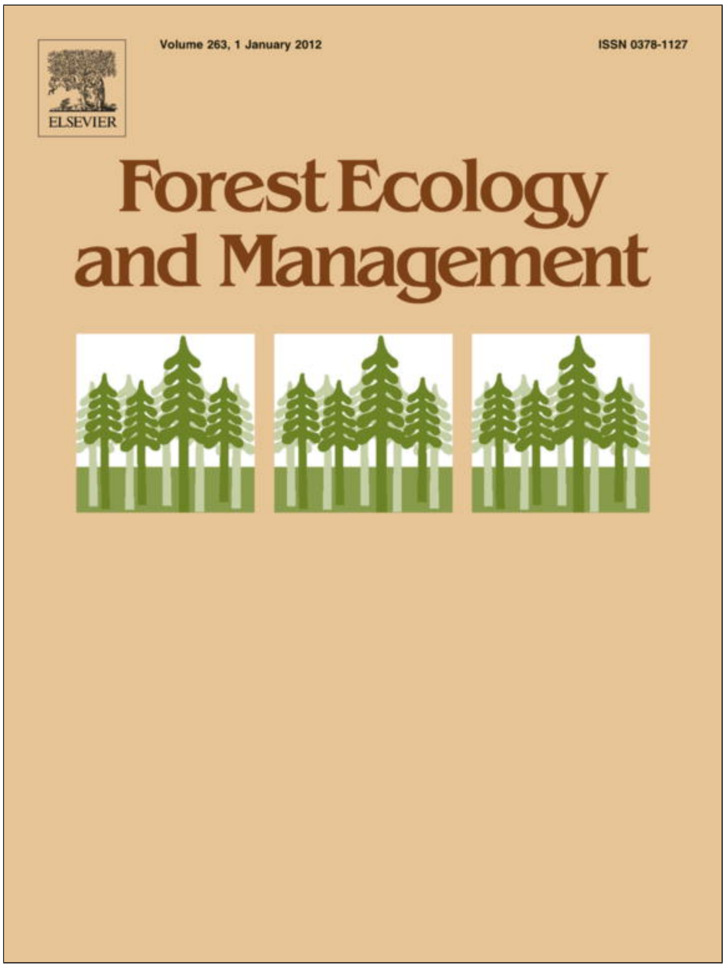
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Forest stand composition and impacts associated with *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) and *Agrilus coxalis* Waterhouse in oak woodlands

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ABSTRACT

From 2009–2011, we assessed the impact of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer, or its sibling species, *Agrilus coxalis* Waterhouse, at locations in southern California (denoted infested: ICA and uninfested: UCA), southeastern Arizona (AZ), and southern Mexico (MX). Our surveys examined forest composition of oak woodlands; the degree of injury and proportion of oaks infested with either *A. auroguttatus* (ICA and AZ) or *A. coxalis* (MX); and the progression of aerially mapped oak mortality in San Diego Co. (ICA). By most measures of impact that we evaluated, the effect on oaks by the two *Agrilus* spp. was relatively low in their native regions, but significantly higher by *A. auroguttatus* at ICA sites. Larger diameter red oak species have been the preferred hosts of *A. auroguttatus* in AZ and ICA sites, and red oaks greater than approx. 13 cm in DBH throughout California are likely at risk of injury from this invasive pest. At sites in AZ there was no evidence of infestation by *A. auroguttatus* on living or dead white oak species, whereas at ICA sites we recorded a minor amount of infestation by *A. auroguttatus* on living individuals of a white oak species (*Quercus engelmannii* Greene), but no mortality. In contrast, a white oak from MX sites (*Quercus peduncularis*) was more frequently infested by *A. coxalis* than were indigenous red oaks. Across all ICA sites, *A. auroguttatus* has infested 61% of the live larger diameter oaks and killed 13% of the oak component of the forest (vs. 4% infested and 2% dead in AZ, respectively). At survey plots near the predicted origin of the outbreak in CA, over 90% of the larger diameter red oaks have been infested. Nearly 90% of the dead oaks surveyed across all ICA sites showed evidence of previous injury symptoms from *A. auroguttatus*. Aerial oak mortality polygons associated with *A. auroguttatus* have expanded ~50 km in nine years, but our analysis confirms that the outbreak appears to still be confined to San Diego Co. The distance of oak mortality polygons from the predicted origin of the outbreak explained the most variance in a principal component analysis. The invasive population of *A. auroguttatus* is a significant conservation and ecological threat to the oak woodlands of California and should be managed accordingly, especially by restricting firewood movement.

1. Introduction

Stem-infesting *Agrilus* spp. (Coleoptera: Buprestidae) phloem/xylem borers have played key roles in historic cases of oak decline and mortality in the eastern USA and Europe (Nichols, 1968; Stringer et al., 1989; Hartmann and Blank, 1993; Führer, 1998; Oszako, 1998; Thomas et al., 2002). Damage from most *Agrilus* spp. is associated with oak trees already in decline. For example, in the eastern USA, the native twolined chestnut borer, *Agrilus bilineatus* Weber, frequently attacks oaks weakened by high levels of defoliation from Lepidoptera, infection by *Armillaria* sp. (Fr.) Staude root rot, injury from frost, or drought (Chapman, 1915; Hursh and Haasis, 1931; Knull, 1932; Baker, 1941; Staley, 1965; Dunbar and Stephens, 1975; Wargo, 1977) and is typically regarded as a secondary pest on stressed oaks (Dunn et al., 1986; Haack and Acciavatti, 1992; Muzika et al., 2000). In Europe, the native oak splendor

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beetle, *Agrilus biguttatus* (F.), regularly interacts with the impacts of insect defoliators, canker fungi, late winter frosts, or drought to cause oak mortality (Jacquiot, 1976; Gibbs and Greig, 1997; Moraal and Hilszczański, 2000; Vansteenkiste et al., 2004; Hilszczański and Sierpinski, 2007).

Oak mortality in northern California, USA over the past 15 years has been well-documented and attributed to Sudden Oak Death, caused by *Phytophthora ramorum* S. Werres et al. (Rizzo and Garbelotto, 2003). Because *Agrilus* spp. diversity is low in California (Fisher, 1928; Furniss and Carolin, 1977), there has been no record of native stem-infesting *Agrilus* spp. interacting with the oak mortality attributed to *P. ramorum* (Swiecki and Bernhardt, 2006). However, beginning around 2002, a second center with elevated levels of oak mortality emerged in southern California (San Diego Co.). In this area, which is devoid of *P. ramorum*, an estimated 22,171 trees died over 212,460 ha (USDA Forest Service and Forest Health Monitoring, 2010). The primary cause of this mortality is the invasive goldspotted oak borer, *Agrilus auroguttatus* Schaeffer, which is aggressively colonizing and killing coast live oak, *Quercus agrifolia* Née, California black oak, *Quercus kelloggii* Newb., and canyon live oak, *Quercus chrysolepis* Liebm. across all land ownerships in San Diego Co. (Coleman and Seybold, 2008). Engelmann oak, *Quercus engelmannii* Greene, a white oak, occurs in this area as well and is also injured on rare occasions, but not killed, by *A. auroguttatus* (Coleman and Seybold, 2011). Coleman and Seybold (2011) hypothesized that *A. auroguttatus* was introduced inadvertently into southern California between the mid-1990's and 2000 via movement of infested firewood from southeastern Arizona or northern Mexico. Prior to the discovery of *A. auroguttatus*, the observed high oak mortality in the area was attributed solely to acute drought that occurred during 2002–2003 (Coleman and Seybold, 2008; Coleman et al., 2011); additional abiotic and biotic factors that contribute unequivocally to this southern California oak mortality have not been reported.

A. auroguttatus was described in 1905 from specimens collected in southeastern Arizona (Schaeffer, 1905; Fisher, 1928), whereas a sibling species, *Agrilus coxalis* Waterhouse, had been described in 1889 from specimens collected in Oaxaca, Mexico (Coleman and Seybold, 2011). Since the collection of the type specimens, additional collecting of *A. auroguttatus* in the 20th Century established its native distribution as southeastern Arizona and the southern tip of Baja California Sur, Mexico, though suspected populations in western New Mexico and northern Mexico have yet to be confirmed (Coleman and Seybold, 2011). In contrast, the native range of *A. coxalis* extends from central Mexico to Guatemala (Coleman and Seybold, 2011). DNA sequence analysis of gene fragments from mitochondrial cytochrome oxidase I and nuclear 28S ribosomal DNA suggest that the population of *A. auroguttatus* in California is genetically more similar to populations in Arizona than to populations (of *A. coxalis*) collected in southern Mexico (Coleman et al., 2012). Because of the relatively extreme sequence divergence of both the mitochondrial and nuclear gene fragments, this molecular analysis supports the species status of *A. auroguttatus* and *A. coxalis*, which previously was based solely on morphological characters (Coleman et al., 2011; Hespenheide et al., 2011).

No life history or impact data were available for either *A. auroguttatus* or *A. coxalis* when *A. auroguttatus* was first collected in southern California in 2004 (Westcott, 2005) and associated with dying oaks there in 2008 (Coleman and Seybold, 2008). We now know that large numbers of the larvae of *A. auroguttatus* girdle the main stem and larger branches of oaks by feeding primarily on the surface of the xylem, injuring the cambium and phloem. Infested trees are identified by thinning crowns, D-shaped emergence holes, bark damage from woodpecker foraging, and bark staining (Coleman et al., 2011; Hishinuma et al., 2011). Following several years of repeated and extensive injury, oaks eventually succumb to this larval herbivory.

Although initial surveys in southeastern Arizona revealed that Emory oak, *Quercus emoryi* Torrey, and silverleaf oak, *Quercus hypoleucoides* A. Camus, are susceptible to injury caused by *A. auroguttatus*, only low levels of infestation and tree mortality were observed in this native region of the beetle (Coleman and Seybold, 2011). In southern Mexico, *Quercus conzatti* Trel. and *Quercus peduncularis* Nee were confirmed recently as hosts for *A. coxalis* (Coleman et al., 2012). Thus, in California, the invasive population of *A. auroguttatus* is associated with host oak species for which it had no prior co-evolutionary relationship in Arizona, and the extent of the potential short- and long-term impacts of *A. auroguttatus* on California's oak woodlands is unknown.

