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RESEARCH PAPER

Hardwood injury and mortality associated with two shot hole borers, *Euwallacea* spp., in the invaded region of southern California, USA, and the native region of Southeast Asia

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Abstract

• ***Key message*** **We assessed the impact of the polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus* (Schedl), and Kuroshio shot hole borer (KSHB), *E. kuroshio* Gomez and Hulcr, on hardwood trees in southern California, southwestern China, and northwestern Vietnam. The highest levels of mortality were recorded from 10 of 39 tree species in the survey, and these were primarily native tree species.**

• ***Context*** Two invasive shot hole borers represent relatively recent introductions in southern California, USA, and continue to spread and cause injury and mortality to several native and ornamental tree species. They originate from Southeast Asia.

• ***Aims*** Knowledge of tree species susceptibility to these wood-boring beetles is essential to inform better pest management and to evaluate future risk for urban and wildland forests.

• ***Methods*** From 2012 to 2016, ground surveys were conducted in the invaded and native regions at PSHB/KSHB-infested and PSHB/KSHB-uninfested sites to record levels of tree injury and mortality on native and ornamental tree species.

• ***Results*** In California, several native species of maple, *Acer*, willow, *Salix*, and sycamore, *Platanus*, were infested by either PSHB or KSHB at high rates (> 70%), and comparative rate of infestation by KSHB in all trees and in native trees surpased that by PSHB, whereas rate of infestation by PSHB in ornamental trees surpassed that by KSHB. Mortality of two maple species caused by PSHB exceeded 20%, whereas background mortality rate of hardwoods was 2% in uninfested areas.

• ***Conclusion*** These data should inform land managers about the tree species at most risk to injury and mortality, facilitate detection ground surveys, and direct prophylactic treatments for these invasive woodborers.

Keywords Ambrosia beetles · Hardwood tree mortality · Impact assessment · Invasive species

This article is part of the topical collection on *Entomological issues during forest diebacks*

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Contributions of the co-authors: T. Coleman: designed and led the study, and collected, consolidated, and summarized the field data.
Y. Chen: contributed to field work and performed statistical analyses.
A. Poloni and S. Seybold: contributed to field work in California.
R. Rabaglia: provided insect taxonomic support.
R. Rabaglia, G. Man, J. Sun, Q. Li, and P. Q. Thu: contributed to field work in China and Vietnam.
R. Rabaglia, G. Man, J. Sun, and P. Q. Thu: coordinated work in China and Vietnam.
T. Coleman, A. Poloni, and S. Seybold: wrote the manuscript.
All authors contributed to writing or revising the manuscript approved for the publication.

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1 Introduction

Invasive insects have caused widespread ecological and economic damage to North American forests (Wallner 1996; Mayfield et al. 2019). However, short-term ecological impacts, including intensity and speed of tree dieback and mortality, reduced populations of susceptible hosts, and loss of prominent canopy or keystone species, often highlight the impact of invasive species; gain the attention of the public; and demand and direct integrated pest management responses (Rizzo and Garbelotto 2003; Tisserat et al. 2009; Herms and McCullough 2014; Barnes et al. 2018). There has been a long history of establishment of invasive forest insects and diseases in the USA, primarily in the northeastern region of the country (Liebhold et al. 2013). Yet, the Pacific Coast region of the USA, specifically California, has also had a considerable number of introductions of invasive species that damage trees (Lee et al. 2007; Seybold et al. 2016, 2019a, b).

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Two invasive ambrosia beetles, *Euwallacea* spp. Hopkins (Coleoptera: Scolytinae) (or (Coleoptera: Scolytidae) (Bright 2014; Bright 2019)), were first linked to tree injury and mortality in the early 2010s in southern California (Umeda et al. 2016). The polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus* (Schedl) (previously referred to as *Euwallacea* nr. *fornicatus* sp. No. 1 Eichhoff; O'Donnell et al. 2015), was first collected in 2003 in the region (Rabaglia et al. 2006; Seybold et al. 2016; Gomez et al. 2018b) but gained considerable attention when injury symptoms were first detected in 2012 on ornamental avocado trees, *Persea americana* Mill., in Los Angeles County (Eskalen et al. 2012). PSHB in California was identified initially as the tea shot hole borer (TSHB), *Euwallacea fornicatus* (Eichhoff) (previously referred to as *Euwallacea fornicatus* sp. No. 2; O'Donnell et al. 2015), because of their morphological similarity (Eskalen et al. 2013; Chen et al. 2017). However, DNA sequences from mitochondrial cytochrome oxidase *c* subunit 1 (COI) and cuticular hydrocarbon profiles support the status of PSHB and TSHB as separate taxa (O'Donnell et al. 2015; Chen et al. 2017; Stouthamer et al. 2017). Stouthamer et al. (2017) reported that the native range of PSHB may encompass Northern Thailand, Vietnam, China, Taiwan, and Okinawa.

Three symbiotic fungi, *Fusarium euwallaceae* S. Freeman, Z. Mendel, T. Aoki & O'Donnell; *Graphium euwallaceae* Lynch et al.; and *Paracremonium pembeum* Lynch et al. have been isolated from the mycangia of PSHB and from infected wood (Eskalen et al. 2013; Lynch et al. 2016). Among these fungal species, *Fusarium euwallaceae* was recovered at higher frequencies from the mycangia of PSHB and was the most prominent fungus found in the xylem of attacked trees (Cooperband et al. 2016; Lynch et al. 2016). Eskalen et al. (2012) referred to tree injury associated with PSHB and this fungus as "Fusarium dieback."

Kuroshio shot hole borer (KSHB), *E. kuroshio* Gomez and Hulcr (previously referred to as *Euwallacea* nr. *fornicatus* sp. No. 5; O'Donnell et al. 2015, Gomez et al. 2018b), is a second exotic ambrosia beetle that was first detected in 2013 in urban forests of San Diego County (Chen et al. 2017; Stouthamer et al. 2017). KSHB is similar morphologically to PSHB and TSHB but differs in cuticular hydrocarbon phenotype (Chen et al. 2017) and in DNA sequence from the COI region (Stouthamer et al. 2017); it also carries novel *Fusarium* sp. and *Graphium* sp. symbionts (O'Donnell et al. 2015). KSHB populations in California are similar to populations in Taiwan and Okinawa, suggesting a possible origin for this species (Stouthamer et al. 2017).

Early collection records of TSHB originate from Southeast Asia where it has been associated with numerous economically important host species (Danthanarayana 1968; Wang and Yuan 2003; Kumar et al. 2011; Li et al. 2016; Gomez et al. 2019). However, there are limited host impact data associated with these, and other previous, host records. Tea shot hole borer has been introduced to several regions of the world, including Oceania, North and Central America, Africa, and Hawaii (Rabaglia et al. 2006; Mendel et al. 2012; CABI 2018; Paap et al. 2018). An *Euwallacea* sp. was recovered from an empty shipping container in Australia, further supporting the proclivity for spread of species in this genus (Stanaway et al. 2001). Danthanarayana (1968) provided an extensive list of 99 tree species in 36 families injured by TSHB in Southeast Asia, but TSHB is capable of reproducing in only 21 species.

Haack (2006) reported that in 2004 R.L. Penrose found *E. fornicatus* (i.e., PSHB) attacking species of maple, *Acer* L., alder, *Alnus* Mill., sycamore, *Platanus* L., and black locust *Robinia* L. in Los Angeles County. Since this initial survey, PSHB has been recorded in southern California from hundreds of tree species, and *F. euwallaceae* has been isolated from more than 100 tree species, but the beetle only reproduces in approximately 40 native, ornamental, and agriculturally important hardwood species (Eskalen et al. 2013; Boland 2016; Cooperband et al. 2016; UC Riverside 2018b). The discrepancy between the capacity to injure and the capacity to reproduce was also foretold with TSHB in Southeast Asia by Danthanarayana (1968). Host preference and susceptibility are still undefined and needed for developing integrated pest management options for these two invasive species.

PSHB and KSHB likely complete several generations a year in southern California (Cooperband et al. 2016; Chen et al. unpublished data). PSHB reproduce via arrhenotokous haplodiploidy (defined as the development of unfertilized haploid eggs into males and fertilized diploid eggs into females) and mate with siblings, which produces a collection of progeny that is female-biased and already mated by the time the new adult females emerge from a tree (Cooperband et al. 2016; Dodge et al. 2017). Newly emerged females have been observed to re-attack the same tree if the host is still a suitable substrate for the symbiotic fungi (TWC, unpublished data).

External injury symptoms associated with PSHB and KSHB entrance holes (attacks) can be observed primarily along the main stem and larger branches of trees and can also occur on exposed roots and from the root collar to the small diameter (< 2.5 cm) branches. Adult entrance holes are round and about 0.85 mm in diameter, and fine white boring dust emanates from the holes as tightly packed cylindrical columns, likely a result of the beetles usually attacking vigorous trees with moist xylem, or frass can be found at the base of trees (Coleman et al. 2013a). Depending on the tree species attacked, PSHB and KSHB injury symptoms can be identified either by wet discoloration, gumming, or sugary exudate near adult entrance holes on the outer bark of trees (Coleman et al. 2013a). High levels of PSHB/KSHB attacks on a tree can cause severe branch and crown dieback; epicormic growth along the stem and at the base of the tree; stem or branch failure; and eventual tree death (Coleman et al. 2013a).

PSHB and KSHB have caused injury and/or mortality to thousands of trees in southern California (CFPC 2015), mostly ornamental species in urban forests and native tree species in adjacent riparian forests located in the wildland-urban interface. However, the level of injury and risk to tree species from these invasive shot hole borers to ornamental and native tree species of southern California and elsewhere in the USA, are largely unquantified. Boland (2016) provided a thorough overview of KSHB attacks in one riparian corridor in San Diego County, but the tree injury and mortality data were not analyzed statistically and similar areas impacted by PSHB have not been assessed.

The absence of host preference, tree injury, and mortality data from invaded and native areas presents an obstacle to developing an integrated pest management program against these insect-disease complexes and assessing the risk of these complexes for other regions (Venette et al. 2010). The objective of this study was to assess the impact of PSHB and KSHB to ornamental and native tree species in southern California and in PSHB's native region of China and Vietnam (Stouthamer et al. 2017; Smith et al. 2018). This information can assist with developing and focusing management actions on the most susceptible trees, reducing unwarranted treatments, and developing risk models.

2 Materials and methods

2.1 Survey locations

From May 2012 to April 2016, tree surveys were conducted to assess the impact (i.e., presence/absence and levels of infestation, tree injury, and tree mortality) from PSHB and KSHB in southern California forests. The impact of PSHB was assessed at 18 sites in urban and native forests in four infested counties (Los Angeles, Orange, Riverside, and San Bernardino). The impact of KSHB was assessed at three sites in urban and native forests in San Diego County. Each site included multiple survey plots (Fig. 1a). From 10 to 26 April 2015, surveys were also conducted to assess tree injury associated with PSHB in southwestern China and northwestern Vietnam to document impact of this beetle in its native region. Four infested sites were surveyed in southwestern China and five in northwestern Vietnam (Fig. 1b). Infested stands were identified from recorded distributional data (UC Riverside 2018a); through collection of *Euwallacea* spp. adults from infested trees; from trap captures on white elm bark beetle sticky panel traps (Synergy Semiochemicals, Delta, British Columbia, Canada, Product No. 4019); and through local knowledge by our coauthors.

Urban trees were surveyed along city streets, in neighborhoods, and in city and county parks, whereas trees in native forests were located mostly adjacent to or in riparian areas at the wildland-urban interface. These infested native stands were localized primarily at lower elevations and adjacent to infested urban areas. Native PSHB-infested forest sites were not only located principally on the Los Angeles Ranger District of the Angeles National Forest but also occurred in city, county, and wilderness parks and recreation areas. Across all sites, trees were chosen arbitrarily for assessments due to the diverse tree arrangements encountered (e.g., intensively managed parks, street trees, and dense forested areas immediately adjacent to creeks), but at least 50 trees were surveyed at a plot. Surveys encompassed all tree species in the area regardless of injury condition, and at least ten trees of a species were observed if available. Tree species could not be represented proportionately mostly due to the wide diversity of ornamental plantings found across the urban sites. Both ornamental and native tree species were found in the urban areas, whereas only a few ornamental or invasive plant species were found in the native areas. Latitude and longitude coordinates were recorded at all survey sites. Avocado groves maintained by California State Polytechnic University, Pomona were surveyed for PSHB injury in Los Angeles County as PSHB had spread to the university campus. Sites that were beyond the leading edge of spread of *Euwallacea* or had apparently escaped invasion (=uninfested sites) were surveyed to provide a baseline level of tree injury and mortality from other abiotic and biotic issues. These uninfested urban and native stands were located in Riverside, San Bernardino, and San Diego Counties. and on the San Gabriel Ranger District, Angeles National Forest and Front Country Ranger District, San Bernardino National Forest.

