



# Escalating threat: increasing impact of the polyphagous shot hole borer beetle, *Euwallacea fornicatus*, in nearly all major South African forest types

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**Abstract** The polyphagous shot hole borer (PSHB; *Euwallacea fornicatus*), is an invasive ambrosia beetle and poses a significant threat to a wide range of tree species globally. Despite its potential impact, research on the beetle's spread and impacts in natural ecosystems remains limited. This study examines the interactions between PSHB and native forest ecosystems in two regions in South Africa. Over 5 years, PSHB invaded all but one forest type with colonization being recorded on numerous native tree species, often resulting in severe infestations and sometimes mortality. Many tree species and families had higher than expected infestation rates. An increase in PSHB-attacked trees and infestation severity was observed over the course of the study with trees having a ~7.5% increased chance of PSHB infestations per year and PSHB holes increasing by over 10% annually.

Significant temporal and regional effects on PSHB infestations were also noted. There were higher infestation levels in the tropical KwaZulu-Natal region than in the more temperate Western Cape. Monitoring plots closer to PSHB source populations had higher infestation rates. Higher tree species richness resulted in lower PSHB attacks, whereas higher densities of competent host species led to increased infestations. This study underscores the importance of extended monitoring of invasive species and provides key insights for the potential management of PSHB in natural forest ecosystems. The ecological effects of this invasion may be severe, with many important tree species sustaining infestations. Over time this invasion could have adverse effects to ecosystem functioning and resilience.

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## Introduction

Forests are a fundamental part of many natural environments and healthy forests provide humans with essential ecological, social, and spiritual benefits (FAO 2022). Healthy forests are spatially and temporally heterogeneous and encompass a network of successional patches that include all stages of naturally occurring disturbance and recovery (Trumbore et al. 2015; Sambaraju et al. 2024). Natural disturbances such as drought, fire, insect damage and diseases are essential parts of forest functioning and create a wide array of habitats that promote diversity (Winder and Shamoun 2006; Grossiord et al. 2014; Burkle et al. 2015; Silva Pedro et al. 2016). In the twenty-first century global forest health is at risk from multiple mega disturbances such as climate change, overexploitation, and invasive species, which are increasing in frequency, extent, and severity (Dale et al. 2001; Millar and Stephenson 2015; Guégan et al. 2023). Understanding the role of disturbance, the difference between natural and human-induced disturbances, and how much disturbance forests can tolerate is important in protecting global forest health (Raffa et al. 2009; Thom and Seidl 2016).

One of the biggest threats to forest health is invasive species (Aukema et al. 2010; Castello and Teale 2011; Ramsfield et al. 2016; Freer-Smith and Webber 2017). The introduction and range expansion of insect, plant, and fungal pests has caused substantial disturbance to many forest ecosystems globally (Sturrock et al. 2011; Ploetz et al. 2013; Ayres and Lombardero 2018; Guégan et al. 2023). Introduced non-native organisms can remain undetected during their establishment, allowing them to multiply and spread unchecked (Simberloff 2009), and once established, the management of pests in natural forests is difficult and costly. Some of the most invasive organisms in forests are bark and ambrosia beetles (Coleoptera: Curculionidae, Scolytinae) (Brockerhoff et al. 2006; Ploetz et al. 2013; van Wilgen et al. 2020). Introductions of these insects have significantly increased over the past century (Pureswaran et al. 2004; Cudmore et al. 2010; Ploetz et al. 2013), and surveys conducted at borders and ports of entry around the world have shown the majority of Coleopteran interceptions involve scolytine beetles (Haack 2006; Brockerhoff et al. 2006; Ploetz et al. 2013). These insects are highly destructive and may

carry pathogenic fungal symbionts that can have devastating effects on the trees they attack (Fraedrich et al. 2007; Ploetz et al. 2013; Duan et al. 2018). The invasion patterns of bark and ambrosia beetles have been studied extensively (Haack and Rabaglia 2013; Lantschner et al. 2020) and the tree diseases caused by them are some of the most economically and ecologically damaging known to man (Ploetz et al. 2013; Kirkendall et al. 2015; Rassati et al. 2016). Due to increased invasions by these beetles, there is a growing body of research concerning them and their vectored pathogenic symbionts (Hulcr and Dunn 2011; Kirkendall et al. 2015).

The polyphagous shot hole borer (PSHB), *Euwallacea fornicatus* (Eichoff), is an ambrosia beetle native to Southeast Asia. Over the past decade, it has become highly invasive in the United States of America and Israel as well as being introduced into Australia and parts of South America (Eskalen et al. 2013; Cook and Broughton 2023; Ceriani-Nakamura-kare et al. 2023). In 2017 the PSHB was discovered in Pietermaritzburg, South Africa, and has since been confirmed in all but one province of the country. It has been recorded attacking ornamental street trees, some agricultural species, and native tree species (Paap et al. 2018; van Rooyen et al. 2021; Engelbrecht et al. 2024; Townsend et al. 2024). Once female beetles bore into a host tree they release their fungal symbiont, *Neocosmospora euwallaceae* (previously *Fusarium euwallaceae*) (Hypocreales; Nectriaceae), which they cultivate in galleries as a source of food. If the fungus establishes within a host tree the female beetle begins laying eggs after which she and her brood will create tunnel systems within the tree, spreading the fungus (Eskalen et al. 2013; Cooperband et al. 2016). The fungus is pathogenic and grows within the xylem vessels of a host tree and can cause a disease known as Fusarium dieback which can lead to tree death (Freeman et al. 2013). Currently, the PSHB beetle has been recorded on 162 tree species in South Africa, 78 of which are indigenous. Of these 162 species recorded 84 are “competent” and 78 are “*Fusarium* colonised” host species (discussed below) (Paap et al. 2018; van Rooyen et al. 2021; Townsend et al. 2024). If this beetle continues to spread it poses a major risk to agriculture, urban trees, and indigenous forests throughout Africa (Paap et al. 2018; van Rooyen et al. 2021; Engelbrecht et al. 2024; Townsend et al. 2024).

PSHB is an aggressive ambrosia beetle, and its spread is highly dependent on host tree availability. Therefore, understanding this beetle's host tree preferences and movement through landscapes is important. There is a significant body of research investigating the spread, impacts, and mitigation of PSHB in agricultural and urban environments (Eskalen et al. 2013; Lynch et al. 2021; Engelbrecht et al. 2024; Roberts et al. 2024), providing a good understanding of how the beetle and its fungal symbiont interact with ornamental and agricultural trees. There is, however, a severe lack of research concerning the beetle's spread and impacts in natural and indigenous landscapes. One study in the USA found that a close relative of PSHB, *Euwallacea Kuroshio* (Gomez & Hulcr), caused severe damage to native willows (*Salix* spp.) in the Tijuana River Valley (Boland 2016), and Bennett (2020) tracked the dispersal and expansion of PSHB in a riparian system along the Santa Clara river (California), investigating PSHB host preferences and susceptibility. In 2019 Townsend et al. (2024) established 51 permanent monitoring plots in an indigenous Afrotropical forest complex in the Western Cape, South Africa, to monitor the spread, host range, impact, and drivers of invasion of the PSHB in indigenous forests. Over 2 years of study, it was found that PSHB invaded the forest and attacked various indigenous trees, with breeding colonies of PSHB being present in 10% of monitored tree species. Key factors influencing the invasibility of sites were identified, including the proximity of monitoring plots to PSHB source populations and the abundance of host trees within plots. It was also found that natural disturbances such as damage to trees and increased distances from surface water resulted in increased infestation of individual trees. This study offered a valuable snapshot of the PSHB populations in natural forests at an early stage of the invasion process. It also revealed important trends that warrant further investigation. However, to provide a more comprehensive understanding of the current and future dynamics of the PSHB invasion into natural forest ecosystems, it is necessary to gather extended, longer term data not only of Afrotropical forests but of multiple forest types.

The main aims of this study were to use monitoring plot data to 1) determine the current PSHB infestation levels, 2) determine host tree preferences of the PSHB beetle in native forests, 3) determine the progression of

infestations over 5 years of monitoring, and 4) determine the factors that increase invasion success by PSHB in two different climatic regions in South Africa: Southern Afrotropical forests in the winter-rainfall dominated Western Cape Province, and coastal, mangrove, sand, and swamp forests in the summer-rainfall dominated KwaZulu-Natal province. We evaluated the factors that may affect the invasibility of these forests and the factors that may affect the susceptibility and severity of infestations of individual trees.

