Urban Forestry & Urban Greening 112 (2025) 128980

Contents lists available at ScienceDirect

Urban Forestry & Urban Greening

journal homepage: www.elsevier.com/locate/ufug

Original Article

Factors that influence the flight activity, abundance and infestation severity of the polyphagous shot hole borer beetle (PSHB, *Euwallacea fornicatus*) in an urban-agricultural fringe setting

Elise Roberts [a,*], Trudy Paap [b,1], Francois Roets [a,2]

[a] *Department of Conservation Ecology and Entomology, Stellenbosch University, Stellenbosch, South Africa*
[b] *Department of Biochemistry, Genetics and Microbiology, Forestry and Agricultural Biotechnology Institute, University of Pretoria, Pretoria, South Africa*

ARTICLE INFO

Keywords:
Biological invasion
Pest and pathogen
Trees
Monitoring
Management
Peri-Urban
Euwallacea fornicates

ABSTRACT

The polyphagous shot hole borer (PSHB, *Euwallacea fornicatus*) has invaded multiple countries, including South Africa. Along with its fungal mutualist, PSHB has caused the death of a wide range of tree species. Unmitigated costs of invasion in South Africa are estimated to be high. This study consisted of a 26-month PSHB monitoring programme using baited traps in an urban-agricultural fringe setting in the Western Cape province, focusing on revealing the factors most important to flight activity, beetle abundance, and infestation severity. It also tested the validity of felling infested trees as a management option to reduce beetle numbers (propagule pressure). More than half of the 94 study plots evaluated had PSHB-infested trees. Beetle flight activity was highest in summer and negligible in winter, with flight activity being positively correlated with temperature, beetle developmental degree days and beetle flight hours. The surrounding abundance of infested hosts was positively correlated with beetle abundance and infestation levels, though “saturation” in the infestation of a focal host tree may be a deterrent to dispersing beetles. Trees in plots that experience water stress (seasonal flooding) had higher dispersing beetle abundance and infestation levels, suggesting that tree stress might play a role in attracting beetles or making trees more vulnerable to infestation. Beetle activity during tree felling echoed the overall seasonal trend, and higher numbers of dispersing beetles on the day of tree felling in summer suggest that felling activities should best be conducted in winter. For three host tree species, infestation severity increased with decreasing tree size, which may be due to larger trees having thicker bark or other better defence systems. This study provides insight into the ecology of PSHB in this region of South Africa, which is important for developing monitoring and management strategies.

1. Introduction

Due to globalisation and increased global trade, the number of forest pest invasions is increasing worldwide (Liebhold et al., 2012). Wood-boring insects such as bark- and ambrosia beetles (Curculionidae; Scolytinae), are some of the most common and destructive invasive alien species globally (Haack, 2006; Roques, 2010). Long-term monitoring programmes are critical to understand the drivers behind these species' population dynamics in invaded ranges. This generates information that can be used to evaluate the potential impacts of invaders and inform management strategies.

The polyphagous shot hole borer beetle (PSHB) (*Euwallacea fornicatus*; Coleoptera: Curculionidae: Scolytinae) is native to Southeast Asia but has spread to multiple countries where it has emerged as a damaging tree pest (van Rooyen et al., 2021). PSHB was first identified in South Africa in 2017 (Paap et al., 2018), but it has been present in the country since at least 2012 (Stouthamer et al., 2017). The invasion in South Africa represents the most widespread outbreak of this species in the world, reaching every province except Limpopo (van Rooyen et al., 2021). The species likely arrived at South African harbours with infested

---

Abbreviations: AICc, Second-order Akaike's information criterion; CBH, Circumference at breast height; GLMM, Generalized linear mixed models; LOWESS, Locally Weighted Scatter-plot Smoother; PSHB, Polyphagous shot hole borer.

* Corresponding author.
E-mail address: robertselisen@gmail.com (E. Roberts).
[1] https://orcid.org/0000-0003-1364-4350
[2] https://orcid.org/0000-0003-3849-9057

https://doi.org/10.1016/j.ufug.2025.128980
Received 28 February 2025; Received in revised form 26 July 2025; Accepted 27 July 2025

wood packaging material or other wood products, but dispersal within the country has since been aided by the formal and informal firewood trade (van Rooyen et al., 2021).

The PSHB is an ambrosia beetle characterised by a developmental dependence on fungal mutualists. Female beetles bore into woody host trees and deposit their fungal symbionts into the xylem from specialised organs called mycangia (Hulcr and Dunn, 2011; Six, 2012). The fungi use host tree resources and grow into fungal gardens within beetle galleries, upon which the larvae and adult beetles feed (Hulcr and Dunn, 2011; Joseph and Keyhani, 2021). Male PSHB are haploid and cannot fly, so dispersal to new hosts is limited to the diploid females (Umeda et al., 2016). One female PSHB can produce over 50 female offspring in 7 weeks, and PSHB colonies produce and maintain multiple overlapping generations per year (Cooperband et al., 2016). *Fusarium euwallaceae* is the primary mutualistic fungal symbiont of the dominant haplotype of the PSHB in numerous invaded countries, including South Africa (Bierman et al., 2022; Freeman et al., 2016; Lynch et al., 2016; Paap et al., 2018). *Fusarium euwallaceae* is phytopathogenic to many hosts as it can block tree vasculature and cause dieback disease (Fusarium dieback) in highly susceptible trees (Eskalen et al., 2013; Na et al., 2018). Non-reproductive host tree species are those in which the fungus can grow after inoculation by the beetle, but the beetles are unable to establish viable colonies (Eskalen et al., 2013). These host trees usually survive PSHB colonisation attempts. Tree species within which the beetle can reproduce often die from Fusarium dieback (Eskalen et al., 2013). This pest-disease complex has caused host mortality across a very diverse range of tree species (Gomez et al., 2019). In South Africa, 83 tree species (indigenous and alien) have been shown to support viable PSHB colonies (FABI, 2023).

Total social cost due to unmitigated PSHB invasion in South Africa over the next 10 years is expected to be around 18 billion dollars, or about 0.6 % of the country's gross domestic product (de Wit et al., 2022). Most of this cost will be incurred in urban areas, but native forests and agricultural crops are also vulnerable. For example, the expected loss to the avocado industry due to PSHB invasion in South Africa over the next 10 years is estimated at 28 million dollars (de Wit et al., 2022). Apple (de Jager and Roets, 2022), stone fruit (de Jager and Roets, 2023), pear (Engelbrecht et al., 2024) and pecan nut trees (de Beer and Fell, 2022) have also recently been identified as reproductive hosts for PSHB, but the potential economic effects of these invasions have not yet been quantified (Neethling et al., 2024).

To mitigate the spread and impact of PSHB, there is a strong need to understand the factors that influence its flight activity, abundance and infestation severity. Like with many other insects, PSHB flight activity may be strongly linked to seasonal changes in abiotic conditions, such as changes in temperature, precipitation and number of daylight hours (Berryman, 1986; Régnière et al., 2012). For example, aspects of increasing temperature were found to increase flight activity in the tea shot hole borer (a close relative of PSHB) in its native range, and reduction of aerial numbers was found in the coldest months of the year (Calnaido and Thirugnanasuntharau, 1966). In contrast, the flight activity of PSHB and two closely related species was lowest in warmer months and highest in colder months in Taiwan (Liu et al., 2022). Although not yet tested, flight activity is expected to peak during warmer months in South Africa, though as the previous results show, PSHB flight activity may vary in different locations, and especially between its natural environment and invaded regions. Seasonal changes also impact the state of potential host trees, especially for deciduous species (Berryman, 1986; Na et al., 2018). In addition to climatic conditions, numerous local site- and biological factors may influence PSHB flight activity. For example, tree canopy cover and understory cover may impact local temperature and habitat suitability. The above factors may influence fungal growth and beetle development, therefore impacting beetle emergence and flight behaviour (Dodge and Stouthamer, 2021; Hulcr et al., 2007; Umeda and Paine, 2018).

Numerous biotic and environmental factors may be important to PSHB abundance and infestation severity in different locations. In accordance with the biotic resistance hypothesis, areas with increased tree species richness may be more resilient to PSHB invasion (Fridley et al., 2007). Alternatively, increased availability, abundance and density of preferred host tree species is expected to positively influence the chances of invasion of an area and subsequent PSHB abundance as there will be increased availability of resources (Lynch et al., 2018; Townsend et al., 2024). Higher numbers of infested reproductive hosts could also increase the likelihood of PSHB infestation on less preferred hosts, due to increased propagule pressure and a tendency to alight on tree species seemingly at random (Lynch et al., 2021; Mendel et al., 2012; 2017). This is especially relevant in agricultural areas where crop species may become infested when they are surrounded by infested reproductive hosts. It is also thought that the overall health status and stress level of host trees may influence host susceptibility to colonisation (Hulcr and Dunn, 2011; Mendel et al., 2012). Increased PSHB abundance and infestation levels are therefore expected in areas with a greater abundance of stressed reproductive hosts such as those negatively influenced by natural or human impacts including water availability, storm damage or tree pruning (Boland, 2016; Hulcr and Stelinski, 2017; Mendel et al., 2021; Townsend et al., 2024). There is also mounting evidence that larger trees suffer higher numbers of attacks than smaller trees for some ambrosia beetles (Choudhury et al., 2020; Haas et al., 2016; Mayfield and Brownie; 2013), although this has not yet been clearly demonstrated for PSHB (Townsend et al., 2024). The impact of many of these factors on PSHB infestation levels has recently been evaluated in a native forest in South Africa (Townsend et al., 2024). However, the impact of these factors on PSHB abundance and infestation levels has not been evaluated in an agricultural or urban setting in South Africa.

Higher infestation levels on reproductive hosts are expected to positively correlate with a higher abundance of dispersing PSHB individuals, particularly in the warmer summer months. This will likely lead to increased chances of higher infestations and dispersal to new hosts and sites (Howe et al., 2021; Kautz et al., 2016). Many managing authorities and scientists therefore recommend the removal of highly infested reproductive host trees (Chen et al., 2020; Jones and Paine, 2015), especially since there is currently no effective way of eradicating PSHB from infested individuals (Greer et al., 2018; Paap et al., 2020; Roberts et al., 2024). However, there is also concern, especially from homeowners, that tree removal practices may lead to increased abundance of dispersing individuals following disturbance within galleries due to tree felling activities, even though the recommended subsequent chipping of wood would kill most beetle individuals (Chen et al., 2020; Jones and Paine, 2015). Therefore, there is still a need to demonstrate the reductive effect of infested tree removal on local PSHB numbers and to determine the best-suited time for tree felling to avoid unintended dispersal.

1.1. Research objectives

This study included a two-year monitoring programme with the overall objective to understand the factors behind PSHB population dynamics in an invaded area. The study site was a peri-urban landscape, which was directly adjacent to an urban area and itself maintained a hybrid landscape of scattered urban, rural and agricultural elements. It first aimed to elucidate factors that influence PSHB flight activity (when beetles fly), abundance of dispersing PSHB individuals (propagule pressure), and timing of infestations. It is hypothesized that beetle flight activity, the abundance of dispersing individuals, and the rate of infestation on tree individuals will increase during warmer periods. Hereafter, the factors that may affect PSHB propagule pressure and infestation severity were evaluated at a local site scale. The progression of infestations at the plot level was followed to determine which of these factors lead to a faster increase in PSHB colonisation. The influence of tree felling on PSHB propagule pressure was then evaluated. If the numbers of active beetles (propagule pressure) are correlated to infestation levels, it is hypothesised that the removal of highly infested reproductive hosts will reduce the number of active beetles at a site. If the numbers of active beetles increase in summer and decrease in winter, it is hypothesised that tree felling activities will produce higher unintended dispersal activity in summer than in winter. Factors that may influence the severity of infestations of individual host trees in a plot were then investigated for three selected host species: English oak, Australian beefwood and Chinese poplar.

2. Methods and materials

2.1. Study site

This study was conducted on Lourensford Estate, a 4000-hectare, privately owned property in Somerset West (S34°04’47.0” E18°53’12.3”), in the Western Cape province of South Africa (Fig. 1), after confirmation of PSHB infestation in January 2021. However, it is likely that the beetle has been present on the property since 2020 just after it was locally detected by the PSHB Research Network. The region maintains a Mediterranean climate, characterised by hot, dry summers and cold, rainy winters, and it has a naturally Fynbos-dominant landscape (Cowling and Holmes, 1992). Monthly temperature and rainfall data during the study period are presented in Fig. A1. The most abundant tree species within the estate are presented in Table S1. Several of the tree species listed in Table S1 have previously been recorded as either PSHB reproductive hosts or as preferred hosts (FABI, 2023; Gomez et al., 2019). Reasons for host susceptibility are not yet well understood but may include phylogenetic affinities to other susceptible host species (Lynch et al., 2021; Townsend et al., 2025). Cultivated areas maintain commercial crop species (mainly deciduous fruit species) and tree species used as windbreaks, many of which are PSHB reproductive hosts (Table S1). Transition areas are found scattered between cultivated and ornamental zones, many of which are semi-natural and invaded by alien woody host species (Table S1). Ornamental areas maintain tree species for gardens and recreation, many of which are also reproductive hosts (Table S1).

2.2. Data collection

Monitoring traps were constructed using two plastic bottles joined at the openings using a short piece of hosepipe (Fig. 2). The top bottle had a volume of 2 L, was orientated upside down and had a large window cut out into the side. It was placed upside down to act as a funnel and catching panel (Fig. 2). Arthropods that flew into the trap (through the window) were funnelled down into a smaller 1 L collection bottle, which contained *ca.* 200 ml undiluted propylene glycol to euthanise and preserve catches (Fig. 2). Traps were suspended on metal poles 1.24 m high from the ground, corresponding to general flight height observed for PSHB in a previous study (Byers et al., 2017). Traps were baited with a slow-release Quercivorol ((1S,4 R)-p-menth-2-en-1-ol) lure (Synergy Semiochemicals Corp.) (Byers et al., 2020; Dodge et al., 2017). The efficacy of Quercivorol lures for attracting *Euwallacea* species reduces substantially after 9 weeks (Owens et al., 2019a). Therefore, lures were replaced every 8 weeks throughout the study period.

Fig. 1. An outlined map of South Africa with study area indicated in red.

