructive (Maloney et al., 2005), are generally located in ravines and river valleys at low elevations, whereas mixed evergreen forests, dominated by broadleaf hardwoods, are located predominantly on moist slopes in lower montane zones and higher elevations (Meentemeyer et al., 2008; Davis et al., 2010). The fire regime history for the region is not well characterized, but the return interval between fires is thought to range from 5 to 75 yr with an average return of 24 yr (Davis et al., 2010). In the summer and fall of 2008, wildfires burned large sections of the Big Sur region: The Basin Complex-Indians Fire was ignited by lightning strikes in June and burned more than 95,000 ha until it was contained in late July; the Chalk Fire, located to the south of the first wildfire

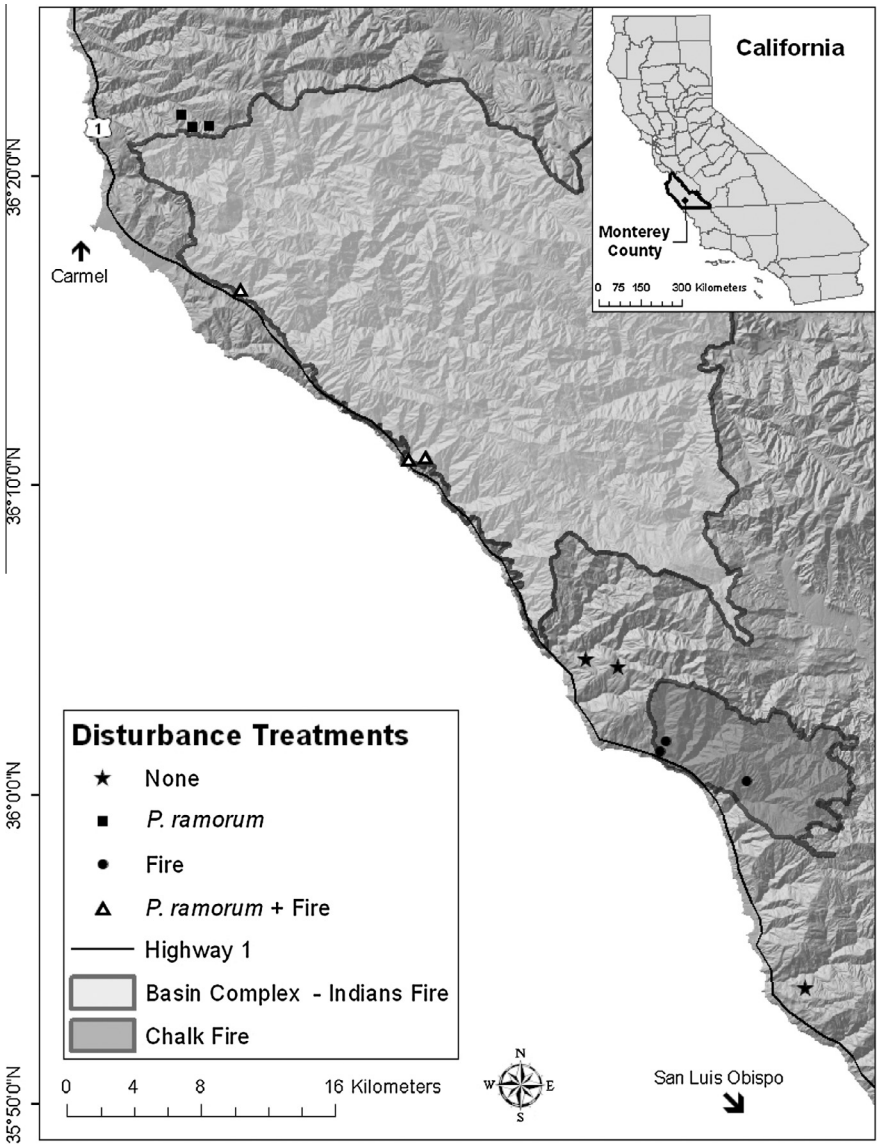

Fig. 1. Location of the study area; beetle trapping plots with associated disturbance treatments; and the Basin Complex-Indians Fire and Chalk Fire perimeters in the Big Sur region, Monterey Co., CA.

(Fig. 1), began in September and burned an additional 6400 ha before it was contained later that month (USDA Forest Service, 2008).

We conducted our research in the Big Sur Forest Monitoring Network, a collection of 280 plots established in 2006 and 2007 to examine the feedbacks among *P. ramorum*, its various hosts, and the physical environment of Big Sur (Haas et al., 2011; Metz et al., 2011, 2012). The plots were 500 m^2 and distributed in a stratified-random design across redwood-tanoak and mixed-evergreen forest types in areas with and without *P. ramorum* (Haas et al., 2011; Metz et al., 2012). Within each plot, we originally measured all stems $\geqslant$1 cm diameter at breast height (dbh) (1.37 m), confirmed the presence of the pathogen or other pests, estimated cover class by species, and measured the cylindrical volume of logs $\geqslant$20 cm in diameter (Metz et al., 2011). Immediately following containment of the Basin Complex-Indians Fire, burn severity was quantified in 61 of the 121 plots burned in the wildfires by using the Composite Burn Index (Key and Benson, 2006; Metz et al., 2011). In the summer of 2009, all stems $\geqslant$1 cm dbh were surveyed again for survival and health, and the live and dead basal area of each host was calculated by using size measurements from plot establishment (Metz et al., 2012).

2.2. Experimental design

Scolytids and other subcortical beetles were sampled from 12 forest plots in August–November of 2009 (="fall" 2009 trapping season) and in March–June of 2010 (=spring 2010 trapping season), approximately 1 and 1.5 yr, respectively, following the fires. We used a balanced, fully crossed two-factor design based on three replicate plots for each of four disturbance combinations: (1) *P. ramorum* and fire disturbance absent = *no disturbance*; (2) *P. ramorum* disturbance present and fire disturbance absent = *P. ramorum disturbance*; (3) *P. ramorum* disturbance absent and fire disturbance present = *fire disturbance*; and (4) *P. ramorum* and fire disturbance present = *mixed disturbance*.

The 12 plots used in this study were chosen for their relatively high density of pre-fire tanoak [each plot had at least 15–25% tanoak cover (Mueller-Dombois and Ellenberg, 1974; Kent and Coker, 1992); see Appendix Table A1 for more details], and all but two of the research plots were located in redwood-tanoak type forests. Nevertheless, the species composition in our plots was generally quite diverse and none of the plots approached a tanoak monoculture. Of the six plots with *P. ramorum*, the percentage of *P.*

ramorum-symptomatic tanoak prior to the fires averaged 70%, and of those burned plots located within the Basin Complex-Indians Fire perimeter, the mean Composite Burn Index ranged from 1.85 to 2.18 on a scale of 0–3 (Appendix Table A1). The total basal area (m^2/plot) and the proportion of *P. ramorum* host basal area that died between the time of plot establishment in 2006/2007 and fall of 2009 was greatest in the *mixed disturbance* plots and the *fire disturbance* plots (Appendix Table A1). The elevations of the plots range from 119 to 670 m, and the minimum distance between plots is 400 m, although the distances between most plots are on the scale of kilometers (Fig. 1, Appendix Table B1). The spatial distance between plots was chosen to ensure independence for pathogen effects and beetle activity, but because neither sudden oak death nor wildfire was randomly distributed among the plot network, there is some clustering of disturbance conditions over the large spatial scale of the network (Fig. 1). Burned plots are necessarily within one of two different fire perimeters, whereas *P. ramorum* infestation is more common in the north of Big Sur than in the south (Fig. 1). However, we checked model residuals in the analyses described below for spatial autocorrelation by using Moran's I and the *spdep* package in the programming language R (R Development Core Team, 2009; Bivand, 2013) and found no evidence of spatial autocorrelation.