## Methodology

### Site selection

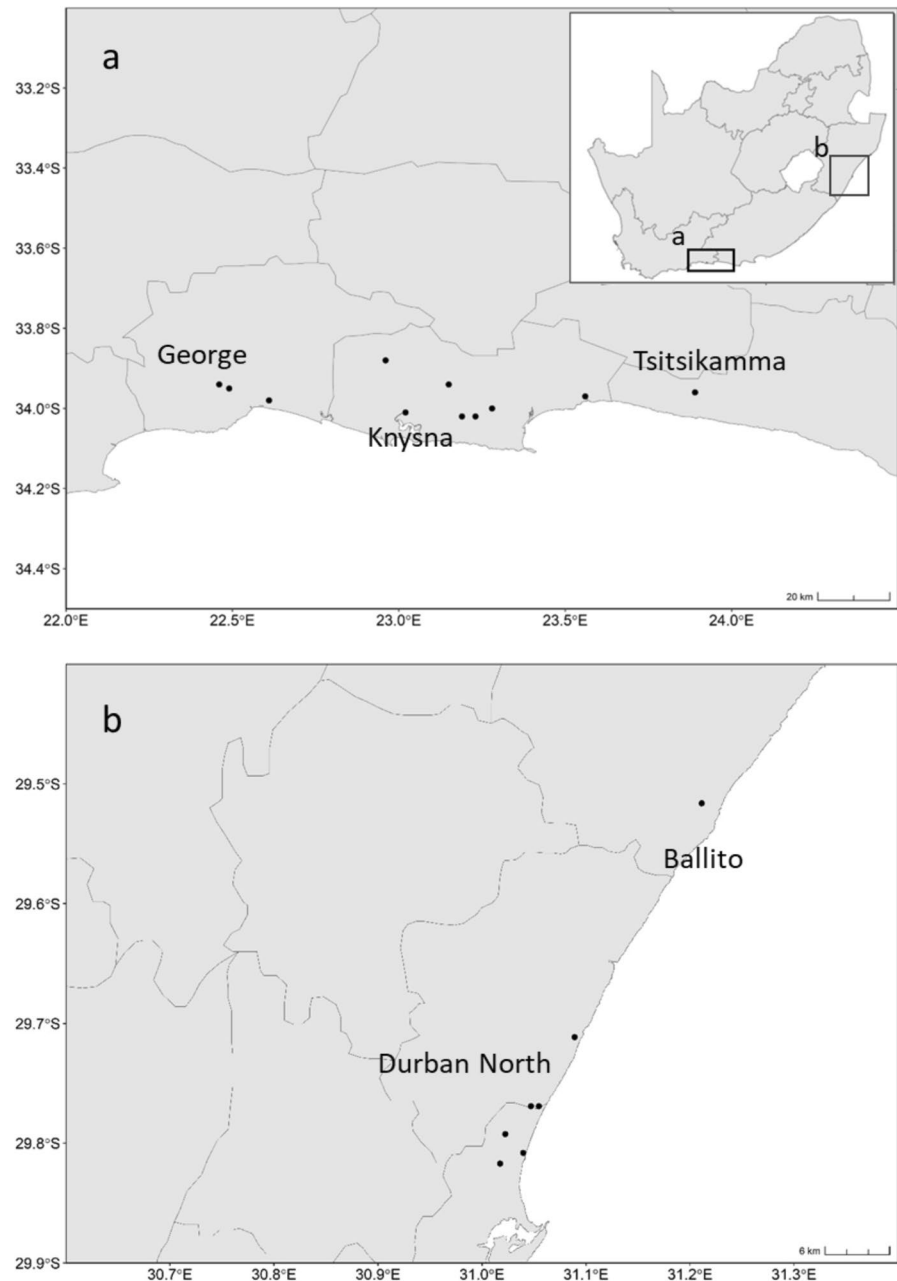
Surveys assessing the level and progression of PSHB infestations were conducted in two regions in South Africa. In the Southern Cape, 51 permanent monitoring plots were established at 11 sites in a Southern Afrotropical forest complex spanning from George (33°56'35.2''S 22°27'36.7''E) to Tsitsikamma (33°57'58.5''S 23°53'45.1''E). Surveys took place between June 2019 and January 2023 (Fig. 1a). In KwaZulu-Natal, 27 permanent monitoring plots were established at 7 sites in coastal, mangrove, sand, and swamp forests from Durban North (29°49'00.3''S 31°01'01.9''E) to Ballito (29°30'43.4''S 31°13'02.0''E). These surveys occurred between September 2019 and January 2023 (Fig. 1b). Sites were selected to capture diverse natural and human impacts and ecologies, including areas frequented by humans (picnic spots with fireplaces in mature forests, areas next to roads susceptible to PSHB spread through human assistance), urban zones already invaded by PSHB, and hiking trails less likely to have PSHB introduced by human activities. The number of plots at each site varied from 1 to 6 ( $n=78$ ). Each plot measured 15 m × 10 m, with at least a 30 m separation between plots, and was chosen to represent various tree species growing under different conditions (e.g., varying distances to surface water or nearest human impact).

### Data collection

#### Monitoring

All permanent monitoring plots were surveyed once annually during the study period ( $n=5$  monitoring events). Surveys comprised all living trees/shrubs

**Fig. 1** The two study regions, **a** the Garden Route in the Western Cape Province and, **b** Durban in KwaZulu-Natal Province, and their location within South Africa. Black dots represent sites ( $n = 18$ ) where permanent monitoring plots ( $n = 78$ ) were established



found in a plot that had a diameter at breast height of  $\geq 30$  mm regardless of health condition. Following the methods of Townsend et al. (2024), individual tree data variables collected included; diameter at breast height (mm), canopy health (% as an average of estimation by two observers) and broad health category (ranging from 1 to 5, with 1 = being a tree that was close to death and 5 = tree in near perfect condition). Distance to the nearest surface water source

(km) was also measured, as water availability and drought/flood stress have been shown to affect ambrosia beetle attacks on certain tree species. The degree of natural impact on trees (i.e. snapped branches or main bole, herbivory, etc.) and the degree of human impact (i.e. cut branches, bark collection, vandalism, etc.) was recorded as a percentage of the tree affected. Survey year was also noted, with the first year (2019) used as a reference point. Following Townsend et al.

(2024), plot-level data variables that were recorded included; distance to surface water from the middle of each plot, distance to the border of closest known infestations (usually nearest urban border or a known infested competent host, as defined below), the abundance of trees of species that were confirmed or suspected as hosts of the PSHB beetle, discussed below (Table 2) at any time throughout the study, canopy cover (% as an average of estimation by two observers), degree of natural impact (e.g. storm damage, fallen trees) scored as the percentage of trees in a plot that had signs of damage by natural causes, degree of physical human impact scored as the percentage of trees in a plot that had signs of damage caused by humans (e.g. cutting of branches, digging up of roots), total tree species richness and abundance, tree density (number of trees/m<sup>2</sup>) (LaBau and Cunia 1990), forest type (defined by tree species composition and successional stage (Mucina and Geldenhuys 2006)), and the number of trees showing signs of PSHB colonisation, discussed below.

If an infested tree was found, the number of PSHB holes was counted (standardized from the base to the breast height of the tree (ca. 1.5 m)). The mean flight height of PSHB is ca. 1.24 m (Byers et al., 2017). A standard sampling height ensured consistency and allowed for more trees to be surveyed. This also allowed us to calculate a survey surface area for each tree using the tree radius and the survey height of 1.5 m. Tree surface area was included as an individual tree-level variable.

#### *Infested tree confirmation*

All trees were inspected for PSHB colonisation or attempted colonisation by evaluating the trunks for entry holes of the correct size (ca. 0.85 mm) or other symptoms of boring beetles such as sap flow, presence of frass, or the presence of PSHB beetles on the tree (van Rooyen et al. 2021). When holes were present, the bark was removed from the affected area using a sterile chisel to reveal any necrotic tissue in the cambium and deeper wood tissues. Boring activity/colonisation attempts were confirmed by the presence of an entry hole of the expected size for PSHB under the bark that may or may not have been accompanied by wood staining around the gallery (indicative of fungal growth). Based on the notion that *F. euwallaceae* is a host species-specific symbiont of *E.*

*formicatus* in South Africa and that it cannot spread without the help of its symbiotic beetle vector, confirmation of host status/successful colonisation was based on the presence of *F. euwallaceae* within these galleries in wood. To encourage global consistency in host tree species classification we followed the criteria of Lynch et al. (2021). The host status of species was based on the ability of PSHB to establish *F. euwallaceae* and to reproduce within trees. Non-host species are those trees on which no signs of PSHB attack were observed. *Fusarium*-colonised hosts are those in which fungal transmission from PSHB is possible but beetles do not reproduce within the tree. On these hosts, removal of the outer bark reveals necrotic tissue caused by the pathogen, but there are no signs of beetles in attempted galleries. Competent hosts are those in which the beetle can establish a natal gallery and produce offspring. These were all species that contained at least one individual with more than 10 PSHB entry holes, showed signs of extensive gallery formation when opening the wood, and in which either the beetle or *F. euwallaceae* could be isolated from at least one sampling site or in previous studies in South Africa (Townsend et al. 2024; van Rooyen et al. 2021). Kill-competent hosts included all tree species where at least one individual has been shown to die because of PSHB and *F. euwallaceae* infestations within our monitoring plots or in South Africa.

For all samples collected from potentially infested trees, wood that contained a part of the gallery and any fungal-stained wood was removed and isolated following the methods of Paap et al. (2018). For genetic analysis, DNA was extracted from mycelia using the modified cetyltrimethylammonium bromide (CTAB) extraction (Lee et al., 1988; Wu et al., 2001). Thermocycling conditions followed Na et al. (2018) and O'Donnell et al. (1998). Amplification products were purified and sequenced by Macrogen Europe, Amsterdam, Netherlands, and compared to reference sequences available on GenBank for species confirmation.

#### Statistical analyses

We employed generalized linear mixed models (GLMMs) to investigate patterns of PSHB infestation, host preferences, and factors influencing infestation severity at the species and family levels. All models were fitted using the *glmmTMB* package in

R (Brooks et al. 2017), with binomial error distributions and logit link functions unless stated otherwise. Prior to analysis, all predictor variables were assessed for multicollinearity using Variance Inflation Factor (VIF) values from the ‘performance’ package (Lüdtke et al. 2021), with a threshold of  $VIF > 3$  being used (Zuur et al. 2010). No predictor variables in any of the models used were found to exceed this threshold (Table S2, Supplementary material). To ensure sufficient variation the variability of each predictor was also assessed by calculating the Coefficient of Variation (CV), no predictor variables with a CV value below 20% (0.2) were included in our models (Table S2, Supplementary material). Model fit was assessed using a hypothesis testing approach. Residual diagnostics from the ‘DHARMA’ package (Hartig 2018), and fixed effect significance was determined using Likelihood Ratio Tests (LRT) via the ‘Anova’ function in the ‘car’ package (Fox et al. 2019). Marginal effects plots were generated using the ‘ggeffects’ package (Lüdtke 2018) to visualize key relationships between response and predictor variables.

#### Host preferences: host species selection and utilisation

Although PSHB has a broad host range, field observations and previous studies suggest that the beetle exhibits some degree of host species preference (Lynch et al. 2021; Townsend et al. 2024). To evaluate if PSHB is preferentially selecting specific tree species, we analysed two response variables: the proportion of infested trees per species and the proportion of PSHB entry holes per species. The number of infested trees and the number of entry holes were divided by their respective totals per plot to calculate proportions. A community-weighted relative abundance of each tree species was calculated for each plot by dividing the number of individuals of a species by the total number of trees. This was used to test whether the proportion of total infested trees and the total PSHB holes per tree species within each plot was frequency-dependent. If the number of infested trees is frequency-dependent the beetle may not be targeting specific tree species, but rather beetle attacks are directly correlated to tree abundance.

