

# Goldspotted oak borer effects on tree health and colonization patterns at six newly-established sites

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- Abstract**
- 1 Newly-established populations of invasive wood-inhabiting insects provide an opportunity for the study of invasion dynamics and for collecting information to improve management options for these cryptic species.
  - 2 From 2011 to 2013, we studied the dynamics of the goldspotted oak borer *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), a new pest of oaks in southern California, at six sites that had been colonized recently.
  - 3 At all sites, the percentage of coast live oaks *Quercus agrifolia* Née, colonized by *A. auroguttatus* increased between 2011 (6–33%) and 2013 (23–40%), although beetle densities did not grow rapidly at most sites.
  - 4 From 2011 to 2013, there were minor changes in signs and symptoms of *A. auroguttatus* infestation (adult emergence holes, bark staining, and evidence of woodpecker foraging), except at one site where an outbreak occurred. At some sites, noticeable negative changes in oak crown health occurred 1 year prior to positive *A. auroguttatus* population growth.
  - 5 Among sites, most of the *A. auroguttatus* population density (66–93%) was produced by a small number of heavily-infested trees (= brood trees). Early identification and removal of brood trees in newly-invaded areas could slow the growth of *A. auroguttatus* populations.

**Keywords** *Agrilus auroguttatus*, brood trees, insect population dynamics, invasion dynamics, newly-established invasive species, oak pest, per capita rate of increase.

## Introduction

As the number of invasive alien species that are moving about the globe continues to increase, so does the number of invasive alien insects that feed beneath the bark of woody plants (Aukema *et al.*, 2010). These insects are often moved inter- and intra-continentially via wood-packing material or firewood (Haack, 2006; Haack *et al.*, 2010; Herms & McCullough, 2014). Opportunities for studying invasive subcortical insects once they have caused extensive and noticeable damage to their new habitat are more frequent than opportunities for studying newly-established populations. Invasive borers may not be noticed for several years, possibly because founder populations are small, borers have cryptic habits and detection tools are poor, or some combination of these factors. Nonetheless, researchers

have taken advantage of opportunities to study new populations of invasive borers (Mercader *et al.*, 2009; Siegert *et al.*, 2010; Dodds & Orwig, 2011; Fierke *et al.*, 2013), often using external symptoms on recently colonized trees to detect nascent infestations (Corley *et al.*, 2007; Dodds *et al.*, 2010). Such studies enhance our understanding of the biology and ecology of invasive borers in their new habitats and can lead to the development of effective management strategies.

Goldspotted oak borer *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is a new invasive phloem- and wood-boring beetle in southern California (Coleman & Seybold, 2008, 2011). To date, *A. auroguttatus* has killed more than 25 000 oaks (mostly coast live oak *Quercus agrifolia* Née; California black oak *Quercus kelloggii* Newberry; and some canyon live oak *Quercus chrysolepis* Leibmann) in eastern San Diego County (Coleman *et al.*, 2012a; USDA Forest Service FHM, 2014). *Agrilus auroguttatus* is native to southeastern Arizona, where it feeds on Emory oak *Quercus emoryi* Torrey and silverleaf oak *Quercus hypoleucoides* A. Camus; and it likely

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occurs throughout the distribution of *Q. emoryi* in New Mexico, Texas and Mexico (Coleman & Seybold, 2011; Coleman *et al.*, 2012a). Movement of firewood is the suspected pathway of introduction for *A. auroguttatus* from Arizona to California (Coleman *et al.*, 2012b; Lopez *et al.*, 2014a,b).

Recently, the life history and diagnosis of damage by *A. auroguttatus* have been characterized. In southern California, generation time for the majority of individuals is 1 year (Haavik *et al.*, 2013a). Adults are captured in flight from May to October (Coleman & Seybold, 2008; Haavik *et al.*, 2013a; Coleman *et al.*, 2014). Females oviposit in bark cracks or crevices; small larvae chew through bark and migrate to the interface between the phloem and xylem where they feed in a meandering pattern, undergo a total of four instars and form dark, frass-filled galleries (Coleman & Seybold, 2008; Hishinuma *et al.*, 2011; Flint *et al.*, 2013; Haavik *et al.*, 2013a). Larvae overwinter in a chamber just under the outer bark in a doubled-over hairpin position (also called J-larvae). If individuals have a 2-year life cycle, earlier instars may overwinter within the larval gallery at the phloem/xylem interface. Pupation occurs in the overwintering chamber, and adults chew out of this pupal cell and through the outer bark to emerge. Emerging adults create characteristic D-shaped holes, approximately 4 mm wide, which are clearly visible on the bark surface (Coleman & Seybold, 2008; Hishinuma *et al.*, 2011; Flint *et al.*, 2013; Haavik *et al.*, 2013a). Additional external signs and symptoms of *A. auroguttatus* infestation include bark staining (sometimes coincident with pathogenic fungi; Lynch *et al.*, 2014) and evidence of woodpecker foraging on the bark surface that tracks larval feeding galleries (Coleman & Seybold, 2008; Hishinuma *et al.*, 2011).

Studies of *A. auroguttatus* populations in newly-invaded areas will advance knowledge of its invasion dynamics and inform management decisions. Such studies can determine how rapidly population densities grow or spread, how beetles are distributed among trees, and how well visual signs and symptoms associated with changes in oak infestation reflect changes in beetle densities. To search for temporal patterns in *A. auroguttatus* population densities in newly-invaded areas, we studied the symptoms of infestation among *Q. agrifolia* (a favoured host) and estimated *A. auroguttatus* population densities annually for 3 years at six sites where the beetle had likely recently established. The recency of colonization was determined from annual ground and aerial surveys of oak mortality (Fig. 1) (Coleman & Seybold, 2011; USDA Forest Service FHM, 2014). Specific objectives were to: (i) determine whether signs and symptoms of *A. auroguttatus* infestation changed over a 3-year period; (ii) quantify changes in oak health through visual surveys; (iii) document changes in the density and growth of *A. auroguttatus* populations; and (iv) describe how *A. auroguttatus* individuals were distributed among oaks.