2.3. Beetle sampling

Beetles were sampled by using 14 × 20 cm yellow sticky cards (Alpha Scents Inc., Portland, OR, USA) attached to three live tanoaks per plot (=trap trees). Two sticky cards were used per trap tree, and each one was placed approximately at breast height (1.37 m) on the east- and west-facing side of the tree bole, for a total of 6 traps per plot. Although we endeavored to use only trap trees larger than 20 cm dbh in this study, the dbh's of trap trees ranged from 8 to 83 cm with a mean of 42.5 [±3.19 (S.E.)] cm. The three trap trees per plot provided a consistent number of tanoak sample units across the full range of tree species diversity available on the 12 research plots. In some instances, plots may only have had four or five live tanoak trees available in the appropriate size class.

The three tanoaks selected for trap trees within each plot were representative of the overall tanoak in that plot. For instance, within fire disturbance plots, the boles of trap trees were totally or partially charred, and within *P. ramorum* disturbance plots, *P. ramorum* cankers were present on some, but not all, trap trees. Within mixed disturbance plots, most trap trees were charred and some were known to have *P. ramorum* cankers prior to the fires (the post-fire charring made it difficult to see their current canker status), and in control plots, trap trees were neither burned nor diseased. As the damage from the disturbances differed among plots (as shown in Appendix Table A1), the damage level and health of the trap trees also differed among plots.

Sampling in 2009 commenced in mid-August in most plots and concluded in early November, whereas sampling in 2010 ran from mid-March to the second half of June (Appendix Table B1). During the two sampling seasons, the sticky cards were collected periodically to assess beetle landing rates and replaced with clean sticky cards. The deployment lengths of sticky cards ranged from 7 to 31 days, with a mean deployment period of 18 days in fall 2009 and 24 days in spring 2010 (Appendix Table B1). In some instances, different tanoaks were used as trap trees during the spring 2010 season compared to the fall 2009 season; this was due primarily to structural failure or death of trap trees during the winter of 2009–2010.

During the fall 2009 sampling season, sticky cards were attached to the trap trees with green horticultural wire (Woodstream Co., Lititz, PA, USA) wrapped tautly around the tree bole at both the top and bottom of the cards. During the spring 2010 sampling season, rectangular "cages" made of vinyl-coated hexagonal chicken wire (dimensions of 17 × 23 × 3 cm with 2.2 × 2.2 cm openings) were used to surround the sticky cards and prevent the unintended bycatch of birds, mammals, and reptiles. The cages were attached to the trap trees with horticultural wire and the sticky cards were positioned inside the cages so that they were flush against the tree bole while the cage extended about 3 cm from each side of the sticky card surface.

Trap catches on the sticky cards were transported to the laboratory (Davis, CA) for beetle removal and identification. To extract the beetles from the sticky card surface, a droplet of xylenes (EMD Chemicals, Gibbstown, NJ, USA) was placed atop each specimen to dissolve the adhesive, and the point of a scalpel was used to lift the beetles from the card. All beetles from the same plot and deployment period were stored in a vial of xylenes for several days to dissolve any residual sticky trap adhesive. Prior to species identification by microscopy, vacuum filtration through filter paper was used to separate the specimens from the solvent. All scolytids were identified by MMB and SJS by using taxonomic keys and species descriptions (Bright and Stark, 1973; Wood, 1982; Hobson and Bright, 1994), except for one specimen of *Cyclorhipidion bodoanum* (Reitter) (=*Xyleborus californicus* Wood), which was identified by D.E. Bright (Colorado State University, Fort Collins, CO). Buprestid beetles were identified by R. Westcott (Oregon Department of Agriculture, Salem, OR) and S. Bílý (Department of Entomology, National Museum, Prague, Czech Republic). Other subcortical beetles were identified to the species or family level by MMB and SJS. Voucher specimens have been deposited with the Bohart Museum of Entomology, University of California, Davis, CA; the California Academy of Sciences, San Francisco, CA; and the National Museum, Prague, Czech Republic (Buprestidae only).

In this paper, we have elected to use the original family-level nomenclature for bark and ambrosia beetles (Coleoptera: Scolytidae) based on the argument presented in Wood (2007) and a more extensive treatment of the issue developed by D.E. Bright (personal communication), which is to be published in his third supplement to the world catalog of the Scolytidae and Platypodidae (Bright, 2014). In essence, morphological and fossil evidence of adult scolytids support the family-level treatment, whereas similarity in scolytid and curculionid larval morphology supports a subfamily placement. Because this issue is not entirely resolved, we prefer to take the more conservative and economical approach of using the original nomenclature.

2.4. Data analyses

Within each field season, we analyzed the landing rates of (1) all scolytid species combined, and (2) each of the four most abundant scolytid species in the trap catches, by using pooled counts of trap catches from each sticky card deployment period from each of the four disturbance treatments. The seasonal activity of the beetles was presented by plotting these measures versus the mode collection dates of the sticky cards in each trapping season. For analysis of the relationship between scolytid catches and disturbance type, we summed trap catches from all sticky card deployment periods within each field season per plot for each beetle species or the family and then divided by the total number of weeks of trapping in that plot. We compared these standardized landing rates (i.e., the number of beetles trapped/plot/week) with a two-factor analysis of variance (ANOVA) and the crossed factors of *P. ramorum* and fire. Tukey's "honestly significant difference" (HSD) test was used for post hoc pairwise comparisons among treatment means. All tests and analyses were performed with the statistical programming language R (R Development Core Team, 2009) and significance was determined for critical values of $\alpha = 0.05$, although results with $P < 0.1$ were also noted to indicate suggestive trends in the data.

Prior to performing the ANOVAs, each standardized data set was tested for homoscedasticity by using a test for outlying variance (a 'Cochran test') contained in the R package 'outliers' (Komsta, 2011), and those data sets that did not meet the assumptions of homoscedasticity were transformed. Data were also examined for normality by evaluating the model residuals. In most cases, a logarithmic transformation [$x' = \log(x + 1)$] was used, but in certain instances, other transformations were required in order to make the data homoscedastic and meet assumptions of normality in the model residuals, including a square root transformation ($x' = \sqrt{x}$) and a rank transformation (Conover, 1980). There was one instance of species data that remained heteroscedastic despite transformation and on which an ANOVA was not performed [*Monarthrum scutellare* (LeConte) landing rates from spring 2010].

