What Determines Host Range and Reproductive Performance of an Invasive Ambrosia Beetle *Euwallacea fornicatus*; Lessons From Israel and California

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This study examined the polyphagous shot hole borer (PSHB) *Euwallacea fornicatus* (Coleoptera; Scolytinae) native to Southeast Asia and concentrated on its wide host range in two of the invaded areas, California and Israel. Among the 583 examined tree species, 55.9% were characterized as "non-reproductive hosts" and only 13.8% were characterized as "reproductive hosts," suitable for the *E. fornicatus* reproduction. Families that included ≥20 species and genera with ≥10 were considered for further analysis. The highest percentage of tree species suitable for reproduction was obtained for Salicaceae and Sapindaceae, whereas the lowest percentage of tree species belonging to this category were within the Rosaceae, Myrtaceae, and Magnoliaceae. The genera *Acer*, *Quercus* and *Acacia* displayed the highest percentage within the "reproductive host" category, with the former significantly higher from all seven of the studied genera. We found that all *Brachychiton* and *Erythrina* were attacked and none of the examined 20 *Eucalyptus* spp. were suitable for *E. fornicatus* reproduction. The results suggest discordance between host tree phylogeny and susceptibility to the *E. fornicatus*, indicating that trait correlation of susceptibility of different tree species to the *E. fornicatus* are the results of convergent evolution and not of a common descent. A theoretical model, suggesting the different possibilities of potential tree species becoming attractive or non-attractive to *E. fornicatus* attack, is described. It is suggested that the beetle reproduction success rate over a wide host range, as well as the long list of species belonging to the "non-reproductive host" category, is the outcome of interactions between the beetle fungal symbiont, *F. euwallaceae*, and sapwood of the attacked tree. The model suggests that a tree selected by the *E. fornicatus* may fall in one of three groups, (i) those in which *F. euwallaceae* is unable to develop, (ii) those tree species that slow the development of the fungus, and (iii) those that enable *F. euwallaceae* to thrive. Hence, the host range suitable for beetle reproduction is determined by development of *F. euwallaceae*. In general, PSHB does not distinguish between host species of the "non-reproductive host" and "reproductive host" categories.

Keywords: *Euwallacea fornicatus*, host range, ambrosia beetle, symbiotic fungus, *Fusarium*

INTRODUCTION

Ambrosia beetles represent the earliest origin of fungus farming in insects (approximately 50 Myr), which emerged long after the origin of the subfamily Scolytinae (100–120 Myr) (Coleoptera: Curculionidae). Later origins include the species rich Xyleborini tribe (Curculionidae: Scolytinae), dating back to 21 Myr (Jordal and Cognato, 2012). The habit of feeding on colonized fungi located in the nutritionally poor xylem by ambrosia beetles likely evolved several times with the feeding on fungal fruiting structures and spores, mostly with shifts to angiosperm hosts (Farrell et al., 2001). Ambrosia beetles generally occur as secondary insects in diseased trees or felled timber (Francke-Grosmann, 1967). The majority of ambrosia fungi and beetles are only able to colonize declining and freshly killed trees, and are not competitive in trees colonized by general wood-decaying fungi. Furthermore, collapse of the tree physiology boosts the development of wood decaying basidiomycetes, which compete with mutualistic fungi (Frankland, 1998), significantly limiting the time ambrosia beetles can remain in the wood. That in turn restricts evolution of family and social dynamics among the insects; nearly all ambrosia beetle species are only able to develop a single generation on a given tree, and all new individuals must thereafter disperse. Therefore, the most common relationship of ambrosia beetles with host trees is colonization of freshly killed tissues. However, there are also those that attack living trees, and those that survive in rotting tissues with a wood-decaying symbiont; most of these strategies are driven by fungal symbionts' metabolism (Hulcr and Stelinski, 2017).

Although healthy trees are normally unsuitable to attack by bark and ambrosia beetles, some species are reported to attack and eventually kill live, apparently healthy non-coniferous trees, but this represents a minority of species to date (Grousset et al., 2020). Among the ambrosia-feeding scolytids, Xyleborini are the most numerous and widely distributed tribe. Their cryptic nature; polygamous, sib-mating system; and wide host range foster their distribution through commerce and establishment in new areas (Rabaglia et al., 2006). In scolytine-fungus ectosymbioses, the fungi are inoculated by the beetles into plant tissues where they grow for a period of time independent of the host, before being reacquired by offspring as callow adults (Six, 2012). The mycangia, structures in the beetles' mandible, mesonotum, or elytron that harbor the symbiotic fungi, play a critical role in this process (Skelton et al., 2019).

For ambrosia beetles, the adoption of a strictly mycophagous habit may have led to extensive species radiations in the Xyleborini (Jordal et al., 2000). However, these radiations occurred mainly in tropical rainforests, where both warm temperatures and high humidity favor fungal development (Atkinson and Equihua-Martinez, 1986). The high species richness of the tropical rainforests may have shaped the strategy of fungi-beetles symbiont partnerships allowing colonization of large number of host tree species, which also makes them successful invaders. Ambrosia beetles that attack live trees are mostly those surviving under stressed conditions. Stress may arise from various abiotic factors; including flooding, drought, mechanical damage (such as windbreak and snowbreak),

freezing, ozone exposure, graft incompatibility, non-suitability for development in particular site conditions, excessive or improperly timed nutrient supplies, and biotic factors caused by pathogens and other insect pests (Ranger et al., 2010; Ploetz et al., 2013; Hulcr and Stelinski, 2017). Ploetz et al. (2013) referred to the alarming increase in ambrosia beetle–associated diseases and of trees in various environments, and coined their surprising impacts and dramatic increases as "black swan events" in tree health.

Many of the studied invasive species of the Xyleborini tribe seem to attack living and/or apparently healthy trees growing within non-native ornamental, horticultural, and forested habitats (Weber and McPherson, 1984; Atkinson et al., 1988; Oliver and Mannion, 2001; Henin and Versteirt, 2004; Keshavareddy et al., 2008). For example, in the United States, camphor trees seemed to be more resistant to vascular wilt disease caused by *Raffaelea lauricola*, native to areas of the fungal host *Xyleborus glabratus*, than American species of Lauraceae (Fraedrich et al., 2014). Native Xyleborini in turn attack live exotic tree species as demonstrated in the case of *Euwallacea perbrevis* in Sri Lanka (mentioned as *Xyleborus fornicatus*, Danthanarayana, 1968; Walgama, 2012) or *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) in India (Mote and Tambe, 1991), China (Li et al., 2016), and in Vietnam (Anon., 2014). This phenomenon was also evident in other groups of ambrosia beetles; for example, *Megaplatypus mutatus* (Platypodinae) native to Argentina that causes serious wilting of exotic *Casuarina cunninghamiana* in Argentina and *Populus* spp. in Italy (Alfaro et al., 2007). Hulcr and Dunn (2011) suggested that virulence of ambrosia beetles in invaded ranges is often triggered when three factors coincide: (i) invasion into territories with naïve trees, (ii) ability of the associated fungus to either overcome resistance of the naïve host or trigger a suicidal over-reaction, and (iii) an "olfactory mismatch" in the insect whereby a subset of live trees is perceived as "weakened," thus suitable for colonization.