## Materials and methods

### Study sites and tree surveys

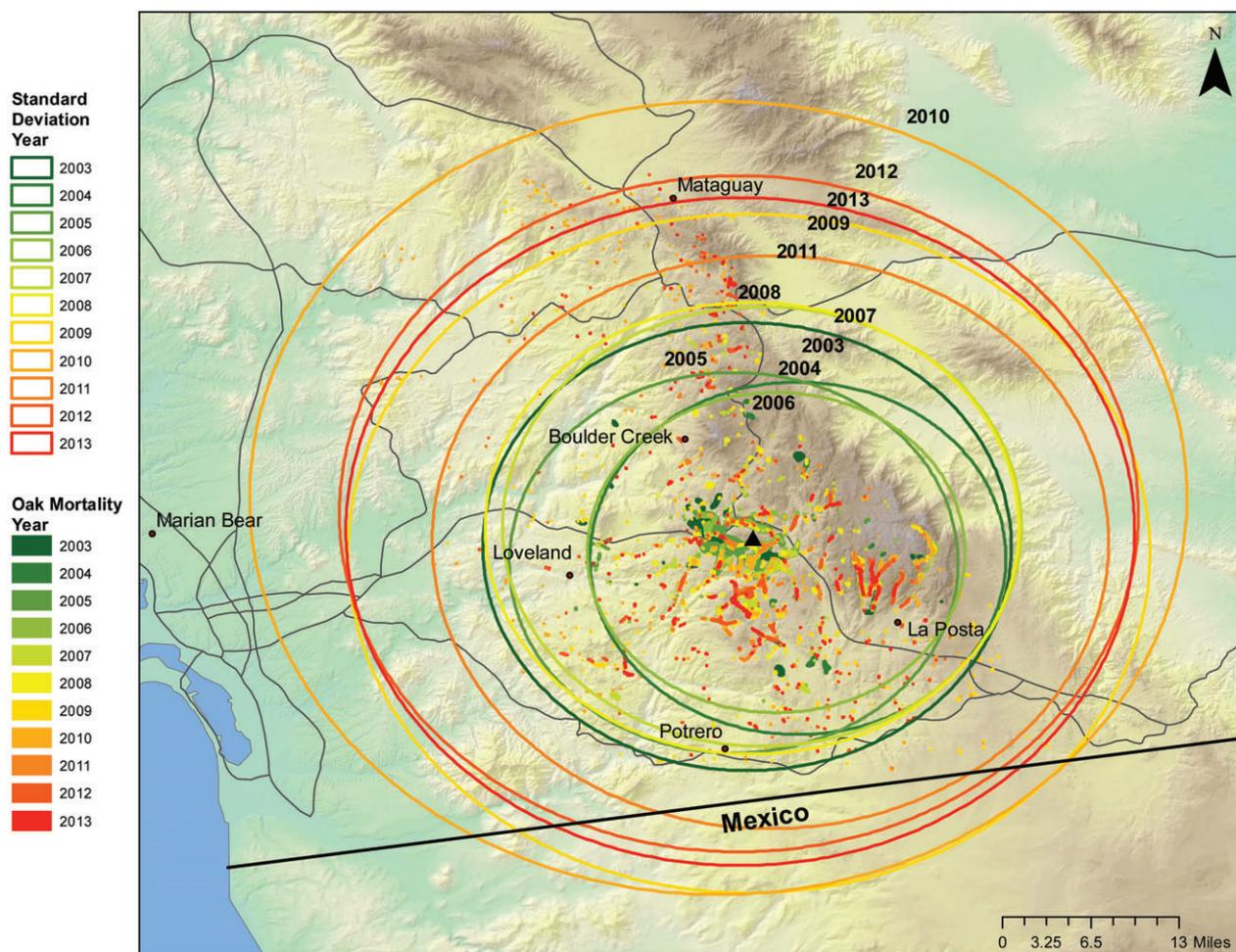
The *A. auroguttatus* infestation is considered to have originated in the vicinity of the Descanso Ranger District (Cleveland National Forest) in the communities of Descanso, Pine Valley and Guatay, and at Cuyamaca Rancho State Park; these were

areas where oak mortality associated with the beetle was first detected (Coleman & Seybold, 2011). The main area of infestation extends out approximately 10–15 km radially from this core. In 2011, we selected five sites on the periphery of this core in the Cleveland National Forest, and one isolated site in western San Diego Co. (Marian Bear Memorial Park, North Clairemont, California) (Fig. 1). *Quercus agrifolia* was the only oak and often the only tree species at all sites (Table 1): three were flat, upland sites that contained open-grown oaks, and three were steeply sloped, closed-canopied forests with oaks growing up-slope from a creek drainage. At each site, we tagged and surveyed all trees in a circular or rectangular area, depending upon topography (Table 1). Circular areas were surveyed at relatively flat sites; rectangular areas were surveyed at sites with varied topography to avoid extremely steep slopes. Boulder Creek had a small population of *Q. agrifolia* surrounded by desert shrubs and herbaceous vegetation; all trees at this site were sampled. Trees at Marian Bear were surveyed in a smaller area compared with the other sites because terrain was too rough and steep with ample growth of poison oak *Toxicodendron diversilobum* (Torr. & A. Gray) Greene (Anacardiaceae), in the understory. Other tree species were rare (0–9% of trees sampled at a site): the most abundant was western sycamore *Platanus racemosa* Nutt. (Platanaceae). A total of 722 oaks were surveyed and affixed with unique identification tags in 2011 and subsequently were re-visited in 2012 and 2013.

Tree surveys were completed in the fall (November to December) of 2011, 2012 and 2013, after cessation of adult flight, to facilitate complete annual estimates of the emerging adult population. At the onset of the present study, diameter at breast height (cm) (dbh; 1.4 m from the ground) was measured for each tagged tree. Survey information collected each year included: (i) degree of crown dieback (categories: 1, < 10% dieback; 2, 10–25% dieback; 3, > 25–50% dieback; 4, > 50% dieback; 5, dead); (ii) presence/absence of evidence of woodpecker foraging in the phloem; (iii) presence/absence of bark staining; and (iv) counts of adult D-shaped emergence holes (below 2 m on main stem) (Coleman *et al.*, 2011; Hishinuma *et al.*, 2011). Compared with other phloem or wood borers commonly found in California oaks, the emergence hole of *A. auroguttatus* is distinctive (Flint *et al.*, 2013; Haavik *et al.*, 2014). Adult emergence holes were marked with permanent paint markers during annual surveys so that new holes could be easily differentiated from old ones. Woodpeckers forage in the outer phloem (near the bark surface) for late-stage larvae, and fresh foraging can be distinguished by its bright red colour from old foraging, which darkens as the exposed phloem tissue oxidizes and dries (for a suitable image, see Hishinuma *et al.*, 2011). Bark staining appears wet and shines when fresh; dry and dull when old (Hishinuma *et al.*, 2011). Site size (area of sampled *Q. agrifolia* population in ha) was measured on the ground with a measuring tape (m) and used to calculate tree density (stems per ha) and basal area (m<sup>2</sup>/ha).