One hundred traps were placed in various strategic areas on the property (Fig. 3). Trap areas were identified based on the monitoring needs of the estate, following some of the borders of the property, various connecting roads, open spaces between garden and agricultural areas, and within fruit orchards. Traps were placed at least 60 m apart to avoid trap interference (Owens et al., 2019b), but inter-trap distances were often greater than this minimum. Trap catches were collected and the number of PSHB individuals counted monthly; the first half of the traps were collected after the first two weeks of every month, and the rest were collected at the end of every month. Traps were set from February 2021 to April 2023 (n = 26 monthly catches for every trap). Individual PSHB were morphologically identified using a stereomicroscope following Gomez et al. (2018), Smith et al. (2019) and Stouthamer et al. (2017).

A circular plot (20 m diameter) was established around each trap. The 20 m plot diameter was chosen to ensure that trap catches and beetle activity only corresponded to environmental variables in the immediate surroundings (Byers et al., 2018). The following variables were recorded within each plot: tree species richness, surface water availability (surface water always available to trees within the plot [including when trees were regularly irrigated], never available or seasonally available), vegetation type (cultivated [including windbreak zones], transition [including semi-natural areas], or ornamental), canopy cover (as a percentage) and understory cover (as a percentage). The following variables were recorded for every tree that was over 3 cm in circumference at breast height (CBH) (~1.37 m above ground level) within each plot (n = 900 trees in total): tree species, CBH, crown health (as a percentage), tree damage (as a percentage of the crown and/or trunk affected), overall tree health (scored from 1 to 5, [1 = healthy, no damage; 5 = dead/dying]), distance to surface water (0 m when regularly irrigated), distance (m) to natural impact (e.g., fallen tree), and distance (m) to human impact (e.g., road or building).

Trees were visually inspected for signs of PSHB infestations (on known reproductive hosts) or *F. euwallaceae* inoculations (on known non-reproductive hosts), detected by looking for entry holes (~0.85 mm (van Rooyen et al., 2021)), and/or other signs of beetle attack including frass, oozing, or resin flow (Eskalen et al., 2013; Mayorquin et al., 2018). Upon recognising these symptoms, the outer bark of the tree around an entry hole was removed for at least one hole to verify fungal staining as expected from *F. euwallaceae* (usually a vertical stain 1–2 mm wide, ranging from red to dark brown). When in doubt, especially when a possible new host was detected, a piece of the fungus-infested wood was collected and the identity of the fungus was confirmed as *F. euwallaceae* following procedures outlined in de Jager and Roets (2022). The number of PSHB entry holes (from the base of the tree up to 3 m height) was recorded for each infected tree (*F. euwallaceae* – non-reproductive host) and/or infested (PSHB reproductive host). These surveys were repeated in autumn (April/May) and spring (September/October) for two years, starting in May 2021 (n = 4 repeats). Spring was chosen because it corresponds to the first signs of yearly beetle activity, and autumn was chosen because it corresponds to when beetle activity decreases (F. Roets, pers. observ.). In successive surveys, any changes to relevant variables were recorded. The time since the first colonisation of a

Fig. 2. (A) Front view and (B) side view of baited traps showing slow-release lure containing Quercivorol ((1S,4 R)-p-menth-2-en-1-ol) (arrow).

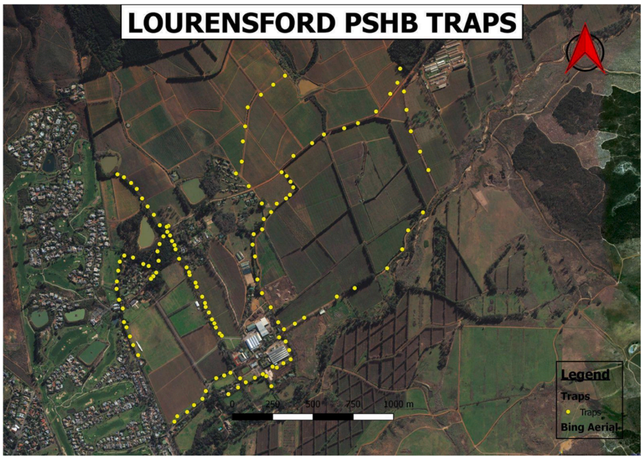

Fig. 3. A map of Lourensford Estate with baited trap locations indicated in yellow.

particular tree was calculated as either time 1 (when the tree was infested at the start of the survey period), time 2 (when the tree was newly infested in April/May 2021) or time 3 (when the tree was newly infested in April/May 2022).

Ninety-six PSHB-infested trees were felled on Lourensford Estate in winter (June through August) and summer (December through February) between 2021 and 2023. Trees with close to or over 50 PSHB entry holes up to a 3 m height were chosen for removal. Trees selected for felling also had a health score of ≥ 3, indicating that they were unhealthy and likely declining due to PSHB infestation and Fusarium dieback. Sixty-two trees were removed in summer (December through February) and 34 trees were removed in winter (June through August). Between 7 and 16 trees were removed on the same date ($x = 9$ harvesting events, 3 harvesting events in winter and 6 harvesting events in summer). The felling procedure followed guidelines in Jones and Paine (2015), with felled material chipped into a large plastic casing and left to solarise for between 6 weeks and 4 months, depending on the average ambient temperature. The following was recorded for every tree: species, CBH and number of infested hosts within a 20 m diameter. One Quercivorol-baited bottle trap was placed 5 m from each tree. The temperature (peak and daily average) and the number of beetles present were recorded daily for seven days before and seven days after each tree was felled (15 total days of monitoring).

2.3. *Statistical analyses*

Hourly temperature data used in analyses were obtained from Ileaf Weather stations (Mérieux NutriSciences, South Africa) located on the estate. All data were analysed using R programming software (R Development 9 Core Team, 2020; version 3.6.3). For all analyses, a confidence level of 5 percent ($P \leq 0.05$) was used to determine statistical significance.

2.3.1. *Factors that influence PSHB flight activity, abundance of dispersing individuals and timing of infestations*

The total number of beetles collected in each trap per month was compared between different collection months across the study period. The distribution of monthly abundance data was first evaluated for normality using a Shapiro-Wilks (1965) test (using the package "*nortest*" (Gross and Ligges, 20150) whereafter beetle catches were compared between months using a Kruskal-Wallis (1952) test followed by a Dunn's (1964) post-hoc test with p-values adjusted with the Benjamini-Hochberg method (using the package "*FSA*" [Ogle, 2017]). To elucidate the relationship between the abundance of dispersing individuals and temperature, a Spearman's rank correlation test was performed between beetle numbers per trap per month and the mean monthly temperature (Cohen et al., 2009). A LOWESS (Locally Weighted Scatter-plot Smoother) line was fitted to this data (using the "*stats*" package (Lüdecke et al., 2021)).

Temperature data were used to calculate the daily mean temperature for each 24-hour period (calculated from the daily maximum and minimum temperatures). Hereafter the number of degree days and dispersal hours for PSHB beetle development was calculated for each month as outlined in Liu et al. (2022). The species can develop between 13.34°C and 33.08°C (Cooperband et al., 2016; Umeda and Paine, 2019). When the mean daily temperature fell within this range, the number of degree days were calculated as the mean daily temperature minus the lower limit for beetle development, otherwise it was regarded as zero. *Euwallacea* species are known to actively disperse between 20°C and 30°C (Calnaido, 1965), and in Sri Lanka and in Florida, most beetle individuals only dispersed between 11:00 and 16:00 (Calnaido, 1965; Kendra et al. 2017; Owens et al. 2019b). Although not tested for South Africa, it is assumed that dispersal hours would be similar. For each day, the total number of hours spent between 20°C and 30°C was calculated. Hereafter the total number of degree days per month and the number of dispersal hours per month were compared with the number of beetles collected per trap and per month, and the total numbers of beetles collected in all traps per month using Spearman's rank correlation tests fitted with LOWESS lines (Cohen et al., 2009).

The numbers of additional attacks on trees since the first survey (April/May 2021) were calculated until the final survey (September/October 2022). Only plots that contained known reproductive and nonreproductive host tree species were considered for these analyses. The number of host tree individuals per plot was summed and divided by the number of holes gained over the entire survey period to obtain an average number of new PSHB holes per host tree in these plots. A Spearman's correlation with a fitted LOWESS line was then used to compare the average number of new holes per host with the total number of dispersing beetles collected between the first and the last surveys.

2.3.2. Factors that influence the numbers of dispersing PSHB individuals collected at a site (propagule pressure) and the infestation levels of a site (number of PSHB holes in trees)

The effect of selected plot characteristics on the number of actively dispersing PSHB individuals and the infestation levels of a site was assessed for all plots except those in which trees were felled during the study period. The final data set consisted of 94 sites. Beetle abundance data consisted of the total number of beetles collected in each trap over the entire collection period. Data on the total numbers of beetles collected per trap were evaluated for normality using a Shapiro-Wilks test and then used as the response variable in generalized linear mixed models (GLMM's) fitted to a zero-inflated Poisson distribution using the "*glmmTMB*" package in R, chosen because the count data was right-skewed and contained many zeroes (Brooks et al., 2017). Plot variables (listed in the previous section) recorded from the last survey point (September/October 2022) were incorporated as fixed effects. The full model included fixed effects of vegetation type (cultivated, transition or ornamental), surface water availability (always, seasonally or never), percentage canopy and understory cover, tree species richness (number of species), number of damaged trees, number of reproductive host trees, number of infested reproductive host trees (at the end of the monitoring period), and number of inoculated non-reproductive host trees (at the end of the monitoring period). Spatial autocorrelation was assumed due to the patchy distribution of highly infested hosts, and including plot number as a random effect substantially improved the models based on Second-order Akaike's information criterion (AICc), which was used to rank all possible combinations of candidate models. The model with the lowest AIC value was retained. After performing Tukey tests to determine significance of categorical variables, categories were separated using the packages "*emmeans*" (Lenth et al., 2018), "*multcomp*" (Hothorn et al., 2008) and "*multcompView*" (Graves et al., 2012). These analyses were repeated to assess the effect of all plot variables on the total number of holes in PSHB-infested trees per site to give an indication of factors that influence infestation levels at the plot level. The full model incorporated the same fixed and random effect(s) as above, but omitted the number of infested reproductive hosts.

2.3.3. Factors that lead to increases in the numbers of dispersing PSHB individuals collected at a site and increased rates of infestation in a site

The effect of selected plot characteristics (as above) on the increase in number of actively dispersing PSHB individuals and to the increase in infestations from the start of monitoring to the end of the study period were assessed for the 94 sites. For these analyses, data for plot characteristics taken at the first assessment (April/May 2021) were used as fixed effects and plot number was used as random effect in GLMM's fitted to a zero-inflated Poisson distribution using the "*glmmTMB*" package in R after evaluating the distribution of the data for normality using a Shapiro-Wilks test. Response variables in models were either the increase in number of PSHB holes in a plot (number of holes at the end of the study minus the number of holes at the beginning of the study) or the increase in beetle catches after this first assessment of plot characteristics (total number of beetles collected per trap at the end of the study minus the total number of beetles collected per trap before April/May 2021). Model selection procedures and post-hoc testing followed those outlined in the previous section.

2.3.4. Influence of tree felling on PSHB propagule pressure

A Spearman's correlation test was used to determine whether the number of PSHB holes in trees per plot at the end of the study period was significantly correlated with the total number of beetles collected per trap over the entire experimental period. Daily PSHB capture data in plots in which infested trees were felled were then analysed as the response variable in GLMM's fitted to a zero-inflated Poisson distribution after testing for normality using a Shapiro-Wilks test. The full model included season (summer or winter), day classification (before, during, or after harvest), the interaction between the season and day variables, average daily temperature, and daily maximum temperature as fixed effects. Tree number nested within the harvesting event was included as a random effect. Second-order AICc was used to rank all possible combinations of candidate models and the model with the lowest AIC value after using stepwise model selection procedures was retained. Levels within factors for categorical variables retained after model selection were separated using the procedures and packages previously outlined.

2.3.5. Factors that influence the severity of infestations of individual host trees

The effect of tree and plot characteristics on the severity of PSHB infestations at the end of the monitoring period were assessed for selected individual reproductive host tree species. The tree species assessed were chosen if they had at least 30 infested individuals. These species included English oak ($n = 36$ individuals), Australian beefwood ($n = 41$ individuals) and Chinese poplar ($n = 34$ individuals).

The density of holes on a tree was calculated by using the circumference of the tree at breast height (m) to calculate the surface area of that tree as a function of a cylinder 3 m tall (up to the height for which holes were counted in surveys). The number of holes in the tree up to 3 m was then divided by the surface area and expressed as holes/m^2. The addition of plot number as a random factor substantially lowered the fit based on AIC value, so the holes/m^2 value was used as the response variable in generalized linear models (GLM). After testing the continuous data for normality using a Shapiro-Wilks test, the model was fitted to a gamma distribution because it was right-skewed and provided a better fit over log distribution based on lower AIC value. Predictor variables assessed in these analyses included: tree size (CBH), the number of surrounding reproductive hosts, the number of surrounding infested reproductive hosts, distance to natural or human impact, percentage canopy cover, percentage understory cover, percentage focal tree damage at start of surveying (April/May 2021), focal tree health status at the start of surveying, surface water availability (always, seasonally or never), vegetation type (cultivated, transition or ornamental), and beetle activity (total number of beetles collected in the surrounding trap over the experimental period). Model selection and post-hoc testing followed those previously outlined.

These analyses were repeated for the increase in density of infestations on trees from the start to the end of the survey period. This was represented by data on the number of holes gained between April/May 2021 and September/October 2022, which was used as the response variable for model selection procedures. Predictor variables assessed in these analyses were the same as above: tree size (CBH), the number of surrounding reproductive hosts, the number of surrounding infested reproductive hosts, distance to natural or human impact, percentage canopy cover, percentage understory cover, percentage focal tree damage at start of surveying (April/May 2021), focal tree health status at the start of surveying, surface water availability (always, seasonally or never), vegetation type (cultivated, transition or ornamental), and beetle activity (total number of beetles collected in the surrounding trap over the experimental period). However, PSHB beetle activity in this case only included the total numbers of beetles caught in traps between April/May 2021 and September/October 2022. Model selection and post-hoc testing followed those previously outlined.

3. Results

3.1. Factors that influence PSHB flight activity, abundance of dispersing individuals and timing of infestations

Beetle numbers varied considerably between months and traps. The highest number of dispersing beetles collected in a single trap was 13 621, collected during the month of February. The lowest number of beetles collected in a trap was zero and was often the case in June – August. Data on the total number of beetles collected in each trap across all monitoring months was nonparametric (Shapiro-Wilks W = 0.844, $P < 0.0001$). Month had a significant influence on the numbers of beetles collected within traps (Kruskal-Wallis $Chi^2 = 44.736$, Df = 11, $P < 0.0001$) (Fig. 4). Dispersing beetle abundance was higher during the warmer late summer to early autumn months (Jan – March) than in the colder winter months (June - August) (Fig. 4; Fig. A1). Congruently, monthly abundance of beetles collected in all traps was strongly correlated with monthly mean temperatures (Spearman $r_s = 0.8886$, $P < 0.0001$) (Fig. 5; Fig. A1).