The objective of this study was to characterize the forest stand conditions in infested and uninfested areas in California by focusing specifically on three factors: the oak composition; the current levels of infestation and tree mortality; and the degree of tree injury associated with *A. auroguttatus* in the San Diego Co. region where it has been introduced. These data were compared to the same data recorded from plots in the native region of *A. auroguttatus* in southeastern Arizona, and from plots in the native region of *A. coxalis* in southern Mexico. Annual oak mortality aerial survey data were also analyzed to assess site characteristics associated with oak mortality polygons and the rate of spread of San Diego Co. oak mortality from this new invasive species.

This information provides short-term impacts (level of tree injury and mortality) and identifies factors associated with higher risk of *A. auroguttatus* infestation in southern California. These data can help land managers focus on susceptible host species and time their management activities to prevent and slow tree injury and mortality at high-value sites. This work also establishes baseline conditions in long-term plots, which will be revisited in the future by using the same sampling protocols.

2. Methods

2.1. Site selection

During 2008–2010, sites were established in oak and pine-oak woodlands in southeastern Arizona, southern California (uninfested and infested areas), and southern Mexico (Fig. 1). In Arizona (AZ), sites were established in the foothills of the Santa Rita (Pima/Santa Cruz Cos.), Huachuca (Cochise Co.), and Chiricahua (Cochise Co.) mountain ranges of the Coronado National Forest ($N = 19$). Historical collection records of *A. auroguttatus* from AZ were used to locate sites in areas where populations of the beetle might be present (Coleman and Seybold, 2011). Areas where we observed current oak mortality were assessed for forest stand conditions to capture the impact of *A. auroguttatus*. Sites were selected in low elevation (1280–1859 m) oak woodlands dominated by *Q. emoryi* and *Quercus arizonica* Sarg. A mean annual maximum temperature of 22.9 °C and minimum temperature of 6.4 °C were recorded in this area (Chiricahua National Monument, AZ). Mean annual precipitation of 48.5 cm was recorded and characterized as monsoonal with peak rainfall occurring from July to August across the AZ sites (WRCC, 2011).

Historical collection records from southern Mexico (MX) were also used to locate sites in areas where populations of *A. coxalis* might be present (Coleman and Seybold, 2011). Surveys were limited to the Mexican states of Oaxaca and Chiapas where most historical specimen records were concentrated (Coleman and Seybold, 2011). Sites were established in Altamirano, Comitan de Dominguez, Laguna de Montebello National Park, Ocosingo, San Cristobal de las Casas, and Teopisca (Chiapas), and Ayutla and Mitla (Oaxaca) ($N = 8$). Sites were established primarily on private land or within national park boundaries in low elevation oak and pine-oak woodlands (Mir-

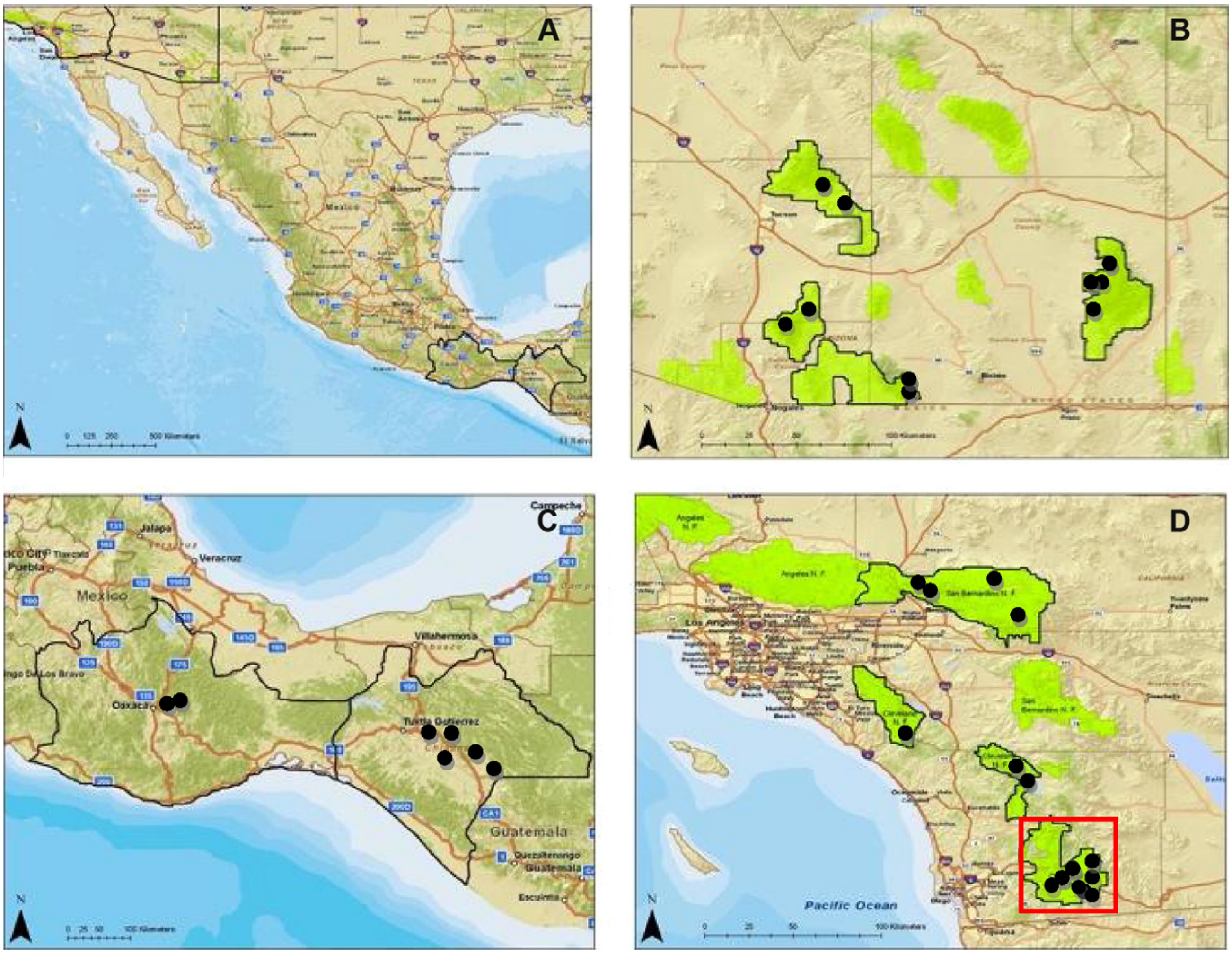

Fig. 1. Forest stand assessments for *Agrilus auroguttatus* were conducted in its native region of Arizona (AZ), introduced region of southern California (ICA), and uninfested region of California (UCA); assessments were conducted for the sibling species, *A. coxalis*, in its native region of southern Mexico (MX) (A, states are in dark outline). The native region for *A. auroguttatus* on the Coronado National Forest where surveys were conducted (B); the native region for *A. coxalis* in Oaxaca and Chiapas, Mexico where surveys were conducted (C); and the introduced and uninfested regions for *A. auroguttatus* in southern California (D). Points (●) note general location of forest stand assessments in each region and the red boxed area denotes the ICA sites in southern California.

anda, 1975). The foothills of southern Mexico (Comitan, Chiapas) were characterized by a mean annual maximum temperature of 25 °C and minimum temperature of 4.6 °C. Mean annual precipitation of 106 cm, occurring primarily from May to October, was recorded in the foothills of the Sierra Madre Mountains (CTI, 2011).

To assess the impact of *A. auroguttatus* in forest stands where the beetle had been introduced, established, and spread, sites were selected in San Diego Co., California on the Descanso Ranger District of the Cleveland National Forest (infested CA: ICA) ($N = 22$). These sites were selected randomly within the zone of infestation, except that areas impacted by the 2003 Cedar wildfire were avoided. Additional southern California sites were established outside the zone of infestation for *A. auroguttatus* (uninfested CA: UCA) on the Cleveland National Forest (Riverside and San Diego Cos.), the Santa Rosa Plateau (Riverside Co.), and the San Bernardino National Forest (San Bernardino Co.) ($N = 16$). In California, sites were selected in stands dominated primarily by *Q. agrifolia*, *Q. kelloggii*, and *Q. chrysolepis*. Sites were established between 915 and 1828 m in oak woodlands and mixed conifer forests. A mean annual maximum temperature of 18.6 °C, a minimum temperature of 4.6 °C, and a mean annual rainfall of 90.2 cm were recorded within the ICA area (Cuyamaca, CA). Precipitation is winter-dominated and falls predominantly in the region from December to March (WRCC, 2011). Similar climate data pertain to the UCA sites.

2.2. Ground surveys: forest stand composition

Forest stand assessments were made in February 2009 and March 2010 at the AZ sites; late March to early April 2010 at the MX sites; March 2009 and June and August 2010 at the UCA sites; and March, August, and September 2009 and March 2010 at the ICA sites. Deciduous oak species in UCA and ICA sites were only surveyed during the summer months after spring leaf flush, whereas evergreen oak species found across all regions were surveyed primarily before leaf flush.

Forest stand assessments were made on overstory, understory, and ground layer plots. First, three to six fixed-radius 0.04 ha (1/10 ac) overstory plots were selected arbitrarily within a stand. These plots were established in a straight line transect with at least 50 m between plot centers. All tree species >12.5 cm diameter at breast height (DBH, 1.47 m) were recorded in overstory plots. Each overstory plot also included one 0.004 ha (1/100 ac) understory plot and one 0.0004 ha (1/1000 ac) ground layer plot positioned at the 0.04 ha plot center to evaluate presence of smaller diameter trees. The understory plots were used to assess tree species with a diameter between 0.1 and 12.4 cm DBH. The ground layer plots focused only on regenerating tree species (<1.47 m tall).