### Analysis of signs and symptoms of *A. auroguttatus* infestation and tree health

To determine whether there were differences in the proportion of *Q. agrifolia* exhibiting signs and symptoms of *A. auroguttatus*



**Figure 1** Location of research sites in southern California relative to the distribution of oak mortality documented annually by aerial sketch mapping (USDA Forest Service FHM, 2014) and modified from Coleman *et al.* (2012a). Large circles represent the standard distance, a measure of the degree that oak mortality was concentrated or dispersed around its geometric mean centre (i.e. the black triangle), and characterize the area potentially affected by *Agrilus auroguttatus* by year.

infestation (woodpecker foraging, bark staining and the presence of emergence holes) at each site over time (by year), we used generalized linear models, which assumed a binomial distribution of residuals (i.e. logistic regression) in the R statistical environment, version 2.15.0 (R Development Core Team, 2012). The proportion of trees exhibiting signs and symptoms in 2011 likely represented symptoms that had accumulated from the time *A. auroguttatus* arrived at each site (probably < 10 years previously) (Fig. 1). In 2012 and 2013, only trees with fresh, current signs and symptoms were included in this proportion. Each sign/symptom was tested separately. We applied Bonferroni correction factors to account for inflation of possible Type I errors from multiple pairwise comparisons (i.e. 2011 versus 2012, 2011 versus 2013 and 2012 versus 2013). To achieve an overall  $\alpha$ -level of 0.05,  $P$ -values were adjusted by a factor of 2, whereby the null hypothesis was rejected if  $P < 0.025$ .

To search for relationships among signs/symptoms and *A. auroguttatus* density among sites, we applied Pearson's correlations to the frequencies of bark staining and woodpecker foraging versus *A. auroguttatus* population density (total number of

emergence holes per m<sup>2</sup> of bark surface sampled). The number of *Q. agrifolia* in each crown dieback category was reported by year at each site. Changes in crown health were calculated as the percentage of *Q. agrifolia* transitioning to a different dieback category between years of survey.

#### *Analysis of A. auroguttatus* population density and growth

Unlike other tree-killing *Agrilus* spp. (Balch & Prebble, 1940; Haack *et al.*, 1983; Loerch & Cameron, 1984), *A. auroguttatus* larvae concentrate their feeding activity in the lower bole (below 3 m; Haavik *et al.*, 2012) and branches are rarely colonized (Coleman & Seybold, 2008; Jones *et al.*, 2013). To facilitate a survey of the large number of trees in the present study, we only counted *A. auroguttatus* emergence holes on the lower bole (below 2 m: the height at which adult emergence holes could be marked and identified when standing on the ground). *Agrilus auroguttatus* population density was expressed as number of adult emergence holes per m<sup>2</sup> of *Q. agrifolia* bark sampled at

**Table 1** Site information, tree count, oak basal area (BA) and cumulative percentage of *Quercus agrifolia* colonized by *Agrilus auroguttatus* at the start and end of the present study

Site name	Site topography	Plot shape	Coordinates (°N, °W)	Size (ha)	Number of trees	<i>Quercus agrifolia</i> BA (m <sup>2</sup> per ha)	<i>Quercus agrifolia</i> colonized by <i>Agrilus auroguttatus</i> initially <sup>a</sup> (%) <sup>b</sup>	<i>Quercus agrifolia</i> colonized by <i>Agrilus auroguttatus</i> 2013 (%)
Potrero	Flat	Circular	32.61542, 116.59539	3.14	93	11.31	16	31
Mataguay	Flat	Circular	33.19218, 116.64507	1.76	175	29.70	7	23
Marian Bear	Slope <sup>c</sup>	Rectangular	32.84277, 117.20361	0.25	53	25.78	6	23
Loveland	Slope <sup>c</sup>	Rectangular	32.79943, 116.75993	2.10	169	15.02	11	26
La Posta	Flat	Circular	32.74894, 116.41222	2.00	161	17.48	33	40
Boulder Creek <sup>d</sup>	Slope <sup>c</sup>	Rectangular	32.94349, 116.63758	0.29	71	49.10	14	28

<sup>a</sup>Initially = 2011.

<sup>b</sup>Includes only trees with confirmed colonization (i.e. emergence holes present).

<sup>c</sup>Trees located up-slope from drainage.

<sup>d</sup>Site affected by 2003 Cedar fire.

each site. This was likely an underestimate of true population density. However, because the same portion of boles was sampled from all trees at all sites, we expected that the magnitude of underestimation was similar among trees and sites (Haavik *et al.*, 2012). Population density estimates in 2011 represented the cumulative number of *A. auroguttatus* that had emerged from trees subsequent to the beetle arriving at each site.

It was possible that trees were infested with *A. auroguttatus* and showed external signs of current attack (bark staining and woodpecker foraging) before colonization was confirmed via the presence of adult emergence holes (Coleman *et al.*, 2011). These trees were included in analyses for signs and symptoms of *A. auroguttatus* infestation, although they were not included as colonized trees in analyses of population density. We assigned infestation level (un-infested, lightly infested or heavily infested = brood tree) *a posteriori* for purposes of comparison among trees that were not colonized by *A. auroguttatus*, trees that produced few adults, and trees that produced many adults. We defined brood trees as oaks that produced large numbers of beetles relative to other oaks at a site. These were the most heavily-infested 5% of trees (median number of emergence holes per m<sup>2</sup> bark = 11.36; range = 1.59–65.63). These oaks were often attacked repeatedly by successive generations, allowing populations to build rapidly, as has been described for other wood-boring insects (Linsley, 1959). All non-brood trees colonized by *A. auroguttatus* were categorized as lightly infested (median number of emergence holes per m<sup>2</sup> bark = 0.65; range = 0.13–8.68).

We calculated population growth, per capita rate of increase ( $R$ ), between 2012 and 2013 at the site level according to (Berryman, 1981):

$$R = \frac{N_t - N_{t-1}}{N_{t-1}}$$

where  $N_t$  is the number of emergence holes from the current generation (2013) of *A. auroguttatus*, and  $N_{t-1}$  is the number of emergence holes from the previous generation (2012). When  $R$  was greater than zero, populations increased; when  $R$  was

