Title
Ecology of the invasive shot hole borer (Euwallacea whitfordiodendrus) in a coastal California riparian system

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Ecology of the invasive shot hole borer (*Euwallacea whitfordiodendrus*) in a coastal California riparian system

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by

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ABSTRACT

Ecology of the invasive shot hole borer (*Euwallacea whitfordiodendrus*) in a coastal California riparian system

by

Shelley Bennett

Invasive species threaten biodiversity and ecosystem processes, with varying impacts among introduced regions. The polyphagous shot hole borer (*Euwallacea whitfordiodendrus*) (Coleoptera: Scolytinae) is an ambrosia beetle native to southeast Asia that has become recently established in southern California, infesting riparian, agricultural and urban tree species. A large dieback event at the Tijuana River Valley in 2016 was attributed to the beetle and their symbiotic fungi (*Fusarium euwallaceae*), but it is unclear whether this is expected to occur in other riparian areas throughout southern California or if, instead, beetle populations are exhibiting a boom-and-bust type population decline. This thesis characterizes the spread and impact of *E. whitfordiodendrus* in a major river in southern California, the Santa Clara River (SCR), by evaluating regional expansion over three years, testing the effects of host water availability and host species on beetle preference, examining host susceptibility to beetles or their symbiotic fungi among riparian host species and tracking the progression of a local riparian infestation over four years. We found that after an initially rapid expansion, *E. whitfordiodendrus* dispersal has tapered off. Beetles exhibited no preference among hosts with differing water status or among different host species. We did, however, find that that host species differed in their susceptibility to beetle tunneling activity, which was explained in part by differences in wood density. Susceptibility to growth of the beetle's symbiotic fungus also differed between species, with *Populus fremontii* being the least susceptible to fungal growth. Differences in host susceptibility may result in differing infestation severities in riparian areas which can vary in dominant tree species throughout a floodplain. Infestation rates at the SCR increased from 2017-2019 but were stabilized or lower in most plots by 2020. *Salix lasiolepis* was the most commonly and severely infested species in the field, however many infested individuals were resprouting by 2020. Overall, we did not find evidence to support a large-scale dieback event at the SCR and *E. whitfordiodendrus* populations may be entering a population 'bust,' yet more work is needed to confirm this.

Introduction:

Globalization has led to an increase in the movement of species worldwide, some of which become invasive and can threaten biodiversity and ecosystem processes (Meyerson and Mooney 2007). Introduced species can cause damage to native ecosystems by inflicting direct mortality to native species or otherwise altering species competition, biogeochemistry and ecosystem structure. However, abiotic and biotic factors can vary regionally across a species introduced range, which can influence their local impact (Crowl et al. 2008). The scale and severity of impact depends on the life history characteristics of the invader, the diversity and structure of the invaded community and environmental conditions that may be more or less suitable for the invasive species (Dukes and Mooney 1999). With recently established invaders, studies are often needed to develop a predictive understanding of a species ecological interactions and potential impacts, which can then be used to guide regional management plans.

In North America, wood-boring xylemycetophagous ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) are among the most frequently intercepted insects at trading ports (Haack 2006). Their cryptic lifestyle contributes to their success as invaders by allowing them to travel undetected in logs, lumber, nursey stock or wood packing material (Haack 2006, Marini et al. 2011, Haack and Rabaglia 2013). These beetles typically feed on symbiotic fungi that they carry and inoculate into host trees. Most are secondary colonizers of stressed or dying trees and facilitate decomposition, although several species have become problematic in their introduced ranges with devastating impacts on native trees (Hulcr and Dunn 2011).

The polyphagous and Kuroshio shot hole borers (*Euwallacea whitfordiodendrus* and *E. kuroshio*, respectively) are genetically distinct ambrosia beetle species with virtually identical morphologies (Gomez et al. 2018) that are native to subtropical Southeast Asia, including Vietnam and Taiwan (Stouthamer et al. 2017). They have recently become established in southern California. Although first detected in 2003, *Euwallacea* species detections increased drastically in 2012 starting in Los Angeles and San Diego Counties and have since spread south to northern Mexico, northwest to Santa Barbara County and east to San Bernardino County. The beetles are considered invasive due to their quick range expansion, fast population growth, due in part to their haploid-diploid reproduction combined with brother-siter mating, and impact on riparian, agricultural and urban tree species (Eskalen 2013, Boland 2016). It is currently speculated that the two species are ecologically very similar as the beetles share reproductive host trees (Eskalen 2020). Their symbiotic fungi (*Fusarium* spp. and *Graphium* spp.) provide the food source for adult beetles and developing larvae (Cooperband et al. 2016). *Fusarium* species can grow into the tree's xylem, block water transport and cause branch dieback or host mortality, a disease referred to as *Fusarium* dieback (Umeda et al. 2016). Susceptible hosts include over 200 native or economically important woody plant species, with 65 identified as reproductive hosts that allow for complete beetle development and reproduction (Eskalen 2013, Eskalen 2020). In 2015, a large-scale dieback event at the Tijuana River Valley (TRV) was attributed to the shot hole borer/*Fusarium* dieback (SHB-FD) pest-disease complex and affected over 140,000 willow trees (*Salix* spp.) (Boland 2016). However, a dieback event of this scale has not been observed in other California riparian systems to date and little is known about the mechanisms driving infestations at the individual host level, such as beetle host choice preferences and differences in host susceptibility.

Euwallacea species are generalists, like most other ambrosia beetles (Rassati et al. 2016) and can colonize many types of unrelated host species. Despite this, hosts often differ in their attractiveness to and suitability for ambrosia beetles and their symbiotic fungus, leading to host preferences and differential colony success among tree species (Ranger et al. 2015, Dathanarayana 1968, Pena et al. 2012). For example, it is known that tree water stress can influence ambrosia beetle attack rates. Ranger et al. (2013) showed that flood intolerant tree species exposed to flooded conditions were more likely to be attacked by ambrosia beetles. These trees also produced more ethanol in leaf tissues than flood tolerant species. Ethanol is a primary kairomone that is indicative to insects of plant stress and, therefore, lowered host defenses (Owens et al. 2017) It is one of the most common volatile cues utilized by ambrosia beetles to indicate host suitability for colonization (Ranger et al. 2018, Reding et al. 2017). Drought stressed trees also emit ethanol, which has been shown to drive bark beetle host choice in pine trees (Kelsey et al. 2014). However, initial observations of *Euwallacea* species suggest that beetles were more likely to be found in well-watered or irrigated host trees (Akif Eskalen, personal communication). In the TRV, Boland (2016) found that one year after establishment, beetles were primarily in wetter areas, but by the second and third year, the beetles had moved into drier areas (Boland 2018). Umeda (2017) found no influence of host water availability on beetle preference for *Liquidambar styraciflua* or potted *Acer negundo*. Thus, it is currently unclear how water status affects beetle preference or colony success in riparian host trees.

Besides host water status, ambrosia beetles use other cues from hosts, such as visual and chemical traits not related to host stress (Vite and Bakke 1979). Trees have unique volatile profiles that may be attractive to certain types of beetles (Vite and Bakke 1979). The closely related tea shot hole borer (*Euwallacea fornicatus*) is widespread throughout southeast Asia but has been noted to preferentially infest tea (*Camellia sinensis*) and castor bean (*Ricinus communis*) (Danthanarayana 1968) likely due to attraction to their volatile profiles (Vite and Bakke 1979). For *E. whitfordiodendrus*, Jones and Paine (2017) found that attack rates differed among avocado varieties in a laboratory setting.

Just as important as beetle's host choice is the host tree's susceptibility, which is dependent both on the beetle's ability to tunnel and form galleries within the host (Sivapalan 1985) as well as the ability of the host tree to resist fungal infection from the beetle's symbiotic fungi (Kumar et al. 1995). Jones and Paine (2017) also found that beetles had differing success at forming galleries in avocado varieties. However, the mechanisms driving beetle success are not known. Wood density could affect a tree's susceptibility to beetle tunneling (Boland and Woodward 2019), but this has not been tested experimentally. In addition, there are no studies examining the success of the *E. whitfordiodendrus*' symbiotic fungi within galleries of different host species.

Knowledge of this species and its ecological interactions in riparian systems remains poorly understood. Understanding *E. whitfordiodendrus* host choice, colonization and susceptibility of its hosts as well as how beetle abundances increase in individual hosts over time and rates of dispersal to naïve hosts (Boland 2020) will be important for determining their dispersal throughout the landscape and predicting outbreaks (Kausrud et al. 2011). Besides the infestation tracking at the TRV, there have been no other long-term datasets that analyze infestation progression of *E. whitfordiodendrus* at a local scale in riparian systems. More studies are needed to predict whether large-scale dieback events, such as that at the TRV, can be expected or whether there is evidence that *E. whitfordiodendrus* is exhibiting a solitary boom and bust invasion cycle in which introduced populations show rapid growth and expansion followed by a sudden population crash (Strayer et al. 2017).

This manuscript characterizes the spread and impact of *E. whitfordiodendrus* in a major river in southern California, the Santa Clara River (SCR), by evaluating regional expansion over three years, experimentally testing the effects of host water availability and host species on beetle preference, examining host susceptibility among riparian host species and tracking the progression of a local riparian infestation over four years. The goals are to determine whether there is evidence to predict a large-scale outbreak, whether there are preferences among trees as the beetles arrive, based on water status or tree species, and whether regional and local expansion continue to grow or show evidence of tapering off.

The specific questions addressed include:

1) How did the distribution and expansion of SHB in the SCR change over a three-year period after initial establishment?
2) Does host water status affect SHB colonization?
3) Does SHB colonization differ between native riparian host species in a controlled laboratory environment? Do tree species vary in susceptibility to beetle colonization and subsequent fungal growth?

4) How do SHB infestations grow over time? Does beetle abundance in infested trees continue to increase over time and are infestation patterns consistent among tree species?

Methods:

Site Description

The Santa Clara River (SCR) flows from the Transverse Ranges in Northern Los Angeles County west to the Pacific Ocean in Ventura County and the watershed drains an area of approximately 4150 km^2. This region has a Mediterranean climate, characterized by cool winters and hot, dry summers, with most precipitation occurring in the winter. The Ventura County region has an average annual rainfall of 360 mm and average annual temperature of 16 C. The SCR receives a majority of water input in short, and sometimes high intensity storm events during the winter months. Notably, it is the only river in southern California that retains elements of natural hydrology. It has not been heavily channelized, although other modifications such as small dams and diversions do affect its hydrology. Further, it is affected by encroaching urban and agricultural development, levee construction and invasive plant species, and is designated as one of the most threatened rivers in the U.S. (American Rivers 2005). *Euwallacea whitfordiodendrus* was first detected in the SCR in late 2015 (Ben Faber, UC Cooperative Extension, pers. comm.).

Distribution and Dispersal

Detection traps were used to track the distribution and spread of SHB within the Santa Clara River. A total of 54 inverted 2-L bottle traps baited with quercivorol, an attractant specific to the *Euwallacea* species complex (Dodge et al. 2017), were deployed throughout the watershed in riparian areas with reproductive host trees present, with three traps placed in an avocado orchard adjacent to the SCR. Forty-two traps were initially deployed in Ventura County between September and October 2016. Twelve additional traps were deployed in the upper watershed in northern Los Angeles County in October 2018. Traps were placed in areas we could obtain access in attempt to achieve broad coverage of the SCR. Traps were monitored biweekly from the time of their deployment until July 2019. After approximately one year of consistent detections at a location, monitoring of that location ceased and presence was assumed for the years following. In all years, traps were not monitored during the months of December through March as beetles are not active and no new detections were expected to occur. For each trap, quercivorol lures were changed every 6 weeks and propylene glycol was used to preserve specimen in the capture vials (**Figure 1**). Specimens from trap catches were sorted and those identified morphologically as *Euwallacea* spp. were then genetically identified using a high-resolution melt analysis (Rugman-Jones and Stouthamer 2016) by the Stouthamer lab at the University of California, Riverside. A binomial generalized linear model was used to analyze the difference in proportion of traps with positive detections between years using the lme4 package in R (version 4.0.0).