Species, count, and DBH were recorded for all woody plants in the overstory and understory plots, whereas species and count were recorded in the ground layer plots. Tree status (living or dead) was recorded in overstory plots, whereas only living trees were surveyed in the understory and ground layer plots. Forest stand assessments followed the protocols of the Field Sampled Vegetation Common Stand Exam (USDA Forest Service, 2003). Several species of oaks were identified only to genus in Mexico due to the lack of information and high incidence of hybridization. These unidentified species represented only 6% of the trees surveyed in MX sites (Table SD1 in Appendix I, Supplementary Data). From the raw survey data, basal areas (m^2/ha) and tree densities (No. stems/ha) were calculated for all tree species, for oak, for infested oak, for dead oak, and for dead oak with either *A. auroguttatus* or *A. coxalis* injury in overstory plots across the four regions. Similar measurements were calculated for only live trees and oaks in understory plots. Density of seedlings (all species/plot and oak/ha) was determined in ground layer plots.

2.3. Ground surveys: injury to oaks by A. auroguttatus and A. coxalis

Presence and severity of *Agrilus* spp. injury symptoms were assessed to determine the level of infestation and to characterize oak health on an areawide basis. Crown thinning and dieback, density of bark staining and D-shaped adult emergence holes, and evidence of woodpecker foraging (presence/absence) were used to rate the level of injury from both *Agrilus* spp. (Coleman et al., 2011; Hishinuma et al., 2011). The five crown rating classes were ranked as: (1) full, healthy crown with no apparent leaf loss; (2) minor twig dieback or light thinning, 10–25% leaf loss; (3) moderate twig dieback and thinning, 25–50% leaf loss; (4) severe dieback progressing to larger branches, >50% leaf loss; and (5) complete tree mortality, no green foliage. Five stain rating classes for the lower portion (<2.5 m) of the primary bole were: (0) no staining; (1) 1–5 stained areas; (2) 6–10 stained areas; (3) >10 stained areas; and (4) staining present and bark cracking away from the xylem. The four D-shaped emergence hole ratings for the lower portion (<2.5 m) of the primary bole were: (0) no emergence holes; (1) 1–9 emergence holes; (2) 10–25 emergence holes; and (3) >25 emergence holes.

Due to the limited distribution of *Q. engelmannii* on the Descanso Ranger District of the Cleveland National Forest, and the low frequency of individuals (29 trees) encountered in ICA sites, an additional ground survey was conducted between September 2010 and October 2011 on a 284 ha parcel of private land (Japatul Valley, CA, 32°48.604′ N, 116°38.997′ W, 939 m elev.) in an open-canopied woodland of *Q. agrifolia* and *Q. engelmannii* to examine the relative rates of infestation by diameter class for these species. A total of 386 *Q. agrifolia* and 289 *Q. engelmannii* were surveyed at this site within the zone of infestation for *A. auroguttatus*. This survey followed the protocol outlined above for assessing oak infestation and injury, but was a complete survey of the oaks on the site. The landowner reported to us that during a period of several years prior to the survey, approx. 50 dead *Q. agrifolia* had been removed. The cause of the mortality was likely infestation by *A. auroguttatus*. Thus, at the time of our survey, no dead *Q. agrifolia* were present at the site.

To confirm the presence of *Agrilus* spp. in declining oaks in AZ and MX, bark was removed to expose meandering larval galleries on the xylem surface or the presence of any life stage of this beetle genus (Coleman and Seybold, 2008). Phloem- or wood-boring insect injury, especially from *Agrilus* spp., is not well documented in these areas and this destructive sampling technique of bark removal was necessary to confirm the presence of the life stages and injury symptoms of this genus (Coleman and Seybold, 2011; Coleman et al., 2012). Woodpecker foraging holes that expose *A. auroguttatus* larval galleries and/or D-shaped emergence holes on the main stem are definitive for *A. auroguttatus* infestation in San Diego Co., California and were required to classify an oak as infested (Brown and Eads, 1965; Swiecki and Bernhardt, 2006; Coleman et al., 2011). Standing dead oaks were also assessed in overstory plots for the presence of *A. auroguttatus*/*A. coxalis* injury symptoms, which were primarily D-shaped emergence holes or larval galleries. These data were used to determine the density of dead oaks impacted previously by these species.

2.4. Aerial surveys: mortality of oaks in San Diego Co.

Aerial surveys were conducted annually between July and September in California in high-wing, single-engine airplanes. Data were recorded from approximately 305 m above the ground and at 185 km/h. Sketch mapping was used to note tree mortality primarily in forested areas on public lands and adjacent ownerships. In 2010, a special survey was flown in May to capture oak mortality in San Diego Co. outside the normal survey area and closer to the urban areas of San Diego. A subset of the oak mortality polygons were ground checked annually from 2008–2011 to verify the causal agent.

Aerial data were collected by utilizing digital systems that consisted of a tablet PC (Motion Computing, Austin, TX), a georeferenced digital map, and a global positioning system (GPS) receiver (Geolink®, Paris, France). A Geolink® mapping program was linked with the GPS signal to track location on background maps. Background maps included 1:100 K topographic maps and aerial imagery after 2005. Presence/intensity of tree injury (e.g., defoliation, top kill, and flagging) or mortality was noted on background maps or imagery. For each instance of injury or mortality, we also noted the estimated number of trees or species that were impacted. If the causal agent of the injury or mortality was readily apparent (e.g., insect or pathogen species or fire), we also noted this on the maps. Aerial survey data (USDA Forest Service and Forest Health Monitoring, 2010) mapped during 2000–2010 in California were queried for oak mortality. Oak mortality in San Diego Co. that was initially attributed to drought (2002–2007) and *A. auroguttatus*-associated oak mortality (2008–2010) were used in the analyses. Mortality agents such as fire and storm damage were excluded from the analysis, as were polygons mapped during the 2002–2003 drought period that contained both conifer and hardwood mortality interspersed within the polygons. The removal of these conifer and hardwood polygons from the dataset limited the aerial survey data available for the analysis to the period from 2003–2010.

2.5. Statistical analyses

Unless otherwise indicated, all statistical procedures were conducted with SAS vers. 9.1 (SAS Institute Inc., 2004); all procedures were conducted at a critical level of $\alpha = 0.05$. Sites (AZ = 19, MX = 8, UCA = 16, ICA = 22) were used as experimental units ($N = 65$) with plots as subsamples. A generalized linear model was used to compare differences in forest stand characteristics and in impact of *A. auroguttatus* in introduced, native, and uninfested regions and in impact of *A. coxalis* in its native region (PROC GLM). Assumptions of normality were checked for all data by using the Shapiro–Wilk test (PROC UNIVARIATE). All data were transformed [$\log_{10}(x + 1)$] to meet assumptions of normality. Homogeneity of variances was checked by plotting residuals (PROC UNIVARIATE). All comparisons of mean responses were performed on the transformed data. Significant treatment differences were analyzed by using the REGWQ procedure (Day and Quinn, 1989).

Diameters (DBH) of uninfested and *A. auroguttatus*/*A. coxalis*-infested oaks were compared within a species from overstory plots for AZ and ICA sites, for all plot sizes for MX sites, and for the Japatul Valley, CA (PROC TTEST). Homogeneity of variances for these data was assessed by using the Folded F method. When variances were found to be equal, the Pooled Method was used. When variances were found to be unequal, the results from the Satterthwaite Method were used. A chi-squared test for comparing two proportions was used to assess differences between uninfested and infested trees at the Japatul Valley, CA site. The relationship between the percentage of infested *Q. agrifolia* and diameter class at this site was analyzed by polynomial regression; a Spearman's rank correlation between these two variables was also calculated (both PROC REG, SAS Institute Inc., 2010). The proportion of infested trees and dead trees with *A. auroguttatus* or *A. coxalis* injury in an oak species were analyzed by using a chi-squared test with Marascuilo comparisons across all regions (Marascuilo, 1966).

A series of multinomial models were employed to determine the influence of region on oak injury associated with either *A. auroguttatus* or *A. coxalis* (PROC GENMOD with CUMLOGIT as the link function). Each model had one independent variable (Region) with four conditions or states (AZ, MX, UCA, ICA), but the single dependent variable in each model differed among models (crown condition, categories of 1–5; bark staining, categories of 0–4; or emergence holes, categories 0–3). Because *A. auroguttatus* emergence holes did not occur in the UCA sites, there were only three conditions for the independent variable in the emergence hole model. Following each model analysis, contrasts were used to determine statistical significance for specific comparisons among the regions. Ratings for crown thinning were found to correlate with the level of *Agrilus* spp. injury, and can be a generalized response for the health of hardwood trees (Katovich et al., 2000; Vansteenkiste et al., 2004; Coleman et al., 2011). Furthermore, crown condition, bark staining, and emergence holes were the main predictors of oak health associated with *A. auroguttatus* infestation in California (Coleman et al., 2011). Uninfested California (UCA) sites were not included in analyses focusing on *A. auroguttatus*-specific assessments as to not unnecessarily inflate the degrees of freedom. Non-transformed data are presented in the tables and figures.

Aerial survey data were analyzed with the Spatial Analyst and Spatial Statistics (Standard Distance) tools (ESRI, ArcMapp 10.0). A 30-m digital elevation model was used via Spatial Analyst to determine mean aspect, elevation, and slope (%) of oak mortality polygons from San Diego Co. Number of dead oaks mapped in each polygon was extracted from the aerial survey data. The geometric mean of all oak mortality polygons in a given year was determined by Standard Distance during 2003–2010. A standard deviation of two was used in the analysis to include 95% of the aerial polygon data. The geometric mean was plotted for the 8-yr period (2003–2010) with the predicted center. The predicted center was used in the following analyses as the reference for the origin of the outbreak.

Principal component analysis (PCA) was used to assess patterns of oak mortality between 2003 and 2010 across the landscape (PC-ORD, McCune and Mefford, 1999). A total of 1111 oak mortality polygons were used in the analysis. Aspect, elevation, slope (%), number of dead oaks, and distance of a polygon to the predicted center of the outbreak (see Standard Distance analysis) were included in the analysis. Circular aspect data were transformed to a 16 point scale with north–northeast being most mesic and south-southwest most xeric. Elevation data ranged from 179 to 1843 m; slope ranged from 0 to 95%; number of dead oaks ranged from 1 to 5329; and distance of polygons to the predicted outbreak origin ranged from 106 to 74,341 m. Eigenvalues are presented to show the variance extracted by environmental parameters. Eigenvalues with a broken stick value <1 and eigenvectors <±0.5 were not discussed.