3. Results

3.1. Species collected

Over the course of the 2009 and 2010 trapping seasons, a total of 2779 scolytids were collected and identified from the sticky traps attached to tanoak; 75% of these scolytids were trapped during the fall 2009 season (Table 1). This collection comprised seven species, five of which are ambrosia beetles and two of which are bark beetles. Two of the ambrosia beetle species, *X. saxesenii* and *Gnathotrichus pilosus* (LeConte), made up 48% and 40% of the total scolytid catch, respectively. *M. scutellare* and *M. dentiger* (LeConte), also ambrosia beetles, were the next most frequently trapped scolytids, making up 6% and 5% of the total scolytids, respectively. The remaining 1% of the trapped scolytids was split among three species: *P. pubipennis* and *Hylocurus hirtellus* (LeConte), both bark beetles, and *C. bodoanum*, an ambrosia beetle.

In addition to these scolytid species, a variety of other subcortical beetles were collected from the sticky cards. The most abundant of these beetles were several species of *Anthaxia* (Buprestidae), including *A. cupriola* Barr, *A. retifer* LeConte, and *A. strigata* LeConte (Table 1). These buprestids were trapped exclusively in the spring 2010 trapping season and primarily in the *mixed disturbance* plots (Table 1). *Anthaxia retifer* (108 of 148 identified specimens) was the dominant species (Table 1). Other beetles trapped in small numbers included: *Scobicia declivis* (LeConte) (Bostrichidae); *Colydima lineola* Say (Zopheridae); *Ptilinus basalis* LeConte (Anobiidae); and members of the following families: Anobiidae, Ciidae, Elateridae, Monotomidae, and Tenebrionidae. Larger woodborers typically associated with hardwoods in California [e.g., the flatheaded appletree borer, *Chrysobothris femorata* (Olivier) (Buprestidae), the oak cordwood borer, *Xylotrechus nauticus* (Mannerheim), and *Neoclytus conjunctus* (LeConte) (both Cerambycidae)] were not trapped in our study (Swiecki and Bernhardt, 2006).

3.2. Seasonal flight activity

Within each field season, peak landing rates on tanoak trap trees were variable for different beetle species as well as within individual species in different disturbance treatments. For all scolytid species combined in fall 2009, the peak landing rate on tanoak in the *mixed disturbance* plots occurred between August 24 and September 3, but there was no definitive peak catch for any of the other treatments (Fig. 2A). The peak in the *mixed disturbance* plots was largely driven by the extreme spike in the number of *X. saxesenii* caught during this time period (Fig. 3A), though *M. scutellare* also had a prominent peak catch at this time (Fig. 3C). During the 2010 field season, the highest catches for all scolytid species combined and across all disturbance treatments were recorded between May 29 and June 22 (Fig. 2B). This trend was influenced by catches of *X. saxesenii* (Fig. 4A), *G. pilosus* (Fig. 4B), and *M. dentiger* (Fig. 4D).

Table 1
Trap catches of Scolytidae and Buprestidae collected from sticky traps in four forest disturbance treatments during the fall 2009 and spring 2010 trapping seasons in the Big Sur region, Monterey Co., CA.

Beetles collected	Field season	Disturbance treatments				Totals from all treatments
		None	*P. ramorum*	Fire	Mixed	
Scolytidae						
Xyleborinus saxesenii (Ratzeburg)	2009	0	62	217	757	1036
	2010	1	1	51	247	300
Gnathotrichus pilosus (LeConte)	2009	1	47	16	810	874
	2010	0	1	19	217	237
Monarthrum scutellare (LeConte)	2009	0	18	3	117	138
	2010	0	19	0	21	40
Monarthrum dentiger (LeConte)	2009	0	4	16	5	25
	2010	0	4	46	68	118
Pseudopityophthorus pubipennis (LeConte)	2009	0	0	0	1	1
	2010	0	0	3	5	8
Hylocurus hirtellus (LeConte)	2009	0	0	0	0	0
	2010	0	0	0	1	1
Cyclorhipidion bodoanum (Reitter)[a]	2009	0	0	0	1	1
	2010	0	0	0	0	0
Total scolytids	**2009**	**1**	**131**	**252**	**1691**	**2075**
	2010	**1**	**25**	**119**	**559**	**704**
Buprestidae						
Anthaxia spp.[b]	2009	0	0	0	0	0
	2010	8	0	13	141	162

Bold values are used for the numbers of total scolytids.
[a] *Cyclorhipidion bodoanum* (Reitter) (=*Xyleborus californicus* Wood).
[b] Of the 162 *Anthaxia* spp. collected, 148 specimens were curated and identified as: *A. retifer* LeConte (108 specimens; 99 in mixed, 8 in Fire, and 1 in No disturbance); *A. strigata* LeConte (39 specimens, all in Mixed); and *A. cupriola* Barr (1 specimen in Mixed).

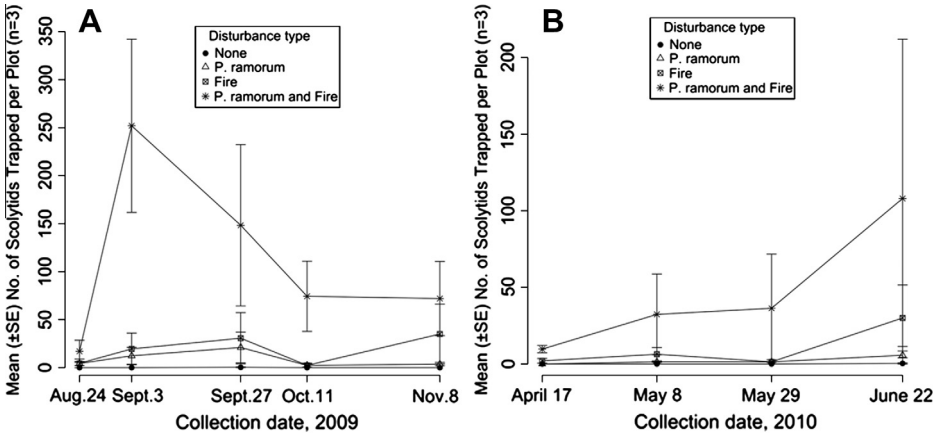

Fig. 2. Mean (±SE) number of total scolytids trapped per plot ($n = 3$) on sticky cards in four forest disturbance treatments at different collection dates in fall 2009 (A) and spring 2010 (B) in the Big Sur region, Monterey Co., CA. The collection dates listed for each trapping season are the mode collection dates for all 12 plots.