In southwestern China (Kunming, Yunnan Province), four urban sites were surveyed. They included the Southwestern Forestry University campus, Yunnan University, CuiHu Park, and Kunming city streets (Table 1). In northwestern Vietnam, six black wattle, *Acacia mangium* Willd., plantations at four sites with previously known PSHB-caused injury were assessed (Table 1). These plantations ranged from 3 to 7 years old; black wattle plantations are harvested in year seven. Although PSHB is likely native to these regions, mostly introduced ornamental and wood production species were surveyed in both countries, resulting in the documentation of novel host interactions for PSHB. At some of the urban sites, all trees were surveyed due to the limited number of trees available at a site.

2.2 Data collection

We recorded data from all trees surveyed, including tree genus or species; diameter at breast height (DBH (in cm at 1.37 m)); tree status (living or dead); PSHB/KSHB infestation (yes or no); degree of crown thinning and dieback (ratings of 1: healthy, no apparent leaf or branch dieback; 2: minor twig dieback (10–25% leaf loss); 3: moderate branch dieback

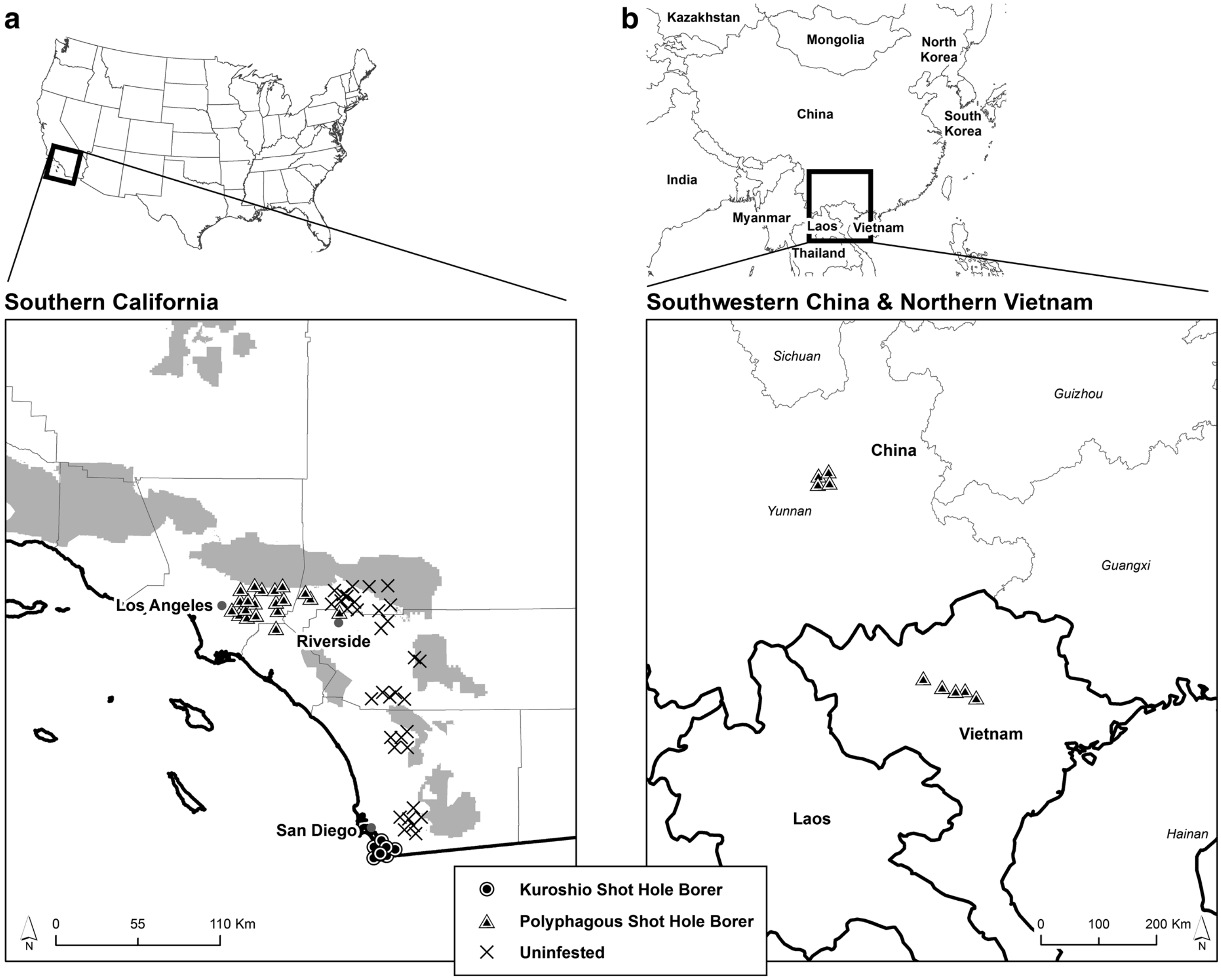

Fig. 1 Locations of surveys to assess the impact of two *Euwallacea* spp. ambrosia beetles on native and ornamental hardwood trees in southern California (**a**) and southwestern China and north Vietnam (**b**). Shaded areas represent national forest land in southern California

Table 1 Locations of polyphagous shot hole borer (PSHB)-infested, *Euwallacea whitfordiodendrus*, and Kuroshio shot hole borer (KSHB)-infested, *E. kuroshio*, sites surveyed to assess impact

Country	Species surveyed	State/province	County/city
USA	PSHB	California	Los Angeles
	PSHB		Orange
	PSHB		Riverside
	PSHB		San Bernardino
	KSHB		San Diego
China	PSHB	Yunnan	Kunming
Vietnam	PSHB	Lao Cai	Nam Tha
	PSHB	Tuyen Quang	Doi Can
	PSHB	Yen Bai	Mau A
	PSHB		Tan Houng

(26–50% leaf loss); 4: severe branch dieback (> 50% leaf loss); and 5: dead, no living crown); density of PSHB/KSHB injury along the main stem (0: no injury; 1: minor injury (1–10 attacks); 2: moderate injury (11–30 attacks); and 3: severe injury (> 30 attacks)); and other insect injury for infested and uninfested trees. The level of stem injury on moderately to severely injured and dead trees was quantified by recording the density of PSHB entrance holes in all three countries involved in the study. In California, entrance hole density was recorded within a 232-cm^2 area at breast height (1.37 m) and at 0.3 m above the root collar. In southwestern China and northwestern Vietnam, entrance hole density measurements were only recorded at breast height because of time constraints. Measurements were taken on the north side of the tree to standardize our procedure, or were taken on the closest accessible area that was free of branches. Tree species, status, and DBH were noted for all trees with entrance hole density measurements. Crown ratings were not recorded for some tree species in the KSHB-infested sites in southern California because surveys were conducted during the winter season when leaves were absent, but all infested tree species were observed again during the growing season and rated for crown health. As a result, crown health ratings are available for each tree species surveyed. Variable radius prism plots (10 basal area factor) and fixed radius plots (0.04 ha) were established in black wattle plantations in northwestern Vietnam to characterize current forest stand conditions, including tree species present and tree status.

2.3 Statistical analyses

All statistical analyses were conducted in R (R Core Team 2016). A critical level of $\alpha = 0.05$ was used for all analyses unless otherwise noted. The Kolmogorov-Smirnov test (R package "nortest") and Levene's test (R package "car") were used to test normality and homogeneity of variances, respectively, where necessary. Proportion tests (R package "base") were used for many comparisons, and the null hypothesis was equal percentages among groups (e.g., 50%:50% if comparisons were between two groups and 25%:25%:25%:25% if comparisons were among four groups). When analyzing proportion of infestation among tree species, only species with greater than five trees surveyed were included to meet the accuracy requirement of greater than 5 in each cell. Tree species only surveyed five times or greater were included in all analyses (see Table 2), but all data were presented to show potential trends.

For trees at infested sites in California, infestation rates between PSHB and KSHB and between ornamental and native trees were analyzed by proportion tests. Assessments between ornamental and native trees were analyzed to compare the potential impact in native and ornamental forested areas. Crown ratings between the PSHB- and KSHB-infested sites were compared by proportion tests, separately for each rating (from "1" to "5"). Stem injury ratings between the PSHB- and KSHB-infested sites were also compared by proportion tests, separately for each rating (from "0" to "3"). For tree species that occurred in both the PSHB- and KSHB-infested sites, comparison of infestation rates between PSHB and KSHB was conducted by a proportion test, separately for each species. No comparisons were made for tree species that occurred uniquely in either a PSHB- or KSHB-infested site.

For trees in the PSHB- and KSHB-infested sites, the following analyses were conducted separately for the PSHB- and KSHB-infested sites. Infestation rate was analyzed by a proportion test (i.e., if the rate deviated from 50%). Infestation status (i.e., infested or uninfested) and mortality by tree types (i.e., native or ornamental) were analyzed by proportion tests. DBH by infestation (i.e., infested or uninfested), DBH by tree status (i.e., live or dead), DBH by tree types (i.e., native or ornamental), DBH by tree species, and DBH by stem injury rating were either analyzed by Wilcoxon-Mann-Whitney tests if there were two groups or by Kruskal-Wallis rank sum tests if there were more than two groups. Differences in percentages of trees among various crown ratings or stem injury ratings were analyzed by proportion tests. Crown ratings or stem injury ratings among tree species were analyzed by Kruskal-Wallis rank sum tests. Entrance hole density (number of holes/232 cm^2 on the bark surface at 1.37 and 0.3 m) between two heights and between tree types (i.e., ornamental or native) was analyzed by Wilcoxon-Mann-Whitney tests and among tree species was analyzed by Kruskal-Wallis rank sum tests. Density of entrance holes was not different between the height measurements for the southern California data, so data were pooled when analyzing effects of tree types and tree species on density.

For data collected in southwestern China, difference in DBH between tree species and differences in colonization density between tree species were analyzed by Kruskal-Wallis rank sum tests. Difference in DBH between infested and uninfested trees was analyzed by a Wilcoxon-Mann-Whitney test.

For data collected in northwestern Vietnam, difference of DBH between infested and uninfested trees was analyzed by a Wilcoxon-Mann-Whitney test. Difference in percentage of trees in various stem injury classes was analyzed by a proportion test.

3 Results

3.1 Southern California

A total of 5644 trees representing 39 tree species were surveyed in the PSHB/KSHB-infested and PSHB/KSHB-uninfested stands in southern California (Table 2). Of the 4535 trees from the PSHB sites, 2052 and 2483 were from the PSHB-uninfested and PSHB-infested sites, respectively. Of the 1109 trees from the KSHB sites, 519 and 590 were from the KSHB-uninfested and KSHB-infested sites, respectively. Mean DBH of all surveyed trees was 21.1 cm (± 0.28). All the following comparisons were made within the infested sites only unless otherwise noted.

Rate of infestation by KSHB was significantly higher than rate of infestation by PSHB across all species (Table 3 (Infestation)). Rate of infestation by PSHB in ornamental trees was significantly higher than KSHB in ornamental trees (Table 3 (Infestation)). Rate of infestation by KSHB in native trees was significantly higher than PSHB in native trees (Table 3 (Infestation)).