Ambrosia beetles belonging to the Xyleborini are typically recognized as stenophagous (feeding on few species of fungi) whereas the polyphagous nature of their fungal symbionts is an acquired property in diverse habitats such as the tropical rainforests (Beaver, 1977, 1979; Kirkendall, 1983; Atkinson et al., 1990). Thus, many of the studied Xyleborini are found on a large number of tree species (Wood and Bright, 1992). Browne (1961) who studied the *Euwallacea* spp. (as *Xyleborus* spp. in the group *Euwallacea*) in Malaysia (Malaya) indicated that in natural conditions the species are not, as a general rule, highly selective in their choice of hosts. For example, Browne (1961) listed 19 hosts in 14 families in Malaysia for *Euwallacea similis*. However, some of them such as *E. fornicatus* (s.l.) showed signs of distinct preferences to certain host trees. Hulcr et al. (2007) examined host specificity of ambrosia beetles from a lowland rainforest in Papua New Guinea and found that they are broad generalists as 95% of the species did not show any preference for a particular host species or clade. *Xylosandrus compactus* is known to infest more than 225 species of plants, belonging to 62 families (Ngoan et al., 1976; CABI, 2020). *Xylosandrus crassiusculus* also occurs in a very wide variety of host plants;

Schedl (1963) listed 94 tree species in 28 families in Africa, and 63 tree species in 34 families outside Africa. *Xyleborus affinis* has a pan-tropical distribution infesting some 300 woody hosts (Schedl, 1963; Wood, 1982; Rabaglia et al., 2006), 150 species in Africa alone (Francke-Grosmann, 1967). *Xylosandrus germanus* exhibits the capability of attacking a diverse range of more than 200 tree species (Weber and McPherson, 1983).

Euwallacea is a monophyletic genus that is morphologically diverse (Storer et al., 2015). The first description of *Xyleborus fornicatus* Eichh. (*Euwallacea fornicatus*), a twig boring ambrosia beetle, was made by Eichhoff in 1868 from a specimen collected in Sri Lanka (then Ceylon) from an unknown plant (Speyer, 1917). During the past two decades, exotic Asian *Euwallacea* spp. have been detected in several areas in the West where they attack and reproduce in living woody hosts. At first, the main concern was the avocado industry, however, later it was found that these species inflict serious damage on native and exotic trees in urban landscapes and even in native forests (O'Donnell et al., 2015; Boland, 2016; Mendel et al., 2017; Paap et al., 2018). A recent taxonomic review of the species complex by Smith et al. (2019) proposed the following classification: *Euwallacea fornicatus* [=*E. tapatapaoensis* (Schedl, 1951); =*E. whitfordiodendrus* (Schedl, 1942) syn. res.]. Members of the *Euwallacea fornicatus* species complex and their variety of ambrosia symbiotic fungi further confirms that the relationship between the beetles and fungi are more likely promiscuous in native areas, as opposed to strictly obligate with a specific combination of fungi of any of the beetle species, as observed in invaded areas (Carrillo et al., 2019).

Stouthamer et al. (2017) reported that the native range of the polyphagous shot-hole borer (PSHB), *Euwallacea fornicatus* might encompass Northern Thailand, Vietnam, China, Taiwan, and Okinawa. Three symbiotic fungi: *Fusarium euwallaceae*, *Graphium euwallaceae*, and *Paracremonium pembeum* were detected in the larvae and adult PSHBs and from the brood galleries of the beetles in four tree species (Freeman et al., 2012, 2019; Lynch et al., 2016). The mutualism between xyleborine beetles within the genus *Euwallacea* and members of the Ambrosia *Fusarium* Clade (AFC) represents one of 16 known evolutionary origins of fungiculture by ambrosia beetles (O'Donnell et al., 2015; Aoki et al., 2019). AFC symbionts are unusual in that some are plant pathogens that cause significant damage in naïve natural and cultivated ecosystems (Kasson et al., 2013).

Fusarium euwallaceae is a well-characterized fungal symbiont of *E. fornicatus* inciting Fusarium dieback on many host plants in Israel, California, and South Africa. The discovery of additional fungal symbionts within ambrosia beetle mycangia was expected as already Baker and Norris (1968) showed that as a complex, the three fungi provided the nutrients essential for reproduction of *Xyleborus ferrugineus*; thus, suggesting that *G. euwallaceae* and *P. pembeum* together with *F. euwallaceae* occur as a community for beetle proliferation and survival (Lynch et al., 2016; Freeman et al., 2019).

Many bark and ambrosia beetle species are attracted by ethanol (e.g., Rabaglia et al., 2006; Reding and Ranger, 2020). Ethanol is present in some tissues of healthy trees, but in weakened trees, it increases dramatically due to limited oxygen availability resulting from a variety of physiological stresses (Kimmerer and Kozlowski, 1982; MacDonald and Kimmerer, 1991). Some Xyleborini species are considered non–ethanol-responsive ambrosia beetles that may exploit host volatiles induced by the symbiotic fungi (Hulcr et al., 2011) or those volatiles related directly to the host chemistry (Martini et al., 2017). Observations in Israel suggested that PSHB does not respond to ethanol (Mendel and Freeman, unpublished data). Attraction to host volatiles may be misleading as the beetles often attack host trees unsuitable for reproduction (Kendra et al., 2011; Mendel et al., 2017). The PSHB is capable of colonizing living tissues of angiosperm hosts, which may help explain the beetle's unique semiochemical ecology (Kendra et al., 2017). However, data of Li et al. (2016) did not suggest that the beetle is an aggressive colonizer of living and healthy trees, since nearly all individuals were collected in that study from weak, diseased, or dead host plants. Cooperband et al. (2017) identified two pheromone compounds, 2-heneicosanone and 2-tricosanone, for the three members belonging to the *E. fornicatus* species complex present in North America. Gomez et al. (2019a) suggested that these are probably involved in social behavior with colonized galleries.

The effect of imitating the PSHB attack by multiple inoculations of its symbiont *Fusarium euwallaceae* clearly indicated that the fungus colonizes host plant tissues in a localized manner and is not systemically transmitted throughout the xylem tissues (Freeman et al., 2019). Multiple attacks by beetles are needed to weaken main limbs and branches of avocado "Hass" (Mendel et al., 2017) as well as other tree species (authors' observations in both California and Israel). To the contrary, *Xyleborus glabratus* in North America represents an extreme case: the spores of its symbiont, *Raffaelea lauricola* migrate passively through the xylem, causing the tree to respond with gums and tyloses, which impede water transport and cause foliage wilting and branch dieback; complete seedling wilt and plant mortality can occur within a few weeks (Inch and Ploetz, 2012; Inch et al., 2012).

This study concentrates on the wide host range of PSHB in two of the invaded areas including 207 and 52 tree species in California (Eskalen et al., 2013) and Israel (Mendel et al., 2017), respectively, and more new records, accumulated since these studies were published. The objectives of the present work were: (i) to analyze results of the surveys that were conducted in Israel and California urban areas and parks totaling 583 tree species, (ii) to clarify the distinct susceptibility between host species, and (iii) to suggest a model which may explain the lack and differences in reproduction success of the PSHB in different host tree species.

MATERIALS AND METHODS

Host Plant Survey

The surveys were conducted in Israel between 2013 and 2020 in different growth habitats, including public parks, botanical gardens, home backyards, ornamental landscapes of different Kibbutzim and commercial avocado orchards with the

surrounding woody vegetation. Interactions with stakeholders, landscape managers and gardeners initiated many visits to the beetle infested trees. The surveys were also based on information conveyed by foresters and landscape inspectors regarding susceptible indigenous tree species in their natural habitats; maples and oaks in particular (see also Mendel et al., 2017). In California, most of the trees were visited and identified to species at the LA Arboretum and the Huntington Library, Art Collections and Botanical Gardens in Los Angeles County, and native and urban forests. Each botanical garden covers approximately 48 ha and in general, the species collections housed in each location are different and genetically diverse (see also Eskalen et al., 2013).

