

Review

Polyphagous Shot Hole Borer, a Global Threat to Forest Plantations, Green Infrastructure, and Biodiversity: Status, Challenges, and Solutions

Bernard Dell ^{1,2,*}, Wei Xu ³ and Nguyen Minh Chi ⁴¹ Centre for Crop and Food Innovation, Murdoch University, Murdoch, WA 6150, Australia² Forest Protection Research Centre, Vietnam Academy of Forest Sciences, Hanoi 11910, Vietnam³ School of Agricultural Sciences, Murdoch University, Murdoch, WA 6150, Australia; w.xu@murdoch.edu.au⁴ Institute of Forest Tree Improvement and Biotechnology, Vietnam Academy of Forest Sciences, Hanoi 11910, Vietnam; nguyenminhchi@vafs.gov.vn

* Correspondence: b.dell@murdoch.edu.au

Abstract

Global trade and climate change are accelerating the spread and impacts of invasive forest pests worldwide. The Polyphagous Shot Hole Borer (*Euwallacea fornicatus*) is among the most destructive invasive ambrosia beetles, attacking approximately 680 woody plant species across five continents and causing substantial ecological and economic losses. This review synthesizes the current knowledge of PSHB taxonomy, biology, fungal symbiosis, host range, invasion history, surveillance and management. Evidence indicates that eradication is rarely feasible once populations become established, while existing chemical and biological control measures remain of limited effectiveness, making early detection and rapid response essential. This review highlights major knowledge gaps in invasion biology, host susceptibility, fungal interactions and chemical ecology, and identifies research priorities to improve surveillance, risk prediction and integrated management. Advancing these areas will strengthen global biosecurity and enhance protection of forests, urban trees and commercial orchards.

Keywords: ambrosia beetle; *Euwallacea fornicatus*; invasive forest pest; management; *Neocosmospora euwallaceae*; orchards; research gaps; review; tree dieback; urban forestry

1. Introduction

The world's forests are facing increasing pressure from human intervention [1,2], climate change [3–6], and invasive alien species (IASs) [4,7]. Invasive species can markedly impact biodiversity [8], substantially altering ecosystem functioning [9–11], the provision of ecosystem services [12], and carbon cycling [13]. In recent decades, there has been a notable increase in the number of invasive forest insect pests and pathogens impacting forests globally [7,14,15]. For instance, during the period 2011 to 2020, 14 new emerging insect pests and 3 new emerging pathogens were documented in forest plantations in Vietnam [16]; and 18 pests and 38 pathogens were reported in the UK, which included 23 new pests and pathogens over a span of 25 years [17]. It is noteworthy that alien insects represent the largest share of invasive species within the animal kingdom [18]. Furthermore, the Kunming-Montreal Global Biodiversity Framework has established a goal to reduce invasive alien species by 50% by the year 2030.

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The long-distance dispersal and establishment of IASs are increasingly supported by the rise in globalization and trade [19,20]. These biological invasions result in significant economic repercussions [9], with one global assessment estimating that invasive insects inflict approximately USD 70 billion (hereinafter, \$) in damages each year [21]. Destructive non-native insects and pathogens are progressively emerging as substantial threats to both planted [22] and native forests [7,23], as well as urban forests [7] and commercial orchards [24]. This situation is likely to worsen due to climate change [5,25]. From 2002 to 2020, the global forest area impacted by insects and diseases was approximately 34 and 9.2 million hectares per year, respectively [6].

Bark and ambrosia beetles (Coleoptera: Curculionidae) represent some of the most destructive insects affecting forests, and urban and orchard trees, leading to significant economic losses and environmental issues worldwide. In contrast to bark beetles that consume the phloem within the inner bark, ambrosia beetles create a network of tunnels within the xylem, where they engage in a mutualistic relationship with various fungi [26–28]. Ambrosia beetles pose substantial biosecurity threats in numerous countries, particularly those involved in the trade of wood and wood products [29,30].

Ambrosia beetles belonging to the genus *Euwallacea* are of particular concern because certain species have the capability to attack and kill a diverse array of living tree taxa. In addition, invasive species are spreading globally, and their small size renders them challenging to detect within the round-wood and lumber industries. *Euwallacea* maintain nutritional relationships with a specific group of fungi referred to as the Ambrosia *Fusarium* Clade (AFC) symbionts [31–33]. These fungi are carried in specialized structures called mycangia, located on the heads of female adults. A small number of these fungi are pathogenic and can cause tree mortality [34,35].

Euwallacea fornicatus (commonly known as the Polyphagous Shot Hole Borer or PSHB) was selected for this review for four reasons: (i) it ranks among the most destructive species within the Xyleborine group [36], resulting in economic losses exceeding one billion \$ annually [37]; (ii) it is an invasive alien species that impacts hundreds of live woody species [38,39]; (iii) it is globally disseminating across five continents [40,41]; and (iv) it adversely affects trees in many environments, including forest plantations, orchards, urban parks, biodiversity reserves, and native forests [42]. The aim of this review is to deliver a thorough evaluation of the current global situation regarding PSHB, as well as to pinpoint significant gaps in knowledge, biosecurity arrangements, and management that urgently require further attention. This review is intended to benefit a diverse array of professionals, including field ecologists, forest protection researchers, forest managers, arboriculturists, and horticulturalists.

2. Methodology

A comprehensive literature search was performed utilizing Scopus, CAB Abstracts, Web of Science Core Collection, and Google Scholar to identify relevant peer-reviewed publications. Searches used combinations of the following keywords: “*Euwallacea fornicatus*”, “polyphagous shot hole borer”, “PSHB”, “ambrosia beetle”, “*Fusarium dieback*”, “*Neocosmospora euwallaceae*”, “invasive forest pest”, “urban forest”, “biosecurity”, “host range”, “chemical ecology”, “surveillance”, and “management”. The final literature search was completed on 30 April 2026. The initial searches retrieved approximately 680 records. After removing duplicates and screening titles and abstracts for relevance, publications that focused on the taxonomy, biology, fungal symbiosis, host range, invasion history, surveillance, chemical ecology, management, modeling, and biosecurity of *E. fornicatus* (PSHB) or its associated fungal symbionts were selected. Studies dealing exclusively with other ambrosia beetle species were included only when they provided broader biological or management insights directly relevant to PSHB.

Publications using outdated or ambiguous taxonomy without sufficient evidence to confirm that the species investigated was *E. fornicatus* (PSHB) were excluded where species identity could not be verified. Government reports, international biosecurity documents, and authoritative online databases were also consulted where they provided important information on current distribution, host records, management, or policy.

Following screening, approximately 280 publications and official reports were considered sufficiently relevant for inclusion in this review. Given the recent taxonomic clarification of the *E. fornicatus* species complex, particular care was taken when interpreting older literature. Studies published before the current taxonomy was established were only included when the identity of the taxon could be reasonably confirmed.

3. PSHB Taxonomy

Due to the confusing taxonomic history of *Euwallacea fornicatus*, this section briefly provides a concise examination of the specific epithet and the taxonomic challenges that have emerged over time. The taxon was initially described as *Xyleborus fornicatus* by Eichhoff in 1868, based on specimens collected in what is currently known as Sri Lanka. In 1989, Wood transferred the species into the genus *Euwallacea*. Earlier citations of the species can be found in several works [43–45].

Significant genetic variation was identified among invasive populations of shot hole borers from Florida and California which conformed to the morphological characteristics of *E. fornicatus* [46,47]. These observations implied that the populations may represent different species, leading to the establishment of the common name for PSHB in California. In parallel, O'Donnell et al. [48] performed DNA-based phylogenetic analyses on invasive populations around the world, and concluded that *E. fornicatus* comprises a complex of at least five morphologically indistinguishable species.

In an effort to clarify the *E. fornicatus* species complex, three distinct clades were identified: the tea shothole borer (TSHB), the polyphagous shothole borer (PSHB) and Kuroshio shothole borer (KSHB) [40]. Subsequently, a taxonomic revision of the species complex, using both molecular and morphological data along with specimens collected from the *E. fornicatus* type locality, identified four species [49]: *E. fornicatus* Eichhoff 1868, *E. fornicator* Eggers 1923, *E. whitfordiodendrus* Schedl 1942, and *E. kuroshio* Gomez and Hulcr [49]. Upon the discovery of a syntype of *Xyleborus fornicatus* (the holotype was destroyed in World War II), the species complex underwent a thorough reassessment, confirming the exclusive use of PSHB for *Euwallacea fornicatus* [50].

Considering the substantial alterations in the usage of the *E. fornicatus* name and its related common name since 1917 [51], it is imperative to exercise caution when evaluating older literature concerning the genuine identity of the taxa under investigation. This is crucial as voucher specimens are rarely utilized in biological and management publications. The evolution of nomenclature over time has posed a significant challenge for biosecurity and regulatory bodies [52], including the European Food Safety Authority (EFSA).

4. Fungi Associated with PSHB

Female PSHB adults harbor fungal symbionts, also known as mutualists, within paired mandibular mycangia, which are subsequently cultivated in xylem galleries of woody plants, supplying nutrition essential for the beetle's life cycle [53,54]. Generally, the Ambrosia *Fusarium* clade (AFC) encompasses the primary fungal symbionts associated with *Euwallacea fornicatus* [26,48]. The main fungus carried by *E. fornicatus* was described as *Fusarium euwallaceae* based on isolates from Israel (the type locality) and the

USA (California) [55]. This species was subsequently renamed *Neocosmospora euwallaceae* [56], and this name is used hereafter in this review even though it has not been universally accepted [57]. PSHB may also transport *Graphium euwallaceae* and *Paracremonium pembeum* [32]. In their natural environment, damaging *Euwallacea* species may associate with a broader array of fungal symbionts compared to regions where they have been introduced and become invasive [39]. For example, *Neocosmospora kuroshium*, which was initially described from KSHB in California [58], has been recognized as the primary symbiont in *E. fornicatus* infesting mango trees in Japan [59].