Most trees in the survey had healthy crowns (crown rating of "1") (Fig. 2), a significantly lower proportion of trees in the KSHB sites had healthy crowns when compared with trees at

Table 2 Impact of polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus*, and Kuroshio shot hole borer (KSHB), *E. kuroshio*, assessed as rates of infestation, stem injury, and tree mortality of tree species surveyed in southern California, USA (A), southwestern China (B), and northwestern Vietnam (C)

Region	Tree species	Injury agent	n^a	DBH (± s.e.) (cm)	Infestation rate (%)	Stem injury rating (%)				Tree mortality (%)
						0	1	2	3	
A	Tree of heaven, *Ailanthus altissima* (Mill.) Swingle[b]	PSHB	4	12.0 (± 0.81)	100	0.00	0.00	0.00	100	50.0
	Boxelder maple, *Acer negundo* L.	PSHB	187	12.9 (± .026)	92.5	7.49	5.35	5.35	81.8	26.7
	Castorbean, *Ricinus communis* L.	PSHB	34	7.05 (± 0.46)	71.4	28.6	10.7	3.57	57.1	21.4
	Bigleaf maple, *Acer macrophyllum* Pursh	PSHB	63	24.0 (± 0.87)	73.0	27.0	22.2	4.76	46.0	20.6
	Arroyo willow, *Salix lasiolepis* Benth.	PSHB	84	20.4 (± 0.36)	83.3	16.7	66.7	8.33	8.33	16.7
	Red willow, *Salix laevigata* Benth.	PSHB	335	13.1 (± 0.24)	80.1	19.8	17.2	16.6	46.4	15.9
	Gooding's black willow, *Salix gooddingii* C.R. Ball	PSHB	104	19.6 (± 0.36)	77.3	22.7	47.0	10.6	19.7	7.58
	Fremont cottonwood, *Populus fremontii* S. Watson	PSHB	329	27.7 (± 0.36)	56.2	43.8	42.7	3.37	10.1	5.62
	London plane, *Platanus* x *acerifolia* (Alton) Willd.	PSHB	361	33.0 (± 0.33)	84.8	15.2	52.1	14.7	14.1	5.54
	California bay laurel, *Umbellaria californica* (Hook. & Am.) Nutt.	PSHB	29	15.1 (± 0.75)	10.3	89.7	10.3	0.00	0.00	3.45
	Western sycamore, *Platanus racemosa* Nutt.	PSHB	1135	34.0 (± 0.23)	80.0	20.2	35.8	18.1	25.9	2.59
	White alder, *Alnus rhombifolia* Nutt.	PSHB	378	28.2 (± 0.35)	41.7	58.3	29.2	5.95	6.55	0.60
	Avocado, *Persea americana* Mill.	PSHB	128	25.6 (± 0.66)	91.4	66.7	84.4	7.03	0.00	0.00
	American sycamore, *Platanus occidentalis* L.	PSHB	6	43.2 (± 2.99)	50.0	16.7	16.7	16.7	0.00	0.00
	Engelmann oak, *Quercus engelmannii* Greene[b]	PSHB	2	49.4 (± 8.85)	50.0	50.0	0.00	0.00	50.0	0.00
	Hickory, *Carya* spp. Nutt.	PSHB	11	15.7 (± 0.78)	45.5	54.6	36.4	9.09	0.00	0.00
	Lombardy poplar, *Populus nigra 'Italica'* L.	PSHB	10	1.14 (± 0.35)	40.0	60.0	40.0	0.00	0.00	0.00
	Blue elderberry, *Sambucus mexicana* C. Presl ex DC.	PSHB	36	18.9 (± 0.97)	36.7	63.3	36.7	0.00	0.00	0.00
	Velvet ash, *Fraxinus velutina* Torr.	PSHB	54	19.4 (± 0.70)	28.6	71.4	26.2	2.38	0.00	0.00
	American sweetgum, *Liquidambar styraciflua* L.	PSHB	51	30.5 (± 0.40)	25.5	74.5	19.6	3.92	1.96	0.00
	Southern California black walnut, *Juglans californica* S. Wats.	PSHB	43	20.2 (± 0.91)	23.5	76.5	20.6	0.00	2.94	0.00
	Evergreen ash, *Fraxinus uhdei* (Wenz.) Lingl.	PSHB	232	35.9 (± 0.69)	23.0	77.0	12.9	4.32	5.76	0.00
	Coast live oak, *Quercus agrifolia* Nee	PSHB	649	48.4 (± 0.39)	22.8	77.2	18.3	2.42	2.08	0.00
	Canyon live oak, *Quercus chrysolepis* Liebm.	PSHB	32	42.9 (± 1.66)	14.3	85.7	14.3	0.00	0.00	0.00
	Holly oak, *Quercus ilex* L.	PSHB	8	28.3 (± 2.35)	12.5	87.5	12.5	0.00	0.00	0.00
	White mulberry, *Morus alba* L.	PSHB	90	37.2 (± 0.84)	10.5	89.5	10.5	0.00	0.00	0.00
	Pepper tree, *Schinus molle* L.	PSHB	61	60.8 (± 1.70)	4.92	95.1	4.92	0.00	0.00	0.00
	Chinese elm, *Ulmus parvifolia* Jacq.	PSHB	49	33.8 (± 0.77)	0.00	100	0.00	0.00	0.00	0.00
	Live oak, *Quercus virginiana* Mill.[b]	PSHB	1	16.5	0.00	100	0.00	0.00	0.00	0.00
	Peach, *Prunus* sp. L.[b]	PSHB	3	6.52 (± 0.50)	0.00	100	0.00	0.00	0.00	0.00
	Silver maple, *Acer saccharinum* L.[b]	PSHB	3	54.1 (± 6.95)	0.00	100	0.00	0.00	0.00	0.00
	Southern magnolia, *Magnolia grandifolia* L.	PSHB	7	31.9 (± 0.48)	0.00	100	0.00	0.00	0.00	0.00
	California black oak, *Quercus kelloggii* Newb.[b]	PSHB	1	14.5	0.00	100	0.00	0.00	0.00	0.00
	Gum tree, *Eucalyptus* sp. L'Hér.	PSHB	5	23.3 (± 0.64)	0.00	100	0.00	0.00	0.00	0.00
	Narrowleaf willow, *Salix exigua* L.	PSHB	10	14.7 (± 0.13)	0.00	100	0.00	0.00	0.00	0.00
	Fremont cottonwood, *Populus fremontii* S. Watson	KSHB	91	18.9 (± 0.47)	46.2	53.9	13.6	9.62	23.1	9.62
	Gooding's black willow, *Salix gooddingii* C.R. Ball	KSHB	35	24.9 (± 0.60)	81.0	19.1	9.52	28.6	42.9	9.52
	Arroyo willow, *Salix lasiolepis* Benth.	KSHB	326	18.1 (± 0.16)	72.1	27.4	11.8	8.10	52.7	8.10
	London plane, *Platanus* x *acerifolia* (Alton) Willd.	KSHB	47	24.3 (± 0.66)	74.5	25.53	38.3	12.8	23.4	4.26
	Western sycamore, *Platanus racemosa* Nutt.	KSHB	230	21.4 (± 0.40)	78.9	22.8	14.0	19.3	43.9	3.51
	White alder, *Alnus rhombifolia* Nutt.[b]	KSHB	2	27.4 (± 1.20)	100	0.00	0.00	0.00	100	0.00
	Golden medallion, *Cassia leptophylla* Vogel	KSHB	20	15.8 (± 0.51)	95.0	5.00	10.0	5.00	80.0	0.00
	Castorbean, *Ricinus communis* L.	KSHB	7	11.9 (± 0.42)	60.0	40.0	0.00	0.00	60.0	0.00

Table 2 (continued)

Region	Tree species	Injury agent	n[a]	DBH (± s.e.) (cm)	Infestation rate (%)	Stem injury rating (%)				Tree mortality (%)
						0	1	2	3	
	Southern California black walnut, *Juglans californica* S. Wats.	KSHB	9	23.9 (± 0.77)	33.3	66.7	33.3	0.00	0.00	0.00
	Coast live oak, *Quercus agrifolia* Née	KSHB	67	43.6 (± 1.19)	33.3	66.7	33.3	0.00	0.00	0.00
	Southern magnolia, *Magnolia grandifolia* L.	KSHB	11	18.1 (± 0.55)	9.09	90.9	0.00	9.09	0.00	0.00
	African sumac, *Searsia lancea* (L.f.) F.A. Barkley	KSHB	18	22.9 (± 0.55)	0.00	100	0.00	0.00	0.00	0.00
	American sweetgum, *Liquidambar styraciflua* L.	KSHB	11	16.8 (± 0.70)	0.00	100	0.00	0.00	0.00	0.00
	Chinese wingnut, *Pterocarya stenoptera* C. DC.	KSHB	5	37.2 (± 6.80)	0.00	100	0.00	0.00	0.00	0.00
	Blue elderberry, *Sambucus mexicana* C. Presl ex DC.	KSHB	38	8.83 (± 0.29)	0.00	100	0.00	0.00	0.00	0.00
	Engelmann oak, *Quercus engelmannii* Greene	KSHB	5	29.1 (± 1.54)	0.00	100	0.00	0.00	0.00	0.00
	Gum tree, *Eucalyptus* spp. L'Hér.[b]	KSHB	2	23.6 (± 0.80)	0.00	100	0.00	0.00	0.00	0.00
	Evergreen ash, *Fraxinus uhdei* (Wenz.) Lingl.	KSHB	8	8.48 (± 0.80)	0.00	100	0.00	0.00	0.00	0.00
	Moreton bay fig, *Ficus macrophylla* Desf. ex Pers.[b]	KSHB	1	48.8	0.00	100	0.00	0.00	0.00	0.00
	Narrowleaf willow, *Salix exigua*. L.	KSHB	146	11.1 (± 0.18)	0.00	100	0.00	0.00	0.00	0.00
	Red willow, *Salix laevigata* Benth.	KSHB	30	9.32 (± 0.31)	0.00	100	0.00	0.00	0.00	0.00
B	*Wisteria* sp. Nutt.	PSHB	1	5.84	100	100	0.00	0.00	100	100
	Chinese banyan, *Ficus microcarpa* L.f.[b]	PSHB	2	13.2 (± 1.27)	100	0.00	0.00	0.00	100	0.00
	Trident maple, *Acer buergerianum* Miq.	PSHB	45	24.7 (± 1.58)	55.8	40.0	26.7	2.20	31.1	0.00
	Oriental plane, *Platanus orientalis* L.	PSHB	47	48.1 (± 2.08)	57.5	42.6	19.1	4.20	34.0	0.00
	Japanese maple, *Acer palmatum* Thunb.	PSHB	10	2.69 (± 0.46)	0.00	100	0.00	0.00	0.00	0.00
	Mulberry, *Morus* sp. L.[b]	PSHB	2	33.0 (± 6.86)	0.00	100	0.00	0.00	0.00	0.00
	Prunus sp. L.	PSHB	10	7.62 (± 0.04)	0.00	100	0.00	0.00	0.00	0.00
	Willow, *Salix* sp. L.	PSHB	37	32.0 (± 2.31)	0.00	100	0.00	0.00	0.00	0.00
	Chinese sweetgum, *Liquidambar formosana* L.	PSHB	14	17.9 (± 0.93)	0.00	100	0.00	0.00	0.00	0.00
C	Black wattle, *Acacia mangium* Willd.	PSHB	116	13.6 (± 0.23)	29.3	72.4	16.4	4.31	6.90	1.72

Tree species within a country (USA, southwestern China, northwestern Vietnam) and within an injury agent (PSHB or KSHB) were ranked and listed by mortality rate (%) and then by infestation rate (%)

[a] Total tree counts across all sites, including infested and uninfested areas

[b] Tree species surveyed less than five times were not included in the analyses

Table 3 Comparison of infestation rates across all tree species, crown and stem injury ratings, and infestation rates of individual tree species by two invasive ambrosia beetles, polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus*, and Kuroshio shot hole borer (KSHB), *E. kuroshio*, in southern California, USA. Only tree species occurring in survey plots for both PSHB and KSHB are included in this analysis