Host Tree Type Definition

We defined three categories of host trees with respect to the PSHB. The "reproductive host" was termed when eggs, larvae, pupae or callow adults of the PSHB were detected in the exposed galleries of attacked tree species and *Fusarium euwallaceae* was isolated. The "non-reproductive host" referred to typical attack symptoms on tree species, viz., lesions and/or penetration holes that were observed and (in most cases) *F. euwallaceae* was isolated without any signs of beetle reproduction. The "non-attacked host" referred to individuals of tree species that were not affected although they were observed in the vicinity (a radius of 25 m) of attacked trees, observed under similar conditions, on at least two separate sites. Owens et al. (2019) found that 80% of marked *Euwallacea* nr. *fornicatus* were recaptured within 30–35 m of the release point. "Attacked tree species" was termed for "suitable for reproduction" and "non-reproductive," combined.

Examination of the Sampled Trees

In Israel, the bark of suspect infested trees was removed to expose the beetle's gallery. Beetles were collected and identified, and in most examined trees a core sample (0.5×10 cm) was removed with a tree increment borer (Haglöf group, Långsele, Sweden) or knife for isolation of the common symbiotic fungus, *Fusarium euwallaceae*, as described by Freeman et al. (2012). Tree species that were termed as highly susceptible, produced extensive beetle populations and significant numbers of these hosts were eventually killed (Mendel and Freeman, unpublished data). All trees characterized as "non-reproductive" were grown on sites with ascertained "reproductive hosts." In California, tissue samples from each tree species showing symptoms characteristic of dieback (one tree per species) were collected by extracting symptomatic tissue from the trunk with a sterilized knife to a depth beyond the cambium. Samples were returned to the laboratory (University of California, Riverside) for morphological and molecular identification of the beetle, the fungus, or both. If visible, beetles were collected and placed immediately into 95% ethanol for further molecular identification (Eskalen et al., 2013).

Data Analysis

The 583 tree species included in the analyses with their specific affiliation included; their family, genera, category with respect to the beetle attack and area of examination, as listed in Supplementary Table 1. The tree species were sorted according to category, and the occurrence of trees of all three categories within each family and genus, according to number of examined species in each taxa. Indigenous sampled tree species for California and Israel were also analyzed separately. The tree category patterns, analyzed for the eight families, included 20 or more species and eight genera, which included 10 or more species. Overall association between species and category and between genera and category was established by the Likelihood Ratio (LR) Chi-square Test. Following significant association in both cases ($\chi^2_{(14)} = 117.6$, $p < 0.0001$, $\chi^2_{(14)} = 65.7$, $p < 0.0001$, respectively), pairs of species and pairs of genera were compared for incidence of each of the three categories separately by χ^2 LR Test with one degree of freedom.

RESULTS

General Information About the Sampled Trees

The 583 examined tree species fell into the three host categories, the majority of which 55.9% were designated as "non-reproductive hosts" while only 13.8% as "reproductive hosts," suitable for the PSHB reproduction (**Table 1**). Occurrences of trees belonging to all three categories in a certain family or a genus is related to the sampling size. Thus, only 3.1% of the examined genera and 23.2% of the examined families nested species of all three categories. However, when genera with ≥ 5 species and families with ≥ 10 species were assessed, these values rose to 30 and 88.9% for genera and families, respectively (**Table 1**). The number of examined tree species varied markedly between the representative genera and families, therefore, only genera that included ≥ 10 species or families with ≥ 20 (**Table 2**) were considered for further analysis. **Supplementary Table 1** (as **Supplementary Data**) lists all examined tree species with respect to their taxonomic affiliation (genus and family), susceptibility to the PSHB and geographic location; 451 species were examined in California, 97 in Israel and an additional 35 in both locations.

TABLE 1 | Summary of host tree information.

Taxonomic level of hosts	Groups	Number examined	% included all three host categories
Species	Total	583	–
	"Suitable for reproduction" category	81	–
	"non-reproductive" category	326	–
	"Not attacked" category	176	–
Genera	Total	259	3.1
	Including 1–4 sampled tree species	238	0.8
	Including ≥5 sampled tree species	21	33.3
Families	Total	82	23.2
	Including 1–9 sampled species	64	6.2
	Including ≥10 sampled species	18	88.9

The examined indigenous tree species sampled in each area are listed in **Table 3**; they represent a small fraction of the total species examined. The percentage of tree species associated with the "reproductive" category is similar to both California and Israel, and all belong to the same four genera: *Acer*, *Platanus*, *Populus*, and *Quercus* (**Table 3**).

Family Level Examination

Among the eight analyzed botanical families of the examined trees, only Fagaceae and Myrtaceae were significantly different within the three host categories. Some families did not differ from each other in any of the categories for the two following groups: (1) between Fabaceae, Magnoliaceae, and Malvaceae, and (2) between Fagaceae, Sapindaceae, Salicaceae, and Rosaceae (**Table 4**). Fagaceae significantly differed from Myrtaceae in all three tree categories; any other pair comparisons displayed a significant difference only for one or two of the categories (**Table 4**). Comparison of occurrences of tree species suitable for reproduction and all attacked tree species (attacked tree species = suitable for reproduction + "non-reproductive") of

TABLE 2 | Families studied with respect to number of genera and related host species information according to the three categories of susceptibility to the PSHB.

Family	Genera	Reproductive	Non-reproductive	Not attacked	Family	Genera	Reproductive	Non-reproductive	Not attacked
Adoxaceae	2	–	1	2	Lauraceae	8	1	8	2
Altingiaceae	1	1	1	–	Lythraceae	2	–		3
Anacardiaceae	8	1	4	6	Magnoliaceae	2	2	27	2
Apocynaceae	5	–	1	4	Malpighiaceae	2	–	2	
Aquifoliaceae	3	1	2	–	Malvaceae	15	3	21	2
Araliaceae	2	–	2	–	Meliaceae	4	–	3	1
Arecaceae	13	2	6	7	Melianthaceae	1	–	1	
Asparagaceae	2	–	1	1	Menispermaceae	1	1	1	
Asphodelaceae	2	–		2	Monimiaceae	1	–	1	
Asteraceae	3	–	2	1	Moraceae	3	3	7	1
Betulaceae	5	1	5	4	Moringaceae	1	–	1	
Bignoniaceae	3	2	3	3	Myrtaceae	10	1	9	29
Boraginaceae	1	–	2	1	Nyssaceae	1	–		1
Bougainvilliidae	1	–	–	1	Oleaceae	5	–	8	4
Buddlejaceae	1	–	1	–	Onagraceae	1	–	2	
Burseraceae	2	–	1	1	Papaveraceae	1	–	1	
Cactaceae	1	–	–	1	Papaveraceae	1	–		1
Cannabaceae	1	1	2	2	Papilionaceae	1	–		1
Caprifoliaceae	1	–	–	1	Pinaceae	3	–	4	6
Casuarinaceae	1	–	1	–	Pittosporaceae	2	–	2	2
Celastraceae	2	–	–	2	Platanaceae	1	7	2	
Cercidiphyllaceae	1	–	–	1	Poaceae	2	–	1	1
Clethraceae	1	–	–	1	Podocarpaceae	2	–	1	4
Combretaceae	1	–	1	–	Polygalaceae	1	–		1
Cornaceae	4	–	6	–	Proteaceae	4	–	2	2
Corynocarpaceae	1	–	–	1	Quillajaceae	1	–		1
Cunoniaceae	1	–	1	–	Rhamnaceae	5	–	7	
Cupressaceae	8	–	3	8	Rosaceae	8	–	16	9
Ebenaceae	1	–	2	1	Rutaceae	7	–	3	8
Elaeocarpaceae	2	–	2	–	Salicaceae	6	9	8	4
Ericaceae	1	–	1	2	Sapindaceae	8	12	10	3
Euphorbiaceae	5	1	6	2	Sciadopityaceae	3	–		1
Fabaceae	31	16	71	6	Scrophulariaceae	1	–		2
Fagaceae	3	12	20	9	Simaroubaceae	1	1		
Fouquieriaceae	1	–	–	1	Solanaceae	3	–	1	2
Garryaceae	1	–	–	1	Tamaricaceae	1	–		1
Ginkgoaceae	1	–	–	1	Taxodiaceae	1	–	1	
Hernandiaceae	1	–	–	1	Theaceae	3	1	13	3
Iteaceae	1	–	–	1	Ulmaceae	3	–	7	1
Juglandaceae	3	2	4	1	Urticaceae	1	–	1	
Lamiaceae	1	–	–	1	Verbenaceae	3	–	3	1