This was then used to determine the relationship between tree relative abundance and PSHB infestation rates and counts for each species allowing

us to evaluate if PSHB infestations and counts are higher or lower than expected based on the relative abundance of trees. This allowed us to estimate the probability of a specific tree species being attacked and utilised relative to the species around it. The relationship between PSHB infestation (proportion of infested trees or PSHB holes) and tree species abundance was modelled as a function of the relative community-weighted abundance of each tree species using GLMMs (model 1 and 2; Table S2, Supplementary material). Both models included random slopes for ‘year’ and random intercepts for ‘plot’ nested within ‘region’ and ‘species’ within ‘plot’.

Data from both of the above analyses was used to visualise the relationship between the proportion of infested trees and the proportion of PSHB holes per tree both relative to the community-weighted relative abundance of each tree species per plot along with the sample sizes for each tree species.

#### Host preferences: host family selection

To evaluate if PSHB is selecting host trees at the family level and to determine if certain plant families show higher than expected infestation levels, we applied a similar approach, calculating the proportion of infested trees per family by dividing the number of infested trees per family by the total number of infested trees in each plot. As with the species-level analyses, a community-weighted relative abundance of each tree family was calculated, and the proportion of PSHB-infested trees per family was modelled against this predictor (model 3; Table S2, Supplementary material). This was then used to determine the relationship between tree relative abundance and number of PSHB-infested trees for each plant family allowing us to evaluate if infestation probability was higher or lower than expected based on the relative abundance of trees, effectively assessing the proportional relationship between the number of PSHB-infested trees per family and family abundance per plot. To account for differences in the potential infestation probability of each family a random slope for ‘family’ was included, along with a nested random intercept for ‘plot’ nested in ‘region’ and ‘region’ nested in ‘year’ (Bolker et al., 2009).



### Factors that influence the severity and probability of infestations by PSHB on individual trees

To evaluate the factors associated with PSHB infestations on individual trees ( $n=2313$ ), the influence of selected variables on the number of PSHB holes on trees was tested using a GLMM with a negative binomial distribution, the model also incorporated a hurdle component (Brooks et al. 2017) (model 4; Table S2, Supplementary material). Hurdle models are designed to account for excess zeroes in the response variable (i.e. the number of PSHB holes per tree). This first component models the probability of each tree having zero (0) or non-zero (1) number of PSHB holes using a binomial distribution, while the second component models the non-zero counts using a zero-truncated negative binomial distribution (Brooks et al. 2017). Both models incorporated the same fixed effects including diameter at breast height (dbh), canopy health (ch), broad health category (bhc), distance to the nearest water source ( $dH_2O$ ), degree of natural impact (ni), the surface area of trees (sa) and year. Initially, the broad health category (bhc) and degree of natural impact (ni) were included as fixed effects, however, these models generated convergence issues due to the lack of variation in PSHB counts concerning each predictor. Repeated measurements taken from the same trees over time at the different sampling sites were accounted for using a subject-specific random intercept term (at the individual-tree level), while potential spatial non-independence of sites was accounted for using a site-specific random intercept term. Lastly, a correlated random slope was included to allow for each tree species to differ in the extent to which they are colonised by PSHB over time. For the binomial model component, we dropped the 'species' and 'area' random intercept terms due to a zero estimate for both terms. This estimate does not necessarily mean that the between-group variability for each term was zero, instead, it means that the variability was not sufficient to warrant inclusion in the model (Speyer et al., 2023).

### Factors that influence the proportion of PSHB-infested trees in plots

To evaluate the factors associated with the prevalence of PSHB in monitoring plots ( $n=78$  plots), the influence of selected variables on the proportion of

infested trees per plot was tested using Generalized Linear Mixed Models (GLMM's) fitted to a binomial distribution, with plot number and year as random variables (Brooks et al. 2017) (model 5; Table S2, Supplementary material). The overall model incorporated the fixed plot effects of distance to potential source population (dsp), number of host trees (no\_hosts), percentage of trees with human impact (hi), percentage of trees with natural impact (ni), overall tree species richness (sprich), canopy cover (canopy), distance to nearest surface water ( $dH_2O$ ) and tree density (dens, i.e. number of trees/ $m^2$ ). Repeated measurements taken from the different sampling sites were accounted for using a subject-specific random intercept term (at the site level).

## Results

### PSHB infestation levels

PSHB infestations were recorded at 15 of the 18 monitoring sites in indigenous forests over the 5-year monitoring period and within all five main forest types monitored (Table 1). Out of the 78 monitoring plots, 48 (60%) contained infested trees in 2023, an increase of 23 plots (29%) from the first monitoring event in 2019 (Table 2). These plots were spread across the survey area. A total of 2313 trees were monitored representative of 148 species. Of these, 176 (7%) trees representing 43 species (and seven unidentified species) were found to have PSHB infestations (Table 3). In 2019 at the beginning of the study, we recorded 100 infested trees across all survey sites. In 2023 we recorded 176—a mean increase of 15 (0.6%) trees per year. When comparing the two survey regions, KwaZulu-Natal (Fig. 1b) had a higher proportion of infested trees (0.11%) and all monitoring sites had PSHB present. The Western Cape (Fig. 1a) had a lower proportion of infested trees (0.06%) with eight of the eleven monitoring sites having PSHB present. In total, 18 species were recorded as competent hosts of PSHB (being able to support PSHB reproduction), 8 as kill-competent hosts (can be killed by PSHB), 24 can be colonised by *Fusarium euwallaceae* but not the PSHB, and 107 species showed no signs of attack by PSHB throughout the study (Table 2). Increases in the number of PSHB-infested trees were recorded in 42 out of the 78 monitoring plots, while 36 plots showed no increases in

**Table 1** A summary of the forest types monitored in the KwaZulu-Natal Province (KZN) and the Afrotropical forest types monitored in the Western Cape Province (WC; broken down into climax forest types, distinguished by the dominant plant species present). The region (KZN/WC), number of sites and plots, tree species richness, the total number of trees, the total number of PSHB host trees and tree species (including Fusarium-colonised, competent and kill-competent), the number of plots with PSHB infested trees in 2019 and 2023 and the increase in the number of infested plots over this period. The number of infested tree species, the total number of trees with PSHB infestations in 2019 and 2023 and the increase in the number of infested trees over this period

Forest type	Region	Sites	Plots	Tree species	Trees	Host trees	Host species	Infested plots 2019	Infested plots 2023	Infested species	Infested trees 2019	Infested trees 2023
Coastal dune forest	KZN	1	3	25	70	17	3	2	3	6	6	9
Northern coastal forest	KZN	4	16	66	339	48	15	9	12	18	22	48
Swamp forest	KZN	1	6	14	153	55	6	3	6	6	5	20
Mangrove forest	KZN	1	2	7	69	0	3	0	0	0	0	0
*Disturbed moist high forest	WC	1	3	11	38	18	3	2	3	3	4	6
*Disturbed medium moist high forest	WC	1	2	17	37	9	2	0	0	0	0	0
Early successional forest	WC	1	10	13	423	94	10	9	9	6	33	51
Moist high forest	WC	3	7	34	225	59	7	3	3	8	5	12
Medium moist high forest	WC	3	14	31	518	76	14	3	3	2	4	6
Very dry scrub forest	WC	2	15	52	441	99	15	8	9	14	20	32

\*Disturbed sites were located in Wilderness and Natures Valley where monitoring plots were erected around camping sites to determine the impact of fire-making facilities and human activities



**Table 2** A summary of the species and family names of all plants on which PSHB infestations or *Fusarium* infections were recorded. The type of host a species represents, and the number of infested individuals recorded throughout the study are also shown

Family	Species	Host type	Total no. trees	No. infested trees
Achariaceae	<i>Xylothea kraussiana</i>	Fusarium colonised	27	5
Anacardiaceae	<i>Sclerocarya birrea</i>	Competent	4	2
	<i>Searsia chirindensis</i>	Fusarium colonised	12	2
	<i>Searsia lucida</i>	Fusarium colonised	36	2
	<i>Searsia</i> sp.	Fusarium colonised	4	1
Apocynaceae	<i>Voacanga thouarsii</i>	Competent	53	14
Celastraceae	<i>Gymnosporia buxifolia</i>	Fusarium colonised	92	9
Ebenaceae	<i>Diospyros dichrophylla</i>	Fusarium colonised	37	2
	<i>Diospyros glabra</i>	Kill competent	68	21
	<i>Diospyros whyteana</i>	Fusarium colonised	18	1
Euphorbiaceae	<i>Croton sylvaticus</i>	Fusarium colonised	5	1
	<i>Macaranga capensis</i>	Fusarium colonised	4	1
Fabaceae	<i>Albizia adianthifolia</i>	Fusarium colonised	10	1
	<i>Albizia</i> sp.	Competent	1	1
	<i>Baphia racemosa</i>	Kill competent	20	9
	<i>Dichrostachys cinerea</i>	Kill competent	8	8
	Unknown	Competent	3	1
	<i>Virgilia oroboides</i>	Kill competent	17	4
Fagaceae	<i>Quercus robur</i>	Fusarium colonised	7	5
Loganiaceae	<i>Strychnos henningsii</i>	Fusarium colonised	1	1
Malvaceae	<i>Cola natalensis</i>	Competent	9	2
	<i>Grewia occidentalis</i>	Kill competent	2	2
	<i>Sparrmannia africana</i>	Fusarium colonised	8	3
Meliaceae	<i>Ekebergia capensis</i>	Fusarium colonised	14	3
	<i>Trichilia emetica</i>	Fusarium colonised	26	3
Metteniusaceae	<i>Apodytes dimidiata</i>	Kill competent	43	3
Moraceae	<i>Ficus trichopoda</i>	Fusarium colonised	4	1
Penaeaceae	<i>Olinia ventosa</i>	Fusarium colonised	8	1
Phyllanthaceae	<i>Antidesma venosum</i>	Fusarium colonised	2	2
	<i>Bridellia micrantha</i>	Fusarium colonised	16	1
Podocarpaceae	<i>Afrocarpus falcatus</i>	Competent	78	8

infested trees throughout the study. Table 3 shows the 11 individual trees that died as a result of PSHB infestations over the course of this study. Some tree individuals died very rapidly (within 2–5 years of first infestation) and some died with relatively few infestations (e.g. *Sparrmannia africana*).

