Osborn et al.: Global xyleborine ambrosia symbioses

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Symbiotic fungi associated with xyleborine ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) and the imperative of global collaboration

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Abstract

Ambrosia beetles from the tribe Xyleborini are part of nearly all forest ecosystems. Because of their small size, haplodiploid mating structure, and protected lives inside the sapwood of woody plants, they have a unique ability to expand into new regions via inadvertent human transport. A small number of invasive xyleborines cause significant damage to forests, lumber concerns, and agricultural systems. Most ambrosia pests damage or kill trees by the accumulation of beetle attacks, one is known to cause tree death through the introduction of pathogenic fungus into susceptible Lauraceae trees. The relationships between ambrosia fungi and their beetle vectors range from mutualistic symbiosis to facultative association, but most remain unstudied. Unresolved taxonomies, convergent morphologies and the difficulty of sampling ambrosia fungi over their entire global ranges make comprehensive surveys of ambrosia fungi difficult to achieve. Ambrosia fungi from Europe and North America are moderately well documented, however we have yet to sufficiently document those from Africa, Asia, Australia, and South America. Worldwide cooperation to improve and standardize scientific study of the ambrosia symbioses are needed to better understand these impactful organisms.

Keywords: invasive species, pests, symbiosis, Xyleborini

Introduction: Ambrosia symbioses in historical and ecological context

Forests experience a constant cycle of death, decomposition, and renewal which provides a steady supply of dead trees as a ubiquitous source of carbon and nutrients (Klemm et al. 2005, Ulyshen 2016). Cellulose, hemicellulose, and lignin that form plant cell walls are a potentially abundant source of carbon but are indigestible to most animals (Coughlan 1985) and may inhibit access to limiting nutrients like nitrogen and phosphorus and other minerals (French and Roeper

1973). Conversion of these plant polysaccharides into shorter sugars is achieved by the enzymatic apparatus of a few insects (Martin 1983, 1991, Calderón-Córtez 2012, Tanimora et al. 2013, Sade et al. 2018) but is mostly dominated by bacteria, fungi, and some protists (Flint et al. 2008, Ulyshen 2016).

Several groups of insects have independently evolved different strategies to gain access to the nutrients within plant cell walls. Most termites employ a highly structured community of bacteria, archaea, and co-evolved protozoa that allow them to degrade plant cell walls more efficiently than any other herbivorous animal (Brune and Okhuma 2011). Other insects use plant-degrading fungi to convert plant material into nutritional molecules. The relationships between wood-degrading fungi and these insects range from obligate mutualism with attine ants and macrotermitine termites, to facultative associations with the bee species *Scaptotrigona depilis* (Moure), and many beetles including silphine staphylinids, lymexylids, attalabids from the genus *Euops* Schoenherr, and *Doubledaya* White erotilid beetles (Kobayashi et al. 2008, Paludo et al. 2019, Biedermann and Vega 2020, Toki and Aoki 2021).

Bark and ambrosia beetles from the curculionid subfamily Scolytinae contain species that span this continuum of relationships. Many phloem-feeding bark beetles transmit fungal spores and maintain an opportunistic association with these fungi as they cohabitate inside the same host plants (Six 2003, Harrington 2005). Scolytine species that maintain a mutualistic symbiosis with fungi are called ambrosia beetles (Figure 1). Despite the common narrative in the scientific literature, most ambrosia fungi are poor wood degraders (Licht and Biedermann 2012, Huang et al. 2019), and may cooperate with bacteria and yeasts to maintain their symbiosis with the beetles (Ibarra-Juarez et al. 2020). Ambrosia fungi, which derive carbon from a variety of simple wood compounds, efficiently colonize freshly dead wood before the presence of wood degraders such as white and brown rot species (Huang et al. 2019, Skelton et al. 2020). Ambrosia fungi benefit from this association because they are given access to suitable growing substrates with appropriate nutrient and moisture levels (Rassati et al. 2016, Nuotclá et al. 2021). Independent phylogenetic analyses have found that the ambrosia nutritional strategy has evolved at least 14 times in Scolytinae and once in the weevil subfamily Platypodinae (Jordal and Cognato 2012, Gohli et al. 2017, Johnson et al. 2018, Pistone et al. 2018, Cognato et al. 2021). Although not all ambrosia beetle lineages are diverse, fungus farming may have contributed to species richness in several groups (Jordal and Cognato 2012, Gohli et al. 2017).

Figure 1. Xyleborine ambrosia beetle *Euwallacea fornicatus* in gallery. Photo by You Li.

Ecology of Xyleborini. The Xyleborini contains ~1260 species (S. M. Smith, unpublished), all of which are ambrosia beetles. They are found in forested habitats worldwide and have experienced rapid speciation events on more than one continent (Jordal et al. 2000, Jordal and Cognato 2012, Cognato et al. 2018, Eliassen and Jordal 2021). Facilitated by a suite of biological characters that make them uniquely equipped for transport and proliferation in novel environments, xyleborines invade novel habitats at a higher rate than other scolytines (Rabaglia et al. 2019, Lantschner et al. 2020). Female xyleborines lay unfertilized eggs that mature into flightless haploid males which mate with their sisters inside their natal gallery. Extreme inbreeding is the largest contributing factor to their invasive success (Jordal et al. 2001, Gohli et al. 2017, Lantschner et al. 2020). During long-distance dispersal via ocean currents (Cognato 2013, Jordal 2015, Cognato et al. 2018) or trade (Seebens et al. 2017, Grousset et al. 2020, Osborn et al. 2022b), xyleborines are well protected from hostile conditions by their location inside the sapwood. When the females leave the fungal garden, they carry the fungal symbionts with them inside mycangia (Francke-Grosmann 1956, Schedl 1962). Ambrosia fungi associated with the most successful invaders can grow on many species of trees given favorable environmental and moisture conditions, so dispersing females often find suitable hosts in new environments if the climate is relatively similar to that in their native range (Rassati et al. 2016). At least 45 xyleborine species have established populations beyond their native ranges due to human accidental introduction (Table 1) (Rabaglia et al. 2006, Kirkendall and Faccoli 2010, Haack and Rabaglia 2013, Gomez et al. 2018b, Lin et al. 2021).

Table 1. Introduced Xyleborini, their native region, and region(s) of introduction inferred from Wood and Bright 1992, Pennacchio et al. 2003, Rabaglia et al. 2006, Kirkendall and Ødegaard 2007, Wood 2007, Cognato and Rubinoff 2008, Kirkendall and Faccoli 2010, Knížek 2011, Haack and Rabaglia 2013, Faccoli et al. 2016, Gomez et al. 2018a, 2018b, Schiefer 2018, Mandelshtam et al. 2019, Smith et al. 2019, Barnouin et al. 2020, Rabaglia et al. 2020, Rugman-Jones et al. 2020, Smith et al. 2020, Eliasson and Jordal 2021, Lin et al. 2021, Urvois et al. 2021, Smith and Cognato 2021, Colombari et al. 2022, Marchioro et al. 2022, Polyphagous 2022, Smith and Cognato 2022, Smith et al. 2022, and Thurston et al. 2022. * Denotes dubious records of *Coptoborus* introduced to Africa (see Smith and Cognato 2021). ** Denotes dubious record of *Tricosa abberrans* introduced to Brazil (see Smith et al. 2022).

Genus	**species**	**Common Name, Notes**	**Origin Region(s)**	**Introduced Region(s)**
Amasa	nr. *truncata*		Asia	Europe (France, Portugal Spain), South America (Brazil, Chile, Uruguay)
Ambrosiodmus	*lewisi*		Asia	North America (USA)
Ambrosiodmus	*minor*	punky wood ambrosia beetle	Asia	North America (USA)
Ambrosiodmus	*rubricollis*		Asia/East Asia	Europe (Italy), North America (Mexico, USA)
Ambrosiophilus	*atratus*		Asia/East Asia	Europe (Italy), North America (USA)
Ambrosiophilus	*osumiensis*		Asia	North America (USA)
Anisandrus	*dispar*		Europe	North America (USA)
Anisandrus	*maiche*		Asia	North America (USA)
Cnestus	*mutilatus*	camphor shot borer	Asia	Europe (Italy), North America (USA)
Coptoborus	*coartatus*		Central and South America	Africa*
Coptoborus	*crinitulus*		South America	Africa*
Genus	**species**	**Common Name, Notes**	**Origin Region(s)**	**Introduced Region(s)**
Coptoborus	*ricini*		Central America, North America (Florida, USA), and West Indies	Africa*
Cyclorhipidion	*bodoanum*		North Asia	Europe, North America (USA)

Cyclorhipidion	*californicum*		Asia	North America (USA)
Cyclorhipidion	*distinguendum*	(= *fukiense*)	Asia	Europe (France), North America (USA)
Cyclorhipidion	*nemesis*		Asia	North America (USA)
Cyclorhipidion	*pelliculosum*		Asia	North America (Canada, USA)
Cyclorhipidion	*tenuigraphum*		Asia	North America (USA)
Diuncus	*haberkorni*		Asia	Africa
Dryocoetoides	*cristatus*		South America, West Indies	Africa
Dryoxylon	*onoharaense*		Asia	Europe (Italy), North America (USA)
Eccoptopterus	*spinosus*		Asia	Africa
Euwallacea	*fornicatus*		Asia	Australia, Central America, Hawaii, North America (USA), South America (Brazil)
Euwallacea	*interjectus*		Asia	North America (USA)
Euwallacea	*kuroshio*		Asia	North America (USA)
Euwallacea	*perbrevis*		Asia	Central America, Hawaii, North America (USA)
Euwallacea	*similis*		Africa, Asia	North America (USA), South America (Brazil)
Euwallacea	*validus*		Asia	North America
Heteroborips	*seriatus*	(= *Xyleborus seriatus*)	Asia	North America (USA)