Figure 1. Inverted two-liter bottle trap used to track detection and spread of shot hole borer. Traps were baited with a quercivorol lure (seen as the plastic pouch inside the trap) and propylene glycol was used in the capture vial to preserve specimen.

Experimental Test of Influence of Water Availability on Colonization

Salix lasiolepis pole cuttings were used to test whether *E. whitfordiodendrus* prefer to colonize well-watered trees. Pole cuttings were collected from sixteen uninfested trees at the SCR in Santa Paula, CA in late July 2017. Each of these poles was cut in half to test treatments on genetically identical individuals. Pole cuttings had a mean diameter of 52 mm +/- 5 mm and were cut to a standard 1.25 m length, then potted in 4:1 sand to soil mixture and propagated in the nursery at the Hedrick Ranch Nature Area (HRNA) with a standardized watering regime (watered approx. every other day). Pole cuttings were established in 0.5 m x 0.125 m rectangular pots after two weeks. Following this, pots were deployed near heavily colonized conspecific host trees (with >20 beetle entry holes) that could provide a source of beetles to infest the experimental cuttings. Pole cuttings were experimentally manipulated with a wet (watered to saturation every seven days) or dry (watered to saturation every 21 days) treatment using a paired design in which cuttings from the same tree were imposed with one wet and one dry treatment. A total of four cuttings (two wet and two dry treatments) were chosen randomly using a random number generator and arranged in cardinal directions around a source tree (**Figure 2**). This design was repeated for a total of 32 pole cuttings and 16 replicate pairs. The number of beetle entry holes on source trees (within a 1 m length of area centered at 1.3 m from the ground's surface) and distance of pole cuttings to nearest surface water were measured at the beginning of the experiment. Pole cuttings were censused for beetle entry holes weekly for eight weeks. Soil moisture in pots was not measured. For each pair, the difference of cumulative entry holes after eight weeks between wet and dry treatments was calculated. Differences were averaged for cuttings near the same source tree and compared to a population mean of zero using a one-sample t-test. The number of entry holes was compared between treatments using a multiple linear regression, with initial number of entry holes on source tree and distance to water as covariates. Wet and dry treatments were then separated, and linear models were run for each and plotted together to examine whether treatments diverged in their response to both covariates. Lastly, initial number of entry holes on source trees was correlated with distance to water. All analyses were conducted in R (version 4.0.0).

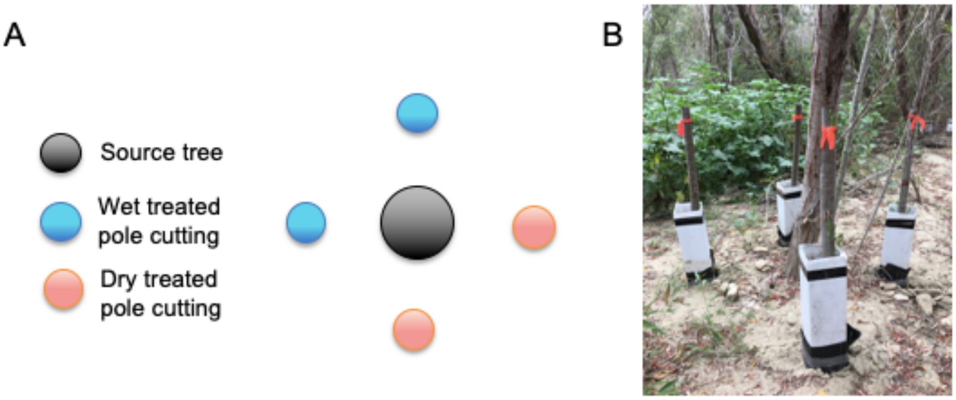

Figure 2. (A) Experimental design of water preference experiment. The black circle represents an infested source tree, blue circles represent pole cuttings treated with a high watering regime (wet) and red circles represent pole cuttings treated with a low watering regime (dry); ‘a’ and ‘b’ represent different genotypes. (B) Photo of the experimental set-up in the field, with experimental *Salix lasiolepis* pole cuttings deployed near an infested source tree.

Host Species Preference and Susceptibility

Choice trials modified from Jones and Paine (2017) were conducted to test beetle preference and host susceptibility to shot hole borers/Fusarium dieback (SHB-FD). Naïve female *E. whitfordiodendrus* were exposed to mature stem samples of five common, native southern California riparian species (*Platanus racemosa*, *Populus fremontii*, *P. trichocarpa*, *Salix laevigata* and *S. lasiolepis*). Stem samples were collected from host trees at the Santa Clara River near Santa Paula, CA. Branches were all collected from different individual trees and ranged from 5.2 to 7.4 cm in diameter and were cut into sections 25 cm long. Beetles were also collected from the SCR and reared in the laboratory on artificial media (Biedermann et al. 2009) made with avocado sawdust. Second generation female beetles were used in the experiment.

Ten trials were conducted inside clear, plastic 0.076 m^3 enclosures, with each experimental unit consisting of branch sections from each of the five host species (10 total reps). Sections were arranged in a circle inside the enclosure in a randomly generated order and stood upright with ends covered in parafilm to reduce moisture loss. An open container of water (approx. 8 oz) was added to each enclosure to increase relative humidity and encourage growth of the beetle's symbiotic fungi. Fifty beetles were released into the center of the enclosures and given seven days to select a branch section to infest, begin creating a gallery, inoculate their symbiotic fungus and lay eggs. After the allotted time, each enclosure was placed in a -40C freezer to kill beetles and halt fungal growth and egg development.

Beetle preference and host susceptibility to SHB-FD were measured for each branch section. Preference was measured by counting the number of beetle entry holes present (**Figure 3A**). The branch sections were then destructively sampled to measure the following susceptibility factors (**Figure 3B**). For each entry hole, the gallery length extending from the entry point was measured and the presence of eggs was recorded for each gallery. These variables were used as proxies for susceptibility to beetle activity, with larger galleries and presence of eggs indicating higher susceptibility to beetle activity. The presence of symbiotic fungus was recorded visually for each gallery, either by the presence of white fungal mycelia, necrotic tissue or both. This was used as a proxy for susceptibility to *Fusarium* dieback, with presence of fungus after seven days indicating higher susceptibility to fungal growth. Due to the destructive nature of sampling potentially causing the loss of some eggs, the presence of eggs was omitted from analysis, although eggs were only detected in one *P. fremontii* and one *S. lasiolepis* gallery, with two and three eggs, respectively.

A sample of each branch section that had not been affected by beetle tunneling was used to measure wood density. Bark was stripped from each sample and volume was measured using the water volume displacement method (Chave 2005). Samples were dried in an oven for seven days at 60C and then weighed. Density was calculated as Density (g/ml) = [dry weight (g)]/ [Volume (ml)].

For each trial, the percent of entry holes was calculated for each species by dividing the number of entry holes on that species by the total number of entry holes on all branches within the same trial. Standardizing by branch size did not produce different results as all branches were very close in size. Beetle host preference was analyzed using a one-way ANOVA, with species as the independent variable and percent entry holes as the dependent variable. Gallery length was averaged for each branch section and mean gallery length among species was analyzed using a one-way ANOVA, with species as the independent variable and average gallery length as the dependent variable. The difference in the proportion of galleries with fungal growth was compared between species using a binomial generalized linear model. Correlation between wood density and gallery length was evaluated using linear regression. Mean wood density between species was analyzed using a one-way ANOVA. All analyses were computed in R (version 4.0.0).

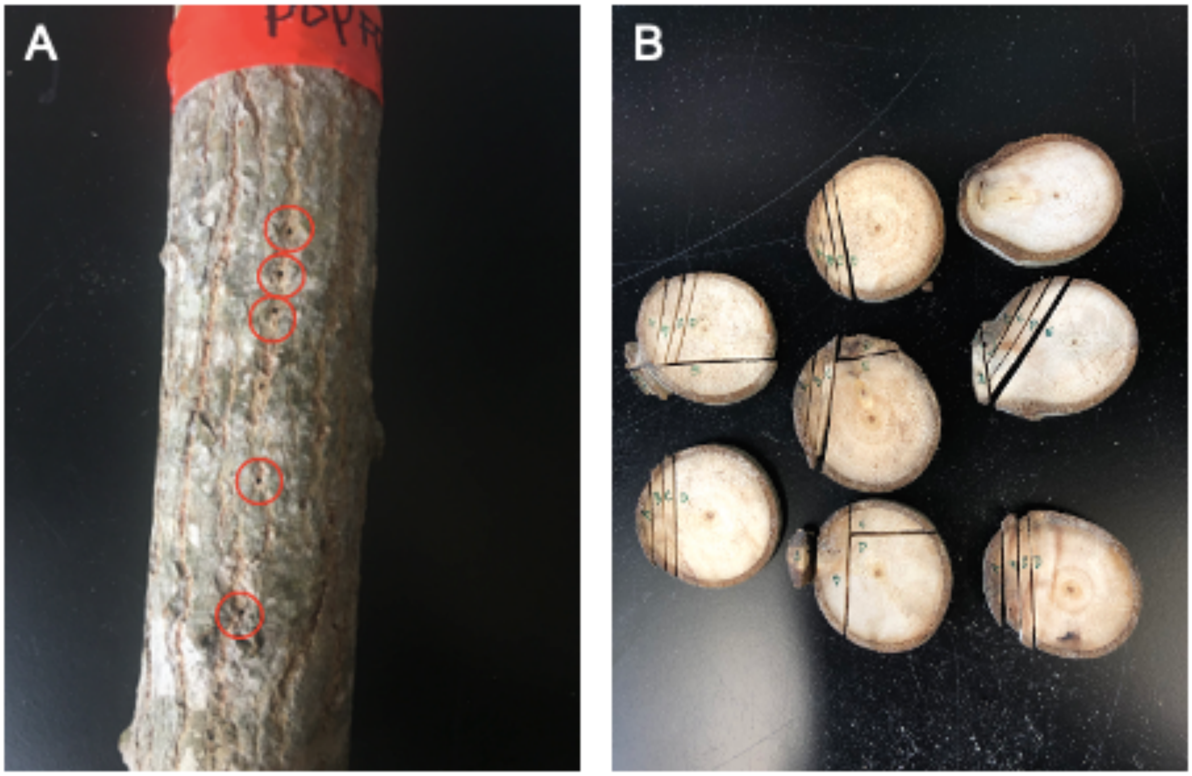

Figure 3. (A) *Populus fremontii* branch section with *Euwallacea whitfordiodendrus* entry holes circled in red. (B) Destructive sampling of *E. whitfordiodendrus* galleries to measure length and record presence of fungi within the tunnel.