Infestations involving *N. euwallaceae* and *E. fornicatus* can lead to considerable mortality of a wide range of tree species [60–62]. The fungus was previously regarded as the primary pathogen causing Avocado Dieback Disease in California [63]. It has been described as a “moderately virulent pathogen” [64]. However, more recent findings indicate that the fungus acts as a pseudo-pathogen, being incapable of inducing disease without the involvement of the beetles [65]. Nonetheless, inoculation experiments have shown that lesion formation can take place even in the absence of PSHB, as observed in apple [66] and avocado branches [67]. In summary, it is the interaction between *N. euwallaceae* and PSHB that is responsible for the mortality observed in a diverse array of woody plant taxa [60,61].

Graphium euwallaceae and *P. pembeum* were described from cultures taken from the heads and galleries of *E. fornicatus* in California [32]. The three fungal symbionts seem to exhibit distinct behaviors throughout the life cycle of PSHB. For instance, both fungi were found in the mycangia of developing beetles, but were supplanted by *N. euwallaceae* in mature adults [60]. Furthermore, this research indicated that larvae thrived on the mycelia of *N. euwallaceae* and *G. euwallaceae* but not on that of *P. pembeum*. Through the inoculation of avocado trees, it was demonstrated that *N. euwallaceae* predominantly remained within the galleries of PSHB and was viable in functioning xylem for more than 2 years [65]. In contrast, *G. euwallaceae* and *P. pembeum* disappeared two months post-inoculation from live wood, yet persisted in dead wood [65].

The nutritional relationships between ambrosia beetles and their fungal symbionts have not been fully examined [48]. In addition, the potential for symbiont switching raises concerns about the emergence of more virulent beetle–fungus associations. Evidence suggests that *Euwallacea* species may acquire and cultivate fungi from closely related species, potentially leading to novel and more damaging interactions [68,69]. There is also a small risk that harmful *Euwallacea*-associated fungi could be transmitted by lateral transfer to other vectors [70,71].

The broader microbiome associated with PSHB remains insufficiently studied. While more attention has been paid to fungal partners, bacterial communities are increasingly recognized as important components of the ambrosia beetle system. These bacterial assemblages appear to be species-specific and vary across beetle life stages, mycetangia, and fungal gardens, yet their functional roles are largely unknown [72]. Advanced molecular approaches, including metagenomics and transcriptomics, are needed to clarify how these microbial communities influence beetle fitness, symbiosis stability, and invasion success.

Host-associated microbiomes are also an important but underexplored factor. Woody plants harbor diverse fungal and bacterial endophytic communities that can influence resistance to pests and pathogens [73]. However, the role of these endophytes in determining PSHB host susceptibility remains largely unknown. Lynch [74] suggested that integrating host microbiome data into invasion models could improve predictions of spread, refine risk assessments, and identify new management opportunities.

5. Life Cycle of PSHB

The life cycle of PSHB is described in many documents [53,75,76] and the main features are summarized in Figure 1. Briefly, host trees are attacked by a female adult carrying ambrosia fungi. The female beetle initially bores a hole through the bark and subsequently tunnels into the sapwood. In non-reproductive hosts, penetration holes are made [39] but galleries are not produced [77]. In reproductive hosts, these tunnels create an ideal environment for spore germination and mycelial growth of ambrosia fungi. The symbiont derives its nutrients from non-lignified components of the sapwood. The developing fungal biomass serves as the exclusive food source for PSHB. The life cycle is defined by haplodiploidy, where fertilized eggs develop into diploid females, while unfertilized eggs transform into haploid males [47]. The degree to which the reproductive cycle is moderated over time in infested trees remains uncertain. There exists plasticity in the formation of new colonies as: (i) colonizing female adults may have been fertilized prior to dispersal, and (ii) unfertilized females can produce their initial brood through parthenogenesis. This breeding system leads to a significantly skewed female sex ratio, resulting in the presence of typically one male and numerous female beetles within a gallery [78].

The sexual dimorphism of PSHB has important ecological and management implications. Females are larger (approximately 2 mm long), fully winged, and solely responsible for dispersal and colonization of new host trees, whereas males are smaller, wingless, and typically remain within their natal galleries where they mate with females before dying (Figure 1). Consequently, dispersal is almost entirely female-mediated, and flight-based surveillance systems, including lure-baited sticky and funnel traps, only capture dispersing females. This female-biased dispersal strategy facilitates establishment because a single fertilized female, or even an unfertilized female through arrhenotokous parthenogenesis, can initiate a new colony. Understanding this reproductive biology is therefore fundamental for interpreting trap captures, modeling invasion dynamics, and developing surveillance and management strategies.

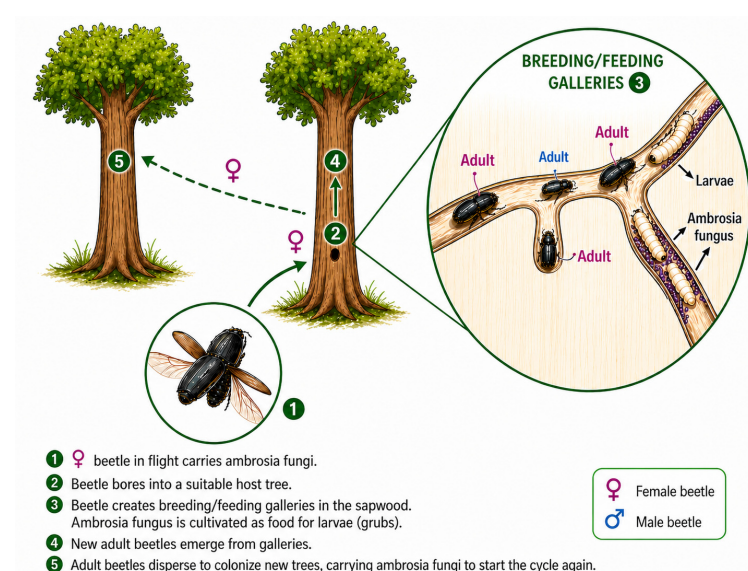


Figure 1. The life cycle of PSHB involves a female that flies to new host trees and burrows into the sapwood where, given suitable conditions, reproductive colonies are formed. Subsequently, other females emerge to establish additional colonies in the same tree or to spread to nearby hosts. Female beetles measure approximately 2 mm in length, while males are smaller than females, wingless and less abundant.

Cardinal temperatures necessary for the development of PSHB were established through a laboratory study, revealing values of $T_{min} = 13.24\text{ }^{\circ}\text{C}$, $T_{max} = 33.08\text{ }^{\circ}\text{C}$, and $T_{opt} = 27.51\text{ }^{\circ}\text{C}$ [79,80]. The authors determined that 398 degree days are required for the development of PSHB from egg to adult. In South Africa, the flight activity of the beetle showed a positive correlation with degree days, peaking in the summer months [42]. However, field studies conducted in the Northern Hemisphere indicated that peak trapping occurred during the winter (dry season) in Taiwan [80,81], while in Vietnam, trapping rates were highest in April (spring) and October (autumn) [82]. In Israel, the beetles were most active in spring and summer [83]. Additionally, short-term fluctuations in temperature can influence the dispersal of PSHB [84].

One central question is the role of abiotic stress in mediating host susceptibility. Environmental stressors such as drought, temperature extremes, and mechanical damage possibly increase tree vulnerability by altering host physiology and defense capacity. However, the extent to which these factors influence PSHB attack dynamics across different environments is not fully understood. Addressing this gap is critical for predicting outbreak risk under changing climatic conditions. Similarly, fundamental aspects of PSHB population biology remain unclear, including the number of generations per year under different climatic regimes, the potential use of degree-day models to predict life-cycle timing, and the frequency of sexual reproduction in this predominantly haplodiploid, inbreeding species [36]. These gaps limit our ability to model population growth and seasonal dispersal patterns.

6. Chemical Interactions

Chemical cues (semiochemicals) mediate insect behaviors such as mating, feeding, and oviposition [85]. Host-derived volatile compounds (VOCs) may play a critical role in insect host selection. Compared to healthy trees, stressed or damaged trees emit compounds such as ethanol, acetaldehyde, and terpenoids, which may act as kairomones attracting dispersing PSHB females [86,87]. Ethanol is widely recognized as a signal of host stress and suitability for colonization, although its behavioral effect varies with concentration and context [88,89]. These VOCs can guide beetles during the critical host-seeking phase, especially when solitary foundresses disperse to establish new galleries [39,90]. Variation in VOC profiles among different tree species, and even among individuals, likely results in differential host attack [91]. Differences in metabolic pathways (e.g., terpenoids and phenylpropanoids) can influence both attractiveness and suitability [92,93]. Environmental factors such as drought, temperature, and mechanical damage may further modify VOC emissions, increasing the susceptibility of trees to PSHB attack.

The tripartite interaction between tree-, insect-, and fungal-derived compounds jointly determines colonization success. Fungal symbionts contribute to this chemical profile by producing VOCs that may reinforce host suitability or act as aggregation cues. For example, quercivorol has been identified from fungal cultures and frass of the oak ambrosia beetle *Platypus quercivorus* and can attract PSHB and related species [47,94,95]. Such compounds may facilitate population build-up once a suitable host is colonized. Concurrently, host trees respond to infestation via their chemical defenses, including phenolics, resins, and oxidative compounds. The colonization success of PSHB depends on whether the beetle–fungus complex can overcome or tolerate these defenses, enabling fungal establishment and brood development [58,96].

Chemical interactions among the beetle, host trees, and associated microbiota are still largely unexplored in ambrosia beetles, limiting our ability to develop effective behavior-based management strategies [97]. One major challenge is the limited understanding of how PSHB locates and evaluates suitable hosts under natural conditions. Bark and

ambrosia beetles that attack healthy trees often rely on two key strategies: coordinated mass attack and the introduction of pathogenic or symbiotic fungi that weaken host defenses [98]. However, the chemical cues underlying these processes in PSHB are not well investigated. It remains unclear whether host selection is driven by single compounds (e.g., ethanol) or by complex blends of volatiles that form a species-specific “signature bouquet” as suggested for other ambrosia beetles such as *Xyleborus glabratus* [99,100].