Genus	**species**	**Common Name, Notes**	**Origin Region(s)**	**Introduced Region(s)**
Tricosa	*abberrans*	(= *Xyleborus abberrans*)	Asia	South America (Brazil)**
Xyleborinus	*andrewesi*		Asia	Hawaii, North America (USA)
Xyleborinus	*artestriatus*		Asia	North America (USA)
Xyleborinus	*attenuatus*		Asia	Europe, North America
Xyleborinus	*exiguus*		Asia	Africa, Central America
Xyleborinus	*gracilis*		Asia	Africa
Xyleborinus	*octiesdentatus*		Asia	North America (USA)
Xyleborinus	*saxesenii*		Asia, Europe	Africa, Australia, Hawaii, New Zealand, North America (Canada, USA), South America
Xyleborus	*affinis*		South America	Africa, Asia, Australia, Europe, Hawaii, North America (USA)
Xyleborus	*bispinatus*		Central and South America	Europe

Xyleborus	*ferrugineus*		North and South America	Africa, Asia, Australia, Europe, Hawaii
Xyleborus	*glabratus*	redbay ambrosia beetle	Asia	North America (USA)
Xyleborus	*monographus*		Africa, Asia, Europe	North America (USA)
Xyleborus	*pfeilii*		East Asia	Europe, New Zealand, North America
Xyleborus	*spinulosus*		Central and South America	North America (USA), Hawaii
Xyleborus	*xylographus*		North America	Africa (Canary Islands), Asia (Turkey)
Xylosandrus	*compactus*	black twig borer	Asia	Africa, Central America, Europe, Hawaii, New Zealand, North America (USA), South America
Genus	**species**	**Common Name, Notes**	**Origin Region(s)**	**Introduced Region(s)**
Xylosandrus	*crassiusculus*	granulate ambrosia beetle	Asia	Africa, Australia, Central America, Europe, Hawaii, North America, South America
Xylosandrus	*germanus*		Asia/East Asia	Europe, North America
Xylosandrus	*morigerus*		Asia	Africa, Central America, Europe, Hawaii, Middle East (Jordon, Lebanon), North America, Pacific Islands, South America

History of research regarding ambrosia fungi. Ambrosia beetles have long been understood to cause ecological and financial harm to forests and the lumber industry in Europe and North America (Schmidberger 1836, Hubbard 1897). Early researchers noted that ambrosia beetles differed from their bark beetle counterparts because ambrosia beetles eat a white powered substance that was never observed to be associated with bark beetles (Schmidberger 1836; Ratzeburg 1839). Schmidberger (1836) established the term “ambrosia” to describe the beetles’ diet because of its fruity odor and the fact that he suspected it was made by females out of tree sap and saliva to feed her offspring (Beling 1873). When Hartig (1844) documented the fungal nature of ambrosia he classified the fungus associated with *Anisandrus dispar* (Fabricius) as

Monilia candida (Persoon). More than five decades later, Hubbard (1897) recognized that ambrosia fungi provide nutrition to the beetles and are actively cultivated in a symbiotic relationship (Francke-Grosmann 1967).

Before the middle of the twentieth century, investigations into the ambrosia symbioses were generally flawed with misidentifications of ambrosia fungi (e.g., Neger 1911, Muller 1933, Verrall 1943). As ambrosia research continued and the precision of culturing and microscopy improved, ambrosia fungi were reclassified into eight genera, of which three were known to associate with xyleborines: *Ascoidea* Brefeld, *Ambrosiella* Brader ex von Arx and Hennebert, and *Monacrosporium* Oudem (Batra 1967).

Modern ambrosia research has continued to reveal the varied range of relationships shared between xyleborine ambrosia beetles and fungi (Kostovcik et al, 2015, Skelton et al. 2018). This includes the identification of many previously unknown fungal symbionts (von Arx and Hennebert 1965, Harrington et al. 2008, Freeman et al. 2013, Harrington et al. 2014, Li et al. 2016, Lynch et al. 2016, Simmons et al. 2016a, 2016b, Aoki et al. 2018, 2019, Lynn et al. 2020, Mayers et al. 2020a, 2020b, Aoki et al. 2021, Araújo et al. 2022) and recognition that the same species of ambrosia fungus might grow in the galleries of non-xyleborine beetles as well as those of xyleborines (Gebhardt et al. 2004). Since the discovery and identification of the mycangium (Francke-Grosmann 1956, Schedl 1962, Batra 1963), research has revealed the central role this organ plays in the development and maintenance of ambrosia symbioses (Mayers et al. 2022). The evolution of mycangia is associated with the ambrosia lifestyle throughout Scolytinae (Mayers et al. 2015) and mycangial morphology of several ambrosia beetle lineages is correlated with symbiosis with specific ambrosia fungal lineages (Johnson et al. 2018, Mayers et al. 2020b). The mycangia of *Xylosandrus* beetles selectively interact with fungi to ensure vertical transmission of the most desirable mycological partners (Skelton et al. 2019). Stability of fungal cultivar extends beetles' ability to survive variable conditions such as changing moisture levels (Hulcr and Dunn 2011, Nuotclá et al. 2021).

Fungi associated with Xyleborini

Xyleborines have established mutual symbioses with a taxonomically diverse group of fungi within three ascomycete orders and one from Basidiomycota (Table 2; Figure 2) (Bateman 2018). Given the beetles' unique capacity for range expansion, these fungi have access to similarly large geographical ranges. Evidence indicates that the first fungus farming xyleborines appeared ~21 million years ago followed by a rapid evolutionary radiation fueled by global warming during the early Miocene (Jordal and Cognato 2012). This timing is incongruent with the origins of the xyleborine fungal lineages. Phylogenetic analysis of *Raffaelea sensu lato* isolates shows that the three ambrosia clades currently recognized as *Raffaelea, Harringtonia,* and *Dryadomyces* (de Beer et al. 2022) emerged 86, 67, and 33 million years ago respectively, considerably predating the current estimate for the origin of Xyleborini (Vanderpool 2017). Similarly, the Ambrosia *Fusarium* clade (AFC), which includes both *Fusarium* Link and *Neocosmospora* Smith species, is ~24 million years old (O'Donnell et al. 2015). Mayers et al. (2020b) determined the first appearance of the *Ambrosiella* lineage associated with xyleborines to be ~12 Million years ago, ~9 million years after the origin of Xyleborini. The age of the ambrosia fungus *Irpex subulatus* (Ryvarden) has not been estimated but investigation of the timing of its entrance into ambrosia symbiosis could further illuminate the mechanisms of ambrosial evolution.