Shot Hole Borer Infestation Progression and Change over Time

To characterize how infestations progress and change over time, nine permanent 30m^2 plots were established at the SCR in Santa Paula, CA to track the growth of local infestations (infection of naïve hosts) as well as infestation growth within individual hosts (change in beetle entry holes) over four years (**Figure 4**). Plot locations were chosen where previous vegetation surveys had been conducted in order to compare changes in vegetation pre- and post-arrival of *E. whitfordiodendrus*, however those analyses are not included here. Plots were established and initially monitored in August 2017, then monitored once each year for the following three years. All plots are characterized as riparian forest dominated by *Salix* *lasiolepis* with several other riparian tree species commonly occurring, including *Platanus racemosa, Populus trichocarpa* and *S. laevigata*. In each plot, 30 reproductive host trees were selected and tagged. Trees were chosen systematically by establishing three transects radiating from the center point of the plot in the N, SE and SW directions. The first ten trees encountered along each transect were chosen, with trees ranging from <1 m to 6 m apart. Each plot had a variety of host tree species in varying sizes, some infested and some not. Tagged trees were monitored for (a) diameter at breast height (dbh, measured 1.3 m from the ground surface), (b) number of beetle entry holes (measured in a 1m length centered around the dbh line), (c) whether infested or not infested, and (d) displaying symptoms of SHB-FD (staining, exudate, frass and canopy dieback). Infestation rates per plot (percent infested out of 30 potential hosts) were calculated to quantify infection of naïve hosts over time. The number of entry holes for each species was binned into three infestation severity categories: low (<50 beetle entry holes), moderate (50-200 entry holes) and severe (>entry holes) (Eskalen 2013).

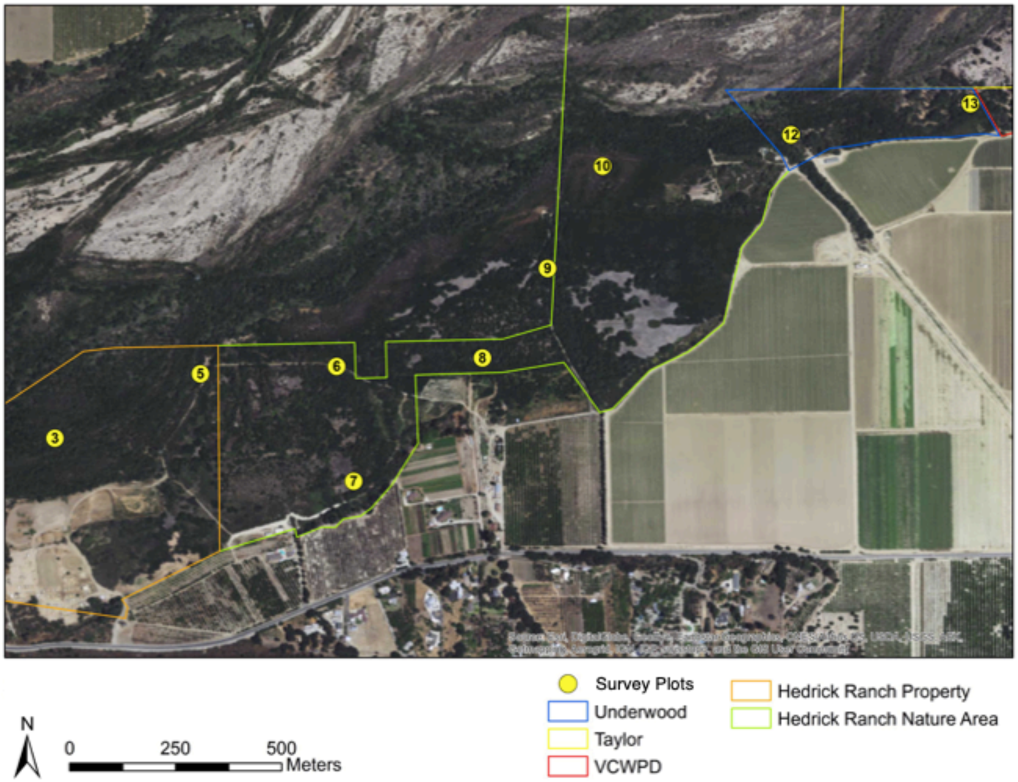

Figure 4. Map of permanent 30 m^2 plots used for monitoring *Euwallacea whitfordiodendrus* infestations over time. Plots are located in Santa Paula, CA.

Results:

Distribution and Dispersal

Euwallacea whitfordiodendrus was detected at a total of 29 out of 42 trap locations by the end of the study period (**Figure 5**), with fourteen initial detection locations in 2016. While beetles initially continued to spread, with twelve new detection locations in 2017, detections slowed with three new detection locations in 2018 and none in 2019. The proportion of traps with *E. whitfordiodendrus* differed significantly between years (χ^2 (3)=8.84, p=0.032; **Figure 6**). Cumulative presence significantly increased between 2016 and 2018 and between 2016 and 2019, but not between 2017 and any later years, supporting a decline in beetle dispersal after 2017 as there were still several traps near positive detections that the beetles did never reached (**Figure 7**).

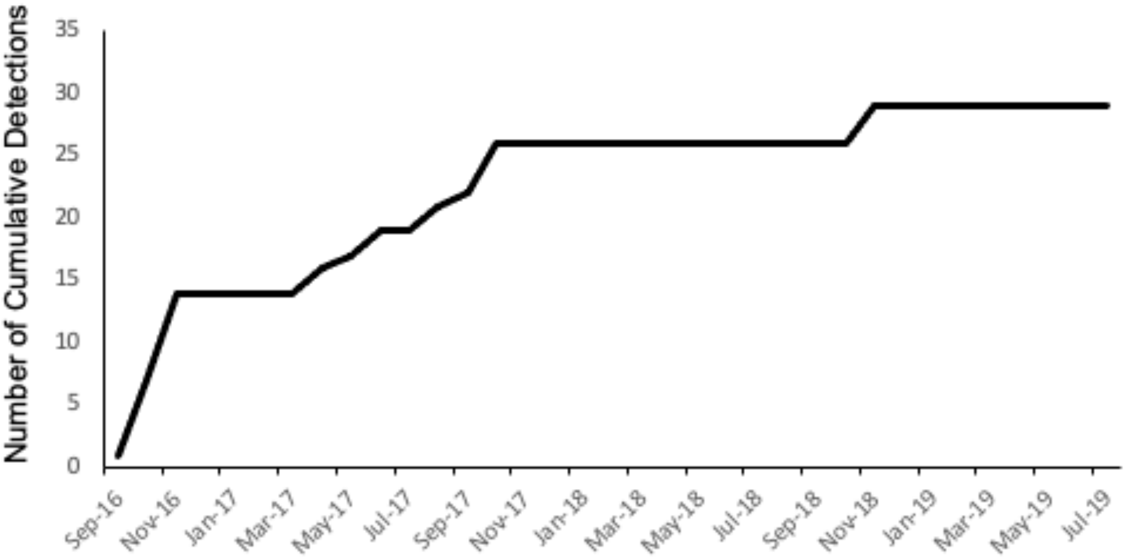

Figure 5. Cumulative number of traps with *Euwallacea whitfordiodendrus* detections deployed in the Santa Clara River from September 2016 to July 2019. Forty-two traps were initially deployed between August and October 2019, while twelve additional traps were deployed in October 2018. All traps with detections continued to catch beetles following the initial detection.

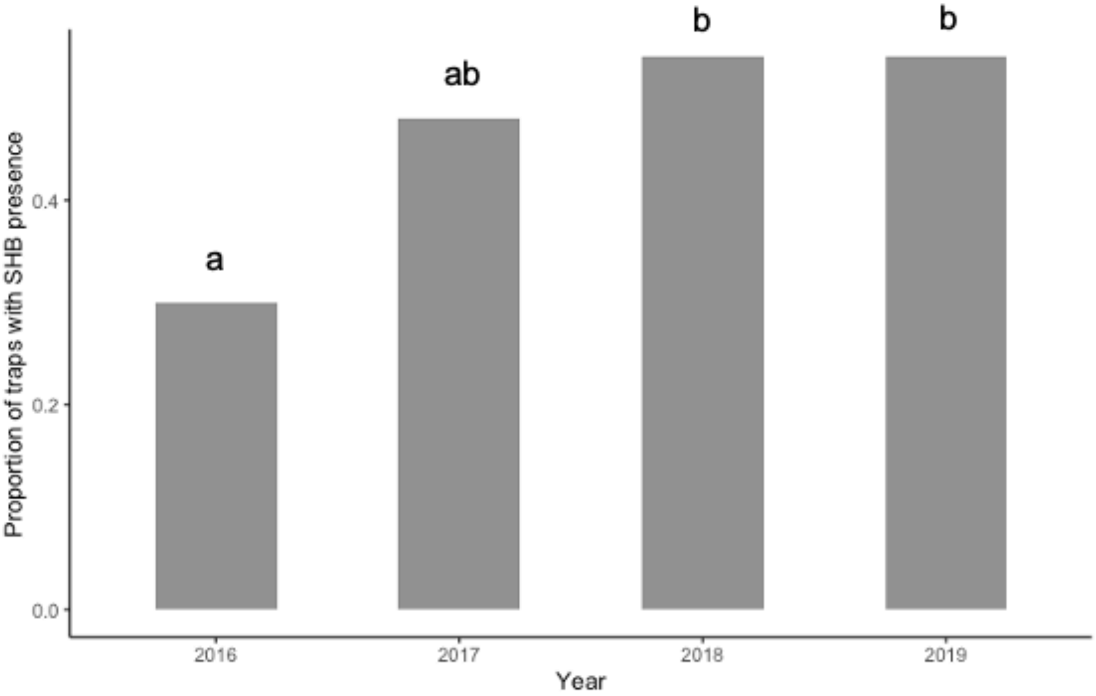

Figure 5. Proportion of traps with shot hole borer presence from traps deployed in the Santa Clara River from September 2016 to July 2019. Forty-two traps were initially deployed between August and October 2019, while twelve additional traps were deployed in October 2018. Shot hole borer presence differed significantly between years (χ^2 (3) = 8.84, p=0.032). Different letters represent significant differences.