Parameter	Species		X_1^2	*P* value
Infestation	PSHB	KSHB		
Total	59.3% (1473/2483)	65.1% (384/590)	6.38	0.01
Native trees	60.4% (963/1594)	70.1% (326/465)	14.0	< 0.01
Ornamental trees	57.4% (510/889)	46.4% (58/125)	4.9	0.03
Crown rating				
1	61.3% (1523/2483)	53.3% (252/473)	10.4	< 0.001
2	17.7% (439/2483)	17.1% (81/473)	0.00	1
3	8.62% (214/2483)	19.5% (92/473)	49.1	< 0.001
4	5.44% (135/2483)	1.69% (8/473)	12.2	< 0.001
5	5.64% (140/2483)	7.82% (37/473)	2.99	0.08
Stem injury rating				
1	30.8% (764/2483)	13.2% (78/590)	72.9	< 0.001
2	8.74% (217/2483)	9.49% (56/590)	0.25	0.62
3	20.1% (498/2483)	41.9% (247/590)	122	< 0.001
Infestation by species				
American sweetgum, *Liquidambar styraciflua* L.	25.5% (13/51)	0% (0/10)	1.90	0.17
Evergreen ash, *Fraxinus uhdei* (Wenz.) Lingl.	23.0% (32/139)	0% (0/8)	1.20	0.27
Arroyo willow, *Salix lasiolepis* Benth.	83.3% (10/12)	72.1% (235/326)	0.25	0.62
Fremont cottonwood, *Populus fremontii* S. Watson	56.2% (50/89)	46.2% (24/52)	0.95	0.33
Gooding's black willow, *Salix gooddingii* C.R. Ball	77.3% (51/66)	81.0% (17/21)	0.003	0.96
Southern magnolia, *Magnolia grandifolia* L.	0.00% (0/7)	9.09% (1/11)	0.00	1.00
Western sycamore, *Platanus racemosa* Nutt.	80.0% (340/425)	79.0% (45/57)	0.00	1.00
Castorbean, *Ricinus communis* L.	71.4% (20/28)	60.0% (3/5)	0.00	1.00

the PSHB sites (Table 3 (Crown rating)). Crown dieback differed significantly between the PSHB and KSHB sites for all crown ratings except for a crown rating "2" (Table 3 (Crown rating)). Overall rate of tree mortality (crown rating of "5") caused by both KSHB and PSHB was low, and not different between the two species (Table 3 (Crown rating)). An additional 3 (0.63%) and 32 (1.29%) trees were found dead in the KSHB and PSHB sites, respectively, but with no injury from either ambrosia beetle species. Stem injury was significantly different between the PSHB-infested and KSHB-infested sites for minor (rating of "1") and severe stem injury (rating of "3") (Table 3 (Stem injury rating)). Stems were injured more severely at the KSHB-infested sites.

PSHB infested 25.5% of American sweetgum, *Liquidambar styraciflua* L., and 23.0% of evergreen ash, *Fraxinus uhdei* (Wenz.) Lingl., whereas KSHB did not infest either of the two tree species (Tables 2 and 3 (Infestation by species)). The differences in infestation between the two beetle species for American sweetgum, evergreen ash, arroyo willow, *Salix laevigata* Benth., Fremont cottonwood, *Populus fremontii* S. Watson, Gooding's black willow, *Salix gooddingii* C.R. Ball, southern magnolia, *Magnolia grandifolia* L., western sycamore, *Platanus racemosa* Nutt., and castorbean, *Ricinus communis* L., were not significant (Table 3 (Infestation by species)). Twenty tree species did not have KSHB injury but had varying levels of PSHB injury (Table 2). Golden medallion, *Cassia leptophylla* Vogel, was infested (95%, 19/20) by KSHB but was not surveyed in the PSHB-infested sites.

At the PSHB-infested sites, significantly more trees were infested than uninfested and the infestation rate on native trees did not differ from that on ornamental trees (Fig. 3a). Mortality of native trees was significantly greater than that of ornamental trees (Fig. 3a). DBH (mean (±s.e.)) of the PSHB-infested trees ranged from 0.25 to 122 cm but did not differ from that of the PSHB-uninfested trees (Fig. 3b). DBH of dead trees was smaller than that of living trees (Fig. 3b). DBH of the PSHB-infested ornamental trees was greater than that of the infested native trees (Fig. 3b). DBH of the infested trees differed among tree species ($X_{26}^2 = 586$; $P < 0.001$) and among stem injury ratings (no injury, 34.3 cm (± 21.6); minor, 30.4 cm (± 0.72); moderate, 34.7 cm (± 1.48), and severe, 27.1 cm (± 0.94)) ($X_3^2 = 36.4$; $P < 0.001$).

At the PSHB-infested sites, the percentages of crown ratings of all trees and PSHB-infested trees deviated from 20%

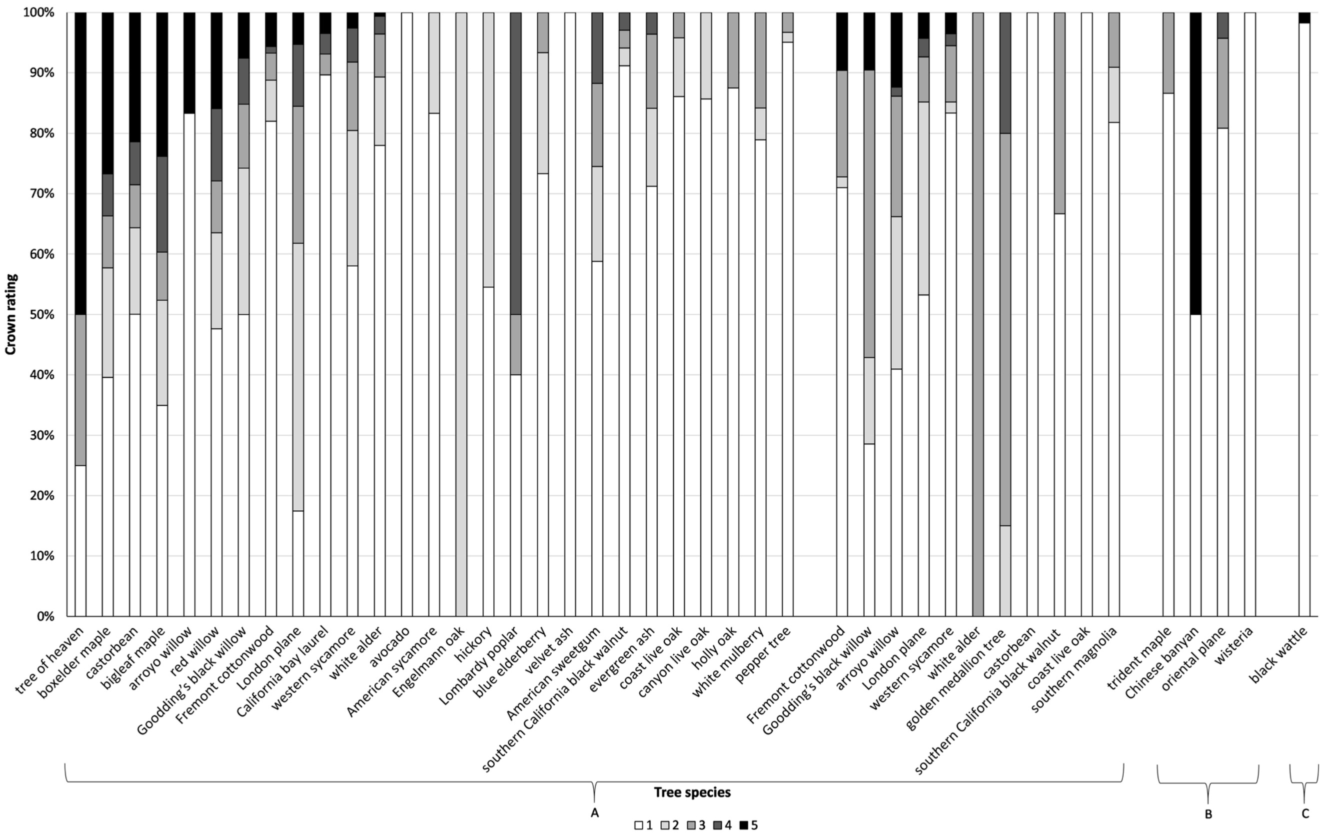

Fig. 2 Crown health ratings (%) for tree species that were infested by polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus*, and Kuroshio shot hole borer (KSHB), *E. kuroshio*, in southern California (**A**, PSHB first set of species and KSHB second set of species), southwestern China (**B**), and northwestern Vietnam (**C**). Degree of crown thinning and dieback were rated for individual trees on a scale of 1 to 5 (1: healthy, no apparent leaf or branch dieback; 2: minor twig dieback (10–25% leaf loss); 3: moderate branch dieback (26–50% leaf loss); 4: severe branch dieback (> 50% leaf loss); and 5: dead, no living crown). Scientific names for each tree species can be found in Table 2

(i.e., equal percentages for each crown category) ($X_4^2 = 2764$; $P < 0.001$ and $X_4^2 = 878$; $P < 0.001$, respectively). At these sites, the majority of all trees had healthy crowns (61.3%) followed by minor dieback (17.7%), moderate dieback (8.62%), severe dieback (5.44%), and dead trees (5.64%). Similarly, the majority of the PSHB-infested trees had healthy crowns, 47.7% (703/1473) followed by minor dieback, 23.8% (351/1473); moderate dieback, 11.6% (171/1473); severe dieback, 7.33% (108/1473); and dead trees, 9.50% (140/1473). Eleven tree species were killed by PSHB, including boxelder maple, *A. negundo* L., castorbean, bigleaf maple, *A. macrophyllum* Pursh, arroyo willow, red willow, *Salix laevigata* Bebb, Goodding's black willow, Fremont cottonwood, London plane, *Platanus x acerifolia* (Alton) Willd., California bay laurel, *Umbellaria californica* (Hook. & Am.) Nutt., western sycamore, and white alder, *Alnus rhombifolia* Nutt., (Table 2). Mortality rates for boxelder maple, castorbean, and bigleaf maple exceeded 20% (Fig. 4a).

At the PSHB-infested sites, no stem injury (40.4%) was most the frequent survey outcome followed by minor injury (30.8%), severe injury (20.1%), and moderate injury (8.74%); these percentages deviated from 25% ($X_3^2 = 556$; $P < 0.001$). Of the 1473 PSHB-infested trees, 51.5, 14.7, and 33.8% trees had a stem injury ratings of 1, 2, and 3, respectively; these percentages deviated from 33.3% ($X_2^2 = 880$; $P < 0.001$).

At the PSHB-infested sites, stem injury differed among tree species ($X_{105}^2 = 1617$; $P < 0.001$). PSHB severely injured boxelder maple, castorbean, bigleaf maple, arroyo willow, red willow, Goodding's black willow, Fremont cottonwood, London plane, California bay laurel, western sycamore, and white alder (Table 2). Branch and stem failure were observed on western sycamore and white alder following severe PSHB stem injury during the surveys (Fig. 4b). High levels (> 20%) of severe stem injury were recorded on boxelder maple, castorbean, bigleaf maple, red willow, and western sycamore by PSHB (Table 2).