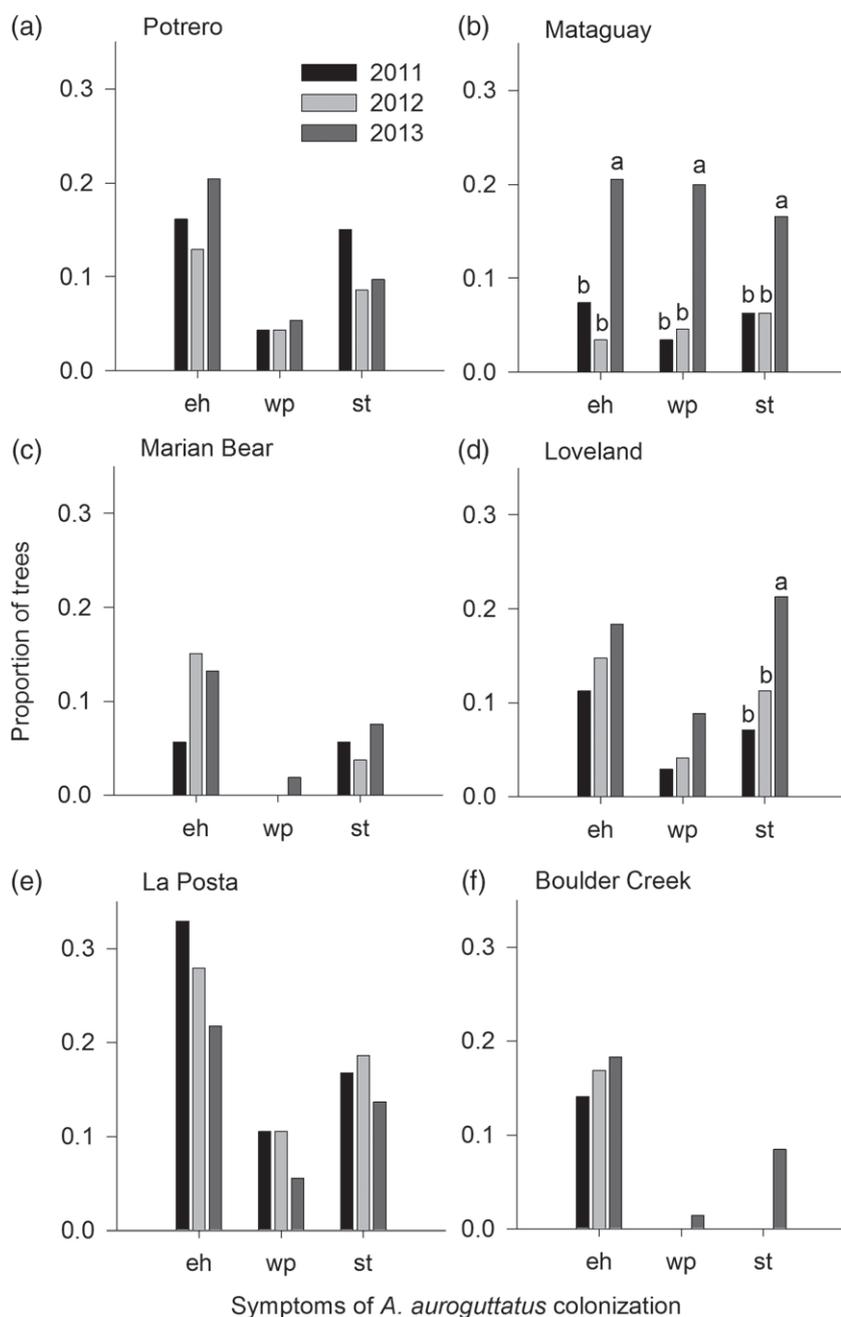
approximately zero, populations were stable; and when  $R$  was less than zero, populations declined (Berryman, 1981).

## Results

### *Signs and symptoms of A. auroguttatus infestation and tree health*

Tree mortality was low: only five of the 722 trees (<1%) died during the course of the study from *A. auroguttatus* infestation (all brood trees), and four of these died at Mataguay in 2013. Unrelated to *A. auroguttatus* at riparian sites, three understory trees were shaded out and died [mean  $\pm$  SE dbh = 16.5  $\pm$  1.7cm], and another died from unknown causes (dbh = 48.3 cm). At the start of the study (representing 2011 and preceding years), 6–33% of oaks were colonized by *A. auroguttatus*; by 2013, 23–40% were colonized (Table 1).

At four of the six sites, the proportion of oaks exhibiting signs and symptoms of *A. auroguttatus* infestation subsequent to the beetle arriving at the site (2011 survey) did not change significantly over the next 2 years (Fig. 2). The mean  $\pm$  SE proportion of oaks, among all sites, with adult emergence holes was 0.16  $\pm$  0.02; with woodpecker foraging was 0.05  $\pm$  0.01; and with bark staining was 0.10  $\pm$  0.01. Only at Mataguay (all signs and symptoms) and Loveland (bark staining) were there significant changes in the proportion of *Q. agrifolia* with signs and symptoms among years (Fig. 2b,d). At Mataguay, the proportion of oaks with *A. auroguttatus* signs and symptoms was significantly greater in 2013 than in 2012 or 2011 (0.21 versus 0.03 or 0.07 of oaks with emergence holes, Deviance ( $D$ ) = 29.62, d.f. = 2,518,  $P$  < 0.001; 0.20 versus 0.05 or 0.03 of oaks with evidence of woodpecker foraging,  $D$  = 33.59, d.f. = 2,518,  $P$  < 0.001; 0.17 versus 0.06 or 0.06 of oaks with bark staining,  $D$  = 12.40, d.f. = 2,502,  $P$  = 0.005; in 2013 versus 2012 or 2011, respectively) (Fig. 2b). Bark staining was found on significantly more trees at Loveland in 2013 than in previous years (0.21 of trees versus 0.11 or 0.07 in 2013 versus 2012 or 2011, respectively;  $D$  = 14.51, d.f. = 2,497,  $P$  < 0.001) (Fig. 2d), coincident with positive *A. auroguttatus* population growth that



**Figure 2** (a–f) Proportion of *Quercus agrifolia* with signs and symptoms of *Agrilus auroguttatus* infestation at each site by year. Symptoms in 2011 were cumulative from the time *A. auroguttatus* arrived at a site; those in 2012 and 2013 were current for each respective year. Eh, *A. auroguttatus* emergence holes; wp, woodpecker foraging; st, bark staining. Each symptom of infestation was analyzed separately within a site. Different letters above bars indicate significant differences among years ( $\alpha = 0.025$ ).

year ( $R = 0.62$ ) (Table 2). The general stasis in these symptoms among the four other sites was consistent with relatively stable *A. auroguttatus* population growth ( $R = -0.53$  to  $0.46$ ) (Table 2).

Woodpecker activity varied across sites from none (Marian Bear and Boulder Creek in 2011 and 2012) to foraging amongst nearly all trees with emergence holes (Mataguay in 2012 and 2013) (0–97%) (Fig. 2) and was more frequent at sites with greater *A. auroguttatus* densities in 2011 ( $r = 0.843$ ,  $P = 0.0352$ ) and in 2013 ( $r = 0.970$ ,  $P = 0.001$ ) but not in 2012 ( $r = 0.55$ ,  $P = 0.258$ ). Bark staining was recorded more frequently at some sites (La Posta and Potrero) than others (Boulder Creek and Marian Bear) (0–20% of trees) (Fig. 2). There were no significant correlations

between frequency of bark staining and *A. auroguttatus* density among sites.