To date, only a few attractants—primarily quercivorol and α -copaene-enriched lures—are commercially available, and their effectiveness varies depending on beetle population density and environmental conditions [94,100,101]. While combinations of these lures can produce additive or synergistic effects, they likely do not fully replicate the natural host odor profile. Identifying additional host-derived terpenoids and volatile blends from preferred host species (e.g., avocado, *Annona* spp., or alternative highly attractive hosts such as *Jacaranda mimosifolia*) may be an important research priority for improving detection and monitoring systems [100,102].

Further complexity arises from unresolved questions regarding the specificity and optimization of semiochemicals. For example, the active isomer(s) of quercivorol (p-menth-2-en-1-ol) responsible for attraction remain unclear, and responses may differ among members of the PSHB species complex [91]. Similarly, the role of α -copaene—naturally present in certain hosts such as avocado—requires further investigation to determine its attractiveness across different populations and environments. These uncertainties highlight the need for more precise chemical identification, behavioral assays, and field validation.

Therefore, future research should prioritize: (i) characterizing the full spectrum of VOCs produced by host trees, beetles, and fungal symbionts; (ii) identifying behaviorally active compounds and their optimal blends; and (iii) understanding how environmental factors influence semiochemical production and perception.

7. Distribution

The natural range of PSHB spans from India through Southeast (SE) Asia to China and Japan [31,40,50]. Apart from observations made in plantations and orchards, there is limited knowledge regarding the presence of PSHB in both primary and secondary forests throughout this extensive region. In the past few decades, the beetle has been introduced to North and South America, Australia, South Africa, the Middle East, and Europe (Table 1), where it has become an invasive species. Its spread has been particularly rapid in South Africa and South America (Argentina, Brazil, Uruguay), while its distribution in the USA (Hawaii, CA, USA), Western Australia and the Middle East (Israel, Palestine, Türkiye) remains more restricted. In Western Europe, PSHB has been detected in greenhouses across five nations (Italy, Germany, the Netherlands, Poland, Spain), as well as in urban trees in southern Spain.

Table 1. Timeline of the worldwide dissemination of *Euwallacea fornicatus* beyond its native range in Asia.

Country	Year Observed	Host	Reference
USA (California)	2003	<i>Robinia pseudoacacia</i>	Rabaglia et al. [103]
Israel	2005	<i>Persea americana</i>	Mendel et al. [104]
South Africa	2012	-	van Rooyen et al. [76]
(Pietermaritzburg)	2017	<i>Platanus × acerifolia</i>	Paap et al. [78]
Mexico (Baja California)	2015	-	García-Avila et al. [105]

Poland (Poznan)	2017	<i>Ficus religiosa</i> (Botanic Garden)	Schuler et al. [106]
Brazil (Minas Gerais)	2019	<i>Acacia mangium</i> , <i>Khaya grandifolia</i> , etc.	Covre et al. [107]
State of Palestine	2019	<i>Persea americana</i>	Salman et al. [108]
Italy (Merano)	2020	<i>Annona muricata</i> , <i>Bixa orellana</i> and others (Tropical greenhouse)	Schuler et al. [106]
USA (Big Island, O`ahu)	2020	<i>Macadamia</i>	Rugman-Jones et al. [109]
Australia (East Fremantle, Western Australia)	2021	<i>Acer negundo</i>	IPPC [110]; Moir et al. [111]
Germany (Erfurt and Berlin)	2021	<i>Mangifera indica</i> , <i>Tectona grandis</i> (Tropical greenhouses)	Schuler et al. [106]
Netherlands (Zuid-Holland)	2021	<i>Artocarpus altilis</i> , <i>Ficus macrocarpa</i> (Commercial greenhouse)	NPPO [112]
Argentina (Buenos Aires)	2021 2022	- <i>Acer negundo</i> , <i>Casuarina cunninghamiana</i> , <i>Platanus × acerifolia</i>	Ceriani-Nakamurakare et al. [113],[114]
Spain (Andalusia)	2022	<i>Acer negundo</i>	Goldarazena et al. [115]
Uruguay	2023	<i>Acer japonicum</i>	Ceriani-Nakamurakare et al. [116]
Türkiye (Istanbul)	2024	<i>Acer negundo</i> , <i>A. platanoides</i> , <i>Platanus acerifolia</i>	Acer et al. [117]

Molecular profiling indicates that the invasion history of PSHB differs among geographical regions, with evidence supporting both independent introductions from the native range and subsequent regional spread following establishment. For example, Spain contains a single haplotype that is phylogenetically closely related to populations from China, Japan and Vietnam [115,118], suggesting a recent introduction from Asia rather than spread from another invaded region. Similarly, the haplotype detected in Western Australia is closely related to one from Taiwan [111], indicating an independent introduction. In contrast, South Africa contains at least two distinct haplotypes, one corresponding to populations established in California, Israel and Vietnam, and another closely related to populations from China and Vietnam [41]. The presence of multiple genetically distinct lineages strongly suggests that South Africa has experienced more than one introduction event.

In South America, populations in Argentina, Brazil and Uruguay share closely related haplotypes [113], which may indicate either repeated introductions from a common Asian source or secondary spread among neighboring invaded countries after initial establishment. Distinguishing between these scenarios will require higher-resolution population genomic analyses, as currently available mitochondrial markers have limited power to resolve invasion pathways. Likewise, the occurrence of genetically similar populations in several invaded regions raises the possibility that international movement of infested wood, nursery stock or untreated wood packaging materials may have facilitated secondary dispersal following the initial introduction.

Understanding these invasion pathways has important implications for global biosecurity. Evidence of multiple independent introductions indicates that border biosecurity remains the primary defence against new incursions, requiring continued surveillance of high-risk trade pathways and stricter phytosanitary measures. Conversely, evidence of secondary spread between invaded regions highlights the need for coordinated international surveillance, harmonized diagnostic protocols, and timely information sharing among national plant protection organizations. Population genomic studies, integrated with trade pathway analyses and interception records, will further improve source attribution, strengthen pathway risk assessments, and support more

effective prevention strategies against future introductions of PSHB and other invasive ambrosia beetles.

Typically, initial reports concerning new introductions of PSHB focus on identifying the insect pest and potential sources, while the associated symbiotic fungi are less often investigated in early collections. Nonetheless, several studies have examined both the beetle and its symbiotic partner together. For instance, in South Africa, PSHB was initially documented as an invasive species carrying *N. euwallaceae* [78]. In Western Australia, *E. fornicatus* was shown to be carrying *G. euwallaceae*, which was closely linked to molecular sequences from collections in the USA and Vietnam [111]. In Hawaii, *N. euwallaceae* and *G. euwallaceae* were isolated from PSHB, and the DNA sequences matched those from PSHB in California [109].

Outside Asia, PSHB may occur in the same geographical region as several other non-native *Euwallacea* pest species. For instance, both *E. fornicatus* and *E. perbrevis* are present in avocado orchards located in Hawaii [109]. Additionally, in South Africa, *E. fornicatus* and *E. piceus* have been discovered to coexist [119]; and in Southern Spain, *E. fornicatus* and *E. similis* were found in neighboring provinces [118].

8. Host Range

As introduced earlier (Section 5), plant species are categorized into three groups: (i) competent or reproductive hosts; (ii) non-competent or non-reproductive hosts; and (iii) species that are not affected by PSHB [39]. In reproductive hosts, both PSHB and the fungal symbiont can thrive and reproduce successfully. Non-reproductive hosts are subject to attack by PSHB, and although the fungal symbiont may sometimes exist, the beetles are unable to reproduce. Most reproductive and non-reproductive hosts are flowering trees and shrubs, with only a very small number of palm and conifer species being affected.

The categorization into host groups is affected by the methods and criteria used, which have not been consistently defined across different geographical regions and research teams. Mendel et al. [39] state that a reproductive host is identified when PSHB is found in the galleries of attacked trees, and the fungal symbiont is isolated. Non-reproductive host trees are characterized as having typical attack symptoms (lesions and/or penetration holes) from which the fungal symbiont is isolated in most instances. van Rooyen et al. [76] include DNA fingerprinting in all host determinations. The classification of hosts into reproductive and non-reproductive categories has relied exclusively on the beetle [38,46]. DPIRD [120] outlines six categories of host susceptibility ratings: four pertaining to reproductive hosts and two related to non-reproductive hosts; however, the methodology is lacking in detail.

PSHB impacts around 680 species of woody plants [16,38–40,46,76,121–126], with approximately 30% of these serving as reproductive hosts. These reproductive hosts are distributed among 105 genera within 52 plant families. Among these, ten species are categorized as highly susceptible. The five families that contain the highest number of reproductive hosts, listed in descending order, are Fabaceae, Salicaceae, Sapindaceae, Myrtaceae, and Fagaceae. At the time of writing, the genera containing the greatest number of susceptible species are *Quercus*, *Ficus*, and *Salix*.

In many of the invaded regions, PSHB is affecting both exotic and native plant species. For example, in the Perth area of Western Australia, reproductive hosts comprise 69.9% exotic plant species, 8.7% of species that are indigenous to the region, and a further 21.3% are being cultivated from other parts of Australia [126]. By contrast, in South Africa 50% of reproductive hosts are indigenous species [127]. In the recent incursion in Uruguay, 60% of the native hosts were recorded as reproductive hosts [113]. The list of

identified reproductive and non-reproductive hosts is growing rapidly, and inventories are consistently being refreshed on multiple websites [126,127].

Variation in host resistance remains poorly understood. Studies in other tree–insect systems indicate that resistance can be influenced by plant chemistry, structural traits, and associated microbiota [128], yet comparable work for PSHB hosts is limited. Identifying the factors that confer resistance or tolerance in certain tree species or genotypes could provide valuable insights for management and breeding programs.