At the KSHB-infested sites, significantly more trees were infested than uninfested, and the infestation rate on native trees was significantly greater than that on ornamental trees (Fig. 3a). The mortality rate of native trees did not differ from that of ornamental trees (Fig. 3a). DBH of KSHB-infested trees ranged from 2.79 to 53.6 cm, which was significantly greater than the DBH of KSHB-uninfested trees (Fig. 3b). DBH of trees killed by KSHB was smaller than that of living

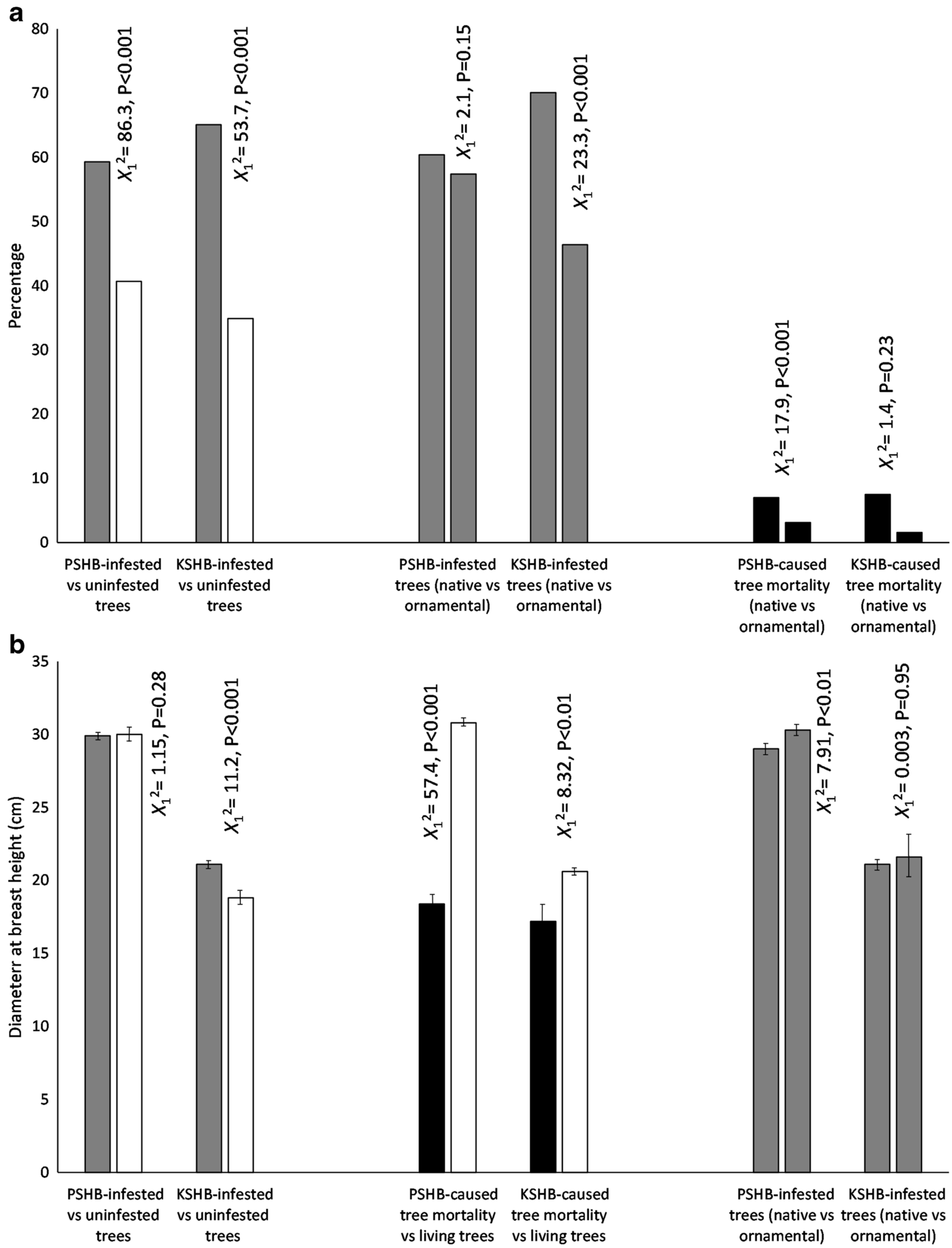

Fig. 3 Injury and mortality associated with polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus*, and Kuroshio shot hole borer (KSHB), *E. kuroshio*, evaluated in native and ornamental tree species (**a**) and by tree size (diameter at breast height (DBH)) (**b**) in southern California, USA

trees (Fig. 3b). DBH of infested trees differed among tree species ($X_{10}^2 = 81.2$; $P < 0.001$) but not among stem injury ratings (no injury, 18.6 cm (± 2.86); minor, 21.4 cm (± 1.17); moderate, 23.2 cm (± 1.44); and severe injury, 20.6 cm (± 0.56)) ($X_3^2 = 2.02$; $P = 0.57$).

Of the 473 trees with a recorded crown rating at the KSHB sites, the percentages of healthy crowns (53.3%); minor (17.1%), moderate (19.5%), severe dieback (5.44%), and dead trees (5.64%) deviated from 20% ($X_4^2 = 444$; $P < 0.001$). Of the 274 KSHB-infested trees surveyed with crown ratings, 90

Fig. 4 Elevated injury and mortality caused by polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus*, to trees in a native stand of boxelder maple, *Acer negundo* L., (**a**) and branch and stem failure caused by PSHB to western sycamore, *Platanus racemosa* Nutt., (**b**) in southern California. Moderate injury caused by PSHB to trident maple, *Acer buergerianum* Miq., in an urban park in southwestern China (**c**), and survey of 3-year-old black wattle, *Acacia mangium* Willd., plantation for PSHB injury in northwestern Vietnam (**d**)

(32.8%), 58 (21.2%), 81 (29.6%), 8 (2.92%), and 37 (13.5%) had healthy crowns to dead trees, respectively, and the percentages deviated significantly from 20% ($X_4^2 = 128$; $P < 0.001$). Fremont cottonwood, Goodding's black willow, arroyo willow, London plane, and western sycamore were killed by KSHB (Table 2). Fremont cottonwood had the highest tree mortality associated with KSHB (9.62%) and the other four species ranged from 3.51 to 9.52% (Table 2).

At the KSHB-infested sites, 34.9% of trees had no stem injury, 13.2% had minor injury, 9.49% had moderate injury, and 41.9% had severe injury; these percentages deviated from 25% ($X_3^2 = 182$; $P < 0.001$). Of the KSHB-infested trees, most had severe stem injury (1, 78 (20.3%); 2, 56 (14.6%); and 3, 247 (64.3%)); these percentages deviated from 33.3% ($X_2^2 = 347$; $P < 0.001$).

At the KSHB-infested sites, stem injury differed among tree species ($X_{105}^2 = 199$; $P < 0.001$). No entrance holes were observed in ten of the tree species (Table 2). Over 20% of golden medallion, castorbean, arroyo willow, western sycamore, Goodding's black willow, Fremont cottonwood, and London plane had severe stem injury (Table 2).

To gauge entrance hole densities, 49 trees from eight species (i.e., avocado, bigleaf maple, boxelder maple, castorbean, coast live oak, red willow, western sycamore, and white alder) were surveyed in southern California. Mean DBH of the trees surveyed was 19.2 cm (± 2.4). Mean entrance hole density (count/232 cm^2) across all tree species was 17.3 (± 2.3) and 15.3 (± 2.4) holes at 1.37 and 0.3 m, respectively ($X_1^2 = 0.98$; $P = 0.32$), so data were pooled for the two measurements (Table 4). Mean entrance hole densities (pooled over two heights) on native trees (15.2 (±2.59)) did not differ from those on ornamental trees (21.6 (± 4.27)) ($X_1^2 = 2.82$; $P = 0.09$). Entrance hole densities differed among tree species ($X_7^2 = 21.2$; $P < 0.01$); density was significantly higher on boxelder maple and lower on red willow (Table 4).

At sites that had no evidence of infestation by *Euwallacea*, tree mortality was low (2%) and healthy crown ratings dominated the individual tree conditions (PSHB, 98.3% (510/519); KSHB, 99.2% (2036/2052)). Common willow agrilus, *Agrilus politus* (Say), was the most prominent injury agent, other than PSHB/KSHB, found attacking arroyo willow (6×) and red willow (9×) in uninfested and infested stands (13×). Only two dead arroyo willows were found with common willow agrilus injury. American black bear, *Ursus americana* (Pallas), injury (i.e., claw marks) was the second dominant tree injury surveyed on white alder (7×), white mulberry (3×), and western sycamore (4×). Carpenterworm, *Prionoxystus robiniae* (Peck), injury was observed twice on coast live oak, *Quercus agrifolia* Née (one living and one dead tree) (Swiecki and Bernhardt 2006).

3.2 Southwestern China

A total of 168 trees representing nine species were surveyed at four sites in Kunming. DBH (mean (± s.e.)) of all surveyed trees was 30.1 cm (± 1.36; $n = 168$), and DBH differed among tree species surveyed ($X_8^2 = 107$; $P < 0.001$) (Table 2). Infestation rates were highest on trident maple, *Acer buergerianum* Miq., (55.8%) and oriental plane, *Platanus orientalis* L., (57.5%) (Table 2, Fig. 4c). One stem of wisteria, *Wisteria*, Nutt., stem (5.84 cm DBH) and two Chinese banyan, *Ficus microcarpa* L.f., (mean DBH 13.21 cm (± 1.27)) were infested by PSHB. One Chinese banyan had severe crown dieback. DBH (mean (±s.e.)) of infested trees was 37.2 cm (± 1.90; $n = 56$), which was significantly greater than that of uninfested trees (26.1 (±

Table 4 Density of polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus*, and Kuroshio shot hole borer (KSHB), *E. kuroshio*, entrance holes (mean (±s.e.) per 232 cm^2) on trees surveyed in southern California, USA, southwestern China, and northwestern Vietnam

Country	Factor		Number	Entrance hole density[a]
USA	Forest type	Native trees	39	15.2 (±2.59)a
		Ornamental trees	10	19.7 (±4.43)a
	Tree species	Boxelder maple, *Acer negundo* L.	5	45.1 (±5.91)a
		Bigleaf maple, *Acer macrophyllum* Pursh	4	24.1 (±7.42)b
		Coast live oak, *Quercus agrifolia* Née	1	19.5
		Castorbean, *Ricinus communis* L.	9	21.1 (±4.72)b
		Western sycamore, *Platanus racemosa* Nutt.	8	15.7 (±4.49)b
		Avocado, *Persea americana* Mill.	1	7.5
		White alder, *Alnus rhombifolia* Nutt.	2	11.5 (±11.5)bc
		Red willow, *Salix laevigata* Bebb	19	5.50 (±1.27)c
China	Tree species	Trident maple, *Acer buergerianum* Miq.	7	20.7 (±2.84)a
		Chinese banyan, *Ficus microcarpa* L.f.	1	20.0
		Oriental plane, *Platanus orientalis* L.	2	15.0 (±0.00)a
Vietnam	Tree species	Black wattle, *Acacia mangium* Willd.	8	10.6 (2.65)

Entrance holes were recorded at 1.37 and 0.3 m height along the tree stem in southern California and at 1.37 m only in China and Vietnam

[a] Means (± s.e.) followed by the same letters within each table sub-section are not significantly different

1.76 cm) ($n = 112$)) ($X_1^2 = 17.0$; $P < 0.001$). DBH of infested trees ranged from 5.8 to 86.4 cm. Crown thinning and dieback were only evident on trees with severe PSHB injury.

Branch dieback and partial death of the main stem from PSHB was evident on numerous trident maple and oriental plane trees (Table 2; Fig. 4c). The majority of trees surveyed had healthy crowns (Fig. 2). Moderate (14.8%, 7/47) and severe (4.26%, 2/47) dieback were observed on oriental plane during the surveys. New plantings of oriental plane along the street suggested previous tree mortality associated with PSHB, which was verified by Li. Moderate dieback of trident maple (13.3% (6/45)) was recorded during the surveys, whereas crowns of remaining tree species were all healthy (Fig. 3). Severe stem injury from PSHB was recorded on wisteria (100% (1/1)), oriental plane (34.0% (16/47)), and trident maple (31.1% (14/45)) (Table 2). Oriental plane and trident maple also had stem injury that could be classified as minor (26.7% (12/45); 19.1% (9/47), respectively) and moderate (2.22% (1/45); 4.26% (2/47), respectively). Entrance hole densities of PSHB (per 232 cm^2) on the stem at 1.37 m across the three species was 18.5 (± 3.76) and did not differ among the species (i.e., trident maple, Chinese banyan, and oriental plane) ($X_2^2 = 4.98$; $P = 0.08$).

3.3 Northwestern Vietnam

A total of 116 black wattle trees were surveyed in six plantations at four sites in northwestern Vietnam and low levels of tree injury were associated with PSHB at these sites. Most of the black wattle plantations surveyed were four to 5 years old; one plantation was 7 years old (Fig. 4d). DBH of the PSHB-infested trees ranged from 4.57 to 42.9 cm. DBH (mean (±s.e.)) of the infested and uninfested black wattle ($n = 116$) was 13.6 cm (± 0.23), and DBH of the infested black wattle ($n = 34$) was 11.3 cm (± 0.98), which was significantly smaller than uninfested trees (14.6 cm (± 0.68)) ($X_1^2 = 8.44$; $P < 0.01$) (Table 2). Mean total basal area of black wattle plantations surveyed was 11.2 m^2 ha^{-1} (± 0.34). Mean basal area of trees injured by PSHB was 0.55 m^2 ha^{-1} (± 0.13), representing 4.9% of the basal area in the plantations. Mean stem density in the plantations was 532 ha^{-1} (± 99.9) with 15.2 ha^{-1} (± 13.2) infested, representing a 2.9% infestation rate. Only 1% of the surveyed black wattle were killed by PSHB (Table 2).