There was a significant positive correlation between dispersing beetles per month and per trap and the number of developmental degree days per month (Spearman $r_s = 0.5992$, $P < 0.0001$) (Fig. 6a), as well as between dispersing beetles per month and per trap, and flight hours per month (Spearman $r_s = 0.5864$, $P < 0.0001$) (Fig. 6b). The correlation between the total number of beetles per month (all traps combined) and the monthly degree days, as well as the monthly flight hours, were significantly positive (Spearman $r_s = 0.8828$, $P < 0.0001$ [Fig. 6c]; $r_s = 0.8072$, $P < 0.0001$ [Fig. 6d], respectively).

The total number of new PSHB holes in host trees per plot (increase in holes over the monitoring period) was significantly correlated with the number of beetles collected in traps over the survey period (Spearman $r_s = 0.2518$, $P < 0.0002$) (Fig. 7). However, this correlation was not particularly strong. This is likely because there was an initial strong positive correlation between these two variables up to about 70 holes, whereafter the number of dispersing beetles did not positively correlate with increased number of holes in host trees (Fig. 7).

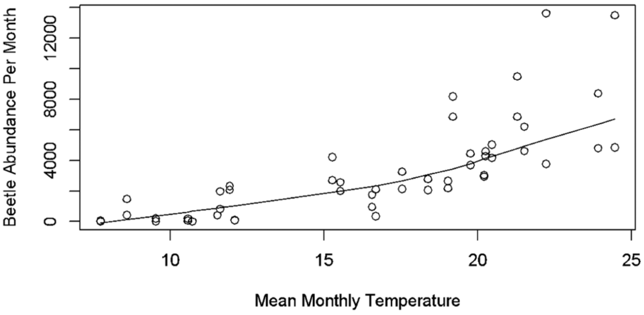

Fig. 5. Scatterplot showing the relationship between beetle abundance and mean monthly temperature. A LOWESS line is fitted to the data.

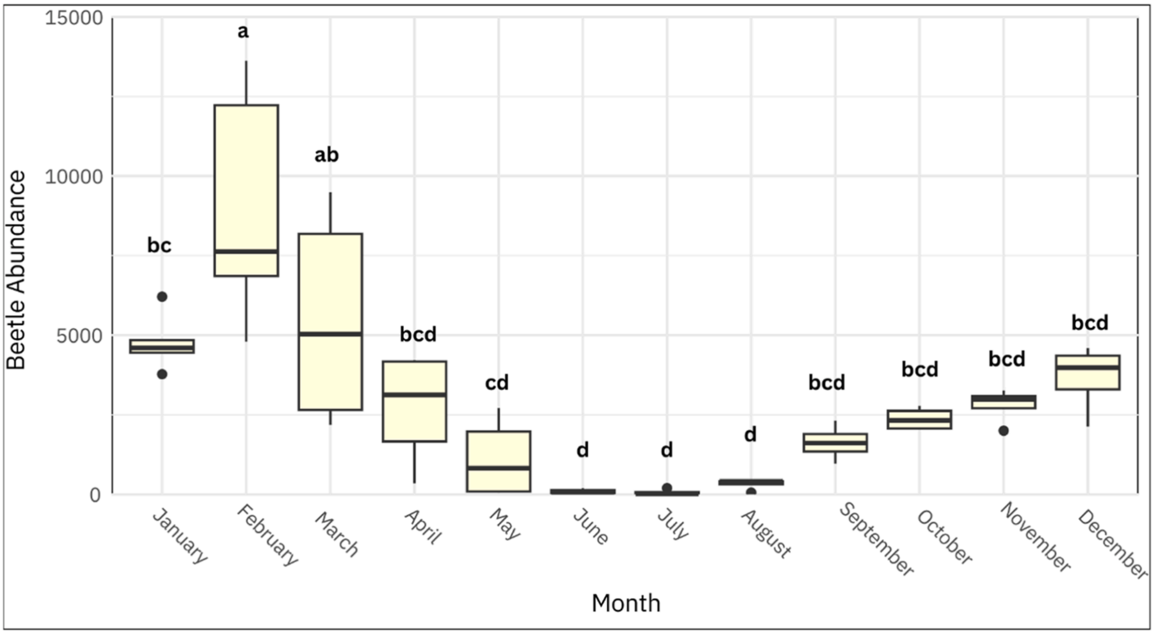

Fig. 4. Box plot showing the differences in beetle abundance per trap across different months. Different letters above bars indicate significant differences between months. Box indicates 25–75 % data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers.

3.2. Factors that influence the numbers of dispersing PSHB individuals collected at a site (propagule pressure) and the infestation levels of a site (number of PSHB holes in trees)

Due to tree felling activities, 6 of the 100 intial study plots were removed from analysis, leaving 94 total plots. Data on the total number of dispersing PSHB individuals per trap were nonparametric (Shapiro-Wilks W = 0.84, $P < 0.0001$). After model selection, the best-fit model retained vegetation type, surface water availability, percentage understory cover, number of reproductive host trees, and number of infested reproductive host trees as fixed effects, with plot number as a random effect (AIC = 1538.8, BIC = 1561.7, deviance = 1520.8, Df = 85). The percentage understory cover (Z = 0.00493, P = 0.0007) (Fig. A2a) and the number of infested reproductive host trees (Z = 3.110, P = 0.0019) (Fig. A2b) were positively correlated with total numbers of dispersing beetles. Vegetation type and surface water availability also had a significant influence on the total numbers of dispersing beetles (Fig. A3). More beetles were collected at sites containing transition vegetation than cultivated or ornamental vegetation, but this was only significantly

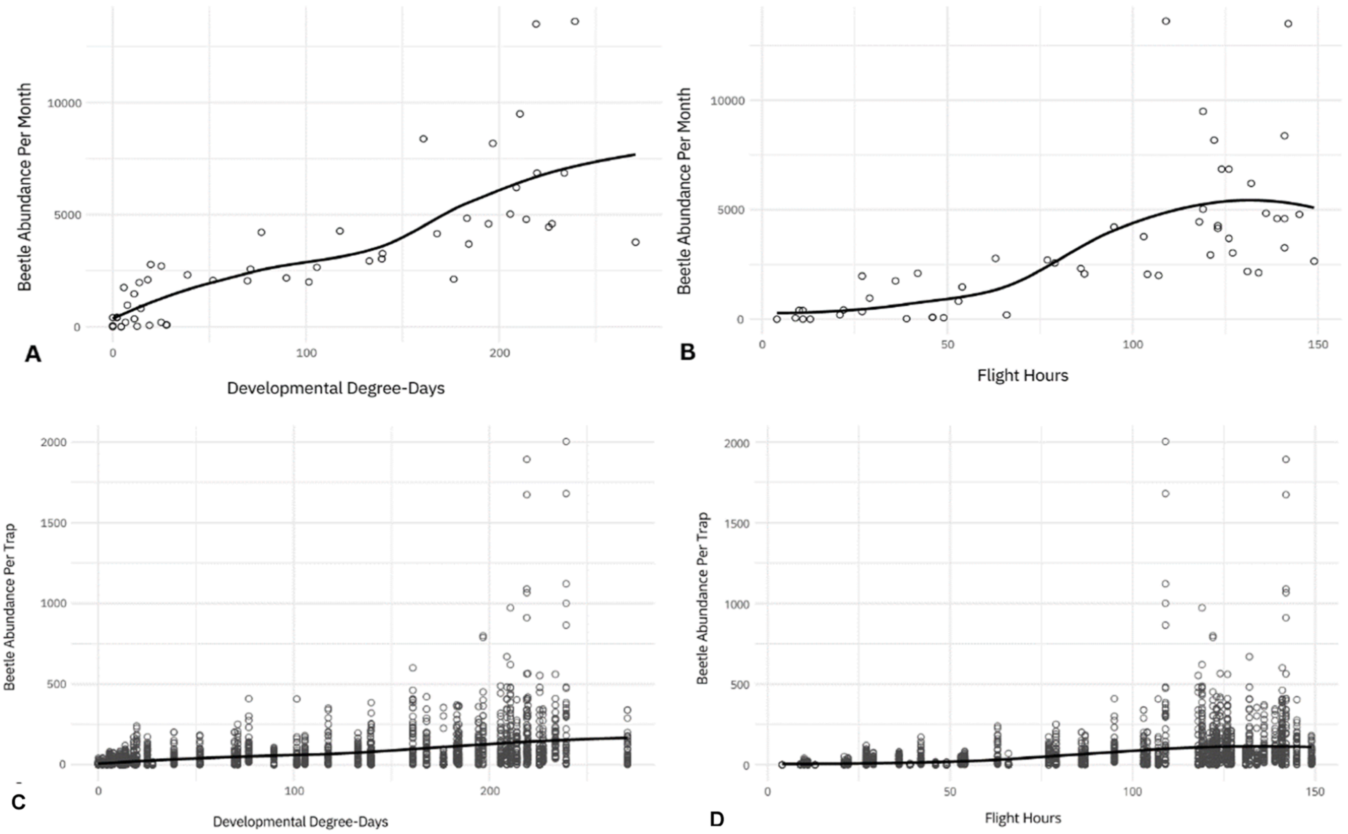

Fig. 6. Scatterplot showing the relationship between beetle abundance per month and per trap and (A) developmental degree days per month and (B) flight hours per month as well as the relationship between total beetle abundance and (C) developmental degree days per month and (D) flight hours per month. LOWESS lines are fitted to the data.

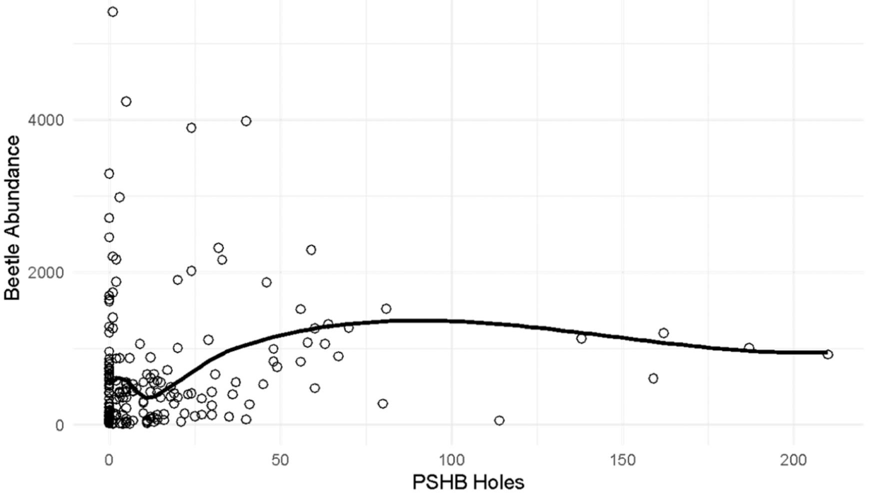

Fig. 7. Scatterplot showing the relationship between total abundance of dispersing beetles per plot and the increase in numbers of holes caused by infestation in host trees over the monitoring period. A LOWESS line is fitted to the data.

evident when compared to cultivated zones (Fig. A3a). Significantly more beetles were collected at sites with seasonal water availability (seasonal flooding) than at plots that always or never had surface water available (Fig. A3b).

The best-fit model for infestation level data (total number of holes in host trees in plots at the end of the surveying period) retained vegetation type, surface water availability and tree species richness, as well as plot number as a random effect (AIC = 823.3, BIC = 841.1, deviance = 809.3, Df = 87). Species richness was significantly positively correlated with infestation levels in sites (Z = 2.203, P = 0.0276) (Fig. A2c). Plots with seasonal access to surface water were associated with higher infestation levels than plots that always or never had access, but this was only significantly evident against those that always had access (Fig. A3c). Post-hoc testing showed no significance between levels in different vegetation types.

3.3. Factors that lead to increases in the numbers of dispersing PSHB individuals collected at a site and increased rates of infestation in a site

The best-fit model for data on the increase in the number of dispersing PSHB individuals over the monitoring period retained vegetation type, surface water availability, percentage understory cover, and the number of infested reproductive hosts as fixed effects, and plot number as a random effect (AIC = 1419.9, BIC = 1440.2, deviance = 1403.9, Df = 86). Percentage understory cover and the number of infested reproductive host trees were significantly positively correlated with an increase in dispersing PSHB beetle numbers (Z = 2.365, P = 0.018; Z = 3.507, P = 0.0005, respectively) (Fig. A2d). Vegetation type and surface water availability also had a significant impact, with the transition vegetation type and seasonal water availability having the highest association with increased beetle abundance (Fig. A3d & A3e).

The best-fit model for data on the increase in infestations between the first survey and the last survey included vegetation type, the number of reproductive host trees, and the number of infested reproductive hosts as fixed effects, and plot number as a random effect (AIC = 730.4, BIC = 745.6, deviance = 718.4, Df = 88). The number of infested reproductive host trees was significantly positively correlated with an increase in infestations in plots (Z = 6.480, P < 0.0001) (Fig. A2e). Plots with seasonal access to surface water (seasonal flooding) had increased infestation levels compared to plots that never or always had surface water access (Fig. A3f). Post-hoc testing showed no significance between levels in different vegetation types.

3.4. Influence of tree felling on PSHB propagule pressure

Beetle propagule pressure (number of beetles collected per trap over the entire monitoring period) was significantly positively correlated with infestation levels (number of holes at the end of the monitoring period) (Spearman $r_s = 0.5189$ & $P < 0.0001$) (Fig. 8). The numbers of beetles and infestation levels were strongly positively correlated up to ~150 holes or 3000 beetles, whereafter the association seemingly disappeared (Fig. 8).

Daily PSHB dispersing individual abundance data was found to be nonparametric (Shapiro-Wilks W = 0.4964, P < 0.0001). The best-fit model for these data retained season (summer or winter), day classification (before, during, or after tree removal), the interaction between the season and day classification, and daily maximum temperature as fixed effects, as well as tree number nested within the harvesting event as a random effect. The daily average temperature was removed before analysis because it was significantly correlated with maximum temperature and the latter provided a better model fit (AIC = 7577.9, BIC = 7620, deviance = 7561.9, Df = 1432). Post-hoc testing of the interactive effects of tree felling on PSHB abundance revealed that overall numbers of beetles did not differ before, during or after tree removal in winter (Fig. 9), although numbers were significantly lower in winter than in summer (Fig. 9). In summer, beetle numbers increased on the day of tree removal, but thereafter were significantly lower than pre-tree removal numbers (Fig. 9). An increase in maximum daily temperature led to higher dispersing beetle numbers (Z = 46.30, P < 0.0001) (Fig. A4).

