REVIEW

Recent advances toward the sustainable management of invasive *Xylosandrus* ambrosia beetles

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Abstract

We provide an overview of both traditional and innovative control tools for management of three *Xylosandrus* ambrosia beetles (Coleoptera: Curculionidae: Scolytinae), invasive species with a history of damage in forests, nurseries, orchards and urban areas. *Xylosandrus compactus*, *X. crassiusculus* and *X. germanus* are native to Asia, and currently established in several countries around the globe. Adult females bore galleries into the plant xylem inoculating mutualistic ambrosia fungi that serve as food source for the developing progeny. Tunneling activity results in chewed wood extrusion from entry holes, sap outflow, foliage wilting followed by canopy dieback, and branch and trunk necrosis. Maintaining plant health by reducing physiological stress is the first recommendation for long-term control. Baited traps, ethanol-treated bolts, trap logs and trap trees of selected species can be used to monitor *Xylosandrus* species. Conventional pest control methods are mostly ineffective against *Xylosandrus* beetles because of the pests' broad host range and rapid spread. Due to challenges with conventional control, more innovative control approaches are being tested, such as the optimization of the push–pull strategy based on specific attractant and repellent combinations, or the use of insecticide-treated netting. Biological control based on the release of entomopathogenic and mycoparasitic fungi, as well as the use of antagonistic bacteria, has yielded promising results. However, these technologies still require validation in real field conditions. Overall, we suggest that management efforts should primarily focus on reducing plant stress and potentially be combined with a multi-faceted approach for controlling *Xylosandrus* damage.

Keywords Forest health · Integrated pest management · Invasive species · Scolytinae · Xyleborini

Key Message

- *Xylosandrus* spp. cause severe damage to plants growing in various environments.
- We provide a comprehensive review of current knowledge on *Xylosandrus* spp. management.
- Traps/lures combinations, ethanol-treated bolts and trap logs/trees are useful for monitoring.
- Host stress reduction is the most effective behavior-based management strategy.
- Attractants and repellents, insecticide-nets and microbial control are promising tools.

Biology and ecology of problematic *Xylosandrus* species

Ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) are widespread colonizers of physiologically stressed or weakened plants (Kühnholz et al. 2001; Ranger et al. 2015a, 2016a). The group includes highly successful invaders (Hulcr and Dunn 2011; Hulcr and Stelinski 2017), and although most ambrosia beetle invasions remain unnoticed due to the lack of visible impacts, new reports documenting

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introductions into areas located outside their native range are increasing (Roques et al. 2009; Haack et al. 2013; Hulcr et al. 2021). The trend toward more introductions is linked to increasing global trade of wood products and climate change (Marini et al. 2011; Meurisse et al. 2019; Biedermann et al. 2019; Grousset et al. 2020; Inward 2020; Lantschner et al. 2020; Zeng et al. 2020), and it is not expected to stop in the near future (Liebhold et al. 2017; Urvois et al. 2021). Some species can also cause severe damage to a broad range of host trees growing in various ecosystems, including plant nurseries, orchards and natural forests (Kirkendall and Faccoli 2010; Sauvard et al. 2010; Hulcr and Dunn 2011; Vannini et al. 2017). Consequently, interest in ambrosia beetles by scientists and plant protection organizations is increasing exponentially.

At present, more than 50 ambrosia beetles are known to be established outside their native range (Lantschner et al. 2020). Most of non-indigenous ambrosia beetles belong to the tribe Xyleborini, including the genus *Xylosandrus* that contains several important invasive species (Dole and Cognato 2010; Greco and Wright 2015; Ranger et al. 2016a; Rassati et al. 2016). Specifically, *Xylosandrus compactus* (Eichhoff), *Xylosandrus crassiusculus* (Motschulsky), and *Xylosandrus germanus* (Blandford) are three species native to subtropical Asia that have been established in several other countries around the world (Haack et al. 2013; Rassati et al. 2016a; Lantschner et al. 2020; Smith et al. 2020). Attacks of these species can occur in different environments including forests, ornamental plant nurseries, orchards, and

urban areas (Ranger et al. 2016a; Agnello et al. 2017; Galko et al. 2019; Gugliuzzo et al. 2019a). Adult females bore galleries into the xylem of twigs, branches, stems, trunks, and exposed roots of a wide variety of woody plants (Greco and Wright 2015; Ranger et al. 2016a). Mutualistic ambrosia fungi are introduced into these galleries by adult females and provide the food source for developing larvae and adult offspring (Kinuura 1995; Hulcr and Stelinski 2017; Biedermann and Vega 2020). The effect of *Xylosandrus* colonization differs between live and dead trees, as do the symptoms. In both cases, sawdust in the form of frass (for *X. compactus*) or compacted "noodles" (for *X. crassiusculus* and *X. germanus*) is extruded from trees, but attack on living trees also produces sap flow, twig wilting followed by canopy dieback, and branch and trunk necrosis.

The black twig borer, *X. compactus*, is currently widely distributed in Africa, Asia, Southeastern USA, and South America (Fig. 1). Introductions of *X. compactus* have occurred in the Pacific Islands, and more recently in Europe (EPPO 2020a). *Xylosandrus compactus* females are minute and shiny black, approximately 1.4–1.8 mm long and 0.7–0.8 wide (Rabaglia et al. 2006). Adults of this species have been recorded from more than 220 host plants, including agricultural crops, trees, shrubs and nursery plants (EPPO 2020a). In particular, *X. compactus* has become an emerging pest of several Mediterranean maquis trees and various ornamental shrubs widespread in southern Europe (Pennacchio et al. 2012; Francardi et al. 2017; Vannini et al. 2017; Gugliuzzo et al. 2019b; Contarini et al. 2020; Leza
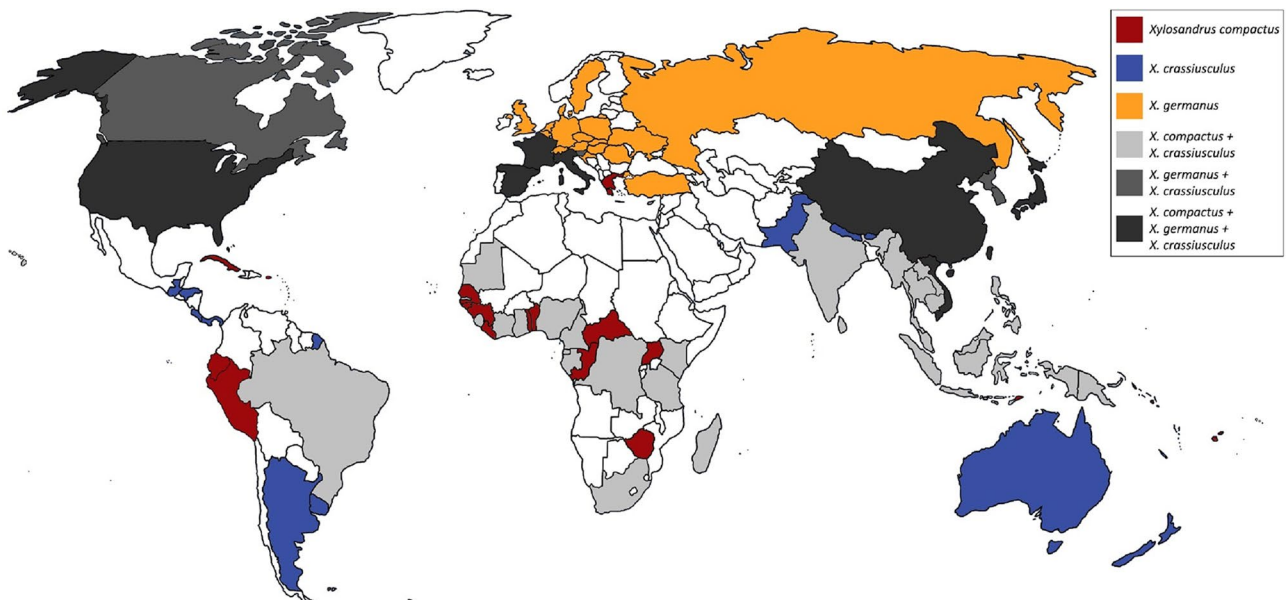

Fig. 1 Current global distribution (as January 11th 2021) of *Xylosandrus compactus*, *X. crassiusculus* and *X. germanus*. Different colors indicate single- or multi-species occurrence of the three ambrosia beetles among countries. The combination of *X. compactus* + *X. ger-* *manus* without *X. crassiusculus* was not found for any country (EPPO 2020b). Colored areas refer to political country areas, not to biogeographical distribution

et al. 2020). Moreover, *X. compactus* has raised serious concerns as a threat to coffee production in East and Central Africa (FAO 2013; IACO 2013; ICO 2014).

The granulate ambrosia beetle, *X. crassiusculus*, has been reported in the USA, Central and South America, Africa, Oceania and Europe (EFSA 2020) (Fig. 1). Female *X. crassiusculus* are on average larger (2.1–2.9 mm in length and about 1.2 mm wide) than the other two *Xylosandrus* species considered in this review. They are reddish-brown, becoming darker brown from the distal half of the elytra (Pennacchio et al. 2003; Rabaglia et al. 2006; Gallego et al. 2017). *Xylosandrus crassiusculus* attacks at least 120 woody host species (Schedl 1963). However, thin-barked deciduous species are attacked more frequently, including nursery ornamental (Ranger et al. 2015a) and cultivated fruit trees (Carrillo et al. 2012).

Xylosandrus germanus is now established in 21 European countries (Fig. 1), along with Russia, 35 US states, and six Canadian provinces (Bousquet et al. 2013; Ranger et al. 2016a; Gomez et al. 2018; Galko et al. 2019; Rabaglia et al. 2019; Webster et al. 2020). The beetle has several common names including black stem borer, black timber bark beetle, and tea root borer. Adult females are dark brown to black, shiny, and semi-cylindrical; they are 2.0–2.4 mm long and about 1.0 mm wide (Rabaglia et al. 2006). Over 200 trees and shrubs are among its broad host range (Weber and McPherson 1983a). The most severely attacked hosts are woodland trees, nursery-grown ornamentals, and orchard tree fruit (Cheng and Guo 1994; Yang et al. 2008). Thin-barked deciduous species are preferred (Ranger et al. 2016a). Galko et al. (2019) reported also attacks of *X. germanus* on fresh lumber.

These three *Xylosandrus* spp. also cause damage in their native grounds in southeast Asia. For example, *X. compactus* attacks twigs of tea (*Camellia sinensis* L.), coffee (*Coffea arabica* L. and *Coffea canephora* Pierre ex A. Froehner), and many ornamental plants (Kaneko et al. 1965; Lin et al. 1994; Gao et al. 2017; Wu et al. 2007); *X. crassiusculus* cause damage to rubber tree (*Hevea brasiliensis* (Willd. ex A. Juss.) Müll. Arg.) and *Morus alba* L. (A 2012; Zhou et al. 2020); and, *X. germanus* is an important pest of tea, grape (*Vitis vinifera* L.) and Chinese chestnut (*Castanea mollissima* Blume) (Kaneko et al. 1965; Yang et al. 2008; Cheng and Guo 1994).

The term "host range" is not just a list of species. It is important to distinguish host trees that are colonized after their death when the defense mechanisms cease, from tree species that are colonized while still alive. The latter is typically a much more restricted list than the total host range in the literature, but those tree species are more important from the management perspective. Some authors also distinguish reproductive hosts from non-reproductive hosts. This difference has not been explored well in *Xylosandrus* compared to other ambrosia beetle pests (e.g., Eskalen et al. 2013; Martini et al. 2017; Paap et al. 2020), but the reproductive hosts are likely to be more important for management. Moreover, the geographic distribution of vulnerable host trees and the physio-climatic classification of related native and invaded regions are key factors in the context of the invasion success of these pests.

Males of these three *Xylosandrus* spp., like other ambrosia beetles belonging to the tribe Xyleborini, are smaller than females, flightless, with a radically reduced thorax (Rabaglia et al. 2006). They are rarely observed outside the brood gallery and sibling mating dominates reproduction (Peer and Taborsky 2005; Keller et al. 2011). Multiple asynchronous emergences of *Xylosandrus* beetles from the same gallery (Oliver and Mannion 2001) may suggest some internal intersection of galleries within the wood, potentially allowing some non-sibling mating. Larvae develop from eggs laid in the system of galleries excavated by the foundress female. They feed on species-specific fungal mutualists (Vega and Biedermann 2020) that are carried by females in a dedicated fungus-spore-carrying structure (mycangium or mycetangium, as suggested by Vega and Biedermann 2020), and inoculated during gallery excavation (Hulcr and Stelinski 2017; Li et al. 2019; Biedermann and Vega 2020). Female oviposition occurs only after feeding on the fungal mutualist that is established within the gallery (Weber and McPherson 1983b; Kinuura 1995).

Each of the three *Xylosandrus* spp. is consistently associated with one primary mycetangial mutualist from the genus *Ambrosiella* (Microascales: Ceratocystidaceae) (Masuya 2007; Alamouti et al. 2009; Mayers et al. 2015; Ito and Kajimura 2017; Skelton et al. 2019). Specifically, *A. xylebori* Brader ex Arx and Hennebert, *A. grosmanniae* C. Mayers, McNew and T.C. Harr. and *A. roeperi* T.C. Harr. and McNew occur with *X. compactus, X. germanus* and *X. crassiusculus*, respectively (Harrington et al. 2014; Mayers et al. 2015; Bateman et al. 2016). Other microorganisms can be found in association with these ambrosia beetles, most commonly *Fusarium* spp., yeasts, and many transient fungi and bacteria. Their ecology has not been studied well, and they appear to be commensals or even antagonists (Dute et al. 2002; Hulcr and Cognato 2010; Hulcr et al. 2012; Bateman et al. 2016; Rassati et al. 2019a; Grubbs et al. 2020). A few fungal species isolated from galleries infested by these three *Xylosandrus* spp. are plant pathogens, such as species of the genus *Ophiostoma*, *Fusarium*, *Phomopsis* and *Raffaelea* (Kinuura 1995; Dute et al. 2002; Ploetz et al. 2013; Carrillo et al. 2014; Bateman et al. 2016; Egonyu et al. 2017; Gugliuzzo et al. 2020; Morales-Rodríguez et al. 2020). The extent to which they contribute to tree damage or death remains untested.

The key feature often highlighted for the invasion success of Xyleborini is inbreeding-mating among siblings in

maternal galleries (Jordal et al. 2000; Grousset et al. 2020). Females arriving in a new environment are already fertilized and ready to establish a new population. However, only a fraction of Xyleborini, as well as only a fraction of *Xylosandrus*, are widespread invasive (Dole and Cognato 2010). There are over 50 species of *Xylosandrus*, but only these three have colonized most of the world; the remaining ones are rarely collected outside of their native range, and most of them remain rare. There are exceptions, such as, for example, *Xylosandrus amputatus* and *Xylosandrus morigerus* whose ranges are also expanding, but not as rapidly as the previous three (Cognato et al. 2011; Rassati et al. 2016).

What allows these three *Xylosandrus* species to become effective invaders is thus still a matter of speculation. The general fact of feeding on fungal mutualists is an unlikely reason, because most ambrosia beetles are not invasive; on the contrary, the mutualists' microenvironmental demands further restrict the ecological niche breadth. What may provide the key ecological advantage are the main fungal mutualists which these three beetle species carry in their mycetangia. Although there is a different association between specific fungal species and each of these invasive beetles (Skelton et al. 2019), it appears that all three species are abundant in natural areas, which then often spill over into human-made landscapes including nurseries and orchards (Reding et al. 2015).