At all sites (Fig. 3), negative changes in crown health occurred throughout the study, although, by 2013, at least half of *Q. agrifolia* remained in the lowest dieback category (<10% dieback). At the start of the study, over half of the *Q. agrifolia* at La Posta (Fig. 3e) (the site with the highest initial *A. auroguttatus* population density) exhibited >10% crown dieback, yet many of these trees remained in the same dieback category throughout the study. Similarly, at Boulder Creek (Fig. 3f), a site affected by recent wild-fire, many *Q. agrifolia* (61%) were initially in a state of advanced dieback (>25%) but remained in the same dieback categories from 2011 to 2013. There were no positive

**Table 2** Density of *Agrilus auroguttatus* adult emergence holes below 2 m on the main stem of *Quercus agrifolia* from 2011 (initial) to 2013 (total among all trees sampled at each site), estimated population growth rate (*R*) and change in infestation status of colonized trees

Site	Initial per m <sup>2</sup> bark	2012 per m <sup>2</sup> bark	2013 per m <sup>2</sup> bark	Initial to 2013 cumulative per m <sup>2</sup> bark	2012–2013 site <i>R</i> <sup>a</sup>	2011 trees not after (%) <sup>b</sup>	2012 trees new, not current (%) <sup>c</sup>	2013 trees new, not current (%) <sup>d</sup>
Potrero	0.25	0.13	0.20	0.58	0.46	21	54,42	54,17
Mataguay	0.06	0.09	1.75	1.90	18.90	6	6,18	79,6
Marian Bear	0.19	0.29	0.28	0.75	-0.03	0	50,0	30,40
Loveland	0.46	0.49	0.79	1.75	0.62	8	36,22	42,28
La Posta	1.65	0.57	0.27	2.49	-0.53	21	16,33	14,28
Boulder Creek	0.37	0.19	0.14	0.70	-0.28	20	25,25	31,25

<sup>a</sup>*R* = per capita rate of increase (population growth).

<sup>b</sup>Of lightly-infested trees, percentage of trees colonized in previous years (i.e. up to and including 2011) but with no emergence in 2012 or in 2013.

<sup>c</sup>Of lightly-infested trees, percentage of newly-colonized trees in 2012, percentage of trees not colonized in 2012 that were colonized in previous years (i.e. up to and including 2011).

<sup>d</sup>Of lightly-infested trees, percentage of newly-colonized trees in 2013, percentage of trees not colonized in 2013 that were colonized in 2012.

Population densities were likely underestimated (see Materials and methods).

changes in crown health at four of the six sites in 2012; 2% and 3% of trees transitioned to a less severe dieback category at Marian Bear and Mataguay, respectively. In 2013, positive changes in crown health were slightly more frequent, where 17% of trees at Boulder Creek transitioned to a less severe dieback category. Smaller improvements in crown health (3–6% of trees) occurred at the remaining sites.

#### *Agrilus auroguttatus* population density and growth

Among all oaks combined, infested or un-infested, the number of beetles that emerged per m<sup>2</sup> of *Q. agrifolia* bark ranged from 0.06 to 1.65 among sites in 2011 (cumulative), 0.09 to 0.57 in 2012 and 0.20 to 1.75 in 2013 (Table 2). The population density of *A. auroguttatus* (1.65 beetles per m<sup>2</sup> of *Q. agrifolia* bark) (Table 2) and the percentage of oaks colonized (33%) (Table 1) at La Posta in 2011 was the highest amongst the sites, although the cumulative beetle density by 2013 had not increased as much as that at Loveland and Mataguay (Table 2). During the course of the study, there was a 1.5- versus 1.9- and 3.8-fold increase in *A. auroguttatus* density at La Posta versus Loveland and Mataguay, respectively. From 2011 to 2013, the cumulative percentage of oaks colonized by *A. auroguttatus* also increased less at La Posta (by 7%) than at Loveland (by 15%) and Mataguay (by 16%) (Table 1). Among all sites, from 2011 to 2013, the Boulder Creek and Potrero *A. auroguttatus* population densities increased the least (an increase of 0.33 beetles per m<sup>2</sup> of *Q. agrifolia* bark at both sites); Mataguay increased the most (an increase of 1.84 beetles per m<sup>2</sup> of *Q. agrifolia* bark).

Overall, *A. auroguttatus* populations were relatively stable among sites between 2012 and 2013, with slightly negative or positive growth (Table 2). At Mataguay, however, the *A. auroguttatus* population erupted in 2013 with a per capita rate of increase from the 2012 population of almost 19 beetles. Some newly-colonized trees were detected at all sites in 2012 and 2013 (6–79% of lightly-infested trees) (Table 2), although some trees that were colonized at the start of the study (in 2011) exhibited no evidence of colonization (adult emergence holes) on the lower bole in 2012 or in 2013 (up to 21% of lightly-infested

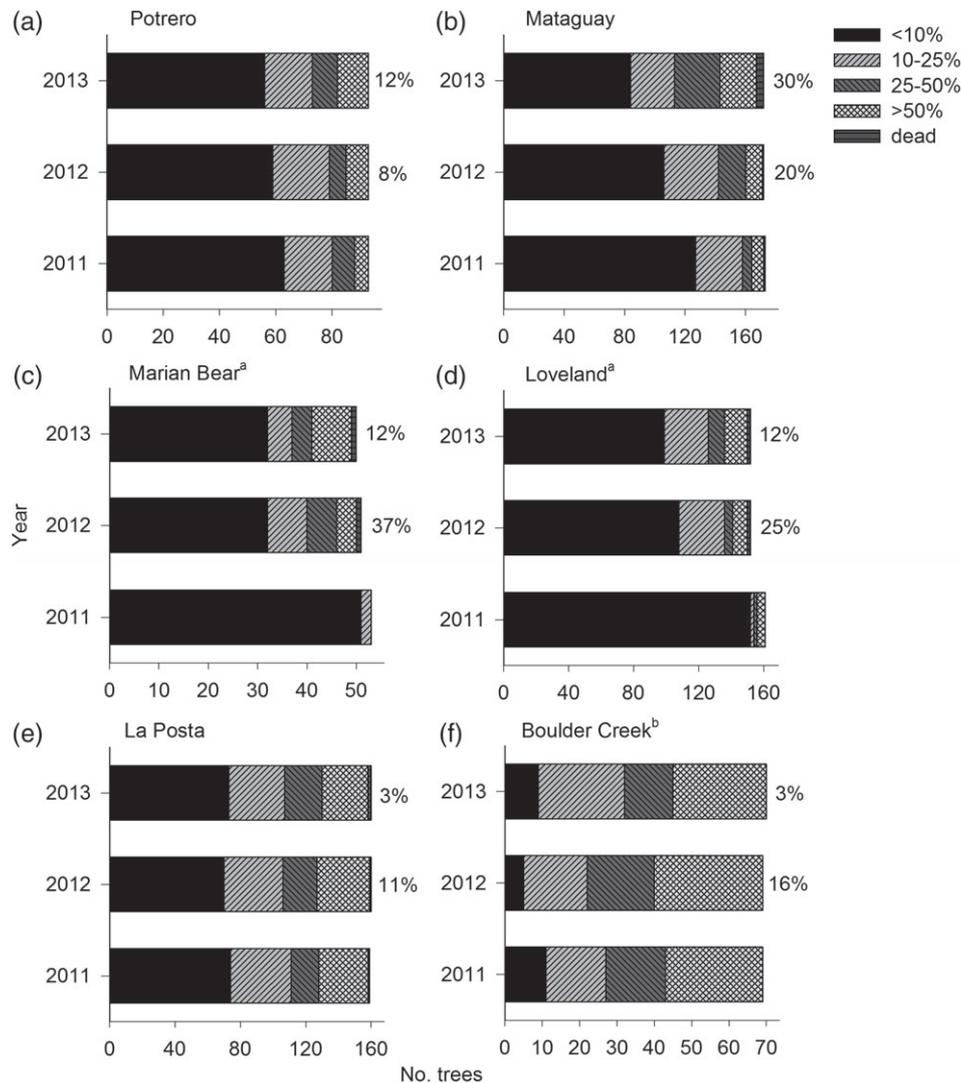
trees) (Table 2). Although variable (between 0% and 79% of lightly-infested trees), on average, the infestation status (i.e. the presence or absence of new emergence holes) of approximately one-third of lightly-infested trees changed from 1 year to the next (Table 2).