3.5. Factors that influence the severity of infestations of individual host trees

Data on the overall hole density and the increase in hole density between the first and last survey periods were both nonparametric for all three tree species analysed (Table 1), and the best-fit models for these three species are presented in Table 2.

The overall hole density of English oak trees was significantly negatively correlated with tree size (Table 2a; Fig. A5a). Cultivated zones had higher hole density for this species than ornamental or transition zones, however this was only significantly apparent against transition zones (Table 2a; Fig. 10). The increase in English oak hole density between the first and last survey events was significantly negatively correlated with tree size (Table 2b; Fig. A5b). Cultivated zones experienced the highest increase in hole density, and trees with an initial health category of 2 experienced the highest increase in hole density (Table 2b; Fig. 11).

The overall hole density of Australian beefwood trees was significantly negatively correlated with tree size and distance to the nearest impact (Table 2a; Fig. A5c & A5d). The increase in the number of holes in Australian beefwood between the first and the last survey events was also negatively correlated with tree size and distance to impact (Table 2b; Fig. A5e & A5f). Though the number of infested host trees initially indicated significance, visual inspection showed that this was a false positive result.

The overall hole density of PSHB on Chinese poplar trees was significantly negatively correlated with tree size (Fig. A5g) and percentage canopy cover (Fig. A5j), while being significantly positively correlated with the number of surrounding reproductive host trees (Fig. A5h) and percentage understory cover (Table 2a; Fig. A5i). The increase in hole density on Chinese poplar between the first and last survey events was significantly negatively correlated with tree size

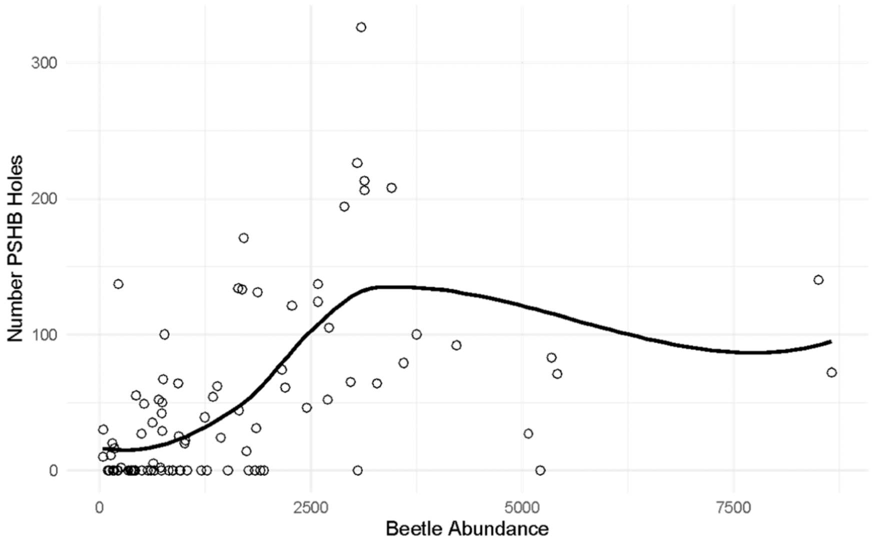

Fig. 8. Scatterplot showing the relationship between beetle abundance and infestation levels over the experimental period. A LOWESS line is fitted to the data.

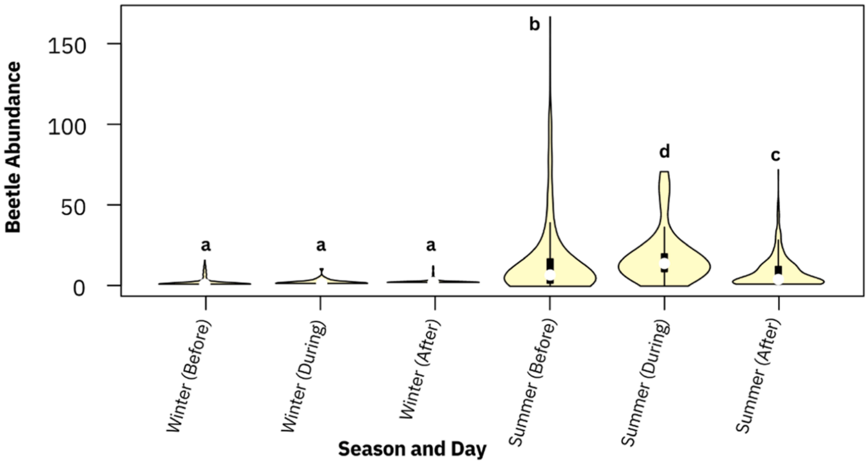

Fig. 9. Violin plot showing the differences between daily beetle numbers across summer and winter and before, during and after tree removal. Different letters above bars indicate significant differences between events. Box indicates 25–75 % data range, whiskers indicate 1.5 times the interquartile range, white dots represent medians.

Table 1
The Shapiro-Wilks test results of overall hole density and hole density between survey points for selected reproductive host tree species.

Host species	Overall hole density		Hole density between the first and the last survey periods	
	W-value	P-value	W-value	P-value
English oak (*Quercus robur*)	0.6165	< 0.0001	0.6641	< 0.0001
Australian beefwood (*Casuarina cunninghamiana*)	0.7131	< 0.0001	0.75158	< 0.0001
Chinese poplar (*Populus simonii*)	0.8656	0.0019	0.8252	0.0003

(Fig. A5k) and percentage canopy cover (Fig. A5n), and was positively correlated with the percentage understory cover (Fig. A5m) and beetle abundance between the first and last survey points (Table 2b; Fig. A5l).

4. Discussion

The PSHB and its primary fungal mutualist, *F. euwallaceae*, are responsible for the death of a wide range of tree species in multiple countries, including South Africa. In South Africa, the costs of unmitigated PSHB invasion are predicted to be high (de Wit et al., 2022). Although much of these costs would be sustained in the country's urban areas, native and agricultural systems are also threatened because many species in these systems have been confirmed as reproductive hosts (de Beer and Fell, 2022; de Jager and Roets, 2022; 2023; FABI, 2023; Engelbrecht et al., 2024; Neethling et al., 2024; Townsend et al., 2024). To mitigate negative effects, more information is needed on the factors that influence PSHB's ecology and invasion success in these different environments. This 26-month study investigated the flight activity, abundance and infestation severity of PSHB in an urban-agricultural fringe environment in the Western Cape province of South Africa. It further tested the impact of tree-felling on dispersal activity in different seasons. Overall, beetle numbers and infestations increased throughout the monitoring period, with the highest monthly catch being over 13000 individuals. About 37 percent of all plots had infested trees at the beginning of monitoring, which increased to more than 65 percent by the end of the monitoring period, encompassing 17 tree species. Even when trees weren't infested within a plot, at least one PSHB was found in all traps over the study period. Three important fruit tree species (avocado, pear and plum) also had signs of infestation by the end of monitoring, which indicates that agricultural crops in the Western Cape province with high PSHB propagule pressure are at risk (Neethling et al., 2024).

4.1. Factors that influence PSHB flight activity, abundance of dispersing individuals and timing of infestations

Monthly PSHB trap catches are representative of overall flight activity. Therefore, as expected, based on the developmental and flight temperature ranges of PSHB or closely related species (Calnaido, 1965; Cooperband et al., 2016; Umeda and Paine, 2019) and its previous invasion success in other Mediterranean climates (Boland, 2016; Mendel et al., 2017), overall flight activity was higher during the warmer and drier summer months and lower in colder and wetter winter months, with the highest trap catches in February and the lowest in June and July. Interannual population dynamics were not considered in this analysis, however, patterns were similar between the different years, as evident by the relatively low level of variance in trap catches, especially during the cooler months. Flight activity was highly positively correlated with temperature, which aligns with their developmental and flight temperature ranges, as well as with a previous study on the flight patterns of the closely related tea shot hole borer (Calnaido and Thirugnanasuntharan, 1966). These same parameters (developmental degree days and flight hours) proved highly significantly correlated with actively dispersing beetle numbers in this study. However, these results oppose those of a recent study comparing the flight activity of PSHB and two closely related species to degree days and flight hours (calculated using the same ranges) in Taiwan (Liu et al., 2022). Liu et al. (2022) theorised that high temperatures and summer rains in their experimental region may have depressed dispersal by flight, and/or that an increased need for brood care may have delayed female flight (Peer and Taborsky, 2007). Brood care is expected in the same season in both Taiwan and the Western Cape province in South Africa, while the Western Cape experiences winter rain, so the present study suggests that high temperatures and summer rains in Taiwan are the most likely of these options. Liu et al. (2022) found that midday temperatures in Taiwan were frequently higher than the 30°C dispersal threshold, and that summer rains and the increased humidity it causes could have deterred or prevented beetle flight.

While the correlation between the number of attacks on trees versus beetle abundance was significant, the positive association was relatively weak, thus there are likely multiple influences. One factor may be that beetles are not always using dispersal by flight, but sometimes just walk

Table 2

Model results for factors that influence the severity of infestations of individual host trees based on (A) total hole density at the end of the survey period and (B) increase in hole density from the first until the last survey period.

A) Best-fit model

Host species	AIC	Residual deviance	Degrees of freedom	Variables (significance*)	Z-value	P-value
English oak (*Quercus robur*)	127.7	49.74	60	Tree circumference*	−6.429	< 0.0001
				Vegetation category*	NA	NA
				Health category	NA	NA
Australian beefwood (*Casuarina cunninghamiana*)	231.3	37.89	51	Tree circumference*	−3.991	0.0002
				Distance to impact*	2.570	0.0131
				Percentage understory	1.926	0.0597
Chinese poplar (*Populus simonii*)	78.53	9.8382	21	Tree Circumference*	−2.545	0.0188
				Vegetation category	NA	NA
				Number of surrounding reproductive hosts*	−2.643	0.0152
				Percentage understory*	−2.469	0.0222
				Percentage canopy*	−2.021	0.0562
				Overall beetle number	NA	NA

B) Best-fit model

Host species	AIC	Residual deviance	Degrees of freedom	Variables (significance*)	Z-value	P-value
English oak (*Quercus robur*)	160.3	45.47	59	Tree Circumference*	−6.626	< 0.0001
				Health Category*	NA	NA
				Vegetation Category*	NA	NA
Australian Australian beefwood (*Casuarina cunninghamiana*)	275.4	27.88	50	Tree Circumference*	−4.740	< 0.0001
				Number of surrounding infested hosts*	2.011	0.0497
				Distance to impact*	−2.809	0.0071
				Number of beetles between survey points	NA	NA
Chinese poplar (*Populus simonii*)	101.5	29.90	20	Tree Circumference*	2.249	0.0359
				Vegetation category	NA	NA
				Number of surrounding reproductive hosts	NA	NA
				Number of surrounded infested hosts	NA	NA
				Percentage understory*	−3.949	0.0008
				Percentage canopy*	−2.415	0.0255
				Beetle number*	−2.988	0.0073

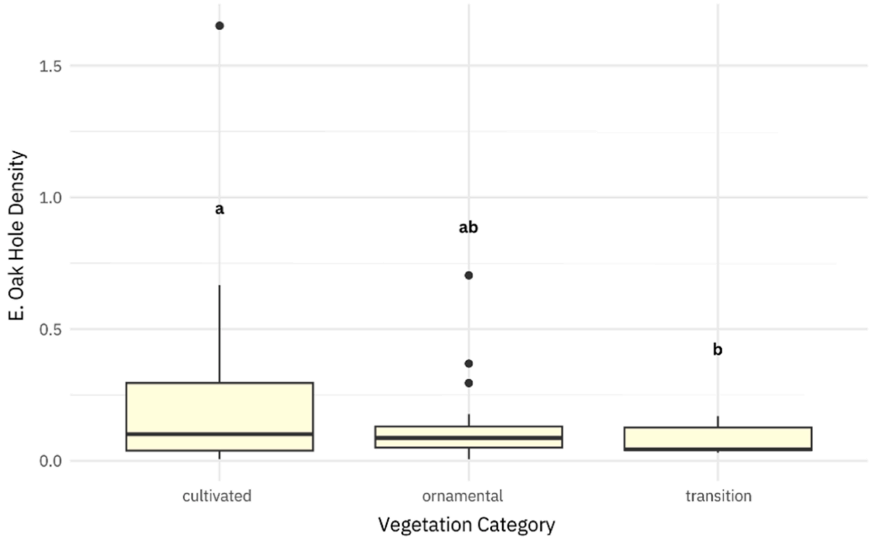

Fig. 10. Box plot showing the differences between English oak (*Quercus robur*) tree hole density at the end of the survey period across vegetation categories. Different letters above bars indicate significant differences between categories. Box indicates 25–75 % data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers.