9. Damage Inflicted

In reproductive hosts, damage can range from branch wilting and dieback to complete tree mortality depending on the reproductive host species and level of infestation. The entry and exit holes are small, <1 mm in diameter, and can extend vertically for several meters, occasionally reaching up to 16 m [113]. Other notable external symptoms include extruded noodle-like frass, sap exudates (sugars, gums, resin), and staining of the bark [129,130]. Dissection of the wood reveals the labyrinth of tunnels containing the beetle and its fungal symbiont. Abiotic stress may heighten the vulnerability of trees to damage from PSHB, yet the underlying mechanisms remain unclear. In non-reproductive hosts, entry holes and often lesions are typically observed [39]. Further long-term investigations are needed to determine whether the penetration holes facilitate the entry of canker and other fungal pathogens which could lead to tree decline.

9.1. Orchards

Commercial avocado orchards located in California, Israel, and South Africa, along with macadamia groves in Hawaii, can be adversely affected by PSHB [46,104,109,131,132]. Branch necrosis and mortality in vulnerable avocado cultivars lead to a notable decrease in fruit yield. Other fruit and nut species susceptible to PSHB include apple [66], citrus [76], stone fruit [66,133], pecan nut [134], walnut [135], and almond [46,76,121,123]. Hence, there are concerns for future impacts of PSHB on the commercial production of these commodities [135]. The pathogenicity of *N. euwallaceae* has been established in avocado [136], apple [66], nectarine and plum [133], as well as almond [121]. On the other hand, inoculation of detached macadamia branches did not cause significant fungal lesions [123].

9.2. Plantation Forests

In Vietnam, PSHB is a significant pest affecting exotic *Acacia mangium* (Figure 2a) and *A. auriculiformis* plantations, as well as their hybrids, leading to a mortality rate of 10–15% in 3–5-year-old stands located in central and northern Vietnam [137]. PSHB also targets *A. crassicarpa* plantations in southern Vietnam; however, the damage observed so far is minor [138]. Similarly, *A. mearnsii* plantations in north-western regions of the country are largely unaffected [135], but remain a concern in South Africa [37].

9.3. Native Forests

PSHB is having a deleterious impact in native riparian forests and *Acer negundo* stands in California [135,139], and in many forest types in South Africa [61]. In California, mortality rates were 5.6% across all hardwood species but was as high as 25% in highly susceptible species [135]. Research conducted in South Africa has uncovered a diverse range of temperate vegetation types impacted by PSHB, along with newly identified reproductive host species [61,140]. Notably, locations with greater tree species diversity encountered fewer attacks, highlighting the importance of forest community structure in the spread of this pest [69]. Inevitably, an increasing number of new hosts will be

recognized as the pest infiltrates more deeply into natural ecosystems. In Western Australia, PSHB is encroaching upon urban native bushlands (Figure 2b), and considering that some vulnerable native hosts have a wide geographical range, it seems unavoidable that it will have a considerably larger impact on the health of conservation reserves and national parks in the future.

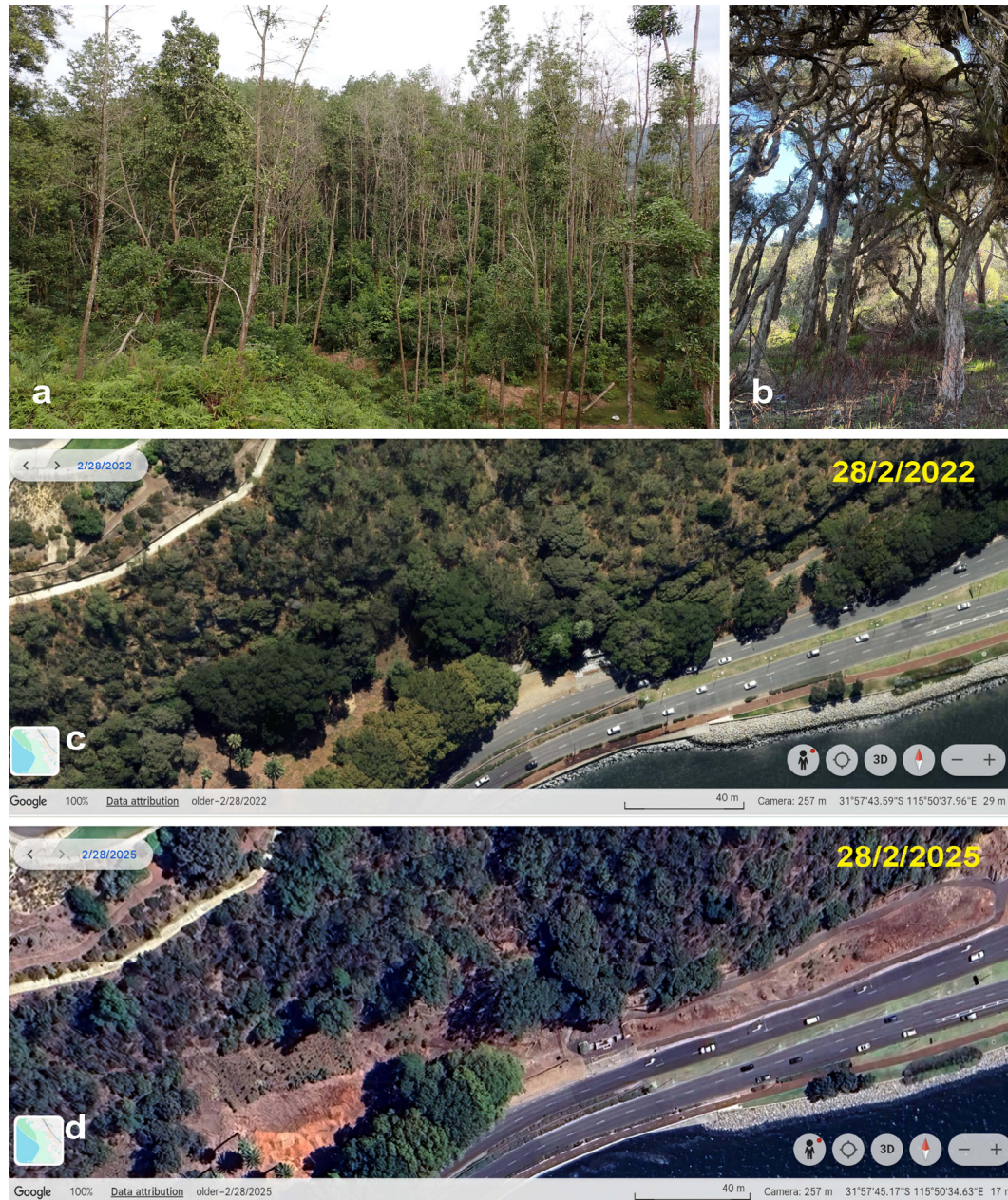


Figure 2. Damage inflicted by PSHB in different land use types. (a) Collapse of 5-year-old *Acacia mangium* plantation, Phu Tho province, Vietnam. (b) *Melaleuca preissiana*-dominated urban wetland forest susceptible to PSHB, Perth, Australia. (c,d) Loss of canopy cover due to removal of infested *Ficus macrophylla* at the base of King's Park, Perth, Australia.

9.4. Urban Forests

Many reproductive host species have been planted as ornamental trees in urban environments. Being close to likely points of PSHB introduction, early reports of damage describe canopy decline and tree death [38,53,76,135]. The impact of PSHB is very evident when infested trees are removed from streetscapes, parks, and private gardens. The resulting loss of vegetation cover (Figure 2c,d) is of significant concern due to the

ecosystem services that trees provide, such as reducing air pollution, mitigating urban heat islands, and enhancing the mental health of residents.

10. Economic Impact

Avocado production is a significant sector in the global horticulture industry, with an estimated gross production value of about USD 1.6 billion (hereinafter, \$) in 2024 [141]. The Hass variety, which is currently under threat from PSHB, holds the largest market share [142]. The potential economic repercussions of PSHB on avocado production in California, Israel, South Africa, and Western Australia remain uncertain. However, based on current FAOSTAT [141] data and Avocados Australia [143], and assuming a 10% decline in productivity due to yield loss or decrease in fruit quality, PSHB might result in a loss of approximately \$130 million in gross annual production.

The economic effects of PSHB on plantation forestry have yet to be assessed. Currently, Vietnam's forestry sector is particularly vulnerable due to its large-scale cultivation of *Acacia mangium* and several hybrids, with PSHB found in nearly 50% of these plantations. The potential loss in production could reach hundreds of millions of dollars per annum. In 2025, the export value of acacia wood was recorded at \$2.85 billion. Another forest industry that may be at risk due to PSHB invasion is *A. mearnsii*, a reproductive host for PSHB, which is grown for the production of tannin, fuelwood, and woodchips [144].

The complete global economic impact of PSHB invasions and their associated damage have yet to be fully assessed. However, preliminary regional cost estimates reveal a significant financial burden on governments at all levels, as well as local businesses and communities. In Southern California, it was estimated that the death of 11.6 million trees due to borer damage would result in a \$616.8 million annual loss in ecosystem services [145].

In South Africa, economic modeling has projected social costs of USD 18.45 billion over a decade, focusing on the removal and disposal of infested urban trees [37]. In Western Australia (WA), the estimated cost for eradication in 2023 was \$32 million, with ongoing management expenses reaching up to \$4.8 million annually [146]. These cost estimates do not consider the long-term management costs of regreening affected cities. Despite these financial efforts, the spread of PSHB continues unabated, and the window for eradication has now passed. In November 2025, the National Management Group sanctioned an expanded Transition to Management (T2M) Response Plan for PSHB, allocating \$16.5 million to T2M activities [147]. The WA government has earmarked \$18.8 million for the 2025–26 period, along with \$5.1 million for a tree recovery initiative [126,148]. To date, the total eradication/management budget for WA from all funding sources has surpassed \$92 million. The transition from eradication to long-term management in the Perth Metropolitan Area will impose significant additional expenses on local governments and communities for the removal and replacement of trees.

11. Surveillance

The early detection of PSHB is essential for tracking incursions and the dissemination of PSHB, in addition to facilitating management. A variety of surveillance methods are accessible (Figure 3). The primary strategy involves the physical inspection of trees for PSHB damage, coupled with the trapping of female beetles during flight. The costs associated with human resources can be high unless the public is encouraged to engage.