Another reason for the spread of these three *Xylosandrus* spp. is climate change which causes unpredictable weather conditions and drastic fluctuations in temperature and precipitation in different parts of the world (Urvois et al. 2021). This creates stress conditions for trees (i.e., flood, drought, etc.) and make them vulnerable for beetle attacks. These invasive *Xylosandrus* spp., and more specifically *X. crassiusculus* and *X. germanus* which are specialized on freshly dead or stressed trees, are therefore able to find suitable tree hosts, and are likely to continue spreading. The majority of the life cycle of *Xylosandrus* spp., including pupation, occurs within the host plant galleries in the wood. Adults spend very little time outside of trees for dispersal and host selection. However, *Xylosandrus* beetles readily take flight after emergence and have been shown to be good flyers (Gugliuzzo et al. 2019a). Furthermore, their broad host range, their efficiency at locating and colonizing trees under physiological stress, and the lack of effective natural enemies in newly invaded environments render beetle management challenging and often ineffective. Reviews dedicated to the management of ambrosia beetles have focused on *X. compactus* with emphasis on coffee in Hawaii (Greco and Wright 2015), as well as *X. crassiusculus* and *X. germanus* in ornamental plant nurseries (Ranger et al. 2016a). These have been implemented more recently following the publication of several important advances in understanding of the biology, ecology, and control strategies of these invasive fungus-farming beetles.

However, several aspects concerning the real effectiveness and the possible improvement of some management strategies against *Xylosandrus* spp. are still under evaluation. The purpose of this review is to summarize, discuss, and explore global advances and current implementations for the sustainable management of emerging ambrosia beetles in the genus *Xylosandrus* (Fig. 2).

Cultural control

Weakened, dying or physiologically stressed trees are the main hosts of the opportunistic *X. crassiusculus* and *X. germanus* (Ranger et al. 2016a). Therefore, maintaining tree health and vigor is a crucial first step for reducing the risk of ambrosia beetle infestations. Maintenance of plant health to prevent attack is particularly true for these two species, which are poor colonizers of vigorous plants, but can locate vulnerable hosts in the early stage of physiological stress (Weber and McPherson 1983b; Ranger et al. 2015a, b). As recommended for other wood borers, reducing the tree density can strengthen the vigor of individual trees (Jactel et al. 2009) and thus their susceptibility to *Xylosandrus* attacks. The rate of attack of *X. germanus* and *X. crassiusculus* on completely healthy trees is statistically negligible (Ranger et al. 2010). Unlike *X. crassiusculus* and *X. germanus*, *X. compactus* is one of the few exceptions which preferentially colonize healthy or recently stressed trees (Chong et al. 2009; Greco and Wright 2015; Gao et al. 2017; Vannini et al. 2017). Its colonization success, however, has not been examined under experimentally controlled conditions to determine the influence of host quality or host stress (Ranger et al. 2021).

Among abiotic factors predisposing trees to attack by *Xylosandrus* spp., flooding and freezing events are the most representative (La Spina et al. 2013; Ranger et al. 2013a, 2015a, 2019). Trees intolerant of flooding are preferentially attacked over flood tolerant species (Ranger et al. 2015a). Consequently, monitoring soil moisture levels in regions where potential hosts occur could allow risk forecasting for infestations and provide a possible preventative tool. For example, Frank and Ranger (2016) observed fewer ambrosia beetle attacks on flood-intolerant container-grown nursery trees with substrate moisture levels of 30% and 50% compared to those grown in 70% or 90%. These results were confirmed by Frank et al. (2017), whereby infestations of *Xylosandrus* spp. were reduced on ornamental trees maintained at 50% or lower water holding capacity of the container substrate. Empirical evidence of extreme frost events (i.e., freezing-related necrotic tissues) preceding large-scale ambrosia beetle attacks on European beech (*Fagus sylvatica* L.) in Western Europe (La Spina et al. 2013), and on thin-barked deciduous trees in the USA, also highlight the
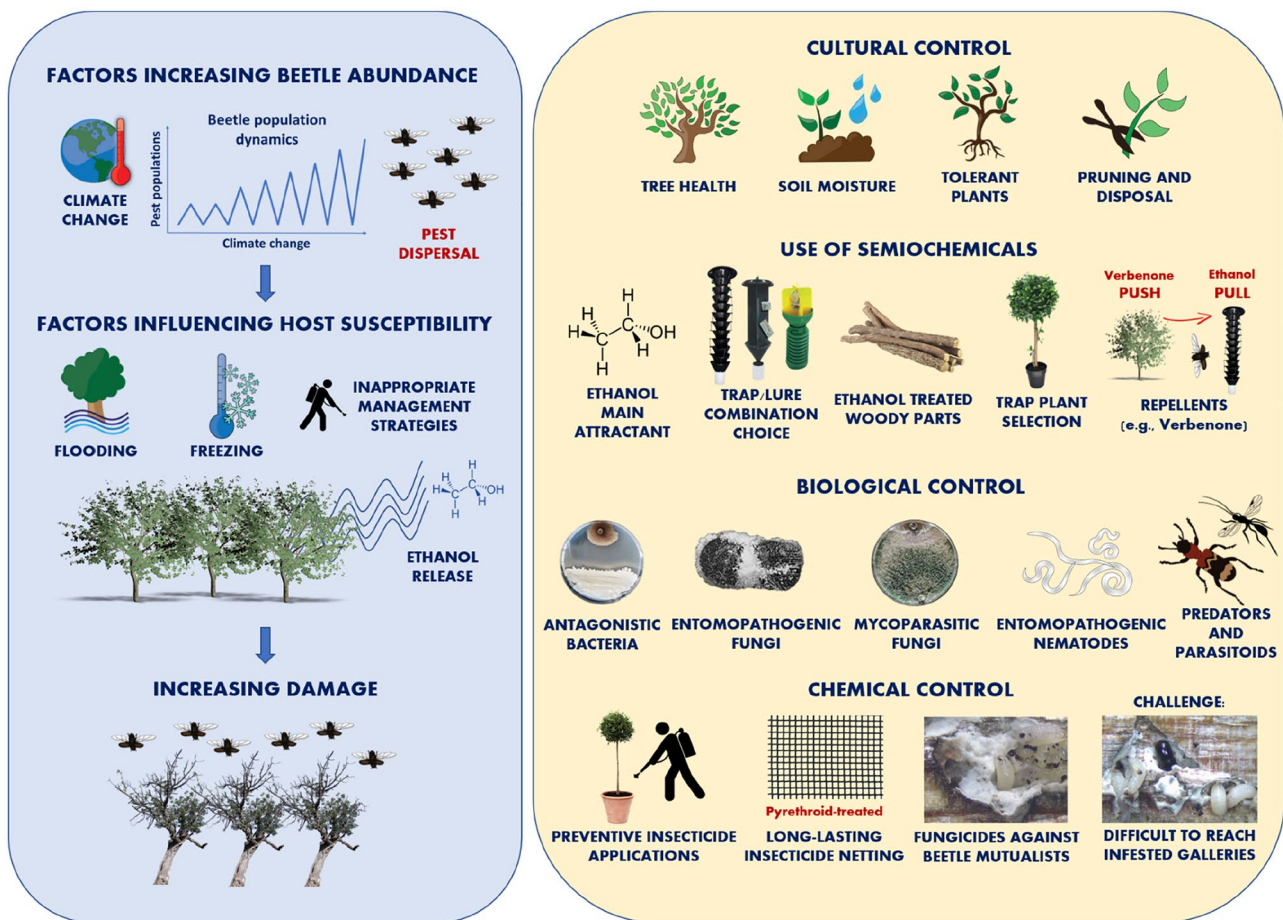
Fig. 2 Overview of the main factors influencing *Xylosandrus* spp. abundance and management

possible influence of frost events on tree attractiveness and/or susceptibility, especially when mild winters were followed by late-spring freezes (Ranger et al. 2015b, 2019). La Spina et al. (2013) demonstrated that *X. germanus* was more attracted to bark tissue of beech trees experimentally injured by freezing compared to undamaged bark. Similarly, in the USA, *X. crassiusculus* and *X. germanus* rapidly attacked container-grown trees that were experimentally freeze-stressed, while no attacks occurred on control trees (Ranger et al. 2019). Consequently, proper selection and matching of plant species or cultivar with growing region will contribute toward higher plant tolerance to low temperatures and/or to other abiotic stressors and thus prevent secondary beetle injuries.

Along with abiotic factors, biotic factors also can induce the production and emission of ethanol (Kelsey and Joseph 1998; Kelsey 2001; Kelsey et al. 2016), which attracts *Xylosandrus* spp. (Ranger et al. 2021). For instance, trees infected by the oomycete *Phytophthora ramorum* Werres, de Cock and Man in't Veld, the causal agent of sudden oak death disease, were more attractive to certain ambrosia

beetles than uninfected trees as a result of a higher ethanol concentration in wood tissues (McPherson et al. 2005, 2008; Kelsey et al. 2016). Similar observations are recorded for plant fungal pathogens and *Xylosandrus* spp. (Ranger et al. 2021). Whether the presence of a fungal pathogen in wood tissue can affect beetle fitness by competing with its main mutualist remains unclear (Fernandez-Conradi et al. 2018). Previous studies showed a mixed response depending on the fungal pathogen and the ambrosia beetle species (Menocal et al. 2017, 2018a; Fraedrich et al. 2018), but no study targeting *Xylosandrus* spp. has been performed so far. The role of phytopathogens in the associations with *Xylosandrus* spp.in host selection and colonization success is an important aspect to consider for improving cultural control strategies.

Most initial infestations by *X. compactus* occur on twigs and small branches rather than larger branches and trunks (Masuya 2007; Greco and Wright 2015; Gugliuzzo et al. 2019c). Therefore, proper tree pruning including removal of tissues exhibiting initial signs of attack (e.g., wilting, necrosis, entry holes, etc.) can be a potential cultural control

strategy, as suggested by Gugliuzzo et al. (2020). Similarly, non-target infested plant material, including trap plants growing in the vicinity of the cultivated crop, or plants becoming infested within ornamental nurseries should be promptly removed and destroyed to prevent adult beetle emergence and re-infestation (Ranger et al. 2016a).

Use of semiochemicals

Lures

Ethanol is the most studied semiochemical involved in the attraction of ambrosia beetles to susceptible host plants. Several studies demonstrated that ethanol is attractive to *Xylosandrus* beetles and serves as a cue for females to locate suitable hosts (Miller and Rabaglia 2009; Ranger et al., 2010, 2012). Ethanol is released by plants under stress (Kimmerer and Kozlowski 1982; Ranger et al., 2013a, 2019), often as a result of anaerobic respiration, and it is one of the most attractive semiochemicals for many Xyleborini, including some *Xylosandrus* spp. (Burbano et al. 2012; Reding et al., 2013a; Ranger et al. 2021). Ethanol also is emitted by *Fusarium solani* (Mart.) Sacc., a fungal symbiont of *X. compactus* (Egonyu and Torto 2018). Besides its role in attracting ambrosia beetles, ethanol contained in woody tissues influences the colonization success of *Xylosandrus* spp., notably by promoting the growth of some of their mutualistic fungi, such as *A. grosmanniae* and *A. roeperi* associated with *X. germanus* and *X. crassiusculus*, respectively (Ranger et al. 2018). Interestingly, ethanol also has been shown to inhibit the growth of fungal garden competitors (Ranger et al. 2018; Lehenberger et al. 2020). For instance, *X. germanus* did not produce fungal gardens or broods in trees baited with ethanol, but gardens and brood were established in living stem tissues containing ethanol introduced through irrigation (Ranger et al. 2018). The concentration of ethanol in wood tissue might also facilitate niche-partitioning. In a field experiment involving ethanol-soaked logs, the number of entry holes decreased with increasing ethanol concentration for *X. germanus* and increased for *Xyleborinus saxesenii* (Ratzeburg) (Rassati et al. 2020); in addition, the number of galleries with brood was higher for *X. germanus* than for *X. saxesenii*, even though the attack rate was significantly higher for the latter species (Rassati et al. 2020).

Lures for monitoring *Xylosandrus* species generally consist of sealed polyethylene sachet or pouch-style dispensers, or capped polyethylene vials, filled with 70–95% ethanol. These dispensers are designed to maintain a steady release rate over time, but may possibly be perforated (in the upper part of the pouch, or in the cap of the vials) to facilitate ethanol volatilization and increase release rates. Ethanol release rate is obviously a key variable affecting the efficacy of the lures. Both standard-release (release rate of 65 mg/day at 30 °C) and ultra-high-release (0.6 g/day at 25–28 °C) ethanol lures are commercially available (Miller and Rabaglia 2009; Reding et al. 2013b). A positive correlation between ethanol release rate and trap captures or attacks by *Xylosandrus* spp. was shown in previous studies (Ranger et al. 2012, 2015b), although this pattern was not evident for *X. germanus* when ethanol-soaked logs were used (Rassati et al. 2020). The optimal release rate of ethanol may vary depending on the beetle species, and it is necessary to conduct further studies to elucidate these mechanisms. Commercially available releasers alleviate the need for lure preparation by the grower and some of the challenges associated with rapid ethanol evaporation (Oliver and Mannion 2001; Reding et al. 2011). Commercial lures of high release ethanol rate have notably been used in Spain, for the monitoring of *X. crassiusculus* and *X. compactus* (Gallego et al. 2017; Leza et al. 2020). The addition of conophthorin and α-pinene to ethanol was evaluated for improving the attraction of *Xylosandrus* spp., but the results were inconsistent and do not justify the increased cost of resultant lures (Miller and Rabaglia 2009; Ranger et al. 2011a, 2014; Burbano et al. 2012; Miller et al. 2015a, 2018, 2020). Other experiments comparing single and multi-lure traps showed that *X. crassiusculus* was trapped exclusively with ethanol-only lures compared to those baited simultaneously with ethanol, frontalin, ipsenol/ipsdienol, and (-)α-pinene (Rassati et al. 2014). More recently, a specific multi-lure trapping strategy for *X. crassiusculus* and *X. compactus* is being developed and tested in Europe (Gallego, unpublished).

Traps in combination with lures can be reliably used as monitoring devices for the presence of *Xyleborus* spp., another genus of important pests belonging to the tribe Xyleborini. Nevertheless, so far they have been ineffective for mass trapping. In fact, for bark and ambrosia beetles in general, mass trapping is only possible with sexual or aggregation pheromones, which are orders-of-magnitude more attractive than tree produced kairomones, including ethanol (Miller and Rabaglia 2009). Furthermore, even in the pheromone-based systems, mass trapping has rarely been shown as cost-effective (Grégoire et al. 2001). In addition, *Xylosandrus* spp. are not coordinated in their attacks, as the mass-attacking conifer bark beetles are (Blomquist et al. 2010), and instead colonize stressed trees individually.

Traps

Ethanol-baited traps are the predominant method for monitoring ambrosia beetle populations, including *Xylosandrus* spp. in ornamental nurseries (Reding et al., 2010, 2011, 2015), forests (Hauptman et al. 2019; Martínez et al. 2019; Marchioro et al. 2020), and urban landscapes and parks (Klingeman et al. 2017; Gugliuzzo et al. 2019a). Several

types of traps are commercially available, and homemade inexpensive bottle traps can be easily made and baited with lures (Egonyu and Torto 2018; Owens et al. 2019b). Among most simple models, Baker-type traps can be made by cutting openings (windows) in 2-L soft drink bottles. The ethanol-based lure is usually suspended within the upper part of the bottle and diluted soapy water, or low toxicity antifreeze (propylene glycol), is used as killing and preservative agents in the reservoir created within the bottle.