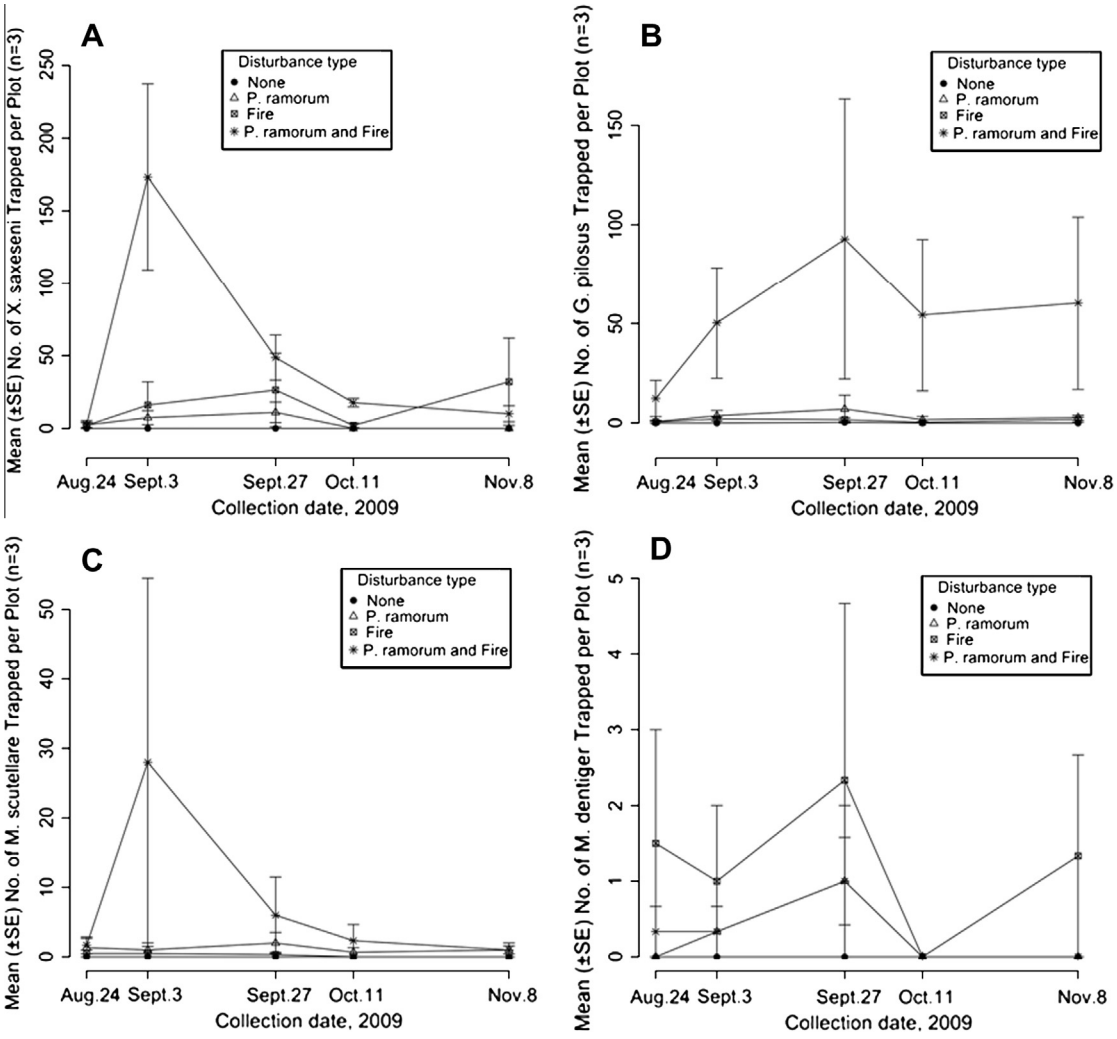

Fig. 3. Mean (±SE) number of *Xyleborinus saxesenii* (A), *Gnathotrichus pilosus* (B), *Monarthrum scutellare* (C), and *Monarthrum dentiger* (D) trapped per plot ($n = 3$) on sticky cards in four forest disturbance treatments at different collection dates in fall 2009 in the Big Sur region, Monterey Co., CA. The collection dates listed are the mode collection dates for all 12 plots.

3.3. Effects of disturbances and their interaction

All scolytids. In fall 2009, 81% of all scolytids collected during that season were trapped on tanoak in the *mixed disturbance* plots, 92% more scolytids were collected in *fire disturbance* plots compared to *P. ramorum disturbance* plots, and only one scolytid beetle was trapped in the plots with no disturbances (Table 1). Log-transformed landing rates of all scolytid species combined differed