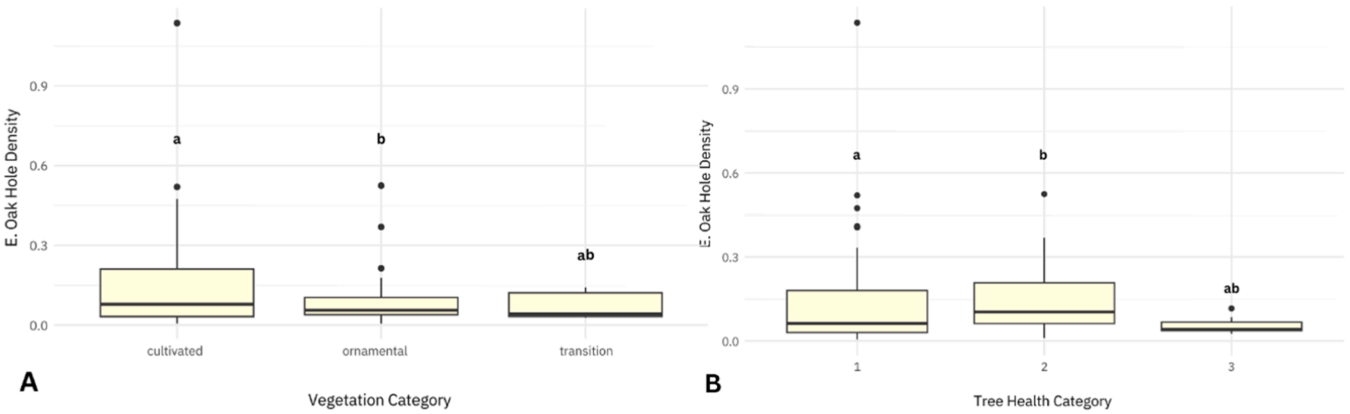

Fig. 11. Box plot showing the differences between the increase in the number of holes on English oak (*Quercus robur*) trees from the beginning to the end of the survey period across (A) vegetation categories and (B) tree health categories. Different letters above bars indicate significant differences between categories. Box indicates 25–75 % data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers.

to start new galleries on the same host tree (Dodge et al., 2017; Liu et al., 2022), therefore triggering discrepancies between beetles caught in traps versus new holes observed. The possibility of host tree saturation may have also played a role. At the lower end of beetle abundance, the number of holes on infested host trees increases with the number of beetles, yet as beetle numbers grow increasingly higher, the number of holes remains constant. This observation supports the theory that as a host tree becomes more infested, the deteriorating condition of the tree may encourage individuals to disperse (leading to higher beetle abundance), and deter dispersing individuals from colonising that same host (leading to lower numbers of new holes on the focal host tree) (Cooperband et al., 2016). The exact cues used by PSHB beetles that encourage them to disperse and deter them from colonising a saturated host tree are still unknown and need to be further investigated.

4.2. Factors that influence the numbers of dispersing PSHB individuals collected at a site (propagule pressure) and the infestation levels of a site (number of PSHB holes in trees)

Beetle numbers increased with a higher abundance of infested reproductive host trees in plots, a tendency that aligns with other observations of the PSHB in different invaded regions and environments (Byers et al., 2017; Townsend et al., 2024). This may help explain why the transition vegetation plots, which were considered semi-natural and invaded by mostly alien species, had greater beetle abundance than either of the other vegetation types. These transition zones were often populated by infested PSHB reproductive host species (e.g., *Quercus* spp., *Acacia* spp. and *Populus* spp.), which also occurred at a higher density than trees in the heavily managed ornamental and cultivated zones. This finding supports the hypothesis that PSHB may be attracted to volatiles produced by its fungal associates at nearby infestations. This is supported by Cooperband et al.'s (2017) finding that Quercivorol, the chemical used as an attractant in PSHB lures, is also produced by the beetle's fungal symbionts.

Dispersing PSHB beetle abundance was positively correlated with the percentage of understory cover in plots. These results contradict the theory that ambrosia beetles prefer open spaces with less understory cover and therefore fewer obstacles between hosts and more opportunity for wind-mediated dispersal (Chen et al., 2010; Townsend et al., 2024). One reason for the difference found in this study is that many plots in which understory cover was higher were also in the less managed zones which, as mentioned above, had a higher density of infested reproductive hosts than other zones. The percentage of understory cover was also less than 30 percent for many of the plots, with a few outliers having both far more coverage and more beetle abundance. These outliers may therefore be overrepresented in the data.

Plots with seasonal access to surface water had significantly higher dispersing beetle abundance and infestation levels. Studies on PSHB (or near relatives) have not yet provided clarity on their preference for trees based on water availability (Bennett, 2020; Boland, 2018; Umeda, 2017). In this case, however, plots with seasonal access to surface water may be more of an indication of trees with water stress than overall water access. These plots were often located along the farm's artificial canal system, which experienced oscillating periods of overflow and drought (e.g., inundation during winter). This likely puts the trees in these areas, especially those that are relatively flood-intolerant, under stress. Some bark and ambrosia beetles have shown a preference for water-stressed trees (Kelsey et al., 2014; Ranger et al., 2013), especially in non-native regions (Ranger et al., 2015). However, this attraction is often in response to ethanol, a stress volatile produced by these trees, whereas PSHB was observed not responding to ethanol, at least not in high concentrations (Byers et al., 2018). Regardless, trees under stress would have compromised defence systems (Gely et al., 2019; Hulcr and Stelinski, 2017), making it easier for pests to overcome tree defences.

As the number of tree species increased in plots, so did infestation levels. This contradicts with what was hypothesised based on the biotic resistance theory (Fridley et al., 2007). This is also opposite to the trends observed for ambrosia beetles in forest ecosystems in Italy (Rassati et al., 2016) and for PSHB in the Afro-temperate forests in South Africa (Townsend et al., 2024). Townsend et al. (2024) theorised that the reason for decreasing infestations with increasing species richness was because suitable host tree species decreased. Therefore, one reason for the discrepancies between previous studies and the current one could be that even when tree species richness increased within plots, the majority of the species were still hosts for PSHB. The biotic resistance theory may therefore be more relevant for predicting PSHB invasion in species-rich native vegetation than in species-poor urban and agricultural settings.

4.3. Factors that lead to increases in the numbers of dispersing PSHB individuals collected at a site and increased rates of infestation in a site

Some of the same factors that were significant in explaining overall propagule pressure (dispersing beetle numbers) and infestation levels (total number of holes in trees) were also significant explanatory variables for greater rates of increases in dispersing individuals and rates of infestations over the monitoring period. These included the positive correlations with percentage of understory cover and the number of infested reproductive hosts, with faster rates of increase in beetle abundance and infestations in transition vegetation types and with seasonal surface water. The similarities between overall beetle abundance and infestations versus the rates of their increase were expected since there was a significant positive correlation between propagule pressure and infestation levels over the entire experimental period. This leads to a positive feedback loop between beetle infestations and beetle abundance, therefore if there is uncolonised host material available, greater beetle abundance will lead to more infestations, and vice versa.

4.4. *Influence of tree felling on PSHB propagule pressure*

Tree pruning and removal are often recommended for heavily infested PSHB material (Chen et al., 2020; Jones and Paine, 2015), but the effect of tree felling on local beetle activity before and after removal and between seasons has not been evaluated. The daily numbers of dispersing beetles in winter were low across all monitoring days, which was expected. The results of tree felling in summer showed that beetle numbers were statistically lower in the days after tree removal than the days before, which aligns with the hypothesis and advice that infested tree felling is helpful in reducing local beetle activity (propagule pressure). In summer, beetle numbers were statistically higher on the day of tree removal than the days before or after removal, indicating that the activities of tree removal stimulate beetle flight activity. Although the exact cause of this is unknown, it has been theorised that bark beetles have sensitive vibration detectors which they may use to communicate between conspecifics within the tree (Hofstetter et al., 2019). Thus, it could be that the mechanical disturbance caused by tree removal creates vibrations that cue the beetles to emerge and disperse.

The above results also indicate that, as hypothesised, beetle numbers in winter were significantly lower than the days before, during, and after tree felling in summer. This correlates with the previous results surrounding beetle catches across the months which show much higher numbers in summer than in winter, and those that show beetle abundance being positively correlated with temperature. Overall, these results indicate the felling of infested trees, while important for reducing local beetle activity, may be best conducted in seasons of low beetle activity or overall lower temperatures. If tree felling in summer is necessary, further studies could determine whether the time-of-day impacts beetle activity during felling activities, whether due to changes in temperature or general PSHB flight times.

4.5. *Factors that influence the severity of infestations of individual host trees*

All three of the tree species analysed separately here, English oak, Australian beefwood and Chinese poplar, are considered reproductive hosts for PSHB (FABI, 2023). Results showed that the negative association between tree size and overall infestations, as well as the rate of increase in infestation severity, was consistent amongst all species. This is surprising because there are prevailing theories that larger host trees may be easier for bark and ambrosia beetles to find and that they may have more resources available for colonisation (Choudhury et al., 2020; Mayfield and Brownie, 2013). One explanation could be that these studies have looked at the incidence of disease or beetle presence across tree trunks of different diameters, whereas the present study uses the density of holes on trees based on trunk surface area. Another reason could be that the observed trees of the three tree species in the present study, and especially those of English oak, have much thicker bark as they grow larger. Boland and Woodward (2021) found that a near relative of PSHB avoided boring into thicker bark in willow (*Salix* sp.) trees. Aside from mechanical deterrence, bark can also maintain layers of chemicals that can be toxic or repellent to pests (Franceschi et al., 2005; Thomas, 2014) which could be more abundant or more effective when there is a larger quantity of bark. It therefore follows that, because larger trees with thicker bark were often found growing next to smaller trees of the same species, PSHB preferentially infested the trees with thinner bark. Infestations could therefore also increase in larger trees in the future as the smaller trees die and there is less host material from which to select.

English oak trees also experienced higher overall infestations and rates of increase in infestations in cultivated areas. This varies from overall beetle abundance and infestations which were significantly higher in the transition zones. However, there was a greater abundance and higher density of English Oak trees in cultivated areas, and cultivated areas had few other available host trees and species. This aligns with the previously mentioned theory that PSHB may select host material according to availability (Carlsson et al., 1990; Choudhury et al., 2020).

In Australian beefwood trees, overall infestations and rates of infestation severity were negatively associated with distance to human or natural impact. This echoes the sentiment that areas that are negatively impacted by human or natural disturbances will experience higher rates of infestation (Boland, 2016; Hulcr and Stelinski, 2017; Mendel et al., 2021; Townsend et al., 2024). In the case of this species, the majority of these disturbances were roads. The negative impact of roads on most ecosystems is in fragmentation and edge creation. Many bark and ambrosia beetles first occupy the edges of a natural system (Didham, 1997), and this tendency held true for PSHB in the natural forest areas (Townsend et al., 2024). In this study, increased wind speeds and even wind tunnels created by roads may have been important, because this area is known for instances of high wind speed. This could have increased wind-mediated dispersal along roads.

The number of surrounding infested hosts demonstrated significance for increasing rates of infestation severity in Australian beefwood, and the beetle abundance along with the number of surrounding reproductive hosts were important to infestation levels in Chinese poplar. These factors again align with previous observations about host material availability and possible beetle attraction to nearby infestations. Interestingly, host abundance and infested host abundance did not indicate significance for English oak. English oak is considered a highly susceptible reproductive host (FABI, 2023), and the PSHB is known to quickly amplify within it and cause its death. Therefore, PSHB may preferentially select an English oak and cause severe infestation, regardless of its proximity to other infested hosts.

4.6. *Conclusions*

The overall invasion of PSHB at this study site continued to intensify throughout the 26-month monitoring period. The highest flight activity periods occurred in the drier summer months and the lowest activity periods were in the wetter winter months, with flight activity being positively associated with temperature, developmental degree days and flight hours (within previously determined general flight times for a near relative of PSHB). These results corroborate previous theories of PSHB activity in Mediterranean climates and confirm that most of the increasing invasion severity will occur in summer. However, these results are limited to this climatic region, and further studies will be needed to determine PSHB population dynamics in other climatic zones. Even when PSHB flight activity is lower, infestations may still be increasing if individual beetles walk to start new galleries on the same host tree. Host tree saturation may be an important deterrent to further colonisation of highly infested hosts. The factor most important to beetle dispersal and infestation levels, as well as the rates of increase to both, was greater abundance and density of infested reproductive host trees, and therefore removing host tree material is important to preventing infestations and stemming infestation levels. Tree stress, such as water stress, may also play a role, but this needs to be further investigated to be confirmed. Beetle activity was significantly higher during tree removal periods in summer than in winter, and there was more beetle activity on the day of tree removal than on the days before or after felling during summer. Felling activities may therefore be better conducted in winter, though further research could ascertain whether the time-of-day has an influence. More studies are also needed to determine the feasibility of tree felling at larger scales across different landscapes, as it is resource intensive and proved to be logistically complex during this study. Smaller trees were more likely to become infested and increase in infestation severity, which may be due to larger trees having thicker bark or better tree defences. Larger trees are however still at risk as host availability may reduce host selective pressures on PSHB.

CRediT authorship contribution statement

Elise Roberts: Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Trudy Paap:** Supervision, Resources, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Francois Roets:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Formal analysis, Conceptualization.

Declaration of Competing Interest

All authors, Elise Roberts, Francois Roets, Trudy Paap, have no conflicts of interest to declare.

Acknowledgements

The authors thank Lourensford Fruit Company for financial support for this study and Lourensford Estate for providing the space and equipment to conduct experiments. Vergelegen Estate is acknowledged for partial funding of equipment used.

Appendix A

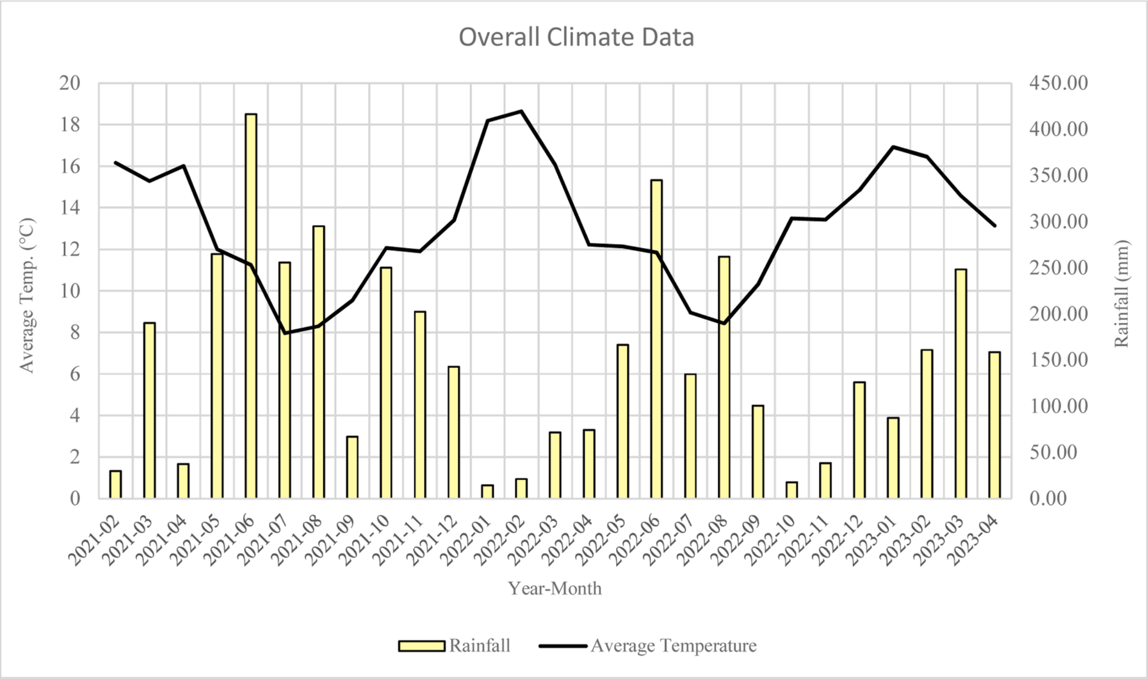

Figure A1. Combination chart showing the monthly average temperature (black line) and the cumulative monthly rainfall (yellow bars) over the entire study period