A single-window bottle trap baited with ethanol-based hand sanitizers effectively attracts and catches *X. crassiusculus* (Steininger et al. 2015). Moreover, a modified Baker-type trap employing a bottle connector to connect the mouths of two bottles allows easier recovery of trap contents than single bottle designs (Reding et al. 2011). More commonly, Lindgren funnel traps are used for Scolytinae beetles including many invasive Xyleborini (Miller and Duerr 2008). Lindgren traps consist of a variable number of interconnected vertical funnels through which beetles reach a collecting cup attached at the lowest funnel (Lindgren 1983). Lindgren traps traditionally have been black in color since many borers are attracted to dark silhouettes (Campbell and Borden 2006, 2009). However, other Lindgren trap colors (e.g., green, purple) also have been used to trap other wood-boring insects like emerald ash borer (*Agrilus planipennis* Fairmaire), and these alternative colors also will generally collect *Xylosandrus* spp. as long as the trap is baited with an ethanol lure (Francese et al. 2013; Rassati et al. 2019b; Cavaletto et al. 2020; Marchioro et al. 2020). Indeed, most ethanol-baited traps have been shown suitable for monitoring the presence or absence of ambrosia beetle. However, identifying a most efficient trap type is difficult. As earlier studies have identified forest composition and other factors to affect relative trap efficacy in catching ambrosia beetles (Miller et al. 2018).

Japanese beetle traps were more effective than Lindgren funnel traps, both baited with 95% ethanol, for monitoring *X. compactus* in *Coffea arabica* L. plantations and *Acacia koa* A. Gray nurseries in Hawaii (Burbano et al. 2012). The traditional Japanese beetle trap consists of a yellow-colored funnel with four vertical blades connected to a green plastic collection canister. Miller et al. (2018) caught larger numbers of *X. crassiusculus* in multiple-funnel traps (baited with ethanol and conophthorin) than in bottle traps in Eastern USA, but the same trials yielded variable results with *X. germanus*. Also, Gugliuzzo et al. (2019a) showed that red, cross-shaped sticky traps baited with ethanol were effective for monitoring flight activity of *X. compactus* in infested carob trees (*Ceratonia siliqua* L.). Werle et al. (2014) found red or opaque corrugated plastic with sticky glue, and ethanol baits were significantly more attractive to multiple ambrosia beetles (including *Xylosandrus* spp.) than yellow or white, but were not significantly different from other colors like black, blue, brown, clear, gray, green, lavender, orange, or purple. This general preference of *Xylosandrus* spp. for dark colors over light colors, especially yellow, was confirmed also using colored-panel traps (Cavaletto et al. 2020). Cross-vane sliding and sticky-coated traps (Cross-trap®, Econex, Spain) have been developed by improving the classical traps used for mass trapping of *Monochamus galloprovincialis* (Olivier), the vector of pine wilt nematode (*Bursaphelenchus xylophilus* (Steiner & Buhrer) Nickle) (Álvarez et al. 2015). This trap model is currently under evaluation with promising preliminary results for the mass trapping of *X. crassiusculus* and *X. compactus* (Gallego, unpublished).

Several other factors can affect catch rates of *Xylosandrus* spp., including trap placement (Reding et al. 2010; Klingeman et al. 2017; Marchioro et al. 2020; Miller et al. 2020). Traps placed 0.5 m above the ground capture more *X. germanus* than those placed at 1.7 or 3.0 m (Reding et al. 2010). Similarly, Miller et al. (2020) demonstrated that understory traps capture more *X. crassiusculus* than canopy traps. Traps hung on trees at a 1.5 m height are effective for *X. compactus* detection (Burbano et al. 2012). Reding et al. (2015) observed that overwintered *X. germanus* females occur earlier in proximity to wooded areas adjacent to nurseries and later within nurseries, hypothesizing that forests serve as the reservoir for dispersal of beetles in the spring.

Menocal et al. (2018b) showed most *X. crassiusculus* dispersal in avocado (*Persea americana* Mill.) orchards occurs near dusk with females initiating flight 30 min before sunset as light intensity and wind speed decrease. Thorough understanding of daily flight periodicity and optimal trap placement should be described for other invasive *Xylosandrus* spp., to further optimize monitoring and/or mass trapping strategies (Sheehan et al. 2019; Ulyshen and Sheehan 2019; Miller et al. 2020).

Trap trees and ethanol-treated tree bolts

Artificial alteration of tree (or selected tissues) attractiveness to modify host location behavior of *Xylosandrus* spp. is another strategy for beetle monitoring or possible direct management. For example, Ranger et al. (2010, 2012, 2013a, b) enhanced the attractiveness of 4-year-old *Magnolia virginiana* L. by injecting their stems with a concentrated ethanol solution (e.g., 75 ml of 90% ethanol) or by artificially causing flood stress. Reding et al. (2017) confirmed the effectiveness of such "trap trees" created by ethanol injection (75 ml of 90% ethanol) using a wide range of deciduous trees species. Moreover, Addesso et al. (2019) documented considerably higher attacks in trees injected with high doses of ethanol than in adjacent mildly stressed trees (injected with a lower ethanol dose to simulate common stress occurring in nursery). These studies demonstrate that a wide range of

host plant material can potentially be used to attract, monitor and potentially manage exotic ambrosia beetles, including *Xylosandrus* spp.

Ethanol treatment also increases *Xylosandrus* beetle attacks on bolts (i.e., tree stem sections). Indeed, Reding and Ranger (2020) observed that tree bolts immersed in 10% ethanol for at least 24 h or filled with 10 ml of 95% ethanol by drilling a chamber in the wood before deployment, both captured more *X. germanus* than ethanol-baited bottle traps. Similar results were demonstrated for *X. crassiusculus*; however, drilled bolts filled with ethanol were often less attractive than traps and infused bolts (Reding and Ranger 2020). Furthermore, Rassati et al. (2020) and Cavaletto et al. (2021) demonstrated that the ethanol concentration in tissues of ethanol-soaked bolts affects *Xylosandrus* spp. host selection and colonization success.

Overall, ethanol-treated bolts, trap logs, and trap trees of selected species can be used to attract and trap *Xylosandrus* species selectively, i.e., with low non-target catches (Mayfield et al. 2013; Reding et al. 2017; Addesso et al. 2019; Rassati et al. 2020; Reding and Ranger 2020). Manipulation of tree attractiveness to beetles with the aim to develop monitoring strategies or to reduce colonization of the cultivated target crop could emerge as an innovative behavior-based management strategy. For example, selective behavioral modification could be used to reduce beetle infestations on susceptible host plants in nurseries, orchards, and natural tree stands. Another possible use of ethanol-treated bolts could be for insecticide residue studies or evaluation of potential repellents (Brown et al. 2020).

Push–pull strategies

Another semiochemical-based strategy, more recently evaluated for *Xylosandrus* ambrosia beetles, combines ethanol-baited traps (or trap trees) placed at a distance from the vulnerable host plants and repellents appropriately placed on or in close proximity to the protected crop (Ranger et al. 2013b; Addesso et al. 2019; Werle et al. 2019). This management strategy, known as push–pull, manipulates the behavior of insects by combining the two forces: (1) a repellent to 'push' them away from the cultivated host and (2) an attractant to 'pull' them into a trap crop or artificial trap (Cook et al. 2007). However, efforts to use ethanol lures or trap trees (i.e., ethanol-injected or flood-stressed plants) as a 'pull' attractant and synthetic repellents as a 'push' component has had inconsistent results (Ranger et al. 2013b; Addesso et al. 2019; Werle et al. 2019; Rivera et al. 2020).

The bark beetle anti-aggregation pheromone, verbenone, has shown promising results as a multi-species repellent, with activity against *X. compactus*, *X. crassiusculus* and *X. germanus* (Burbano et al. 2012; VanDerLaan and Ginzel 2013; Ranger et al. 2014). A 97% reduction in catches

was observed for *X. germanus* when ethanol-baited traps also contained verbenone dispensers releasing 50 mg/day (Ranger et al. 2013b). Attraction to ethanol-baited traps is also significantly reduced for both *X. germanus* and *X. compactus* with the addition of verbenone dispensers releasing 2 mg/day (Burbano et al. 2012; Ranger et al. 2014). Ethanol-injected trap trees had 85% fewer ambrosia beetle attacks when treated with verbenone dispensers compared to trap trees without them, demonstrating the effective repellence of the verbenone (Ranger et al. 2013b). A similar reduction of tree infestation was documented with *Xyleborus grabratus* Eichhoff after treating host trees or bolts with verbenone dispensers (Hughes et al. 2017; Martini et al. 2019), indicating the broad-spectrum effectiveness of this repellent against ambrosia beetles. Agnello et al. (2017) observed evidence of reduced *X. germanus* attacks with verbenone in plots that were also treated with permethrin during management trials in apple (*Malus* spp.) orchards. Moreover, other volatile organic compounds (VOCs), such as limonene and terpinolene, have been shown to reduce attraction of *X. compactus* and *X. germanus* to ethanol lures (Burbano et al. 2012; Ranger et al. 2014).

Although both ethanol and verbenone have been widely evaluated as attractants and repellents for *Xylosandrus* species, respectively, their combined use for push–pull beetle management requires further investigation. Werle et al. (2019) did not observe an additive or synergistic effect of combining verbenone and ethanol in evaluations of push–pull against *Xylosandrus* spp. among woodlots of five different USA states. Similarly, Addesso et al. (2019) did not find ethanol-injected trap trees reduced attacks on adjacent, less attractive trees; varying densities of perimeter ethanol-baited traps also failed to protect ethanol-injected trap trees. However, Rivera et al. (2020) observed a significant reduction in *Xyleborus* spp. ambrosia beetle captures (vectors of laurel wilt [*Raffaelea lauricola* T. C. Harr., Fraedrich & Aghayeva]) in commercial avocado push–pull plots treated with verbenone dispensers (SPLAT®, ISCA Technologies, Riverside, CA) and co-deployed with ethanol lures along plot borders compared to plots treated with verbenone or ethanol alone. Similar promising results were observed with early development of push–pull for other ambrosia beetle species, including *Euwallacea fornicatus* (Eichhoff) in avocado (Byers et al. 2021).

Therefore, further optimization of the push–pull strategy for *Xylosandrus* ambrosia beetles is warranted. The main challenge facing recent attempts to develop push–pull against ambrosia beetle species has been relatively weak activity of the repellents tested to date. In cases where efforts were made to understand mechanisms of efficacy, the effective repellent radius of verbenone-releasing dispensers has been quantified as less than 1 m (Byers et al. 2018; Rivera et al. 2020). Accordingly, it would need a high density of

these repellent dispensers per treated area for effective management, which would likely be impractical and not economically sustainable. Identification of more potent repellents and/or development of appropriate formulations that could achieve a high deployment density per area of treated crop should be explored. Another biological challenge is the dispersal capabilities of ambrosia beetles. These minute insects can disperse long distances over brief periods (ca. 20–80 m / 24 h; with maximum distances recorded from 200-400 m) without wind assistance (Seo et al. 2017; Owens et al. 2019a). Therefore, a behavioral manipulation strategy will require potent active compounds to thwart colonizing beetles that could arrive from long distances. While push–pull is unlikely to adequately manage beetle populations as a stand-alone treatment, benefits are possible if it is integrated in association with additional preventive measures such as conservation biological control, removal of infected and stressed trees, or application of protective treatments like insecticides. In this framework, future studies should consider repellent release technology, the use of alternative or synergic repellents, the effect of different ethanol-baited trap designs, and the practical applications within different growing environments, e.g., nurseries, tree fruit, and/or forest stands.

Microbial control

Entomopathogenic fungi

Among promising biocontrol agents of ambrosia beetles, commercial strains of *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium brunneum* Petch (Ascomycota: Hypocreales) have shown high virulence against *X. crassiusculus* and *X. germanus* in different laboratory trials (Castrillo et al. 2011, 2013, 2016). Laboratory studies on comparative virulence using direct spray applications to foundresses showed that strains of *B. bassiana* Naturalis® (= ATCC 74040) and *M. brunneum* F52® (= ARSEF 5198) at a dosage of 600 conidia/mm^2 significantly affected the survival and brood production of *X. germanus*, resulting in ≥ 60% mortality at 6 days post-exposure compared to controls (Castrillo et al. 2011). Laboratory studies with *X. crassiusculus* showed that this species is even more susceptible to these pathogens with 50% mortality occurring a day earlier at less than half the dosage required for *X. germanus* (Castrillo et al. 2011, 2013). Moreover, exposure of *X. crassiusculus* and *X. germanus* females to beech (*Fagus* spp.) stems treated with the same biocontrol agents resulted in lower survival rates, fewer galleries, and reduced brood production (Castrillo et al. 2013, 2016). Some of the progeny produced also became infected by fungal conidia produced on female cadavers, further reducing effective brood size

(Castrillo et al. 2013). A natural infection of *X. compactus* by *B. bassiana* in the absence of field applied formulations was observed by Balakrishnan et al. (1994) on coffee in India. In the same study, spray applications of *B. bassiana* spores caused 21% infection of surveyed beetles two weeks after application.

Beauveria bassiana and *M. anisopliae* (Metch) Sorokin also were found among the fungal flora associated with *X. germanus* females in hazelnut orchards (Tuncer et al. 2017). Isolates of *B. bassiana* (TR-217) and *M. anisopliae* (TR-106) were sampled from *X. germanus* cadavers and tested against the pest in the laboratory. Eighty and 100% mortality was obtained following *B. bassiana* and *M. anisopliae* topical applications, respectively, both at 1×10^8 conidia ml^{-1} dosages (Tuncer et al. 2019). Moreover, another entomopathogenic fungus, *Isaria fumosorosea* Wize (strain TR-78–3) (Ascomycota: Hypocreales), significantly reduced survival of *X. compactus* in laboratory trials both after direct application to the beetles and indirect treatment of hazelnut branches (Kushiyev et al. 2018). Avery et al. (2018) confirmed the susceptibility of *X. crassiusculus* to *B. bassiana*, *I. fumosorosea* and *M. brunneum* commercial strains, but spore acquisition by treated beetles was significantly higher after exposure to *B. bassiana* compared to the other two fungi. Mukasa et al. (2019) observed more than 70% mortality of *X. compactus* in laboratory and field tests with an atoxigenic L-strain of *Aspergillus flavus* Link (Eurotiales: Trichocomaceae) isolated from Robusta coffee (*Coffea canephora* Pierre ex A. Froehner) farms in Uganda.

However, the efficacy of these entomopathogenic fungi against *Xylosandrus* spp. under field conditions remains to be properly assessed though they produce promising results under the laboratory conditions. Preliminary field studies testing *B. bassiana* and *M. brunneum* against *X. germanus*, *X. crassiusculus* and *Cnestus mutilatus* (Blandford) on excised beech bolts suggest that further studies are needed to develop economical strategies and to improve the efficient delivery of these microbials in the field (Castrillo et al., unpublished). Given that insect host–fungal pathogen interactions are determined by variables such as fungal species, strain and dosage, insect life stage, physiology and behavior, and environmental conditions (i.e., relative humidity, UV light, temperature, host plant) (Castrillo 2018; Mann and Davis 2020), field tests are also needed to determine optimal application strategies of these control agents (i.e., formulation type, application mode, rate, and frequency based on beetle phenology). Surveys for naturally occurring pathogens and strains associated with these beetles may offer alternatives that could be more virulent to the beetles or more adapted to their natural habitats rather than commercial ones. However, the cost and length of time required to develop (i.e., mass production and formulation studies) and register these naturally associated strains as new commercial

products could be a hindrance to their rapid deployment in the field. In contrast, commercially available strains such as *B. bassiana* GHA and *M. brunneum* F52 that have been proven to be pathogenic against these beetles offer readily available products compatible with available application technologies. As with other control options, the use of these fungi needs to be integrated with other control strategies required for optimal beetle control under a given habitat or cropping system.

Mycoparasitic fungi and antagonistic bacteria

Xylosandrus ambrosia beetles perform most of their life cycle within host wood, living in nutritional mutualism with *Ambrosiella* fungi. Therefore, altering the microbial community associated with beetles, through the release of microbial antagonists, could potentially offer an important tool for developing sustainable management strategies. Targeted growth suppression of beetles' mutualistic fungi has been observed with antagonistic agents like mycoparasitic fungi and antagonistic bacteria, which reduce development of beetle progeny (Castrillo et al. 2016; Eatough Jones et al. 2017; Kushiyev et al. 2020).