TABLE 3 | Examined indigenous tree species in California and Israel, and category as related to their susceptibility to the PSHB.

Category	California (25 species)	Israel (18 species)
"Reproductive[1]"	*Acer macrophyllum*	*Acer obtusifolium*
	A. negundo	*Platanus orientalis*
	Platanus racemosa	*Populus euphratica*
	Populus fremontii	*Quercus calliprinos*
	P. trichocarpa	*Q. infectoria*
	Quercus agrifolia	*Q. ithaburensis*
	Q. engelmannii	
	Q. lobata	
%	32.0	33.0
"Non-reproductive"	*Juglans californica*	*Cercis siliquastrum*
	Pithecellobium glandulosa	*Olea europaea*
	Prunus ilicifolia	*Pistacia atlantica*
	P. mexicana	*P. palestina*
	Umbellularia californica	*Populus alba*
		Quercus look
		Rhamnus alaternus
		Ziziphus spina-christi
%	20.0	44.4
"Non-attacked"	*Bocconia arborea*	*Cupressus sempervirens*
	Bursera odorata	*Pinus halepensis*
	Calocedrus decurrens	*Pistacia lentiscus*
	Euonymus bungeanus	*Pyrus amygdaliformis*
	Maytenus boaria	
	Myoporum laetum	
	Pinus torreyana	
	Quercus emoryi	
	Sambucus mexicana	
	S. nigra	
	Sequoia sempervirens	
	Umbellularia californica	
%	48.0	22.6

[1]*A "reproductive tree" was termed when eggs, larvae, pupae or callow adults of the PSHB were detected in the exposed galleries of attacked trees and Fusarium euwallaceae was isolated. An "Non-reproductive tree" referred to typical attack symptoms, viz., lesions and/or penetration holes that were observed and (in most cases) F. euwallaceae was isolated without any signs of reproduction; A "non-attacked tree" referred to those where intact adult tree species were observed in the vicinity of attacked trees, observed on at least two separate sites.*

the eight examined botanical families is displayed in **Table 5**. The highest percentage of tree species suitable for reproduction was obtained for Sapindaceae and Salicaceae, whereas the lowest percentage of tree species belonging to this category was within the Rosaceae, Myrtaceae, and Magnoliaceae. With regards to percentage of attacked tree species, in Fagaceae, Magnoliaceae and Malvaceae more than 90% of the tree species were included, whereas the lowest percentage of attacked tree species was recorded for Myrtaceae and Rosaceae, 25.6 and 64.0%, respectively.

Figure 1 displays a cluster analysis of the tested botanical families based on the proportion of the three tree categories as compared with the schematic phylogenetic tree of these families, based on analysis made by Soltis et al. (2011). These authors constructed a 17-gene data set for 640 species representing 330

families using genes from the nuclear, plastid, and mitochondrial genomes. While the tested families were grouped according to their proportional tree categories, the cluster is dissimilar to the phylogenetic relationship (as suggested by Soltis et al., 2011).

Genus Level Examination

Among the 28 possible combinations of eight examined genera, 13 did not indicate significant differences within any of the three species categories (**Table 6**). The genera *Acer*, *Quercus*, and *Acacia* displayed the highest percentage within the "reproductive host" category, with the former significantly different from all seven of the studied genera; none of the examined 20 *Eucalyptus* spp. were suitable for PSHB reproduction (**Table 7**). However, concerning the percentage of affected trees (combination of species of "reproductive hosts" and "non-reproductive hosts"), we found that all *Brachychiton* and *Erythrina* were attacked; while on the other extreme were the *Eucalyptus* spp. with the lowest percentages of attacked tree species (**Table 7**).

In **Figure 2** the cluster analyses of the tested botanical genera was performed in an identical manner to that done at the family level. The tested genera were grouped according to their proportional tree categories of the relevant tested species. One cluster included *Acer* and *Quercus* displaying the highest percentage of "reproductive host" category, along with *Eucalyptus* with the highest percentage of non-attacked tree category. The other group included the other examined genera with similar percentages of trees of from each category (**Table 6**). The overall clustering is dissimilar to the phylogenetic pattern (as derived from Soltis et al., 2011).

DISCUSSION

Attraction to a wide host range by the PSHB was well demonstrated in the present study and in others (Eskalen et al., 2013; Mendel et al., 2017; Gomez et al., 2019b). Similarly, a wide host range was recorded for the two other *Euwallacea* spp. of the *fornicatus* complex, *E. perbrevis* (= TSHB) and *E. kuroshio* (= KSHB) (Boland, 2016; Owens et al., 2018; Carrillo et al., 2019; Boland and Uyeda, 2020) as well as for *Euwallacea similis* (Browne, 1961). Wide and diverse host range characterizes many other members of the tribe Xyleborini. For example, Horn and Horn (2006) found that *Xylosandrus crassiusculus* reproduced on 124 host species of 48 families, including distinct taxa such as pine, cocoa, coffee, mahogany, rubber, tea, and teak. Many other examples demonstrating the wide host range of Xyleborini are mentioned in the introduction section (Schedl, 1963; Ngoan et al., 1976; Beaver, 1977, 1979; Kirkendall, 1983; Weber and McPherson, 1983; Atkinson et al., 1990; Wood and Bright, 1992; Rabaglia et al., 2006; Hulcr et al., 2007; Owens et al., 2018; CABI, 2020). Kuhnholz et al. (2001) raised the question of how ambrosia beetles became capable of attacking living trees that appear to be fully resistant. These authors suggested that if the introduced beetle or its tree host beetle or the host itself is introduced to a new location, lack of coevolution with the beetle imparts the potential to become more aggressive than toward

TABLE 4 | Comparison of % tree species of each category between eight botanical families.