3. Results

3.1. Ground surveys: forest stand composition

In the ground survey portion of this study a total of 2737 trees, representing 36 species/genera (there were trees that were only identified to genus), were surveyed across the four regions (Table SD1 in Appendix I, Supplementary Data). *Q. arizonica* was the most abundant oak species surveyed in AZ followed by *Q. emoryi*, *Q. hypoleucoides*, and *Q. grisea* Liebm. (Appendix I). At the sites in MX, *Quercus peduncularis* was the most abundant oak species surveyed followed by *Q. rugosa* and *Q. conzatti* (Appendix I). In UCA sites, *Q. kelloggii* was the most frequently encountered oak species followed by *Q. chrysolepis*, *Q. agrifolia*, and *Q. engelmannii* (Appendix I). However, in ICA sites, *Q. agrifolia* was the most frequently occurring oak in the survey followed by *Q. kelloggii*, *Q. chrysolepis*, and *Q. engelmannii* (Appendix I).

Total basal area in the overstory plots was highest in UCA and ICA sites when compared to sites in AZ (41% less than UCA) and MX (46% less than UCA) (Table 1A). Similar significant differences were observed for total overstory basal area in AZ (37% less) and MX (41% less) when compared to sites in ICA. In UCA and ICA sites, oak overstory basal area was 87% and 75% greater than in AZ, and 2× and 1.8× greater than in MX sites, respectively (Table 1A). Oak overstory basal area in AZ was also significantly greater than in MX sites (61%). The oak component represented the dominant overstory basal area surveyed in each region (AZ: 75%; MX: 50%; UCA: 82%; and ICA 83%, Table 1A). Total tree density in the overstory plots was significantly greater in AZ when compared to sites in MX (46%), UCA (75%), and ICA (1×) (Table 1A). A similar trend was observed for oak densities across the four regions; sites in AZ had 72% more oaks per unit area than sites in MX, 1.5× more oaks than UCA, and 1.3× more oaks than ICA sites.

In understory plots, total basal area was highest in MX sites (Table 1B), but this was not significantly different when compared to other regions. Total understory basal area was significantly lower at sites in UCA (90%) and ICA (93%) when compared to sites in AZ (Table 1B). The ANOVA was not significant in understory plots for any of the other forest stand characteristics. *Agrilus* infestation was only observed at MX sites in the understory size class, but even these observations were rare. Tree and oak density were highest in ground layer plots at UCA sites (Table 1C), but were not significantly greater than the other sites in AZ and ICA. Ground layer data were not collected in MX.

3.2. Ground surveys: injury, rates of infestation and mortality, and stand-level effects on oaks by A. auroguttatus and A. coxalis

3.2.1. Injury on oaks by A. auroguttatus and A. coxalis

In the analysis of oak injury as a consequence of *Agrilus* colonization, the multinomial models for crown condition ($\chi^2_3 = 379.8$; $P < 0.001$), bark staining ($\chi^2_3 = 412.6$; $P < 0.001$), and emergence holes ($\chi^2_2 = 393.8$; $P < 0.001$) were all significant. The proportional allocations of oaks at ICA sites to the various classes for each of these dependent variables were significantly different than the allocations of oaks from the three other regions (all $P < 0.001$) (Figs. 2A–C). The proportional allocation of oaks at UCA sites to the various crown condition classes also differed significantly from the allocations of oaks from AZ ($P < 0.001$) and MX ($P < 0.001$) sites (Fig. 2A). Healthy crowns were the most abundant in AZ, MX, and UCA sites (Fig. 2A). Although the majority of oak crowns (28%) were also classified as healthy in ICA sites, almost as many dis-

Table 1
Forest stand characteristics (mean ± s.e.) associated with the impact of *Agrilus auroguttatus* (*Aa*) in native (AZ), introduced (ICA), and uninfested California (UCA) oak woodlands, and with the impact of *A. coxalis* (*Ac*) in native southern Mexican oak woodlands[a].

Characteristic	Region				ANOVA[b]	
	Arizona (AZ)	Mexico (MX)	Uninfested CA (UCA)	Infested CA (ICA)	F_{df}	*P*
A. Overstory plots						
Basal area (m^2/ha)						
Total	23.12 ± 2.63 b	21.59 ± 5.11 b	39.78 ± 5.66 a	36.51 ± 2.76 a	$7.96_{3,62}$	<0.001
Oak	17.33 ± 2.19 b	10.76 ± 6.07 c	32.49 ± 5.65 a	30.33 ± 3.19 a	$16.43_{3,62}$	<0.001
Infested oak w/ *Aa* or *Ac*	1.69 ± 0.62 b	0.12 ± 0.21 b	–	23.15 ± 2.80 a	$61.52_{2,46}$	<0.001
Dead oak	2.41 ± 0.62 ab	0.28 ± 0.28 c	0.75 ± 0.44 bc	9.18 ± 2.19 a	$10.35_{3,62}$	<0.001
Dead oak w/ *Aa* or *Ac*	1.60 ± 0.57 b	2.62 ± 2.39 b	–	8.21 ± 2.15 a	$6.30_{2,46}$	0.004
Tree density (No. stems/ha)						
Total	67.85 ± 8.12 a	46.54 ± 10.30 b	38.80 ± 4.11 b	28.62 ± 2.25 b	$9.59_{3,61}$	<0.001
Oak	53.77 ± 6.81 a	31.20 ± 10.82 b	21.05 ± 3.50 b	23.17 ± 1.88 b	$7.16_{3,61}$	0.003
Infested oak w/ *Aa* or *Ac*	1.92 ± 0.72 b	0.78 ± 0.33 b	–	14.22 ± 1.31 a	$42.36_{2,46}$	0.001
Dead oak	5.53 ± 1.30 a	0.38 ± 0.27 c	1.50 ± 0.56 bc	3.47 ± 0.63 ab	$6.52_{3,62}$	<0.001
Dead oak w/ *Aa* or *Ac*	1.14 ± 0.51 b	0.38 ± 0.27 b	–	3.01 ± 0.57 a	$8.49_{2,46}$	<0.001
B. Understory plots						
Basal area (m^2/ha)						
Total	1.29 ± 0.86 a	1.77 ± 0.92 ab	0.13 ± 0.07 b	0.09 ± 0.03 b	$3.72_{3,61}$	0.02
Oak	0.34 ± 0.22	1.11 ± 0.81	0.13 ± 0.08	0.06 ± 0.03	$2.66_{3,61}$	0.06
Infested oak w/ *Aa* or *Ac*	0	0.08 ± 0.08	–	0	$2.75_{2,46}$	0.07
Tree density (No. stems/ha)						
Total	30.71 ± 10.34	87.69 ± 41.21	10.32 ± 5.61	19.16 ± 7.00	$2.06_{3,61}$	0.1
Oak	13.89 ± 9.62	46.79 ± 27.51	7.49 ± 6.00	17.78 ± 7.12	$1.02_{3,52}$	0.4
Infested oak w/ *Aa* or *Ac*	0	1.26 ± 1.26	–	0	$2.75_{2,46}$	0.08
C. Ground layer plots						
Tree density (No. stems/ha)						
Total	188.86 ± 78.68		1247.83 ± 736.98	237.61 ± 104.16	$1.77_{2,55}$	0.2
Oak	146.80 ± 63.95		605.22 ± 366.11	180.89 ± 87.96	$1.59_{2,50}$	0.2

[a] Stand data are presented by overstory (>12.5 cm DBH), understory (<12.5 cm DBH), and ground layer (<1.47 m tall) size classes.

[b] Threshold for significance is $\alpha = 0.05$; when the ANOVA was significant, rows with different bold, lower-case letters denote statistically significant different means.

played minor thinning (24%), moderate thinning (20%), or complete loss of the crown (18% were dead); 10% had severe thinning (Fig. 2A). Absence of bark staining was the most prevalent condition across all regions (AZ: 96%, MX: 100%, UCA: 96%, and ICA: 57%; Fig. 2B). Although most oaks were allocated to the lower bark staining classes in AZ, MX, and UCA sites, more oaks were allocated to classes 1 through 4 in ICA sites than in the other three regions (Fig. 2B). Absence of emergence holes was also the most prevalent condition across all regions (AZ: 98%, MX: 99%, UCA: 100%, and ICA: 59%; Fig. 2C). Although most oaks were allocated to the lower emergence hole classes in AZ, MX, and UCA sites, more oaks were allocated to classes 1 (34%), 2 (5%), and 3 (2%) in ICA sites than in the other three regions (Fig. 2C).

3.2.2. Rates of infestation and mortality on oaks by *A. auroguttatus* and *A. coxalis*

The mean overall rates of infestation by *A. auroguttatus* among large diameter live red oaks >12.5 cm DBH (in AZ and CA) and by *A. coxalis* among live white oaks (in MX) were 61% (ICA), 4% (AZ), 3% (MX), and 0% (UCA) (Fig. SD-1 in Appendix I, Supplementary Data, Table 1A). The highest infestation rates observed at individual sites were 39% at AZ, 4% at MX, and 91% at ICA sites. Some uninfested plots were encountered in all regions, but only one uninfested site was surveyed among ICA sites. At sites in AZ, mean DBH of infested *Q. emoryi* was significantly greater (62%) than mean DBH of uninfested *Q. emoryi* (Table 2). The DBH range of infested *Q. emoryi* was 14.9 to 73.7 cm. Infested *Q. hypoleucoides* were numerically larger in diameter than uninfested *Q. hypoleucoides*, but this difference was not statistically significant. The DBH ranges of infested and uninfested *Q. hypoleucoides* were 20.8–60.9 cm and 11.4–43.2 cm, respectively. *A. auroguttatus* injury was not observed on the white oak species (section *Quercus*) at AZ sites.

At sites in MX, only *Q. conzatti* and *Q. peduncularis* were observed with signs of *A. coxalis* infestation (Table 2). A single live infested red oak, *Q. conzatti* (10.7 cm DBH), was observed in this survey. Only three dead individuals of *Q. peduncularis* were observed with evidence of prior infestation by *A. coxalis*, and their DBH's ranged from 9.9 to 20.8 cm (Table 2). Mean DBH of *A. coxalis*-infested *Q. peduncularis* was 19% greater than uninfested *Q. peduncularis*, but this difference was not statistically significant.