Among mycoparasitic fungi, several *Trichoderma* species and strains (Ascomycota: Hypocreales) that exhibit multiple modes of action (mycoparasitism, spatial and nutrient competition, antibiosis by enzymes and metabolites) are mainly used against plant fungal pathogens (Verma et al. 2007; Vinale et al. 2008). However, little has been documented on the use of *Trichoderma* spp. against ambrosia beetles. The antagonistic activity of various *Trichoderma* fungi against *Ambrosiella* mutualists, specific to each *Xylosandrus* species, was initially observed in in vitro tests and subsequently evaluated in complementary beetle bioassays (Castrillo et al. 2016). Specifically, *Trichoderma harzianum* Rifai (commercial strain T-22) significantly reduced brood production in *X. crassiusculus* and *X. germanus* after foundresses were exposed to treated beech stems (Castrillo et al. 2016). Beetle galleries in *T. harzianum*-treated beech stems had sparse symbiont growth and many had no or only a small number of eggs present (Castrillo et al. 2016). Laboratory trials suggest that various *Trichoderma*-based biofungicides can also affect brood production of *X. compactus* by outcompeting other fungal mutualists within galleries (Gugliuzzo et al., in prep.). Mycoparasitic *Trichoderma* spp. obtained from soil samples of the Black Sea Region of Turkey, including isolates of *T. harzianum*, *T. hamatum* (Bonord.) Bainier, *T. asperellum* Samuels, Lieckf. & Nirenberg and *T. atroviride* P. Karsten, Finl. Mögelsvamp, significantly inhibited growth of *A. grosmanniae* in both Petri dish assays and within *X. germanus* galleries (Kushiyev et al. 2020). Moreover, a slight reduction of ambrosia beetle attacks was observed by Brown et al. (2019) under field conditions when evaluating

T. harzianum (strain T-22) + *Trichoderma virens* (J.H. Mill., Giddens & A.A. Foster) Arx, Beihefte zur Nova Hedwigia (strain G-41) (RootShield Plus®) for *Phytophthora* root rot control on flowering dogwoods (*Cornus florida* L.) after flood events. Future investigations should focus on evaluation of *Trichoderma* species and strain affinity for host plant wood. Indeed, Gugliuzzo et al. (in prep.) observed significantly higher impact of *T. atroviride* SC1 on brood production of *X. compactus* compared to other commercial species/strains tested, irrespective of application rate. The SC1 strain was isolated from decaying hazelnut wood, and it is characterized by rapid growth, germination, and wood colonization (Longa et al. 2008).

Among antagonistic bacteria, *Bacillus* spp. are known for their ability to dominate within an ecological niche/substrate via production of antimicrobial compounds, and they can be readily formulated as storage resistant spores (Cawoy et al. 2011; Pérez-García et al. 2011). However, their use against ambrosia beetles has been seldomly investigated. Eatough Jones et al. (2017) obtained short-term control of *Euwallacea* sp. with a *Bacillus subtilis* (Ehrenberg) Cohn-based biofungicide in field trials. Concerning *Xylosandrus* spp., the use of two *Bacillus*-based biofungicides (Serenade max: *B. subtilis* QST 713; Amylo-X: *Bacillus amyloliquefaciens* [ex Fukumoto 1943] Priest et al. 1987 emend. Wang et al. 2008 D747) significantly affected mycelial growth of *Ambrosiella xylebori* Brader ex Arx and Hennebert in laboratory assays, reducing development of *X. compactus* progeny (Gugliuzzo et al., in prep.).

Future investigations should identify and enumerate naturally occurring microbial species and strains co-occurring with mutualists that may possess antagonistic properties. Following isolation from naturally infested beetle galleries, evaluations with beetle mutualists can be performed in competitive assays in vitro. Selection of naturally occurring strains that exhibit effectiveness against beetle mutualists could lead to identification of novel biological agents with greater efficacy than current commercial formulations. Moreover, the activity and practical application of newly identified antagonists may yield practical tools for host plant systems where they do not naturally occur. However, as for other biological control agents (e.g., entomopathogenic fungi), practical field applications of mycoparasitic fungi and antagonistic bacteria will have to consider some specific microbial traits (e.g., persistence on tree surface, survival in fluctuating moisture conditions, tolerance to ultraviolet light in sunlight, non-pathogenicity to host plant, and ability to colonize infested galleries), which vary according to the species and strain. Future field applications also need to overcome some of these limitations by means of innovative solutions facilitating the microorganism colonization

and persistence (e.g., gel formulations, UV protectants, pressurized sprays, etc.).

Biological control by predators and parasitoids

No descriptions could be found in the literature of specific predators or parasitoids attacking *Xylosandrus* spp. However, various opportunistic predators feed on bark and ambrosia beetles, including invasive Xyleborini (Weber and McPherson 1983b; Kenis et al. 2004; Greco and Wright 2015; Wegensteiner et al. 2015; Gossner et al. 2019; Jiang and Kajimura 2020). Among them, the predatory beetle, *Callimerus* spp. (Coleoptera: Cleridae), feeds on all biological stages of *X. compactus* within infested coffee branches, exhibiting preference for larvae in more detailed laboratory assays (Sreedharan et al. 1992). Similarly, the beetle, *Cryptamorpha desjardinsi* (Guérin-Méneville) (Coleoptera: Silvanidae), attacks *X. compactus* larvae infesting coffee trees (Greco 2010). More recently, the flat bark beetles, *Carthartus quadricollis* (Guérin-Méneville) (Coleoptera: Silvanidae) and *Leptophloeus* spp. (Coleoptera: Laemophloeidae), have been identified as fortuitous, but likely minor, predators of *X. compactus* in coffee, macadamia nut (*Macadamia* spp.), and mixed coffee-macadamia nut farms (Brill et al. 2020). Egonyu et al. (2015) demonstrated that the ant, *Plagiolepis* sp. (Hymenoptera: Formicidae), is an indigenous predator able to colonize over 18% of *X. compactus* galleries in Uganda. Moreover, the predatory ant, *Pheidole megacephala* (Fabricius) (Hymenoptera: Formicidae), feeds on all life stages of *X. compactus* in laboratory bioassays, but the predator was unable to enter infested galleries. However, in field manipulative experiments, the presence of *P. megacephala* on coffee twigs reduced beetle presence by 22-fold (Ogogol et al. 2017), likely through deterring or removing adult beetles before they bored into the plant. Schedl (1963) observed the curculionid, *Scolytoproctus schaumi* Faust & J. (Coleoptera: Curculionidae), invading and laying eggs inside galleries of *X. crassiusculus*, but its impact on beetle survival and brood development is unknown. As a novel predator at the order level, Jiang and Kajimura (2020) demonstrated that the earwig, *Anisolabella* (*Gonolabis*) *marginalis* (Dohrn) (Dermaptera: Anisolabididae), preys upon adults of seven species of ambrosia beetles, including *X. crassiusculus* and *X. germanus*, in laboratory bioassays.

Among parasitoids, *Tetrastichus* spp. (Hymenoptera: Eulophidae) and *Tetrastichus xylebororum* Domenichini were reported in association with *X. germanus* in Germany and *X. compactus* in Indonesia, respectively (Weber and McPherson 1983b; Balakrishnan et al. 1989). Moreover,

an undescribed bethylid (Hymenoptera: Bethylidae) was recorded in association with *X. compactus* in Indonesia (Balakrishnan et al. 1989). However, *Eupelmus* spp. (Hymenoptera: Eupelmidae) was most frequently associated (> 20%) with *X. compactus* in India (Balakrishnan et al. 1989). More recently, a single specimen of the braconid wasp, *Heterospilus leptostoma* Fischer (Hymenoptera: Braconidae), was isolated from a laurel (*Laurus nobilis* L.) twig infested by *X. compactus* larvae in Italy, but the role of this ectoparasitoid is still unclear (Pennacchio et al. 2012).

Although none of the above-described predators or parasitoids have been reported to effectively suppress populations of *Xylosandrus* spp., there is a general lack of information about their roles in various ecosystems and within their respective plant-host–predator tritrophic interactions and such investigations are needed. For instance, various clerids are attracted by ethanol-baited traps (Miller et al. 2015b), i.e., the kairomones active for ambrosia beetles, and these predators could have value for managing pest *Xylosandrus* beetles. Most predator species are difficult to breed in the laboratory and this makes their study challenging. Moreover, integration of ecological services, such as beneficial arthropods for management of *Xylosandrus* spp., requires thorough investigation of potential new associations that may arise between these beetles and predators or parasitoids following invasion into new environments. It would be of particular interest to test whether the diversity of tree species, which is generally known to confer associational resistance to forest insect pests (Jactel et al. 2020), could be used to strengthen the control of *Xylosandrus* spp. by their natural enemies, in the framework of conservative biological control.

Chemical control

Insecticides

Currently, chemical control of *Xylosandrus* ambrosia beetles consists of preventive insecticide applications to host trees. In addition, direct injection of systemic insecticide into tree trunks has shown efficacy against bark beetle attacks in conifers; however, soil applications of systemic insecticides are generally ineffective (Fettig et al. 2013; Reding et al. 2013a). Chemical control targeting *Xylosandrus* spp. should be strictly timed with beetle flight activity during spring and performed before observation of the initial attacks on plants by overwintering adults, because these treatments are likely to be more effective if used before beetles have successfully tunneled into the wood (Oliver and Mannion 2001; Reding et al. 2013b). Gallery abandonment also has been reported following permethrin applications (Schultz et al. 2002; Reding et al. 2013a; Reding and Ranger 2020),

suggesting some potential for its use as a rescue treatment post-attack. Although preventive treatments with conventional insecticides can reduce *Xylosandrus* spp. attacks, near complete protection should not be expected. All insecticide treatments are likely to be more effective when underlying factors like tree stress and associated ethanol production are minimized (Frank et al. 2017).

The pyrethroids bifenthrin, cypermethrin, and permethrin have been shown as among the most effective insecticides against *X. crassiusculus* and *X. germanus*, but results were often inconsistent (Frank and Sadof 2011; Reding et al. 2013a; Ranger et al. 2016b; Reding and Ranger 2018; Brown et al. 2020). Mizell and Riddle (2004) obtained greater reduction of *X. crassiusculus* attacks on attractive hardwood bolts treated with cypermethrin and bifenthrin than bolts treated with permethrin, chlorpyrifos, and esfenvalerate, while acephate, cyfluthrin, endosulfan, fenpropathrin, imidacloprid, and thiamethoxam were ineffective. Chlorpyrifos also was not effective against *X. crassiusculus* (Frank and Bambara 2009). *Xylosandrus germanus* attacks were significantly reduced by chlorpyrifos, lambda-cyhalothrin, and permethrin treatments in a single apple tree trial, but similar treatment efficacy could not be repeated in other locations (Agnello et al. 2017). Moreover, chlorpyrifos caused > 80% mortality of all *X. compactus* stages infesting twigs of flowering dogwood in Florida (Mangold et al. 1977). Abamectin injection at 1.8% concentration at multiple points in the tree trunk was not completely effective against *X. compactus* infesting carob trees (Leza et al. 2020).

Reding et al. (2013a) observed fewest *Xylosandrus* spp. attacks on highly attractive ethanol-injected trees treated with permethrin but, conversely, no efficacy was observed following substrate drenches or trunk sprays of certain systemic insecticides (chlorantraniliprole, cyantraniliprole, tolfenpyrad and dinotefuran). Moreover, pre-treatment of trees with permethrin can disrupt *X. germanus* colonization of flood-stressed trees, but this treatment did not completely prevent beetle attacks (Ranger et al. 2016b). Frank and Sadof (2011) suggested repeated permethrin treatments during peak flight periods of ambrosia beetles for greatest efficacy. However, pyrethroid application timing should also involve consideration of residual activity (Brown et al. 2020). In this regard, Reding and Ranger (2018) observed consistently reduced *X. germanus* attacks up to 31 days post-application in permethrin residual efficacy trials using ethanol-injected *Magnolia* trees, and Brown et al. (2020) found permethrin residues ≤ 17 days were optimal for preventing *X. crassiusculus* attacks using ethanol-filled *Liriodendron tulipifera* L. bolts. In contrast, bifenthrin produced inconsistent results, and its efficacy lasted only about 10 days; consequently, this compound would require more frequent applications (Reding and Ranger 2018).

Tree coverage is thought to affect efficacy of insecticide treatments and focus has been placed on treatment of tree trunks, which are the main targets attacked by *X. crassiusculus* and *X. germanus* (Reding et al. 2010; Ranger et al. 2013a, b; 2015b; Gallego et al. 2017). However, similar efficacy was observed when permethrin was applied with a precision sprayer directed to the trunk versus by airblast application (Frank and Sadof 2011). The efficacy and residual activity of precision insecticide applications to the tree trunk against wood-boring beetles vary depending on both active ingredient and formulation of the commercial product. Specifically, emulsifiable concentrates (EC) are generally more effective than wettable powders (WP) (Fettig et al. 2013). Moreover, recurrent rainfall events and water deposition on tree trunks through certain irrigation systems can negatively impact residues of some insecticides depending on formulation, particularly for non-systemic insecticides. Insecticides like permethrin are somewhat resistant to irrigation removal after drying (Brown et al. 2020).

Use of broadcast insecticide applications against ambrosia beetles can cause unintentional negative impacts, including reduction of populations of opportunistic predators and parasitoids (Frank and Sadof 2011). In this regard, more selective compounds should be sought for integration into sustainable programs for *Xylosandrus* spp. management. Among possible alternatives, some botanical formulations can be effective in reducing ambrosia beetle attacks (Ranger et al. 2011b; Reding et al. 2013a) and their application in organic production would represent one of the few available management options. Specifically, certain commercial plant-derived essential oils have been shown to discourage ambrosia beetles from initiating attacks (Ranger et al. 2011b). Therefore, further evaluation of essential oils in other crops, against other potential target species, and in possible combinations with insecticides could offer interesting advances for developing innovative management strategies. Deterrent particle films, such as kaolin clay, also may represent a biorational alternative to insecticides for ambrosia beetle management. While initial investigations suggest that kaolin clay alone does not reduce beetle galleries, treating trees with the combination of kaolin + bifenthrin has shown improved efficacy (Werle et al. 2017).

The wide variation in efficacy among insecticide products and trials likely indicates some insecticides are not effective at all against these beetles, or that insecticide efficacy may be influenced by a variety of other factors like beetle attraction to the host, pest population at the site, environmental conditions, timing and age of residues, etc. Although insecticides may have some utility when used in an integrated pest management context, especially for high-value tree crops undergoing sporadic periods of environmental stress,

they may impact non-target organisms (Desneux et al. 2007; Varikou et al. 2019); thus, the first line of defense against *Xylosandrus* beetles should remain the maintenance of vigorously growing and stress-free plants.

Long-lasting insecticide netting

An alternative to broadcast insecticide sprays for ambrosia beetle management is insecticide-treated nets. Polyester or polyethylene nets are usually infused or surface coated with insecticides (mainly pyrethroids), and the active ingredient is slowly released over the course of several months (Curtis et al. 2006; Marianelli et al. 2019). Scolytinae crawling on or through these nets dislodge insecticide active ingredient residues that can repel or kill the beetle (Skrzecz et al. 2015). These nets are placed around the main tree trunk or stem to protect the areas where beetles normally form galleries (Franjević et al. 2016; Galko et al. 2019; Ranger et al. 2021). Consistent effectiveness of insecticide-treated nets has been demonstrated for management of a wide variety of agricultural pests (Biondi et al. 2015; Marianelli et al. 2019). The nets may be useful in landscape environments with limited numbers of trees, orchards where long-term tree protection is a goal, or for protection of high-value trees in nurseries, but net and deployment labor costs may be impractical in nursery settings with large numbers of low-value trees.