	Fagaceae	Magnoliaceae	Malvaceae	Myrtaceae	Rosaceae	Salicaceae	Sapindaceae	Families
Tree Categories								
A attacked	**0.0011***	0.23	0.74	**<0.0001**	0.19	**0.0010**	**0.0008**	Fabaceae
N non-host	**0.0169**	0.97	0.81	**<0.0001**	**0.0005**	0.08	0.38	
R reproductive	0.06	0.17	0.58	0.06	–**	**0.0108**	**0.0016**	
A attacked		**0.0012**	**0.0117**	**0.0236**[a]	0.20	0.47	0.54	Fagaceae
N non-host		0.09	0.17	**<0.0001**	0.20	0.83	0.34	
R reproductive		**0.0199**[a]	0.09	**0.0079**	–	0.35	0.17	
A attacked			0.48	**<0.0001**	**0.0493**[a]	**0.0006**	**0.0006**	Magnoliaceae
N non-host			0.83	**<0.0001**	**0.0126**	0.18	0.48	
R reproductive			0.48	0.44	–	**0.0052**	**0.0019**	
A attacked				**<0.0001**	0.21	**0.0054**	**0.0055**	Malvaceae
N non-host				**<0.0001**	**0.0275**[a]	0.28	0.64	
R reproductive				0.16	–	**0.0243**[a]	**0.0092**	
A attacked					**0.0016**	0.22	0.15	
N non-host					**0.0031**	**0.0002**	**<0.0001**	Myrtaceae
R reproductive					–	**0.0024**	**0.0011**	
A attacked						0.08	0.09	Rosaceae
N non-host						0.21	0.06	
R reproductive						–	–	
A attacked							0.89	Salicaceae
N non-host							0.51	
R reproductive							0.73	

Effect Likelihood Ratio Tests (probability of χ^2, n = 1).
*Families sharing the value in bold differ significantly in proportion of tree species of the same tree category; **No tree species of reproductive category; [a]insignificant after being subjected to Bonferroni correction.

its native host tree. Current analyses of the host range of the PSHB in Israel and California indicate that both native and exotic tree species for both areas are attacked and many among them successfully allowed beetle reproduction and associated fungal colonization; the indigenous tree genera attacked by the beetle are the same in both locations. While in California the PSHB killed more native trees than ornamental (planted out of their native habitats) ones (Coleman et al., 2013), in Israel, the situation is to the contrary (Mendel et al., 2017). Trees of the few genera, such as *Acer* and *Platanus*, were frequently attacked and killed in California and Israel but also in Southern China (Li et al., 2015). Although *Ficus microcarpa* was reported as a reproductive host in China (Coleman et al., 2019), attack of this tree was never observed in Israel or California, despite high occurrence of this ornamental species in both locations.

In the presumed natural range of the PSHB and the two other members of the *Euwallacea fornicatus* complex, attacks on live trees were reported on exotic tree species (Kalshoven, 1958; Walgama, 2012; Stouthamer, 2014). Kovach and Gorsuch (1985) suggested that most native ambrosia beetles found in peach orchards in South Carolina are more a symptom of other stress factors although the invasive species displayed aggressive behavior toward young "healthy looking" trees. However, the borderline between secondary and primary attack is not always
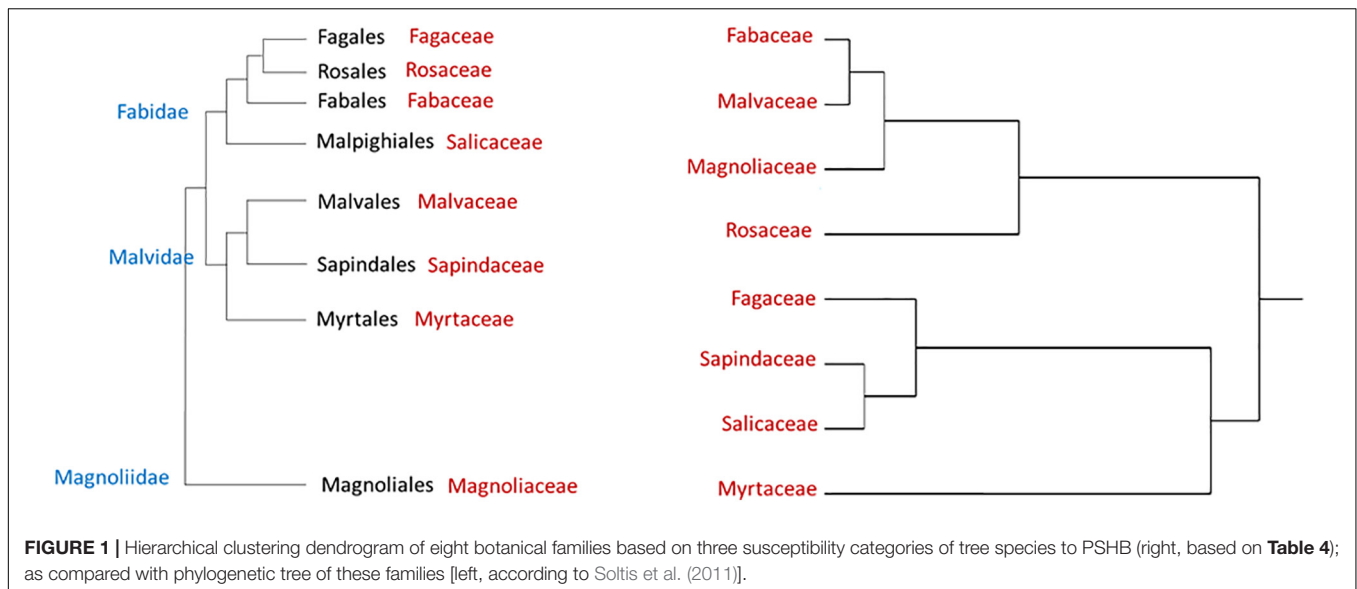
clear; *Euwallacea destruens* native in Java attacks fast-growing teak trees in plantations and therefore is considered a primary pest of this native tree species (Kalshoven, 1981).

Two significant factors may define the process that determines host range of the PSHB (and other Xyleborini), host location

TABLE 5 | Comparison of occurrences of tree species suitable for reproduction and all attacked tree species of the eight examined botanical families.

Family	Number of examined tree species	% tree species suitable for reproduction	% all affected tree species; suitable for reproduction + attacked alone
Fabaceae	92	16.5 bc*	93.4 a
Fagaceae	41	30.9 ab	78.6 bc
Magnoliaceae	31	6.4 c	93.5 a
Malvaceae	26	12.0 bc	92.0 ab
Myrtaceae	39	2.6 f	25.6 d
Rosaceae	25	0 c	64.0 c
Salicaceae	21	42.7 a	81.0 abc
Sapindaceae	25	48.0 a	88.0 abc

*Means sharing the same letter do not significantly differ (probability of $\chi 2$, n = 1). Normal approximations used for ratio confidence limits effects: Tests and confidence intervals on odds ratios are Wald based.