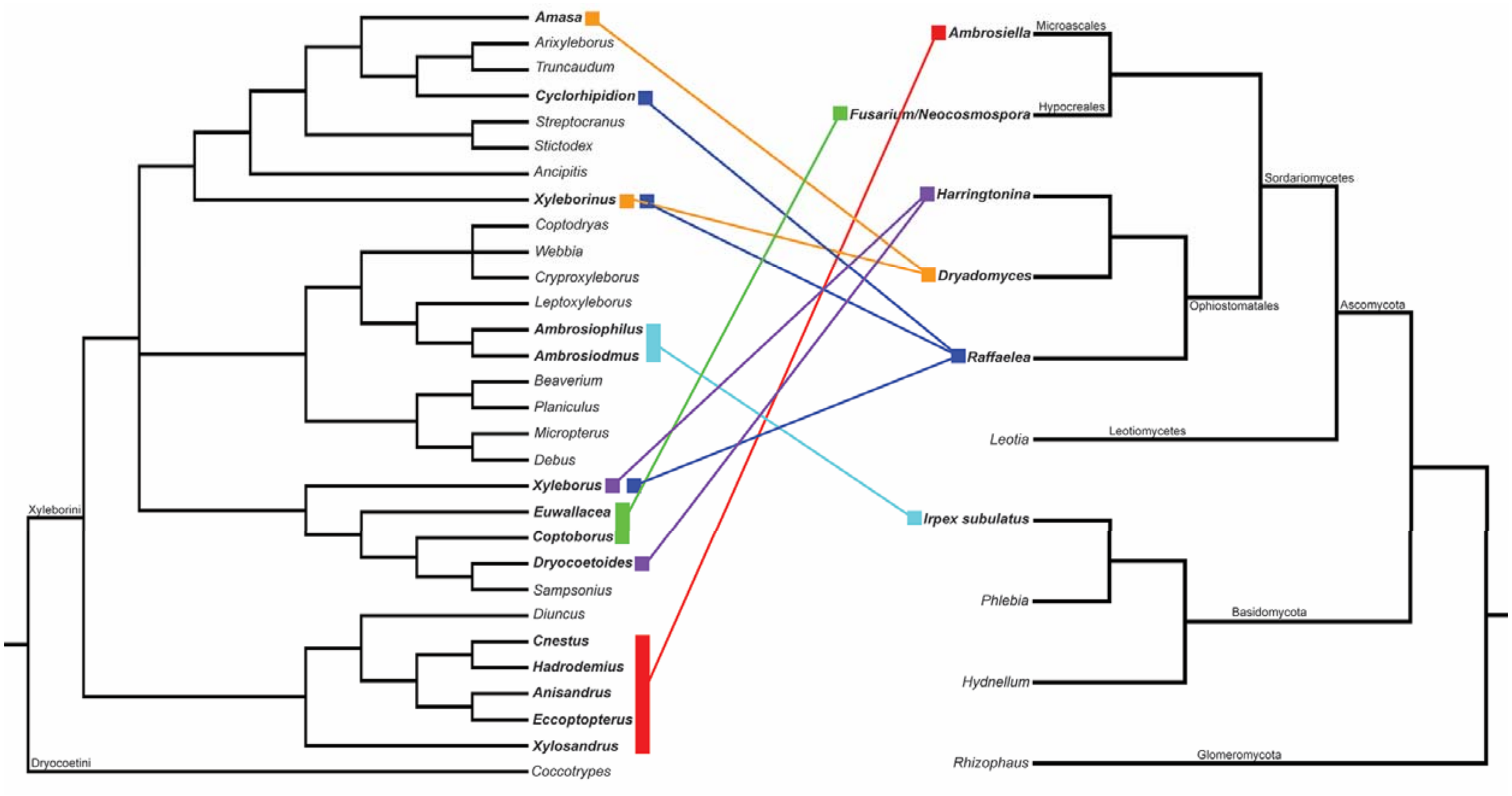

Figure 2. Schematic representation of Ambrosia associations between xyleborine and fungal genera. Cladogram of the Xyleborini summarized from Cognato et al. 2011, Cognato et al. 2018, and Johnson et al. 2018. Fungal cladogram summarized from Binder et al. 2013, Spatafora et al. 2016, and Hongsanan et al. 2017. Relationships between the beetles and fungi from von Arx and Hennebert 1965, Batra 1967, Scott and du Toit 1970, Brayford 1987, Gebhardt et al. 2005, Harrington et al. 2008, Six et al. 2009, Harrington et al. 2010, Kasson et al. 2013, Mayers et al. 2015, O'Donnell et al. 2015, Simmons et al. 2016a, 2016b, Lin et al. 2017, Mayers et al. 2017, Na et al. 2018, Carrillo et al. 2019, Lynn et al. 2020, Nel et al. 2021, de Araújo et al. 2022, Osborn et al. 2022a.

Table 2. Ambrosia fungal species with nutritional associations with xyleborine beetles and their beetle partners (von Arx and Hennebert 1965, Batra 1967, Scott and du Toit 1970, Brayford 1987, Gebhardt et al, 2005, Harrington et al. 2008, Six et al. 2009, Harrington et al. 2010, Kasson et al. 2013, Mayers et al. 2015, O'Donnell et al. 2015, Simmons et al. 2016a, 2016b, Lin et al. 2017, Mayers et al. 2017, Na et al. 2018, Carrillo et al. 2019, Lynn et al. 2020, Nel et al. 2021, Osborn et al. 2022b).

Genus	species	Beetle(s)	Notes
Ambrosiella	*batrae*	*Anisandrus sayi*	
Ambrosiella	*beaveri*	*Cnestus mutilatus*	
Ambrosiella	*catenulata*	*Eccoptopterus* spp., *Hadrodemius* spp.	
Ambrosiella	*cleistominuta*	*Anisandrus maiche*	
Ambrosiella	*grosmanniae*	*Xylosandrus germanus*	
Ambrosiella	*hartigii*	*Anisandrus dispar*	
Ambrosiella	*nakashimae*	*Xylosandrus amputatus*	
Ambrosiella	*roeperi*	*Xylosandrus crassiusculus*	
Ambrosiella	*xylebori*	*Xylosandrus compactus*	
Dryadomyces	*amasae*	*Amasa concitata*, *Amasa* aff. *glaber*	
Dryadomyces	*sulphureus*	*Xyleborinus saxexenii*	*= Raffaelea sulphurea*
Fusarium	AF-6	*Euwallacea* sp.	
Fusarium	*duplospermum* [AF-8]	*Euwallacea* sp.	
Fusarium	AF-9	*Coptoborus* spp. *Xyleborus ferrugineus*	
Fusarium	*drepaniforme* [AF-10]	*Euwallacea fornicatus*	*= Fusarium bugnicourtii*
Fusarium	*papillatum* [AF-11]	*Euwallacea* sp. from Taiwan	
Fusarium	AF-13	*Euwallacea* sp. from Taiwan	
Fusarium	AF-14	*Euwallacea* sp. from Taiwan	
Fusarium	AF-15	*Euwallacea* sp. from Taiwan	
Fusarium	AF-16	*Euwallacea* sp. from Taiwan	
Fusarium	AF-17	*Euwallacea* sp.	
Fusarium	AF-18	*Euwallacea* sp.	
Harringtonia	*ambrosioides*	*Dryocoetoides capucinus*	
Harringtonia	*lauricola*	*Xyleborus glabratus*	*= Raffaelea lauricola*

Irpex	*subulatus*	*Ambrosiodmus* spp., *Ambrosiophilus* spp.	*= Flavodon ambrosius*
Neocosmospora	*ambrosia* [AF-1]	*Euwallacea fornicatus*	*= Fusarium ambrosium*
Neocosmospora	*euwallaceae* [AF-2]	*Euwallacea* sp.	*= Fusarium euwallaceae*
Neocosmospora	*floridana* [AF-3]	*Euwallacea interjectus*	*= Fusarium floridanum*
Neocosmospora	*oligoseptata* [AF-4]	*Euwallacea validus*	*= Fusarium oligoseptatul*
Neocosmospora	*obliquiseptata* [AF-7]	*Euwallacea* sp.	*= Fusarium obliquiseptatum*
Neocosmospora	*kuroshio* [AF-12]	*Euwallacea* sp.	*= Fusarium kuroshium*
Neocosmospora	*rekana* [AF-19]	*Euwallacea perbrevis*	*= Fusarium rekanum*
Raffaelea	*arxii*	*Xyleborus affinis, Xyleborus volvulus* (= *X. torquatus*), *Xyleborinus saxesenii*	
Raffaelea	*campbelli*	*Xyleborus glabratus*	
Raffaelea	*cyclorhipidia*	*Cyclorhipidion ohnoi*	
Raffaelea	*ellipticospora*	*Xyleborus glabratus*	
Raffaelea	*fusca*	*Xyleborus affilis, Xyleborus glabratus*	
Raffaelea	*promiscua*	*Xyleborinus saxesenii, Xyleborus affinis*	
Raffaelea	*subalba*	*Xyleborus glabratus*	
Raffaelea	*subfusca*	*Xyleborus glabratus*	
Raffaelea	*xyleborina*	*Xyleborinus andrewesii*	

Current knowledge of the dissimilar patterns of emergence between the Xyleborini and their ambrosia fungi in *Raffaelea/Harringtonia/Dryadomyces, Fusarium/Neocosmospora* and *Ambrosiella* suggests that xyleborine beetles obtained their current ambrosia fungi through lateral transmission (partner switching) (O'Donnell et al. 2015, Peris et al. 2021). *Raffaelea/Harringtonia/Dryadomyces* is known to have experienced frequent partner switching (Miller et al. 2019) including at least three independent transitions into symbiosis with xyleborine beetles (Vanderpool 2017). Frequent partner switching, including a recent shift to Neotropical Xyleborini was found to be the most likely explanation for the confused phylogenetic patterns in *Fusarium* (AFC) (O'Donnell et al. 2015, Peris 2021, Osborn et al.

2022a). A constrained lineage of *Ambrosiella* was also found to have transferred from their historical platypodine beetle hosts to *Xylosandrus* Reitter within Xyleborini (Mayers et al. 2020a).

After the first appearance of the invasive xyleborine *Xyleborus glabratus* Eichhoff and the destructive fungus *Harringtonia lauricola* (Harrington, Fraedrich and Aghayeva) in the United States, surveys detected *H. lauricola* in the mycangia of several beetles that commonly inhabit the same tree hosts as *X. glabratus* including species of *Xyleborus*, *Xylosandrus*, and *Ambrosiodmus* (Carrillo et al. 2014, Ploetz et al. 2017). *Xyleborus bispinatus* Eichhoff was also shown to successfully feed and reproduce when experimentally reared in a fungal garden of *H. lauricola* (Saucedo et al. 2017). The fungus is also known to cohabitate with *Raffaelea* both inside the mycangium and upon beetle gallery walls (Harrington et al. 2010, 2011, Simmons et al. 2016b). These studies are compelling evidence that the fungal symbiont of one beetle can enter the mycangium of a different species when the galleries exist in the same tree, provided that the fungus belongs to the same clade and is compatible with the beetles' nutritional requirements (Huang et al. 2019).

Current and emerging pestiferous xyleborine beetle-fungus partnerships

Xyleborus glabratus-Harringtonia lauricola. The invasive *X. glabratus* was first detected in North America in 2002 in Chatham County, Georgia (Table 3) (Haack 2006, Rabaglia et al. 2006). Though its association with host trees throughout its large native range in Southeast Asia is not well understood (Cognato et al. 2019), it is known to attack healthy Lauraceae trees throughout the southeastern United States (Haack 2006, Harrington et al. 2011, Ploetz et al. 2017). *X. glabratus* carries several ophiostomatalean fungi originally assigned to the genus

Table 3. Harmful Xyleborini, their nutritional symbionts, associated harmful fungi, native region, year of first report in introduced regions, and significant plant hosts (Blandford 1894a, Hagedorn 1908, Hoffmann 1941, Groschke 1953, Anderson 1974, Kessler et al. 1974, Hara and Beardsley 1979, Wood 1982, Weber and McPherson 1983, Nirenburg 1990, Pennacchio et al. 2003, Haack 2006, Rabaglia et al. 2006, Kirkendall and Ødegaard 2007, Cognato and Rubinoff 2008, Olivera et al. 2008, Eskalen et al. 2012, Garonna et al. 2012, Mendel et al. 2012, Stilwell et al. 2014, Egonyu et al. 2015, Mayers et al. 2015, Li et al. 2015, Nageleisen et al. 2015, Flechtmann and Atkinson 2016, Simmons et al. 2016a, Gallego et al. 2017, Li et al. 2017, Kavčič 2018, Paap et al. 2018, Schiefer 2018, Carreras-Villaseñor et al. 2022, Osborn et al. 2022b). Note that *Harringtonia lauricola* is the only confirmed phytopathogen associated with a xyleborine ambrosia beetle (Freeman et al. 2019, Araújo et al. 2022).