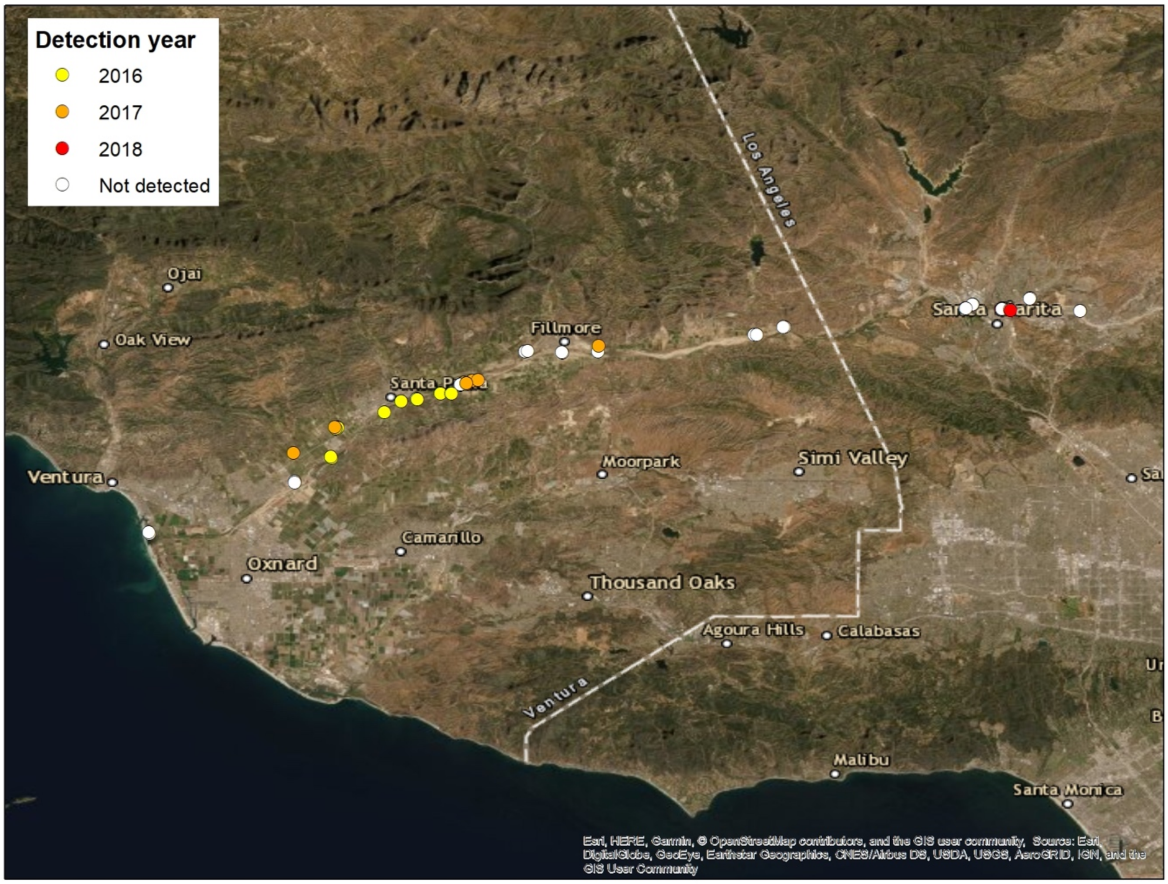

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Figure 7. Distribution of *Euwallacea whitfordiodendrus* (SHB) at the Santa Clara River in Ventura and Los Angeles Counties indicated by year of first detection. Traps in Ventura County were deployed in September 2016 and traps in Los Angeles County were deployed in October 2018. Yellow circles indicate locations where SHB was first detected in 2016, orange circles indicate where SHB was first detected in 2017 and red circles indicate where SHB was first detected in 2018. White circles indicate where a detection trap was deployed but no SHB has been detected.

Experimental Test of Influence of Water Availability on Colonization

Ten out of sixteen dry treated pole cuttings were infested with a mean of 14.8 (+/- 23.4 standard deviation) entry holes. Similarly, twelve wet treated pole cuttings were infested but with a mean of only 7.8 (+/- 10.2 standard deviation) entry holes. Dry treated pole cuttings had a maximum of 71 entry holes while wet treated pole cuttings had a maximum of 31 entry holes. Although there was a trend of higher colonization in dry cuttings, the difference between treatments was not significantly different from zero (t(7)=-1.44, p=0.19;

Figure 8). The initial number of entry holes on source trees ranged from 20 to 309 holes per 1 m of surface area centered at 1.3m from the ground's surface (mean = 110 entry holes +/- 102 holes). The number of entry holes on experimental pole cuttings was higher in areas with higher source tree infestation severity (F(1, 28)=13.65, p<.001). Linear regressions were plotted for wet (R^2 = 0.28 p=0.02) and dry treated cuttings (R^2 = 0.56, p<0.001) and the difference in regression lines at higher source tree infestation indicates a trend towards more entry holes on dry cuttings than wet (**Figure 9**). Distance to water ranged from 1.01 m to 18.05 m (mean =6.93 m +/- 5.77m SD). The number of entry holes on experimental cuttings was higher in areas closer to surface water (F(1, 28)=4.20, p=0.05) and in this case there was no difference between the wet (R^2 = 0.27 p=0.02) or dry treated cuttings (R^2 = 0.26, p=0.02). (**Figure 10**). Overall the multiple linear model significantly explained the number of entry holes on cuttings (F(3, 28) = 10.48, R^2=0.48 , p<0.001). The initial number of entry holes on source trees was significantly correlated to the distance to nearest surface water (F(1,30)=6.23, p=0.018; R^2=0.14; **Figure 11**).

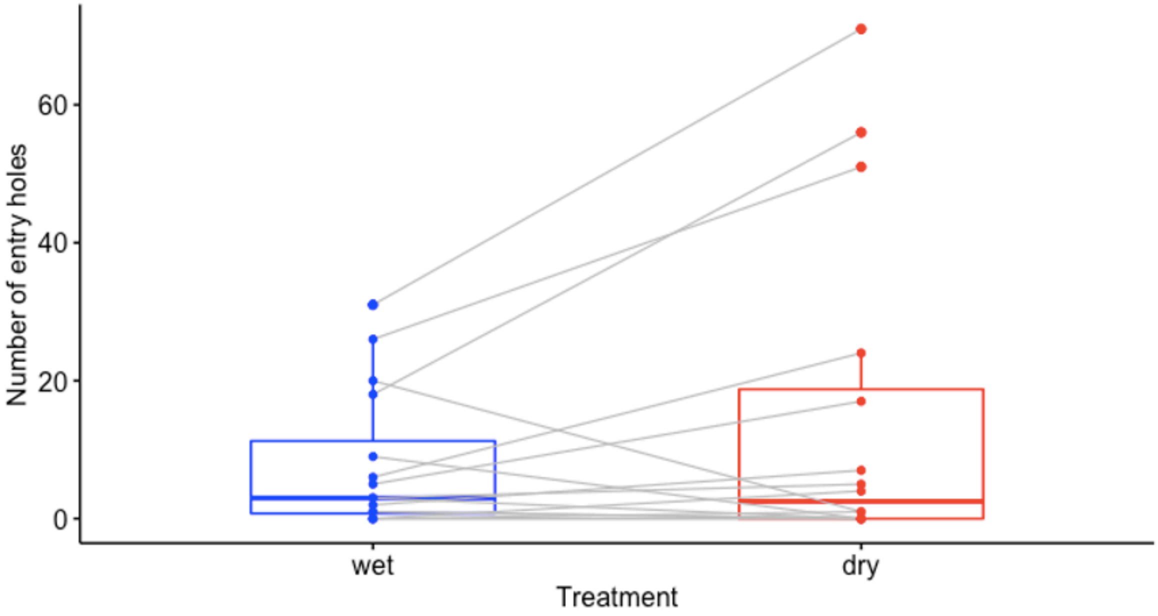

Figure 8. Number of *Euwallacea whitfordiodendrus* entry holes on *Salix lasiolepis* pole cuttings under different watering treatments. There is a trend towards higher beetle colonization rate in the dry cuttings, however differences between the treatments was not significantly different from zero (t(7)=-1.44, p=0.19).

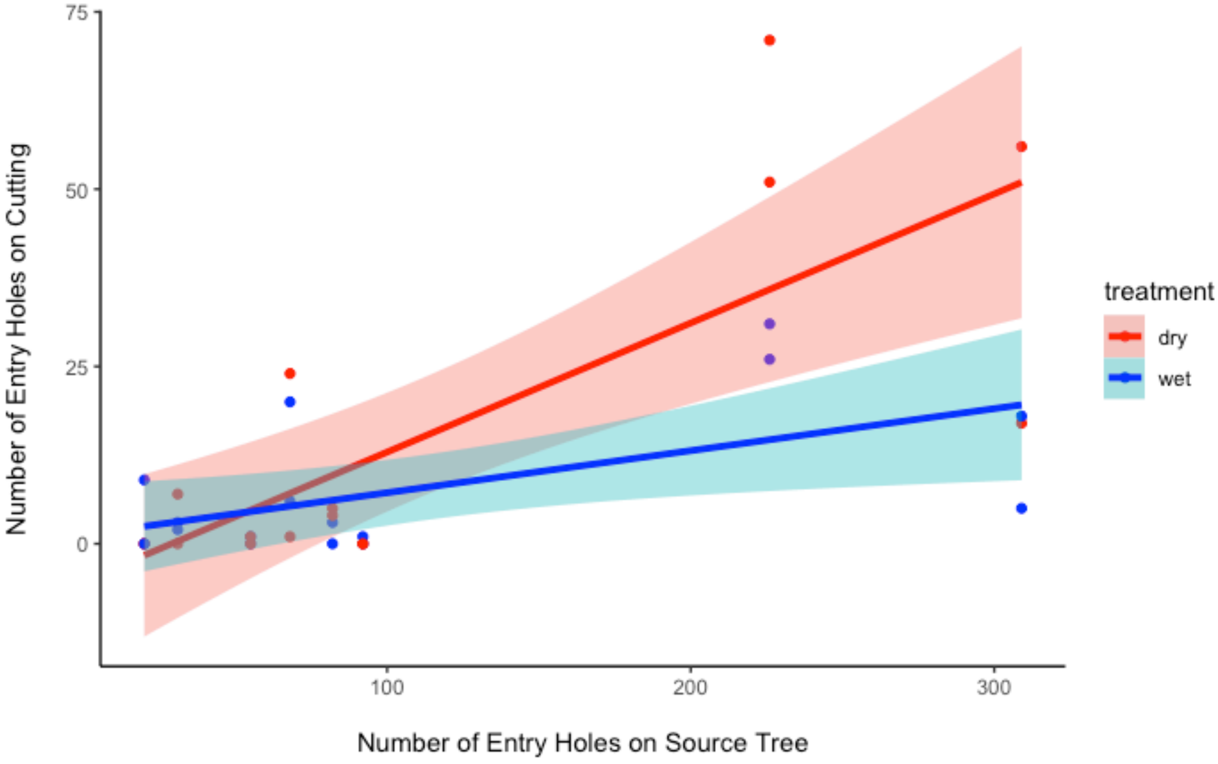

Figure 9. Regression analysis modeling the relationship of source tree infestation (number of entry holes) and number of entry holes on wet (blue line, $R^2 = 0.28$ p=0.02) or dry treated cuttings (red line $R^2 = 0.56$, $p < 0.001$). Overall there was a significant effect of source tree infestation on the number of entry holes on cuttings (F(1, 28)=13.65, p<.001). Difference in regression lines at higher source tree infestation indicates a trend towards more entry holes on dry cuttings than wet. Regression lines are plotted with 95% confidence intervals shown by shaded regions.

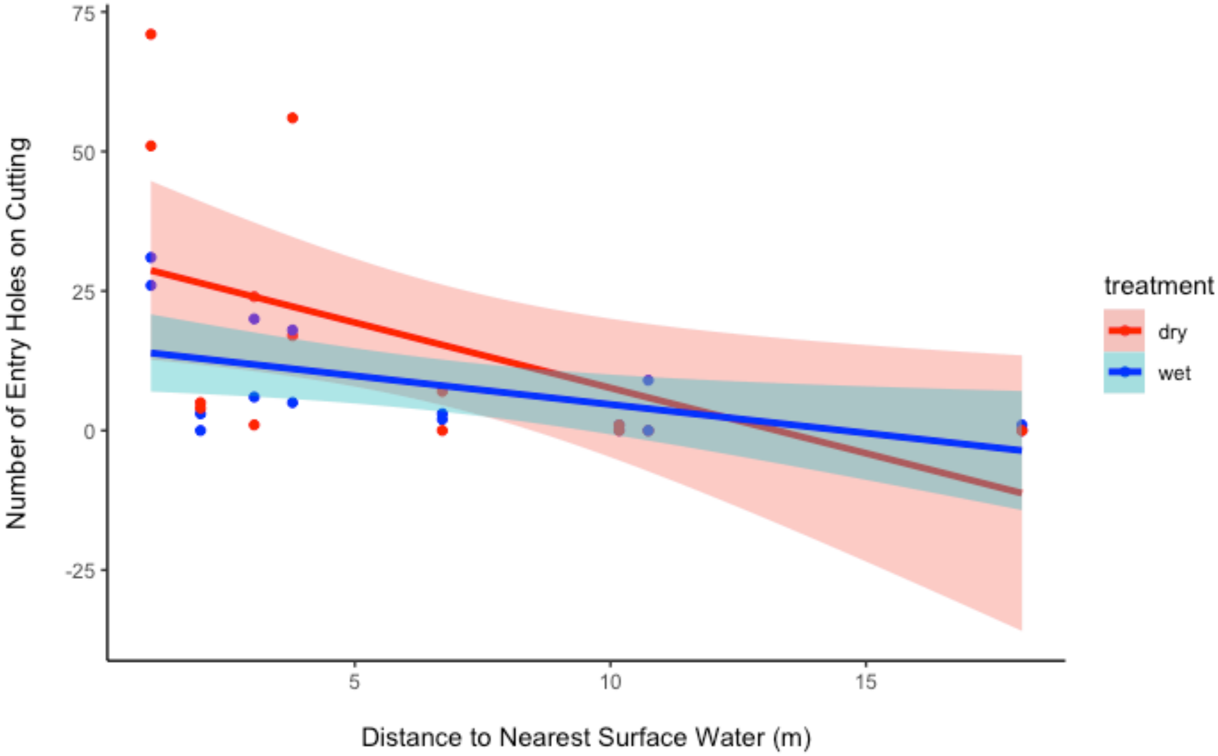

Figure 10. Regression analysis modeling the relationship of distance to nearest surface water (m) and number of entry holes on wet (blue line, $R^2 = 0.27$ p=0.02) or dry treated cuttings (red line $R^2 = 0.26$, p=0.02). Distance to nearest surface water had a significant effect on number of entry holes overall (F(1, 28)=4.20, p=0.05), but there was no difference between the treatments (F(1, 28)=2.29, p=0.14). Regression lines are plotted with 95% confidence intervals shown by shaded regions.