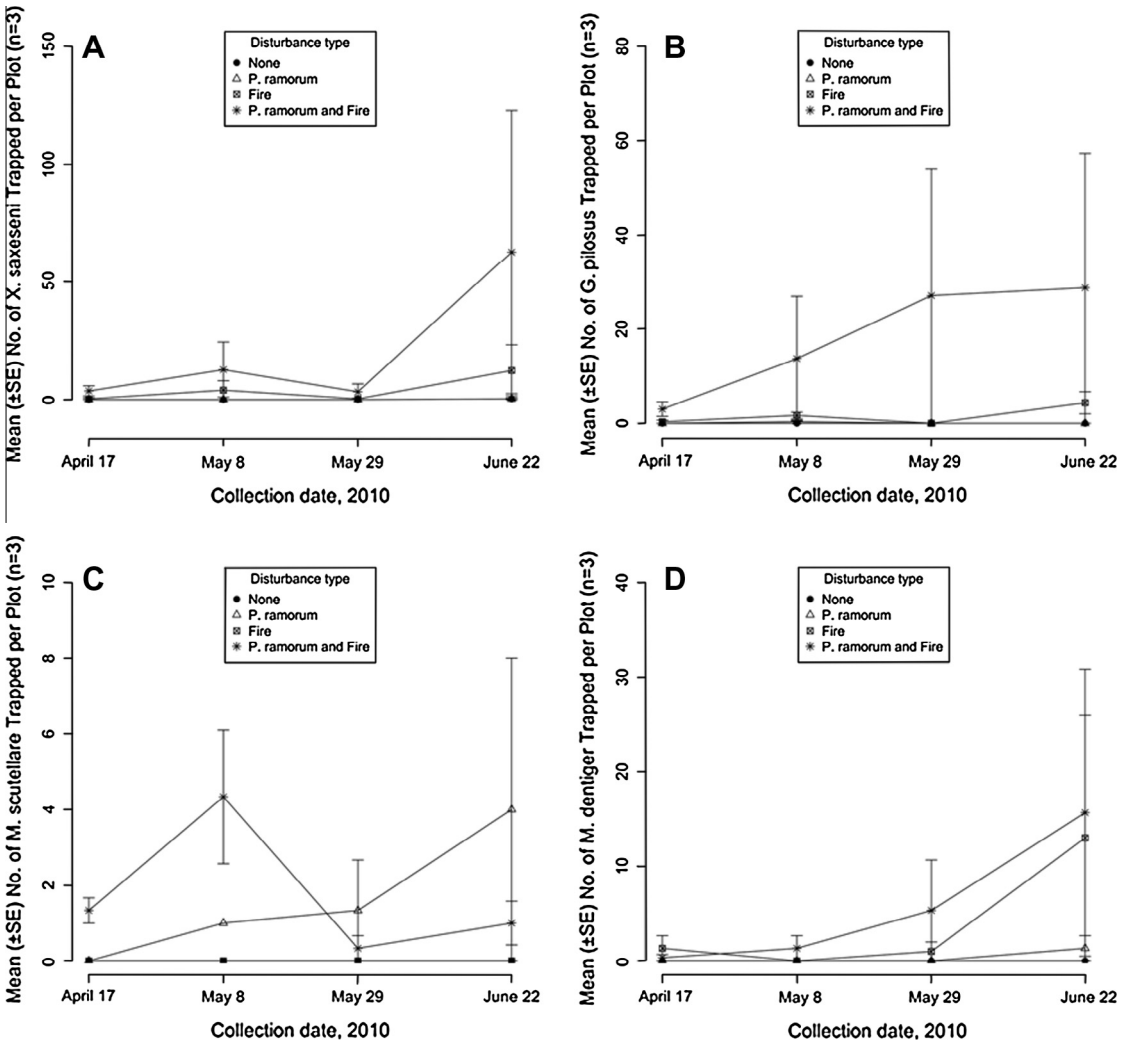

Fig. 4. Mean (±SE) number *Xyleborinus saxesenii* (A), *Gnathotrichus pilosus* (B), *Monarthrum scutellare* (C), and *Monarthrum dentiger* (D) trapped per plot ($n = 3$) on sticky cards in four forest disturbance treatments at different collection dates in spring 2010 in the Big Sur region, Monterey Co., CA. The collection dates listed are the mode collection dates for all 12 plots.

significantly with *P. ramorum* disturbance ($P = 0.01$) and fire disturbance ($P = 0.006$) (Table 2), and the mean landing rate per week per plot was significantly higher in the *mixed disturbance* plots than in the *no disturbance* and *P. ramorum disturbance* plots (Table 3). However, even though landing rates on trap trees in the *mixed disturbance* plots were more than an order of magnitude larger than those in the other plots, the interaction term in the ANOVA model was not significant (Table 2). This was likely due to the fact that the logarithmic transformation that we employed most frequently (and is appropriate for data in which the mean and variance are positively correlated) often eliminates significant interaction terms because relationships that are multiplicative on a linear scale are additive on a logarithmic scale (Gotelli and Ellison, 2004).

In spring 2010, there were fewer scolytids trapped than in fall 2009, but the majority of scolytids (79%) were still collected in the *mixed disturbance* plots (Table 1). In plots with only one disturbance, 476% more scolytids were trapped on tanoak in the fire-disturbed plots than in the *P. ramorum*-disturbed plots, and, as in 2009, only one scolytid beetle was trapped in the plots with no disturbances (Table 1). In the ANOVA model for all scolytids trapped in spring 2010, neither of the disturbance factors nor their interaction were significant, although fire disturbance fell just short of being considered significant at $P = 0.05$ (Table 2). There were no significant differences in mean catches per week among the treatment groups (Table 3).

Individual species. The effects of the disturbances on landing rates of the four most abundant ambrosia beetle species were, for the most part, similar to the results for all scolytid species combined (Tables 2 and 3). There were three results that were notably different for individual species than for all scolytids. First, in the fall 2009 trapping season, *G. pilosus* was the only species collected in this study in which both disturbance factors were significant (*P. ramorum*: $P = 0.006$; fire: $P = 0.014$) *and* the interaction between these disturbances was close to significant ($P = 0.058$) in the ANOVA model of landing rates (Table 2). The mean *G. pilosus* landing rate per week per plot was significantly greater in the *mixed disturbance* plots than in all other treatments, including fire (Table 3). Second, in contrast to the trends noted for the other species trapped in this study, more *M. scutellare* were trapped overall in the *P. ramorum disturbance* plots than in the *fire disturbance* plots in both trapping seasons (Table 1). *P. ramorum* disturbance was the only significant factor ($P = 0.017$) in the 2009 ANOVA model of *M. scutellare* catches (Table 2). Third, *M. dentiger* was the only species collected in this study in which the greatest total catch in a trapping season did not occur in the *mixed disturbance* plots. In the case of *M. dentiger* in 2009, the majority of individuals were trapped in the *fire disturbance* plots (Table 1).

Table 2
ANOVA model[a] for landing rates per plot per week of all scolytid species pooled and for the four most abundant scolytid species trapped in fall 2009 and spring 2010 in the Big Sur region, Monterey Co., CA, with *Phytophthora ramorum* disturbance, fire disturbance, and the interaction of *P. ramorum* and fire disturbances as factors.

Source	Field season	Transformation[c]	Disturbance factors[b]		
			P. ramorum	Fire	*P. ramorum* × fire
All scolytids	2009	$x' = \log(x+1)$	$11.07_{1,8}$; 0.01*	$14.07_{1,8}$; 0.006**	$1.03_{1,8}$; 0.34^{NS}
	2010	$x' = \log(x+1)$	$0.98_{1,8}$; 0.35^{NS}	$5.31_{1,8}$; 0.05†	$0.12_{1,8}$; 0.74^{NS}
Xyleborinus saxesenii	2009	None	$4.45_{1,8}$; 0.068†	$10.53_{1,8}$; 0.012*	$2.82_{1,8}$; 0.13^{NS}
	2010	$x' = \log(x+1)$	$0.57_{1,8}$; 0.47^{NS}	$3.71_{1,8}$; 0.09†	$0.57_{1,8}$; 0.47^{NS}
Gnathotrichus pilosus	2009	$x' = \log(x+1)$	$13.72_{1,8}$; 0.006**	$9.84_{1,8}$; 0.014*	$4.84_{1,8}$; 0.058†
	2010	Rank	$0.60_{1,8}$; 0.46^{NS}	$29.17_{1,8}$;<0.001***	$0.10_{1,8}$; 0.77^{NS}
Monarthrum scutellare	2009	Rank	$8.95_{1,8}$; 0.017*	$4.78_{1,8}$; 0.06†	$0.12_{1,8}$; 0.74^{NS}
	2010	NA[d]	–	–	–
Monarthrum dentiger	2009	$x' = \sqrt{x}$	$0.036_{1,8}$; 0.86^{NS}	0.54$_{1,8}$; 0.48^{NS}	$0.86_{1,8}$; 0.38^{NS}
	2010	$x' = \log(x+1)$	$0.08_{1,8}$; 0.79^{NS}	$1.78_{1,8}$; 0.22^{NS}	$0.003_{1,8}$; 0.96^{NS}

[a] ANOVA model: $Y_{ijk} = \mu + (P.\ ramorum)_j + (\text{fire})_j + (P.\ ramorum \times \text{fire})_{ij} + \varepsilon_{ijk}$ where Y_{ijk} is the landing rate in replicate plot k (#1–3) with disease treatment i (2 levels, present/absent) and fire treatment j (2 levels, present/absent); μ is the true grand mean and ε_{ijk} is the error term. There was no spatial autocorrelation detected in the residuals of any of the nine ANOVA models (all $P > 0.81$, Moran's I Test).

[b] For each table entry in the 'disturbance factors' columns, the first number is the *F*-value with degrees of freedom as subscripts, and the second number is the *P*-value with a significance symbol: †$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

[c] Data for the standardized catches were transformed to meet the assumptions of homogeneity of variances prior to ANOVA, except in the instance of *X. saxesenii* in fall 2009. Homogeneity of variance was confirmed following transformation with a Cochran test; normality was confirmed by an examination of model residuals.