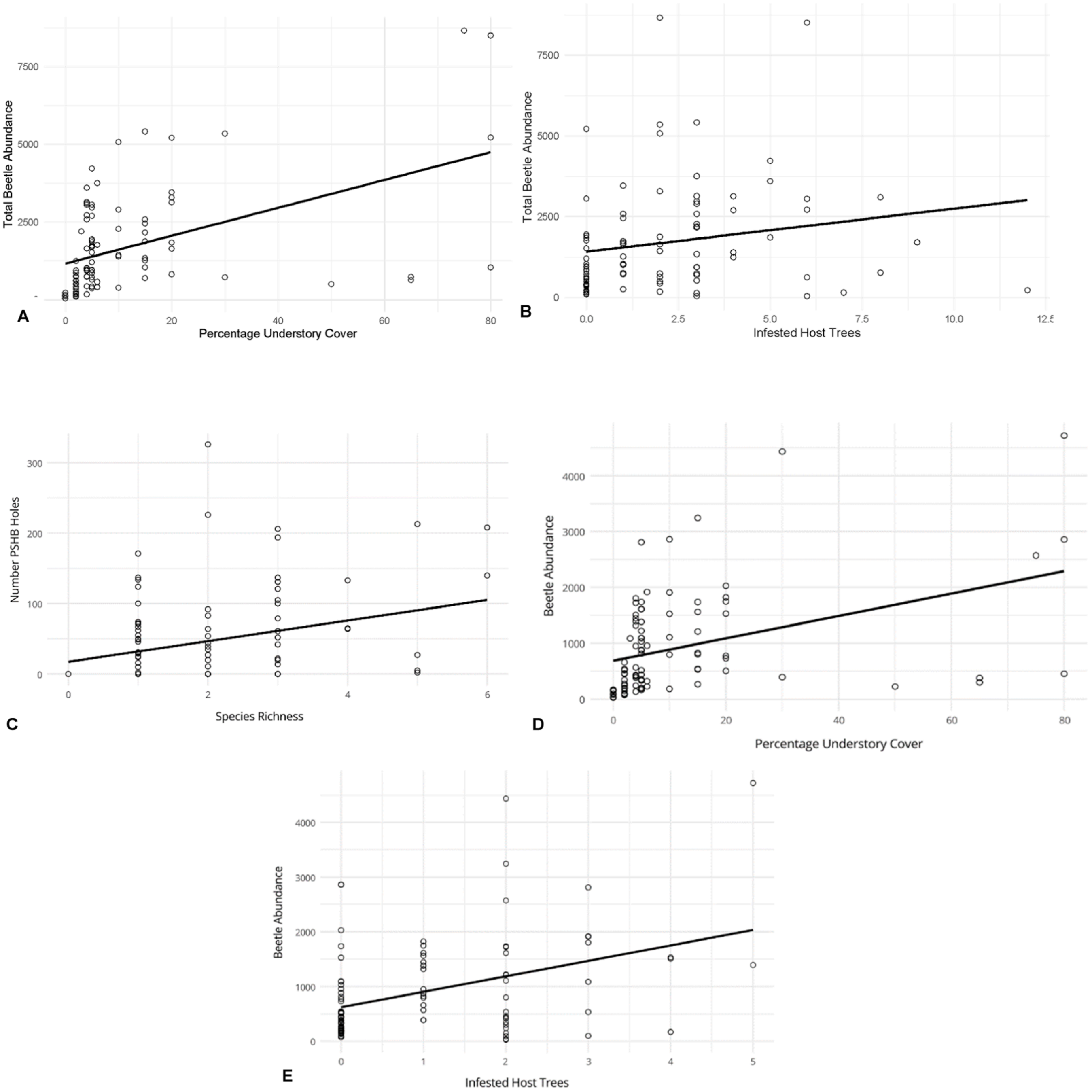

Figure A2. Scatterplots showing the relationship and direction of association (fitted line) between (A) total beetle abundance up to the end of the survey period versus percentage understory cover and (B) total beetle abundance up to the end of the survey period versus the number of infested reproductive host trees in plots (C) total infestation levels (number of holes) at the end of the survey period versus plot tree species richness (D) beetle abundance versus plot percentage understory cover and (E) beetle abundance versus the number of infested reproductive host trees in plots

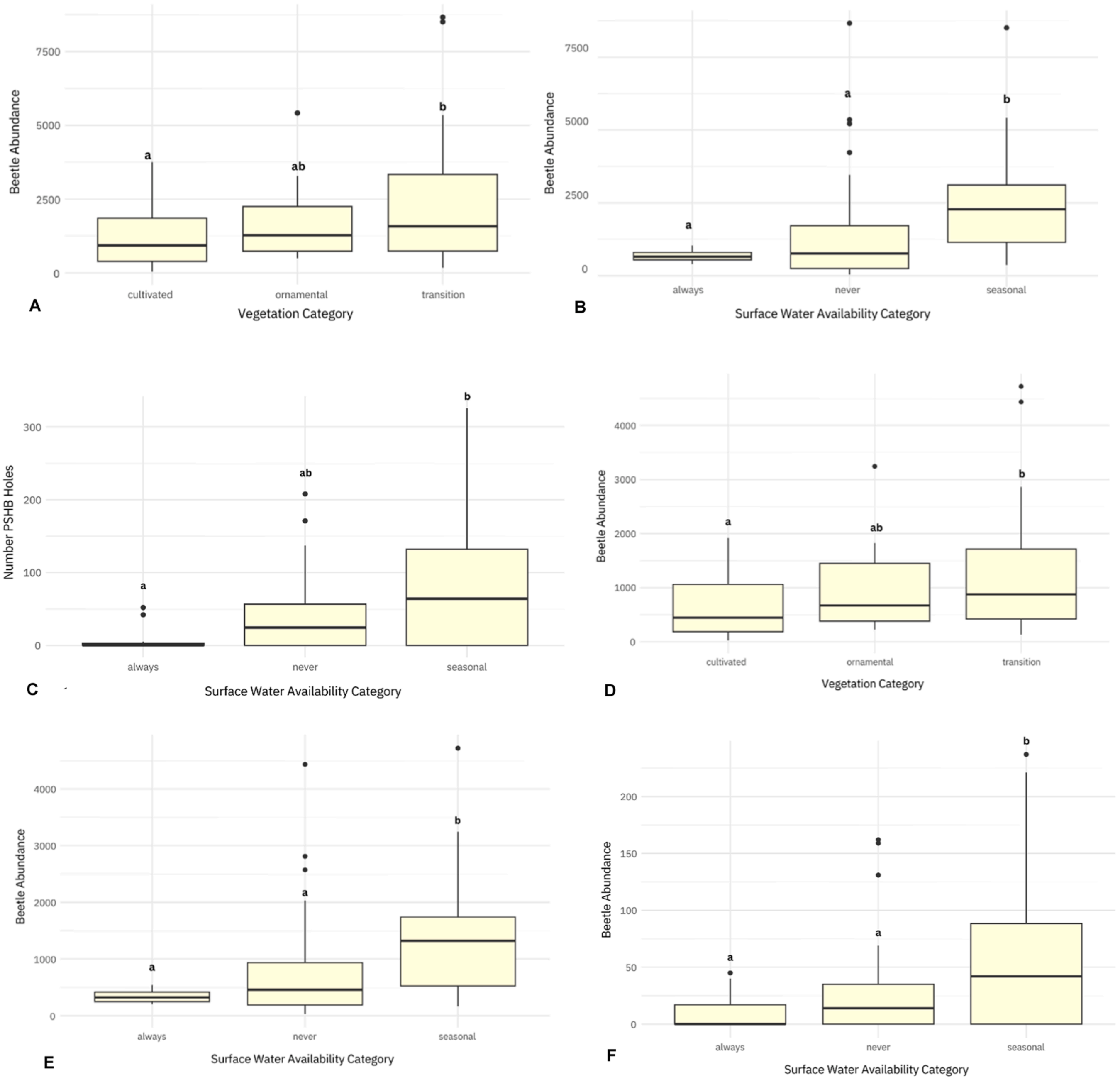

Figure A3. Box plots showing the differences between (A) total beetle abundance up to the end of the survey period across vegetation type categories (B) total beetle abundance up to the end of the survey period across surface water availability categories (C) total infestation levels (number of holes) at the end of the survey period across surface water availability categories (D) total beetle abundance across vegetation type categories (E) total beetle abundance across surface water availability categories and (F) increased number of infestations up to the end of the survey period across surface water availability categories. Different letters above bars indicate significant differences between categories. Box indicates 25–75 % data range, whiskers indicate 1.5 times the interquartile range, dots represent outliers

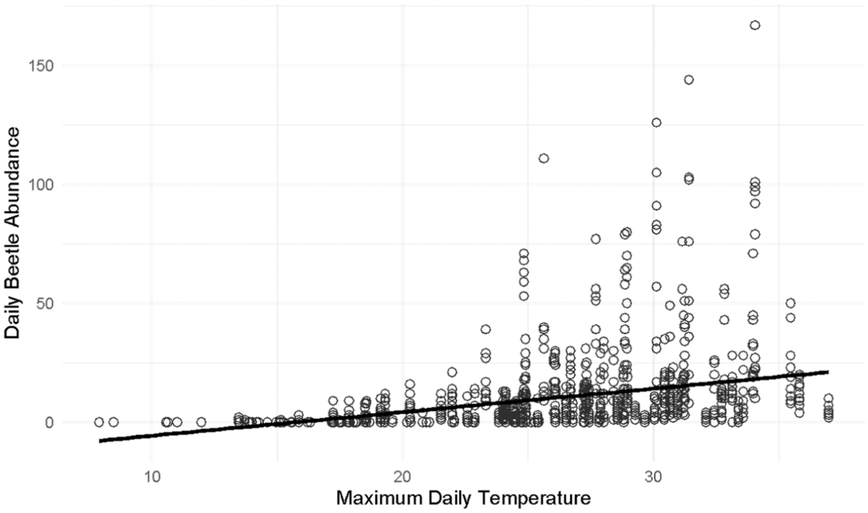

Figure A4. Scatterplot showing the relationship and the linear fit between daily abundance of dispersing beetles and maximum daily temperature

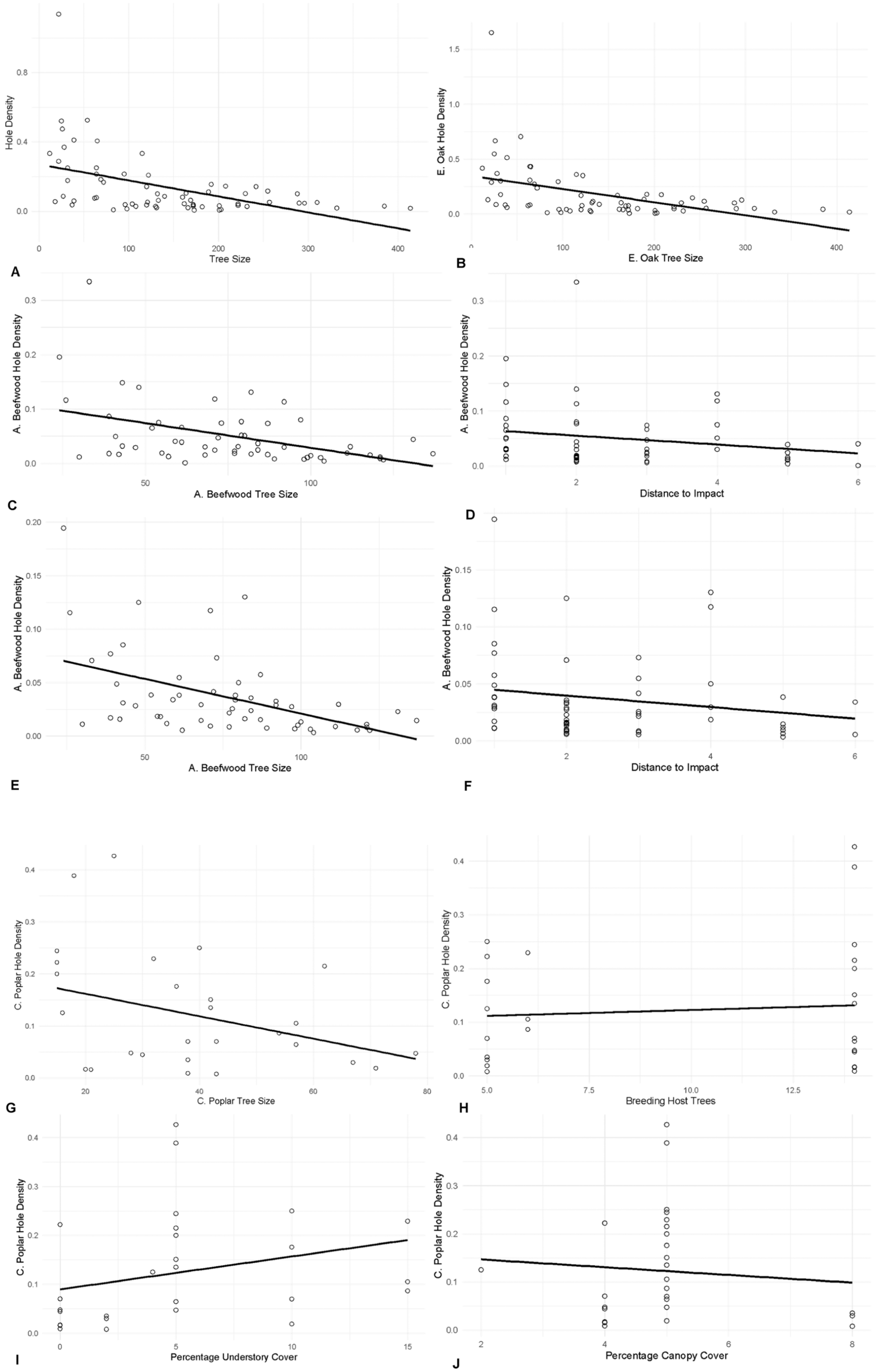

Figure A5. Scatterplot showing the relationship and the linear fit between (A) English oak (*Quercus robur*) tree size and hole density at the end of the survey period (B) the increase in the number of holes on English oak (*Quercus robur*) trees and tree size from the beginning to the end of the survey period (C) the hole density on Australian beefwood (*Casuarina cunninghamiana*) trees at the end of the survey period versus tree size (D) the hole density on Australian beefwood (*Casuarina cunninghamiana*) trees at the end of the survey period versus distance to nearest impact (E) the increase in hole density on Australian beefwood (*Casuarina* *cunninghamiana*) trees from the beginning to the end of the survey period versus tree size (F) the increase in hole density on Australian beefwood (*Casuarina cunninghamiana*) trees from the beginning to the end of the survey period versus distance to nearest impact (G) the hole density on Chinese poplar (*Populus simonii*) trees at the end of the survey period versus tree size (H) the hole density on Chinese poplar (*Populus simonii*) trees at the end of the survey period versus number of surrounding reproductive hosts (I) the hole density on Chinese poplar (*Populus simonii*) trees at the end of the survey period versus percentage understory cover (J) the hole density on Chinese poplar (*Populus simonii*) trees at the end of the survey period versus percentage canopy cover (K) the increase in hole density on Chinese poplar (*Populus simonii*) trees from the beginning to the end of the survey period versus tree size (L) the increase in hole density on Chinese poplar (*Populus simonii*) trees from the beginning to the end of the survey period versus beetle abundance (M) the increase in hole density on Chinese poplar (*Populus simonii*) trees from the beginning to the end of the survey period versus percentage understory cover and (N) the increase in hole density on Chinese poplar (*Populus simonii*) trees from the beginning to the end of the survey period versus percentage canopy cover