#### Host preferences: host species selection and utilisation

In both models (Model 1 and Model 2, Table S2, Supplementary material), there was a statistically

significant effect of tree relative abundance on PSHB infestation and hole counts, indicating a frequency-dependent relationship.

In model 1 there was evidence for a statistically significant effect of tree relative abundance ( $X^2=41.651$ ,  $df=1$ ,  $P<0.001$ ) on the proportion of infested trees per tree species per plot, indicating a frequency dependence. The beta coefficient ( $\beta=16.69$ ) of the regression indicated that as the relative abundance of trees per species per plot increased by 1%, there was a 17% increase in the

**Table 3** Individual trees that died as a result of PSHB infestation and/or Fusarium dieback their species names, diameter at breast height (DBH), and the number of PSHB entry holes recorded on each tree during different survey years (2019–2023). Bold numbers indicate the year the tree was recorded as dead

Species	DBH (cm)	No. holes				
		2019	2020	2021	2022	2023
<i>Dichrostachys cinerea</i> <i>Dichrostachys cinerea</i>	134	300	300	300	500	<b>500</b>
<i>Dichrostachys cinerea</i>	141	300	300	300	659	<b>659</b>
<i>Dichrostachys cinerea</i>	145	24	24	24	24	<b>26</b>
<i>Dichrostachys cinerea</i>	41	6	6	6	14	<b>14</b>
<i>Diospyros glabra</i> *	207	210	<b>230</b>			
<i>Ficus tricophoda</i>	502	0	0	0	240	<b>240</b>
<i>Gymnosporia buxifolia</i>	178	32	32	32	<b>32</b>	
<i>Sparmannia africana</i>	218	12	<b>12</b>			
<i>Trichelia emetica</i>	430	0	200	1000	1000	<b>1000</b>
<i>Vepris lanceolata</i>	252	0	250	300	<b>300</b>	
<i>Vepris lanceolata</i>	291	0	0	0	300	<b>320</b>

\*This individual's main bole died as a result of PSHB infestation but the plant re-sprouted and continued growing less than 1 year after dying back

proportion of infested trees per species per plot averaged over regions, plots and years (Fig. 2).

Of the 43 PSHB-attacked tree species, 20 had statistically higher than expected proportions of PSHB-infested trees (including five kill-competent hosts and seven competent hosts). 23 species statistically had the expected number of infested trees (including four kill-competent hosts and one competent host), relative to their abundances.

In model 2 there was evidence for a statistically significant effect of tree relative abundance ( $X^2=101.88$ ,  $df=1$ ,  $P<0.001$ ) on the proportion of PSHB holes per tree species per plot, indicating a frequency dependence. The beta coefficient ( $\beta=30.89$ ) of the regression indicated that as the relative abundance of trees per species per plot increased by 1%, there was a 31% increase in the proportion of PSHB holes per species per plot averaged over regions, plots, and years (Fig. 3).

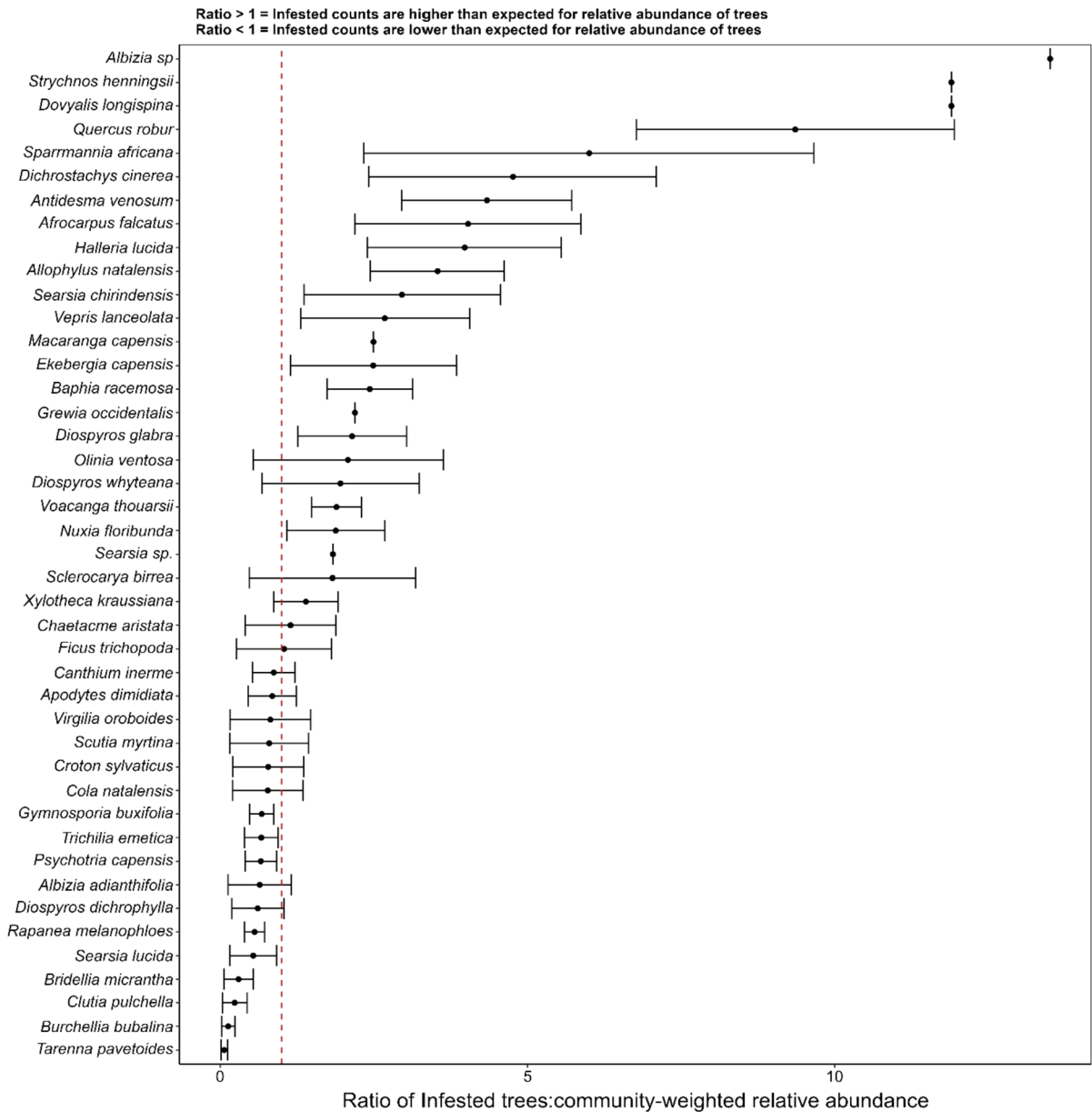
Of the 43 PSHB-attacked tree species 13 had statistically higher than expected proportions of PSHB holes (including five kill-competent hosts and seven competent hosts). 30 species had the expected number of PSHB holes (including two kill-competent hosts and two competent hosts), and 16 species had lower than expected infestations (including one kill-competent host and one competent host), relative to their abundances. Of the 23 species that are seemingly

selected for (Fig. 2), 13 also had higher utilization by PSHB than expected by chance (Fig. 3). These include *A. falcatus*, *A. natalensis*, *Albizia* sp., *B. racemose*, *D. cinerea*, *D. glabra*, *H. lucida*, *Q. robur*, *S. africana*, *S. henningsii*, *V. lanceolata*, *V. thouarsii* and *X. kraussiana*. The correlation between the mean proportion of infested hosts and mean proportion of PSHB holes per host indicated that all kill-competent host species, besides *Q. robur*, have a higher proportion of PSHB holes than their proportion of infested trees (Fig. 4).

#### Host preferences: host family selection

In this model (model 3, Table S2, Supplementary material), there was evidence for a statistically significant effect of the relative abundance of specific tree families ( $X^2=45.9$ ,  $df=1$ ,  $P<0.001$ ) on the proportion of PSHB-infested trees per plant family per plot, indicating a frequency dependence. The beta coefficient ( $\beta=7.19$ ) of the regression coefficient indicated that as the relative abundance of trees per family per plot increases by 1% there is a 1326% increase in the proportion of PSHB-infested trees per family per plot averaged over regions, plots and years (Fig. 5).

Of the 24 plant families included in these analyses, seven had statistically higher than expected