Species	**Nutritional symbiont**	**Harmful fungus**	**Asia**	**North America**	**Africa**	**Europe**	**Central/South America**	**Oceania**	**Significant hosts**
Xyleborus glabratus	*Harringtonia lauricola*	*Harringtonia lauricola*	Native	2002	N/A	N/A	N/A	N/A	Lauraceae, *Persea*
Xylosandrus crassiusculus	*Ambrosiella roeperi*	…	Native	1700s?	1700s?	2003	1996	N/A	*Carica, Cinnamomum, Coffea, Hevea, Magnifera, Prunus, Swietenia, Tectona, Theobroma*
Xylosandrus compactus	*Ambrosiella xylebori*	*Fusarium solani* sp.	Native	1941	1700s?	2011	1970s	1961 (Hawaii)	*Ceratonia, Coffea, Laurus, Magnifera, Persea, Theobroma,*

Species	**Nutritional symbiont**	**Pathogenic fungus**	**Asia**	**North America**	**Africa**	**Europe**	**Central/South America**	**Oceania**	**Significant hosts**
Xylosandrus morigerus	*Ambrosiella* sp.	*Fusarium solani* sp.	Native	unknown	unknown	unknown	unknown	Native	*Coffea, Cacao, Fabaceae, Persea, Swietenia, Tectona*
Xylosandrus germanus	*Ambrosiella grosmanniae*	*Fusarium solani* sp.	Native	1941	N/A	1951		2007 (Hawaii)	*Castanea Malus, Pinus, Vitis*
Euwallacea spp.	*Fusarium* spp. (AFC)	*Fusarium* spp. (AFC)	Native	2006	2018	Native	1980s	Native/1980s	*Persea*
Coptoborus ochromactonus	*Fusarium* sp. AF-9	*Fusarium* sp. AF-9	N/A	N/A	N/A	N/A	Native	N/A	*Ochroma*
Ambrosiodmus minor	*Irpex Subulatus*	…	Native	2015	N/A	N/A	N/A	N/A	…

Raffaelea. De Beer et al. (2022) recently described the new genus *Harringtonia* to accommodate three former *Raffaelea* species: *Raffaelea aguacate* Simmons, Dreaden and, Ploetz, *Raffaelea brunnea* Batra (associated with Corthylini ambrosia beetles), and *Raffaelea lauricola* Harrington Fraedrich and Aghayeva, the causal agent of laurel wilt (Fraedrich et al. 2008, Harrington et al. 2008). Only *H. lauricola* is a pathogen, while other *Harringtonia* species appear harmless (Araújo et al. 2022). *Harringtonia ambrosioides* Araújo, Li, and Hulcr was recently described after being isolated from the Neotropical xyleborine *Dryocoetoides capucinus* (Eichhoff) (Araújo et al. 2022). *Harringtonia lauricola* quickly spreads throughout its tree host after inoculation and can prevent water transport by blocking the xylem, causing wilt symptoms within 14 days (Inch et al. 2012). This beetle-phytopathogen partnership likely originated in Asia and the two were imported together to the southeastern United States (Harrington et al. 2011) where laurel wilt disease causes widespread damage to forest ecosystems (Ploetz et al. 2017, Wingfield et al. 2017) and commercial avocado (*Persea americana* Miller) plantations (Inch et al. 2012). *COI* gene analysis of *X. glabratus* across its US population revealed only one haplotype, suggesting that the beetle-fungal pair was introduced once to southern North America (Hughes et al. 2017) followed by rapid proliferation to 11 southern states besides Georgia (Olatinwo et al. 2021). In 20 years, the beetle and fungus advanced into the US interior from eastern Texas and north to Kentucky, killing over 300 million trees, mainly red bay tree, but also sassafras (Hughes et al. 2017, Olatinwo et al. 2021). The beetle and fungus may eventually extend their range as far north as Michigan, given the trend of global warming (Formby et al. 2017).

Harringtonia lauricola is commonly found in the mycangia of cohabitating xyleborine species and has been shown to support survival and reproduction of the closely related species *Xyleborus bispinatus* Eichhoff (Carrillo et al. 2014, Saucedo et al. 2017). Thus, the fungus may be likely to expand its range by jumping to other beetle partners, especially those with preoral mycangia (Ploetz et al. 2017). Investigators have developed rapid field detection techniques (Abdulridha et al. 2018, Hamilton et al. 2021) and begun to increase the understanding of the pathogenicity of *H. lauricola* with molecular screening (Zhou et al. 2020) and metabolic examination (Joseph et al. 2021). However, effective methods for controlling the movement of *X. glabratus* and other vectors are very limited (Rivera et al. 2020), and there are few effective treatments for trees infected with *H. lauricola* (Olatinwo et al. 2021). Thus, laurel wilt continues to cause significant ecological and economic damage in the southeastern United States (Hughes et al. 2017). If the range of *X. glabratus* and *H. lauricola* expands to Mexico and Central and South America, native Lauraceae and commercial avocado trees throughout the Neotropics would be threatened.

Xylosandrus-Ambrosiella. The genus *Ambrosiella* is one part of three lineages in the Microascales family Ceratocystidaceae that independently evolved ambrosial associations with beetles (Mayers et al. 2015, Mayers et al. 2020b). Each of the 11 *Ambrosiella* species are ambrosia fungi that maintain tight associations with one ambrosia beetle species (Miller et al. 2019, Mayers et al. 2020b). Due to their long evolutionary history with ambrosia beetles, the genus is highly adapted to the convergent ambrosia lifestyle which makes morphology-only based identification and taxonomic assignments unreliable (Cassar and Blackwell 1996, Alamouti et al. 2009, Mayers et al. 2020b). *Ambrosiella* also tends to form relationships with beetles possessing large, intricate mycangia that are associated with internal glands (Harrington et al. 2014, Johnson et al. 2018, Mayers et al. 2020b). The most recent phylogenetic treatment of the genus (Mayers et al. 2020b) identified two clades, one of which has been associated with Scolytoplatypodini (Curculionidae: Scolytinae) ambrosia beetles since the origin of *Ambrosiella* ~18 million years ago. The other, younger clade contains the majority of *Ambrosiella* species and has been carried by several xyleborine genera since its origin ~12 million years ago.

The granulate ambrosia beetle (*Xylosandrus crassiusculus* (Motschulsky)) has a documented history of human-aided range expansion that stretches back a century or more to Africa (Hagedorn 1908), North America (Anderson 1974), and most recently to Central and South America (Kirkendall and Ødegaard 2007, Flechtmann and Atkinson 2016) and Europe (Table 3) (Pennacchio et al. 2003, Nageleisen et al. 2015, Gallego et al. 2017, Kavčič 2018). The ability of *X. crassiusculus* to establish and spread beyond its native range in Asia is fueled by two factors that are difficult to disentangle because of the complex genetic diversity this species possesses in both its native and introduced ranges (Ito and Kajimura 2009, Flechtmann and Atkinson 2016, Storer et al. 2017). First, the beetle quickly proliferates after establishing a new population. This is evidenced by the fact that it was one of the most prevalent ambrosia beetles in Costa Rica just ten years of its first detection in the country (Kirkendall and Ødegaard 2007). Second, repeated introductions of this species are common and this increases the rate of success for nascent populations and expands their geographic range (Rabaglia et al. 2019). Both factors are responsible for the rapid proliferation of the granulated ambrosia beetle throughout North America after its first appearance in Dorchester County, South Carolina, United States in 1974 (Anderson 1974, LaBonte et al. 2005, Flechtmann and Atkinson 2016, Rabaglia et al. 2019), and its range expansion throughout South America and Africa (Flechtmann and Atkinson 2016, Landi et al. 2017, Nel et al. 2020).

Xylosandrus crassiusculus maintains a stable relationship with its fungal symbiont *Ambrosiella roeperi* Harrington and McNew throughout its global geographic range (Harrington et al. 2014, Mayers et al. 2020b, Nel et al. 2020, Saragih et al. 2021). This fungus is not known to cause disease in host plants, however, infestation with *X. crassiusculus* can be associated with unidentified fungal infections that may opportunistically exploit the holes created by dispersing foundresses (Atkinson et al. 1988). The granulated ambrosia beetle impacts ornamental plant nurseries and lumber productivity by killing young saplings (Kirkendall and Ødegaard 2007) and damaging stored logs (Atkinson et al. 2000). It is also capable of attacking and reproducing in a vast range of angiosperms including crop trees such as coffee (*Coffea canephora* Pierre ex Froehner), cacao (*Theobroma cacao* L.), mango (*Mangifera indica* L.), papaya (*Carica papaya* L.), rubber (*Hevea brasiliensis* Willd. Ex Juss), camphor (*Cinnamomum camphora L.*), mahogany (*Swietenia* Jacquin), teak (*Tectona grandis* L.), and stone fruit trees (*Prunus* L.) (Schedl 1963, Atkinson et al. 1988, Wood and Bright 1992). Cavaletto et al. (2021) discovered that host choice of *X. crassiusculus* was more influenced by ethanol levels in the wood than plant taxon. Despite the prediction of Harrington et al. (2014) that *X. crassiusculus* is unlikely to efficiently vector plant pathogens in the genera *Raffaelea* or *Harringtonia,* studies on the lateral transfer of pathogenic fungi between sympatric ambrosia beetles have called this into question. Carrillo et al. (2014) and Ploetz et al. (2017) both discussed the potential for the granulated ambrosia beetle to contribute to the spread of laurel wilt disease after finding its causal agent, *H. lauricola*, inside the mycangia of *X. crassiusculus* specimens.