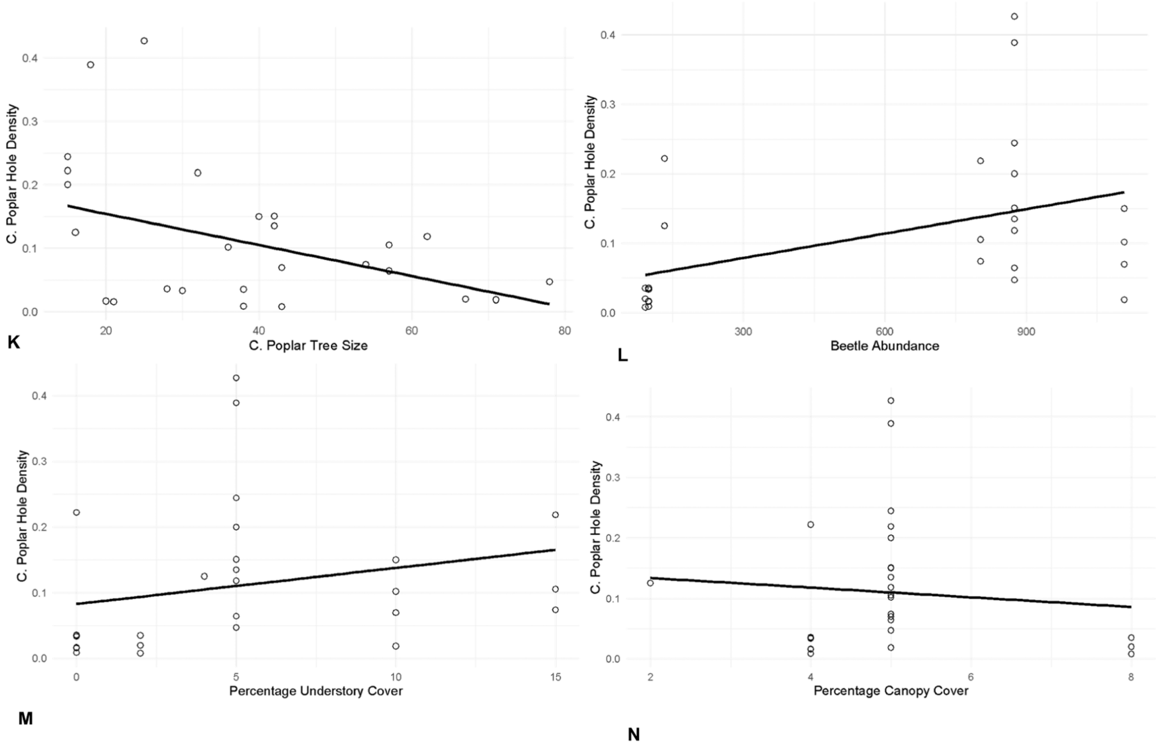

Figure A5. (*continued*).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2025.128980.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

References

de Beer, W. & Fell, S. 2022. The polyphagous shot hole borer (PSHB) now found reproducing in light-stressed branches of older pecan trees. SAPPA SA Pecan, 91:10-12. ⟨https://www.sappa.za.org/publication/volume-91-2022⟩. Accessed 6 June 2023.

Bennett, S.K., 2020. Ecology of the invasive shot hole borer (*euwallacea whitfordiodendrus)* in a coastal california riparian system (Thesis). University of California, Santa Barbara. ⟨https://escholarship.org/content/qt2rp257w2/qt2rp257w2.pdf⟩ (Thesis).

Berryman, A.A., 1986. Population dynamics of forest insects. In: Berryman, A.A. (Ed.), Forest insects: Principles and practice of population management. Plenum Press, New York, pp. 51–77.

Bierman, A., Roets, F., Terblanche, J.S., 2022. Population structure of the invasive ambrosia beetle, *euwallacea fornicatus*, indicates multiple introductions into South Africa. Biol. Invasions 24 (8), 2301–2312. https://doi.org/10.1007/s10530-022-02801-x.

Boland, J.M., 2016. The impact of an invasive ambrosia beetle on the riparian habitats of the tijuana river valley, california. PeerJ 4, 2141. https://doi.org/10.7717/peerj.2141.

Boland, J.M. 2018. The Kuroshio Shot Hole Borer in the Tijuana River Valley in 2017-18 (Year Three): Infestation Rates, Forest Recovery, and a New Model: Final Report. ⟨https://trnerr.org/wp-content/uploads/2018/07/Boland-KSHB-April2018-FINAL.pdf⟩. Accessed 6 June 2023.

Boland, J.M., Woodward, D.L., 2021. Thick bark can protect trees from a severe ambrosia beetle attack. PeerJ 9, e10755. https://doi.org/10.7717/peerj.10755.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. Modeling zero-inflated count data with glmmTMB. BioRxiv, 132753. https://doi.org/10.1101/132753.

Byers, J.A., Maoz, Y., Levi-Zada, A., 2017. Attraction of the *euwallacea* sp. Near *fornicatus* (Coleoptera: Curculionidae) to quercivorol and to infestations in avocado. J. Econ. Entomol. 110, 1512–1517. https://doi.org/10.1093/jee/tox151.

Byers, J.A., Maoz, Y., Fefer, D., Levi-Zada, A., 2020. Semiochemicals affecting attraction of ambrosia beetle *euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) to quercivorol: developing push-pull control. J. Econ. Entomol. 113 (5), 2120–2127. https://doi.org/10.1093/jee/toaa127.

Byers, J.A., Maoz, Y., Wakarchuk, D., Fefer, D., Levi Zada, A., 2018. Inhibitory effects of semiochemicals on the attraction of an ambrosia beetle *euwallacea* nr. *fornicatus* to quercivorol. J. Chem. Ecol. 44, 565–575. https://doi.org/10.1007/s10886-018-0959-8.

Calnaido, D., 1965. The flight and dispersal of shot-hole borer of tea (*xyleborus fornicatus* Eichh., Coleoptera: Scolytidae). Entomol. Exp. Appl. 8 (4), 249–262. https://doi.org/10.1111/j.1570-7458.1965.tb00859.x.

Calnaido, D., Thirugnanasuntharau, K., 1966. Preliminary studies on the shot-hole borer and their relation to the control of the pest. Tea Quart. 37, 28–45.

Carlsson, U., Elmqvist, T., Wennstrom, A., Ericson, L., 1990. Infection by pathogens and population age of host plants. J. Ecol. 78 (4), 1094. https://doi.org/10.2307/2260954.

Chen, Y., Coleman, T.W., Poloni, A.L., Nelson, L., Seybold, S.J., 2020. Reproduction and control of the invasive polyphagous shot hole borer, *euwallacea* nr. *fornicatus* (Coleoptera: Curculionidae: Scolytinae), in three species of hardwoods: effective sanitation through felling and chipping. Environ. Entomol. 49 (5), 1155–1163. https://doi.org/10.1093/ee/nvaa103.

Chen, H., Li, Z., Tang, M., 2010. Laboratory evaluation of flight activity of *dendroctonus armandi* (Coleoptera: Curculionidae: Scolytinae). Can. Entomol. 142 (4), 378–387. https://doi.org/10.4039/n10-018.

Choudhury, R.A., Er, H.L., Hughes, M.A., Smith, J.A., Pruett, G.E., Konkol, J., Ploetz, R. C., Marois, J.J., Garrett, K.A., van Bruggen, A.C., 2020. Host density dependence and environmental factors affecting laurel wilt disease incidence. Plant Pathol. 70 (3), 1–13. https://doi.org/10.1111/ppa.13314.

Cohen, I., Huang, Y., Chen, J., Benesty, J., 2009. Pearson correlation coefficient. In: Benesty, J. (Ed.), Noise reduction in speech processing. Springer, Berlin, pp. 1–4. https://doi.org/10.1109/5.771073.

Cooperband, M.F., Cossé, A.A., Jones, T.H., Carrillo, D., Cleary, K., Canlas, I., Stouthamer, R., 2017. Pheromones of three ambrosia beetles in the *euwallacea fornicatus* species complex: ratios and preferences. PeerJ 5, e3957. https://doi.org/10.7717/peerj.3957.

Cooperband, M.F., Stouthamer, R., Carrillo, D., Eskalen, A., Thibault, T., Cossé, A.A., Castrillo, L.A., Vandenberg, J.D., Rugman-Jones, P.F., 2016. Biology of two members of the *euwallacea fornicatus* species complex (Coleoptera: Curculionidae: Scolytinae), recently invasive in the USA, reared on an ambrosia beetle artificial diet. Agr. For. Entomol. 18 (3), 223–237. https://doi.org/10.1111/afe.12155.

Cowling, R.M., Holmes, P.M., 1992. Endemism and speciation in a lowland flora from the cape floristic region. Biol. J. Linn. Soc. 47 (4), 367–383. https://doi.org/10.1111/j.1095-8312.1992.tb00675.x.

Didham, R.K., 1997. An overview of invertebrate responses to forest fragmentation. In: Watt, A.D., Stork, N.E., Hunter, M.D. (Eds.), Forests and Insects. Chapman & Hall, London, pp. 303–320.

Dodge, C., Coolidge, J., Cooperband, M., Cossé, A., Carrillo, 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. PeerJ 5, 3656. https://doi.org/10.7717/peerj.3656.

Dodge, C., Stouthamer, R., 2021. Effect of temperature on fecundity, development, and emergence of the invasive ambrosia beetle *euwallacea kuroshio* (Coleoptera: Scolytinae). Agr. For. Entomol. 23 (1), 79–86. https://doi.org/10.1111/afe.12407.

Dunn, O.J., 1964. Multiple comparisons using rank sums. Technometrics 6 (3), 241–252.

Engelbrecht, K., Raubenheimer, I., Paap, T., Neethling, E., Roets, F., 2024. 2024. Detection of *fusarium euwallaceae* and its vector *euwallacea fornicatus* on pear (*pyrus communis*) and in deciduous fruit orchards in South Africa. Australas. Plant Dis. Notes 19 (1).

Eskalen, A., Stouthamer, R., Lynch, S.C., Rugman-Jones, P.F., 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 (7), 938–951. https://doi.org/10.1094/PDIS-11-12-1026-RE.

Forestry and Agricultural Biotechnology Institute. 2023. Polyphagous Shot Hole Borer South African host list. ⟨https://www.fabinet.up.ac.za/images/PSHB/PSHB_host_list_v6_20230417.pdf⟩. Accessed 6 June 2023.

Franceschi, V.R., Krokene, P., Christiansen, E., Krekling, T., 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. N. Phytol. 167 (2), 353–376.

Freeman, S., Sharon, M., Dori-Bachash, M., Maymon, M., Belausov, E., Maoz, Y., Margalit, O., Protasov, A., Mendel, Z., 2016. Symbiotic association of three fungal species throughout the life cycle of the ambrosia beetle *euwallacea* nr. *fornicatus*. Symbiosis 68, 115–128. https://doi.org/10.1007/s13199-015-0356-9.

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D., Von Holle, B., 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecol 88, 3–17. https://doi.org/10.1890/0012-9658(2007)88[3:tiprpa]2.0.co;2.

Gely, C., Laurance, S.W., Stork, N., 2019. How do herbivorous insects respond to drought stress in trees? Biol. Rev. https://doi.org/10.1111/brv.12571.

Gomez, D.F., Lin, W., Gao, L., Li, Y., 2019. New host plant records for the *euwallacea fornicatus* (Eichhoff) species complex (Coleoptera: Curculionidae: Scolytinae) across its natural and introduced distribution. J. AsiaPac. Entomol. 22 (1), 338–340. https://doi.org/10.1016/j.aspen.2019.01.013.

Gomez, D.F., Skelton, J., Steininger, M.S., Stouthamer, R., Rugman-Jones, P., Sittichaya, W., Rabaglia, R.J., Hulcr, J., 2018. Species delineation within the *euwallacea fornicatus* (Coleoptera: Curculionidae) complex revealed by morphometric and phylogenetic analyses. ISD 2 (6), 2. https://doi.org/10.1093/isd/ixy018.

Graves, S., Piepho, H.P., Selzer, L. & Dorai-Jai, S. 2012. MultcompView: Visualizations of Paired Comparisons. R Package Version 0.1-5.

Greer, K., Rice, K. & Lynch, S. 2018. Southern California Shot Hole Borers/Fusarium Dieback Management Strategy for Natural and Urban Landscapes. https://sdmmp.com/upload/SDMMP_Repository/0/j02vf5k3qyt49wb16sxnrgcd7hpmz.pd. Accessed 6 June 2023.

Gross, J. & Ligges, U. 2015. Nortest: Tests for Normality. R package version 1.0.4.

Haack, R.A., 2006. Exotic bark-and wood-boring coleoptera in the United States: recent establishments and interceptions. Can. J. For. Res. 36 (2), 269–288. https://doi.org/10.1139/x05-249.

Haas, S.E., Cushman, J.H., Dillon, W.W., Rank, N.E., Rizzo, D.M., Meentemeyer, R.K., 2016. Effects of individual, community, and landscape drivers on the dynamics of a wildland forest epidemic. Ecol 97 (3), 649–660. https://doi.org/10.1890/15-0767.1.