A majority of *A. auroguttatus* adult emergence holes (61–91%) (Fig. 4) were found on the 5% of trees that were most heavily infested (i.e. brood trees; 3–9 trees per site, depending on the number of trees sampled at a site). Over two-thirds of these brood trees also exhibited >50% crown dieback. Among sites, 69% of brood trees were infested with *A. auroguttatus* initially in 2011 and 83% were infested by 2012. Only five of the 36 (14%) brood trees died during the course of the present study. Although evidence of *A. auroguttatus* infestation in the six populations of oaks may not have changed appreciably from 2011 to 2013 (Fig. 2), beetle population density and growth at some sites may have still increased (e.g. Potrero *R*=0.46 and Loveland *R*=0.62) (Table 2) because a very small number of trees (i.e. brood trees, 4–9) harboured a very large portion of the *A. auroguttatus* population at each site (61–91%) (Fig. 4a,d).

*Agrilus auroguttatus*-infested trees were found in most diameter classes at each site but comprised a greater proportion of trees in the larger, rather than the smaller, diameter classes (dbh < 40 cm) (Fig. 5). Brood trees were more frequently in the larger diameter classes (dbh > 41 cm) (Fig. 5).

## Discussion

Signs and symptoms of *A. auroguttatus* infestation and measures of population density and growth at six sites where the beetle was newly-established indicated that, in general, *A. auroguttatus* was not expanding at an alarming rate into new hosts on the periphery of southern California's main infestation. Consistent with this, Lynch *et al.* (2014) also found low levels of oak mortality at some sites that had been infested for comparatively longer, which suggests that *A. auroguttatus* infestation and associated oak mortality is a slow process. *Agrilus auroguttatus* may be present at a site for two decades or more before oak mortality levels are



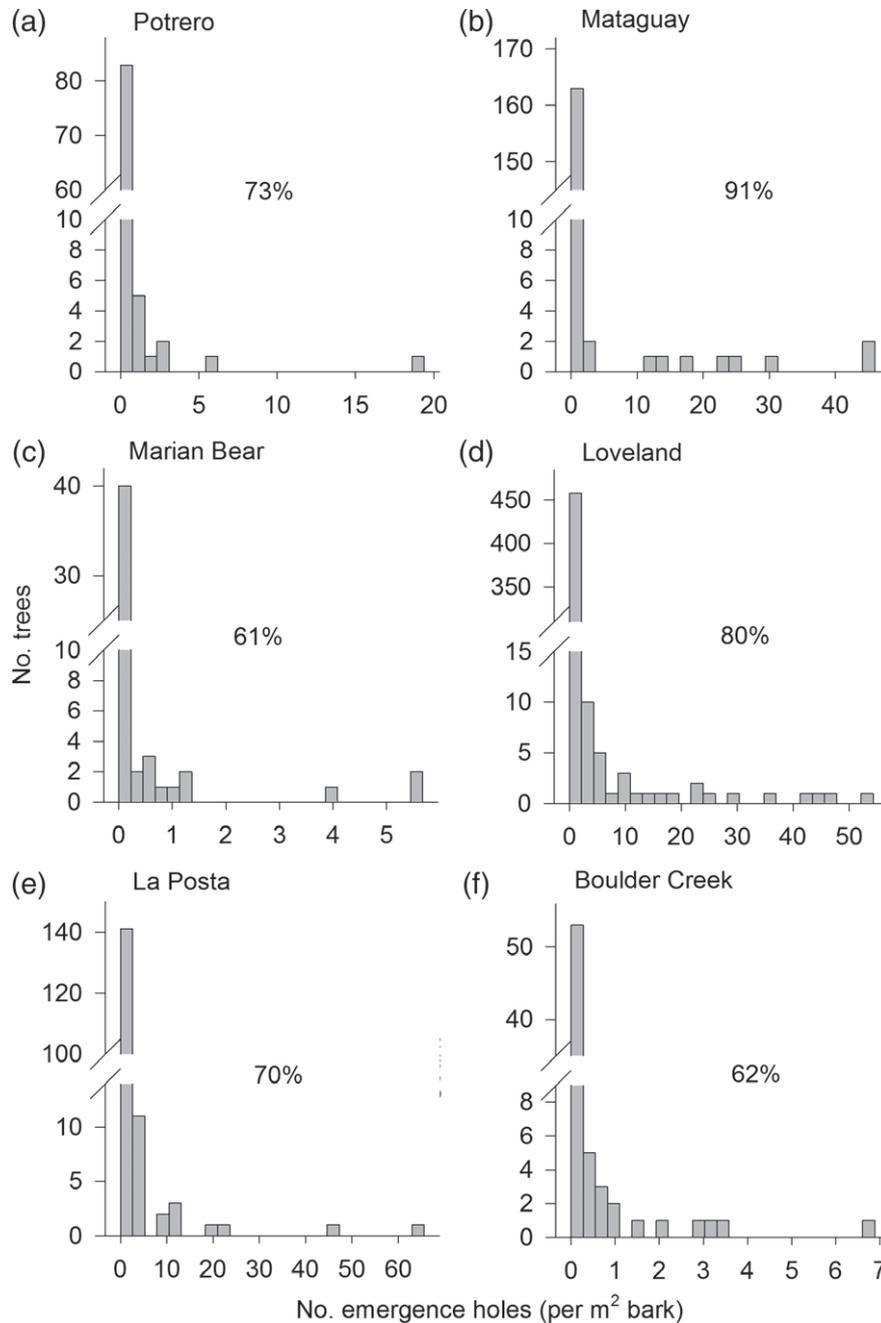
**Figure 3** Number of *Quercus agrifolia* classified by crown dieback category (key upper right next to b) in each year at each site (a–f). Percentage of trees that exhibited negative change in crown health between years is presented to the right of respective bars. <sup>a</sup>Crowded canopy conditions and natural shading out were observed frequently at these sites. <sup>b</sup>The 2003 Cedar fire affected this site.