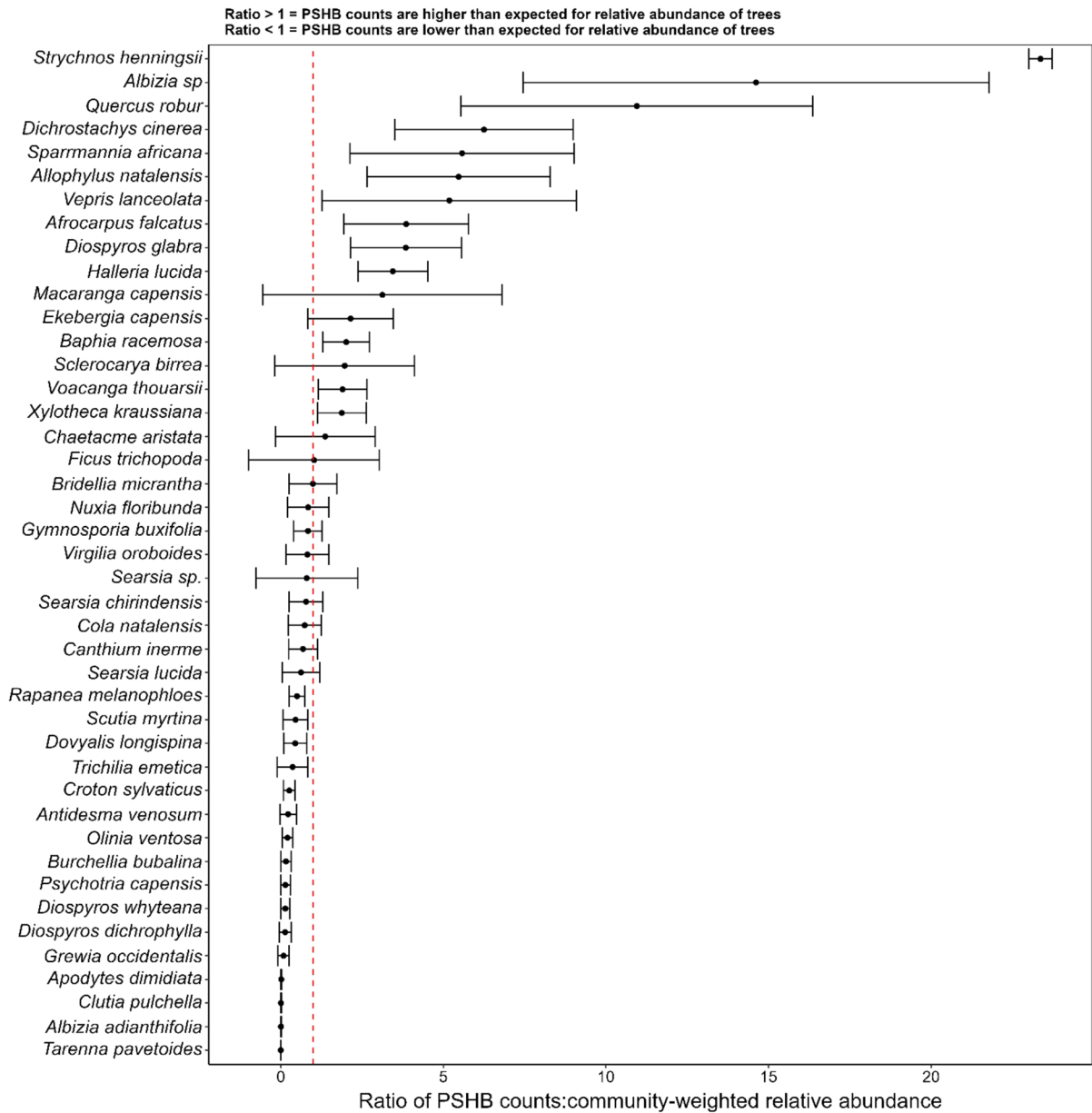
**Fig. 2** Relationship between the ratio of PSHB-infested trees and community-weighted relative abundance of different tree species. Error bars represent the lower and upper confidence intervals for each mean ratio. Points indicate the mean ratio for each tree species. The vertical dashed red line at  $x=1$  denotes the threshold where PSHB-infested tree proportions are equal

to what would be expected based on the relative abundance of trees. Ratios greater than 1 indicate that infested tree proportions are higher than expected for the relative abundance of those species. Ratios less than 1 indicate that infested tree proportions are lower than expected for the relative abundance of those species

proportions of PSHB-colonised trees (these families contained six kill-competent hosts and nine competent host species). 17 families had the expected number of infested trees (containing two kill-competent host species and three competent host species).

Factors that influence the severity of infestations on individual trees

The overall model incorporated both the conditional and zero-inflated components (model 4, Table S2,

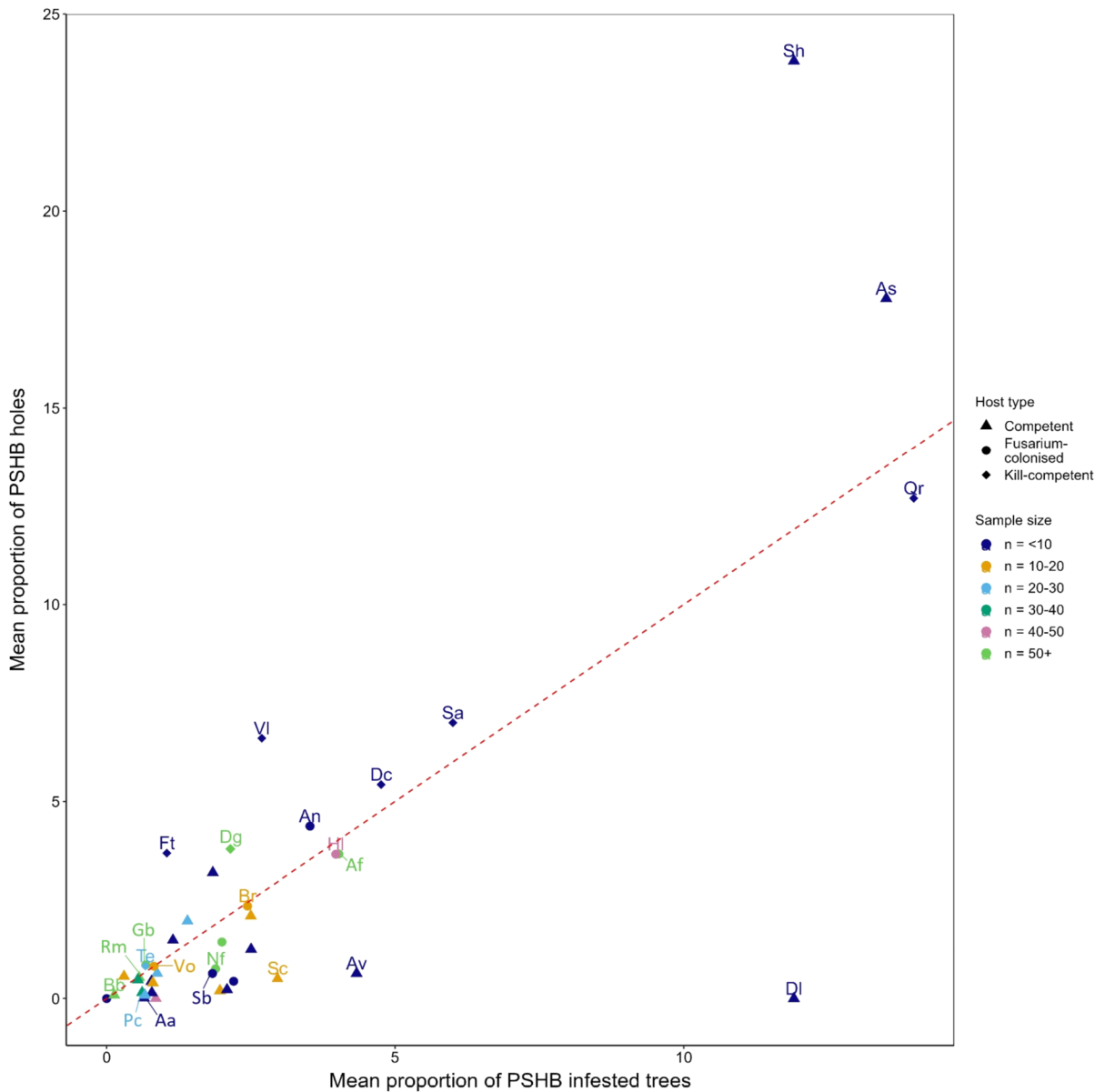


**Fig. 3** Relationship between the ratio of PSHB counts and community-weighted relative abundance of different tree species. Error bars represent the lower and upper confidence intervals for each mean ratio. Points indicate the mean ratio for each tree species. The vertical dashed red line at  $x=1$  denotes the threshold where PSHB hole counts are equal to what

would be expected based on the relative abundance of trees. Ratios greater than 1 indicate that hole counts are higher than expected for the relative abundance of those species. Ratios less than 1 indicate that hole counts are lower than expected for the relative abundance of those tree species

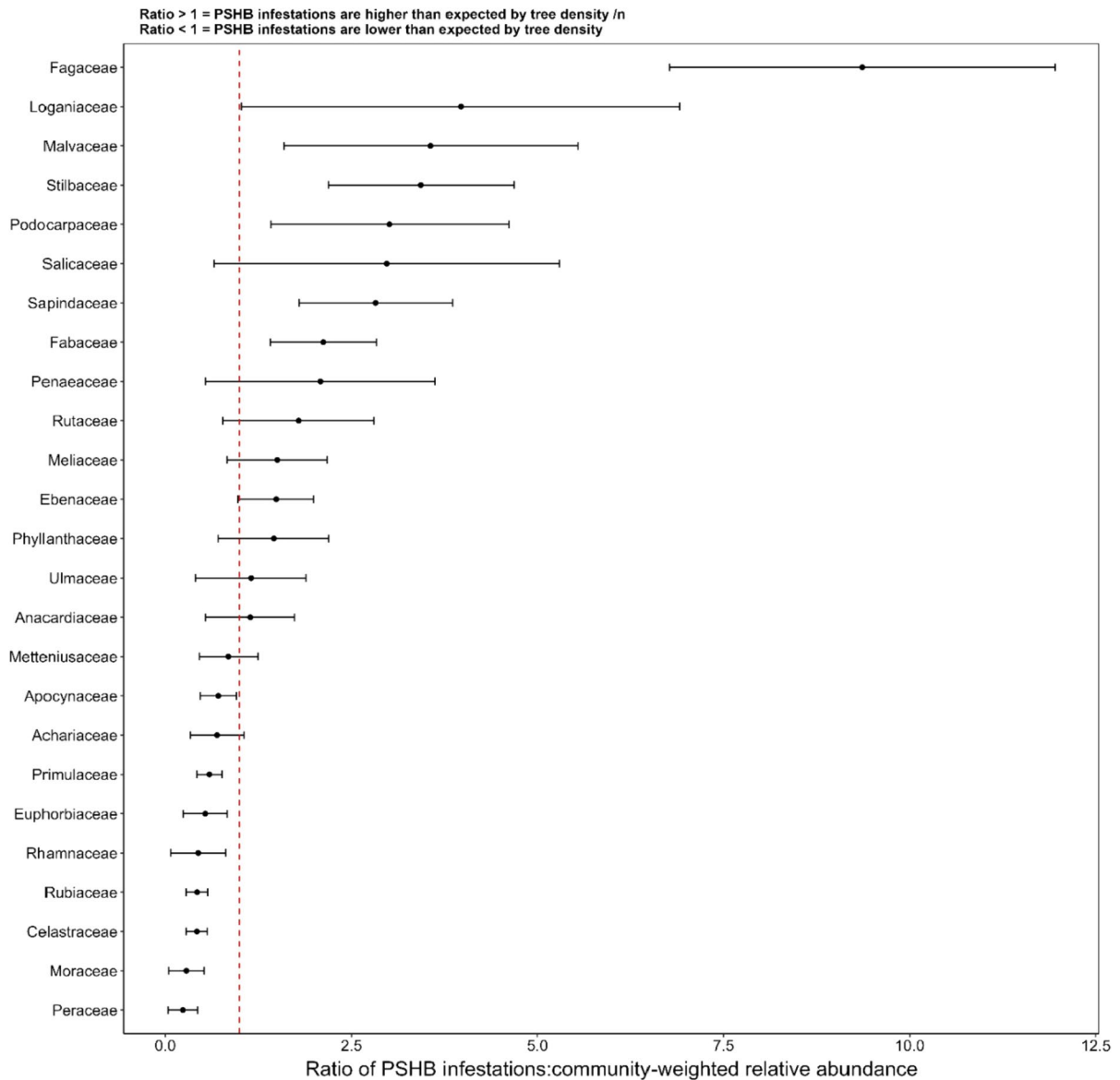
Supplementary material). In the conditional component of the model, there was evidence for a statistically significant effect of diameter at breast height (dbh) ( $X^2=7.598$   $df=1$ ,  $P<0.006$ , canopy health (canhealth) ( $X^2=9.645$ ,  $df=1$ ,  $P<0.002$ ),

distance to surface water (dh2o) ( $X^2=5.960$ ,  $df=1$ ,  $P<0.015$ ), and year ( $X^2=75.339$ ,  $df=1$ ,  $P<0.001$ ) on PSHB. The partial derivatives of the regression coefficients indicated that: (1) a 1 cm increase in DBH increases PSHB counts by