Like *X. crassiusculus,* the black twig borer (*Xylosandrus compactus* (Eichhoff)) uses a wide variety of dicotyledonous angiosperm hosts for the establishment of fungal gardens (Ngoan et al. 1976, Hara and Beardsley 1979). This ambrosia beetle attacks small-diameter twigs and early growth healthy trees of diameter 3 mm or larger (Wood 1982), causing wilting and death in young individuals (Oliviera et al. 2008). It is a significant pest of coffee, cacao, avocado, mango, and many forest and nursery trees (Brader 1964, Ngoan et al. 1976, Oliveira et al. 2008).

The native range of *X. compactus* probably extends through Asia, though it has been widely introduced to many regions and has a pantropical distribution today (Table 3) (Brader 1964, Rabaglia et al. 2006, Haack and Rabaglia 2013, Urvois et al. 2021). In an examination of the biology of this beetle and its impact on coffee plantations, Brader (1964) noted that *X. compactus* was limited to the Paleotropics, but it would eventually spread to the Neotropics. A phylogeographical analysis of global patterns of genetic diversity of *X. compactus* confirmed that two Asian linages independently invaded Africa and the Americas, Pacific Islands and Europe through international trade (Urvois et al. 2021). The introduction to Africa probably occurred several hundred years ago, early in the history of the continent's participation in international trade (Egonyu et al. 2015). The occurrence of *X. compactus* in the Americas, Pacific Islands and Europe is more recent. In North America it was first recorded in Ft. Lauderdale, Florida in 1941 before quickly establishing pestiferous populations in avocado plantations in that state and Georgia (Wood 1982). Estimates place the introduction of the black twig borer to South America as being in the 1970s. It first discovered in Peru in 1973 (Oliviera et al. 2008) and in Brazil during the 1980s (Delgado and Couturier 2017). *X. compactus* was introduced to Oahu, Hawaii in 1961 and has since spread to all the Hawaiian Islands where it threatens coffee crops and several native trees (Hara and Beardsley 1979, Greco and Wright 2015). Most recently, this ambrosia species was discovered to be reproducing in Italy in 2011 (Garonna et al. 2012) and had spread to France, Spain and Greece by 2019 (Contarini et al. 2020, Leza et al. 2020, Faccoli 2021). The population in central Europe causes commercial and ecological damage by attacking bay (*Laurus nobilis* L.) and carob (*Ceratonia siliqua* L.) trees and can produce five generations per year (Gugliuzzo et al. 2020).

X. compactus appears to be associated with two fungi, which lead to several years of confusion as investigators uncovered inconsistent results when culturing samples from the beetles' gallery walls (Hara and Beardsley 1979). Species from two genera have shown the most consistent association with *X. compactus*: *Ambrosiella xylebori* Brader ex von Arx & Hennebert (Mayers et al. 2015, Bateman et al. 2016, Gugliuzzo et al. 2020) and a species of *Fusarium* from the *Fusarium solani* species complex (FSSC) (Muller 1933, Brown 1954, Ngoan et al. 1976, Gugliuzzo et al. 2020, Morales-Rodríguez et al. 2021). Because of it can be reliably found inside the beetle mycangium, and growing in the gallery, *A. xylebori* is likely the primary nutritional symbiont of its beetle partner (Bateman et al. 2016).

However, the role (if any) of the *Fusarium* in the life cycle of the black twig borer, is less clear. A pathogenicity study in Uganda found that a species of *Fusarium* vectored by *X. compactus* are the causal agents of wilting in infested cacao plants (Kagezi et al. 2017). Bateman et al. (2016) found FSSC was consistently recovered from the external surface of the beetles, but not found in the mycangium. They suggest that this may indicate that the FSSC may possess conidiophores that are adapted for insect dissemination and the pathogenicity of FSSC allows *X. compactus* to overcome plant defenses when it attacks healthy hosts. These fungi may be predisposed to developing associations with arthropods because their association with plants commonly puts them into direct contact with insects that also interact with plants. (Aoki et al.

2003, Summerell and Leslie 2011) and is vectored by several insect and mite orders (O'Donnell et al. 2012). However, these possible explanations for the association between *X. compactus* and FSSC are unconfirmed and require further investigation (Bateman et al. 2016). It is clear that the beetle is responsible for vectoring a fungal disease that is capable of causing significant economic and ecological damage (Egonyu et al. 2015).

Xylosandrus morigerus (Blandford) was described in England from specimens taken from infested orchid plants that had originated in Papua New Guinea (Blandford 1894a). Thus, its potential for introduction to many non-native regions was clearly notable from the beginning (Table 3) (Browne 1961, Kalshoven 1961). This ambrosia beetle is probably native to tropical Asia with introduced populations in the Americas, Pacific Islands, Europe, Middle East, and Africa (Wood and Bright 1992, Kirkendall and Ødegaard 2007, Cognato and Rubinoff 2008, Kirkendall and Faccoli 2010). A study of the mitochondrial genetic diversity of the invasive population in Costa Rica suggests that despite widely divergent mitochondrial lineages, *X. morigerus* occupies identical niches throughout the country (Andersen et al. 2012). This ecological generalism probably contributes to the extreme mobility of the species outside of its native range. *X. morigerus* is like *X. compactus* in that it attacks twigs and saplings no more than 15 cm in diameter from a wide variety of angiosperms (Browne 1961, Kalshoven 1961). This can cause significant damage to the coffee, cacao, avocado, mahogany, teak, legumes, and many forest trees (Kalshoven 1961, Carreras-Villaseñor et al. 2022).

Presumably, the nutritional symbiont of *X. morigerus* is an unstudied *Ambrosiella* species, similar to other *Xylosandrus* (Bateman et al. 2018, Skelton et al. 2019). However, the mycangial contents of *X. morigerus* have not yet been studied. Two isolates belonging to the FSSC were recovered from *X. morigerus* collected in Veracruz, Mexico and found to cause wilting and necrosis in coffee, and several forest tree species (Carreras-Villaseñor et al. 2022). The full nature of the relationship between *X. morigerus* and its pathogenic fungus in the FSSC is still uncertain.

Xylosandrus germanus was described by Blandford (1894b) from 16 specimens collected from the island of Honshu in Japan. It was not collected outside of Asia until Felt (1932) reared several hundred from infested grapevines in Nassau County, New York. Initial biological descriptions of this species noted that it occasionally infests healthy trees but enjoys far better success attacking freshly fallen or sick hosts (Table 3) (Hoffmann 1941). Hoffmann (1941) also observed that *X. germanus* relies on a fungus for food and concluded that this fungus was unlikely to be a plant pathogen. As the beetle continued to spread through the eastern United States (Weber and McPherson 1982, LaBonte et al. 2005), *X. germanus* was linked to a *Fusarium* fungal disease killing young walnut plantation trees in southern Illinois, Indiana, Missouri, and Iowa (Kessler et al. 1974). It was first reported in Europe in Germany in 1951 (Groschke 1953) and had established populations thorough central Europe by the 1990s (Wood and Bright 1992). In 2018, the beetle had spread to the Mediterranean scrubland (Contarini et al. 2020). In 2007, *X. germanus* was discovered on Oahu and Hawaii (Cognato and Rubinoff 2008). Phylogeographic analysis across its native and introduced populations indicate that the non-native *X. germanus* in Europe and North America each descend from independent invasions by Japanese founders: Europe having been invaded once, and North America experiencing repeated introductions (Dzurenko et al. 2021). Non-native populations of *X. germanus* are so abundant they are a convenient model for studies about xyleborine sex ratios and inbreeding rates (Peer and Taborsky 2005, Keller et al. 2011).

Though *X. germanus* generally attacks trees that are already physiologically compromised (Ranger et al. 2018) it is a significant pest causing death and dieback in nurseries (Reding et al. 2015), and orchards (Agnello et al. 2017, Reinke and Wilson 2020) in the United States. In Europe, it is cited as causing significant losses in forests (Grégoire et al. 2003), vineyards (Ruzzier et al. 2021), and the lumber industry (Galko et al. 2018), The mycangial symbiont of *X. germanus* is *Ambrosiella grosmanniae* McNew, Mayers, and Harrington which is closely related to *A. roeperi* and *A. xylobori* and has repeatedly been isolated from several specimens from around the United States, Germany, Netherlands, and Switzerland (Mayers et al. 2015). Molecular data from the fungi from *X. germanus* in Japan (within the native range) indicates that there may be more genetic diversity than proposed by Mayers et al. (2015) (Ito and Kajimura 2017).

Additional fungi including two species of *Fusarium* have been recovered from *X. germanus* galleries (Yang et al. 2008) but their relationship to *X. germanus* is currently unknown. Disease in New York apple orchards associated with a *Fusarium* species is thought to be vectored by *X. germanus,* but this link remains unconfirmed because specific identification and pathogenicity studies have not been performed (Agnello et al. 2017).

Like other *Xylosandrus, X. germanus* can live inside an exceptionally wide number of plant hosts and even infests conifers (Weber and McPherson 1983). Multi-year monitoring of non-native *X. germanus* in forests in Slovakia showed that populations did not decline significantly after an exceptionally cold winter, suggesting that they may be capable of continuing to expand into colder areas (Dzurenko et al. 2022). In addition, as global climate change continues to bring milder winters and trigger stress in host trees, this beetle's range will likely continue to expand throughout its non-native range (Henin and Versteirt 2004).

AFC-Euwallacea and AFC-Coptoborus. Three *Xylosandrus* species vector FSSC pathogens that cause a significant global impact but are not nutritional symbionts for the beetles (Carreras-Villaseñor et al. 2022). The genera, *Euwallacea* Hopkins and *Coptoborus* Hopkins maintain nutritional relationships with an unusual group of *Fusarium* species collectively referred to as the Ambrosia *Fusarium* Clade (AFC) (Li et al. 2016, Lynch et al. 2016, Osborn et al. 2022a). These fungi form a monophyletic group that diverged from the FSSC ~21–24 million years ago (Kasson et al. 2013, O'Donnell et al. 2015). The AFC consists of 19 species, 11 of which have been formally described (Gadd and Loos 1947, Nirenberg 1990, Freeman et al. 2013, Aoki et al 2018, Na et al. 2018, Aoki et al. 2019, Lynn et al. 2020, Aoki et al. 2021).