noticeable (T. W. Coleman, personal observation). Oak mortality was low (< 1%) during the present study. The number of trees colonized by *A. auroguttatus* increased between 2011 and 2013, although beetle population densities did not generally increase rapidly at most sites. One site (Mataguay) was the exception, and experienced an outbreak in 2013, with concomitant significant changes in signs and symptoms of *A. auroguttatus* infestation.

Interestingly, the majority of *A. auroguttatus* individuals at all sites were produced by a small number of heavily-infested trees. Of these brood trees, most were colonized initially (in 2011) and repeatedly (in both 2012 and 2013) throughout the present study, and remained alive in 2013, which implied that several generations of beetles were produced by them. Consistent with Coleman *et al.* (2012a), who reported that *A. auroguttatus* was found more frequently in larger diameter (dbh > 50 cm) trees, brood trees (and many lightly-infested trees) in the present study were in the larger size classes (for most, dbh > 41 cm).

Such highly suitable trees that produce large numbers of borers have been observed in studies of other subcortical beetles that feed in hardwoods (Hay, 1974; McCullough & Siebert, 2007; Fierke & Stephen, 2010; Siebert *et al.*, 2010; Dodds *et al.*, 2014). Many hardwood borers in the family Cerambycidae are known to repeatedly attack the same brood tree for several generations (Linsley, 1959; Hanks, 1999; Hu *et al.*, 2009; Fierke & Stephen, 2010). *Agrilus* spp. have also been reported to re-attack the same tree (Barter, 1957; Dunbar & Stephens, 1975; Vansteenkiste *et al.*, 2004).

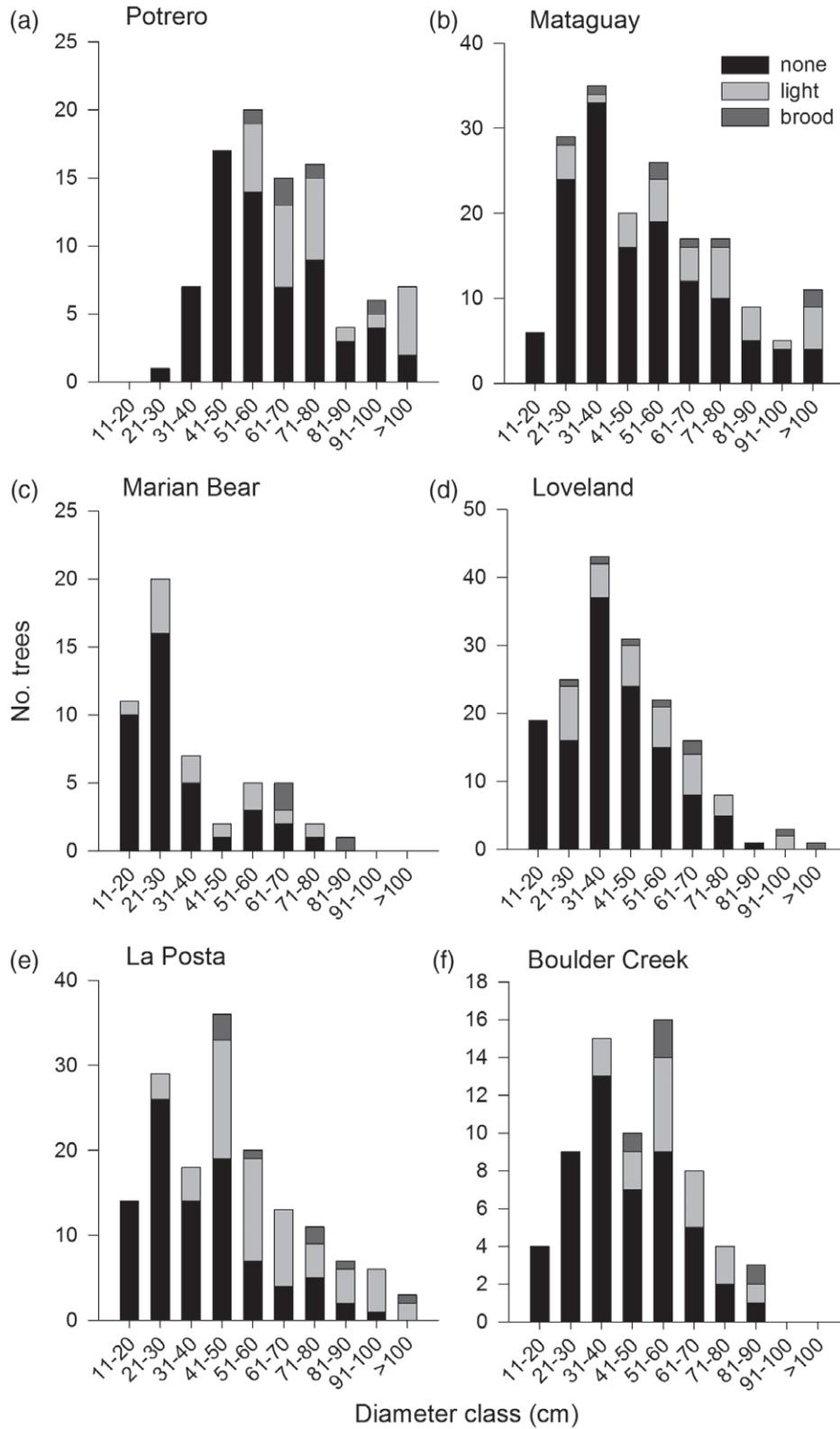
A brood tree in the present study (at Mataguay) produced 327 (45.53/m<sup>2</sup> of *Q. agrifolia* bark) beetles in 1 year. This level of maximum brood production was likely an underestimate because only the lower bole was examined. To produce such a large brood, either a large portion of the egg load from a few ovipositing females (50–600 eggs per female; Haavik *et al.*, 2013b; Lopez & Hoddle, 2014) or a small portion of the egg



**Figure 4** Frequency distributions of *Quercus agrifolia* by estimated cumulative *Agrilus auroguttatus* densities at each site (a–f). Percentage of beetle density produced by the 5% most heavily-infested (i.e. brood) trees at each site is reported in the centre of each panel.

load from many ovipositing females must have survived to adulthood. If the possibility of beetle migration is ignored, the small emerging population at Mataguay in 2012 (0.09 beetles per m<sup>2</sup> of *Q. agrifolia* bark) suggested that a large fraction of the egg load survived from only a few ovipositing females. The use of natal trees as brood trees is beneficial for beetles with respect to saving resources expended during host- and mate-finding, although tree mortality and within-tree competition for phloem becomes increasingly riskier with successive generations.