FIGURE 1 | Hierarchical clustering dendrogram of eight botanical families based on three susceptibility categories of tree species to PSHB (right, based on **Table 4**); as compared with phylogenetic tree of these families [left, according to Soltis et al. (2011)].

and acceptance, and host suitability for reproduction. All three above mentioned *Euwallacea* spp. of the *fornicatus* complex are not attracted to ethanol as opposed to many other members of the Xyleborini tribe (Ranger et al., 2018; Rabaglia et al., 2019; Chen et al., 2021, Mendel and Freeman unpublished data). However, it may be important to note that *F. euwallaceae* was neither facilitated nor compromised by ethanol up to 2% relative to the control (Lehenberger et al., 2021). These authors indicated that *F. euwallaceae* can tolerate ethanol, which is already known for the genus *Fusarium*. Considering the wide host range of the PSHB, initial host detection and selection may be modulated by different types of blends of volatiles typical to each of the hundreds of tree species that are attacked by the beetle. Similarly, Owens et al. (2018) suggested that TSHB might respond to different chemical cues to locate tree species suitable for breeding. Effective baits for the PSHB, TSHB, and KSHB are two natural compounds initially unrelated to these beetles, alpha-copaene and quercivorol (Dodge et al., 2017; Kendra et al., 2017; Mendel et al., 2017). The alpha-copaene is a sesquiterpenoid that was isolated in 1914 from the neotropical tree *Copaifera langsdorffii*, (Kapadia et al., 1963); whereas quercivorol was identified as an aggregation pheromone component of the oak ambrosia beetle *Platypus quercivorus* (Kashiwagi et al., 2006). This apparent random accordance is still unexplained and the attraction to such different compounds suggests that predicting the attraction of PSHB to a certain tree species is still an unresolved challenge. Attraction of the PSHB to suitable host trees is intensified by previous conspecific colonization (Mendel et al., 2017). Hulcr et al. (2011) proved that *X. glabratus*, *X. ferrugineus*, and *Xylosandrus crassiusculus* were attracted to volatiles produced by their own symbiotic fungi, in the case of the former species also a cross attraction was demonstrated. These authors also suggested synergy of fungal produced volatiles with those of their host trees.

Attacks by the PSHB were observed on approximately 70% of the examined tree species in the present study. Since species of the "non-attacked host" category occurred in the vicinity of attacked

tree species we may assume that the beetle was not attracted or even repelled by the tree volatiles or the tree was not "accepted" as a suitable host due to a deterrent effect during the initial boring into the cortex. It appears that under high infestation of the PSHB populations, the variety of attacked tree species is high, including many host species that apparently are not suitable for reproduction (Eskalen et al., 2013; Mendel et al., 2017; Coleman et al., 2019). Among the 407 attacked tree species observed in the present study, approximately 20% were apparently suitable for beetle reproduction.

Although the mechanism of initial attraction of the PSHB to a certain tree species is still unknown, there is little doubt that the PSHB is initially attracted to trees but probably not to ethanol, as opposed to many other ambrosia beetles. Ethanol is a key kairomone in attraction of Platypodinae (Graham, 1968; Moeck, 1970; Elliott et al., 2007) and ambrosia beetles among the Scolytinae (Ranger et al., 2015; Rabaglia et al., 2019). Ranger et al. (2018) demonstrated that ambrosia beetles rely on ethanol for host tree colonization since it promotes the growth of their fungal gardens while inhibiting the growth of "weedy" fungal competitors. Aggressive ambrosia beetles that colonize live trees barely respond to ethanol (Rabaglia et al., 2019).

Figure 3 displays a theoretical model suggesting the different possibility of potential tree species becoming attractive or non-attractive to PSHB attack (but may not necessarily end in successful reproduction). In PSHB native habitats, indigenous tree species are expected to become attractive to the beetle following stress conditions. However, some stressed tree species may lack the volatile combinations that induce attraction, or even produce compounds that may repel the beetle. Exotic tree species in both PSHB native and invasive areas, as well as native tree species in the invasive areas, display the same pattern of relationship as indigenous tree species in PSHB native locations. However, other exotic tree species in both PSHB native and invasive habitats as well as indigenous tree species in PSHB invasive areas are attractive to the beetle without any significant

TABLE 6 | Comparison between of % tree species of each category eight botanical genera.

	Acer	Brachychiton	Camellia	Erythrina	Eucalyptus	Magnolia	Quercus	Genera
Tree categories								
A non-reproductive	**0.0204***	0.32	0.67	0.42	**0.0294[a]**	0.29	0.13	*Acacia*
N non-host	0.96	0.99	0.55	0.99	**0.0041**	1	0.23	
R reproductive	**0.0207**	0.52	0.30	0.68	–**	0.20	0.51	
A non-reproductive		**0.0100**	**0.0085**	**0.0051**	0.69	**0.0005**	0.17	*Acer*
N non-host		0.99	0.59	0.99	**0.0052**	0.95	0.26	
R reproductive		**0.0195**	**0.0061**	**0.0119**	–	**0.0005**	**0.0249[a]**	
A non-reproductive			0.51	0.75	**0.0146**	0.78	**0.0463[a]**	*Brachychiton*
N non-host			0.99	1	0.99	0.99	0.99	
R reproductive			0.77	0.75	–	0.73	0.24	
A non-reproductive				0.68	**0.0119**	0.56	0.06	*Camellia*
N non-host				0.99	**0.0053**	0.46	0.529	
R reproductive				0.51	–	1	0.119	
A non-reproductive					**0.0071**	0.93	**0.0308[a]**	*Erythrina*
N non-host					0.99	0.99	0.999	
R reproductive					–	0.42	0.29	
A non-reproductive						**0.0005**	0.28	*Eucalyptus*
N non-host						**0.0002**	**0.0016**	
R reproductive							0.99	
A non-reproductive							**0.0029**	*Magnolia*
N non-host							0.11	
R reproductive							**0.0326[a]**	

Effect Likelihood Ratio Tests (probability of χ^2, n = 1).
*Genera sharing value in bold differ significantly in proportion of tree species of the same tree category.
**No tree species of reproductive category.
[a] insignificant after being subjected to Bonferroni correction.

stress. Based on our observation in Israel and in California it appears that stressed trees among the latter group lose their attraction to the PSHB.

There is no doubt that the PSHB attacks may cause tree mortality on certain host trees (Hulcr and Dunn, 2011; Mendel et al., 2017; Paap et al., 2018; Coleman et al., 2019). However, the concept of attacks on "healthy" trees is often debated in the literature, as trees that appear healthy may have been previously exposed to some stress (Grousset et al., 2020). Keler (1956) defined primary insects as "those which prefer completely healthy plants in full vigor"; based on this definition, Rudinsky (1962) suggested that most species of bark and ambrosia beetles must be considered secondary insects. In the case of ambrosia beetles of the Platypodinae, Kuhnholz et al. (2001) distinguished between primary and secondary ambrosia beetles and discussed the factors that may be responsible for an increasing prevalence of attack by secondary ambrosia beetles on living trees. The PSHB and its complex members cannot fall into primary or secondary categories since these species attack both weakened and healthy tree species. Coleman et al. (2019) suggested that

tree mortality rates caused by the PSHB among hardwood species were low even though infestation levels by both beetles were exceptionally high. This may be related to colonization of weakened specimens of certain tree species whereas healthy trees can tolerate the attack.

A typical ecological question asked is why tree species related to one genetic group are more susceptible to attack and suitable for reproduction of the PSHB than those related to another genetic group? And, how to explain the distinct susceptibly among member of each taxonomic level, family and genus as demonstrated by the present findings, as well as the extreme differences between genotypes of the same species which was well demonstrated for avocado (*Persea americana*) cultivars (Jones and Paine, 2017; Mendel et al., 2017; Freeman et al., 2019). The question is how to relate the confounding effects of different genetic groups of trees. The clustered taxa of the selected families and genera we compared indicated that differences are apparently independent of their phylogenies. This discordance between host tree phylogeny and susceptibility to the PSHB, as shown in **Figures 1**, **2**, indicates that the trait

Genera	Number of examined tree species	% tree species suitable for reproduction	% affected tree species (suitable for reproduction + non-reproductive)
Acacia	15	20.0 bc*	93.3 ab
Acer	14	64.3 a	92.9 ab
Brachychiton	10	10.0 bcd	100 a
Camellia	15	6.7 bcd	86.7 ab
Erythrina	14	14.3 bcd	100 a
Eucalyptus	20	0.0 d	35 c
Magnolia	30	6.7 cd	93.3 ab
Quercus	38	28.9 b	78.9 b

Means sharing the same letter do not significantly differ (probability of χ2, n = 1). Normal approximations used for ratio confidence limits effects: Tests and confidence intervals on odds ratios are Wald based.

correlation of susceptibility of different tree species to the PSHB are the results of convergent evolution and not of a common descent. However, Lynch et al. (2020) recently demonstrated a strong phylogenetic signal in the relative effects of PSHB and KSHB and their associated fungal symbionts on tree host species in California and South Africa, demonstrating that the severity of multi-host pest impacts in plants can be predicted by host evolutionary relationships. Patterns in the signal indicate that there are several ways to be susceptible, but susceptibility clusters within phylogenetic groups and this clumping becomes more restricted with more impactful interactions. These authors show that the "reproductive" host range was phylogenetically restricted than "non-reproductive" hosts by 62 Myr, and those with devastating impacts were the most constrained, narrower by 107 Myr.