Trapping has become one of the most important tools for the early detection, delimitation, and monitoring of PSHB populations. Because only females disperse by flight, captures in semiochemical traps represent the dispersing reproductive population

rather than the total population within infested trees, and trap catches should therefore be interpreted accordingly. Sticky traps and funnel traps baited with quercivorol are currently the most widely used traps for surveillance programs in urban forests, orchards, and natural ecosystems [47,94,149]. Quercivorol has consistently demonstrated stronger attraction to PSHB than ethanol-based lures in multiple field studies. Ethanol traps may still provide a low-cost alternative for broad ambrosia beetle monitoring, particularly in regions with limited access to commercial lures. However, capture rates for PSHB are generally 10–12% lower compared to quercivorol-baited traps [82,150]. Trap efficacy may vary depending on lure release rate, trap design, host density, climate conditions, and seasonal beetle activity. A better understanding of PSHB biology and chemical ecology may provide insights into developing more efficient approaches for trapping this pest. Future improvements in semiochemical identification, lure optimization, and integration with remote sensing technologies may substantially enhance surveillance sensitivity and biosecurity preparedness.

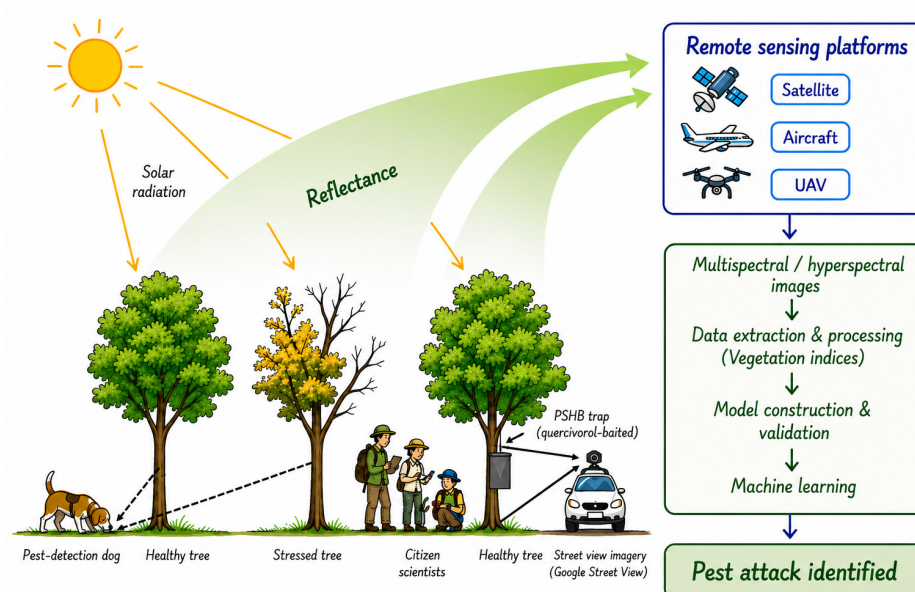


Figure 3. Ground-based and remote sensing options for the detection and surveillance of trees infested with PSHB.

Remote sensing serves as a cost-efficient approach for detecting and monitoring the health of forests [151,152], which includes analyzing the spatial and temporal patterns of borer damage [153,154]. Recent advancements in platforms, sensor technology, spectral indices, and machine learning have enabled surveillance to be performed at the individual tree level [155–157]. Aerial imagery was employed to detect laurel wilt disease in avocado orchards [158], and a subsequent study revealed that remote sensing could differentiate between this ambrosia beetle transmitted disease and damage caused by abiotic stresses [159]. Current remote sensing technologies can be explored further for monitoring PSHB; however, in regions characterized by a Mediterranean-type climate, it will be necessary to differentiate abiotic stresses such as drought.

Detector dogs can be trained to identify insect and fungal pests [160], including borers like the Asian longhorn beetle [161], the emerald ash borer [162], and the laurel wilt pathogen [163]. It would be interesting to establish whether detector dogs could be trained and employed to detect PSHB incursions.

Databases that include the locations of high-risk reproductive hosts in urban settings will aid in the surveillance of PSHB [164]. Recent research emphasizes the use of

multispectral imagery to identify [155–157] identify *Platanus* (a reproductive host) trees in Sydney [165]. Numerous local government authorities are in the process of compiling databases regarding their local trees, which can serve purposes such as disease and pest monitoring, in addition to carbon accounting. These databases may facilitate the targeting of ground-based monitoring of tree health through Google street view [166] and other digital platforms [167].

No single surveillance method is sufficient for detecting PSHB across all stages of invasion (Table 2). Consequently, future surveillance programs are likely to achieve the greatest effectiveness by integrating complementary approaches. Semiochemical trapping can provide early warning of beetle presence, remote sensing can prioritize high-risk locations for inspection, and ground surveys can confirm infestations, while molecular diagnostics such as eDNA offer additional opportunities for early detection and verification.

Table 2. Comparison of current surveillance approaches for PSHB.

Surveillance Method	Strengths	Limitations	Best Application
Visual inspection	Low cost; confirms infestation symptoms; widely applicable	Labor-intensive; requires trained personnel; symptoms appear after infestation	Confirmation of infestations, routine surveys
Semiochemical trapping	Sensitive for dispersing females; standardized; useful for monitoring	Lure performance varies with season, population density and environment	Early detection, delimitation, long-term monitoring
Remote sensing	Rapid landscape-scale assessment; repeated monitoring; detects canopy decline	Cannot distinguish PSHB from other stressors; requires image processing	Large-area surveillance and prioritizing field inspections
Detector dogs	Very high detection sensitivity; detects concealed infestations	Expensive; specialized training required; limited operational capacity	High-value sites, ports, eradication programs
Tree inventories & GIS databases	Identifies high-risk hosts; supports surveillance planning	Does not detect infestations directly; requires regular updating	Risk assessment and surveillance planning
Molecular diagnostics (eDNA/DNA barcoding)	Rapid and highly specific identification; detects early infestations	Currently limited availability and standardization	Biosecurity diagnostics and confirmation

12. Management Options

12.1. Mechanical Control

Currently, mechanical intervention is the foremost approach employed to reduce the dissemination and impact of PSHB. Guidelines [64,168,169] for the removal of infested branches and trees have been developed based on research findings regarding chipping, solarization, and composting [83,170–172]. A management matrix for infested urban trees has been established according to the degree of infestation and the perceived value of the trees [173]. The timing of sanitation activities is critical for reducing the risk of PSHB dispersal. The removal of infested trees is given priority during the season when the beetles are not active in flight, which corresponds to winter in regions with a Mediterranean-type climate [42]. Disposal logistics also present major operational challenges, especially in urban environments where large volumes of infested wood require rapid transport, chipping, solarization, composting, or deep burial under strict biosecurity protocols. Delays in disposal or inappropriate handling of infested material may facilitate further spread of the beetle. However, aside from the removal of infested

branches in avocado orchards, it has not been possible to eradicate the pest using mechanical methods, thus necessitating the development of alternative control strategies.

12.2. Chemical Control

To date, no chemicals have been demonstrated to completely stop PSHB from attacking or reproducing in host trees. A limited number of chemicals has been shown to be somewhat effective in mitigating PSHB attacks (Table 3), along with improving tree health and reducing mortality (Figure 4). The most potent insecticides include bifenthrin, a synthetic pyrethroid, and emamectin benzoate (EB), both of which induce nervous system failure in insects. EB is derived from abamectin, which originates from the soil actinomycete *Streptomyces avermitilis* [174]. These substances kill insects either through direct contact or through residual effects. Interestingly, a study conducted over one year revealed that EB and bifenthrin were effective in reducing PSHB attacks of infested *Platanus racemosa* trees; however, EB demonstrated greater efficacy in trees with severe infestations [175]. Previous research indicated that bifenthrin diminished PSHB attacks and gallery development in castor bean (*Ricinus communis*) branches under laboratory conditions, while also lowering beetle activity in infested plants in natural settings [176]. In a preliminary field study thiamethoxam, a neonicotinoid insecticide, reduced the number of entry/exit holes by 70% in 2–7 year-old *Acacia* stands [138].

Furthermore, several broad-spectrum conazole fungicides, mainly propiconazole and tebuconazole, have been demonstrated to partially mitigate damage caused by the PSHB symbiont (Table 3). For example, propiconazole administered as a trunk injection decreased the length of galleries containing *N. euwallaceae* by approximately 36% in American sweetgum (*Liquidambar styraciflua*) [177], and reduced PSHB attacks in California sycamore (*Platanus racemosa*) by 37%, 45 months post-treatment in a preventative trial [178]. Conazoles impede the production of ergosterol, which is an essential component of fungal cell membranes, thereby hindering fungal proliferation [179].

Table 3. Key studies on the effect of pesticides for the management of PSHB in urban trees.

Host	Treatment *	Treatment Effect	Reference
<i>Liquidambar styraciflua</i>	Bifenthrin (pyrethroid insecticide) TS	Reduced PSHB colonization attempts by ca. 40%	Roberts et al. [177]
	Cypermethrin (pyrethroid insecticide) + Salicylic acid (fungicide) TS	Reduced PSHB colonization attempts by ca. 40%	
	Emamectin benzoate (avermectin) TI	Ineffective	
	Propiconazole (triazole fungicide) TI	Reduced gallery fungal-lesion length by ca. 36%	
<i>Platanus racemosa</i>	Bifenthrin TS + Tebuconazole (triazole fungicide) TI	Reduced PSHB attack 1 month, but not 3 months post-treatment	Eatough-Jones et al. [180]
	Emamectin benzoate TI + Tebuconazole TI	No pesticide treatments were effective after 6 months	
	Bifenthrin TS + Emamectin benzoate TI + Metconazole (triazole fungicide) TS	Reduced PSHB attack up to 3 months post-treatment	
<i>Platanus racemosa</i>	Emamectin benzoate TI	Reduced PSHB attack by 30% after one year in therapeutic trial	Grosman et al. [178]
	Emamectin benzoate TI	Reduced PSHB attack by 65% after 45 months in preventative trial	
	Emamectin benzoate TI + propiconazole TI	Reduced PSHB attack by 73% after 45 months in therapeutic trial	
	Propiconazole TI	Reduced PSHB attack by 37% after 45 months in preventative trial	

* TS trunk spray, TI trunk injection.