Hofstetter, R.W., Aflitto, N., Bedoya, C.L., Yturralde, K., Dunn, D.D., 2019. Vibrational behavior. In: Hill, P.S.M., Lakes-Harlan, R., Mazzoni, V., Narins, P.M., Virant-Doberlet, M., Wessel, A. (Eds.), Biotremology: Studying Vibrational Behavior (Animal Signals and Communication, 6. Springer, Heidelberg, pp. 415–435.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50 (3), 346–363. https://doi.org/10.1002/bimj.200810425.

Howe, M., Carroll, A., Gratton, C., Raffa, K.F., 2021. Climate-induced outbreaks in high-elevation pines are driven primarily by immigration of bark beetles from historical hosts. Glob. Change Biol. 27 (22), 5786–5805. https://doi.org/10.1111/gcb.15861.

Hulcr, J., Dunn, R.R., 2011. The sudden emergence of pathogenicity in insect–fungus symbioses threatens naive forest ecosystems. Proc. R. Soc. B Biol. Sci. 278 (1720), 2866–2873. https://doi.org/10.1098/rspb.2011.1130.

Hulcr, J., Nogia, M., Isua, B., Novtny, V., 2007. Host specificity of ambrosia and bark beetles (Col., Curculionidae: Scolytinae and Platypodinae) in a new Guinea rainforest. Ecol. Entomol. 32, 762–772. https://doi.org/10.1111/j.1365-2311.2007.00939.x.

Hulcr, J., Stelinski, L.L., 2017. The ambrosia symbiosis: from evolutionary ecology to practical management. Annu. Rev. Entomol. 62, 285–303. https://doi.org/10.1146/annurev-ento-031616-035105.

de Jager, M.M., Roets, F., 2022. Pathogenicity of *fusarium euwallaceae* towards apple (*malus domestica*) and grapevine (*vitis vinifera*). Australas. Plant Dis. 17 (1), 1–4. https://doi.org/10.1007/s13314-022-00456-0.

de Jager, M.M., Roets, F., 2023. Pathogenicity of *fusarium euwallaceae*, symbiont of the polyphagous shot hole borer beetle, to selected stone fruit trees in South Africa. Plant Pathol. J. 105 (1), 5–13. https://doi.org/10.1007/s42161-022-01258-0.

Jones, M., Paine, T.D., 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 (4), 1852–1859. https://doi.org/10.1093/jee/tov169.

Joseph, R., Keyhani, N.O., 2021. Fungal mutualisms and pathosystems: life and death in the ambrosia beetle mycangia. Appl. Microbiol. Biotechnol. 105 (9), 3393–3410. https://doi.org/10.1007/s00253-021-11268-0.

Kautz, M., Imron, M.A., Dworschak, K., Schopf, R., 2016. Dispersal variability and associated population-level consequences in tree-killing bark beetles. Mov. Ecol. 4, 1–12. https://doi.org/10.1186/s40462-016-0074-9.

Kelsey, R.G., Gallego, D., Sanchez-Garcia, F.J., Pajares, J.A., 2014. Ethanol accumulation during severe drought May signal tree vulnerability to detection and attack by bark beetles. Can. J. For. Res. 44 (6). https://doi.org/10.1139/cjfr-2013-0428.

Kendra, P.E., Owens, D., Montgomery, W.S., Narvaez, T.I., Bauchan, G.R., Schnell, E.Q., Tabanca, N., Carrillo, D., 2017. α-Copaene is an attractant, synergistic with quercivorol, for improved detection of *euwallacea* nr. *fornicatus* (Coleoptera: Curculionidae: Scolytinae). PLoS One 12 (6), 0179416. https://doi.org/10.1371/journal.pone.0179416J.

Kruskal, W.H., Wallis, W.A., 1952. Use of ranks in one-criterion variance analysis. JASA 47 (260), 583–621. https://doi.org/10.1080/01621459.1952.10483441.

Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2018. Package "Emmeans". R. Package Version 4, 0–3.

Liebhold, A.M., Brockerhoff, E.G., Garrett, L.J., Parke, J.L., Britton, K.O., 2012. Live plant imports: the major pathway for forest insect and pathogen invasions of the US. Front. Ecol. Evol. 10 (3), 135–143. https://doi.org/10.1890/110198.

Liu, F.L., Rugman-Jones, P., Liao, Y.C., Husein, D., Liang, H.H., Tuan, S.J., Stouthamer, R., 2022. Seasonal dynamics of flight phenology of the *euwallacea fornicatus* species complex and an associated parasitoid wasp in avocado Groves in Taiwan. J. Econ. Entomol. 115 (6), 1901–1910. https://doi.org/10.1093/jee/toac144.

Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an r package for assessment, comparison and testing of statistical models. J. Open Source Softw. 6, 60.

Lynch, S.C., Carrillo, J.D., Stouthamer, R., Eskalen, A., 2018. Severity of fusarium Dieback–Shot hole borers analyzed. Grove Winter 46–50 https://ucanr.edu/sites/eskalenlab/files/296160.pdf. Accessed 6 June 2023.

Lynch, S.C., Eskalen, A., Gilbert, G.S., 2021. Host evolutionary relationships explain tree mortality caused by a generalist pest–pathogen complex. Evol. Appl. 14 (4), 1083–1094. https://doi.org/10.1111/eva.13182.

Lynch, S.C., Twizeyimana, M., Mayorquin, J.S., Wang, D.H., Na, F., Kayim, M., Kasson, M.T., Thu, P.Q., Bateman, C., Rugman-Jones, P., Hulcr, J., 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. Mycol 108 (2), 313–329. https://doi.org/10.3852/15-063.

Mayfield, A.E., Brownie, C., 2013. The redbay ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) uses stem silhouette diameter as a visual host-finding cue. Environ. Entomol. 42 (4), 743–750. https://doi.org/10.1603/EN12341.

Mayorquin, J.S., Carrillo, J.D., Twizeyimana, M., Peacock, B.B., Sugino, K.Y., Na, F., Wang, D.H., Kabashima, J.N., Eskalen, A., 2018. Chemical management of invasive shot hole borer and fusarium dieback in california sycamore (*platanus racemosa*) in Southern california. Plant Dis. 102 (7), 1307–1315. https://doi.org/10.1094/PDIS-10-17-1569-RE.

Mendel, Z., Protasov, A., Maoz, Y., Maymon, M., Miller, G., Elazar, M., Freeman, S., 2017. The role of *euwallacea* nr. *fornicatus* (Coleoptera: Scolytinae) in the wilt syndrome of avocado trees in Israel. Phytoparasitica 45 (3), 341–359. https://doi.org/10.1007/s12600-017-0598-6.

Mendel, Z., Protasov, A., Sharon, M., Zveibil, A., Yehuda, S.B., 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 (3), 235–238. https://doi.org/10.1007/s12600-012-0223-7.

Na, F., Carrillo, J.D., Mayorquin, J.S., Ndinga-Muniania, C., Stajich, J.E., Stouthamer, R., Huang, Y.T., Lin, Y.T., Chen, C.Y., Eskalen, A., 2018. Two novel fungal symbionts *fusarium kuroshium* sp. Nov. and *graphium kuroshium* sp. Nov. of kuroshio shot hole borer (*euwallacea* sp. nr. *fornicatus*) cause fusarium dieback on woody host species in california. Plant Dis.10211541164. https://doi.org/10.1094/PDIS-07-17-1042-RE.

Neethling, E., Roets, F., Crous, C., 2024. Early impact assessment of the paninvasive polyphagous shot hole borer beetle on commercial pear production. Èntomol. Exp. Et. Appl. 172, 796–805.

Ogle, D.H. 2017. FSA: Fisheries Stock Analysis. R package version 0.8.17.

Owens, D., Kendra, P.E., Tabanca, N., Narvaez, T.I., Montgomery, W.S., Schnell, E.Q., Carrillo, D., 2019a. Quantitative analysis of contents and volatile emissions from α-copaene and quercivorol lures, and longevity for attraction of *euwallacea* nr. *fornicatus* in florida. J. Pest Sci. 92 (1), 237–252. https://doi.org/10.1007/s10340-018-0960-6.

Owens, D., Seo, M., Montgomery, W.S., Rivera, M.J., Stelinski, L.L., Kendra, P.E., 2019b. Dispersal behaviour of *euwallacea* nr. *fornicatus* (Coleoptera: Curculionidae: Scolytinae) in avocado Groves and estimation of lure sampling range. Agr. For. Entomol. 21 (2), 199–208. https://doi.org/10.1111/afe.12321.

Paap, T., de Beer, Z.W., Migliorini, D., Nel, W.J., Wingfield, M.J., 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 doi:1007/s13313-018-0545-0.

Paap, T., Wingfield, M.J., Wilhelm de Beer, Z., Roets, F., 2020. Lessons from a major pest invasion: the polyphagous shot hole borer in South Africa. S. Afr. J. Sci. 116 (11-12), 1–4. https://doi.org/10.17159/sajs.2020/8757.

Peer, K., Taborsky, M., 2007. Delayed dispersal as a potential route to cooperative breeding in ambrosia beetles. Behav. Ecol. Socio 61, 729–739. https://doi.org/10.1007/s00265-006-0303-0.

Ranger, C., Reding, M., Schultz, P., Oliver, J., 2013. Influence of flood-stress on ambrosia beetle host-selection and implications for their management in a changing climate. Agr. For. Entomol. 15 (1), 56–64. https://doi.org/10.1111/j.1461-9563.2012.00591.x.

Ranger, C.M., Schultz, P.B., Frank, S.D., Chong, J.H., Reding, M.E., 2015. Non-Native ambrosia beetles as opportunistic exploiters of living but weakened trees. Plos One 10 (7), e0131496. https://doi.org/10.1371/journal.pone.0131496.

Rassati, D., Faccoli, M., Haack, R.A., Rabaglia, R.J., Toffolo, E.P., Battisti, A., Marini, L., 2016. Bark and ambrosia beetles show different invasion patterns in the USA. Plos One 11 (7), 1–17. https://doi.org/10.1371/journal.pone.0158519.

Régnière, J., Powell, J., Bentz, B., Nealis, V., 2012. Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. J. Insect Physiol. 58 (5), 634–647. https://doi.org/10.1016/j.jinsphys.2012.01.010.

Roberts, E., Paap, T., Roets, F., 2024. Chemical control of the polyphagous shot hole borer (*euwallacea fornicatus*, PSHB) beetle and *fusarium euwallaceae* in American sweetgum (*liquidambar styraciflua*). J. Plant Pathol. 106, 457–468.

van Rooyen, E., Paap, T., Beer, W.D., Townsend, G., Fell, S., Nel, W.J., Morgan, S., Hill, M., Gonzalez, A., Roets, F., 2021. The polyphagous shot hole borer beetle: current status of a perfect invader in South Africa. S. Afr. J. Sci. 117 (11-12), 1–10. https://doi.org/10.17159/sajs.2021/9736.

Roques, A., 2010. Alien forest insects in a warmer world and a globalised economy: impacts of changes in trade, tourism and climate on forest biosecurity. N. Z. J. For. Sci. 40, 77–94 https://www.scionresearch.com/_data/assets/pdf_file/0015/17160/NZJFS40Suppl.2010S77-S94ROQUES.pdf. Accessed 6 June 2023.

Shapiro, S.S., Wilk, M.B., 1965. An analysis of variance test for normality (complete samples). Biometrika 52 (3/4), 591–611. https://doi.org/10.1093/biomet/52.3-4.591.

Six, D.L., 2012. Ecological and evolutionary determinants of bark beetle—fungus symbioses. Insects 3 (1), 339–366. https://doi.org/10.3390/insects3010339.

Smith, S., Gomez, D., Beaver, R., Hulcr, J., Cognato, A., 2019. Reassessment of the species in the *euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) complex after the rediscovery of the “lost” type specimen. Insects 10 (9), 261. https://doi.org/10.3390/insects10090261.

Stouthamer, R., Rugman-Jones, P., Thu, P.Q., Eskalen, A., Thibault, T., Hulcr, J., Wang, L., Jordal, B.H., Chen, C., Cooperband, M., Lin, C., 2017. Tracing the origin of a cryptic invader: phylogeography of the *euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) species complex. Agr. For. Entomol. 19 (4), 366–375. https://doi.org/10.1111/afe.12215.

Thomas, P., 2014. Trees: Their natural history. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511790522.

Townsend, G., Hill, M., Hurley, B.P., Roets, F., 2025. Escalating threat: increasing impact of the polyphagous shot hole borer beetle, *euwallacea fornicatus*, in nearly all major South African forest types. Biol. Invasions 27, 88. https://doi.org/10.1007/s10530-025-03551-2.

Townsend, G., van Rooyen, E., Hill, M., De Beer, W., Roets, F., 2024. Invasion of an afrotemperate forest complex by the polyphagous shot hole borer beetle. Entomol. Exp. Appl. 172 (4), 354–369. https://doi.org/10.1111/eea.13415.

Umeda, C. 2017. Environmental effects on polyphagous shot hole borer. Dissertation, University of California, Riverside. https://escholarship.org/content/qt243646pn/qt243646pn_noSplash_90eef95d6094ffb3a7fb769f1fbe8ead.pdf. Accessed 6 June 2023.

Umeda, C., Eatough-Jones, M., Paine, T., 2019. Irrigation and its effect on polyphagous shot hole borer attack. Entomol. Exp. Appl. 167 (9), 820–825. https://doi.org/10.1111/eea.12829.

Umeda, C., Eskalen, A., Paine, T.D., 2016. Polyphagous shot hole borer and fusarium dieback in california. In: Paine, T.D., Lieutier, F. (Eds.), Insects and Diseases of mediterranean forest systems. Springer, Switzerland, pp. 757–767. https://doi.org/10.1007/978-3-319-24744-1_26.

Umeda, C., Paine, T.D., 2018. Temperature can limit the invasion range of the ambrosia beetle. Agr. For. Entomol. 21 (1), 1–7. https://doi.org/10.1111/afe.12297.

de Wit, M.P., Crookes, D.J., Blignaut, J.N., de Beer, Z.W., Paap, T., Roets, F., van der Merwe, C., van Wilgen, B.W., Richardson, D.M., 2022. An assessment of the potential economic impacts of the invasive polyphagous shot hole borer (Coleoptera: Curculionidae) in South Africa. J. Econ. Entomol. 1–11. https://doi.org/10.1093/jee/toac061.