Among 407 attacked tree species by the PSHB only approximately 20% were found suitable for reproduction. Upon

attack, the beetle enters the cortex to reach the sapwood. Bark is the first line of defense against wood decay organisms such as fungi and bacteria (Franceschi et al., 2005; Alexander, 2010) and by wounding the bark the beetle allows the invasion of its fungal symbionts. Mechanical wounding is necessary but not sufficient to trigger the full response activated by insects and the damage inflicted by invading microorganisms may trigger the full response by the plant (Maffei et al., 2007). The external response to beetle penetration is typical to tree taxa and the specific wounding response. For example, the attacks on persimmon trees result in secretion of a black viscous gum; species of *Platanus* and *Quercus* respond by oozing out watery transparent gum; while the typical response of avocado is exudation of a white sugar (persitol), which is somehow different from a similar exudation in response to physical wounding (Eskalen et al., 2012, 2013; Mendel et al., 2017). Boland and Woodward (2021) demonstrated that bark thickness influences KSHB attack densities and attack locations and therefore affects KSHB impacts. It is suggested that both mechanical wounding by the beetle and invasion by its fungal symbiont *F. euwallaceae* trigger induced defense responses of the tree.

The above-described symptoms induced by the PSHB attack are conspicuous in cases of both "non-reproductive host" and "reproductive host" categories. It may be important to note that there are marked differences in the performance of the beetles among different host species suitable for reproduction (Mendel et al., 2017; Freeman et al., 2019). For example, while *Acer negundo* is defined as a highly suitable host for reproduction of the PSHB (Eskalen et al., 2013; Mendel et al., 2017; Paap et al., 2018; Coleman et al., 2019), native *Acer obtusifolium* in Israel usually displays reproduction hindrance and offspring development was rarely observed (Mendel and Freeman unpublished data). In the case of avocado, several cultivars seldomly allowed reproduction of the beetle, even in the case of Hass cultivar, usually only secondary and tertiary
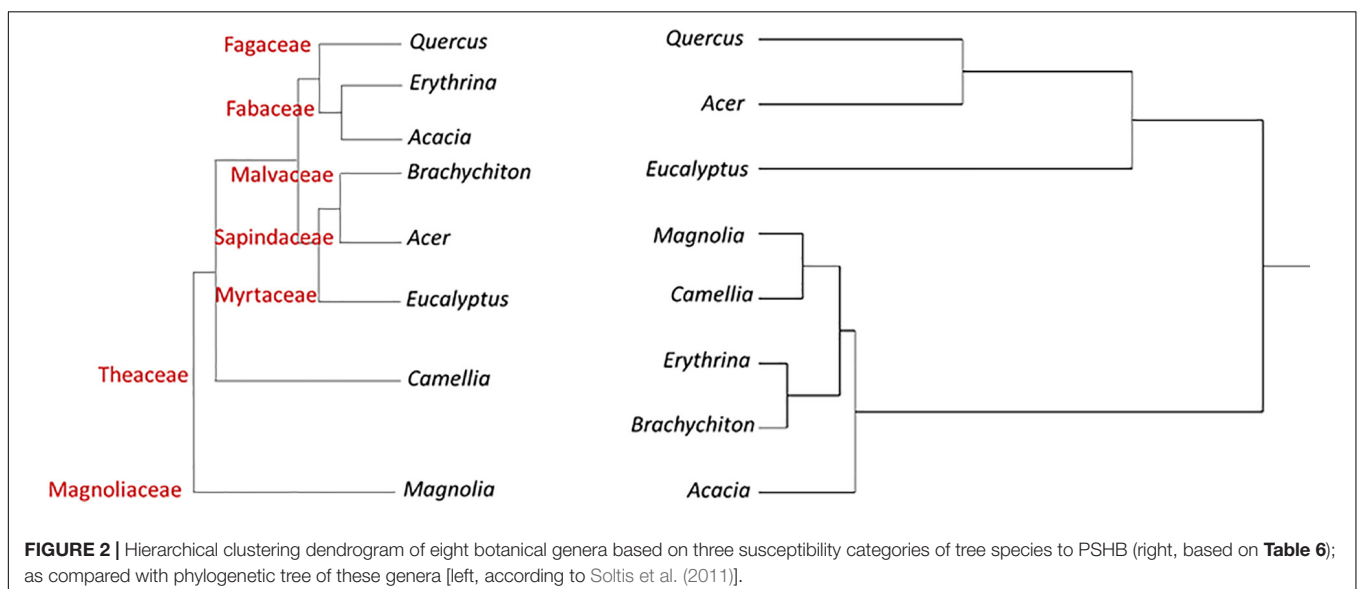
FIGURE 2 | Hierarchical clustering dendrogram of eight botanical genera based on three susceptibility categories of tree species to PSHB (right, based on **Table 6**); as compared with phylogenetic tree of these genera [left, according to Soltis et al. (2011)].
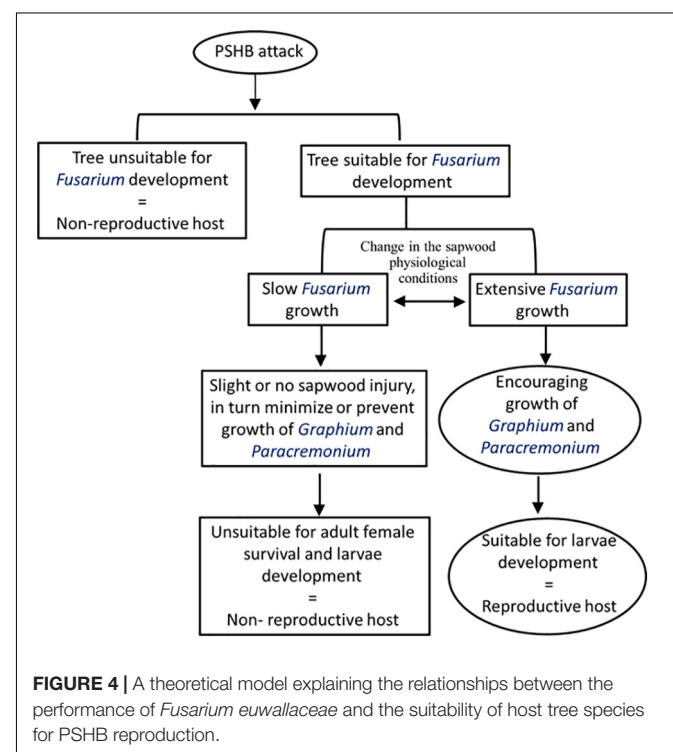
FIGURE 3 | A theoretical model suggesting the probability of a tree species becoming attractive or non-attractive to PSHB attack.
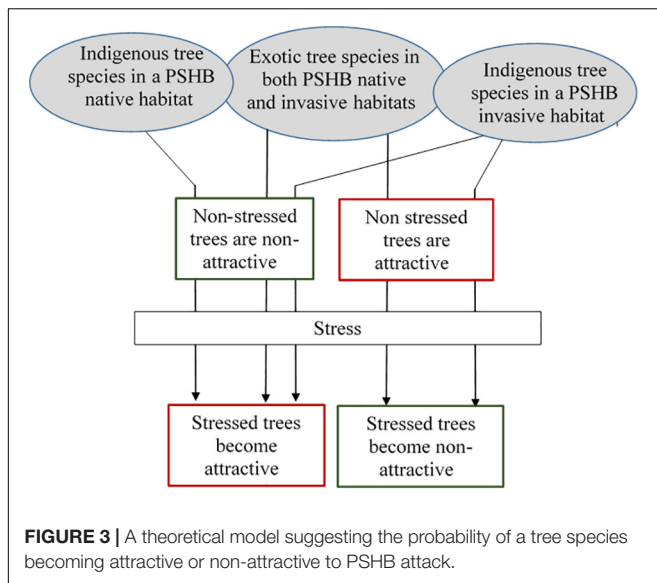
branches permitted reproduction which often occurred on "re-attacked" branches, viz., after previously unsuccessful attacks (Mendel et al., 2017). Unlike the resin flow which serves in pitching out adult bark beetles attacking pine trees almost immediately or in a matter of hours as a reaction to the beetle injury (Berryman, 1972; Smith, 1972), conspicuous sugary exudation in response to the PSHB penetration into avocado woody branches was observed 3–10 days thereafter (Mendel and Freeman unpublished data). Therefore, the exudation obstruction is probably not the mechanism preventing successful colonization of the beetle in hosts belonging to the "attack-tree" category.