Understanding of the ambrosia symbiosis involving *Euwallacea* is confounded by historical misidentifications of pest species (Smith et al. 2019). A pest from this genus traditionally identified as *Euwallacea fornicatus* (Eichhoff) (Figure 1), but currently believed to be *Euwallacea perbrevis* (Schedl), has been a well-documented pest of tea since the late 19th century (Table 3) (Walgama 2012). However, there was little examination of its gallery fungus until Gadd and Loos (1947) described *Monacrosporium ambrosium* Gadd and Loos from beetles infesting tea plantations in Sri Lanka. In 1987, Brayford mistakenly redescribed this fungus as *Fusarium bugnicourtii* (Gadd and Loos) from *E. fornicatus* infesting tea in India (Brayford 1987). These two names were synonymized three years later (Nirenburg 1990) and there was no further discussion of this ambrosia fungus until 2012, when *E. fornicatus* was discovered to cause damage to trees in invaded regions (Eskalen et al. 2012, Mendel et al. 2012).

The symbiotic fugus *Fusarium euwallaceae* Freeman, Mendel, Aoki, and O'Donnell was originally reported as the suspected cause of the so-called Fusarium Dieback Disease in avocado in California, United States (Eskalen et al. 2012). However, subsequent studies have suggested that the fungus is a “Pseudopathogen”, unable to cause disease without the action of the beetles (Freeman et al. 2019).

An inclusive survey examining the fungi from worldwide *Euwallacea* showed that several species including *Euwallacea interjectus* (Blandford), *Euwallacea validus* (Eichhoff), *E. fornicatus*, and other *Euwallacea* species cultivate fungi in the AFC (Kasson et al. 2013). Interestingly, this study also recovered AFC species AF-9 from *Xyleborus ferrugineus* (Fabricius) from Costa Rica (Kasson et al. 2013). Testing for co-cladogenesis in *Euwallacea* and AFC revealed that the AFC are vertically transmitted by the beetles and share a deep and dynamic relationship with *Euwallacea* that includes frequent partner switching (O’Donnell et al. 2015). The beetles and fungi likely became associated close to the origin of *Euwallacea* (19–24 million years ago). However, the nutritional relationship between the beetles and fungi has not been examined and needs investigation (O’Donnell et al. 2015).

Despite the long history of research and monitoring of *E. fornicatus*, identification of this species based on morphology is difficult or impossible (Gomez et al. 2018a, Smith et al. 2019, 2020). The taxonomy of the species has historically been unstable with scientists describing several species with nearly identical diagnoses, placing them into synonymy, and resurrecting some (see Stouthamer et al. 2017 and Gomez et al. 2018a). The rediscovery of a syntype from the initial type series of *Xyleborus fornicatus* Eichhoff provided clarity about the identity of the original description (Smith et al. 2019). However, considerable uncertainty around the diagnosis of *E. fornicatus* and the correct use of its common name, polyphagous shot hole borer remains (Carrillo et al. 2020a, 2020b).

Members of the *E. fornicatus* species complex spread beyond their native Asia and Oceania into Central America in the 1980s (Wood 1982). Between 2006 and 2018, they spread further to North America (California and Florida, United States) (Rabaglia et al. 2006), Israel (Mendel et al. 2012), and South Africa (Paap et al. 2018). Some AFC fungi associated with *Euwallacea* cause plant disease (Eskalen et al. 2012, Mendel et al. 2012, Paap et al. 2018), yet pathogenicity among all members of the AFC has not been evaluated.

Beetles from the Neotropical genus *Coptoborus* were linked to a dieback disease affecting balsa (*Ochroma pyramidale* (Cavanilles ex Lamark)) plantations in Ecuador in the early 1990s (Stilwell et al. 2014). The beetle was described as *Coptoborus ochromactonus* Smith and Cognato after its association with dying balsa trees (Table 3) (Stilwell et al. 2014). Morphological and molecular analysis both identified the fungus associated with this beetle-vectored disease to be a species of *Fusarium* (Stilwell et al. 2014, Castro et al. 2019) and a study of infested balsa plantations in western Ecuador showed that tree age and stress levels had the most influence on infection and mortality rates (Martínez et al. 2020). Osborn et al. (2022a) completed a survey of the fungi in the mycangia of several *Coptoborus* native to Ecuador and concluded that they carry the unnamed species AF-9 from the AFC. Close investigation of the AFC associated with *C. ochromactonus* is still needed to fulfil Koch's postulates for disease causality (Smith 1905).

Ambrosiodmus minor-Irpex subulatus. The sister genera *Ambrosiodmus* Hopkins and *Ambrosiophilus* Hulcr and Cognato are the only xyleborines with documented symbioses with the basidiomycete fungus *Irpex subulatus* (= *Flavodon subulatus*) (Li et al. 2015, Simmons et al. 2016a, Li et al. 2017). The presence of this fungus, which was first assigned to *Flavodon* Ryvarden and recently was moved into *Irpex* Fries by Tian et al. (2022), is very uncommon among the Xyleborini. *Ambrosiodmus minor* (Stebbing) is native to Eastern Asia (Wood and

Bright 1992, Lin et al. 2019), but it has been introduced to the southeastern United States, spreading from Nassau County, Florida to Georgia, Alabama, and Mississippi by 2017 (Table 3) (Schiefer 2018). The ambrosia partnership between *A. minor* and *I. subulatus* could result in unique ecological consequences as the beetle continues to spread. *I. subulatus,* like other white rot fungi, can efficiently degrade lignin, one of the most recalcitrant molecules that is responsible for the rigidity of plant walls (Eriksson et al. 1990). Because this fungus colonizes dead wood efficiently and may outcompete similar native fungi, it may alter the carbon cycle in forests and increase falling limbs and damage to trees in human environments (Gomez and Hulcr 2020, Jusino et al. 2020).

Ambrosia beetle-fungus research in regional centers of biodiversity

By far, there is a greater understanding of introduced xyleborine beetles and their fungi as compared to the species residing in their native range. Approximately 1300 xyleborine species are distributed in the tropics but knowledge of the taxonomy, ecology, and fungal symbioses is lacking for the vast majority (Wood 2007, Smith et al. 2017, Eliassen and Jordal 2021). Similarly, most studies exploring ambrosia fungus diversity and their relationships to ambrosia beetles focus on the minority of fungi that cause economic or ecological harm (Batra 1967, Alamouti et al. 2009, Dreaden et al. 2014, Hughes et al. 2017, Short et al, 2017). In many ways, this bias is necessary because of the urgency required to respond to newly discovered pathogens (Liebhold and Kean 2018). However, future studies aimed at gaining a holistic understanding of the diversity of ambrosia symbioses and the biological mechanisms maintaining them may be the best way to fully understand these partnerships and prevent the ecological consequences of waiting until invasive populations are already established before attempting mitigating action (Hulcr and Dunn 2011, Skelton et al. 2018, Miller et al. 2019, Mayers et al. 2020b).

Europe and North America North of Mexico. Xyleborine diversity has been thoroughly documented in Europe (Pfeffer 1995) and North America north of Mexico (Bright 1968, Wood 1982) given its sparseness in these regions (Figure 3). Most scientific attention has been focused on invasive xyleborines, especially those that vector pathogenic fungi (*e.g.,* Norris 1979, LaBonte et al. 2005, Ploetz et al. 2017, Galko et al. 2018, Schiefer 2018, Rabaglia et al. 2019, Salman et al. 2019, Carrillo et al. 2020a, Faccoli 2021) or cause other significant damage in North America and Europe. Some knowledge gained from these investigations focuses on the identities of ambrosia fungi (Harrington et al. 2008, Freeman et al. 2013, Lynch et al. 2016, Simmons et al. 2016a, 2016b, Aoki et al. 2018, 2019, 2021, Araújo et al. 2022). However, despite considerable historical discourse regarding the classification of ambrosia fungi (see Leach et al. 1940, Francke-Grosmann 1967, Araújo et al. 2022, de Beer 2022), the identities of most xyleborine ambrosia fungi are poorly understood or unknown. Nevertheless, the considerable attention given to invasive species has produced a foundational understanding of the mechanistics and ecology of invading populations (Storer et al. 2017, Miller et al. 2019, Jusino et al. 2020, Dzurenko et al. 2021, Moralez-Rodriguez et al. 2021, Urvois et al. 2022) and the evolution of fungus farming in beetles (Farrell et al. 2001, Biedermann and Vega 2020)