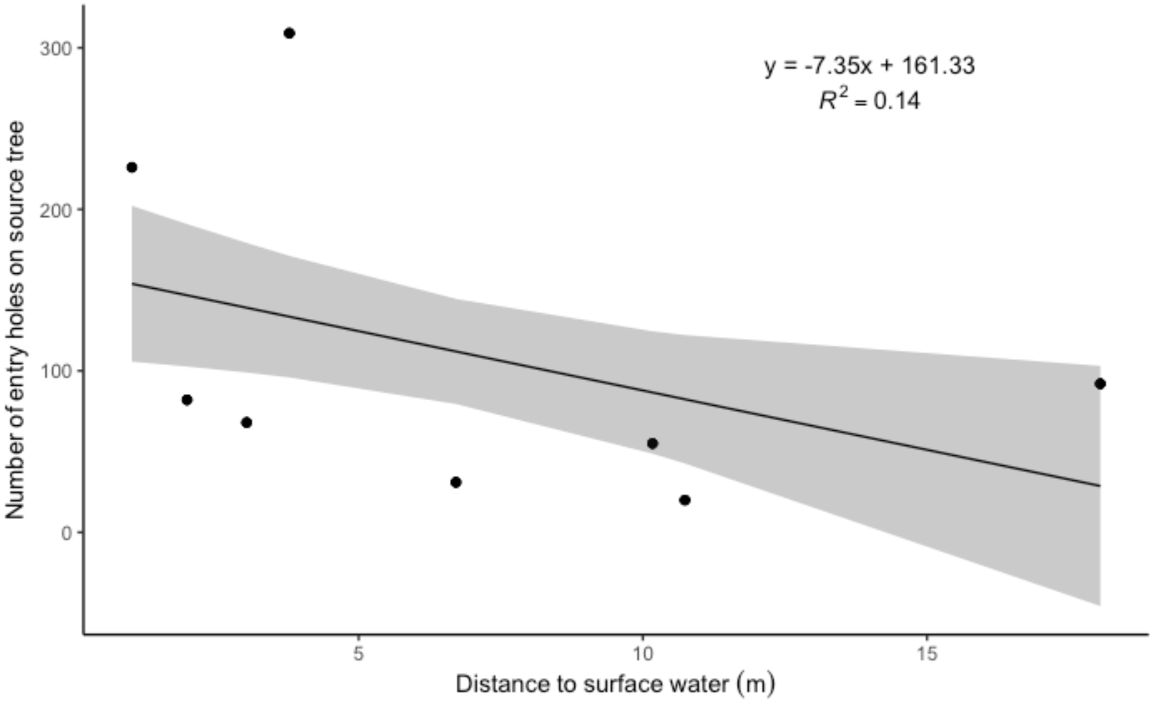

Figure 11. Relationship between distance to nearest surface water (m) and initial number of *Euwallacea whitfordiodendrus* entry holes on source trees. Trees closer to surface water had a higher number of beetle entry holes (F(1,30)=6.23, p=0.018; R^2=0.14). Shaded region indicates 95% confidence interval for the predicted value.

Host Species Preference and Susceptibility

In each trial, an average of 31 out of 50 beetles made a choice (entered one of the branch sections) and all host species had at least one beetle entry hole within each replicate branch (**Figure 12**). Galleries stemming from each entry hole were confirmed to have one beetle occupying them at the time of sampling. There was no significant difference in beetle choice between the host species tested (*Platanus racemosa*, *Populus fremontii*, *P. trichocarpa*, *Salix lasiolegpis*, and *S. laevigata*) (F(4,45)=1.29, p=0.29; **Figure 13**). Gallery length ranged from 2 mm to 64 mm (mean= 13.4mm +/- 8.4 mm). Mean gallery length differed between species (F(4,43)=3.9, p=0.008; **Figure 14**). On average, *Salix laevigata* had the longest galleries while *P. racemosa* had the shortest galleries. The remaining species had similarly intermediate length galleries. Proportion of galleries with fungal growth ranged from 0.2 to 0.31, indicating beetle establishment in the gallery, and there was a significant difference in fungal growth between species ($\chi^2(4) = 19.6$, $p<0.001$; **Figure 15**). Here, *P. racemosa* and *S. laevigata* had the highest proportion of galleries with fungal growth, while *Populus* species tended to have fewer galleries with fungal growth. Wood density differed significantly between species ($F(4,43)=16.18$, $p<0.001$; **Figure 16**) and wood density significantly predicted beetle gallery length ($F(1, 46) = -38.6$, $p<0.001$; $R^2 = 0.32$; **Figure 17**). *Platanus racemosa* had the highest wood density and the shortest galleries, while *S. laevigata* had the lowest wood density and the longest galleries. However, *S. lasiolepis* had significantly higher wood density than *S. laevigata* but similar length galleries and *Populus* species had lower wood density but similarly long galleries compared to *P. racemosa*.

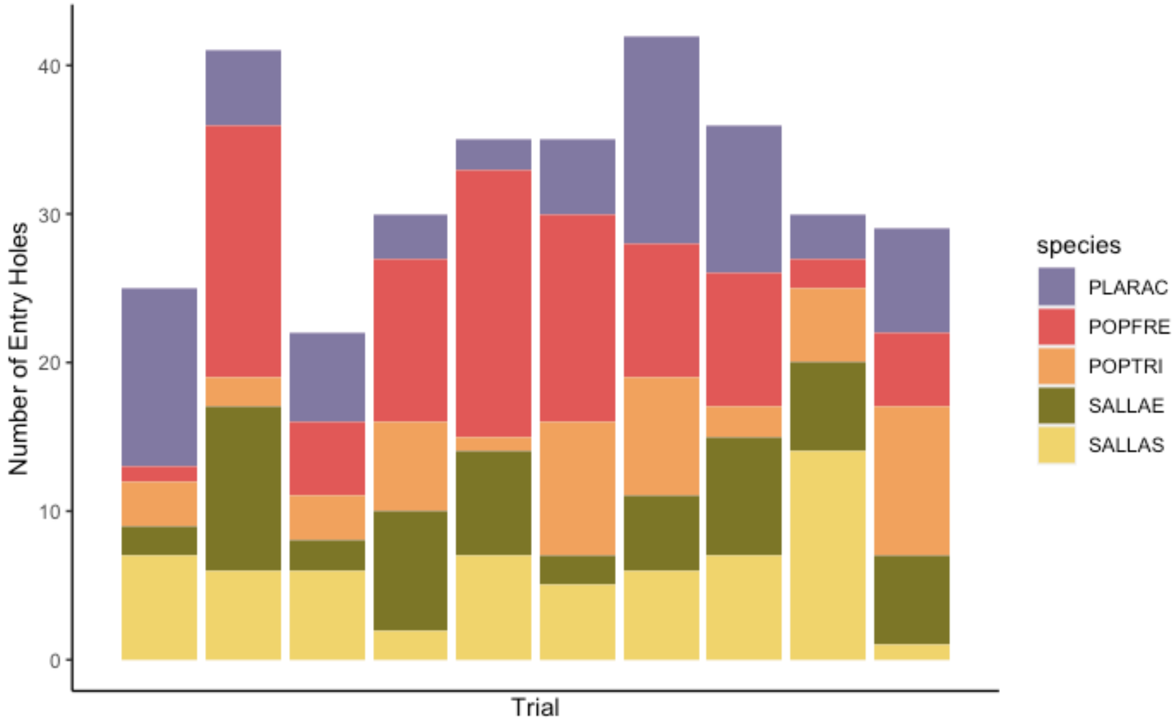

Figure 12. Number of entry holes by species for each choice trial. Species include *Platanus racemosa* (PLARAC), *Populus fremontii* (POPFRE), *Populus trichocarpa* (POPTRI), *Salix laevigata* (SALLAE), and *Salix lasioelpis* (SALLAS).

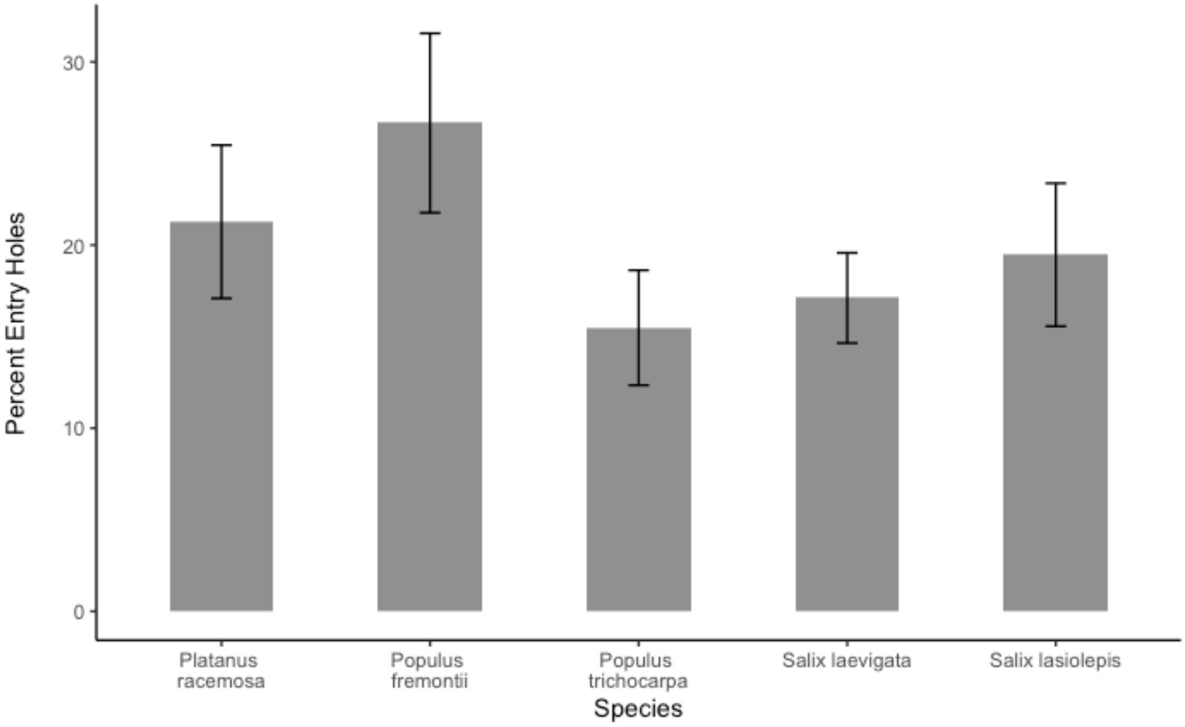

Figure 13. Preference of *Euwallacea whitfordiodendrus* among riparian host species, indicated by mean percent entry holes. There is no difference in beetle choice between the host species (F(4,45)=1.29, p=0.29). Error bars represent one standard error.