In sites in ICA, the red oak species [*Q. kelloggii* (70%) and *Q. agrifolia* (53%), section *Lobatae*] were significantly more infested than the intermediate oak species, *Q. chrysolepis* (48%), section *Protobalanus*, and the white oak species, *Q. engelmannii* (20%), section *Quercus* (Table 2). Mean DBHs of infested *Q. agrifolia* and *Q. kelloggii* were significantly greater (46% and 41%, respectively) than uninfested trees of the same species (Table 2). The same trend was observed for the mean DBH of infested *Q. chrysolepis* (44% greater than uninfested trees), but this difference was only marginally significant (Table 2). Diameters (DBH) of infested oaks ranged from 15.8 to 86.4 cm for *Q. agrifolia*, 20.6 to 193 cm for *Q. kelloggii*, 13.7 to 58.4 cm for *Q. chrysolepis*, and 25.4 to 63.5 cm for *Q. engelmannii*.

In the complete survey of the stand of *Q. agrifolia* and *Q. engelmannii* in Japatul Valley, there was no evidence of infestation by *A. auroguttatus* across the full range of diameter classes of *Q. engelmannii* (Table 2, Fig. 3A). In contrast, *A. auroguttatus* was associated with trees in all but the smallest diameter class of *Q. agrifolia* and the proportion of infested trees increased with diameter class (Fig. 3B). Both the polynomial regression ($F = 85.04$, $P < 0.001$, $R^2 = 0.94$) and the Spearman's rank correlation test ($F = 92.28$, $P < 0.001$, $R^2 = 0.88$) demonstrated that the infestation rates had a significant positive correlation with *Q. agrifolia* diameter class. The diameters of infested *Q. agrifolia* ranged from 14.5 to 162.9 cm. The overall infestation rate of *Q. agrifolia* at the site was 65.5% (Table 2). There were no results for the association of

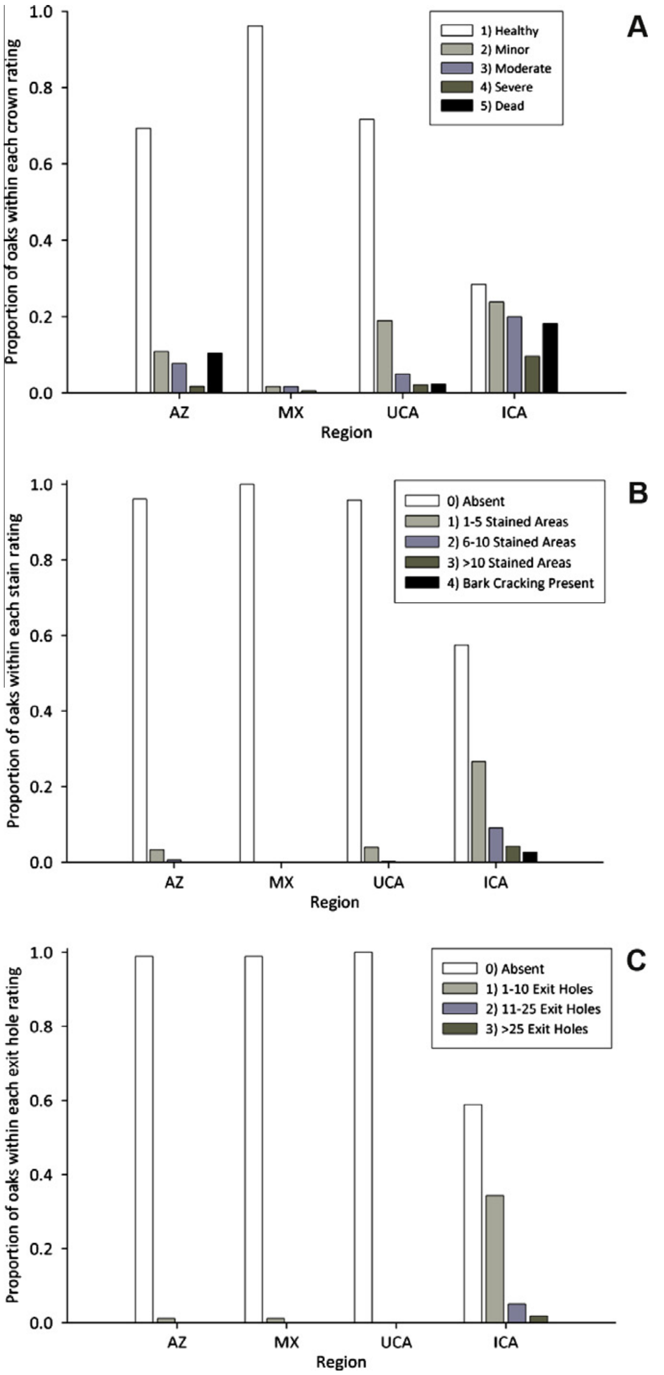

Fig. 2. Crown health (A), bark staining (B), and emergence hole ratings (C) of oaks associated with *Agrilus auroguttatus* in Arizona (AZ); with *A. coxalis* in southern Mexico (MX); and with *A. auroguttatus* in the uninfested (UCA) and introduced, infested (ICA) regions of California.

A. auroguttatus with dead *Q. agrifolia* because dead oaks had been removed from the site over a period of several years prior to the survey.

The mean overall rates of oak mortality attributed to *A. auroguttatus* among large diameter red oaks >12.5 cm DBH (in AZ and CA) and by *A. coxalis* among white oaks (in MX) were 13% (ICA), 2% (AZ), 1% (MX), and 0% (UCA) (Fig. SD-1 in Appendix I, Supplementary Data, Table 1A). The highest rates of *Agrilus*-associated dead oak were 8.09 trees/ha (18%) in AZ, 2.02 trees/ha (8%) in MX, and 9.71 trees/ha (48%) in ICA sites. At ICA sites, oak mortality associated with *A. auroguttatus* injury was significantly more prevalent in the red oaks, *Q. agrifolia* (91%) and *Q. kelloggii* (88%), when compared to *Q. chrysolepis* (60%) and *Q. engelmannii*, the latter of which showed no dead trees associated with signs of *A. auroguttatus* feeding damage (Table 2). Diameters of dead oaks infested with *A. auroguttatus* ranged from 19.8 to 142.2 cm for *Q. agrifolia*, 27.9 to 142.2 cm for *Q. kelloggii*, and 16.5 to 58.4 cm for *Q. chrysolepis*.

3.2.3. Stand-level effects on oaks by A. auroguttatus and A. coxalis

The basal area of oaks infested with *Agrilus* spp. in overstory plots was significantly (13× and 192×) higher at the ICA than at the AZ and MX sites, respectively (Table 1A). The density of *Agrilus*-infested oaks in the overstory plots was significantly greater at sites in ICA than at sites in either of the other regions where *Agrilus* was present (Table 1A). Density of infested oaks was 6x greater at ICA sites than at AZ and 17x greater than at MX sites (Table 1A).

In AZ, the basal area of dead oaks (killed by all causes) was 8× greater relative to MX sites (Table 1A). The basal area of dead oaks killed by all causes did not differ between sites in ICA and AZ, but this basal area was significantly (at least 2.8×) greater at ICA sites than at MX and UCA sites. Basal area of dead oaks that had signs of either *A. auroguttatus* or *A. coxalis* injury was significantly greater at ICA sites than at AZ (4×) or at MX (2×) sites. The density of dead overstory oaks was significantly (14× and 3×) greater at sites in AZ than at sites in MX and UCA, respectively (Table 1A). Densities of dead oaks were significantly lower in MX (89%) when compared to ICA sites. Although the density of dead oaks was 1.3× greater in ICA than UCA sites, the difference was not statistically significant. *A. auroguttatus* injury associated with dead oaks at sites in ICA was 1.6× greater than at sites in AZ and 6.9× greater than *A. coxalis* injury at sites in MX. The majority of dead oaks in each region were: AZ, *Q. emoryi* (46 trees); ICA, *Q. kelloggii* (43 trees); and MX, *Q. peduncularis* (3 trees).

3.3. Aerial surveys: mortality of oaks in San Diego Co.

The estimated center of oak mortality polygons associated with *A. auroguttatus* in California from 2003–2010 is near the communities of Guatay and Pine Valley (Fig. 4). The linear "diameter" of the polygon representing the hypothetical center of the outbreak area spans 11 km. Mean distance of spread for oak mortality polygons increased every year following 2006 to 2010. The mean distance of spread calculated for 2010 polygons represents a 49.7 km expansion from the predicted center of oak mortality detected near Guatay and Pine Valley in 2002. Elevated levels of oak mortality (assessed as ha and number of dead oaks) were mapped continually in San Diego Co. from 2002 to 2010 (Table 3). The number of dead oaks was highest in 2004 at the cessation of the two-year drought. A second peak of oak mortality occurred in 2007 following a moderate drought. Oak mortality associated with *A. auroguttatus* fluctuated from 2008 to 2010, which represented a period of normal precipitation.

The PCA for aerial oak mortality polygons explained 51.2% of the variance along axes 1 and 2 (Table 4). Distance of polygons to the center of outbreak explained the most variance along axis 1. Slope (%) also explained variance along axis 1 (Table 4). Aspect explained the most variance along axis 2 (Table 4). Elevation also contributed to explaining variance along axis 2.

4. Discussion

Historically, *Agrilus* spp. phloem/xylem borers have not played a role in contributing to elevated levels of oak mortality in California. However, our analysis here reveals that the recent introduction of

Table 2
Impact on oaks (*Quercus* sp.) associated with *Agrilus auroguttatus* (*Aa*) in native (AZ) and introduced (ICA) regions, and with *A. coxalis* (*Ac*) in native sites in southern Mexico (MX).