Brood trees could be a source of *A. auroguttatus* for a large area. Early identification followed by removal of these heavily-infested trees (dbh > 41 cm; > 50% crown dieback; and > 60% of the site-level emergence hole density on lower boles) at newly-invaded sites has the potential to slow the growth of *A. auroguttatus* populations. For example, if the most severely-infested brood tree at Potrero had been removed in 2011, then the 2012 population could have been reduced by 60%. If the same procedure had been carried out at Loveland, the 2012 population could have been reduced by 40%. Similar



**Figure 5** Frequency distributions of *Quercus agrifolia* by diameter class at each site (a–f), categorized by cumulative level of *Agrilus auroguttatus* infestation. Brood, brood trees (the most heavily-infested 5% of trees at a site); light, lightly-infested trees (all trees colonized by *A. auroguttatus* that were not brood trees); none, un-infested trees (key upper right next to b).

to our results, McCullough and Siegert (2007) found that large ash trees ( $\geq 26$  cm dbh) accounted for only 6% of the ash population at two *A. planipennis*-infested sites, although they had potential to produce 55–65% of the beetle population at those sites. They recommended the removal of these larger ash trees to slow the short-range spread of *A. planipennis* (McCullough & Siegert, 2007). Brood tree removal as a method of borer population control has been suggested for a wood borer (Cerambycidae) (Donley, 1983) and similar methods have often been used to control bark beetle populations (Fettig *et al.*, 2007). Additionally, study of differences between brood trees and other, apparently less-suitable hosts, would further understanding of characteristics that define a suitable host for *A. auroguttatus*.

Crown health may provide information on *A. auroguttatus* activity in advance of the emerging adult population. Substantial crown dieback occurred the year before the outbreak at Mataguay, confirming evidence from previous studies suggesting that, in combination with other signs and symptoms, crown dieback is a good indicator of *A. auroguttatus* infestation (Coleman *et al.*, 2011; Haavik *et al.*, 2012). Changes in crown health preceded other signs and symptoms of infestation at Mataguay. Similarly, at Loveland, a large portion of trees experienced negative changes in crown health 1 year in advance of positive beetle population growth (2012–2013). During the growing season prior to emergence of a larger adult population, young larvae feed relatively deeply within the subcortical tissues of oaks, disrupting the vascular system, which likely compromises physiological functioning and results in crown dieback. Consistent with this, Coleman *et al.* (2011) found that *A. auroguttatus* infestation may cause drought stress in *Q. agrifolia*. Additionally, a weakly pathogenic agent, *Cryptosporiopsis querciphila* (Dermeateaceae), may act in concert with *A. auroguttatus* larval feeding to exacerbate crown dieback (Lynch *et al.*, 2014). Because Marian Bear and Loveland are riparian sites, it was difficult to determine whether negative changes in crown health were related to *A. auroguttatus* activity or to shading out from crowding in the canopy.

Although variable among sites and between years, the status of many trees fluctuated from un-infested to lightly-infested, or vice versa, between years. As *A. auroguttatus* populations expanded at these newly-invaded sites, more oaks were obviously colonized; however, it is less clear why adults emerged from some trees in (or before) 2011 but not in 2012, or even in 2013. We surmise three possible explanations for this: (i) some *A. auroguttatus* may require 2 or 3 years to complete development; (ii) adult emergence occurred in the mid- or upper-bole and so went undetected; or (iii) there were changes in tree selection by females and/or changes in host suitability. In a previous study, we suggested that generation time may be longer at sites with smaller *A. auroguttatus* population densities (Haavik *et al.*, 2013a) and that this may also translate to individual trees. Similarly, *A. planipennis* generation time is longer on newly-colonized hosts (Cappaert *et al.*, 2005; Siegert *et al.*, 2010; Tluczek *et al.*, 2011). We suspect that some combination of all three of these possible explanations is occurring at our sites.

Knowing whether females alight on one suitable host tree to oviposit their entire egg load or, alternatively, oviposit a portion of their eggs on several potentially suitable hosts, or even

whether oviposition locations are chosen at random, could help to determine the observed patterns of different trees becoming lightly infested in different years. In the laboratory, *A. auroguttatus* females oviposit singly or in small clumps and remain fecund until death (Haavik *et al.*, 2013b; Lopez & Hoddle, 2014). Potential fecundity ranges from approximately 50 to 600 eggs, and depends on female size and diet (Haavik *et al.*, 2013b; Lopez & Hoddle, 2014). Therefore, although unknown at this time, it may be possible for females to oviposit in several locations on the same tree, and potentially even on several different trees. Females of other *Agrilus* spp. are strongly attracted to (and oviposit preferentially on) experimentally- or naturally-stressed trees: trees in which larval survival is optimal (Anderson, 1944; Barter, 1957; Haack & Benjamin, 1982; Dunn *et al.*, 1986, 1987, 1990; McCullough *et al.*, 2009). Female (and male) *A. auroguttatus* landed more frequently on oaks in more advanced stages of crown dieback, which suggests that, similar to other *Agrilus* spp., *A. auroguttatus* may actively select suitable hosts for oviposition (Coleman *et al.*, 2014). A better understanding of the characteristics that define a suitable host would also be helpful in determining the cause of the observed temporal changes in *A. auroguttatus* infestation.

In conclusion, a small number of large-diameter brood trees produced over two-thirds of the *A. auroguttatus* population at all sites. Early identification and removal of brood trees in newly-invaded areas could slow the growth of *A. auroguttatus* populations. Although there was a small but quantifiable increase in *A. auroguttatus* population density at most sites, few changes in symptoms of *A. auroguttatus* infestation (except where an outbreak occurred) were observed. Although negative changes in tree health were frequent, tree mortality levels were low. It was unclear why one site suddenly experienced an outbreak in 2013, when *A. auroguttatus* population growth remained relatively stable at all other sites. We predict that, in general, *A. auroguttatus* populations on the margin of the main infestation in San Diego County will remain stable for the next few years. It is unknown how *A. auroguttatus* populations will be influenced by changing environmental conditions, such as severe drought. The movement of infested oak firewood to new locations remains the greatest threat to geographical expansion of *A. auroguttatus* populations in California (Jones *et al.*, 2013).

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