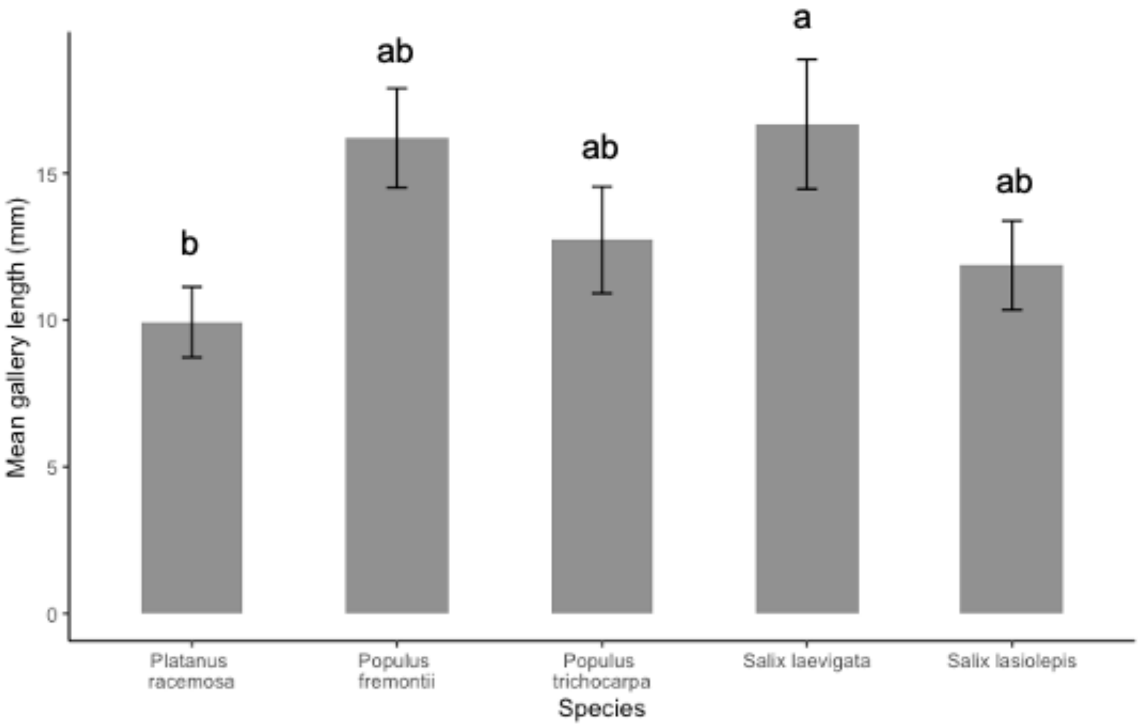

Figure 14. Susceptibility of riparian host species to *Euwallcea whitfordiodendrus,* indicated by mean gallery length (mm). Mean gallery length differed between species (F(4,43)=3.9, p=0.008). Different letters indicate a significant difference in gallery length. Error bars represent one standard error.

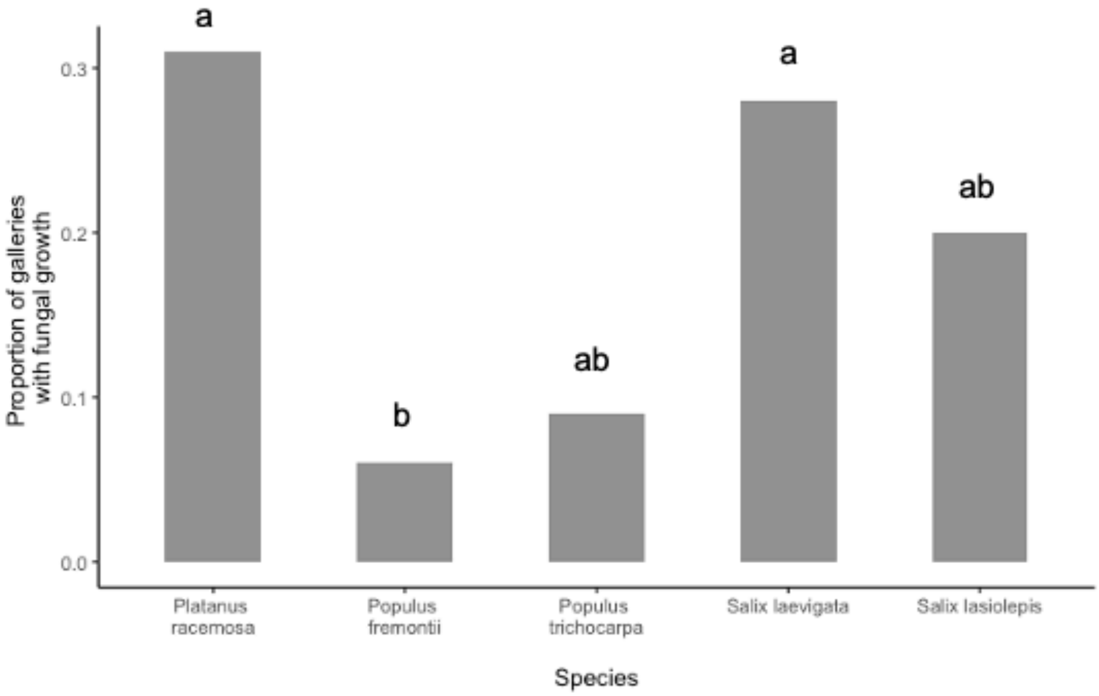

Figure 15. Proportion of galleries with fungal growth across *Euwallacea whitfordiodendrus* riparian host species. There is a significant difference in fungal growth between species ($\chi^2(4) = 19.6$, $p<0.001$). Different letters indicate a significant difference in presence of fungal growth based on Tukey's multiple comparisons test.

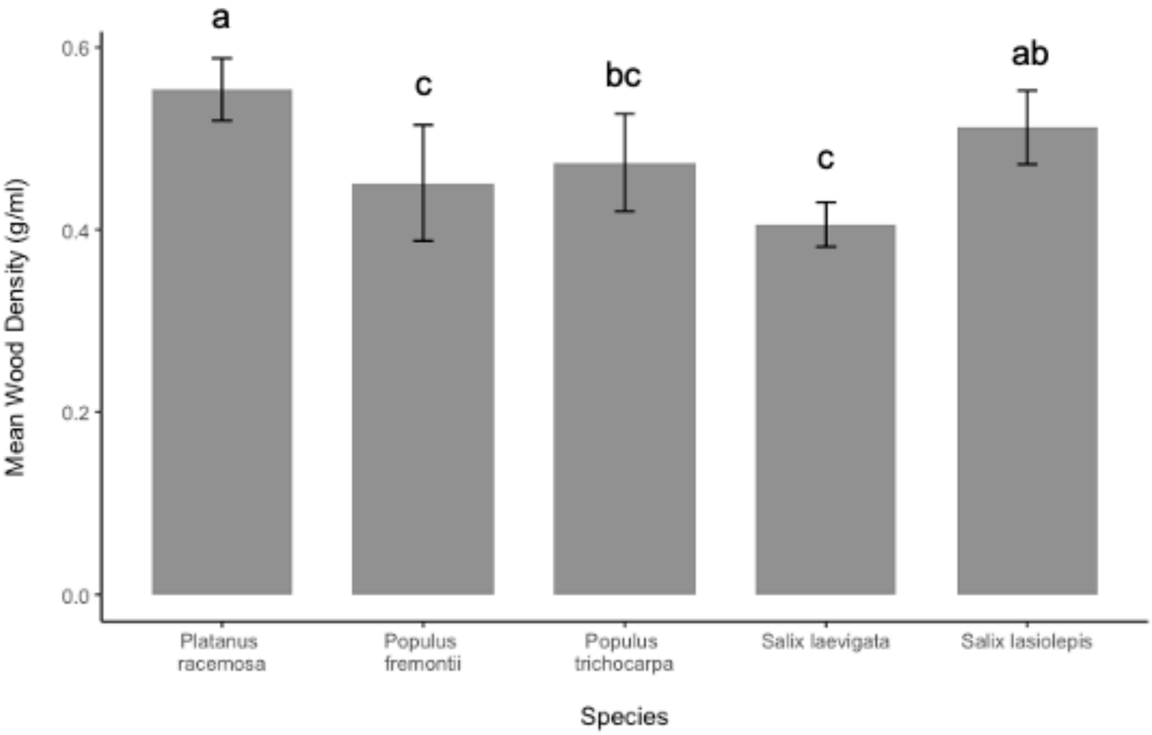

Figure 16. Mean wood density of *Euwallacea whitfordiodendrus* riparian host species. There is a significant difference in density (g/ml) between species (F(4,43)=16.18, p<0.001). Different letters indicate a significant difference in wood density. Error bars represent one standard deviation.

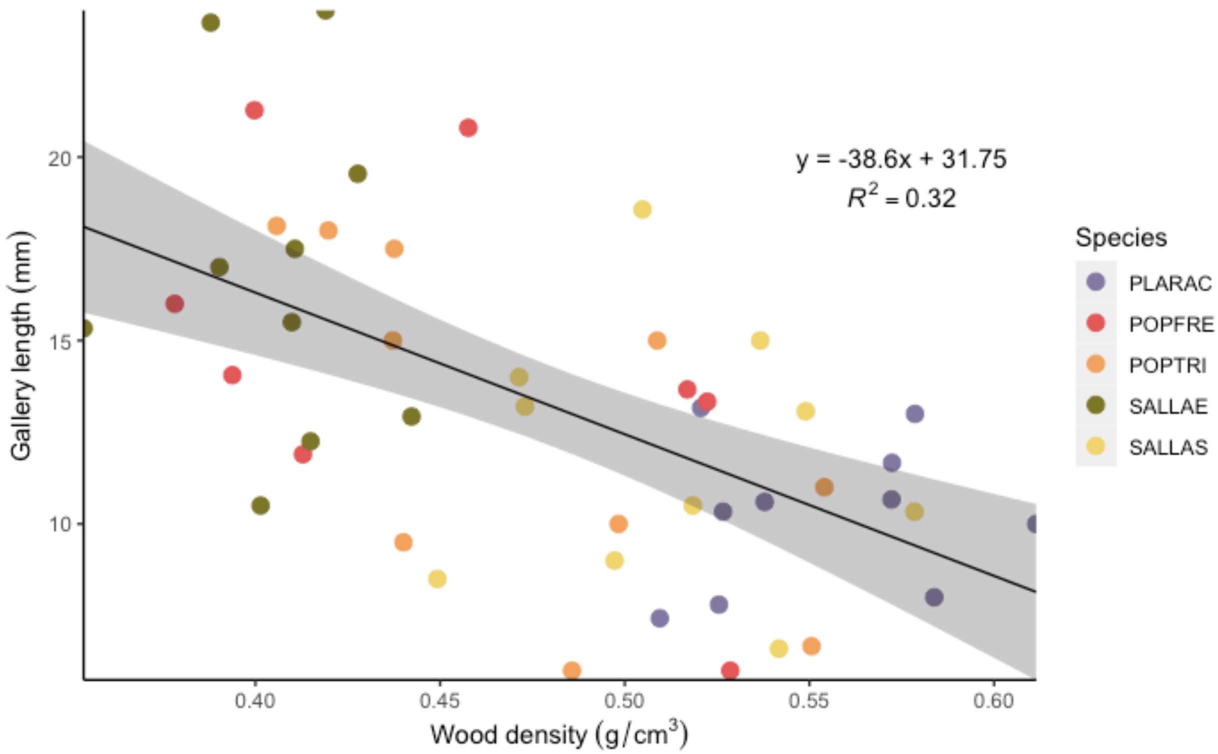

Figure 17. Relationship between host species wood density and *Euwallacea whitfordiodendrus* gallery length. Beetle gallery length (mm) is significantly predicted by wood density (g/cm^3) ($F(1,46) = 22.68$, $p<0.001$, $R^2 = 0.32$). Red dots represent *Platanus racemosa* (PLARAC), blue dots represent *Populus fremontii* (POPFRE), green dots represent *P. trichocarpa* (POPTRI), purple dots represent *Salix laevigata* (SALLAE) and orange dots represent *S. lasiolepis* (SALLAS). Shaded region indicates 95% confidence interval for the predicted value.