Cypermethrin-treated nets effectively prevented attacks by bark and ambrosia beetles, including *X. germanus*, on fresh cut logs evaluated in forests in Croatia, Poland and Slovakia (Skrzecz et al. 2015; Franjević et al. 2016; Galko et al. 2019). More recently, Ranger et al. (2020a, b) obtained variable efficacy by testing two types of deltamethrin-treated nets varying by mesh size (a 'standard mesh' netting of 24 holes/cm^2 and a 'fine mesh' netting of 28 holes/cm^2) for protecting stems of flood-stressed eastern redbud (*Cercis canadensis* L.) from ambrosia beetles. Fewer attacks by *X. germanus* and other ambrosia beetles were observed across different years and/or locations, but inconsistent results were observed in some cases.

Based on the promising results observed in several locations, insecticide-treated netting appears to be a viable tool for incorporation into integrated management programs for *Xylosandrus* spp. More research is needed to optimize net attributes including further research on mesh size, as well as net color, and possible alternative active ingredients. Furthermore, such nets require evaluation with a broader range of *Xylosandrus* spp. in multiple settings.

Fungicides

Fungicides that are used against ambrosia beetle pathosystems target the specific mutualistic relationship between beetles and their mutualistic fungi. In some cases, fungicides also may have repellent properties like insecticides (Brown 2018). Adult females initiate egg laying only after the fungal mutualist is established inside infested galleries and subsequent mycelial growth is necessary for development of the brood (Weber and McPherson 1983b; Kinuura 1995). Fungicides can inhibit fungal growth, which could play a key role in integrated pest management for *Xylosandrus* spp. (Ranger et al. 2016a, b). Several investigations have demonstrated the potential of fungicide applications as a suitable tool for managing ambrosia beetle infestations (Eatough Jones et al. 2017; Addesso et al. 2018; Mayorquin et al. 2018; Brown 2018; Brown et al. 2019; Grosman et al. 2019).

Several fungicides, including chlorothalonil, dimethomorph + mancozeb, and tebuconazole, were shown to effectively inhibit the growth of the mutualist of *X. compactus* in vitro (Kagezi et al. 2015). Joseph et al. (2002) demonstrated that the systemic fungicide, propiconazole, significantly inhibits growth of an unidentified ambrosia fungus associated with *X. compactus* in a laboratory investigation. Significant inhibition of the mycelial growth of the *X. germanus* fungal mutualist was also obtained by Erper et al. (2018) in laboratory trials with azoxystrobin, captan, iprodione, imazalil, prochloraz, thiram and cyprodinil + fludioxonil. Reddy and Verghese (2006) reported that treating grape vines with the fungicide, carbendazim, reduced infestations of *X. crassiusculus* and addition of the insecticides, dichlorvos and acephate, further extended treatment efficacy. Ranger et al. (2016a, b) documented that pre-treatment of highly susceptible flooded trees with azoxystrobin and potassium phosphite significantly reduced ambrosia beetle galleries in areas dominated by *X. germanus* (Ohio and Virginia, USA). Also, Brown et al. (2019) observed a reduction of ambrosia beetle attacks in field trials evaluating the fungicides pyraclostrobin + fluxapyroxad and metalaxyl after flood events. Addesso et al. (2018) demonstrated that a preventative fungicide treatment (pyraclostrobin + boscalid) reduced both Phytophthora root rot disease severity and ambrosia beetle attacks following a simulated flood event, but protection against ambrosia beetles was lower in cases where root rot pathogen was simultaneously infecting plants. *Xylosandrus* tree attacks also were reduced by pyraclostrobin + boscalid applied to *Magnolia* sp. trees 7 days before flood stress or trunk sprays of trifloxystrobin + triadimefon to ethanol-injected trees, but webcam recordings of landing behavior indicated pyraclostrobin + boscalid reduced attacks post-landing (possible short-range toxicity or avoidance) and trunk sprays of trifloxystrobin + triadimefon reduced attacks by pre-landing effects (possible longer-range repellence) (Brown 2018).

More research is needed to identify the most appropriate fungicide classes suitable for the control of fungi specifically associated with *Xylosandrus* spp. or for preventing adult ambrosia beetle tree attacks by repellence. Key factors that

need to be considered for the success of fungicide treatments against these xylomycetophagous pests are: fungal specific mode of action, systemic properties, and bark penetrability of the formulation. Bark-penetrating agents require further investigation and, if optimized, could be a simple attribute of formulations that improves treatment efficacy (Eatough Jones and Paine 2018).

Future research agenda

Despite considerable efforts and investments to discover and develop possible management tools for *Xylosandrus* spp. and the associated microorganisms (Table 1), significant questions remain on virtually all aspects of the spread, development and management of these beetles, as well as on the role of associated fungal pathogens. In some agricultural contexts, it is still unclear which ambrosia beetles transmit their respective pathogens to specific host crops (see for example Laurel wilt in US avocado, Ploetz et al. 2017). Basic information is required on the identity and biology of these fungal vectors, their attraction to their respective hosts, and ability to obtain and transmit the specific fungi, be it mutualistic or not, which cause disease in living hosts. Improved understanding of the host plant × pathogen interactions, disease host range, and application and efficacy of different chemical measures is essential. Improved control measures will rely on advances in all of these areas. Some of these discoveries may help cure disease in existing trees and allow growers and foresters to maintain their current tree inventory remaining in the ground, and this clearly will require thorough understanding of the microbiomes surrounding fungal gardens. To cite one example, functional inhibition of cellulolytic enzyme secreted by fungal symbionts, such as *Fusarium* spp. cultured by *Euwallacea interjectus* (Blandford) attacking fig trees, can be an effective target for host decline (wood degradation) associated with ambrosia beetles (Sakai et al. 2020). Targeted alteration of the beetle's microbiomes with mycoparasitic fungi and antagonistic bacteria could be a critical management tool that circumvent dependence on insecticide treatments as the first line of defense. Alternatively, growers might begin replanting new cultivars or rootstocks, which will require elucidation of factors that may promote host tolerance to beetle infestation and symbiont infection.

The role of environmental biodiversity on *Xylosandrus* populations and individual fitness should also be carefully evaluated. We postulate that more natural and diverse environments are less suitable for these beetle species due to a higher abundance of adult beetle predators and parasitoids, as well as competitors of the beetle nutritional fungi. For example, Rassati et al. (2019a) found that forest habitat structure strongly influenced the composition of the fungal community associated with *X. germanus* individuals; in particular, individuals collected in old growth forests were associated with a more diverse mycobiome compared to individuals collected in restored forests, likely reflecting the community of fungi present in these two different habitats. Despite that most of these fungi may represent transient associations, some of them can potentially compete with the primary mutualists of beetles, and this competition can be expected to occur more often in more natural and diverse forests than in managed forests.

Xylosandrus management is greatly hampered given the cryptic nature of beetles that complete most of their lifecycle protected within galleries in wood. The control of these pests is mainly performed with the goal of preventing gallery establishment considering the protection of the beetles after successful entry. The economic damage threshold for a vector of a disease that causes tree death and/or can ruin fruit production is extremely low, if it exists at all. Because a single breakthrough discovery for managing *Xylosandrus* spp. is unlikely, research should address development of sets of management approaches that can be combined in different ways, optimized and validated for use in different geographic areas, climatic conditions, host availability and type of vegetation, e.g., nurseries, plantations, forests, etc. This approach would allow optimization of management for each situation. The foundation of all management options should be the prevention of host tree stress that initiates the process of *Xylosandrus* attacks. However, this does not fully apply for *X. compactus* that can also attack and infest healthy trees.

Nevertheless, there are many aspects to be covered in the future research agenda on alternative control strategies that are being implemented for other beetle pests. Among these, early beetle detection, especially in the entry areas of raw wood products, solid wood packaging material, or live plants, should be the first step for preventing the establishment of non-native species (Rabaglia et al. 2019). Detection programs aiming at finding, containing, and eventually eradicating an invasive species, before it become widely established in a new area, should also carefully consider specific risk and hazard rating systems. To this aim, it could be crucial to estimate the suitable areas worldwide for different invasive species under the current climate by means of appositely developed prediction models, as recently investigated for *X. compactus* and *X. crassiusculus* (Urvois et al. 2021). Early detection can also be achieved by employing trained detection dogs able to discriminate between beetle infestation and natural forest odors, as demonstrated by Johansson et al. (2019) for the European spruce bark beetle, *Ips typographus* (L.) (Coleoptera: Curculionidae). Canines (*Canis familiaris* (L.)) are an effective proactive management tool because they detect pre-symptomatic avocado trees infested by the invasive redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae)

Table 1 Overview of the main management tools tested against *Xylosandrus compactus*, *X. crassiusculus* and *X. germanus* under laboratory and/or field conditions. ~ indicates unpublished data by at least one of the co-authors of the present manuscript

Management tool	Target species			References
	Xylosandrus compactus	*Xylosandrus crassiusculus*	*Xylosandrus germanus*	
Entomopathogenic fungi				
Beauveria bassiana		x	x	Balakrishnan et al. (1994); Castrillo et al. (2011, 2013, 2016),
Laboratory		x	x	unpublished; Avery et al. (2018) and Tuncer et al. (2019)
Field	x	~	~	
Metarhizium spp.				
Laboratory		x	x	Castrillo et al. (2011, 2013, 2016), unpublished; Avery et al. (2018)
Field		~	~	and Tuncer et al. (2019)
Isaria fumosorosea				
Laboratory	x	x		Avery et al. (2018) and Kushiyev et al. (2018)
Field				
Aspergillus flavus				Mukasa et al. (2019)
Laboratory	x			
Field	x			
Mycoparasitic fungi				
Trichoderma spp.				
Laboratory	~	x	x	Castrillo et al. (2016), Kushiyev et al. (2020) and Gugliuzzo et al.
Field				in prep
Antagonistic bacteria				
Bacillus spp.				
Laboratory	~			Gugliuzzo et al. in prep
Field				
Predators				
Coleoptera Hymenoptera Dermaptera				
Laboratory	x	x	x	Sreedharan et al. (1992), Greco (2010),Egonyu et al. (2015),
Field	x			Ogogol et al. (2017), Brill et al. (2020) and Jiang and Kajimura (2020)
Parasitoids				
Hymenoptera				
Laboratory				Weber and McPherson (1983b) and Balakrishnan et al. (1989)
Field	x		x	
Insecticides				
Synthetic insecticides				
Laboratory		x		Mangold et al. (1977), Mizell and Riddle (2004), Frank and
Field	x	x	x	Bambara (2009), Frank and Sadof (2011), Reding et al. (2013a), Ranger et al. (2016b), Agnello et al. (2017), Reding and Ranger (2018) and Brown et al. (2020)
Insecticide-treated netting				
Laboratory				Skrzecz et al. (2015), Franjević et al. (2016), Galko et al. (2019)
Field		x	x	and Ranger et al. (2020a, b)
Fungicides				
Synthetic fungicides				
Laboratory	x		x	Joseph et al. (2002), Reddy and Verghese (2006), Kagezi et al.
Field		x	x	(2015), Ranger et al. (2016a, b), Brown (2018) and Erper et al. (2018)
Push–pull				
Field		x	x	Addesso et al. (2019) and Werle et al. (2019)

(Mendel et al. 2018). Based on these promising results, future efforts should consider expanding the utility of canine detection to locate chemical volatiles involved in *Xylosandrus* ambrosia beetle infestations.

Classical biological control is currently considered among the most suitable invasive species control strategies (Avtzis et al. 2019; Giorgini et al. 2019; Salas Gervassio et al. 2019). In this case, it could prove effective if host-specific natural enemies of these pests are identified in the areas of *Xylosandrus* origin. Indeed, an unexpected degree of target host specificity has been recently observed for parasitoids of other Scolytinae species (Yousuf et al. 2021). Moreover, among other biological control agents, not previously mentioned in this review, entomopathogenic nematodes (EPNs) represent another potential tool deserving further investigation. Indeed, there is already evidence that significant mortality of *X. germanus* is caused by certain EPN isolates under laboratory conditions (Kepenekci et al. 2018). However, EPNs survival potential, active colonization of beetle infested galleries, and pest control effectiveness under field conditions will have to be carefully evaluated.

Another emerging pest management approach is based on gene silencing through RNA interference (RNAi), which inhibits genes that code for proteins necessary for basic cellular function and stress responses in target insects (Mezzetti et al. 2020). The RNAi approach has proven to be effective in inducing rapid mortality of Scolytinae bark beetles through in vivo laboratory bioassays, including the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and the southern pine beetle, *D. frontalis* Zimmerman (Kyre et al. 2019, 2020). Therefore, RNAi could have potential for controlling other problematic Scolytinae, like ambrosia beetles in the genus *Xylosandrus*. Other genomic manipulations, such as CRISPR/Cas9, have been implemented for mutagenesis studies with beetle pests (i.e., *Tribolium castaneum* (Herbst) and *Leptinotarsa decemlineata* (Say)) (Adrianos et al. 2018; Gui et al. 2020) and might represent a possible tool for future investigations focusing on ambrosia beetles. These or other genomic approaches could also be focused on beetle mutualistic fungi or employed to make tree hosts resistant or repellent to beetles (e.g., inducing bark surface to produce *Xylosandrus* deterrent volatiles).

A holistic management plan is needed that incorporates improved understanding of the potential of biological control, cultural management of pathogen transmission, fungicides and insecticides, all within an overall framework of integrated pest management. Finally, all management interventions are most likely to be successful when integrated with a proper plant maintenance aimed at reducing stress-associated ethanol production.

Author contributions

AG, GTG and AB contributed to the conception of the document. AG wrote the first manuscript draft. DR, JBO, JH, LAC and LLS provided significant original text inputs. All authors participated to various debates and critically reviewed, edited and approved the manuscript.

Declarations

Conflict of interests The authors declare that they have no competing interests. AB is Editor-in-Chief of Journal of Pest Science and was not involved in the journal's review of, or decision related to, this manuscript.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

References

A HC (2012) Hevea rubber trunk pests after cold injury in Honghe and Wenshan of Yunnan province. Trop Agric Sci Technol 35:4–7

Addesso K, Baysal-Gurel F, Oliver J et al (2018) Interaction of a preventative fungicide treatment and root rot pathogen on ambrosia beetle attacks during a simulated flood event. Insects 9:83

Addesso KM, Oliver JB, Youssef N et al (2019) Trap tree and interception trap techniques for management of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in nursery production. J Econ Entomol 112:753–762

Adrianos S, Lorenzen M, Oppert B (2018) Metabolic pathway interruption: CRISPR/Cas9-mediated knockout of tryptophan 2, 3-dioxygenase in *Tribolium castaneum*. J Insect Physiol 107:104–109

Agnello AM, Breth DI, Tee EM et al (2017) *Xylosandrus germanus* (Coleoptera: Curculionidae: Scolytinae) occurrence, fungal associations, and management trials in New York apple orchards. J Econ Entomol 110:2149–2164

Alamouti SM, Tsui CK, Breuil C (2009) Multigene phylogeny of filamentous ambrosia fungi associated with ambrosia and bark beetles. Mycol Res 113:822–835

Álvarez G, Etxebeste I, Gallego D et al (2015) Optimization of traps for live trapping of Pine Wood Nematode vector *Monochamus galloprovincialis*. J Appl Entomol 139:618-626

Avery PB, Bojorque V, Gámez C et al (2018) Spore acquisition and survival of ambrosia beetles associated with the laurel wilt pathogen in avocados after exposure to entomopathogenic fungi. Insects 9:49

Avtzis DN, Melika G, Matošević D, Coyle DR (2019) The Asian chestnut gall wasp *Dryocosmus kuriphilus*: a global invader and a successful case of classical biological control. J Pest Sci 92:107–115

Balakrishnan MM, Vinodkumar PK, Prakasan CB (1989) Impact of the predator *Eupelmus* sp. (Hymenoptera: Eupelmidae) on the incidence of *Xylosandrus compactus*. J Coffee Res 19:88–90

Balakrishnan MM, Sreedharan K, Bhat PK (1994) Occurrence of the entomopathogenic fungus *Beauveria bassiana* on certain coffee pests in India. J Coffee Res 24:33–35