**Fig. 4** Relationship between the mean proportion of PSHB holes and the mean proportion of PSHB-infested trees both relative to the community-weighted relative abundance of different tree species. The red dashed line represents a 1:1 relationship, where the mean proportion of infested trees is equal to the mean proportion of PSHB holes on a species. The letters above each point represent the name of each tree species: *Afrocarpus falcatus* – Af, *Albizia adianthifolia* – Aa, *Albizia* sp. – As, *Allophylus natalensis* – An, *Allophylus* sp. – Asp, *Antidesma venosum* – Av, *Baphia racemosa* – Br, *Burchellia*

*bubalina* – Bb, *Dichrostachys cinerea* – Dc, *Diospyros glabra* – Dg, *Dovyalis longispina* – DI, *Ficus trichopoda* – Ft, *Halleria lucida* – HI, *Nuxia floribunda* – Nf, *Rapanea melanophloes* – Rm, *Quercus robur* – Qr, *Sclerocarya birrea* – Sb, *Searsia chirindensis* – Sc, *Sparmannia africana* – Sa, *Strychnos heningsii* – Sh, *Trichelia emetica* – Te, *Vepris lanceolata* – VI, *Virgilia oroboides* – Vo, *Xylothea krausiana* – Xk. Different colours indicate the number of individual trees sampled for each species (n), and shapes indicate different host types



**Fig. 5** Relationship between the ratio of proportion of PSHB infestations for different plant families and community-weighted relative abundance of plant families within plots. Error bars represent the lower and upper confidence intervals for each mean ratio. Points indicate the mean ratio for each tree family. The vertical dashed red line at  $x=1$  denotes the threshold where PSHB-infested tree proportions are equal to

what would be expected based on the relative abundance of trees. Ratios greater than 1 indicate that PSHB infestations are higher than expected for the relative abundance of those families. Ratios less than 1 indicate that infested tree proportions are lower than expected for the relative abundance of those families

0.12% ( $\beta_{\text{DBH(cm)}}=0.0012$ ), (2) as canopy health increases by 1% PSHB counts decrease by 2.4% ( $\beta_{\text{canhealth}}=-0.024$ ), (3) as distance to the closest water source increases by 10 m, PSHB counts increase by 0.02% ( $\beta_{\text{dh20}}=-0.0002$ ), and (4) for

each additional year surveys were performed PSHB hole counts increased by 11% ( $\beta_{\text{year}}=0.114$ ), on average (Fig. 6).

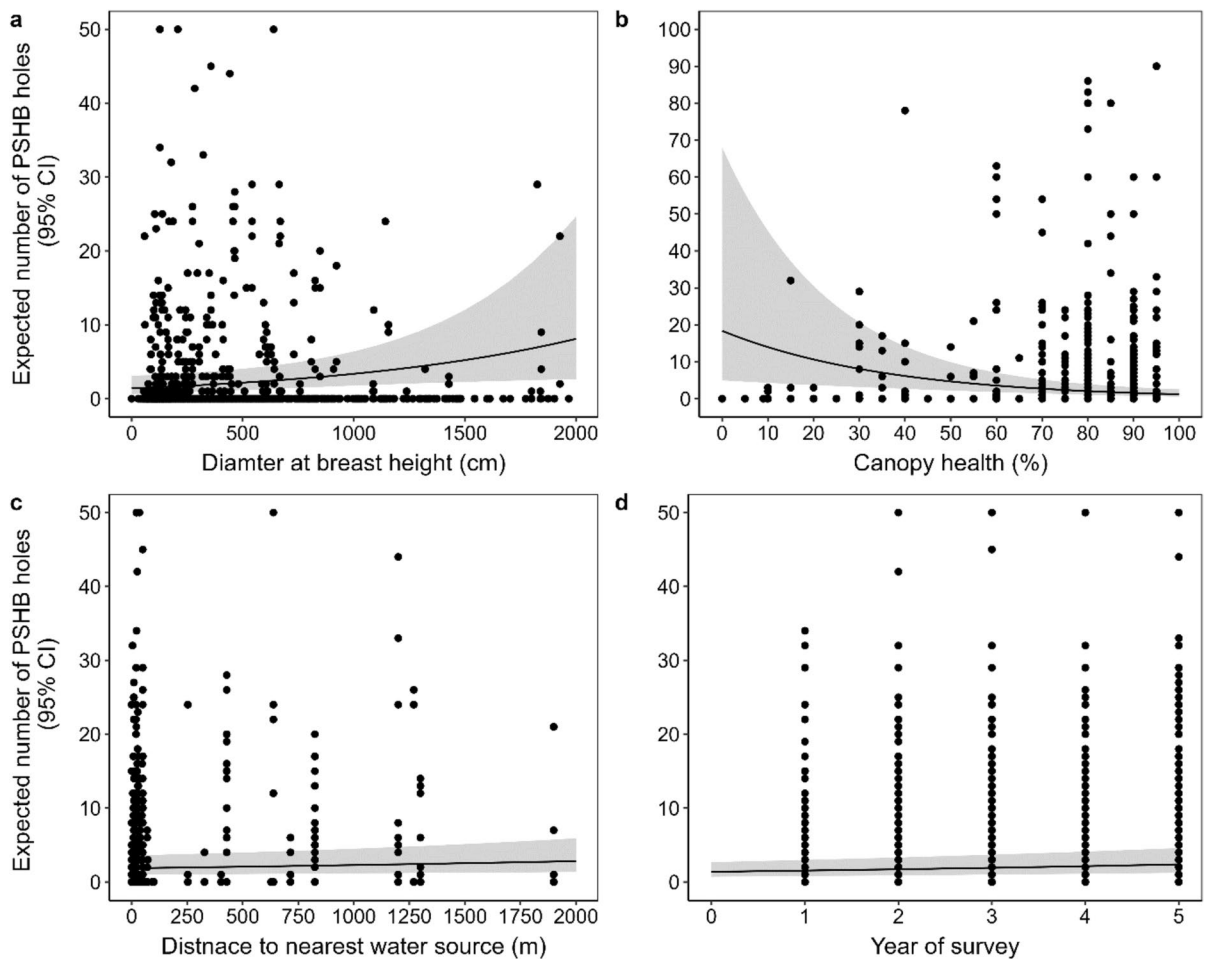


### Factors that influence the probability of infestations on individual trees

In the zero-inflation component of the model, there was no evidence for a statistically significant effect of diameter at breast height ( $X^2=0.09$ ,  $df=1$ ,  $P=0.769$ ), canopy health ( $X^2=1.37$ ,  $df=1$ ,  $P=0.241$ ), or distance to surface water ( $X^2=0.829$ ,  $df=1$ ,  $P=0.363$ ). There was evidence for an effect of year on the presence/absence of PSHB ( $X^2=69.75$ ,  $df=1$ ,  $P<0.001$ ). The partial derivatives of the regression coefficient for the year term indicated that the probability of an individual tree being infested with PSHB increased by 7.6% ( $\beta_{year}=-0.936$ ) per additional year over the survey period, on average.

### Factors that influence the proportion of PSHB-infested trees in plots

In this model (model 5, Table S2, Supplementary material), there was evidence for a statistically significant effect of distance to source population (dsp) ( $X^2=23.887$ ,  $df=1$ ,  $P<0.001$ ), the number of host trees per plot (no\_hosts) ( $X^2=99.35$ ,  $df=1$ ,  $P<0.001$ ) and tree density (dens) ( $X^2=102.1$ ,  $df=1$ ,  $P<0.001$ ) on the proportion of infested trees per plot. The partial derivatives of the regression indicated that: (1) for each 1 km increase in the distance from plots to source populations of PSHB there is a 48% ( $\beta_{dens}=-0.517$ ) decrease in the proportion of infested trees per plot, (2) when the number



**Fig. 6** Marginal effects plots showing the estimated number of PSHB holes on trees in monitoring plots as a function of the predictor variables; **a** The diameter at breast height of trees, **b**