Shot Hole Borer Infestation Progression and Change over Time

Infestation rates increased in all plots from 2017 to 2018 and most plots continued to show increases from 2018 to 2019. By 2020, several plots had lower or stable infestation rate (**Figure 18**). Infestation rates for plots 7, 8, 9 and 13 were not able to be calculated in 2020 either due to site inaccessibility or significant plot changes owing to storm-induced tree fall or tampering of tagged trees.

A total of 270 naturally occurring trees were monitored for beetle presence including six *Alnus rhombifolia*, four *Platanus racemosa*, one *Populus fremontii*, 29 *P. trichocarpa*, 14

Salix laevigata and 216 *S. lasiolepis*. *Alnus rhombifolia*, *P. racemosa*, and *P. fremontii* were omitted from the analysis due to small sample size. There were 90, 165, 155 and 128 total infested trees in 2017, 2018, 2019 and 2020 respectively (**Table 1**). The lower number of infested trees in 2020 is partially explained by an inability to sample trees in plots 7, 8, 9 and 13 in that year. Infestation severity differed among host species in all years (**Figure 19**). Sites were dominated by *S. lasiolepis*, and across all species, most individuals had low to modest infestations, with *S. lasiolepis* being the only species with moderate or severe infestations. Overall, the number of severely infested trees increased from 2017-2018 but, surprisingly, decreased from 2018-2020 (**Figure 20**). Decrease in severity was characterized by fewer visible beetle entry holes and some qualitative evidence of healing holes, such as clumps of dried exudate or frass covering entry holes. Interestingly, eighteen infested individuals of *S. lasiolepis* in site 12 (the site with the highest infestation rate) had severe crown dieback in 2019 and subsequently exhibited vigorous resprouting at their base in 2020, despite continuing beetle presence.

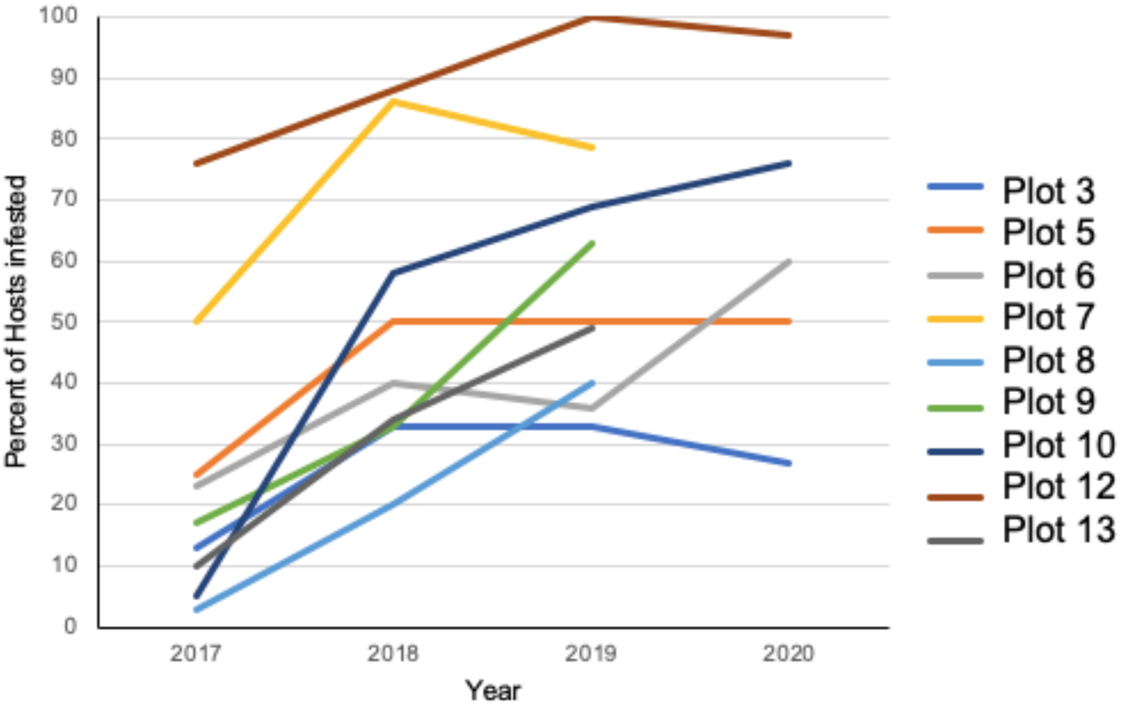

Figure 18. *Euwallacea whitfordiodendrus* infestation rates for nine plots at the Santa Clara River in Santa Paula, CA. Infestation rate was calculated as the percent of hosts infested out of total potential hosts that were monitored. Different colors represent different plots. Not all trees were found in 2020, so data was omitted for plots 7, 8, 9 and 13 in that year.

Table 1. Number of trees infested with *Euwallacea whitfordiodendrus* within monitoring plots at the Santa Clara River from 2017 to 2020.

Year	Total infested trees	*Populus trichocarpa*	*Salix laevigata*	*Salix lasiolepis*
2017	90	2	7	79
2018	165	10	9	140
2019	155	9	7	131
2020	128	6	5	109

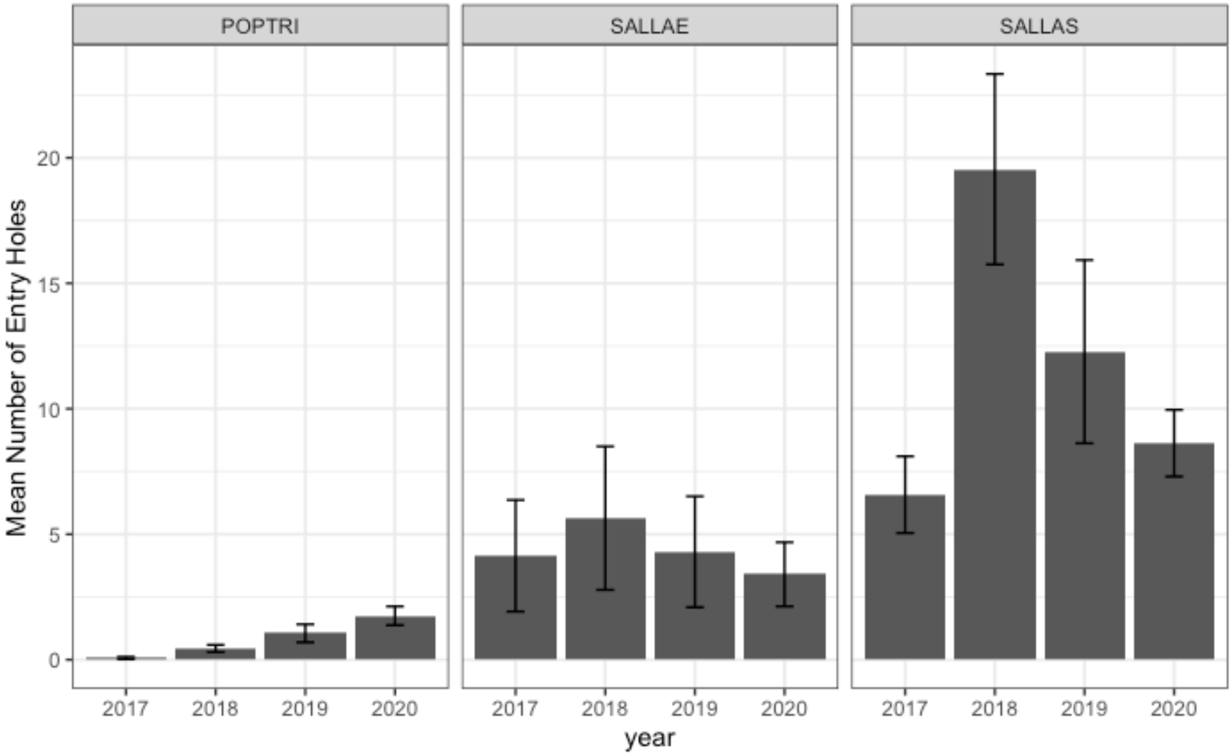

Figure 19. Mean number of *Euwallacea whitfordiodendrus* entry holes for *Populus trichocarpa* (POPTRI), *Salix laevigata* (SALLAE) and *S. lasiolepis* (SALLAS) in 2017, 2018, 2019 and 2020.

Figure 20. Frequency plot of infestation severity levels for *Populus trichocarpa* (POPTRI), *Salix laevigata* (SALLAE) and *S. lasiolepis* (SALLAS) in 2017, 2018, 2019 and 2020. Low infestation severity indicates trees with <50 *Euwallacea whitordiodendrus* entry holes, moderate severity indicates trees with 50-200 beetle entry holes and severe indicates >200 entry beetle holes. Infestation severity scale taken from UCANR 2020.

Discussion:

Distribution and Dispersal

After 2012, *Euwallacea whitfordiodendrus* had a rapid rate of spread throughout southern California (UCANR 2020a). It is thought that this was largely due to human facilitated dispersal through the movement of firewood or other infected plant material (UCANR 2020b). Detection trapping in Ventura County followed this trend, showing a notable increase in beetle detections the first two years after the species was first detected in 2015. The increase in new detections declined in 2018 and the number of locations with *E. whitfordiodendrus* remained stable throughout 2019. In fact, the increase of new detections in

2018 found in this study was potentially due to the deployment of new traps that year to expand coverage of the watershed where it is possible that the beetles were already present prior to 2018. This would further support the pattern of general cessation in beetle spread in the SCR after 2017. The infected range remains fairly widespread, yet patchy, as several sampling locations had no beetle detections despite positive detections up and downriver from them. This is somewhat surprising as the beetles did not reach approximately half the traps that were deployed in their potential habitat.