Bateman C, Šigut M, Skelton J et al (2016) Fungal associates of the *Xylosandrus compactus* (Coleoptera: Curculionidae, Scolytinae) are spatially segregated on the insect body. Environ Entomol 45:883–890

Biedermann PH, Vega FE (2020) Ecology and evolution of insect-fungus mutualisms. Annu Rev Entomol 65:431–455

Biedermann PH, Müller J, Grégoire JC et al (2019) Bark beetle population dynamics in the Anthropocene: challenges and solutions. Trends Ecol Evol 34:914–924

Biondi A, Zappalà L, Desneux N et al (2015) Potential toxicity of α-cypermethrin-treated nets on *Tuta absoluta* (Lepidoptera: Gelechiidae). J Econ Entomol 108:1191–1197

Blomquist GJ, Figueroa-Teran R, Aw M et al (2010) Pheromone production in bark beetles. Insect Biochem Mol Biol 40:699–712

Bousquet Y, Bouchard P, Davies AE, Sikes D (2013) Checklist of beetles (Coleoptera) of Canada and Alaska. Second edition Zookeys 360:1–44

Brill E, Follett PA, Kawabata AM (2020) Feeding habits, movement, and reproduction of the predatory flat bark beetles *Cathartus quadricollis* (Coleoptera: Silvanidae) and *Leptophloeus* sp. (Coleoptera: Laemophloeidae) in Hawaii coffee and macadamia nut. Int J Trop Insect Sci 41:1–10

Brown MS (2018). Reducing nursery tree attractiveness to ambrosia beetles (Coleoptera: Scolytinae) by using stress-mitigating fungicides to target biotic (*Phytophthora* root rot disease) and abiotic (flood stress) factors. Master Thesis. Tennessee State Univ. Nashville, TN

Brown MS, Baysal-Gurel F, Oliver JB, Addesso KM (2019) Evaluation of fungicides and biofungicide to control Phytophthora root rot (*Phytophthora cinnamomi* Rands) and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) on flowering dogwoods exposed to simulated flood events. Crop Prot 124:104834

Brown MS, Addesso KM, Baysal-Gurel F et al (2020) Permethrin residual activity against ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) attacks following field aging and simulated rainfall weathering. J Econ Entomol 113:2418–2426

Burbano EG, Wright MG, Gillette NE et al (2012) Efficacy of traps, lures, and repellents for *Xylosandrus compactus* (Coleoptera: Curculionidae) and other ambrosia beetles on *Coffea arabica*

plantations and *Acacia koa* nurseries in Hawaii. Environ Entomol 41:133–140

Byers JA, Maoz Y, Wakarchuk D et al (2018) Inhibitory effects of semiochemicals on the attraction of an ambrosia beetle *Euwallacea nr. fornicatus* to quercivorol. J Chem Ecol 44:565–575

Byers JA, Maoz Y, Cohen B et al (2021) Protecting avocado trees from ambrosia beetles by repellents and mass trapping (push–pull): experiments and simulations. J Pest Sci Doi: 10.1007/s10340-020-01310-x

Campbell SA, Borden JH (2006) Integration of visual and olfactory cues of hosts and non-hosts by three bark beetles (Coleoptera: Scolytidae). Ecol Entomol 31:437–449

Campbell SA, Borden JH (2009) Additive and synergistic integration of multimodal cues of both hosts and non-hosts during host selection by woodboring insects. Oikos 118:553–563

Carrillo D, Duncan RE, Peña JE (2012) Ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) that breed in avocado wood in Florida. Florida Entomologist 95:573–579

Carrillo D, Duncan RE, Ploetz JN et al (2014) Lateral transfer of a phytopathogenic symbiont among native and exotic ambrosia beetles. Plant Pathol 63:54–62

Castrillo LA (2018) The host population. In: Hajek AE, Shapiro-Ilan D (eds) Ecology of invertebrate diseases. Wiley, Oxford, pp 101–142

Castrillo LA, Griggs MH, Ranger CM et al (2011) Virulence of commercial strains of *Beauveria bassiana* and *Metarhizium brunneum* (Ascomycota: Hypocreales) against adult *Xylosandrus germanus* (Coleoptera: Curculionidae) and impact on brood. Biol Control 58:121–126

Castrillo LA, Griggs MH, Vandenberg JD (2013) Granulate ambrosia beetle, *Xylosandrus crassiusculus* (Coleoptera: Curculionidae), survival and brood production following exposure to entomopathogenic and mycoparasitic fungi. Biol Control 67:220–226

Castrillo LA, Griggs MH, Vandenberg JD (2016) Competition between biological control fungi and fungal symbionts of ambrosia beetles *Xylosandrus crassiusculus* and *X. germanus* (Coleoptera: Curculionidae): mycelial interactions and impact on beetle brood production. Biol Control 103:138–146

Cavaletto G, Faccoli M, Marini L et al (2020) Effect of trap color on captures of bark- and wood-boring beetles (Coleoptera; Buprestidae and Scolytinae) and associated predators. Insects 11:749

Cavaletto G, Faccoli M, Ranger CM, Rassati D (2021) Ambrosia beetle response to ethanol concentration and host tree species. J Appl Entomol. https://doi.org/10.1111/jen.12895

Cawoy H, Bettiol W, Fickers P, Ongena M (2011) *Bacillus*-based biological control of plant diseases. In: Stoytcheva M (ed) Pesticides in the modern world-pesticides use and management. IntechOpen, London, pp 273–302

Cheng L, Guo Y (1994) Biological characteristics of *Xyleborus germanus*. Entomol Knowl 31:94–96

Chong JH, Reid L, Williamson M (2009) Distribution, host plants, and damage of the black twig borer, *Xylosandrus compactus* (Eichhoff), in South Carolina. J Agric Urban Entomol 26:199–208

Cognato AI, Olson RO, Rabaglia RJ (2011) An Asian ambrosia beetle, *Xylosandrus amputatus* (Blandford) (Curculionidae: Scolytinae: Xyleborini), discovered in Florida, USA. Coleopt Bull 65:43–45

Contarini M, Vannini A, Giarruzzo F et al (2020) First record of *Xylosandrus germanus* (Blandford) (Coleoptera: Curculionidae, Scolytinae) in the Mediterranean scrubland in Southern Italy, and its co-presence with the co-generic species *X. compactus* (Eichhoff) and *X. crassiusculus* (Motschulsky). EPPO Bull 50:311–315

Cook SM, Khan ZR, Pickett JA (2007) The use of push-pull strategies in integrated pest management. Annu Rev Entomol 52:375–400

Curtis CF, Maxwell CA, Magesa SM et al (2006) Insecticide-treated bed-nets for malaria mosquito control. J Am Mosq Control Assoc 22:501–506

Desneux N, Decourtye A, Delpuech JM (2007) The sublethal effects of pesticides on beneficial arthropods. Annu Rev Entomol 52:81–106

Dole SA, Cognato AI (2010) Phylogenetic revision of *Xylosandrus* Reitter (Coleoptera: Curculionidae: Scolytinae: Xyleborina). Proc Calif Acad Sci 61:451–545

Dute RR, Miller ME, Davis MA et al (2002) Effects of ambrosia beetle attack on *Cercis canadensis*. IAWA J 23:143–160

Eatough Jones M, Paine TD (2018) Potential pesticides for control of a recently introduced ambrosia beetle (*Euwallacea* sp.) in southern California. J Pest Sci 91:237–246

Eatough Jones M, Kabashima J, Eskalen A (2017) Evaluations of insecticides and fungicides for reducing attack rates of a new invasive ambrosia beetle (*Euwallacea* sp., Coleoptera: Curculionidae: Scolytinae) in infested landscape trees in California. J Econ Entomol 110:1611–1618

EFSA (European Food Safety Authority), Hoppe B, Wilstermann A, Schrader G, et al. (2020) Pest survey card on *Xylosandrus crassiusculus*. EFSA Supporting Publication, Parma. https://doi.org/10.2903/sp.efsa.2020.EN-1903

Egonyu JP, Torto B (2018) Responses of the ambrosia beetle *Xylosandrus compactus* (Coleoptera: Curculionidea: Scolytinae) to volatile constituents of its symbiotic fungus *Fusarium solani* (Hypocreales: Nectriaceae). Arthropod Plant Interact 12:9–20

Egonyu JP, Baguma J, Ogari I et al (2015) The formicid ant, *Plagiolepis* sp., as a predator of the coffee twig borer *Xylosandrus compactus*. Biol Control 91:42–46

Egonyu JP, Mukasa Y, Ogari I et al (2017) Diversity and abundance of twig borers of Robusta coffee and their associated ambrosia fungi in Uganda. Afr Entomol 25:311–318

EPPO (European and Mediterranean Plant Protection Organization) (2020a) Mini data sheet on *Xylosandrus compactus*. https://gd.eppo.int/download/doc/1435_minids_XYLSCO.pdf. Accessed 11th Dec 2020

EPPO (European and Mediterranean Plant Protection Organization) (2020b) EPPO global database https://gd.eppo.int/. Accessed 11 Dec 2020]

Erper İ, Kushiyev R, Türkkan M, Tuncer C (2018) Evaluation of some fungicides against symbiotic fungus *Ambrosiella hartigii* associated with *Anisandrus dispar* Fabricius and *Xylosandrus germanus* Blandford (Coleoptera: Curculionidae: Scolytinae). Selcuk J Agr Food Sci 32:60–66

Eskalen A, Stouthamer R, Lynch SC et al (2013) Host range of *Fusarium* dieback and its ambrosia beetle (Coleoptera: Scolytinae) vector in southern California. Plant Dis 97:938–951

FAO (Food and Agricultural Organisation) (2013) Quarterly early warning bulletin for food and agriculture. http://www.fao.org/3/a-au970e.pdf. Accessed 5 Jan 2021

Fernandez-Conradi P, Jactel H, Robin C et al (2018) Fungi reduce preference and performance of insect herbivores on challenged plants. Ecology 99:300–311

Fettig CJ, Grosman DM, Munson AS (2013) Advances in insecticide tools and tactics for protecting conifers from bark beetle attack in the western United States. In: Trdan S (ed) Insecticides-development of safer and more effective technologies. IntechOpen, London, pp 472–492

Fraedrich SW, Harrington TC, Huang Q et al (2018) Brood production by *Xyleborus glabratus* in bolts from trees infected and uninfected with the laurel wilt pathogen, *Raffaelea lauricola*. For Sci 64:583–594

Francardi V, Noal A, Francescato S et al (2017) Coexistence of *Xylosandrus crassiusculus* (Motschulsky) and *X. compactus* (Eichhoff) (Coleoptera Curculionidae Scolytinae) in the National Park of Circeo (Lazio, Italy). Redia 100:149–155

Francese JA, Rietz ML, Mastro VC (2013) Optimization of multifunnel traps for emerald ash borer (Coleoptera: Buprestidae): influence of size, trap coating, and color. J Econ Entomol 106:2415–2423

Franjević M, Poršinsky T, Đuka A (2016) Integrated oak timber protection from ambrosia and bark beetles: economic and ecological importance in harvesting operations. Croat J For Eng 37:353–364

Frank SD and Bambara S (2009) The granulate [Asian] ambrosia beetle. North Carolina Extension Service. https://www.ces.ncsu.edu/depts/ent/notes/O&T/trees/note111/note111.html

Frank SD, Ranger CM (2016) Developing a media moisture threshold for nurseries to reduce tree stress and ambrosia beetle attacks. Environ Entomol 45:1040–1048

Frank SD, Sadof CS (2011) Reducing insecticide volume and nontarget effects of ambrosia beetle management in nurseries. J Econ Entomol 104:1960–1968

Frank SD, Anderson AL, Ranger CM (2017) Interaction of insecticide and media moisture on ambrosia beetle (Coleoptera: Curculionidae) attacks on selected ornamental trees. Environ Entomol 46:1390–1396

Galko J, Dzurenko M, Ranger CM et al (2019) Distribution, habitat preference, and management of the invasive ambrosia beetle *Xylosandrus germanus* (Coleoptera: Curculionidae, Scolytinae) in European forests with an emphasis on the West Carpathians. Forests 10:10

Gallego D, Lencina JL, Mas H et al (2017) First record of the granulate ambrosia beetle, *Xylosandrus crassiusculus* (Coleoptera: Curculionidae, Scolytinae), in the Iberian Peninsula. Zootaxa 4273:431–434

Gao L, Wu S, Lu G et al (2017) Morphological characteristics and damage survey of *Xylosandrus compactus*. Forest Pest Dis 36:31–34

Giorgini M, Wang XG, Wang Y et al (2019) Exploration for native parasitoids of *Drosophila suzukii* in China reveals a diversity of parasitoid species and narrow host range of the dominant parasitoid. J Pest Sci 92:509–522

Gomez DF, Rabaglia RJ, Fairbanks KE, Hulcr J (2018) North American Xyleborini north of Mexico: a review and key to genera and species (Coleoptera, Curculionidae, Scolytinae). ZooKeys 768:19–68

Gossner MM, Falck K, Weisser WW (2019) Effects of management on ambrosia beetles and their antagonists in European beech forests. Forest Ecol Manag 437:126–133

Greco EB (2010) Developing a monitoring tool to understand the seasonal dynamics and management techniques to estimate a sampling plan for *Xylosandrus compactus* (Eichhoff) in Hawaii. Ph.D. dissertation, University of Hawaii at Manoa, Honolulu

Greco EB, Wright MG (2015) Ecology, biology, and management of *Xylosandrus compactus* (Coleoptera: Curculionidae: Scolytinae) with emphasis on coffee in Hawaii. J Integr Pest Manag 6:7

Grégoire JC, Piel F, De Proft M et al (2001) Spatial distribution of ambrosia-beetle catches: a possibly useful knowledge to improve mass-trapping. Integrated Pest Manag Rev 6:237–242

Grosman DM, Eskalen A, Brownie C (2019) Evaluation of emamectin benzoate and propiconazole for management of a new invasive shot hole borer (*Euwallacea* nr. *fornicatus*, Coleoptera: Curculionidae) and symbiotic fungi in California sycamores. J Econ Entomol 112:1267–1273

Grousset F, Grégoire JC, Jactel H et al (2020) The risk of bark and ambrosia beetles associated with imported non-coniferous wood and potential horizontal phytosanitary measures. Forests 11:342

Grubbs KJ, Surup F, Biedermann PH et al (2020) Cycloheximide-producing *Streptomyces* associated with *Xyleborinus saxesenii* and *Xyleborus affinis* fungus-farming ambrosia beetles. Front Microbiol 11:2207

Gugliuzzo A, Mazzeo G, Mansour R et al (2019b) Carob pests in the Mediterranean region: bio-ecology, natural enemies and management options. Phytoparasitica 47:605–628

Gugliuzzo A, Criscione G, Siscaro G et al (2019a) First data on the flight activity and distribution of the ambrosia beetle *Xylosandrus compactus* (Eichhoff) on carob trees in Sicily. EPPO Bull 49:340–351

Gugliuzzo A, Criscione G, Tropea Garzia G (2019c) Unusual behavior of *Xylosandrus compactus* (Coleoptera: Scolytinae) on carob trees in a Mediterranean environment. Insects 10:82

Gugliuzzo A, Criscione G, Biondi A et al (2020) Seasonal changes in population structure of the ambrosia beetle *Xylosandrus compactus* and its associated fungi in a southern Mediterranean environment. PLoS ONE 15:e0239011

Gui S, Taning CNT, Wei D, Smagghe G (2020) First report on CRISPR/Cas9-targeted mutagenesis in the Colorado potato beetle *Leptinotarsa decemlineata*. J Insect Physiol 121:104013

Haack RA, Rabaglia RJ, Peña JE (2013) Exotic bark and ambrosia beetles in the USA: potential and current invaders. In: Peña JE (ed) Potential invasive pests of agricultural crops. CAB International, Wallingford, pp 48–74