	Diameter (cm DBH, mean ± s.e.)		*t*-test[a]		Proportion of living oaks infested w/*Aa* or *Ac*[b]	Proportion of dead oaks w/*Aa* or *Ac*[b]
Oaks	Uninfested	Infested	t_{df}	*P*		
Arizona (AZ)						
Red oaks (section *Lobatae*)					$\chi^2_3 = 19.2$; $P < 0.001$	$\chi^2_3 = 8.02$; $P = 0.5$
Quercus emoryi (*N* = 247)	26.9 ± 0.86 b	43.5 ± 3.48 a	5.71_{245}	<0.001	0.01 a	0.41
Quercus hypoleucoides (*N* = 58)	23.1 ± 0.99	29.9 ± 7.59	$0.89_{4.13}$	0.4	0.06 a	0.17
White oaks (section *Quercus*)						
Quercus arizonica (*N* = 324)	23.2 ± 0.58	0	nd		0 a	0
Quercus grisea (*N* = 9)	29.9 ± 7.41	0	nd		0 a	0
Mexico (MX)						
Red oaks (section *Lobatae*)					nd	nd
Quercus conzatti (*N* = 17)	16.7 ± 0.78	10.7[cc]	nd		0	0
Quercus rugosa (*N* = 36)	34.3 ± 1.70	0	nd		0	0
White oaks (section *Quercus*)						
Quercus peduncularis (*N* = 97)	20.9 ± 0.74	24.8 ± 5.44	0.92_{95}	0.4	0	1.0
Infested California (ICA)						
Red oaks (section *Lobatae*)					$\chi^2_3 = 22.6$; $P < 0.001$	$\chi^2 = 7.40_2$; $P = 0.025$
Quercus agrifolia (*N* = 274)	37.8 ± 1.85 b	55.0 ± 1.96 a	6.45_{264}	<0.001	0.53 a	0.91 a
Quercus kelloggii (*N* = 182)	35.28 ± 3.81 b	49.8 ± 2.11 a	3.42_{180}	<0.001	0.70 a	0.88 a
Intermediate oaks (section *Protobalanus*)						
Quercus chrysolepis (*N* = 27)	19.4 ± 2.18 b	27.9 ± 3.88 a	$1.92_{20.3}$	0.07	0.48 b	0.6 b
White oaks (section Quercus)						
Quercus engelmannii (*N* = 20)	38.9 ± 3.25	44.4 ± 7.44	0.73_{18}	0.5	0.20 b	0 b
Japatul Valley, Infested California (ICA)						
Red oaks (section *Lobatae*)					$\chi^2_1 = 290.5$; $P < 0.001$	nd
Quercus agrifolia (*N* = 386)	34.3 ± 0.16 b	50.4 ± 0.11 a	7.01_{265}	<0.001	0.66 a	NA
White oaks (section *Quercus*)						
Quercus engelmannii (*N* = 289)	31.1 ± 0.73	0	nd		0 b	0

[a] Threshold for significance is $\alpha = 0.05$; rows with different bold, lower case letters denote statistically significant different means. Some analyses were not conducted (nd) because no infested species were encountered or a single dead tree was found.

[b] Columns with different bold, lower-case letters within the same region denote statistically significant differences in proportions (χ^2 test).

[c] Only one individual in the survey showed evidence of infestation by *A. coxalis*.

the invasive *A. auroguttatus* into southern California oak savanna and mixed conifer landscapes is resulting in injury to the dominant red oak canopy species and is causing increased rates of tree mortality in the region. *A. auroguttatus* and *A. coxalis* do not appear to be aggressive tree killing species in their native regions of southeastern Arizona and southern Mexico, respectively, but the behavior and impact of *A. auroguttatus* in ICA sites is quite different. The effects of *A. auroguttatus* in two relatively naïve ecosystems in southern California make it one of the most profound examples of an indigenous exotic species as defined in Dodds et al. (2010).

4.1. Ground surveys: forest stand composition

Oaks are a dominant component of the forest composition in the areas that we surveyed. Dense stands of small diameter *Q. arizonica* and *Q. emoryi* were most commonly observed in AZ sites and their dominance can be attributed to soil type and depth, low fire frequency, long fire-free periods, and, hypothetically, unreported herbivore pressure from *A. auroguttatus* on the larger diameter red oaks (Borelli et al., 1994; Barton, 1999). In our survey, *Q. peduncularis* frequently held co-dominant canopy positions with *Pinus oocarpa* Schiede ex. Schltdl. at sites in MX, thus limiting the oak component. Low-intensity fires, fuel wood collection, and selective timber harvesting were common disturbance events observed in these areas and likely contributed to shaping the composition, age class, and structure of these Mexican oak stands.

Total and oak basal area in UCA and ICA sites were greater than in the other regions. In southern California, the total and oak basal area estimates were influenced by small numbers of mature, large diameter *Q. agrifolia* in the lower elevation open-canopied savannas, whereas mature *Q. kelloggii* and *Pinus jeffreyi* Grev. & Balf. were prominent contributors to these estimates in the higher elevation mixed conifer forests. *Quercus chrysolepis* also co-dominated higher elevation plots surveyed in UCA sites. Historically, in other areas of California, absence of significant mortality factors, abandonment of agriculture, urbanization, and grazing have favored even-aged stands of large diameter oaks (Brown and Eads, 1965; Bolsinger, 1988), but these factors have not likely been involved in the more montane/chaparral habitats that we surveyed in southern California. The density of oaks in the overstory plots was considerably higher in AZ sites than in the other three regions. We hypothesize that stand species composition, which included greater numbers of co-dominant pines in MX, UCA, and ICA sites, contributed to this difference.

Total understory basal area was highest in plots at MX sites and likely due to canopy gaps from tree felling and canopy disturbances, which allow vegetative growth. Dense canopy cover in higher elevation UCA and ICA sites likely reduced the understory surveyed when compared with AZ sites. Oak regeneration comprised the majority of new seedlings across all regions, but was still observed at low densities. The status of an oak regeneration "problem" in California is not entirely resolved (Tyler et al., 2006), but low regeneration rates may result from numerous abiotic and biotic factors (Callaway and Davis, 1998). In this instance, however, a significant loss of seed bearing trees in ICA sites from colonization by *A. auroguttatus* may reduce natural regeneration because sprouting is not commonly observed on *A. auroguttatus*-attacked and killed trees.

4.2. Ground surveys: injury, rates of infestation and mortality, and stand-level effects on oaks by A. auroguttatus and A. coxalis

Oaks infested with either *A. auroguttatus* or *A. coxalis* were encountered infrequently in their respective native regions of AZ and MX (as assessed by presence and severity of injury symptoms as well as by basal area and stem density of live infested and

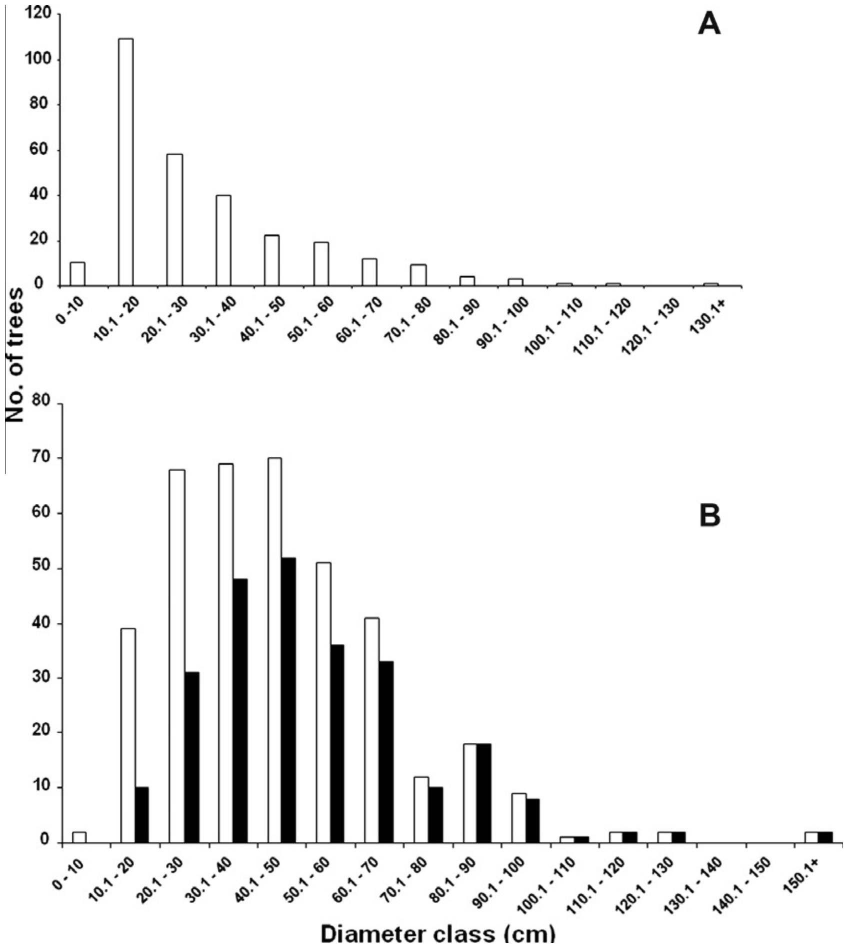

Fig. 3. Frequency distribution by diameter of 289 Engelmann oaks, *Quercus engelmannii* (A) and 386 coast live oaks, *Q. agrifolia* (B) from a survey of a private land parcel (Japatul Valley, California) showing all trees (open bars) and tree infested with *Agrilus auroguttatus* (black bars). Note that none of the *Q. engelmannii* were infested (A) and the proportion of infested *Q. agrifolia* increased with diameter class (B).

previously infested dead trees). Initial surveys by Coleman and Seybold (2011) reported observations of latent activity of *A. auroguttatus* in AZ, which are supported quantitatively in the current study (Tables 1 and 2, Fig. 2A–C, Appendix I). Similarly low levels of activity of *A. bilineatus* were recorded on healthy trees in the eastern USA; this species commonly exploits stressed trees (Dunn et al., 1986, 1990). Low population densities of *A. auroguttatus* and *A. coxalis* in the native regions were also likely reflected in the minimal collection history and previous absence of information on the history and impact (Coleman and Seybold, 2008, 2011). If these insects were pests in their native regions and capable of increasing their population densities and killing large numbers of oaks, then their impacts would have been noticed previously by resource management professionals and survey entomologists.