Distribution of *E. whitfordiodendrus* in its native range is not well documented, so patterns in spatial distribution there are not known. However, the general climate is characterized as tropical to subtropical, with mean annual rainfall ranging from 700 to 5,000 mm, mostly occurring during the rainy season from May to December (Vietnam Assessment Report on Climate). Mean summer temperatures range from about 70 C to 85 C and mean winter temperatures are moderate, usually about 60 C. In the lab, Umeda and Paine (2019) found that *E. whitfordiodendrus* can grow and reproduce in temperatures ranging from 13 to 33 C, with optimal temperature of 24 to 30 C. Although eggs laid at 15C were not able to fully develop, adults could survive at this temperature for 200 days and potentially longer. These beetles live within insulated host trees that are often several degrees warmer than ambient temperatures, further facilitating the beetle's survival in regions with cold winter months (Powell 1967). In Ventura County, the average annual temperature is approximately 16C. This is not optimal for *E. whitfordiodendrus*, but should be sufficient to allow survival year-round, despite sub-optimal conditions for beetle development during the colder winter months when temperatures reach an average low of 7.8C.

The success of symbiotic fungal food sources must also be taken into consideration when evaluating the potential distribution patterns of *E. whitfordiodendrus*. There is evidence that, in general, temperature can influence fungal growth as well as rates of mycophagy (Six and Bentz 2007, Adam and Six 2007), which could also be limiting beetle population growth and dispersal in this system. Microclimate can vary through a river depending on stand structure and has been shown to affect habitat quality and host colonization of saproxylic insects such as bark beetles (Coleoptera: Scolytinae) (Reed and Muzika 2010, Bouget and Duelli 2004, Vodka et al. 2009). This suggests that for *E. whitfordiodendrus*, some microclimates are not as suitable as others for beetle development and dispersal. In addition, the river is highly impacted by agricultural and urban development. Large areas of land lacking host trees may act as dispersal barriers. It is possible that the species have realized their potential distribution in the Santa Clara River watershed under current climate conditions, which explains the plateauing number of locations capturing beetles and declining number of entry holes per tree (Figure 18).

Experimental Test of Influence of Water on Colonization

This study does not support the initial hypothesis that *Euwallacea* species prefer well-watered trees (Akif Eskalen, personal communication). There was no difference in beetle host choice between well-watered or water stressed trees and our study suggest a trend towards preference for dry trees. The results of this study are similar to previous work by Umeda (2017) who found no host preference of the beetle between liquidambars and potted Acer negundo under different water regimes. At the Tijuana River Valley (TRV), *E. kuroshio* was initially found in relatively wetter, *Salix*-dominated areas (Boland 2016), but expanded into dry sites the following year (Boland 2017). At the Santa Clara River, *E. whitfordiodendrus* is found in wet floodplains as well as dry areas where trees were heavily impacted by the 2011-2017 drought (personal observation). In our experiment, distance to water did influence beetle choice of trees and this was likely driven by the greater number of beetles occupying mature trees growing closer to surface water. These beetles colonized these areas more heavily than source trees further from surface water. Beetles may be responding to higher relative air humidity rather than host tree water availability, as has been shown for several ambrosia beetles species found in dry tropical forests of Brazil (Macedo-Reis et al. 2016). Thus, microclimate likely plays a role in *Euwallacea* distribution within a floodplain while tree water status is less important.

While host tree water availability was not a significant determining factor for beetle host choice, it may be important for the host's susceptibility to beetle activity or fungal growth. Boland and Woodward (2019) found that trees closer to the water channel had lower wood densities. Here we found that lower woody density may facilitate greater gallery formation. Fungal growth can have variable effects depending on host tree water availability. In a study analyzing the disease severity of a bark beetle-vectored fungal pathogen (*Endoconidiophora polonica*) in Norway spruce treated with high or low water availability, some strains caused greater disease severity and mortality in seedlings with higher water availability while others had no effect with increased water availability (Linnakoski et al. 2017). In the case of drought-induced stress, a tree's defense capacity is weakened, benefitting ambrosia beetles, and soluble nitrogen is mobilized, making it more available for use by the beetle's symbiotic fungi (Mattson and Haack 1987). Several other studies have found that boring insect colonization increased significantly on stressed trees due to decrease in plant defenses (Koricheva and Larsson 1998, Gely et al. 2019) or reduced bark moisture leading to less incidences of drowning (Huberty and Dunn 2004).

Host Species Preference and Susceptibility

Although *E. whitfordiodendrus* did not exhibit differences in host choice among riparian host species in our lab choice trials, there was a difference in host species susceptibility to beetle activity and fungal growth. Differences in susceptibility to beetle tunneling may be related to wood density. *Platanus racemosa*, the species with the highest wood density, had the shortest beetle galleries. In contrast, *Salix laevigata* had the lowest wood density and the longest beetle tunnels (Figure 16). These results suggest that wood density may be a good predictor of successful beetle activity within a host. Wood density, however, does not appear to be a good predictor of fungal growth. *Platanus racemosa* had the highest susceptibility to fungal growth and highest wood density, followed by *S. laevigata* which had the lowest wood density. The two *Salix* and two *Populus* species were similarly susceptible to beetle tunneling, however *Populus fremontii* is significantly less susceptible to fungal growth, with *P. trichocarpa* having the next lowest proportion of galleries with fungal growth. Fungal growth, however, was not clearly linked to one genus since variation was high within both *Salix* and *Populus*.

Beetle population growth is related to the success of symbiotic fungi in host trees, as beetle brood size and development rate are directly correlated to the presence and quality of their symbiotic fungi (Umeda 2017). Thus, higher beetle success should occur in host species that support more fungal growth, such as *P. racemosa* and *Salix* species. These hosts will likely support larger and faster growing populations of *E. whitfordiodendrus*, allowing for more rapid dispersal of beetle populations from these hosts to nearby hosts. The field experiment conducted in this study showed higher beetle attack frequency for *S. lasiolepis* than any other host species. *Populus* species are less likely to be inoculated with *Fusarium*, suggesting a higher resistance to beetle infestation. This may help to explain the patchy distribution at the SCR.

Shot Hole Borer Infestation Progression and Change over Time

Although there was the potential for a dieback event to occur at the SCR similar to that observed at the TRV because of a similarly abundant availability of hosts, the current evidence is not adequate to support that this will occur. Although infestation rates increased from 2017-2018, many plots had decreased or stabilizing infestations thereafter. In addition, the number of severely infested trees increased from 2017-2018 but decreased from 2018-2020. In the TRV, Boland and Uyeda (2020) also observed a peak in infestation rates during the initial dieback event in 2016 but found declining rates ever since, as trees that were once marked as infested were no longer showing active signs of infestation. Similar to the SCR, the authors also noted that there was no “typical” infestation trajectory, and that infestations progressed differently in different areas along the Tijuana River and that less severe infestations were not necessarily newer.

It is clear the *Salix lasiolepis* has been the most impacted species at the SCR. It was the only species to be moderately or severely infested although it is also the most abundant species through this reach of the river. Boland and Uyeda (2020) also saw higher infestation severities in *Salix* species at the TRV. The reason for lack of severe infestations in *S. laevigata* at the SCR is not clear, but it may be due to lower abundance in the locality that the study was conducted. A lower or moderate severity of infested *Populus* in these plots could be explained by the lower susceptibility to fungal growth. Many individuals from all species that have persisted for several years with a low infestation severity. In the TRV, infestation rates had to be very high (>75%) before significant mortality occurred in those plots (Boland and Uyeda 2020). Infestation rates at most sites in the SCR are lower than this threshold and only 21 trees have died in these plots in which cause of death is likely attributed to *E. whitfordiodendrus*. Interestingly, some infested *Salix* individuals at both the SCR and TRV are resprouting at their base after initial crown dieback, suggesting that infested trees do not necessarily die and may be able to persist (Boland 2018). This may help to lessen the concerns about loss of habitat for wildlife in the area, and may even benefit some listed taxa, such as the southwestern willow flycatcher (*Empidonax traillii extimus*) and least Bell's vireo (*Vireo bellii pusillus*) that prefer shrubby habitat (Kisner 2004). It is possible that infested individuals produce induced chemical defenses that may limit reinfection (Boland 2018), but more work is needed to evaluate this.

Conclusion:

Since their first detections in southern California, *Euwallacea* species had an initially rapid range expansion in the TRV, with consequent severe impacts to riparian trees, that was cause for alarm. The beetles established widely throughout southern California riparian, urban and agricultural areas, including the SCR watershed. Regional dispersal has slowed and based on this study, a large-scale dieback event is not expected to occur. It is still unclear what caused such an event in the TRV. It has been proposed that increased nutrients due to pollution run-off led to a population spike in *Euwallacea kuroshio* (Boland and Uyeda 2020) and that some sort of environmental or other preexisting condition of the trees determined this impact (Hulcr and Stelinski 2017). Although it is hard to predict where these beetles will initially colonize, differences in species susceptibility to beetle infestation can help to predict its dispersal and impact across a landscape, with a faster population growth in *Salix*-dominated stands and slower population growth in *Populus*-dominated stands.

Although more data are needed from different localities and through time, the evidence from these two watersheds suggests that the species is trending towards a boom and bust cycle which has been observed for many invasive species of differing taxa (Strayer et al. 2017, Bennett et al. 2015). Interestingly, infestations of the closely related tea shot hole borer (*Euwallacea fornicatus*) have reportedly come to a “sudden end for unknown reasons” in southeast Asia (Browne 1961). If the species are indeed exhibiting a boom-bust dynamic, this could be due to several reasons. Inbreeding species like *E. whitfordiodendrus* and *E. kuroshio* that exhibit rapid population growth are especially susceptible to population collapse when exposed to a new stressor or change in their environment, as they inherently lack genetic diversity (Strayer et al. 2017). In addition, genetics that favor initial population establishment and dispersal may not be favorable in later stages of invasion (Keller and Taylor 2008). Low genetic diversity can also lead to further inbreeding within occupied patches (Strayer et al. 2017).

Changes to the environment are another common cause of boom-bust cycles in invasive species (Strayer et al. 2017) and in this case, drought could be a factor leading to a population “bust.” *Euwallacea whitfordiodendrus* was reportedly detected in small numbers in Los Angeles County in 2003, but did not become noticeably widespread until 2012, following the induction of a major drought in southern California. Several other regions have been invaded by *E. whitfordiodendrus* following the beginning of a drought, such as in Israel where the beetles were first detected in avocado orchards in 2009 and caused extensive damage during a drought beginning in 2012 (Mendel et al. 2012). In South Africa, the beetles were first detected in 2012, but began having a noticeable impact in 2017, following the beginning of an on-going drought in the region (Paap et al. 2018). With drought, there is an increase in air temperature and decrease in rainfall and humidity. This can make trees more attractive due to changes in volatile emissions, and physiologically suitable for insect growth due to increased soluble nitrogen, while simultaneously making them less able to defend themselves against herbivore attack due to decreased sap production (Mattson and Haack 1987). An increase in drought conditions, and subsequent weakening of trees, has been cited as one factor contributing to bark beetle outbreaks (Bentz et al. 2009)

The apparent “bust” occurring in southern California could be attributed to riparian trees beginning to recover from drought stress. Although the beetles could still thrive in a more mesic environment, similar to their subtropical native ranges, their hosts are better able to defend themselves against attack. This work does not suggest that management of *Euwallacea* species in California is not important. Many trees in the state are still heavily impacted by the pest-disease complex and long-term impacts from this are unknown; to truly characterize this is as a boom-bust dynamic would take several more years of monitoring (Strayer et al. 2017). Furthermore, with climate change predicting more frequent and severe droughts, *Euwallacea* species in California have the potential to cause large-scale dieback events in the future following an environmental change back to drought conditions. More work is needed evaluating the environmental tolerances of *Euwallacea* species and their symbiotic fungi to fully understand the potential range and distribution of the pest-disease complex in varying microclimates of southern California and implications for management. Development of effective, long-term control methods to eradicate the species will be vital, especially in the face of climate change.

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