Crowns of nearly all (98.3% = 114/116) trees in the survey were healthy, suggesting a low level of injury across the plantations. Of the 116 surveyed trees, 84 (72.4%), 19 (16.4%), 5 (4.31%), and 8 (6.89%) had PSHB stem injury ratings of 0, 1, 2, and 3, respectively (Table 2) ($X_3^2 = 143$, $P < 0.001$). We observed two (1.72%) black wattle trees killed by PSHB (mean DBH 5.59 cm (± 1.02)) across all sites and several pruned black wattle stems resting on the forest floor were attacked by PSHB at one site. Castorbean was also observed with severe PSHB injury near Hanoi. Mean DBH (cm) and number of PSHB entrance holes (per 232 cm^2) along the main stem of eight PSHB-infested black wattle was 43.2 (± 14.3) and 10.6 (± 2.65), respectively (Table 3).

4 Discussion

4.1 Southern California

Two invasive shot hole borers represent new threats to native and ornamental tree species in southern California, and potentially outside of this region in the USA and Mexico (García-Avila et al. 2016). Many land ownerships in southern California have already directed labor and funding to manage and remove dead and dying trees associated with PSHB/KSHB (California Legislature 2018). In our impact survey of southern California, each ambrosia beetle species showed high levels of infestation (> 59%), but KSHB caused more impact in its limited distribution in San Diego County. In its invaded range, KSHB has infested more native tree species than PSHB because the KSHB-infested areas have typically been riparian corridors in or near San Diego County parks. In contrast, PSHB has infested more species of ornamental trees than KSHB. This outcome may be a consequence of the spread of PSHB throughout the urban areas of Los Angeles, Orange, Riverside, and San Bernardino Counties.

Although the two shot hole borers are considered different species, the invasive populations of each in California share many biological and ecological similarities with respect to tree injury, tree mortality, and host size and host species preference. For both PSHB and KSHB, the highest infestation rates (> 40%) were recorded on arroyo willow, Fremont cottonwood, Goodding's black willow, western sycamore, white alder, and castorbean (Table 2). Similar infestation rates (0 to 25%) for both beetle species were recorded on several other tree species, including American sweetgum, evergreen ash, and southern magnolia (Table 2).

Even though infestation levels by both beetles were exceptionally high for some tree species, tree mortality rates across all hardwood species were low (KSHB, 7.8%; PSHB, 5.6%) and just above background (2%). Within certain species of maples and willows, however, the mortality rates ranged from nearly 10% (KSHB) to over 25% (PSHB) (Tables 2 and 5). These levels of tree mortality from *Euwallacea* sp. are considerably lower when compared with other invasive species, including the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (13% of oaks; 48% on some survey plots); and the causal agent of sudden oak death, *Phytophthora ramorum* Werres et al. (3.1% for coast live oaks, 2.4% for black oaks, and 5.4% for tanoaks, per year over an 8-year survey interval); and native bark beetles in California (Rizzo and Garbelotto 2003; Rizzo et al. 2005; McPherson et al. 2010; Coleman et al. 2012; CFPC 2014, 2015, 2016, 2017). However, even the loss of a few trees in an urban setting can impact local esthetics considerably and lead to costly management, tree removal, and/or replacement.

Crown ratings have been used frequently in hardwood tree assessments to determine general health (Schomaker et al. 2007; Coleman et al. 2011; Hishinuma 2017), and many (> 53%) of the infested and uninfested trees in the PSHB- and KSHB-infested sites had ratings that suggested healthy crowns (Fig. 2). Minor, moderate, and severe crown dieback were evident in these sites but at lower percentages (< 20%). Moderate dieback was more prevalent in the KSHB-infested sites and likely a consequence of the high population pressure or the duration of infestation of this species in the Tijuana River Valley Regional Park (Boland 2016). Although Boland (2016) first reported instances of tree injury at this location, mortality quickly escalated to hundreds of thousands of trees within a year (CFPC 2017). The level of infestation and mortality from KSHB in this park was not observed elsewhere in the region or from PSHB. The extent of injury may be due to the dense stand conditions of susceptible hosts or other currently unknown contributing factors (e.g., high soil moisture) (Boland 2016).

Stem injury ratings also indicated a more pronounced impact by KSHB. Severe stem injury was prevalent in the KSHB-infested stands (41.9%), whereas stem injury classified as minor (40.4%) and severe (20.1%) occurred in the PSHB-infested stands. Severely injured trees likely will lead to patches of dead cambium, branch and stem failure, or complete tree mortality. Trees with this level of injury in developed sites will likely have to be removed because they cannot be saved with prophylactic or restorative treatments, and infested branches and trees have been shown to be attractive to PSHB (Byers et al. 2017). Stem injury ratings should be modified in the future to include very high densities of entrance holes (> 100), so injury level can be quantified with greater precision.

In southern California, trees do not appear to be succumbing to Fusarium dieback under low levels of injury from either beetle species. Symbiotic fungi carried by either species do not appear to be as pathogenic as the laurel wilt fungus associated with redbay ambrosia beetle, *Xyleborus glabratus* Eichh., on redbay, *P. borbonia* (L.) Spreng, in the southeastern USA (Evans et al. 2014). The combination of mechanical injury from gallery construction by the female parent and fungal inoculation at high densities along the main stem or branches leads to tree mortality. Infestation rate may have been overestimated because trees with low levels of attack may not have been suitable or preferred hosts for either PSHB or KSHB, i.e., these may have been unsuccessful attacks. The success of colonization attempts is difficult to ascertain during surveys without cutting into the xylem of a tree, which is often not an option in urban sites. Evidence of newly produced boring dust may be a second approach to gauge active infestations, but timing of surveys and weather may mask this symptom. Trees that produce a gumming response at the site of entry are often not hosts of either ambrosia beetle (Danthanarayana 1968; Eskalen et al. 2013).

In heavily infested sites, it appears that these ambrosia beetles may attack trees indiscriminately when populations are high, which may explain the elevated numbers of tree species reported previously to harbor entrance holes (Danthanarayana 1968; Eskalen et al. 2013), but relatively few of these have been confirmed as reproductive host species. This trend has been reported with bark beetle species during epidemics (Gibson et al. 2009; Hain et al. 2011), and may likely occur with other non-favored tree species when invasive shot hole borers have reached outbreak levels by attacking numerous favored host species in the vicinity.

PSHB killed more native trees than ornamental trees. Loss of hardwood canopy cover, basal area, and stem density from PSHB and KSHB may affect habitat for some threatened and endangered wildlife species, including arroyo toad, *Anaxyrus californicus* (Camp) and southwestern willow flycatcher, *Empidonax traillii extimius* (Audubon), in native riparian stands of southern California (Hatten and Paradzick 2003; Mitrovich et al. 2011). Thus, management options for PSHB and KSHB may be limited in these riparian corridors (e.g., because of the presence of endangered wildlife species or because of restrictions on insecticide applications near open water).

Both ambrosia beetles attacked trees in a wide range of diameter size classes; even the smallest stems (~ 2.0 cm DBH) were colonized across the three countries. Smaller trees were generally attacked and killed by both species, but the statistical significance of this small diameter difference may not transfer to biological significance. Because both beetle species attack trees in a wide range of diameter size classes, most ornamental and native host species are at risk to injury from the invasive shot hole borers.

Crown health ratings of infested trees detected in the southern California surveys suggested that additional trees will be killed by both species, i.e., the mortality rates may continue with time (McPherson et al. 2010). Eighteen and thirty-one percent of trees had moderate to severe dieback from PSHB and KSHB, respectively. Twelve tree species (PSHB, 12 species; KSHB, 5 species) were killed by at least one of these invasive beetles, and at least 29 individuals each of boxelder maple, castorbean, bigleaf maple, arroyo willow, red willow, Gooding's black willow, Fremont cottonwood, London plane, California bay laurel, western sycamore, and white alder were surveyed in PSHB-infested sites (Table 2). Boxelder maple, castorbean, and bigleaf maple sustained the highest tree mortality (> 20%) from PSHB (Fig. 4a). Paap et al. (2018) reported an invasive populations of PSHB also attacking sentinel plantings of London plane in South Africa. At the KSHB-infested sites, mortality rates of Fremont cottonwood, Gooding's black willow, arroyo willow, London plane, and western sycamore were < 10%, and each species was surveyed as at least 35 individuals (Table 2). Several willow species (i.e., arroyo, red, and Gooding's black) were killed at rates of 8 to 16% by both invasive shot hole borers. Boxelder maple and castorbean have also been attacked by PSHB in Israel (Mendel et al. 2012). *Euwallacea validus* (Eichhoff), another invasive species, was found attacking tree of heaven, *Ailanthus altissima* (Mill.) Swingle and striped maple, *Acer pensylvanicum* L., in the eastern USA (Cognato et al. 2015), suggesting some uniformity in host range for the genus *Euwallacea*.

Severe stem injury was > 33 and > 64% among infested trees at the PSHB- and KSHB-infested sites, respectively. This underscores that tree mortality could continue after our surveys. Severe stem injury from PSHB was recorded on 16 tree species, whereas severe stem injury from KSHB was recorded on eight tree species. Species not killed by PSHB were American sweetgum, southern California black walnut, evergreen ash, and coast live oak. Golden medallion and castorbean had severe stem injury from KSHB, but neither of these species died in the KSHB-infested sites. Only one tree species, California bay laurel, attacked at low levels by PSHB, was killed, but in this isolated instance, contributing factors were likely. No other trees succumbed to PSHB or KSHB with low and moderate levels of stem injury and this same trend was reported in South Africa with PSHB (Paap et al. 2018).

Entrance hole densities recorded from two areas on the main stem of severely injured or dead trees across all tree species and all three regions suggested that a mean density threshold of 18.0 in a 232-cm^2 area likely results in severe crown dieback or tree mortality. Because trees with this level of injury likely cannot be saved with insecticide and/or fungicide treatment, they should be removed and the wood should be handled properly to reduce the population pressure in an area (Jones and Paine 2015; Chen et al. unpublished data). High levels of attacks (6 to 19 per branch) were recorded from TSHB on branches of SOM in India, resulting in branch failure (Kumar et al. 2011). Thus, to facilitate management, a mean of > 18 attacks in a 232-cm^2 sampling area can be used as a threshold to trigger removal of actively infested trees, particularly in southern California where the infestation is still spreading.

4.2 Southeast Asia

The urban settings surveyed in southwestern China were similar to those in southern California. Not surprisingly, PSHB infested a sycamore and a maple species, i.e., oriental plane and trident maple, respectively. Infested trees were generally larger in DBH than uninfested trees, which contradicted data collected in southern California. Previous surveys of PSHB injury in the same areas have recorded injury to smaller diameter trident maple (~ 10 cm DBH). This result may be linked more to population pressure and not to a diameter threshold with the trees (QL, unpublished data). Oriental plane and trident maple in southwestern China had high rates of infestation (> 55%) and severe stem injury. However, previous infestation rates from PSHB in this area were > 80% on trident maple (Li et al. 2015). The decrease in infestation rates may be explained by the loss of older trees to PSHB and the replanting of smaller trident maple. PSHB will likely continue to injure and kill trees in these sites because it is difficult to obtain permission to conduct active management (e.g., the removal of infested branches and trees) in a timely manner in Chinese urban forests.