4.2.1. Injury on oaks by A. auroguttatus and A. coxalis

Overall across three of the four regions, oak crown condition and presence and density of bark staining and emergence holes associated with *A. auroguttatus* or *A. coxalis* were characterized primarily as healthy or absent. However, significant differences in these assessments of injury were observed in ICA sites with the majority of red or intermediate oaks showing detectable symptoms. Crown health of evergreen oaks was slightly poorer in AZ and MX sites when compared to ICA sites, but this might be attributed to surveys conducted prior to leaf flush in the spring. Oaks with crown ratings of “3” and “4” and high densities of emergence holes (ratings of 2–3) are not expected to recover from *A. auroguttatus* injury, so the injury ratings recorded at ICA sites are anticipated to lead to higher levels of tree mortality in this region in the near future. Vansteenkiste et al. (2004) found similar relationships between degree of injury from *A. biguttatus* and progressive crown thinning. These declining oaks in San Diego Co. represent potential hazards to human safety and structures and are not likely to be saved by remedial insecticidal options or cultural control methods.

Low levels of bark staining and emergence hole density were observed in sites in AZ and MX. Nevertheless, there was more bark staining at AZ sites than at UCA sites, and this could be related to current *A. auroguttatus* injury to oaks in AZ or to other decline factors. Bark staining observed in UCA sites was not associated with *A. auroguttatus* infestation. In and outside the zone of infestation in San Diego Co., small amounts of bark staining have been attributed to several *Botryosphaeria* spp. Ces. & De Not. and numerous other fungi (Lynch et al., 2010; Eskalen et al., 2010). In Europe, bark staining associated with *A. biguttatus* was attributed to a wound response, patch killing from *Agrilus* larval feeding, necrotic tissue, secondary infections by fungi, and/or bacterial infection (Moraal and Hilszczański 2000; Vansteenkiste et al. 2004; Denman et al., 2011).

4.2.2. Rates of infestation and mortality on oaks by A. auroguttatus and A. coxalis

The impact that we have measured for *A. auroguttatus* in ICA sites stands in stark contrast to what was recorded in the native region. In ICA sites, mean *A. auroguttatus* infestation level from the

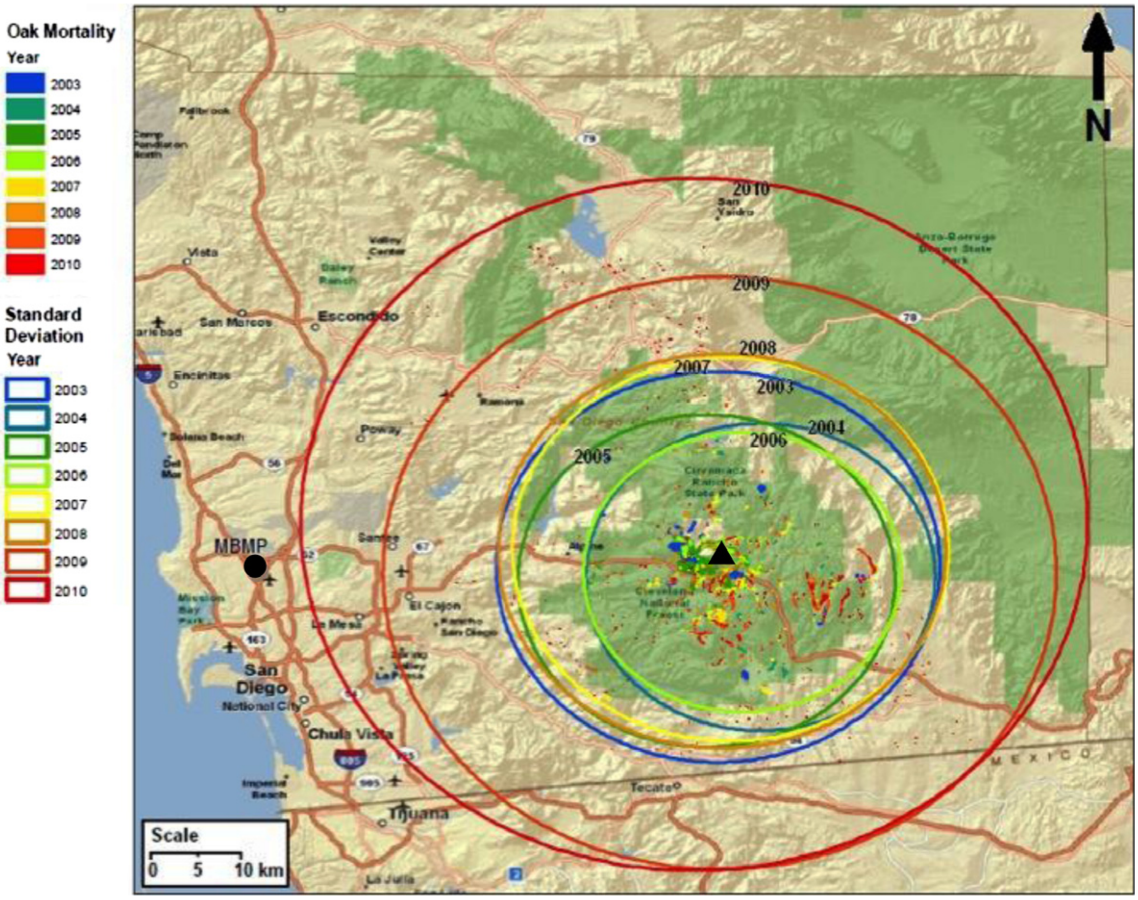

Fig. 4. Standard distance analysis of aerial oak mortality polygons (2003–2010) associated with *Agrilus auroguttatus* in San Diego Co., California, USA. The predicted center of oak mortality polygons from 2003–2010 is noted in the middle of the geometric means (▲). The known satellite infestation in Marian Bear Memorial Park (MBMP) north of urban San Diego is also presented (●).

Table 3
Mortality of aerially mapped *Quercus* spp. by land area and number of trees in San Diego Co., California from 2000–2010.[a]

Year	Oak mortality[b]	
	Hectares	Oaks
2000	0	0
2001	0	0
2002	184	74
2003	4763	370
2004	1145	6000
2005	3061	3805
2006	1114	1365
2007	957	4325
2008	730	1501
2009	669	2851
2010	405	1789
Total	13,027	22,080

[a] Southern California experienced acute drought from 2002–2003 and moderate drought in 2007.
[b] Attributed to *Agrilus auroguttatus*.

Table 4
Principal component analysis of oak mortality polygons associated with *Agrilus auroguttatus* injury in San Diego Co., that were aerially mapped from 2003–2010.

	Axis	
	1	2
Eigenvalue	1.467	1.097
Broken-stick eigenvalue	2.283	1.283
Variance explained (%)	29.3	21.9
Eigenvectors for environmental parameters		
Aspect	0.09	0.71
Distance to center of outbreak	0.64	−0.21
Elevation	0.19	0.54
Number of dead oaks	0.42	−0.21
Slope (%)	0.61	−0.26

survey plots was 61% for larger diameter oaks (>12.5 cm DBH). Higher levels of infestation (91%) were recorded for larger diameter oaks near the center of the outbreak (Pine Valley, CA) where *A. auroguttatus*-associated tree mortality has been present for at least nine years. In the complete survey of *Q. agrifolia* at the Japatul Valley site, which is just south of the center, an infestation rate of 66% was recorded among all diameter classes of *Q. agrifolia*. Coleman and Seybold (2008) reported similar infestation rates (67%) from a smaller pilot study in San Diego Co. Lower levels of infestation (14%) were found for overstory oaks at the outlying sites of the infested area (Lake Morena, CA), which is only 14 km southeast of the center. In this region, the isolation of oak woodlands in mesic valleys by drier, chaparral-dominated hillsides may slow the natural dispersal of *A. auroguttatus* to new areas.

In AZ, *A. auroguttatus* frequently infested larger diameter red oaks, *Q. emoryi* and *Q. hypoleucoides*, whereas no injury was observed on the white oak species. Although *A. bilineatus* is generally thought to have a host range that spans both red and white oak species (Haack and Acciavatti, 1992), under certain circumstances it has shown a significant host preference for red oaks (Haack, 1985; Muzika et al., 2000). In contrast, *A. biguttatus* shows a preference toward white oaks (Moraal and Hilszczański, 2000). The proportion of infested *Q. hypoleucoides* was greater than *Q. emoryi*, but more infested and dead *Q. emoryi* with *A. auroguttatus* injury were surveyed. This difference may be attributed to the limited sample size of *Q. hypoleucoides* ($N = 70$) present in lower elevation oak woodlands. In MX sites, a white oak, *Q. peduncularis*, was found infested by *A. coxalis* more than red oak species. The preference for white oaks may be a behavioral difference between the two sibling *Agrilus* species, but must be confirmed with additional surveys.

In ICA sites, larger diameter *Q. agrifolia*, *Q. kelloggii*, and *Q. chrysolepis* were frequently infested with *A. auroguttatus*. *Agrilus anxius*, *A. bilineatus*, and *A. plannipennis* Fairmaire also show preferences for larger diameter hosts (Balch and Prebble, 1940; Haack and Acciavatti, 1992; Lyons et al., 2009). In the initial report of the discovery of *A. auroguttatus* in California, Coleman and Seybold (2008) reported a lower limit of approx. 12.7 cm DBH for infested red and intermediate oaks in San Diego Co. The current survey largely supports this lower bound for trees that sustain attack by *A. auroguttatus*. In ICA sites, infested trees with the lowest diameter were 13.7 cm for *Q. chrysolepis* and 15.8 cm for *Q. agrifolia*; in the complete survey of the Japatul Valley site, the infested *Q. agrifolia* with the lowest diameter had a DBH of 14.5 cm (Fig. 3B), and there was a clear association between increasing diameter class and probability of infestation. At sites in AZ, *A. auroguttatus* successfully colonized individuals of *Q. emoryi* that were as small as 14.9 cm DBH and *Q. hypoleucoides* that were 20.8 cm DBH. Of all understory plots surveyed, only those in MX showed evidence of *Agrilus* infestation in the smaller diameter oaks. This underscores the potential capability of *A. coxalis* to successfully colonize and develop in smaller diameter trees than *A. auroguttatus*. Tree mortality was not common in these smaller size classes at any of the sites.