[d] Landing rate data for *M. scutellare* in 2010 did not meet the assumptions of homogeneity of variances with any transformation, and thus an ANOVA was not performed.

4. Discussion

Ambrosia beetles composed the vast majority of subcortical beetles collected from sticky cards attached to tanoaks in the Big Sur region and the greatest catches occurred in the fall one year following the wildfires. Illustrating the opportunistic nature of these insects, all but two of the nearly 3000 ambrosia beetles that were collected in this study were trapped in forest plots disturbed by *P. ramorum* and/or fire. Of the two forest disturbances, fire prompted higher beetle landing rates on tanoak than *P. ramorum* disturbance (except for *M. scutellare*), and significantly more ambrosia beetles were trapped on tanoak in forest plots containing both disturbances than in undisturbed plots or plots with only *P. ramorum* disturbance. In the case of *G. pilosus*, the second most abundantly trapped scolytid, significantly more individuals were trapped in the *mixed disturbance* plots than in any of the other treatments. Our results indicate that the novel combination of these two forest disturbances—one that is historically recurring and the other that has been recently introduced—elicited elevated ambrosia beetle landing rates on tanoak trees.

4.1. Subcortical beetle species trapped on tanoak

Of the seven species of scolytids collected from sticky card traps on tanoaks in the Big Sur region, several have never been reported in Monterey County nor had been known to utilize tanoak as a host. *G. pilosus* is a poorly-known species that has been recorded from the southwestern USA and parts of California [although not in the central coast region (Bright and Stark, 1973; Santa Barbara Museum of Natural History, 2013)] and is only known to colonize the limbs of *Quercus* spp. (Bright and Stark, 1973; Wood, 1982; Wood and Bright, 1992). Although we did not confirm in this study whether *G. pilosus* was actually constructing galleries and developing in tanoak (see further discussion in Section 4.3), our results strongly suggest that this ambrosia beetle utilizes tanoak as a host and demonstrate definitively that *G. pilosus* is present in Monterey County. Other beetle species that were collected in this study for which tanoak has not previously been reported as a host include: (1) *C. bodoanum*, an introduced species to California (Wood, 1982; Hobson and Bright, 1994; Wood and Bright, 1992) and one that has not been reported previously from Monterey County (Wood, 1982; Santa Barbara Museum of Natural History, 2013); (2) *H. hirtellus*; and (3) *M. dentiger*. [The latter two species *have* been reported to use oaks and other hardwoods – but not tanoak – as hosts (Bright and Stark, 1973; Wood, 1982; Wood and Bright, 1992; Dallara et al., 2012)].

M. scutellare, *P. pubipennis*, and *X. saxesenii* have all been recorded from tanoak and from Monterey County, specifically in the Big Sur region (Bright and Stark, 1973; Santa Barbara Museum of Natural History, 2013). *X. saxesenii*, the most abundantly trapped scolytid in this study, has a widespread and transcontinental distribution in North America and has been collected on five other continents (Bright and Stark, 1973; Wood, 1982; Wood and Bright, 1992; Rabaglia et al., 2006). It can utilize so many different trees as hosts that "possibly no species is exempt from invasion" (Bright and Stark, 1973). Of the three buprestids species trapped, *A. strigata* has been recorded from Monterey County [the type specimen was collected in nearby Kern County (Nelson et al., 2008)], but *A. cupriola* and *A. retifer* have not (Santa Barbara Museum of Natural History, 2013). Both of the latter species have been collected elsewhere in CA (Bellamy, 2008; Nelson et al., 2008; Santa Barbara Museum of Natural History, 2013). An examination of the holdings of the California State Collection of Arthropods (Sacramento, CA) revealed no specimens of *A. cupriola*, *A. retifer*, or *A. strigata*. There is little information regarding the biology and host preference of

Table 3
Mean (±SE) number of scolytids trapped per plot per week ($n = 3$) on sticky traps in four forest disturbance treatments during the fall 2009 and spring 2010 trapping seasons in the Big Sur region, Monterey Co., CA.

Source	Field season	Disturbance treatments[a]			
		None	*P. ramorum*	Fire	Mixed
All scolytids	2009	0.03 ± 0.03 a	3.51 ± 2.44 a	7.09 ± 6.12 ab	46.42 ± 17.53 b
	2010	0.03 ± 0.03 a	0.61 ± 0.54 a	2.92 ± 2.11 a	13.73 ± 12.26 a
Xyleborinus saxesenii	2009	0 a	1.66 ± 0.92 a	6.07 ± 5.72 ab	20.78 ± 5.17 b
	2010	0.03 ± 0.03 a	0.02 ± 0.02 a	1.25 ± 1.14 a	6.07 ± 5.44 a
Gnathotrichus pilosus	2009	0.03 ± 0.03 a	1.26 ± 1.06 a	0.49 ± 0.09 a	22.24 ± 15.44 b
	2010	0 a	0.03 ± 0.03 a	0.47 ± 0.20 b	5.33 ± 5.18 b
Monarthrum scutellare[b]	2009	0 a	0.48 ± 0.40 ab	0.08 ± 0.05 ab	3.21 ± 3.01 b
	2010	0	0.47 ± 0.39	0	0.52 ± 0.17
Monarthrum dentiger	2009	0 a	0.11 ± 0.07 a	0.44 ± 0.44 a	0.14 ± 0.14 a
	2010	0 a	0.10 ± 0.10 a	1.13 ± 1.13 a	1.67 ± 1.63 a

[a] Data in the same row followed by different letters are significantly different ($P < 0.05$) based on Tukey's HSD test for pairwise comparisons. Refer to Table 2 for type of transformation performed on data from each source and field season.
[b] Pairwise comparisons were not made on the 2010 data due to a lack of homogeneity of variances.

these species, but the larvae of *Anthaxia* spp. generally feed on branches of conifers, hardwoods, and shrubs, whereas the adults are commonly found on yellow or white flowers (Furniss and Carolin, 1977). Species of *Cupressus* and *Pinus* have been listed as larval hosts for *A. retifer* (Barr, 1971; Nelson et al., 2008) and adults of both *A. cupriola* and *A. retifer* have been collected foraging on flowers from a wide array of plant species (Barr, 1971; Nelson et al., 2008). Thus, although their population densities may have been elevated in certain plot types in our study, the responses of these beetles may have been directed toward the color of the sticky card traps (similar in color to flowers) and not to volatiles from the tanoaks in the various disturbance classes.