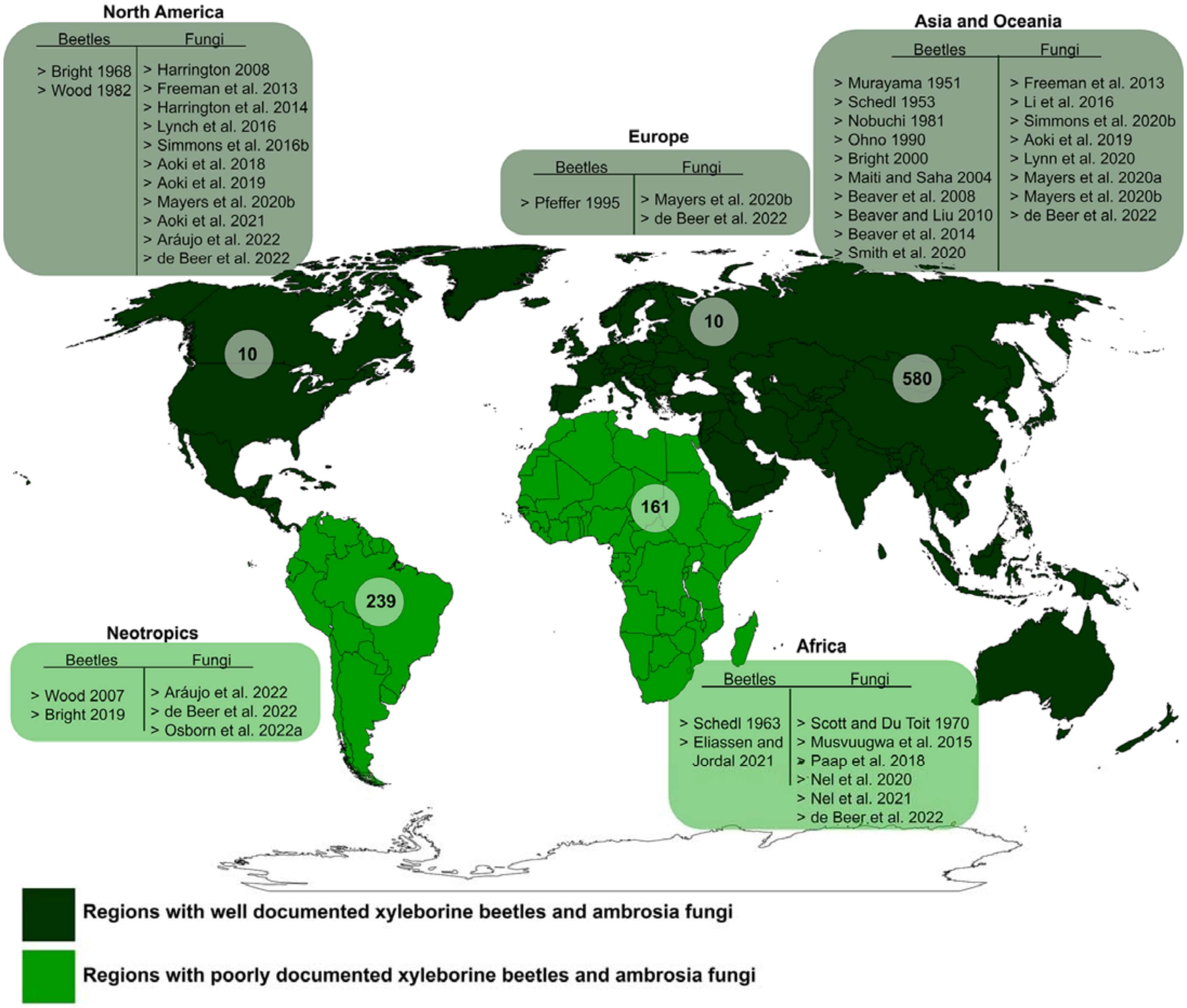
North America
Beetles
Fungi
> Bright 1968
> Wood 1982
> Harrington 2008
> Freeman et al. 2013
> Harrington et al. 2014
> Lynch et al. 2016
> Simmons et al. 2016b
> Aoki et al. 2018
> Aoki et al. 2019
> Mayers et al. 2020b
> Aoki et al. 2021
> Aráujo et al. 2022
> de Beer et al. 2022
Europe
Beetles
Fungi
> Pfeffer 1995
> Mayers et al. 2020b
> de Beer et al. 2022
Asia and Oceania
Beetles
Fungi
> Murayama 1951
> Schedl 1953
> Nobuchi 1981
> Ohno 1990
> Bright 2000
> Maiti and Saha 2004
> Beaver et al. 2008
> Beaver and Liu 2010
> Beaver et al. 2014
> Smith et al. 2020
> Freeman et al. 2013
> Li et al. 2016
> Simmons et al. 2020b
> Aoki et al. 2019
> Lynn et al. 2020
> Mayers et al. 2020a
> Mayers et al. 2020b
> de Beer et al. 2022
10
10
580
161
239
Neotropics
Beetles
Fungi
> Wood 2007
> Bright 2019
> Aráujo et al. 2022
> de Beer et al. 2022
> Osborn et al. 2022a
Africa
Beetles
Fungi
> Schedl 1963
> Eliassen and Jordal 2021
> Scott and Du Toit 1970
> Musvuugwa et al. 2015
> Paap et al. 2018
> Nel et al. 2020
> Nel et al. 2021
> de Beer et al. 2022
Regions with well documented xyleborine beetles and ambrosia fungi
Regions with poorly documented xyleborine beetles and ambrosia fungi

Figure 3. State of current understanding of the ambrosia symbiosis in North America, Europe, the Neotropics, Africa, and Asia and Oceania. Each region is labeled with its number of native xyleborine species as reported in Pfeffer 1995 and Hulcr et al. 2015. The text boxes display important works on beetle and fungal biodiversity for each region.

Neotropics. The study of ambrosia beetles and fungi in South America has emphasized invasive species that damage economically important crops (Burbano-Figueroa et al. 2018, Castro et al. 2019, Martínez and Boira 2021, Carreras-Villaseñor et al. 2022). Increasing discoveries of pestilent bark and ambrosia beetles has sparked a redoubling of collection efforts in South America, development of updated identification tools and various taxonomic changes both at the generic and specific levels of Scolytinae (Wood 2007, Bright 2019, Silva et al. 2020, Smith and Cognato 2021) (Figure 3). The extreme biodiversity of Scolytinae in South America was demonstrated by Dole et al. (2021) who reported that 2500 scolytine specimens collected by Dr. Terry Erwin's canopy fogging project between 1994 and 2006 included more than 400 morphospecies. Taxonomic work on Neotropical Xyleborini has justified the revision of genera (Petrov and Flechtmann 2013, Smith and Cognato 2021), description of new genera (Smith 2017, Cognato 2018), and description of many new species (e.g., Petrov and Mandelshtam 2009, Petrov and Mandelshtam 2018, Petrov 2020, Smith and Cognato 2021, Osborn et al. 2022b). These discoveries indicate that our current understanding of ambrosia beetle diversity in the region is poor (Wood 2007, Smith et al. 2017, Dole et al. 2021), likely because natural areas are under-surveyed in exchange for over-sampling in agricultural areas and tree plantations (Martínez et al. 2019).

We know little about the ambrosia fungi associated with Xyleborini native to South and Central America. Only one study, as described above, surveyed the symbiotic fungi associated native *Coptoborus* (Osborn et al. 2022a). As discussed previously, several xyleborines vector nonsymbiotic fungi that cause plant disease; many of these beetles are introduced pests in South America. *Xylosandrus morigerus*, which vectors the pathogenic fungus *F. solani* in Mexico (Carreras-Villaseñor et al. 2022) was first reported to infest coffee in Colombia in 1959

(Benavides 1961). Sermeño-Chicas et al. (2019) reported the beetle as a potential pest to cacao in El Salvador. Both studies mentioned that *Ambrosiaemyces zeylanicus* Trotter is associated with *X. morigerus* but this fungus is not pathogenic. The black twig borer, *X. compactus*, introduced to South America from Asia is a highly destructive pest of coffee in Brazil that can also use several native tree species as host (Urvois et al. 2021, Túler et al. 2019). Robust research about the symbiotic fungi carried by these invasive ambrosia beetles in South America has not yet been completed.

Avocado is an important crop in many American countries and is vulnerable to several native ambrosia beetle pests that are the subjects of much research attention. Burbano-Figueroa et al. (2018) reported that *Xyleborus volvulus* (Fabricius) is associated with the fungus *Clonostachys pseudochroleuca* Schroers (= *Bionectria pseudochroleuca* Schroers and Samuels), which causes wilting and death in avocado trees in Colombia. This beetle also infests avocado orchards in Colima, Mexico along with *Xyleborus affinis* Eichhoff and *Xyleborus spinulosus* Blandford (Castrejón-Antonio et al. 2017). Avocado plantations in Michoacán, Mexico were found to contain several pests infesting the crop trees including *X. affinis, X. volvulus,* and *X. ferrugineus*, as well as species from several non-xyleborine ambrosia beetle tribes (Ángel-Restrepo et al. 2019). Examination of the mycangial fungi of avocado-infesting *X. affinis* found a variety of *Raffaelea* species including *Raffaelea arxii, Raffaelea fusca,* and an unnamed species (Ángel-Restrepo et al. 2022). A preliminary study of the mycangial contents of *X. affinis, X. volvulus,* and two other native *Xyleborus* (*Xyleborus paralellocollis* Eggers*, and Xyleborus tribulatus* Wood) collected in Ecuador also showed that they are associated with *Raffaelea* (Martínez 2019). It is possible these beetle-fungal associations exist only in the presence of undetected pest beetles that are more consistent vectors of pathogenic fungi. However, the ambrosia symbioses in South and Central America are not well studied enough to definitively explain these preliminary results. Neotropical *Xyleborus* have infested *Theobroma cacao* trees in Costa Rica since the 1960s (Saunders et al 1967, Norris et al. 1968). Recently, *X. ferrugineus* was found to harbor AFC fungi in Costa Rica and Ecuador (Kasson et al. 2013, Martínez 2019). Despite accelerating research, the diversity of Neotropical xyleborine ambrosia fungi is largely unexplored, especially in the Amazon rainforest. More work is required to fully understand the pathology and vector patterns.

Africa. A catalogue of Xyleborini exists for Africa (Schedl 1963) but it is outdated. The formidable task of updating the Afrotropical ambrosia beetle biodiversity has been undertaken by Dr. Bjarte H. Jordal (University of Bergen, Norway) and collaborators. This work includes xyleborines (Jordal and Tischer 2020, Eliassen and Jordal 2021), but most of the tribe has not been revised in several decades (Figure 3).