In specific cases, the application of pesticide combinations has shown enhanced effectiveness when compared to the use of individual treatments. Alongside the studies given in Table 3 and Figure 4, the combination of a mixture of EB (trunk injection), bifenthrin (trunk spray), and metconazole (trunk spray) has been found to be more effective than other treatments in partially reducing PSHB attacks during a 6-month observation period in infested sycamore trees [180]. Nevertheless, the combination of EB or bifenthrin with propiconazole did not lead to a reduction in beetle attacks compared to individual treatments in a separate field study [175].

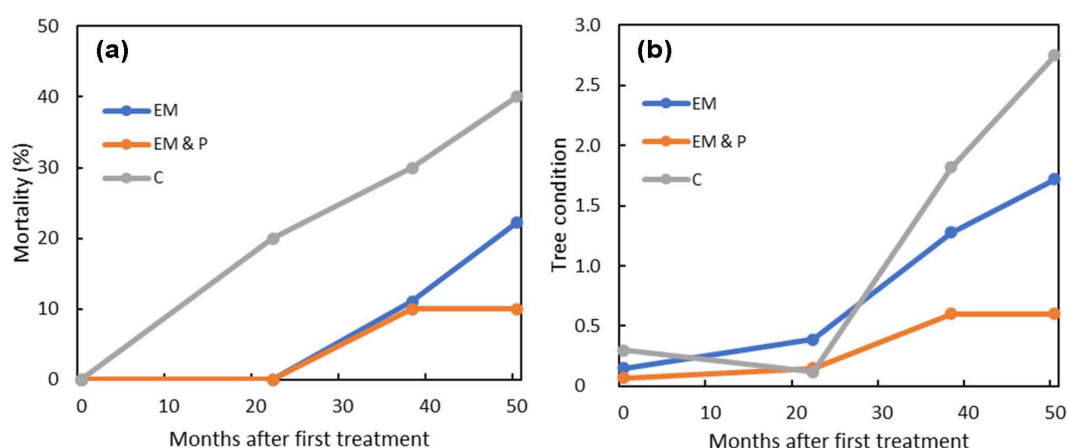


Figure 4. Partial control of PSHB damage expressed as (a) mean tree mortality, and (b) mean tree condition (0 = healthy to 3 = >80% of crown with symptoms) over time in urban *Platanus racemosa* from trunk injections using emamectin benzoate (EM) or EM and propiconazole (EM & P), compared to the untreated controls (C). The treatments were reapplied after 24 months. The figures are drawn from data in Grosman et al. [178].

Environmental concerns must also be considered, including potential non-target impacts on beneficial organisms and soil microorganisms, chemical exposure risks in urban environments, and the sustainability of repeated pesticide use in sensitive ecosystems. So far, bifenthrin and EB have been restricted or banned in a number of countries due to their negative impacts on the environment and human health [181,182]. Also, concern over the long-term impact of neonicotinoids has led to restrictions on their use [183].

Although considerable progress has been made, major knowledge gaps remain regarding chemical management of PSHB. Future research should focus on: (i) enhancing the delivery of insecticides and fungicides to areas of infestation and galleries within trees; (ii) assessing different pesticide formulations such as conazole stereoisomers [179] and novel analogues [184]; (iii) testing pesticide/adjuvant combinations [185]; (iv) discovering more potent chemicals; (v) exploring nanoparticle- and nanocarrier-based delivery systems that may enhance chemical stability and movement within woody tissues; and (vi) assessing RNA interference (RNAi), gene-targeting approaches, and fungal-specific inhibitors as emerging management technologies, among other considerations. No studies have been conducted to quantify the distribution, concentration, and persistence of pesticides applied to combat PSHB in host trees. By contrast, Byrne et al. [186] established a threshold of 300 ng of emamectin benzoate per gram of avocado-based artificial diet for KSHB and utilized this information to ascertain effective concentrations in injected avocado trees. It is advisable to promote integrated pest management programs [177], which take into account chemical treatments, biological agents, and both attractants and repellants [187–190].

12.3. Biological Control

Biological control [191] provides a complementary strategy for managing PSHB, especially where chemical control is: (i) undesirable, such as in urban environments; (ii) uneconomic or impractical, particularly in forest plantations and nature reserves; and (iii) ineffective due to the beetle's cryptic, wood-boring lifestyle. Natural enemies, including predators, parasitoids, and entomopathogens, have been widely explored in bark and ambrosia beetle systems, although their application to PSHB remains relatively limited.

Generalist predators such as clerid beetles, ants, and predatory mites may contribute to mortality of scolytine beetles, primarily during dispersal or at gallery entrances [192,193]. However, their impact on PSHB populations is likely limited because most life stages are protected within host-tree tissues. Similarly, parasitoids have been reported in other ambrosia beetle systems, but there is currently limited evidence of effective, host-specific parasitoids for PSHB [27]. This reflects the ecological challenge of accessing beetle brood within galleries, reducing the potential for classical biological control using parasitoids.

Entomopathogenic fungi [194] represent one of the most promising biological control options for PSHB. Species such as *Beauveria bassiana* and *Metarhizium anisopliae* have demonstrated pathogenicity against a range of bark and ambrosia beetles, causing infection through contact with conidia [195,196]. Laboratory and field studies suggest that these fungi can reduce adult survival and disrupt colonization. However, efficacy under field conditions can be variable, influenced by environmental factors such as temperature, humidity, and UV exposure, which affect fungal persistence and infection rates [197]. In addition, the mutualistic relationship between PSHB and its symbiotic fungi, *N. euwallaceae*, may complicate outcomes, as interactions between pathogenic and symbiotic fungi within galleries remain poorly understood.

Entomopathogenic nematodes (EPNs), including species of *Steinernema* and *Heterorhabditis*, have also been investigated as biological control agents against wood-boring beetles. These nematodes can infect adult beetles during dispersal or at gallery entrances, releasing symbiotic bacteria that rapidly kill the beetle [198]. However, their effectiveness against PSHB is likely limited by the beetle's cryptic habit within woody tissues and the need for adequate moisture to support nematode survival and movement [199].

Another emerging avenue is the use of microbial antagonists targeting the PSHB–fungus symbiosis. Disruption of *N. euwallaceae* establishment could indirectly suppress beetle reproduction, as larvae depend entirely on fungal growth for nutrition. Studies in other ambrosia beetle systems have shown that competition from residents or introduced fungi can limit symbiont establishment and reduce brood success [28,96]. Although still largely unexplored for PSHB, this approach highlights the potential of targeting the tripartite interaction rather than the beetle alone.

Biological control is most likely to be effective when integrated with other management strategies. For example, combining entomopathogenic fungi with semiochemical-based attractants (e.g., quercivorol) may enhance delivery through attract-and-infect or attract-and-kill systems [195]. Despite its potential, biological control of PSHB faces several challenges, including limited knowledge of host-specific natural enemies, difficulty accessing beetles within galleries, and environmental constraints on biocontrol agents.

One key research gap is the identification of highly effective and environment-adapted entomopathogenic agents. Current fungal biological control agents (BCAs) may require high spore loads to achieve infection, limiting practical application. Nel et al. [188] highlighted the need to identify strains better adapted to PSHB microhabitats, which could improve efficacy at lower doses. They also emphasized the importance of targeting

dispersing females—the primary stage vulnerable to infection—through innovative delivery systems such as spore-dissemination traps. However, these approaches are largely preventative, and effective delivery into established gallery systems remains a major unresolved challenge.

Microbial-based strategies targeting the beetle–fungus symbiosis may be another promising direction. Endophytes and bacterial antagonists may suppress fungal symbionts or reduce beetle fitness, but their performance is highly variable and context-dependent [200,201]. Introduced microbes must compete with established host microbiomes, and their persistence under field conditions is often uncertain. Reverchon et al. [202] suggested prioritizing the identification of microbial strains with dual activity (both antifungal and insecticidal) and integrating microbiome-based approaches to manipulate host or beetle-associated microbial communities.

Across all approaches, the lack of effective delivery systems remains a critical bottleneck. Ensuring that BCAs reach target beetles in sufficient quantities and remain viable under field conditions is essential for success. Future work should focus on optimizing delivery strategies, including integration with semiochemical tools (e.g., attract-and-infect systems) to enhance contact with dispersing beetles [188,202]. Therefore, while biological control is unlikely to provide stand-alone suppression of PSHB, it is an important component of integrated pest management.

13. Challenges and Opportunities

13.1. Applied Research

Even though PSHB has been an invasive pest for decades and its global distribution has significantly increased in recent years, there are still significant gaps in our understanding of its invasion biology, ecology, host interactions, and long-term management in the field (Table 4). Significant uncertainties also persist regarding ecology, pathogenicity, transmission dynamics, and environmental adaptation of its fungal symbionts. These knowledge gaps constrain the development of effective surveillance systems, predictive models, and sustainable management strategies. The urgent need for both fundamental and applied research on PSHB and related ambrosia beetle systems has been highlighted by several recent studies [35,203,204].

Table 4. Summary of current knowledge, major knowledge gaps and future research priorities for Polyphagous Shot Hole Borer.