4.2. Seasonal flight activity

We chose to trap subcortical beetles in the fall and spring because peak flight periods for *M. scutellare* and *X. saxesenii* have been previously recorded during these seasons in coastal California (Bright and Stark, 1973; S.J. Seybold, unpublished data). Of these two seasons, far greater total catches of scolytids occurred in the fall (especially during late August and September), indicating that these beetles—in general—disperse more readily in the fall or late summer. [*M. dentiger* was the one exception among the scolytid species, as it was trapped in greater numbers in the late spring of 2010 compared to the fall of 2009, as were the two primary *Anthaxia* spp., which were *only* trapped during the spring months. As was the case in our study, previous collections of *A. strigata* have also been made in the spring (Santa Barbara Museum of Natural History, 2013)]. Fall may be the season most conducive to ambrosia beetle dispersal and gallery initiation in coastal California because trees may be stressed following the drought-like conditions of the typically hot and dry summer. Furthermore, the late fall rainy season may be conducive to the development of these beetles, whose galleries must be moist for the fungus to grow and provide food for the larvae (Ebeling, 1978). Landing rates may also have been greater in fall 2009 because of (1) the potential attractiveness of the trees as a result of the timing of *P. ramorum* infection status or burn status in the trap trees, or (2) potentially higher population densities of scolytids in the trap trees or other trees damaged in the plots by fire in the summer and fall of 2008 (see discussion in Section 4.3). Additionally, the use of wire cages over the sticky card traps in the spring 2010 trapping season may have reduced the rate of scolytid interception. However, the modified traps did capture higher rates of an even larger insect (*Anthaxia* spp.) during the spring of 2010, so it is not likely that there was a reduction in trapping efficiency due to the modification. Because spring 2010 scolytid catches were highest at the end of the trapping period, it is possible that the peak of the spring/summer flight period actually occurred after we concluded trapping.

Although our results suggest that most scolytids in the Big Sur study area disperse in greatest numbers in fall, we cannot make further conclusions about the life histories of the specific scolytid species or the influences of the forest disturbances on scolytid seasonality because: (1) we did not repeat trapping during the spring and fall season in multiple years; (2) trapping was not conducted during the mid-summer or winter; and (3) we did not collect climate data at our research sites. Ambrosia beetles are quite sensitive to temperature, moisture, and other climatic factors, and fluctuations in these variables can have a tremendous influence on the duration of physical development, the number of generations per year, and the timing of dispersal flights for a particular scolytid species (Wood, 1982). For example, variation in the microclimate of research sites located in different disturbance areas (e.g., lower elevation and closer proximity to the ocean in the *mixed disturbance* plots versus higher elevation and further distance from the ocean in *P. ramorum disturbance* plots; see Fig. 1)

may have contributed to differences in scolytid abundance and seasonality among disturbance treatments. Coastal fog and a rapid increase in temperature with higher elevations are characteristic of the marine inversion layer along the Big Sur coastline (Davis et al., 2010), making weather conditions quite variable even among sites located relatively close to one another.

4.3. Effects of disturbances and their interaction

Although ambrosia beetle landing rates on tanoak were significantly higher in forests disturbed both by fire and *P. ramorum*, it is important that the landing rates presented in this study are not interpreted as rates of host colonization because we did not quantify the number of entrance holes on the trap trees or verify that the ambrosia beetle species trapped on the sticky cards were actually constructing galleries and successfully rearing offspring in the tanoaks. One hypothesis of how scolytids find appropriate host trees is that they land randomly on trees and test their suitability by short-range olfaction or gustation (Moeck et al., 1981; Byers, 1995; Graves et al., 2008), and thus the landing rates of ambrosia beetles are not necessarily equivalent to their actual rates of colonization. Nevertheless, signs of ambrosia beetles colonization on tanoaks in the disturbed plots were frequently noted over the course of this study (including on some tanoaks used as trap trees), and, because tanoak is the predominant hardwood component of the forests in our research sites, these observations strongly suggest that ambrosia beetle landing rates on tanoaks were likely correlated with rates of colonization.

We positioned the sticky card traps on the lower stems of tanoaks in this study because we wanted to learn which scolytids were potentially using tanoak as a host, but this methodology also allowed the characteristics of the individual trap trees to influence scolytid landing rates. Semiochemicals emanating from the trap trees very likely affected ambrosia beetle landing rates, as the production of volatile compounds that are attractive to scolytids has been proposed and, in some cases, demonstrated to occur in trees infected with *P. ramorum* and injured by fire. McPherson et al. (2005, 2008) suggested that ambrosia beetle entrance holes are concentrated in the canker region of *P. ramorum*-infected trees because of olfactory responses to volatile compounds produced in the canker region. Ockels et al. (2007) used gas chromatography–mass spectrometry to identify several different volatile phenolic compounds in the exudates of *P. ramorum*-infected coast live oaks that may be involved in host defense responses but also act as attractants to scolytids. Research by Kelsey et al. (2013) demonstrated that ethanol, a compound known to elicit aggregation behavior in a wide range of ambrosia beetles (Kelsey and Joseph, 1999; Seybold et al., 2000; Coyle et al., 2005; Miller and Rabaglia, 2009; Gandhi et al., 2010), was present in higher concentrations in the sapwood of *P. ramorum*-infected coast live oaks near to the canker region compared to sapwood located further from the canker region, as well as compared to sapwood from trees not infected with *P. ramorum*.

Ethanol concentrations in the sapwood of fire-injured ponderosa pines, *Pinus ponderosa* Douglas ex. C. Lawson, have also been found to be much greater than in similar sapwood samples from unburned ponderosa pines, suggesting that scolytids may be attracted to burned conifers as a result of the detection of this ethanol (Kelsey and Joseph, 2003). As trees recover from fire injury, ethanol concentrations have been shown to decline (Kelsey and Joseph, 2003), and this may be another reason that landing rates were lower in the spring 2010 trapping season than the fall 2009 trapping season. However, ethanol concentration are greatest in severely scorched and fire-killed trees (Kelsey and Joseph, 2003), and scolytids have been known to colonize trees for as long as four years post-burn (Jenkins et al., 2008). Additionally, scolytids—including *Gnathotrichus* spp. and other ambrosia beetles—produce aggregation pheromones in suitable situations, and apart from host-produced volatiles, these pheromones are the dominant semiochemicals that stimulate mass attack upon a tree [see Seybold and Vanderwel (2003) and references therein]. The large numbers of scolytids trapped on specific tanoaks at certain times in this study (often when very few beetles were trapped on other trap trees in the same plot) suggests that aggregation pheromones may have been released from trees colonized by ambrosia beetles in the disturbed plots.

To explain why greater numbers of beetles were trapped on tanoak in plots with both disturbances compared to individual disturbances, it may be simpler to examine the overall levels of tree mortality in the different disturbance treatments rather than speculate on the synergistic effects between host volatiles or pheromones produced in *P. ramorum*-infected and burned trees or the volume of scorched wood on the landscape. Although the data on plot-level mortality from the time of plot establishment in 2006/2007 to the fall of 2009 are incomplete, the total basal area as well as the proportion of trees within the plot that died during those two or three years is quite large in the *mixed disturbance* plots (as well as in one of the *fire disturbance* plots) (Appendix Table A1). Greater quantities of moribund and recently-killed trees in a plot, whether from *P. ramorum*, fire-injury, or both, may have led to greater population densities of ambrosia beetles in those areas.

In addition to killing burned trees that would have ordinarily recovered from their injuries, large populations of bark beetles that emerge from fire-injured trees may also disperse to colonize nearby green trees (Furniss and Carolin, 1977; Wood, 1982). This scenario has not been observed with ambrosia beetles in the Big Sur region, nor is it expected to occur due to the opportunistic nature of ambrosia beetles and the ample supply of recently dead and dying trees in the area. However, given the imperiled state of tanoaks in coastal California from *P. ramorum*-caused mortality, even the loss of fire-injured tanoaks to ambrosia beetle colonization would have a major impact on the forests of the Big Sur region. Further research is needed to determine the actual frequency of ambrosia beetle gallery initiation in living tanoaks and whether colonization hastens or leads to tree mortality.