The limited studies on African xyleborine ambrosia fungi were all conducted in South Africa (Scott and Du Toit 1970, Musvuugwa et al. 2015, Paap et al. 2018, Nel et al. 2020, 2021). Seven fungal species from five genera (*Ambrosiella roeperi*, *Ceratocystiopsis lunata* Nel, *Neocosmospora euwallaceae* [AF-2] (Freeman, Mendel, Aoki, and O'Donnell), *Raffaelea promiscua* Nel and van Leeuwenhoek*, Raffaelea arxii* Scott and du Toit, *Dryadomyces sulphurea* (Batra), and *Sporothrix aemulophila* de Beer, Dreyer Roets, and van Leeuwenhoek) have been reported. Of these *C. lunata* and *S. aemulophila* have not previously been shown to be nutritional symbionts of ambrosia beetles and thus likely represent facultative associations.

The most harmful beetle-fungus partnership, and hence the most studied, is that of *E. fornicatus* and *N. euwallaceae.* This beetle and its primary fungal symbiont were first reported from South Africa in 2017 (Paap et al. 2018), although a DNA sequence of *E. fornicatus* was also recovered from a South African specimen collected in 2012 (Stouthamer et al. 2017). Since its invasion into the country over ten years ago, this beetle and fungus has been detected in eight of the nine provinces in South Africa from over 130 plant species (van Rooyen et al. 2021). In general, ambrosia beetles and their fungi are understudied in Africa.

Asia and Oceania. Prior to the 2000s, knowledge of Xyleborini from Asia and Oceania was mainly derived from taxonomic treatments (e.g., Murayama 1951, Schedl 1953, Nobuchi 1981, 1985, Goto 2009, Park et al. 2020) and site-specific surveys (e.g., Ohno 1990, Bright 2000) (Figure 3). Study of specimens was slowed by the distribution of information and type specimens across worldwide journals, in multiple languages, and collections (Bright 1993, Hulcr et al. 2015). Given that the majority of introduced species in Europe and the New World are native to this region, the new millennium brought concentrated effort to revise these faunas for specific genera and regions and to electronically distribute species diagnoses, locality data, and images (e.g., Maiti and Saha 2004, Beaver et al. 2008, Beaver and Liu 2010, Hulcr and Smith 2010, Beaver et al. 2014). These works included monographs for New Guinea and Southeast Asia and associated publicly accessible electronic resources with DNA based phylogenies (Cognato et al. 2019) and DNA identification frameworks (Hulcr and Cognato 2013, Smith et al. 2019, Cognato et al. 2020a, Smith et al. 2020). Many genera and species were described resulting in 315 and 144 species recorded for Southeast Asia and New Guinea, respectively. These publications have increased the rate of recognizing and describing new species which has resulted in a better understanding of species distributions (Smith et al. 2018, Park et al. 2020). However, it is estimated that 30% more species await discovery for Southeast Asia alone (Smith et al. 2020).

Like most other regions, studies on symbiotic fungi in Asia and Oceania focus on those associated with beetle pest species (e.g., Kajimura and Hijii 1992, Jiang et al. 2021). Much of the taxonomic work on Asian ambrosia fungi focuses on the symbionts of xyleborines that have significant non-native populations in other regions, reflecting the importance of Asia to global invasion patterns (Lantschner et al. 2020). Species of *Fusarium* associated with *Euwallacea* (Freeman et al. 2013, Li et al. 2016, Aoki et al. 2019, Lynn et al. 2020), and species of *Ambrosiella* with *Xylosandrus* (Mayers et al. 2020b) have been the subjects of much scientific work. The ambrosia fungi of non-pestiferous xyleborines in Asia and Oceania are understudied.

Study of xyleborine ecology is limited for Asia and Oceania. In China, *Euwallacea* species were studied in context of their economic impact on urban forests (Li et al. 2013, Wang et al. 2021). Hosts and distribution were updated for other pest species (Zheng et al. 2017, Lin et al. 2019, Li et al. 2020). In Thailand and Papua New Guinea, research focused on basic science and addressed ecological factors contributing to ambrosia beetle diversity. Quantitative studies in Thailand demonstrated significantly different ambrosia beetle communities based on forest type (Hulcr et al. 2008). Conversely, studies in Papua New Guinea demonstrated the tree-host generalist tendency for ambrosia beetles and low beta-diversity among ambrosia beetle communities in lowland rainforests (Novotny et al. 2007, Hulcr et al. 2008). These studies, in part, uncovered a new ecological niche, fungus-stealing (mycocleptism) which has independently evolved several times among xyleborines (Hulcr and Cognato 2010).

Global Outlook. Updating of a preliminary species level phylogeny of Xyleborini is needed (Cognato et al. 2011). Although other phylogenies at the generic level provide specific taxonomic and evolutionary information (e.g., Dole et al. 2010, Cognato et al. 2020b, Eliassen and Jordal 2021), a phylogeny including >50% of Xyleborini species sampled across genera and the world is needed in order to make global inferences concerning beetle-fungus symbiosis. During the last two and a half decades, phylogenetic studies of the ambrosia fungi from Hypocreales, Ophiostomatales and Microascales have created increasingly robust classifications of these groups based on isolates obtained from fungal repositories and molecular sequences from GenBank (Cassar and Blackwell 1996, Jones and Blackwell 1998, Alamouti et al. 2009, Dreaden et al. 2014, Vanderpool 2017 Mayers et al. 2020b, de Beer et al. 2022). The global scope of these is useful for understanding broad evolutionary patterns, but finer understanding of the evolutionary interactions between ambrosia fungi and beetles requires the collection of beetles and isolation of the fungi for comparison across geographic space. Studies accomplishing this have centered on beetles from Asia (Gadd and Loos 1947, Brayford 1987, Gebhardt et al. 2005, Li et al. 2016, Lin et al. 2017, Carrillo et al. 2019, Lynn et al. 2020), North America (Six et al. 2009, Harrington et al. 2008, Eskalen et al. 2013, Harrington et al. 2014, Lynch et al. 2016, Simmons et al. 2016a, Mayers et al. 2017, Aoki et al. 2018), or both (Harrington et al. 2010, Freeman et al. 2013, Simmons et al. 2016b, Na et al. 2018, Aoki et al. 2021). A few include specimens from Australia (von Arx and Hennebert 1965, Kasson et al. 2013, Aoki et al. 2019), Europe (Nirenberg 1990, Mayers et al. 2015), and Africa (von Arx and Hennebert 1965, Scott and du Toit 1970, Nel et al. 2021).

Globally relevant ecological studies of these fungi are also rare. There are few quantitative analyses of the symbiotic partners of non-pest xyleborines and the nutrient use of only a few ambrosia fungi have been studied (Kok 1979, Kasson et al. 2016, Skelton et al. 2019). Increasing emphasis on diverse, collaborative scientific research is a hopeful trend and will probably lead to greater understanding of worldwide ambrosia symbioses – especially those in developing agricultural and agroforestry systems.

Enhancing global research on the ambrosia symbiosis.

The nature of the xyleborine ambrosia beetle-fungus relationship remains poorly understood because of varying levels of fidelity or promiscuity, evolutionary histories, and taxonomic diversity of the fungi. Yet xyleborines are found all over the world and are common invaders in every biogeographic region. The first step to understand the beetle-fungus relationship and their pathogenic potential is the identification of the beetle which is often difficult given few and scattered resources. Language barriers between scientists of different nationalities compound this challenge by making scientific literature difficult to share and by discouraging effective international collaboration. Many of the most prolific ambrosia beetle experts of the last century worked alone. Increasing trends toward international scientific teamwork have increased access to foreign language literature, but not every region is well represented. The Facebook group "Frass and Noodles", a community outreach forum for bark and ambrosia beetle research was created to help increase access to sparse taxonomic resources, especially to experts in beetle taxonomy and encourage networking across international borders. The widespread use of social media and increasing improvement of automated translation is a boon for building of a productive ambrosia symbiosis community.

In addition to productive relationships, collaborators could develop resources to train scientists in standard protocols for collecting, identifying, and evaluating ambrosia beetles and fungi (e.g., Hulcr et al. 2022). Not only will this benefit communities with limited resources and expertise, it will also contribute to the standardization of these methodologies. The recent formation of the Bark Beetle Mycobiome collaborative group (Hulcr et al. 2020) and their framework seeks to normalize methods and to further communication so that harmful ambrosia beetles may be studied and mitigated by a global community rather than by individual countries or regions working alone. Invasive ambrosia beetles are monitored and studied by well-established research programs in several regions, but there are parts the world that currently lack such sustained efforts. Many of these are developing nations located around the equator which is where the richest diversity of xyleborine beetles is located. These countries may be the source of future invasive populations as well as suffer from the consequences of new introductions, yet they rarely have robust and enduring programs for studying the ambrosia symbiosis and monitoring for non-native species.

The exchange of specimens for research, has become increasingly challenging due to the demands of biodiversity agreements such as the Nagoya Protocols (Prathapan et al 2018, Acosta and Perez-Gonzalez 2019). The investigation of the xyleborine ambrosia symbiosis has not escaped such bureaucratic inertia in addition to the taxonomic impediment. To better strengthen all regions against harmful new invasive xyleborines and their possibly destructive fungi, research needs to be supported evenly across the globe. The founding consortium of researchers that crafted the Bark Beetle Mycobiome includes a group from several institutions across the United States and South Africa. To maximize its potential, the collaborative relationships codified in its foundation, as cited in this review, should be expanded to benefit research programs in Central and South America, Oceania, Asia and Sub-Saharan Africa (apart from South Africa) should be developed and supported. Partnerships between nations with well-supported scientific institutions and tropical nations, which typically have underfunded or developing scientific infrastructure would be mutually beneficial because resources, local knowledge, and ingenuity can be harnessed to gain knowledge that benefits the global community.

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