Research Area	Current Understanding	Major Knowledge Gaps	Future Research Priorities
Taxonomy & invasion history	Taxonomy has largely been resolved using morphological and molecular evidence. Several invasion pathways and haplotypes have been identified	Cryptic diversity may remain; unresolved haplotypes (e.g., H22 [40,80]); incomplete DNA reference databases; limited surveys in the native Asian range	Expand biodiversity surveys, improve genomic reference databases, integrate morphology with genomics, strengthen international data sharing
Host range & host susceptibility	Approximately 680 woody host species have been identified, including reproductive and non-reproductive hosts	Mechanisms underlying host resistance, susceptibility and host shifts remain poorly understood	Identify resistant tree species/genotypes, investigate host physiology and chemical defenses, develop host-risk prediction models
Tree–beetle–fungus interactions	PSHB depends on <i>Neocosmospora euwallaceae</i> and other fungal symbionts for successful reproduction	Functional roles of fungi, bacteria and host microbiomes remain largely unknown; mechanisms of symbiont switching are unclear	Apply metagenomics, transcriptomics and metabolomics to characterize microbial interactions and identify novel management targets

Chemical ecology	Quercivorol and α -copaene are currently the most effective attractants for surveillance	Host volatile blends, repellents, pheromones, olfactory receptors and behavioral mechanisms remain poorly characterized	Discover new attractants and repellents, develop push–pull strategies, integrate receptor biology with semiochemical discovery
Life history & invasion biology	Basic life cycle, reproductive system and thermal requirements have been described	Population dynamics, dispersal behavior, voltinism and climate adaptation remain uncertain	Develop predictive population models, quantify dispersal, assess climate change impacts and improve invasion forecasting
Surveillance & diagnostics	Visual inspection and lure-based trapping are widely used. Remote sensing and molecular diagnostics are emerging	Low sensitivity during early invasion; limited integration among surveillance technologies	Combine semiochemical trapping, AI, remote sensing, eDNA and molecular diagnostics into integrated surveillance systems
Chemical management	Current insecticides and fungicides reduce attacks but do not eradicate PSHB or its fungal symbionts	Poor pesticide delivery into galleries; unknown resistance risks; limited information on environmental impacts	Develop improved formulations, nanoparticle delivery systems, RNAi technologies and integrated chemical management programs
Biological control	Entomopathogenic fungi and microbial antagonists show promise under laboratory conditions.	Effective natural enemies, field efficacy and delivery systems remain inadequate.	Identify highly effective biological control agents, optimize attract-and-infect systems and target beetle–fungus interactions.
Biosecurity & quarantine	Border inspections and quarantine remain the primary prevention measures	High-risk pathways, early detection capacity and international coordination remain insufficient	Strengthen pathway analysis, molecular diagnostics, international surveillance networks and One Biosecurity approaches
Urban forest resilience & restoration	Tree removal is currently the primary management strategy after infestation	Long-term ecological, economic and social impacts remain poorly quantified	Develop climate-resilient restoration strategies, improve tree selection and quantify ecosystem service recovery
Cross-cutting priorities	Increasing collaboration among researchers, governments and industry	Fragmented datasets and limited interdisciplinary integration	Promote international collaboration, open data, long-term monitoring, stakeholder engagement and integrated management frameworks

Despite extensive research on ambrosia beetles and their associated fungi over recent years, most studies have concentrated on species found in North America and Europe. Indeed, in the natural geographical region in Asia, as well as in certain regions where PSHB has been introduced, our understanding of the native scolytine fauna is either incomplete or has received minimal research attention. Limited research funds and difficulties in accessing many remote areas have contributed to this situation. Recent developments in the combination of morphological and molecular data using convolutional neural networks can aid in this endeavor [205]. In addition, the growth of international collaboration, such as the Bark Beetle Mycobiome [68], could foster and enhance global investigations, particularly in developing nations where financial resources are scarce.

In conjunction with the heightened research efforts that will demand substantial funding support, there is a pressing need to enhance the prediction, monitoring, and biosecurity of forest pests in general [206]. There is an opportunity for researchers, policymakers, land managers, local communities, and others to unite for enhanced

outcomes [204,207]. A new framework has recently been established to facilitate the engagement of scientists with policymakers and to enable the public to champion pre-emptive biosecurity measures and the management of forest health [208]. A blueprint for advancing understanding and management of PSHB is provided in Figure 5, and key topics are explored further in the following sections.

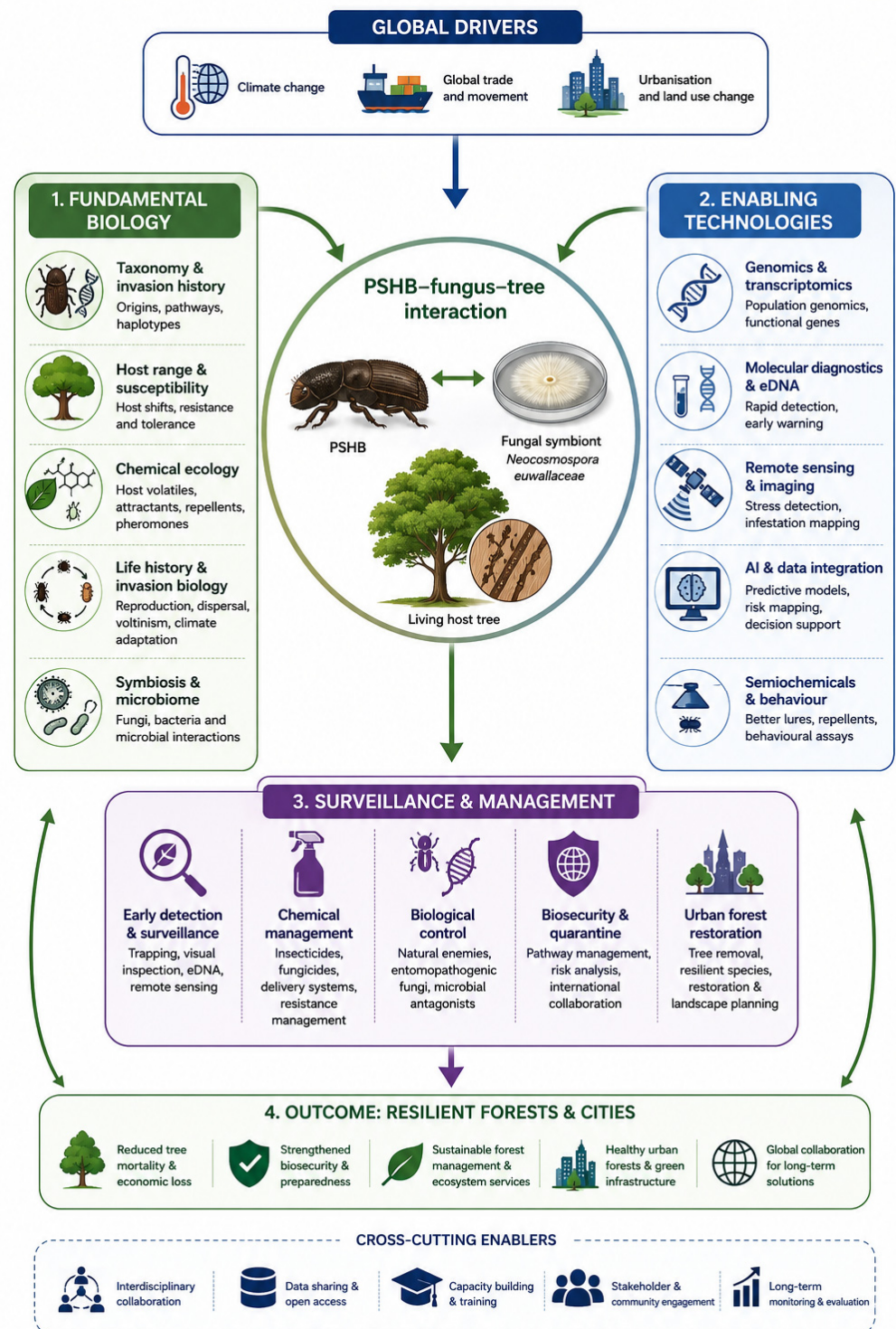


Figure 5. Integrated research framework for advancing the understanding and management of PSHB. Current knowledge gaps and future research priorities are organized into three interconnected components. (1) Fundamental biology focuses on taxonomy, host range, microbial symbiosis, chemical ecology and invasion biology, which underpin understanding of PSHB ecology

and host interactions. (2) Enabling technologies include genomics, environmental DNA (eDNA), remote sensing, artificial intelligence (AI), and semiochemical-based tools that improve detection, diagnostics and research capacity. (3) Management and applications integrate surveillance, chemical and biological control, biosecurity, and urban forest restoration to reduce the impacts of PS HB. Cross-cutting priorities—including interdisciplinary collaboration, long-term monitoring, open data sharing, capacity building and stakeholder engagement—support progress across all research areas. Together, these components provide a pathway from fundamental scientific discovery to sustainable management, improved biosecurity, and resilient forest and urban ecosystems.

13.2. Detection and Diagnosis

The early detection and identification of invasive alien insects is essential for the successful eradication of these species. Greater emphasis can be directed towards the surveillance of trees in urban areas surrounding ports [151,209,210], wood distribution centers, and urban greenspace with high tree species diversity [211]. Furthermore, increased use of aerial and ground-based images and deep learning could enhance the early detection of pest outbreaks [212–214].

Molecular approaches are reliable and essential for the swift and precise identification required to uphold rigorous biosecurity and quarantine protocols. This is relevant to both the beetle and its associated fungi and bacteria. Progress in DNA barcoding, data analysis, and reference libraries is expected to minimize misidentification moving forward [215]. It is hoped that the issue faced in South Africa, where DNA barcoding for PS HB suggested the existence of PS HB five years prior to any field observations being made [216], can be circumvented in the future.

13.3. Management

The recent inability to control and eliminate PS HB in Western Australia underscores the growing need for swift and adaptable management response strategies to address invasive pests in urban settings. Enhancement in surveillance, monitoring (including use of sentinel trees [209]), communication with stakeholders, methods for treating, removing or replacing infested trees, and safeguarding vulnerable species are crucial for implementing best practice management of PS HB incursions. Specific operational protocols are necessary for trees located in orchards, urban green space, plantation forestry, and protected areas. In particular, managing pests in urban trees presents challenges, and it is vital to focus on public engagement when formulating eradication strategies and other responsibilities [217]. Moreover, given that we are unaware of the degree to which a reduction in tree health caused by abiotic stress influences attacks by PS HB, it is prudent to preserve tree health to the greatest extent in urban settings. While there are established guidelines for branch removal in avocado orchards, comparable protocols must be developed for heritage, keystone, or threatened species where branch attack occurs. For protected areas, it is imperative that PS HB strategies are incorporated in their management plans. Given that resources are typically constrained, it has been recommended that surveys concentrate on “areas with different combinations of species representing groups that appear to be most important in the arrival, establishment and spread of the pest–pathogen complex” Lynch et al. [69]. Forecasting the spread of PS HB (see Section 13.8) can assist in pinpointing geographical regions where surveillance may be most economically viable.