As a consequence of the limited number of *Q. engelmannii* and *Q. chrysolepis* encountered in plots at the ICA sites, our assessment of the impact of *A. auroguttatus* on these oak species in California may not be entirely accurate. Further, at ICA sites, the close proximity of *Q. engelmannii* to numerous severely injured *Q. agrifolia* with evidence of high population densities of *A. auroguttatus* may have biased the estimates of *Agrilus*-associated injury for *Q. engelmannii*. Nonetheless, high levels of injury (exit hole ratings of 2–3) were not observed on *Q. engelmannii* at ICA sites. The complete survey of the Japatul Valley site was a direct comparison of *Q. agrifolia* and *Q. engelmannii* growing in close juxtaposition to one another. Although the rate of infestation of *Q. agrifolia* was estimated conservatively at about 66%, none of the *Q. engelmannii*, which were all located in close proximity to infested *Q. agrifolia* showed evidence of colonization by *A. auroguttatus*. This site likely would have had an even higher estimated rate of infestation if the dead and removed *Q. agrifolia* had been accounted for in the survey. Thus, *Q. engelmannii* is not believed to be at significant risk for injury by *A. auroguttatus*. Although *A. auroguttatus* injury was not observed on dead *Q. engelmannii* in this study, injury from this insect (e.g., D-shaped emergence holes and larval galleries on the xylem surface) has been observed elsewhere in San Diego Co. on dead trees of this species (Coleman, unpublished data).

The rates of injury (48%) and proportion of dead individuals with *A. auroguttatus* injury (60%) in *Q. chrysolepis* were relatively high in this survey. At ICA sites, *A. auroguttatus* showed less preference for this intermediate oak species than the sympatric red oak species, which may be due to phloem chemistry, bark thickness, and/or the smaller size of the trees surveyed in ICA sites. Low densities of *Q. chrysolepis* were represented within the ICA sites, but in CA this species is a larger component of forest stands in the Palomar and Transverse Mountain Ranges (UCA sites), which may be invaded in the near future.

4.2.3. Stand-level effects on oaks by *A. auroguttatus* and *A. coxalis*

Total dead oak basal area killed by all causes was greatest in AZ and ICA sites. The basal area of dead oak at MX sites may have been underestimated by the removal of dead trees for fuel wood. Density of all dead oaks was greatest in AZ sites and attributed primarily to dead *Q. emoryi*, but dead trees of this species were not frequently associated with *A. auroguttatus* injury. Injury from *A. auroguttatus* in AZ was recorded from 21% of the dead oaks and limited to *Q. emoryi* and *Q. hypoleucoides*. Thus, in AZ, *A. auroguttatus* is not always playing a role in oak mortality. It is likely a secondary contributor coupled with several long- and short-term and inciting factors (Manion, 1981). Additional studies should examine the decline complex related to injury from *A. auroguttatus* in areas where this insect is native.

Dead oak basal area and stem density, each with evidence of previous *A. auroguttatus* injury, were highest in ICA sites and currently represent 13% of the oak component in these woodlands. The highest level of oak mortality observed in ICA sites was 48% and included predominantly larger diameter *Q. agrifolia* and *Q. kelloggii*. In ICA sites, 87% of the dead oaks surveyed were found with previous injury symptoms from *A. auroguttatus* and those oaks found without injury were mostly old snags that likely had died before the arrival of the new pest. Although it is a native buprestid pest of oaks, similar proportions of dead oaks with symptoms of injury by *A. biguttatus* (70%) have been reported in The Netherlands during periods of high levels of tree mortality (Moraal and Hilszczański, 2000).

A greater density of dead *Q. chrysolepis* was found in denser mixed conifer stands in UCA sites than in ICA sites, and this appears to explain the higher levels of overall tree mortality in the uninfested areas (1.50 + 0.56 trees/ha). The absence of *Q. chrysolepis*-dominated stands found in the ICA sites (Appendix I) could explain the variance between these sites.

A. auroguttatus was not found in oaks in understory plots in AZ and ICA sites. In California, *A. auroguttatus* does not appear as an immediate threat to smaller diameter oaks (<15 cm) (see above). However, *A. coxalis* was discovered infesting understory *Q. peduncularis* and *Q. conzatti* at sites in MX. Although four individual trees were found infested with *A. coxalis*, preference for smaller diameter hosts may reflect an additional behavioral difference between *A. auroguttatus* and *A. coxalis*.

Additional monitoring is required in our plot network in southern California to follow the potential downward progression of *A. auroguttatus*-related health symptoms of oak. Of particular interest will be the time that it takes for trees to reach various states of decline and eventually die from the feeding activity of the beetle larvae. *Q. agrifolia* is often observed with callus tissue in the phloem and it is not known if oaks can withstand low levels of injury, which was frequently observed in ICA sites (34% of oaks with an emergence hole rating of 1), or if fast growing callus tissue can engulf early instar larvae as has been observed with other *Agrilus* spp. (Solomon, 1995; Katovich et al., 2000; Vansteenkiste et al., 2004).

4.3. Aerial surveys: mortality of oaks in San Diego Co.

The area with elevated levels of oak mortality associated with *A. auroguttatus* continues to expand in southern San Diego Co. Since the arrival of the beetle, the mean distance of oak mortality has spread 49.7 km from the predicted initial focus of infestation (near Guatay and Pine Valley, California). Nearly a decade (∼9 yr) may have been required before an incipient founder population could increase to densities to cause noticeably high-levels of injury and elevated levels of oak mortality (48% tree mortality) in the most severely affected forest stands. This relatively slow initial pattern may be explained by the Allee Effect (Taylor and Hastings, 2005), which has characterized the dynamics of the invasion of other exotic forest pests, such as the gypsy moth, *Lymantria dispar* (L.) (Lepdioptera: Lymantriidae) in the eastern USA (Tobin et al., 2007). Active monitoring via ground surveys and adult flight trapping can assist land managers with early detection of infestations and potentially with preservation of high-value sites before *A. auroguttatus* populations reach high-densities and increased tree injury and mortality occurs.

Aerially detected oak mortality from *A. auroguttatus* has fluctuated since 2002, but the level of tree mortality peaked in 2004 and 2007 following two periods of drought. We have ground-checked the San Diego Co. aerial survey data since 2009 and feel confident that it largely reflects the activity of *A. auroguttatus* on the dying oaks. The correspondence of two bouts of elevated oak mortality following two periods of drought suggests that additional stress from drought may have enhanced susceptibility to injury and inflated the levels of oak mortality during this period. This phenomenon has been reported with other *Agrilus* spp. (Katovich et al., 2000; Muzika et al., 2000). Drought stress in southern California may have also allowed the population to establish and proliferate in the early 2000's (Crooks and Soulé, 1999). However, Coleman et al. (2011) found that newly infested and uninfested *Q. agrifolia* at sites in the ICA did not show elevated levels of water stress. Indeed, *A. auroguttatus* was found aggressively attacking vigorous trees, but repeated injury by the larval feeding appeared to elevate water stress in trees with advanced symptoms (Coleman et al., 2011). Thus, it appears that drought stress is not necessary for successful colonization and ultimate mortality of oaks caused by *A. auroguttatus*, but drought may accelerate a decline in tree health by reducing host resistance against beetle attack. In the future, defoliation from California oakworm, *Phryganidia californica* Packard, western tussock moth, *Orgyia vetusta* Boisduval, and fruittree leafroller, *Archips argyrospila* (Walker); infection by *P. ramorum* and *Armillaria* sp.; late frosts; and wildfire injury may further interact with *A. auroguttatus* throughout California to act as long- and short-term and inciting factors, typical of oak decline complexes (Manion, 1981).

5. Conclusion

Lovett et al. (2006) proposed that the impact from an invasive species can be predicted by evaluating the mode of action, host specificity, and virulence of a pest and the importance, uniqueness, and phytosociology of a host species. In California, *A. auroguttatus* is a stem-feeding insect (Mattson et al., 1988) that can cause extensive and fatal injury to several oak species with the greatest impact on larger diameter red oaks. The virulence of this new pest is still being examined, but oak mortality continues in areas that have experienced long-term exposure to this pest. Mortality of these large trees is a process that typically may occur over several years and some host resistance (e.g., formation of callus tissue) (Coleman and Seybold, 2008) and natural enemy activity (Coleman et al., 2012) have been noted in southern California that (along with non-drought periods) could perhaps moderate tree mortality in the future. *Q. agrifolia* is found in pure stands in the foothills and coastal areas of California and Baja California Sur, Mexico, whereas *Q. kelloggii* is a co-dominant species in higher elevation mixed conifer stands throughout California. These red oaks provide unique benefits to wildlife in these ecosystems by providing a large seed crop and suitable habitat for numerous species (McShea et al., 2007). The potential short- and long-term impacts to California oak woodlands from *A. auroguttatus* are likely to be highly detrimental.

No restrictions are currently in place for limiting the movement of oak firewood from San Diego Co. Most of the distribution of *A. auroguttatus* within San Diego Co. can be explained by natural dispersal, but a satellite infestation in Marion Bear Memorial Park (La Jolla, northeast of urban San Diego, and 64 km from the predicted outbreak origin) may represent an isolated introduction via infested firewood (Fig. 4), and could be a harbinger of future satellite infestations outside of San Diego Co. (Coleman and Seybold, 2011). The La Jolla infestation was first detected in 2009 and lies beyond the mean distance for all years of oak mortality mapped (Coleman and Seybold, 2011). Furthermore, the infested stand of *Q. agrifolia* is non-contiguous with the backcountry forests and further isolated by urban development making natural spread unlikely. A second focus of intense oak infestation has been identified at William Heise County Park on the northern edge of the zone of infestation; this site is also thought to have been derived from intra county movement of infested firewood. Without more public education about the potential impacts associated with moving firewood infested with exotic insects, the preference for burning and economic return for selling oak firewood, and no restrictions for transporting oak firewood from San Diego Co., additional satellite outbreaks will likely occur and exacerbate the impact of this pest.

A. auroguttatus has established itself as a significant threat that may impact the oak forests in the Coastal, Transverse, and Sierra Nevada Mountain Ranges of California. Furthermore, intracontinental invasion by other oak-infesting *Agrilus* spp. into California, especially *A. coxalis* from Mexico or *A. bilineatus* from the eastern USA, should be regarded as threats to forest health with the potential to cause significant damage. The threat to the eastern USA from *A. auroguttatus* is difficult to predict because of the potential competitive interaction of the invader with other native stem-infesting *Agrilus* spp., potential host tree resistance, and a potentially diverse natural enemy complex. Nonetheless, firewood movement from the infested areas in California must be addressed to limit future introductions of this pest within California or beyond its borders.

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Appendix I. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.03.011.

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