Harrington TC, McNew D, Mayers C et al (2014) *Ambrosiella roeperi* sp. nov. is the mycangial symbiont of the granulate ambrosia beetle *Xylosandrus crassiusculus*. Mycologia 106:835–845

Hauptman T, Pavlin R, Grošelj P, Jurc M (2019) Distribution and abundance of the alien *Xylosandrus germanus* and other ambrosia beetles (Coleoptera: Curculionidae, Scolytinae) in different forest stands in central Slovenia. IForest 12:451

Hughes MA, Martini X, Kuhns E et al (2017) Evaluation of repellents for the redbay ambrosia beetle, *Xyleborus glabratus*, vector of the laurel wilt pathogen. J Applied Entomol 141:653–664

Hulcr J, Cognato AI (2010) Repeated evolution of crop theft in fungus-farming ambrosia beetles. Evolution 64:3205–3212

Hulcr J, Dunn RR (2011) The sudden emergence of pathogenicity in insect-fungus symbioses threatens naive forest ecosystems. Proc R Soc Lond B Biol Sci 278:2866–2873

Hulcr J, Stelinski LL (2017) The ambrosia symbiosis: from evolutionary ecology to practical management. Annu Rev Entomol 62:285–303

Hulcr J, Rountree NR, Diamond SE (2012) Mycangia of ambrosia beetles host communities of bacteria. Microb Ecol 64:784–793

Hulcr J, Gomez DF, Skelton J et al (2021) Invasion of an inconspicuous ambrosia beetle and fungus may affect wood decay in Southeastern North America. Biol Invasions. https://doi.org/10.1007/s10530-020-02448-6

IACO (InterAfrican Coffee Organization) (2013) Report and decisions of the 53rd annual general assembly of the InterAfrican Coffee Organization. http://www.iaco-oiac.org/sites/default/files/report_and_decisions_aga_53_2.pdf

ICO (International Coffee Organisation) (2014) Report on the critical situation in East and Central Africa caused by black coffee twig borer (BCTB): case of Uganda. http://www.ico.org/documents/cy2013-14/ed-2176e-report-twig-borer.pdf

Inward DJ (2020) Three new species of ambrosia beetles established in Great Britain illustrate unresolved risks from imported wood. J Pest Sci 93:117–126

Ito M, Kajimura H (2017) Landscape-scale genetic differentiation of a mycangial fungus associated with the ambrosia beetle, *Xylosandrus germanus* (Blandford) (Curculionidae: Scolytinae) in Japan. Ecol and Evol 7:9203–9221

Jactel H, Nicoll BC, Branco M et al (2009) The influences of forest stand management on biotic and abiotic risks of damage. Ann For Sci 66:701–701

Jactel H, Moreira X, Castagneyrol B (2020) Tree diversity and forest resistance to insect pests: patterns, mechanisms and prospects. Annu Rev Entomol 66:277–296

Jiang Z, Kajimura H (2020) Earwig preying on ambrosia beetle: evaluating predatory process and prey preference. J Appl Entomol 144:743–750

Johansson A, Birgersson G, Schlyter F (2019) Using synthetic semiochemicals to train canines to detect bark beetle-infested trees. Ann For Sci 76:58

Jordal BH, Normark BB, Farrell BD (2000) Evolutionary radiation of an inbreeding haplodiploid beetle lineage (Curculionidae, Scolytinae). Biol J Linn Soc 71:483–499

Joseph M, Prakasan CB, Vijayalakshmi CK, Sreedharan K (2002) Laboratory evaluation of the systemic fungicide propiconazole (Tilt 25 EC) against the ambrosia fungus, the food of shot hole borer *Xylosandrus compactus* (Eichhoff) (Coleoptera: Scolytidae) attacking coffee. In: Proceedings of the 15th plantation crops symposium placrosym XV (10–13 December 2002), Central Coffee Research Institute, Coffee Research Station, Mysore, India, pp 613–616

Kagezi G, Kucel P, Olal S et al (2015) In vitro inhibitory effect of selected fungicides on mycelial growth of ambrosia fungus associated with the black coffee twig borer, *Xylosandrus compactus* Eichhoff (Coleoptera: Curculionidae) in Uganda. Afr J Agric Res 10:2322–2328

Kaneko T, Tamaki Y, Takagi K (1965) Preliminary report on the biology of some Scolytid beetles, the tea root borer, *Xyleborus germanus* Blanford, attacking tea roots, and the tea stem borer, *Xyleborus compactus* Eichhoff, attacking tea twigs. Jpn J Appl Entomol Zool 9:23–28

Keller L, Peer K, Bernasconi C et al (2011) Inbreeding and selection on sex ratio in the bark beetle *Xylosandrus germanus*. BMC Evol Biol 11:1–6

Kelsey RG (2001) Chemical indicators of stress in trees: their ecological significance and implication for forestry in eastern Oregon and Washington. Northwest Sci 75:70–76

Kelsey RG, Joseph G (1998) Ethanol in Douglas-fir with black-stain root disease (*Leptographium wageneri*). Can J For Res 28:1207–1212

Kelsey RG, Joseph G, Westlind D, Thies WG (2016) Ethanol and acetone from Douglas-fir roots stressed by *Phellinus sulphurascens* infection: implications for detecting diseased trees and for beetle host selection. For Ecol Manag 360:261–272

Kenis M, Wermelinger B, Grégoire JC (2004) Research on parasitoids and predators of Scolytidae–a review. In: Lieutier F et al (eds) Bark and wood boring insects in living trees in Europe, a Synthesis. Springer, Netherlands, pp 237–290

Kepenekci I, Toksöz S, Atay T, Saruhan I (2018) Efficacy of entomopathogenic nematode isolates from Turkey and Kyrgyzstan against black timber bark beetle, *Xylosandrus germanus* (Blandford) (Coleoptera: Curculionidae: Scolytinae) adults. Pak J Nematol 36

Kimmerer TW, Kozlowski TT (1982) Ethylene, ethane, acetaldehyde, and ethanol production by plants under stress. Plant Physiol 69:840–847

Kinuura H (1995) Symbiotic fungi associated with ambrosia beetles. Jpn Agric Res Q 29:57–63

Kirkendall LR, Faccoli M (2010) Bark beetles and pinhole borers (Curculionidae, Scolytinae, Platypodinae) alien to Europe. ZooKeys 56:227

Klingeman WE, Bray AM, Oliver JB et al (2017) Trap style, bait, and height deployments in black walnut tree canopies help inform monitoring strategies for bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae). Environ Entomol 46:1120–1129

Kühnholz S, Borden JH, Uzunovic A (2001) Secondary ambrosia beetles in apparently healthy trees: adaptations, potential causes and suggested research. Integr Pest Manag Rev 6:209–219

Kushiyev R, Tuncer C, Erper I et al (2018) Efficacy of native entomopathogenic fungus, *Isaria fumosorosea*, against bark and ambrosia beetles, *Anisandrus dispar* Fabricius and *Xylosandrus germanus* Blandford (Coleoptera: Curculionidae: Scolytinae). Egypt J Biol Pest Control 28:55

Kushiyev R, Tuncer C, Erper I et al (2020) The utility of *Trichoderma* spp. isolates to control of *Xylosandrus germanus* Blandford (Coleoptera: Curculionidae: Scolytinae). J Plant Dis Prot 128:153–160

Kyre BR, Rodrigues TB, Rieske LK (2019) RNA interference and validation of reference genes for gene expression analyses using qPCR in southern pine beetle *Dendroctonus frontalise*. Sci Rep 9:5640

Kyre BR, Bentz BJ, Rieske LK (2020) Susceptibility of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) to gene silencing through RNAi provides potential as a novel management tool. For Ecol Manag 473:118322

La Spina S, De Cannière C, Dekri A, Grégoire JC (2013) Frost increases beech susceptibility to scolytine ambrosia beetles. Agric Forest Entomol 15:157–167

Lantschner MV, Corley JC, Liebhold AM (2020) Drivers of global Scolytinae invasion patterns. Ecol Appl 30:e02103

Lehenberger M, Benkert M, Biedermann PH (2020) Ethanol-enriched substrate facilitates ambrosia beetle fungi, but inhibits their pathogens and fungal symbionts of bark beetles. Front Microbiol 11:3487

Leza M, Núñez L, Riba JM et al (2020) First record of the black twig borer, *Xylosandrus compactus* (Coleoptera: Curculionidae, Scolytinae) in Spain. Zootaxa 4767:345–350

Li Y, Ruan YY, Stanley EL et al (2019) Plasticity of mycangia in *Xylosandrus ambrosia* beetles. Insect Sci 26:732–742

Liebhold AM, Brockerhoff EG, Kimberley M (2017) Depletion of heterogeneous source species pools predicts future invasion rates. J Appl Ecol 54:1968–1977

Lin Y, Fu Y, Liu F et al (1994) Dynamics and chemical control of *Xyleborus morstatti* Hagedorn. Chin J Trop Crops 15:79–86

Lindgren BS (1983) A multiple funnel trap for scolytid beetles (Coleoptera). Can Entomol 115:299–302

Longa CMO, Pertot I, Tosi S (2008) Ecophysiological requirements and survival of a *Trichoderma atroviride* isolate with biocontrol potential. J Basic Microbiol 48:269–277

Mangold JR, Wilkinson RC, Short DE (1977) Chlorpyrifos sprays for control of *Xylosandrus compactus* in flowering dogwood. J Econ Entomol 70:789–790

Mann AJ, Davis TS (2020) Plant secondary metabolites and low temperature are the major limiting factors for *Beauveria bassiana* (Bals.-Criv.) Vuill. (Ascomycota: Hypocreales) growth and virulence in a bark beetle system. Biol Control 141:104130

Marchioro M, Rassati D, Faccoli M et al (2020) Maximizing bark and ambrosia beetle catches in trapping survey for longhorn and jewel beetles. J Econ Entomol 113:2745–2757

Marianelli L, Paoli F, Sabbatini Peverieri G et al (2019) Long-lasting insecticide-treated nets: a new integrated pest management approach for *Popillia japonica* (Coleoptera: Scarabaeidae). Integr Environ Assess Manag 15:259–265

Marini L, Haack RA, Rabaglia RJ et al (2011) Exploring associations between international trade and environmental factors with establishment patterns of exotic Scolytinae. Biol Invasions 13:2275–2288

Martínez M, Cognato AI, Guachambala M, Boivin T (2019) Bark and ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) diversity in natural and plantation forests in Ecuador. Environ Entomol 48:603–613

Martini X, Hughes MA, Killiny N et al (2017) The fungus *Raffaelea lauricola* modifies behavior of its symbiont and vector, the redbay ambrosia beetle (*Xyleborus glabratus*), by altering host plant volatile production. J Chem Ecol 43:519–531

Martini X, Sobel L, Conover D, Mafra-Neto A, Smith J (2019) Verbenone reduces landing of the redbay ambrosia beetle, vector of laurel wilt pathogen, on live standing redbay tree. Agr Forest Entomol 22:83–91

Masuya H (2007) Note on the dieback of *Cornus florida* caused by *Xylosandrus compactus*. Bull FFPRI 6:59–63

Mayers CG, McNew DL, Harrington TC et al (2015) Three genera in the Ceratocystidaceae are the respective symbionts of three independent lineages of ambrosia beetles with large, complex mycangia. Fungal Biol 119:1075–1092

Mayfield AE III, MacKenzie M, Cannon PG et al (2013) Suitability of California bay laurel and other species as hosts for the non-native redbay ambrosia beetle and granulate ambrosia beetle. Agric Forest Entomol 15:227–235

Mayorquin JS, Carrillo JD, Twizeyimana M et al (2018) Chemical management of invasive shot hole borer and *Fusarium* dieback in California sycamore (*Platanus racemosa*) in southern California. Plant Dis 102:1307–1315

McPherson BA, Mori SR, Wood DL et al (2005) Sudden oak death in California: disease progression in oaks and tanoaks. For Ecol Manag 213:71–89

McPherson BA, Erbilgin N, Wood DL et al (2008) Attraction of ambrosia and bark beetles to coast live oaks infected by *Phytophthora ramorum*. Agric For Entomol 10:315–321

Mendel J, Burns C, Kallifatidis B et al (2018) Agri-dogs: using canines for earlier detection of laurel wilt disease affecting avocado trees in South Florida. Hort Technology 28:109–116

Menocal O, Cruz LF, Kendra PE et al (2017) Rearing *Xyleborus volvulus* (Coleoptera: Curculionidae) on media containing sawdust from avocado or silkbay, with or without *Raffaelea lauricola* (Ophiostomatales: Ophiostomataceae). Environ Entomol 46:1275–1283

Menocal O, Kendra PE, Montgomery WS et al (2018b) Vertical distribution and daily flight periodicity of ambrosia beetles (Coleoptera: Curculionidae) in Florida avocado orchards affected by laurel wilt. J Econ Entomol 111:1190–1196

Menocal O, Cruz LF, Kendra PE et al (2018a) *Xyleborus bispinatus* reared on artificial media using sawdust from avocado or silkbay in presence or absence of the laurel wilt pathogen (*Raffaelea lauricola*). Insects 9:30

Meurisse N, Rassati D, Hurley BP et al (2019) Common pathways by which non-native forest insects move internationally and domestically. J Pest Sci 92:13–27

Mezzetti B, Smagghe G, Arpaia S et al (2020) RNAi: What is its position in agriculture? J Pest Sci 93:1125–1130

Miller DR, Duerr DA (2008) Comparison of arboreal beetle catches in wet and dry collection cups with Lindgren multiple funnel traps. J Econ Entomol 101:107–113

Miller DR, Rabaglia RJ (2009) Ethanol and (−)-α-pinene: Attractant kairomones for bark and ambrosia beetles in the southeastern US. J Chem Ecol 35:435–448

Miller DR, Dodds KJ, Hoebeke ER et al (2015a) Variation in effects of conophthorin on catches of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in ethanol-baited traps in the United States. J Econ Entomol 108:183–191

Miller DR, Crowe CM, Mayo PD et al (2015b) Responses of cerambycidae and other insects to traps baited with ethanol, 2, 3-hexanediol, and 3, 2-hydroxyketone lures in North-Central Georgia. J Econ Entomol 108:2354–2365

Miller DR, Crowe CM, Ginzel MD et al (2018) Comparison of baited bottle and multiple-funnel traps for ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in Eastern United States1. J Entomol Sci 53:347–360

Miller DR, Crowe CM, Sweeney JD (2020) Trap height affects catches of bark and woodboring beetles (Coleoptera: Curculionidae, Cerambycidae) in baited multiple-funnel traps in southeastern United States. J Econ Entomol 113:273–280

Mizell RF, Riddle TC (2004) Evaluation of insecticides to control the Asian ambrosia beetle, *Xylosandrus crassiusculus*. Proc South Nursery Assoc 49:152–155

Morales-Rodríguez C, Sferrazza I, Aleandri MP et al (2020) The fungal community associated with the ambrosia beetle *Xylosandrus compactus* invading the mediterranean maquis in central Italy reveals high biodiversity and suggests environmental acquisitions. Fungal Biol 125:12–24

Mukasa Y, Kyamanywa S, Sserumaga JP (2019) An atoxigenic L-strain of *Aspergillus flavus* (Eurotiales: Trichocomaceae) is pathogenic to the coffee twig borer, *Xylosandrus compactus* (Coleoptera: Curculionidea: Scolytinae). Environ Microbiol Rep 11:508–517

Ogogol R, Egonyu JP, Bwogi G et al (2017) Interaction of the predatory ant *Pheidole megacephala* (Hymenoptera: Formicidae) with the polyphagus pest *Xylosandrus compactus* (Coleoptera: Curculionidea). Biol Control 104:66–70

Oliver JB, Mannion CM (2001) Ambrosia beetle (Coleoptera: Scolytidae) species attacking chestnut and captured in ethanol-baited traps in middle Tennessee. Environ Entomol 30:909–918