13.4. Biosecurity, Quarantine and Trade

Once established, alien forest pests have proven to be extremely difficult to eradicate, even in cases where quarantine measures have been enforced. The recent invasion of

PSHB in Perth, Western Australia serves as an illustration of this. The notable expansion of international trade and tourism in recent years has heightened the demands on border security and biosecurity. Specifically, biosecurity constraints at both the national and international levels can result in the inadvertent introduction of non-native forest insect pests [218]. In many cases, the methods of introduction are not clearly defined. Only a small percentage of the international trade in wood and wood products are subjected to inspection at the point of entry and additional strategies are thus needed to reduce the threat of the introduction of invasive species. This can include a requirement for phytosanitary certificates [30] and stronger engagement through the supply chain, including among plantation managers, traders, shipping agents, and buyers [219]. It has been proposed that concentrating on listed regulated organisms may inadvertently result in the introduction of lesser-known species whose threat status remains undetermined [17,220]. Recommendations for enhancing biosecurity outcomes encompass a heightened emphasis on trade pathways [17,221], enhanced surveillance and trapping around ports [222], establishing national pest surveillance programs [165], and implementing a multi-sectoral strategy such as One Biosecurity [223,224] or One Biosecurity and One Health to enhance regional biosecurity [225]. One Biosecurity has been characterized as “an interdisciplinary approach to biosecurity policy and research that builds on the interconnections between human, animal, plant, and environmental health to effectively prevent and mitigate the impacts of invasive alien species” [226]. Additional improvements to quarantine and biosecurity systems could include stronger inspection of high-risk trade pathways, improved treatment and certification of wood packaging materials, enhanced surveillance around ports and urban entry points, and greater use of rapid molecular diagnostic tools such as environmental DNA (eDNA) for early detection. Increased international collaboration, real-time data sharing, and public awareness programs will also be essential for reducing the spread of PSHB and other invasive forest pests under increasing global trade and climate change pressures.

13.5. Tree Breeding

Cultivating trees that appear to be resilient and flourishing in the field, recognizing resistant varieties, and breeding resistant trees present various medium to long-term opportunities to alleviate the impacts of invasive pests and pathogens. However, many challenges remain in the adoption of these strategies for tree enhancement [227,228], and resistant genotypes have only been deployed in a limited number of plantation forestry and horticultural tree species.

In scenarios where pest species target a narrow selection of woody host species and resources are accessible, there are chances to discover heritable resistance, as in the case of PSHB fungal resistance in avocado [123]. However, the significant number of susceptible hosts that are either compromised or killed by PSHB hinders the selection and breeding efforts for urban forests and conservation areas. Nonetheless, it is essential to consider preserving the genetics of endangered species, as well as heritage trees, which are vulnerable to PSHB attacks.

13.6. Predicting Spread

Forecasting the potential range expansion of current PSHB invasions, along with the probability of new introductions, is crucial for allocating resources towards detection and monitoring in higher-risk regions. A range of models is accessible, including the Generalized Dispersal Kernel (GDK) [229], Maximum Entropy Modeling (MaxEnt) [81,230], CLIMEX [231], and Generalized Linear Model (GLM) [232], among others. Various species distribution models have been employed for ambrosia beetles; however, further global modeling is required to enhance the limited financial resources typically

designated for pest management. Additionally, it is crucial that modeling incorporates projected climate scenarios [233]. Ge et al. utilized CLIMEX in conjunction with the CSIRO-Mk3-6-0a global climate model to predict the future distribution of *E. fornicatus* in China [234]. Their results suggested that any range extension, whether under the current climate or the climate change scenario RCP8.5, would be confined to southern China. Recently, several species distribution models and fuzzy logic have been used to assess the potential distribution of PSHB in Australia [235]. Moreover, the application of a temperature-dependent stage-structured population model suggests that additional regions are climatically appropriate for PSHB [236]. It is especially concerning that these studies point to a probable range expansion of *E. fornicatus* in South Africa, South America, and Australia. These results are already contributing to the formulation of policies and future strategies to address incidents in some regions that are presently free from the pest. Nevertheless, additional modeling is necessary for Africa and South America to enhance future biosecurity measures.

13.7. Afforestation in SE Asia

There is limited knowledge regarding the distribution of PSHB in natural forests across SE Asia, as well as its potential to infest living native trees [34] in both primary and secondary forests. As the utilization of indigenous species in afforestation initiatives increase [237,238], along with the domestication of specific fast-growing species for commercial plantations, it becomes increasingly important to consider threats posed by destructive pests and pathogens. For instance, PSHB is a pest affecting cultivated *Cinnamomum cassia*, *Dalbergia tonkinensis*, and *Styrax tonkinensis* in Vietnam. However, there is no information available regarding the pest status of these species in their natural habitats. Moreover, exotic acacias frequently serve as nurse crops for native tree species during the restoration of degraded lands [239,240], which underscores the necessity for increased understanding of the potential for common pests and their management.

13.8. Restoration of Urban Green Space Impacted by PSHB

PSHB is causing a significant reduction in urban forest canopy, and efforts to restore tree canopies while alleviating the associated rise in land surface temperatures and heat stress among the human population will necessitate substantial ongoing commitment. Urban forests play a crucial role in mitigating urban heat islands and are vital for climate resilience in metropolitan regions [241]. There is a scarcity of research regarding the effects of urban tree insects and pathogens on the cooling advantages provided by trees in urban settings [242], which is also relevant to PSHB. The choice of tree species for the restoration of areas affected by PSHB must be approached with careful thought. Cities that experience similar climatic conditions (for instance, those in Mediterranean climates) frequently feature a number of shared tree species in their urban landscapes, and information regarding their vulnerability to PSHB may have already been documented. Nonetheless, new host species are continually being discovered as PSHB invasions escalate. Consequently, “tree taxa that are not yet widely planted or that exist in regions not significantly affected may not have been thoroughly assessed” [62]. Species identified as reproductive hosts must not be planted in infested locations or in areas with a high risk of infestation. For example, in Perth the public is advised against planting box elder maple (*Acer negundo*), coral tree (*Erythrina × sykesii*), or robinia (*Robinia pseudoacacia*). However, there is currently no guidance regarding the management of the highly susceptible castor bean plant, which is a prevalent invasive weed in disturbed urban environments. In general, there exists an opportunity to enhance the application of strategic decision-making protocols related to tree-planting in order to reduce future risks linked to invasive pests and pathogens [62].

13.9. Community Engagement and Citizen Science

Citizen science [243,244] and extensive community involvement are crucial for the effective surveillance, detection, and monitoring of invasive pests [245,246]. Opportunities exist for greater participation of citizen scientists in forest pest surveillance [247]. Online platforms, such as iNaturalist and eBird, can aid in the early identification of invasive species [248]. Tailored citizen science initiatives are particularly effective. In South Africa, a citizen science initiative utilizing data from iNaturalist proved successful in identifying PSHB infestations [249]. Furthermore, an independent study validated the reliability of citizen science in monitoring PSHB in infested urban trees [250]. In Western Australia, officials were slow to engage the public in PSHB detection, especially in trees adjacent to quarantine areas infested with PSHB. Citizen science efforts were only intensified three years after the initial citizen report of an infested tree in 2021, when residents and visitors were encouraged to report suspected infestations using the MyPestGuide Reporter app. However, significantly more effort is required to build local capacity, and to educate Perth metropolitan landowners on how to identify and manage borer-affected trees on their properties. In contrast, California implemented a collaborative governance framework that facilitated the swift execution of an action plan, five research initiatives, and a comprehensive outreach and education strategy across the state [74]. Future community engagement programs could further benefit from multilingual educational materials, targeted outreach to high-risk industries and neighborhoods, school-based biosecurity education, and improved feedback systems that inform participants about surveillance outcomes and management actions. Long-term public engagement will be essential for improving awareness, increasing reporting rates, and supporting sustainable management of PSHB in urban and natural ecosystems.

14. Conclusions

PSHB has emerged as one of the most serious invasive ambrosia beetles threatening forests, urban green infrastructure, orchards, and biodiversity worldwide. Its broad host range, close association with pathogenic fungal symbionts, cryptic biology, and ability to establish across diverse climatic regions present major challenges for global biosecurity and forest health management. Despite substantial progress in understanding the taxonomy, fungal symbiosis, host range, surveillance, and management of PSHB, significant knowledge gaps remain regarding its invasion, chemical ecology, dispersal biology, climate adaptability, and long-term impacts. Current management approaches continue to rely heavily on sanitation and tree removal, while chemical control strategies remain largely suppressive rather than curative, highlighting the urgent need for more sustainable and integrated management approaches. Future progress will require stronger international collaboration, long-term investment in research and surveillance, and improved integration among science, policy, industry, and community engagement. Emerging technologies such as molecular diagnostics, eDNA detection, remote sensing, machine learning, and AI-assisted surveillance offer promising opportunities to improve early detection and management capacity. The global spread of PSHB highlights the urgent need to transition from reactive eradication programs toward more proactive, adaptive, and resilient forest biosecurity systems capable of responding to increasingly complex invasion risks under accelerating globalization and climate change.

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Abbreviations

The following abbreviations are used in this manuscript:

AFC	Ambrosia <i>Fusarium</i> Clade
BCA	Biological control agent
DNA	Deoxyribonucleic acid
EB	Emamectin benzoate
EFSA	European Food Safety Authority
EPN	Entomopathogenic nematode
IAS	Invasive alien species
KSHB	Kuroshio shot hole borer
PSHB	Polyphagous shot hole borer
SE	Southeast
TSHB	Tea shot hole borer
UK	United Kingdom
USA	United States of America
VOC	Volatile organic compound
WA	Western Australia

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