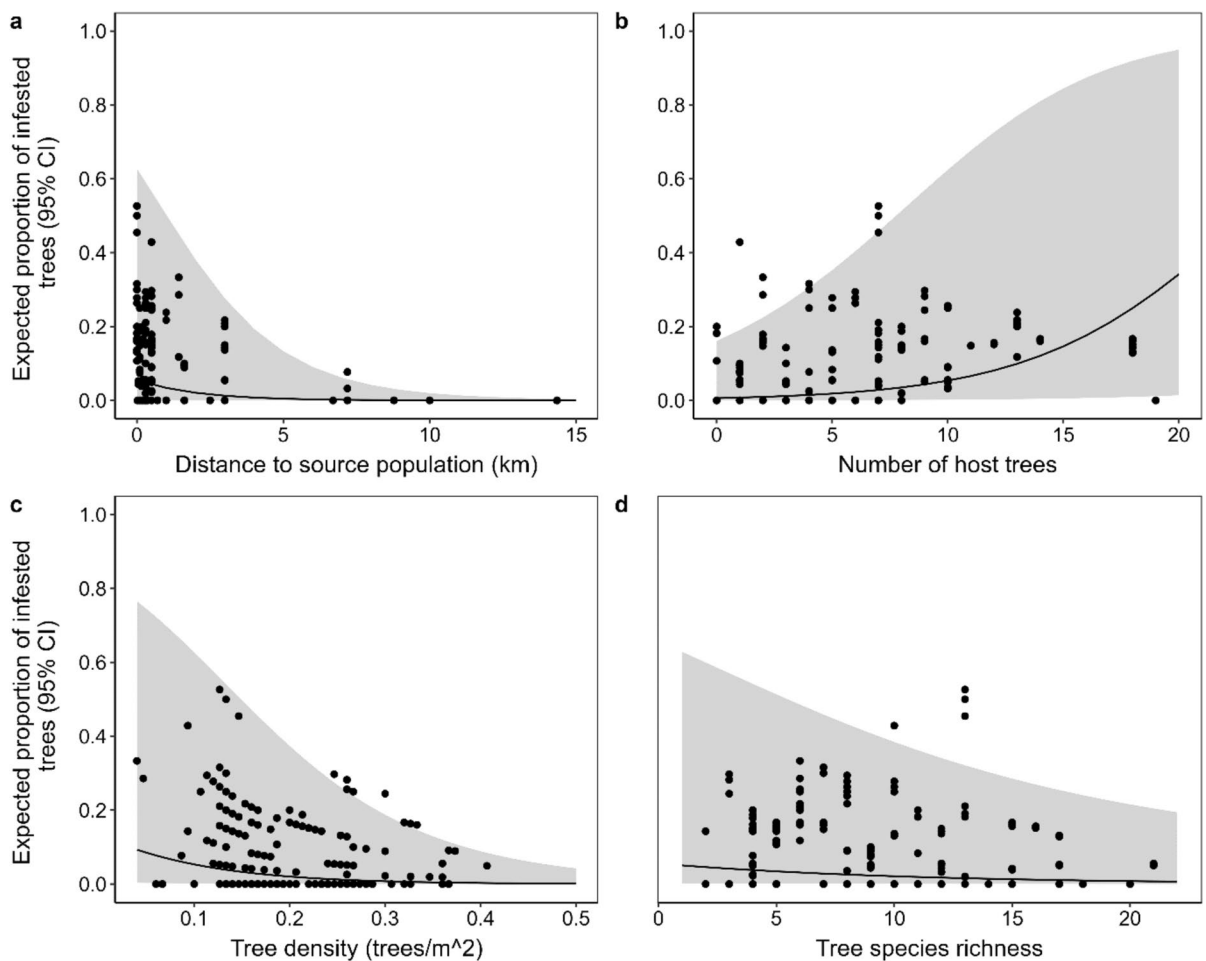
Canopy health, **c** Distance of trees to the nearest water source, **d** The year of sampling

of host trees in plots increases by 1 the proportion of infested trees increases by 9.6% ( $\beta_{\text{nohosts}} = 0.092$ ), (3) when tree density in plots increases by one tree the proportion of infested trees decreases by 5% ( $\beta_{\text{dens}} = -0.051$ ) and (4) when tree species richness in plots increases by one species the proportion of infested trees decreases by 9.7% ( $\beta_{\text{spprich}} = -0.097$ ) (Fig. 7).

## Discussion

This study represents one of only a few investigations of the interactions of the polyphagous shot hole borer (PSHB; *Euwallacea fornicatus*) and native forest

ecosystems, and is the second study done in South Africa since its first report in 2017 (Townsend et al. 2024). PSHB colonisation attempts were recorded on numerous native tree species and families and infestations were often severe. As a result of this host breadth and ideal climatic conditions (Cudmore et al. 2010; Eskalen et al. 2013; Ge et al. 2017), PSHB could invade all forest types monitored here except for the mangrove forests dominated by only a few unsuitable host species. Subsequently, increased numbers of PSHB-attacked trees and increases in the severity of infestations were recorded over the 5 years of monitoring. Although the invasion of this pest into natural forests in South Africa is currently seemingly slow, an increase in the rate of infestations is expected



**Fig. 7** Marginal effects plots showing the estimated proportion of PSHB-infested trees in monitoring plots as a function of the predictor variables; **a** The distance from plots to PSHB

source populations, **b** The number of host tree individuals in plots and **c** The tree density in plots (trees per unit area) in plots

as progressively more competent host individuals are infested. Ecological effects on these forests may be severe as rapid mortality has been recorded for some key tree species with some sensitive to comparatively few attacks. These findings should be considered in a broader context, as this beetle can spread rapidly and could pose a significant threat to a range of forest ecosystems worldwide.

#### Temporal and regional effects on PSHB infestations

We found a significant effect of “survey year” on the proportion of PSHB holes per tree and the probability of trees being infested with PSHB. Tree individuals had more than 7% increased chance of PSHB infestations per year and PSHB holes increased by over 11% annually. Therefore, the longer PSHB is active in the environment the more trees it will infest, the higher its impact will be on hosts, and the higher the number of dispersing individuals produced. This will substantially increase the chances and rates of additional areas becoming infested, especially in areas close to infestation borders. For example, here it was shown that for every kilometre one moves closer to an infested area, a 48% increase in the probability of PSHB infestation can be expected. Consistent with our results, general predictive modelling of the range expansions of forest pests in the USA showed that there appears to be a preferential dispersal of pests to and from areas of high human population density, creating patches of spread around cities. (Hudgins et al. 2017). Investigations into the range expansions of invasive insects in Europe show that those associated with woody plants have a fairly consistent expansion rate after establishment (Roques et al. 2016). Our data as well as data from urban surveys, public reports, and citizen science from throughout South Africa suggests that PSHB populations may be increasing exponentially (Potgieter et al. 2024; Townsend et al. 2024; FABI, 2024) as modelled by de Wit et al. (2021). This mirrors trends seen in other PSHB invaded regions such as the USA and Israel, where once established the beetle can rapidly spread increasing infestation severity over time (Eskalen et al. 2013; Carrillo 2019). Mitigating the increase in infestations of natural ecosystems, even in already infested areas, is therefore critical for PSHB management.

In KwaZulu-Natal we recorded a higher overall proportion of infested trees when compared to the Western Cape. In KwaZulu-Natal there was an increase of *ca.* 6% in infested trees over the 5-year monitoring period compared to a 3% increase in the Western Cape. In the Western Cape, source populations were often found in alien tree species distant from plots, while in KwaZulu-Natal, they were frequently found in indigenous trees within monitoring plots. The fragmented nature of KwaZulu-Natal forests as opposed to the nearly contiguous forests in the Western Cape studied here, and their proximity to urban areas (with high PSHB infestation levels) reduces the urban-natural interface, increasing their susceptibility to PSHB invasion (Coleman et al. 2019). Competent host trees such as *Quercus robur* (English oak), *Acer negundo* (boxelder), *Salix babylonica* (weeping willow), *Platanus x acerifolia* (London plane), *Ricinus communis* (castor bean), and the native *Erythrina caffra* (coral tree) are highly susceptible and common throughout the country. *Erythrina* spp. trees are prevalent in the KwaZulu-Natal region but can be found across South Africa and are important trees in coastal forest ecosystems (Mucina and Geldenhuys 2006).

The most likely explanation for increased infestation levels in KwaZulu-Natal is that the beetle has arrived and established here first. The first recorded data for the presence of PSHB in this region was in 2012 (Paap et al. 2018), whereas the first recorded case of PSHB in the Western Cape was in 2017 (Author obs., Pers. comms. Trudy Paap). It is therefore possible that similarly high infestation levels could be recorded in the Western Cape forests in the next 5 years than is currently the norm in KwaZulu-Natal.

It must be noted that the data in this study span only two eco-regions, which likely differ in many more variables than those measured. Consequently, while our findings offer insights, the reasons behind the differing prevalence of PSHB between these regions are likely more nuanced. The constant dispersal model suggested by Hudgins et al., (2017) proposes that forest pest dispersal could largely be driven by a small number of analogous mechanisms, likely related to human activity such as firewood movement. These mechanisms seem to operate consistently over large scales, providing a consistent means of pest spread. This may be the case for PSHB, and its

longer time in KwaZulu-Natal may have allowed for increased human-mediated dispersal and higher infestation levels in this region.

#### Plot-level effects on PSHB infestations

Generalist pests such as PSHB are not reliant on a single host species to move through the landscape and the community structure of forests is therefore important to determine their establishment, spread, and distribution (Parker et al. 2015; Lynch et al. 2021). Here we showed that higher tree species richness in plots resulted in lower PSHB attacks on trees. This is a recurring finding for PSHB in native forests (Townsend et al. 2024), and may be ascribed to a ‘dilution effect’ where more tree species generally reduce the availability of competent hosts (Johnson et al. 2013; Parker et al. 2015). However, the proportion of PSHB-infested trees per plot is also influenced by the host abundance, and this ‘dilution effect’ could be offset by an increase in competent host species. Higher numbers of certain host trees or higher numbers of species within certain plant families could have an ‘amplification effect’ and lead to higher and more severe PSHB infestations as shown in the current and previous studies (Lynch et al. 2021).

Different scolytine species show preferences for either forest margins or deep forests where forest structure and tree densities differ (Maetô et al. 1999). In our analyses we found that the lower the density of trees within plots the more infested trees could be found. PSHB therefore may preferentially invade forest margins than deeper forest sites as high-density plots may hinder PSHB movement through the landscape. Some ambrosia beetles such as the red bay ambrosia beetle (*Xyleborus glabratus* Eichhoff) use visual cues to locate their hosts (Mayfield and Brownie 2013). A high tree density may limit the ability of these beetles to navigate and target a specific host tree. Since PSHB is also day-active like the red bay ambrosia beetle (Mayfield & Brownie 2013), it likely also uses visual cues for host detection that may be obscured with high tree density. However, the effect of tree density may differ depending on the density of competent hosts within a plot. In our host preference investigations, both analyses of infestation probability and host utilisation indicated a frequency dependence where higher numbers of certain host species result in higher proportions of infested trees

in plots and higher infestation levels on individual trees. Higher densities of these host species in plots may therefore increase the probability of locating a suitable host (Negrón and Wilson 2003; Choudhury et al. 2021).