Owens D, Kendra PE, Tabanca N et al (2019b) Quantitative analysis of contents and volatile emissions from α-copaene and quercivorol lures, and longevity for attraction of *Euwallacea* nr. *fornicatus* in Florida. J Pest Sci 92:237–252

Owens D, Seo M, Montgomery WS et al (2019a) Dispersal behavior of *Euwallacea* nr. *fornicatus* (Coleoptera: Curculionidae: Scolytinae) in avocado groves and estimation of lure sampling range. Agric Forest Entomol 21:199–208

Paap T, Wingfield MJ, de Beer ZW, Roets F (2020) Lessons from a major pest invasion: the polyphagous shot hole borer in South Africa. S Afr J Sci 116:1–4

Peer K, Taborsky M (2005) Outbreeding depression, but no inbreeding depression in haplodiploid ambrosia beetles with regular sibling mating. Evolution 59:317–323

Pennacchio F, Roversi PF, Francardi V, Gatti E (2003) *Xylosandrus crassiusculus* (Motschulsky) a bark beetle new to Europe (Coleoptera Scolytidae). Redia 86:77–80

Pennacchio F, Santini L, Francardi V (2012) Bioecological notes on *Xylosandrus compactus* (Eichhoff) (Coleoptera Curculionidae Scolytinae), a species recently recorded into Italy. Redia 95:67–77

Pérez-García A, Romero D, De Vicente A (2011) Plant protection and growth stimulation by microorganisms: biotechnological applications of Bacilli in agriculture. Curr Opin Biotechnol 22:187–193

Ploetz RC, Hulcr J, Wingfield MJ, De Beer ZW (2013) Destructive tree diseases associated with ambrosia and bark beetles: black swan events in tree pathology? Plant Dis 97:856–872

Ploetz RC, Hughes MA, Kendra PE et al (2017) Recovery plan for laurel wilt of avocado, caused by *Raffaelea lauricola*. Plant Health Prog 18:51–77

Rabaglia RJ, Dole SA, Cognato AI (2006) Review of American Xyleborina (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. Ann Entomol Soc Am 99:1034–1056

Rabaglia RJ, Cognato AI, Hoebeke ER et al (2019) Early detection and rapid response: a 10-Year summary of the USDA forest service program of surveillance for non-native bark and ambrosia beetles. Am Entomol 65:29–42

Ranger CM, Reding ME, Persad AB, Herms DA (2010) Ability of stress-related volatiles to attract and induce attacks by *Xylosandrus germanus* and other ambrosia beetles. Agric Forest Entomol 12:177–185

Ranger CM, Reding ME, Gandhi KJ et al (2011a) Species dependent influence of (−)-α-pinene on attraction of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) to ethanol-baited traps in nursery agroecosystems. J Econ Entomol 104:574–579

Ranger CM, Reding ME, Oliver JB et al (2011b) Comparative efficacy of plant-derived essential oils for managing ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) and their corresponding mass spectral characterization. J Econ Entomol 104:1665–1674

Ranger CM, Reding ME, Schultz PB, Oliver JB (2012) Ambrosia beetle (Coleoptera: Curculionidae) responses to volatile emissions associated with ethanol-injected *Magnolia virginiana*. Environ Entomol 41:636–647

Ranger CM, Tobin PC, Reding ME et al (2013b) Interruption of the semiochemical-based attraction of ambrosia beetles to ethanol-baited traps and ethanol-injected trap trees by verbenone. Environ Entomol 42:539–547

Ranger CM, Reding ME, Schultz PB, Oliver JB (2013a) Influence of flood-stress on ambrosia beetle host-selection and implications for their management in a changing climate. Agric Forest Entomol 15:56–64

Ranger CM, Gorzlancyk AM, Addesso KM et al (2014) Conophthorin enhances the electroantennogram and field behavioural response of *Xylosandrus germanus* (Coleoptera: Curculionidae) to ethanol. Agric Forest Entomol 16:327–334

Ranger CM, Tobin PC, Reding ME (2015b) Ubiquitous volatile compound facilitates efficient host location by a non-native ambrosia beetle. Biol Invasions 17:675–686

Ranger CM, Schultz PB, Frank SD et al (2015a) Non-native ambrosia beetles as opportunistic exploiters of living but weakened trees. PLoS ONE 10:e0131496

Ranger CM, Schultz PB, Reding ME et al (2016b) Flood stress as a technique to assess preventive insecticide and fungicide treatments for protecting trees against ambrosia beetles. Insects 7:40

Ranger CM, Reding ME, Schultz PB, et al (2016a) Biology, ecology, and management of nonnative ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in ornamental plant nurseries. J Integr Pest Manag 7(1).

Ranger CM, Biedermann PH, Phuntumart V et al (2018) Symbiont selection via alcohol benefits fungus farming by ambrosia beetles. Proc Natl Acad Sci 115:4447–4452

Ranger CM, Schultz PB, Frank SD, Reding ME (2019) Freeze stress of deciduous trees induces attacks by opportunistic ambrosia beetles. Agric Forest Entomol 21:168–179

Ranger CM, Werle CT, Schultz PB et al (2020) Long-lasting insecticide netting for protecting tree stems from attack by ambrosia beetles (Coleoptera: Curculionidae: Scolytinae). Insects 11:8

Ranger CM, Reding ME, Addesso K et al (2021) Semiochemical-mediated host selection by *Xylosandrus* spp. ambrosia beetles (Coleoptera: Curculionidae) attacking horticultural tree crops: a review of basic and applied science. Can Entomol 153:103-120.

Rassati D, Toffolo EP, Roques A et al (2014) Trapping wood boring beetles in Italian ports: a pilot study. J Pest Sci 87:61–69

Rassati D, Lieutier F, Faccoli M (2016) Alien wood-boring beetles in Mediterranean regions. In: Paine TD, Lieutier F (eds) Insects and diseases of mediterranean forest systems. Springer, Cham, pp 293–327

Rassati D, Marini L, Marchioro M et al (2019b) Developing trapping protocols for wood-boring beetles associated with broadleaf trees. J Pest Sci 92:267–279

Rassati D, Marini L, Malacrinò A (2019b) Acquisition of fungi from the environment modifies ambrosia beetle mycobiome during invasion. PeerJ 7:e8103

Rassati D, Contarini M, Ranger CM et al (2020) Fungal pathogen and ethanol affect host selection and colonization success in ambrosia beetles. Agric Forest Entomol 22:1–9

Reddy GK, Verghese A (2006) Management of shot hole borer, *Xylosandrus crassiusculus* (Motschulsky) (Coleoptera: Scolytidae) on grapes. Pest Manag Hortic Ecosyst 12:107–115

Reding ME, Ranger CM (2018) Residue age and attack pressure influence efficacy of insecticide treatments against ambrosia beetles (Coleoptera: Curculionidae). J Econ Entomol 111:269–276

Reding ME, Ranger CM (2020) Attraction of invasive ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) to ethanol-treated tree bolts. J Econ Entomol 113:321–329

Reding ME, Oliver JB, Schultz PB, Ranger CM (2010) Monitoring flight activity of ambrosia beetles in ornamental nurseries with ethanol-baited traps: influence of trap height on captures. J Environ Hortic 28:85–90

Reding ME, Schultz PB, Ranger CM, Oliver JB (2011) Optimizing ethanol-baited traps for monitoring damaging ambrosia beetles (Coleoptera: Curculionidae, Scolytinae) in ornamental nurseries. J Econ Entomol 104:2017–2024

Reding ME, Ranger CM, Oliver JB, Schultz PB (2013b) Monitoring attack and flight activity of *Xylosandrus* spp. (Coleoptera: Curculionidae: Scolytinae): the influence of temperature on activity. J Econ Entomol 106:1780–1787

Reding ME, Oliver JB, Schultz PB et al (2013b) Ethanol injection of ornamental trees facilitates testing insecticide efficacy against ambrosia beetles (Coleoptera: Curculionidae: Scolytinae). J Econ Entomol 106:289–298

Reding ME, Ranger CM, Sampson BJ et al (2015) Movement of *Xylosandrus germanus* (Coleoptera: Curculionidae) in ornamental nurseries and surrounding habitats. J Econ Entomol 108:1947–1953

Reding ME, Ranger CM, Oliver JB et al (2017) Ethanol-injection induces attacks by ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) on a variety of tree species. Agric Forest Entomol 19:34–41

Rivera MJ, Martini X, Conover D et al (2020) Evaluation of semiochemical based push-pull strategy for population suppression of ambrosia beetle vectors of laurel wilt disease in avocado. Sci Rep 10:1–12

Roques A, Rabitsch W, Rasplus, et al (2009) Alien terrestrial invertebrates of Europe. Handbook of alien species in Europe. Springer, Dordrecht, pp 63–79

Sakai K, Yamaguchi A, Tsutsumi S et al (2020) Characterization of FsXEG12A from the cellulose-degrading ectosymbiotic fungus *Fusarium* spp. strain EI cultured by the ambrosia beetle. AMB Expr 10:96. https://doi.org/10.1186/s13568-020-01030-6

Salas Gervassio NG, Aquino D, Vallina C, Biondi A, Luna MG (2019) A re-examination of *Tuta absoluta* parasitoids in South America for optimized biological control. J Pest Sci 92:1343–1357

Sauvard D, Branco M, Lakatos F, et al (2010) Weevils and bark beetles (Coleoptera, Curculionoidea). Chapter 8.2. In: Roques A, et al (eds) Alien Terrestrial Arthropods of Europe. BioRisk 4(1), pp 219–266

Schedl KE (1963) Scolytidae und Platypodidae Afrikans. Band 2. Familie Scolytidae. Revista de Entomologia de Moccambique 5:1–594

Schultz PB, Dills MS, Whitaker CS (2002) Managing Asian ambrosia beetles in Virginia. In: Oliver JB (ed) Proceedings of the 47th annual southern nursery Assoc. Res. Conf. 1–2 Aug. 2002, Atlanta, GA, pp 167–169

Seo M, Martini X, Rivera MJ, Stelinski LL (2017) Flight capacities and diurnal flight patterns of the ambrosia beetles, *Xyleborus glabratus* and *Monarthrum mali* (Coleoptera: Curculionidae). Environ Entomol 46:729–734

Sheehan TN, Ulyshen MD, Horn S, Hoebeke ER (2019) Vertical and horizontal distribution of bark and woodboring beetles by feeding guild: is there an optimal trap location for detection? J Pest Sci 92:327–341

Skelton J, Johnson AJ, Jusino MA et al (2019) A selective fungal transport organ (mycangium) maintains coarse phylogenetic congruence between fungus-farming ambrosia beetles and their symbionts. Proc R Soc B 286:20182127

Skrzecz I, Grodzki W, Kosibowicz M, Tumialis D (2015) The alpha-cypermethrin coated net for protecting Norway spruce wood against bark beetles (Curculionidae, Scolytinae). J Plant Prot Res 55(2):156–161

Smith SM, Beaver RA, Cognato AI (2020) A monograph of the Xyleborini (Coleoptera, Curculionidae, Scolytinae) of the Indochinese Peninsula (except Malaysia) and China. ZooKeys 983:1–442

Sreedharan K, Balakrishnan MM, Bhat PK (1992) *Callimerus* sp. (Coleoptera; Cleridae), a predator of the shot-hole borer, *Xylosandrus compactus* (Eichh.). J Coffee Res 22:139–142

Steininger MS, Hulcr J, Šigut M, Lucky A (2015) Simple and efficient trap for bark and ambrosia beetles (Coleoptera: Curculionidae) to facilitate invasive species monitoring and citizen involvement. J Econ Entomol 108:1115–1123

Tuncer C, Kushiyev R, Erper I (2017) Determination of fungal flora on *Anisandrus dispar* Fabricius and *Xylosandrus germanus* Blandford (Coleoptera: Curculionidae: Scolytinae). IX International Congress on Hazelnut 1226:391–398

Tuncer C, Kushiyev R, Erper I et al (2019) Efficacy of native isolates of *Metarhizium anisopliae* and *Beauveria bassiana* against the invasive ambrosia beetle, *Xylosandrus germanus* Blandford (Coleoptera: Curculionidae: Scolytinae). Egypt J Biol Pest Control 29:28

Ulyshen MD, Sheehan TN (2019) Trap height considerations for detecting two economically important forest beetle guilds in southeastern US forests. J Pest Sci 92:253–265

Urvois T, Auger-Rozenberg MA, Roques A et al (2021) Climate change impact on the potential geographical distribution of two invading *Xylosandrus* ambrosia beetles. Sci Rep 11:1339

VanDerLaan NR, Ginzel MD (2013) The capacity of conophthorin to enhance the attraction of two *Xylosandrus* species (Coleoptera: Curculionidae: Scolytinae) to ethanol and the efficacy of verbenone as a deterrent. Agric Forest Entomol 15:391–397

Vannini A, Contarini M, Faccoli M et al (2017) First report of the ambrosia beetle *Xylosandrus compactus* and associated fungi in the Mediterranean maquis in Italy, and new host-pest associations. EPPO Bull 47:100–103

Varikou K, Garantonakis N, Birouraki A (2019) Exposure of *Bombus terrestris* L. to three different active ingredients and two application methods for olive pest control. Entomol Gen 39:53–60

Vega FE, Biedermann PH (2020) On interactions, associations, mycetangia, mutualists and symbiotes in insect-fungus symbioses. Fungal Ecol 44:100909

Verma M, Brar SK, Tyagi RD et al (2007) Antagonistic fungi, *Trichoderma* spp.: panoply of biological control. Biochem Eng J 37:1–20

Vinale F, Sivasithamparam K, Ghisalberti EL et al (2008) *Trichoderma*-plant-pathogen interactions. Soil Biol Biochem 40:1–10

Weber BC, McPherson JE (1983b) Life history of the ambrosia beetle *Xylosandrus germanus* (Coleoptera: Scolytidae). Ann Entomol Soc Am 76:455–462

Weber BC, McPherson JE (1983a) World list of host plants of *Xylosandrus germanus* (Blandford) (Coleoptera: Scolytidae). Coleopt Bull 37:114–134

Webster RP, de Tonnancour P, Sweeney JD et al (2020) New Coleoptera records from eastern Canada, with additions to the fauna of Manitoba, British Columbia and Yukon Territory. Zookeys 946:53–112

Wegensteiner R, Wermelinger B, Herrmann M (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier Academic Press, Cambridge, pp 247–304

Werle CT, Bray AM, Oliver JB et al (2014) Ambrosia beetle (Coleoptera: Curculionidae: Scolytinae) captures using colored traps in southeast Tennessee and south Mississippi. J Entomol Sci 49:373–382

Werle CT, Addesso KM, Sampson BJ et al (2017) Integrating kaolin clay for ambrosia beetle management in ornamental crops of Eastern redbud. HortScience 52:94–98

Werle CT, Ranger CM, Schultz PB et al (2019) Integrating repellent and attractant semiochemicals into a push–pull strategy for ambrosia beetles (Coleoptera: Curculionidae). J Appl Entomol 143:333–343

Wu Y, Yu J, Li X (2007) A new pest *Xylosandrus compactus* in landscape plants. Subtrop Plant Sci 36:13–16

Yang Q, Zhou Z, Li Q et al (2008) Morphological characteristics of the new pest attacking grapevine *Xylosandrus germanus*. Chin Bull Entomol 45:219–223

Yousuf F, Follett PA, Gillett CP et al (2021) Limited host range in the idiobiont parasitoid *Phymasticus coffea*, a prospective biological control agent of the coffee pest *Hypothenemus hampei* in Hawaii. J Pest Sci. https://doi.org/10.1007/s10340-021-01353-8

Zhou Q, Cao H, Xu Y et al (2020) The granulate ambrosia beetle *Xylosandrus crassiusculus* (Motschulsky), a new pest of *Morus alba* L. Plant Quar 34:57–60

Zeng J, Liu Y, Zhang H et al (2020) Global warming modifies long-distance migration of an agricultural insect pest. J Pest Sci 93:569–581

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