In northwestern Vietnam, PSHB was not a major threat to black wattle plantations (1% infestation rate), but small diameter trees were observed with injury. High levels of attack densities appeared to be required to kill black wattle. It was difficult to determine why certain trees were getting attacked and if there were any contributing factors to the infestations and tree mortality in these plantations. A couple of the plantations in the survey were planted on old tea plantations or adjacent to current tea plantations, which was a potential association for future investigation. However, better sanitation of discarded cut stems on the forest floor could reduce localized PSHB populations and subsequent attacks on adjacent living trees. The short growing rotation of these plantations (approx. 7 years) may further limit the extent of tree injury and mortality and could serve potentially as a sanitation cut before new plantings.

4.3 Conclusions and future directions

These survey data represent a snap shot in time of the impacts associated with these two invasive beetles. Follow-up surveys and long-term plots should be established in urban and wildland forests to capture the impacts at newly infested sites. However, tree species observed with high levels of infestation, severe stem injury, and incidences of tree mortality will likely be the most susceptible to PSHB and KSHB as they spread in California (Table 5). The similarities of injury and mortality across several host species from PSHB/KSHB suggest that similar management recommendations and risk models can be developed for the two invasive species in the USA. These data should inform land managers about the tree species at most risk to injury and mortality, facilitate ground surveys, and direct prophylactic treatments.

Future damage by PSHB and KSHB could be forthcoming in California's diverse agricultural crops. Many have raised concern about the potential threat of PSHB to avocado production worldwide, and branch dieback and mortality have been reported in Israel and California (Eskalen et al. 2012; Mendel et al. 2012; Freeman et al. 2013). However, we observed only low levels of injury from PSHB in an infested avocado grove in southern California. Our data suggest avocado is not a preferred host of PSHB, but additional surveys are needed to confirm potential impacts to production. Furthermore, TSHB did not cause damage to avocado plantations in southern Florida (Carrillo et al. 2016). Preliminary host range tests of English walnut, *Juglans regia* L., by our group suggest that multiple cultivars can serve as hosts for PSHB (Coleman et al. 2013b; Chen et al. 2014). Other fruit and nut tree crops grown in California's Central Valley, e.g., almond, *Prunus dulcis* (Mill.) D. A. Webb, persimmon, *Diospyros* spp. L., pistachio, *Pistacia vera* L. pomegranate, *Punica grantum* L., and other *Prunus*, may also be vulnerable to PSHB and KSHB should their distributions expand. The use of sentinel tree plantings of dominant forest and agriculturally important tree species from the USA in the native range of these *Euwallacea* spp. may assist with host testing and future risk assessments (Vettraino et al. 2015).

Invasive shot hole borers (PSHB and KSHB) have spread to additional southern California counties since their initial detections in Los Angeles and San Diego Counties, respectively. Natural flight dispersal, movement of green waste from urban areas (TWC, personal observation), movement of firewood and nursery stock, and a diverse host range may be facilitating the spread of these species. TSHB is already present in the southern USA

Table 5 Southern California tree species most impacted by polyphagous shot hole borer (PSHB), *Euwallacea whitfordiodendrus*, and Kuroshio shot hole borer (KSHB), *E. kuroshio*

Tree species	Family	Agent	Infestation rate (%)	Severe stem injury (%)	Tree mortality (%)
Boxelder maple, *Acer negundo* L.	Sapindaceae	PSHB	92.5	81.8	26.7
Castorbean, *Ricinus communis* L.	Euphorbiaceae	PSHB	71.4	57.1	21.4
Bigleaf maple, *Acer macrophyllum* Pursh	Sapindaceae	PSHB	73.0	46.0	20.6
Arroyo willow, *Salix lasiolepis* Benth.	Salicaceae	PSHB/KSHB	83.3/72.1	8.3/52.7	16.7/8.1
Red willow, *Salix laevigata* Benth.	Salicaceae	PSHB	80.1	46.4	15.9
Fremont cottonwood, *Populus fremontii* S. Watson	Salicaceae	PSHB/KSHB	56.2/46.2	10.1/23.1	5.6/9.6
Goodding's black willow, *Salix gooddingii* C.R. Ball	Salicaceae	PSHB/KSHB	77.3/81.0	19.7/42.9	7.6/9.5
London plane, *Platnus* × *acerifolia* (Alton) Willd.	Platanaceae	PSHB/KSHB	84.8/74.5	14.1/23.4	5.5/4.3
Western sycamore, *Platanus racemosa* Nutt.	Platanaceae	PSHB/KSHB	80.0/78.9	25.9/43.9	2.6/3.5
White alder, *Alnus rhombifolia* Nutt.	Betulaceae	PSHB	41.7	6.55	0.60

The tree species listed had high levels of infestation (> 40%) and stem injury (> 6%), and included at least ten observations at infested sites. They are ranked by their levels of tree mortality (i.e., Florida) (Carrillo et al. 2016). *Euwallacea interjectus* (Blandford), *E. similis* (Ferrari), and *E. validus* have been introduced into the USA to Florida, Georgia, Kentucky, South Carolina, Texas, and Virginia; Texas; and 17 states including nine primarily in the southeastern USA, respectively (Gomez et al. 2018a), suggesting that the distributions of PSHB and KSHB may spread to the coastal regions of the southern USA. Preliminary no-choice host testing for PSHB with tree species from Louisiana (black willow, *Salix nigra* Marshall, red maple, *Acer rubrum* L., and southern red oak, *Quercus falcata* Michx.) and New Mexico, USA (boxelder maple, quaking aspen, *Populus tremuloides* Michx., and narrowleaf cottonwood, *Populus angustifolia* James) revealed susceptible native hardwoods from these southern locations based on the presence of males, larvae, and pupae in a laboratory setting (Coleman et al. 2013b; Chen et al. 2014). This supports the potential for a USA range expansion outside of California. The California Legislature (2018) recently amended a bill (AB-2470) to address the management of the invasive shot hole borers within the state. This action may help limit the spread, address research gaps, and increase the pace of management for these exotic species in urban and native forests.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Barnes I, Fourie A, Wingfield MJ, Harrington TC (2018) New *Ceratocystis* species associated with rapid death of *Metrosideros polymorpha* in Hawaii. Persoonia-Molecular Phylogeny and Evolution of Fungi 40:154–181

Boland JM (2016) The impact of an invasive ambrosia beetle on the riparian habitats of the Tijuana River Valley, California. Peer J 4: e2141. https://doi.org/10.7717/peerj.2141

Bright DE (2014) A catalog of Scolytidae and Platypodidae (Coleoptera), supplement 3 (2000–2010), with notes on subfamily and tribal reclassifications. Insecta Mundi 356:1–336

Bright DE (2019) A taxonomic monograph of the bark and ambrosia beetles of the West Indies Coleoptera: Curculionoidea: Scolytidae and Platypodidae (Coleoptera). Studies on West Indian Scolytidae 7. In: Occasional papers of the Florida State Collection of Arthropods, Gainesville, Florida, 500 pp

Byers JA, Maoz Y, Levi–Zada A (2017) Attraction of *Euwallacea* sp. near *fornicatus* (Coleoptera: Curculionidae) to quercivorol and to infestations in avocado. J Econ Entomol 110:1515–1517

California Forest Pest Council (CFPC) (2014) California forest pest conditions. Sacramento, California. https://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046704. Accessed 26 Sept 2018

California Forest Pest Council (CFPC) (2015) California forest pest conditions. Sacramento, California. https://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046704. Accessed 26 Sept 2018

California Forest Pest Council (CFPC) (2016) California forest pest conditions. Sacramento, California. https://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046704. Accessed 26 September 2018

California Forest Pest Council (CFPC) (2017) California forest pest conditions. Sacramento, California. https://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046704. Accessed 26 Sept 2018

California Legislature (2018) AB-2470 Invasive Species Council of California. https://leginfo.legislature.ca.gov/faces/billTextClient.xhtml?bill_id=201720180AB2470. Accessed 26 Sept 2018

Carrillo D, Cruz LF, Kendra PE, Narvaez TI, Montgomery WS, Monterroso A, De Grave C, Cooperband MF (2016) Distribution, pest status and fungal associates of *Euwallacea* nr. *fornicatus* in Florida avocado groves. Insects 7:573–579

Centre for Agriculture and Biosciences International (CABI) (2018) *Euwallacea fornicatus* distribution map. [WWW document]. URL http://www.cabi.org/isc/datasheet/57163. Accessed 14 August 2018

Chen Y, Coleman, TW, Graves, AD, Meeker, JR, Seybold, SJ (2014) Host range of the invasive polyphagous shot hole borer. California Forest Pest Council Annual Meeting, 12–13 Nov 2014 (http://caforestpestcouncil.org/wp-content/uploads/2014/12/Chen.pdf). Accessed 17 September 2018

Chen Y, Dallara PL, Nelson LJ, Coleman TW, Hishinuma SM, Carrillo D, Seybold SJ (2017) Comparative morphometric and chemical analyses of phenotypes of two invasive ambrosia beetles (*Euwallacea* spp.) in the United States of America. Insect Sci 24:647–662

Chen Y, Coleman TW, Poloni AL, Nelson LJ, Seybold SJ (2019a). Reproduction and control of the invasive polyphagous shot hole borer, *Euwallacea* sp., in three species of hardwoods: effective sanitation through felling and chipping. Agricultural and Forest Entomology (in review)

Chen Y, Coleman TW, Poloni AL, Seybold SJ (2019b) Developing monitoring techniques for the invasive polyphagous shot hole borer, *Euwallacea* sp. (Coleoptera: Curculionidae: Scolytinae). Journal of Economic Entomology (in review)

Cognato AI, Hoekeke ER, Kajimura H, Smith SM (2015) History of the exotic ambrosia beetles *Euwallacea interjectus* and *Euwallacea validus* (Coleoptera: Curculionidae: Xyleborini) in the United States. J Econ Entomol 108:1129–1135

Coleman TW, Grulke NE, Daly M, Godinez C, Schilling S, Riggan PJ, Seybold SJ (2011) Coast live oak, *Quercus agrifolia*, susceptibility and response to goldspotted oak borer, *Agrilus auroguttatus*, injury in southern California. For Ecol Manag 261:1852–1865

Coleman TW, Graves AD, Hoddle M, Heath Z, Chen Y, Flint ML, Seybold SJ (2012) Forest stand composition and impacts associated with *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) and *Agrilus coxalis* Waterhouse in oak woodlands. For Ecol Manag 276: 104–117

Coleman TW, Eskalen A, Stouthamer R (2013a) New pest complex in California: the polyphagous shot hole borer, *Euwallacea* sp., and Fusarium Dieback, *Fusarium euwallaceae*. USDA Forest Service, Pest Alert, R5-PR-032, 4 November 2013, 5 pp. https://cisr.ucr.edu/pdf/pest_alert_pshb_and_fd.pdf. Accessed 24 Sept 2018

Coleman TW, Seybold SJ, Venette RC, Chen Y, Graves AD, Meeker JR (2013b) Host susceptibility and potential for range expansion of the invasive polyphagous shot hole borer (PSHB), *Euwallacea* sp., and Fusarium dieback, *Fusarium euwallaceae*. In: The U.S. Special Technology Development Project No. R5-2014-01, 2014–2016

Cooperband MF, Stouthamer R, Carillo D, Eskalen A, Thibault T, Cossé AA, Castrillo LA, Vandenberg JD, Rugman-Jones PF (2016) Biology of two members of the *Euwallacea fornicatus* species complex (Coleoptera: Curculionidae: Scolytinae), recently invasive in the U.S.A., reared on an ambrosia beetle artificial diet. Agric For Entomol 18:223–237. https://doi.org/10.1111/afe.12155

Danthanarayana W (1968) The distribution and host-range of the shot-hole borer (*Xyleborus fornicatus* Eichh.) of tea. Tea Quarterly 39: 61–69

Dodge C, Coolidge J, Cooperband M, Cossé A, Carillo D, Stouthamer R (2017) Quercivorol as a lure for the polyphagous and Kuroshio shot hole borers, *Euwallacea* spp. nr. *fornicatus* (Coleoptera: Scolytinae), vectors of Fusarium dieback. Peer J 5:e3656. https://doi.org/10.7717/peerj.3656

Eskalen A, Gonzalez A, Wang DH, Twizeyimana M, Mayorquin JS, Lynch SC (2012) First report of a *Fusarium* sp. and its vector tea shot hole borer (*Euwallacea fornicatus*) causing Fusarium dieback on avocado in California. Plant Dis 96:1070. https://doi.org/10.1094/PDIS-03-12-0276-PDN