#### Host species preferences of PSHB

Lynch et al. (2021), to better understand the host range of PSHB, quantified the phylogenetic signal of various host trees. Their analyses showed that hosts with a higher susceptibility are more phylogenetically constrained when compared to those species not attacked, with kill-competent host species showing the highest phylogenetic constraint (Lynch et al. 2021). We identified some of the same families are particularly vulnerable here, including, Ebenaceae, Fagaceae, Fabaceae, Malvaceae, Podocarpaceae, Rutaceae, Sapindaceae and Stilbaceae. Although PSHB has a diverse host range we, along with various other studies (Eskalen et al. 2013; Paap et al. 2018; Lynch et al. 2021; van Rooyen et al. 2021; Townsend et al. 2024), have shown that these families and particular species within them are more susceptible to PSHB. Identification of these taxa will help prioritize surveillance and management activities in vulnerable plant communities throughout PSHB’s invaded ranges.

Host species that were seemingly selected for by PSHB and for tree individuals were attacked at higher levels than expected by chance in the forests studied included *Afrocarpus falcatus*, *Albizia* sp., *Allophylus natalensis*, *Baphia racemosa*, *Dichrostachys cinerea*, *Diospyros glabra*, *Halleria lucida*, *Quercus robur*, *Sparmannia africana*, *Strychnos henningsii*, *Vepris lanceolata* and *Voacanga thouarsii*. All of these except the *Albizia* sp. and *S. henningsii* which are known to be competent or kill-competent hosts. The other two occurred at very low numbers in our plots and may well prove to be competent hosts in the future. It therefore seems as if PSHB can select hosts in which it can reproduce within landscapes. However, some tree species such as *Ekebergia capensis*, *Nuxia floribunda*, *Searsia chirendensis* and *Xylotheca kraussiana* that are not yet recorded as competent hosts were also seemingly preferentially attacked. This could be explained by phylogenetic constraint. *E. capensis*, *S. chirendensis* and *X. kraussiana* all belong to the Rosid clade, while *N. floribunda*

belongs to the closely related Asterid clade (Moore et al. 2010). Species within the Rosid clade have been shown to be particularly susceptible to PSHB infestation (Lynch et al. 2021), and the species above could therefore become competent hosts if individuals are located in areas with high PSHB propagule pressure.

Numerous competent host species such as *Grewia occidentalis*, *Gymnosporia buxifolia*, *Trachelia emetica* and *Virgilia oroboides* were seemingly attacked at random. PSHB may not be able to initially recognize these species as suitable hosts (Kuhnholz et al. 2003; Hulcr and Dunn 2011). Other hosts, like *Apodytes dimidiata*, *Burchellia bubalina*, *Canthium inerme*, *Olinia ventosa*, *Psychotria capensis*, *Rapanea melanophloes*, *Scutia myrtina* and *Searsia lucida* were seemingly attacked by accident or, as for numerous abundant species monitored here such as *Celtis africana*, *Drypetes natalensis*, *Elaeodendron croceum*, *Gonioma kamassi*, *Ilex mitis*, *Ocotea bullata*, *Olea capensis*, *Podocarpus latifolius*, *Pterocelastrus tricuspidatus*, *Tabernaemontana ventricosa*, *Trichocladus crinitus* and others were seemingly not attacked at all. In these species, colonization may initially be deterred. Kairomones or semiochemicals released by certain tree species may deter PSHB beetles (Borden et al. 2001). The interactions between PSHB, its symbiotic fungi and the variety of tree species it encounters involves complex chemical ecology. Additionally, many of the above un-attacked species may only be perceived as suitable hosts when they are stressed or diseased (Kuhnholz et al. 2003), but given the high numbers monitored in this study it is unlikely every individual was in good health. Unfortunately, we were unable to investigate tree health as a predictor for vulnerability to attack by PSHB as many trees were already infested with PSHB before monitoring began, making it impossible to determine whether unhealthy trees identified were targeted because of their poor health or were initially healthy before they were infested. However, observations showed that many infestations were on seemingly healthy individuals. Invasive Scolytinae often perceive healthy trees as weakened hosts and this may also be the case for PSHB (Ploetz et al. 2013; Ranger 2016; Coleman et al. 2019).

Caution should be taken when interpreting the results presented here. The random effects implemented in our host preference models do not allow us to make general inferences about specific tree species.

We sampled a subset of all possible tree species from a much larger existing community. The models therefore only allow for inferences averaged over the subset of species sampled. However, we have demonstrated that numerous tree species in these forests may be at particular risk of PSHB infestations. These included the highly susceptible and kill competent species such as *D. glabra*, *F. trichopoda*, *S. africana*, *T. emetica* and *V. lanceolata*. The PSHB invasion into natural forest ecosystems, although seemingly slow, does not have a net-zero effect. Each native tree species has a specific role in normal ecosystem functioning and supports a unique suite of (Mucina and Geldenhuys 2006; Swart 2020). Even if attacked trees do not die, *Fusarium* infection may weaken them increasing their susceptibility to other pathogens and pests, decreasing their longevity, or reducing their ability to produce fruits and flowers which can have long-term direct and indirect effects on normal ecosystem functioning and resilience (Fensham and Radford-Smith 2021). Loss of trees in natural forests due to pathogens has also been shown to dramatically shift the capacity of forests to fix and store carbon (Paseka et al. 2020). PSHB invasions into natural forests could reduce the ecosystem services they provide.

#### Individual-level effects on PSHB infestations

Although tree species- and family-level traits may be important in host location and establishment, individual tree-level characteristics may be just as important. Here, as with a previous study (Townsend et al. 2024), larger trees showed a higher probability of being attacked. While a definitive preference for larger hosts by PSHB is not experimentally established, our study indicates that PSHB infestation severity increases on larger trees in both study regions. Larger diameter trees have bigger silhouettes and increased kairomone expression which may enhance beetle attraction, similar to findings for the red bay ambrosia beetle (Fraedrich et al. 2007; Mayfield and Brownie 2013; Frank and Ranger 2016). Larger trees also offer more sapwood volume, providing greater brood production resources (Mayfield and Brownie 2013; Ranger 2016; Choudhury et al. 2021). This has also been shown for other scolytine beetles and pathogens, where a higher density of larger hosts correlates with increased pest and disease incidence

(Anderson et al. 1997; Holt et al. 2003; Reynolds and Burke 2011; Choudhury et al. 2021).

We found that trees further away from water sources were seemingly preferentially infested by PSHB. South Africa has recently emerged from a prolonged drought. In the case of drought-induced stress, a tree's defence capacity is weakened, and soluble nitrogen is mobilized, making it more available for pests and pathogens (Mattson et al. 1988). The benefits of water stress on hosts for scolytines has been demonstrated before (Ranger et al. 2015; Boland 2016). Trees further from standing water sources in our study may therefore experience drought stress (either prolonged or seasonally) that increases their PSHB-infestation levels. These results are contradicted by previous studies that showed that the water status of trees has no impact on PSHB attacks (Umneda 2017; Bennett 2020). However, a study in South Africa that aimed to look at the effect of water availability on PSHB attacks found that trees with consistent water had fewer PSHB attacks, while those that only had seasonal water availability experienced the highest PSHB attacks. These findings were mostly driven by a single species, English oak (*Q. robur*), which is sensitive to both flooding and drought (Roberts, unpublished data). Another study found that Xyleborine ambrosia beetles showed preference for flood-stressed over drought-stressed trees. But, after 14 days of drought conditions there were significantly higher beetle attacks on drought-stressed trees when compared to those under standard irrigation. The higher attack rates were attributed in part to flood-stressed trees emitting long-range volatile kairomones while drought-stressed trees did not (Ranger et al. 2023). It is possible that in the absence of flood-stressed trees drought-stressed trees may be more attractive to ambrosia beetles.

A total of 11 trees belonging to seven species located at seven different sites died due to PSHB infestation and *Fusarium* infection during this study. It is also unknown whether these species were stressed before being attacked and if *Fusarium* infection was the sole cause of their deaths. These findings do show that *Fusarium* can kill a variety of tree species over a relatively short period of time. Many trees such as *D. cinerea* and *T. emetica* had high infestation levels prior to death while three smaller individuals of *G. buxifolia*, *S. Africana* and *D. cinerea* succumbed with less than 40 entry holes. One *V. lanceolata*

individual died gradually showing a clear progression of *Fusarium* dieback symptoms over 3 years while a second individual died after 2 years showing very few symptoms. Other species such as *T. emetica*, *F. trichopoda* and *D. cinerea* showed no symptoms of increased infestation before dying. There seems to be a great variability in response to infection between and within tree species, making it impossible to predict which individuals will succumb to infection. This was demonstrated in our study; individuals of infested trees such as *H. lucida* may drop PSHB-infested branches over time. The *D. glabra* individual that died of PSHB infestation resprouted less than a year later while other individuals were heavily infested but showed no signs of *Fusarium* dieback. The *T. emetica* individual died within 1 year of being infested but a second infested individual less than 300 m away showed no signs of dieback. We also recorded the death of an *F. trichopoda* individual due to PSHB, but upon examination of over 30 other individuals no PSHB infestations were found.

Individual trees have unique genotypes which influence their susceptibility to insect and pathogen attacks (Reynolds and Burke 2011; Eller et al. 2016). Specific genotypes of individuals interact differently with the genotypes of pathogens and some trees may be more attractive to pests (Moffett 2009; Marden et al. 2017). This makes natural forests more resilient to PSHB invasions as not all individuals belonging to a 'competent host species' will be susceptible to attack and not all species belonging to a "Fusarium colonised species" will exhibit symptoms of disease. Certain trees infected with *Fusarium* may be able to overcome the infection while in others the infection can spread. This makes it difficult to detect a host-specific structure for PSHB infestations and continued monitoring is needed to assess ecosystem-level impacts of the invasion.

Our findings underscore the importance of understanding local factors such as host species composition, and forest structure, which influence the trajectory of invasion and the extent of damage caused by forest pests. This study provides further evidence that natural forest ecosystems, especially those already facing stress from climate change and habitat fragmentation, are increasingly vulnerable to invasive pests, and highlights the need for more integrated management strategies that consider both ecological and human-mediated drivers of invasion to



maintain forest health and resilience in the face of megadisturbances.

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#### Declarations

**Conflict of interest** The authors have no competing interests to disclose.

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