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Appendix A

See Table A1.

Appendix B

See Table B1.

Table A1
Stand characteristics and disturbance impacts for plots in the study: tanoak abundance, *P. ramorum*-symptom levels, burn severity, and recent mortality levels of *P. ramorum* hosts.

Plot ID[c]	Disturbance treatment	Pre-fire tanoak abundance and infection level		Burn severity	Proportion of basal area of *P. ramorum* hosts with recent mortality[a]		Basal area[b] (m^2/plot) of recent mortality[a] in *P. ramorum* hosts	
		Cover class[d]	% symp-tomatic[e]	CBI, mean[f]	Tanoak only	Other woody hosts[g]	Tanoak only	Other woody hosts[g]
BS 328	None	7	–	–	0.0293	0	0.069	0
BS 407	None	5	–	–	0	0	0	0
BS 408	None	5	–	–	NA[h]	NA[h]	NA[h]	NA[h]
BS 600	*P. ramorum*	7	52%	–	NA[h]	NA[h]	NA[h]	NA[h]
BS 601	*P. ramorum*	4	74%	–	0.0002	0	<0.0001	0
BS 603	*P. ramorum*	7	76%	–	0	0.0001	0	0.0001
296	Fire	4	–	NA[h]	0.0156	0.0007	0.0024	0.0033
A	Fire	NA[h]	–	NA[h]	NA[h]	NA[h]	NA[h]	NA[h]
BS 426	Fire	5	–	NA[h]	0.4208	0.0005	0.6587	0.0012
BS 283	Mixed	7	53%	2.18	0.2065	0.2398	0.2909	0.0289
BS 457	Mixed	5	89%	1.98	0.7757	0.0015	0.5009	0.0091
BS 627	Mixed	5	76%	1.85	0.5503	0.5973	0.3035	0.9195

[a] Recent mortality is defined as trees that have died between the time of plot establishment in 2006/2007 and the fall of 2009.
[b] Basal areas were calculated for each host by using the dbh (diameter at breast height, or 1.37 m above the ground) for every stem $\geqslant$1 cm dbh.
[c] Plot names with 'BS' indicate that the plot is part of the Big Sur Forest Monitoring Network. Plot '296' was located slightly upslope from plot BS 296 for safety reasons. Plot 'A' was created solely for this study because of the lack of a third accessible plot with fire disturbance only in the Big Sur Forest Monitoring Network, and thus pre-fire measurements are not available (NA).
[d] The cover class score indicates what percentage of plot area was covered by tanoak prior to the fires on a scale of 1–7: 1 $\leqslant$ 1%; 2 = 1–5%; 3 $\geqslant$ 5–15%; 4 $\geqslant$ 15–25%; 5 $\geqslant$ 25–50%; 6 $\geqslant$ 50–75%; 7 $\geqslant$ 75% (Mueller-Dombois and Ellenberg, 1974; Kent and Coker, 1992).
[e] Infection level was measured as the percentage of total tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & Oh, trees per plot expressing *P. ramorum* symptoms (either as twig die-back or bole cankers).
[f] Burn severity was rated by using the mean composite burn index (CBI), which uses a continuous value from zero (least severe) to three (most severe) to assess the impacts of fire to five forest strata (substrate, herbs, shrubs, intermediate trees, and dominant trees) [Key and Benson, 2006; see Metz et al., 2011 for more information on burn severity assessment in the Big Sur Forest Monitoring Network]. Only plots within the Basin Complex-Indians Fire were assessed for burn severity in the fall of 2008, so mean CBI scores for the *fire disturbance* plots (all located in the Chalk Fire perimeter) are not available (NA).
[g] Other woody hosts include California bay laurel, *Umbellularia californica* (Hook. & Arn.) Nutt., coast live oak, *Quercus agrifolia* Née, Pacific madrone, *Arbutus menziesii* Pursh., coast redwood, *Sequoia sempervirens* (D. Don) Endl., and Shreve oak, *Q. parvula* var. *shrevei*.
[h] NA = not available.

Table B1
Dates of subcortical beetle trapping periods and sticky card exchanges, and the location and elevation of plots in the Big Sur region, Monterey Co., CA.

Plot ID[a]	Disturbance treatment	Trapping period and sticky card exchange dates in the 2009 and 2010 field seasons		Elevation and coordinates (NAD83, Zone 10) of plots		
		Trapping period	Sticky card exchange dates	El. (m)	Easting	Northing
BS 328	None	September 3–November 8, 2009 March 19–June 22, 2010	September 27, October 11 April 18, May 9, May 29	433	641306	3972920
BS 407	None	August 17–November 8, 2009 March 20–June 22, 2010	August 24, September 4, September 27, October 11 April 16, May 9, May 30	670	630115	3992138
BS 408	None	August 17–November 8, 2009 March 20–June 22, 2010	August 24, September 4, September 27, October 11 April 16, May 9, May 30	375	628187	3992551
BS 600	*P. ramorum*	August 15–November 9, 2009 March 20–June 24, 2010	August 25, September 5, September 28, October 12 April 19, May 7, May 30	549	605699	4024499
BS 601	*P. ramorum*	August 15–November 9, 2009 March 20–June 24, 2010	August 25, September 5, September 28, October 12 April 19, May 7, May 30	603	604677	4024425
BS 603	*P. ramorum*	August 15–November 9, 2009 March 20–June 24, 2010	August 25, September 5, September 28, October 12 April 19, May 7, May 30	491	604005	4025199
296	Fire	August 16–November 8, 2009 March 19–June 22, 2010	August 24, September 3, September 27, October 11 April 18, May 9, May 29	590	637821	3985329
A	Fire	September 3–November 8, 2009 March 19–June 22, 2010	September 27, October 11 April 16, May 9, May 29	230	632681	3987434
BS 426	Fire	August 14–November 8, 2009 March 19–June 22, 2010	August 24, September 3, September 27, October 11 April 16, May 9, May 29	240	632637	3987060
BS 283	Mixed	August 14–November 7, 2009 March 18–June 21, 2010	August 23, September 3, September 26, October 10 April 18, May 10, May 30	606	618664	4004717
BS 457	Mixed	August 14–November 7, 2009 March 18–June 21, 2010	August 23, September 2, September 26, October 10 April 16, May 7, May 28	443	617584	4004573
BS 627	Mixed	August 14–November 7, 2009 March 18–June 21, 2010	August 23, September 2, September 26, October 10 April 16, May 7, May 28	119	607541	4014665

[a] Plot names with 'BS' indicate that the plot is part of the Big Sur Forest Monitoring Network. Plot '296' was located slightly upslope from plot BS 296 for safety reasons. Plot 'A' was created solely for this study because of the lack of a third accessible plot with fire disturbance only in the Big Sur Forest Monitoring Network.

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