Eskalen A, Stouthamer R, Lynch SC, Rugman-Jones PF, Twizeyimana M, Gonzalez A, Thibault T (2013) Host range of Fusarium dieback and its ambrosia beetle (Coleoptera: Scolytinae) vector in southern California. Plant Dis 97:938–951

Evans JP, Scheffers BR, Hess M (2014) Effect of laurel wilt invasion on redbay populations in a martitime forest community. Biol Invasions 16:1581–1588

Freeman S, Sharon M, Mayman M, Mendel Z, Protasov A, Aoki T, Eskalen A, O'Donnell K (2013) *Fusarium euawallaceae* sp. nov.—a symibiotic fungus of *Euwallacea* sp., an invasive ambrosia beetle in Israel and California. Mycologia 105:1595–1606

García-Avila CDJ, Trujillo-Arriaga FJ, López-Buenfil JA, Gonzalez-Gomez R, Carrillo D, Cruz LF, Ruiz-Galvan I, Quezada-Salinas A, Acevedo-Reyes N (2016) First report of *Euwallacea nr. fornicatus* (Coleoptera: Curculionidae) in Mexico. Fla Entomol 99:55–56

Gibson K, Kegley S, Bentz B (2009) Mountain pine beetle. Forest insect and disease leaflet 2 (revised). USDA Forest Service, Portland, Oregon. FS-R6-RO-FIDL No. 2 2002-2009. 12pp

Gomez DF, Rabaglia RJ, Fairbanks KEO, Hulcr J (2018a) North American Xyleborini north of Mexico: a review and key to genera and species (Coleoptera, Curculionidae, Scolytinae). ZooKeys 768: 19–68

Gomez DF, Skelton J, Sedonia Steininger M, Stouthamer R, Rugman-Jones P, Sittichaya W, Rabaglia RJ, Hulcr J (2018b) Species delineation within the *Euwallacea fornicatus* (Coleoptera: Curculionidae) complex revealed by morphometric and phylogenetic analyses. Insect Systematics and Diversity 2. https://doi.org/10.1093/isd/ixy018

Gomez DF, We L, Lei G, You L (2019) New host plant records for the *Euwallacea fornicatus* (Eichhoff) species (Coleoptera: Curculionidae: Scolytinae) across its natural and introduced distribution. J Asia Pac Entomol 22:338–340

Haack RA (2006) Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can J For Res 36: 269–288

Hain FP, Duehl AJ, Gardner MJ, Payne TL (2011) Natural history of the southern pine beetle, pp 13–24. In: Coulson, RN, Klepzig KD (eds) Southern pine beetle II. USDA Forest Service, Southern Research Station General Technical Report SRS-140

Hatten JR, Paradzick CE (2003) A multiscaled model of southwestern willow flycatcher breeding habitat. J Wildl Manag 67:774–788

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu Rev Entomol 59:13–30

Hishinuma SM (2017) Interactions among the walnut twig beetle, *Pityophthorus juglandis*, the pathogenic fungus, *Geosmithia morbida*, and host species in thousand cankers disease in California. Dissertation, University of California, Davis

Jones ME, Paine TD (2015) Effect of chipping and solarization on emergence and boring activity of a recently introduced ambrosia beetle (*Euwallacea* sp., Coleoptera: Curculionidae: Scolytinae) in Southern California. J Econ Entomol 108:1852–1859

Kumar R, Rajkowa G, Sankar M, Rajan RK (2011) A new host for the shot-hole borer, *Euwallacea fornicatus* (Eichhoff) (Coleoptera: Scolytidae) from India. Acta Entomol Sin 54:734–738

Lee JC, Haack RA, Negrón JF, Witcosky JJ, Seybold SJ (2007) Invasive bark beetles. Forest insect and disease leaflet 176. USDA Forest Service, Pacific Northwest Region, Portland, Oregon. 12 pp.

Li Q, Guo H, Zhao Y, Zhang G, He G, Liu B (2015) Damage caused by *Euwallacea fornicatus* (Coleoptera: Scolytidae) and its control techniques in Kunming. China Acad J 41:193–196. https://doi.org/10.3969/j.issn.0529-1542.2015.03.038

Li Y, Gu XY, Kasson MT, Bateman CC, Guo J, Huang YT, Li Q, Rabaglia RJ, Hulcr J (2016) Distribution, host records, and symbiotic fungi of *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) in China. Florida Entomol 99:801–804

Liebhold AM, McCullough DG, Blackburn LM, Frankel SJ, Von Holle B, Aukema JE (2013) A highly aggregated geographical distribution of forest pest invasions in the USA. Divers Distrib 19:1208–1216

Lynch SC, Twizeyimana M, Mayorquin JS, Wang DH, Na F, Kayim M, Kasson MT, Thu PQ, Bateman C, Rugman-Jones PF, Hulcr J, Stouthamer R, Eskalen A (2016) Identification, pathogenicity and abundance of *Paracremonium pembeum* sp. nov. and *Graphium euwallaceae* sp. nov.—two newly discovered mycangial associates of the polyphagous shot hole borer (*Euwallacea* sp.) in California. Mycologia 108:313–329

Mayfield AE III, Seybold SJ, Haag WR, Johnson MT, Kerns BK, Kilgo JC, Larkin DJ, Lucardi RD, Moltzan BD, Pearson DE, Rothlisberger JD, Schardt JD, Schwartz MK, Young MK (2019) Impacts of invasive species in terrestrial and aquatic systems in the USA. In: Poland TM, Patel-Weynand T, Finch D, Ford Miniat C, Lopez V (eds) National assessment of invasive species. Springer Verlag, Berlin, pp 38–108

McPherson BA, Mori SR, Wood DL, Kelly M, Storer AJ, Švihra P, Standiford RB, Rizzo DM (2010) Responses of oaks and tanoaks to the sudden oak death pathogen after 8 y of monitoring in two coastal California forests. For Ecol Manag 259:2248–2255

Mendel Z, Protasov A, Sharon M, Zveibil A, Ben Yehuda S, O'Donnell K, Rabaglia R, Wysoki M, Freeman S (2012) An Asian ambrosia beetle *Euwallacea fornicatus* and its novel symbiotic fungus *Fusarium* sp. pose a serious threat to the Israeli avocado industry. Phytoparasitica 40:235–238

Mitrovich MJ, Gallegos EA, Lyren LM, Lovich RE, Fisher RN (2011) Habitat use and movement of the endangered arroyo toad (*Anaxyrus californicus*) in coastal southern California. J Herpetol 45:319–328

O'Donnell K, Sink S, Libeskind-Hadas R, Hulcr J, Kasson MT, Ploetz RC, Konkol JL, Ploetz JN, Carrillo D, Campbell A, Duncan RE, Liyanage PNH, Eskalen A, Na F, Geiser DM, Bateman C, Freeman S, Mendel Z, Sharon M, Aoki T, Cossé AA, Rooney AP (2015) Discordant phylogenies suggest repeated host shifts in the *Fusarium–Euwallacea* ambrosia beetle mutualism. Fungal Genet Biol 82:277–290

Paap T, de Beer ZW, Migliorini D, Nel WJ, Wingfield MJ (2018) The polyphagous shot hole borer (PSHB) and its fungal symbiont *Fusarium euwallaceae*: a new invasion in South Africa. Australas Plant Pathol 47:231–237

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Rabaglia RJ, Dole SA, Cognato AI (2006) Review of American Xyleborina (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. Ann Entomol Soc Am 99:1034–1056

Rizzo DM, Garbelotto M (2003) Sudden oak death: endangering California and Oregon forest ecosystems. Front Ecol Environ 1: 197–204

Rizzo DM, Garbelotto M, Hansen EM (2005) *Phytophthora ramorum*: integrative research and management of an emerging pathogen in California and Oregon forests. Annu Rev Phytopathol 43:309–335

Schomaker ME, Zarnoch SJ, Bectold WA, Latelle DJ, Burkman WG, Cox SM (2007) Crown-condition classification: a guide to data collection and analysis. General Technical Report SRS-102. Asheville, North Carolina: US Department of Agriculture, Forest Service, Southern Research Station, 78 pp.

Seybold SJ, Penrose RL, Graves AD (2016) Invasive bark and ambrosia beetles in California Mediterranean forest ecosystems. In: Paine TD, Lieutier F (eds) Insects and diseases of Mediterranean forest systems. Springer International Publishing, Cham, Switzerland, pp 583–662. https://doi.org/10.1007/978-3-319-24744-1_21

Seybold SJ, Frankel SJ, Olson DH, Flitcroft R, Kerns BK, Lee JC, Ripley K, Munson AS (2019a) Northwest region summary. In: Poland TM, Patel-Weynand T, Finch D, Ford Miniat C, Lopez V (eds) National assessment of invasive species. Springer Verlag, pp 698–739

Seybold SJ, Graves AD, Frankel SJ, White A, Sutherland C, Munson AS (2019b) Southwest region summary. In: Poland TM, Patel-Weynand T, Finch D, Ford Miniat C, Lopez V (eds) National assessment of invasive species. Springer Verlag, pp 740–786

Smith SM, Rabaglia RJ, Beaver RA, Cognato AI, Thu PQ (2018) Attraction of ambrosia beetles, (Curculionidae: Scolytinae: Xyleborini) to semiochemicals in Vietnam with new records and a new species. Coleopt Bull 72:838–844

Stanaway MA, Zalucki MP, Gillespie PS, Rodriguez CM, Maynard GV (2001) Pest risk assessment of insects in sea cargo containers. Aust J Entomol 40:180–192

Stouthamer R, Rugman-Jones P, Thu PQ, Eskalen A, Thibault T, Hulcr J, Wang LJ, Jordal BH, Chen CY, Cooperband M, Lin CS, Kamata N, Lu S-S, Masuya H, Mendel Z, Rabaglia R, Sanguansub S, Shih H-H, Sittichaya W, Zong S (2017) Tracing the origin of a cryptic invader: Phylogeography of the *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) species complex. Agric For Entomol 19:366–375

Swiecki TJ, Bernhardt EA (2006) A field guide to insects and diseases of California oaks. USDA Forest Service Pacific Southwest Research Station. General Technical Report PSW-GTR-197, Albany, California, 151 pp.

Tisserat N, Cranshaw W, Leatherman D, Utley C, Alexander K (2009) Black walnut mortality in Colorado caused by the walnut twig beetle and thousand cankers disease. Online. Plant Health Progress. https://doi.org/10.1094/PHP-2009-0811-01-RS. http://entnemdept.ufl.edu/pestalert/thousand_cankers_disease_CO_0810.pdf. Accessed 22 Sept 2018.

Umeda C, Eskalen A, Paine TD (2016) Polyphagous shot hole borer and Fusarium dieback in California. In: Paine TD, Lieutier F (eds) Insects and diseases of Mediterranean forest systems. Springer International Publishing, Cham, Switzerland, pp 757–768. https://doi.org/10.1007/978-3-319-24744-1_26

University of California (UC) Riverside (2018a) http://eskalenlab.ucr.edu/distribution.html. Accessed 14 August 2018

University of California (UC) Riverside (2018b) http://eskalenlab.ucr.edu/shotholeborerhosts.html. Accessed 14 August 2018

Venette RC, Kriticos DJ, Magarey R, Koch FH, Baker RHA, Worner SP, Gomez Raboteaux NN, McKenney DW, Dobesberger EJ, Yemshanov D, De Barro PJ, Hutchinson WD, Fowler G, Kalaris TM, Pedlar J (2010) Pest risk maps for invasive alien species: a roadmap for improvement. BioScience 60:349–362

Vettraino A, Roques A, Yart A, Fan JT, Sun JH, Vannini A (2015) Sentinel trees as a tool to forecast invasions of alien plant pathogens. PLoS One 10(3):15. https://doi.org/10.1371/journal.pone.0120571

Wallner WE (1996) Invasive pests ('biological pollutants') and US forests: whose problem, who pays? Bull OEPP/EPPO 26:167–180

Wang WR, Yuan ZY (2003) A new pest of litchi, *Xyleborus fornicatus* and its control. South China Fruits 32:34–35

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