In the present study, species across the "non-reproductive host" category were recognized by the typical injury response and in most cases also by isolation of *F. euwallaceae*, introduced by the beetle. The fundamental question concerns the obstacles responsible for reproductive impediment in many of these cases. However, similar obstacles may play a role in the quality of reproductive performance in the case of species belonging to the "reproductive host" category.

It is suggested that the beetle reproduction success rate over a wide host range, as well as the long list of species belonging to the "non-reproductive host" category, is the outcome of interaction between *Fusarium euwallaceae* and sapwood of the attacked tree. *F. euwallaceae* was defined as a pseudopathogen since typical wilting of the damaged tree occurs only in association with the degree of beetle infestation within the wood (Freeman et al., 2019). Fungal pathogens may be classified as biotrophs, necrotrophs or hemi-biotrophs, fungi of the latter types display both biotrophic and necrotrophic features (Lee and Rose, 2010). Pathogens may switch their strategy of infection from biotrophy to necrotrophy (Chowdhury et al., 2017). *Fusarium euwallaceae* is a wound pathogen that develops on gallery walls excavated by the beetle. It may also be characterized as a weak hemi-biotrophic pathogen as it develops at the onset of colonization on live sapwood tissue, but may remain as an endophyte in

the case of unsuccessful attack or artificial inoculation into healthy sapwood. In addition, it does not progress more than a few mm beyond the inoculated tunnel wall at infection points and is maintained in the dying tissue (Freeman et al., 2019). Weakening of xylem tissue in close proximity of the galleries permits development of the two other fungal symbionts of the PSHB that may survive in the killed dead sapwood for 1 year or even longer (Mendel et al., 2017). It appears that *G. euwallacea* that serves as a food source at the immature beetle stages may thrive in the galleries only after successful development of *F. euwallacea* (Freeman et al., 2019; Carrillo et al., 2020). *Fusarium euwallacea,* similar to many xylem fungi, displays a wide host range in contrast to other fungal pathogens of the same group, such as *F. mangiferae* that colonizes bud tissues of the tree (Freeman et al., 2012). The defense mechanism that constrains pathogen development in the sapwood of many tree species includes constitutive and induced inhibitory compounds, but also cell wall alterations, and occlusion of xylem elements, as well as constitutive and induced micro-environmental conditions in this woody tissue (Beckman, 1987; Gordon and Reynolds, 2017). The trees sense the injured tissue and induce defense responses activated by pathogen infection (Yamada, 2001; Savatin et al., 2014).

A theoretical model proposing the process leading to a dichotomist situation categorizing a host species of the PSHB as "non-reproductive host" or "reproductive host" is demonstrated in **Figure 4**. The model suggests that a tree selected by the PSHB may belong to one of three groups, (1) those in which *F. euwallacea* is unable to develop, (2) those tree species that slow the development of the fungus, and (3) those which

FIGURE 4 | A theoretical model explaining the relationships between the performance of *Fusarium euwallaceae* and the suitability of host tree species for PSHB reproduction.

enable *F. euwallacea* to thrive. Hence, the host range suitable for the beetle reproduction is determined by development of *F. euwallacea*. The ambrosia *Fusarium* clade currently comprises 19 phylogenetically distinct species, most of which are known to be farmed by *Euwallacea* congeneric females (Aoki et al., 2019). Carrillo et al. (2019) reported that the sampled PSHB in Taiwan carried *Fusarium kuroshium*, which is associated with the KSHB in California, whereas the TSHB was found to be associated with six different *Fusarium* spp. in different native and invasive habitats (O'Donnell et al., 2015; Aoki et al., 2019; Lynn et al., 2020). A genetic variation e demonstrated for the fungal symbiont of *X. glabratus* was found in native populations of the beetle in Taiwan, Japan and the United States (Wuest et al., 2017). It has been suggested that members of the *Euwallacea fornicatus* species complex (Carrillo et al., 2019) and also *Xyleborus* spp. (Kostovcik et al., 2015) are more promiscuous in native areas, while in invaded areas this association is apparently limited and species specific. Carrillo et al. (2020) showed that brood of the PSHB and KSHB developed well on their reciprocal fungal symbionts (including *Graphium* spp.), although Freeman et al. (2012) demonstrated that the PSHB brood could not develop on *Fusarium ambrosium*. However, both the PSHB and KSHB are more genetically related than the TSHB (Stouthamer et al., 2017) and similar relationships were revealed between *F. euwallaceae* and *F. kuroshium*. Both the latter fungi are more closely genetically related than the six *Fusarium* spp. symbionts of the TSHB including *F. ambrosium*, based on molecular sequence similarity (Aoki et al., 2019). Therefore, it is plausible to assume that different natural populations of each species among the *Euwallacea fornicatus* species complex may display a varied host species range of the "reproductive host" category that may be dependent on recognition of the *Fusarium* symbiotic species. Our findings suggest that in general the PSHB does not distinguish between host species of the "non-reproductive host" and "reproductive host" categories. However, it appears that host species belonging to one category may be reassigned to another if the PSHB carries a different *Fusarium* symbiont or if site conditions differ in the attacked locations.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/**Supplementary Material**.

AUTHOR CONTRIBUTIONS

ZM: conceptualization, methodology, investigation, writing of manuscript, and raising of partial funding. AE and SL: investigation and editing of the manuscript. AP and MM: assistance with technical field and lab experiments. SF: investigation, writing of manuscript, and raising of partial funding. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2021.654702/full#supplementary-material

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