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REVIEW

What hides beneath the bark? Associations between phytopathogenic fungi and emerging bark beetles in the Mediterranean region

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Abstract

Bark beetles are commonly associated with several fungal symbionts that play mutualistic, commensal or pathogenic ecological roles. In recent decades, reports of serious damage caused by both native and invasive bark beetle species, and the pathogenic fungi they vector, are rapidly increasing worldwide. In particular, new bark beetle–fungus associations are being reported in different contexts, e.g., forests, ornamental plant nurseries, urban areas and orchards. Due to heavy global trade and suitable environmental conditions for alien beetle establishment, the Mediterranean region has recently been invaded by bark beetle species originating from Africa, Asia, Australia and the Americas. *Scolytus amygdali*, *S. rugulosus*, *S. mali*, *Cryphalus dilutus*, *Hylesinus vestitus*, and *Phloeotribus scaraboides* are among the common bark beetles whose infestations are threatening cultivated trees in the Mediterranean area. However, their associations with symbiotic fungi and/or phytopathogenic fungi have been rarely investigated. This literature review aims to summarize knowledge on these species, focusing on the description of their fungal symbionts and also on their ecological roles. Understanding these associations of bark beetles with phytopathogenic fungi is the first step toward developing sustainable management strategies to reduce both beetle infestations and the spread of fungal infections.

Keywords Beetle-fungus association · Fungal symbiont · *Geosmithia* · Mycobiome · *Scolytus* · Wood-boring beetles

Economically important orchards and related bark beetles in the Mediterranean region

The Mediterranean region has a long-standing tradition in the production of temperate and subtropical fruit, which has relevant socio-economic, biodiversity and typicity implications. *Citrus*, grapes (*Vitis vinifera* L.), olive (*Olea europea* L.), apple [*Malus domestica* (Suckow) Borkh.], almond [*Amygdalus communis* L. (= *Prunus dulcis* (Mill.) D.A. Webb*; Prunus amygdalus* Batsch)], peach [*Prunus persica* (L.) Batsch (= *Persica vulgaris* Mill.)], apricot (*Prunus armeniaca* L.), common fig (*Ficus carica* L.), hazelnut (*Corylus avellana* L.) and walnut (*Juglans regia* L. and *J. nigra* L.) are among the most commonly cultivated fruit trees (Mellal et al. 2023; Bassi et al. 2024). In addition, pistachio (*Pistacia vera* L.) and mango (*Mangifera indica* L.) are rapidly emerging as additional key crops of the Mediterranean countries (Benmoussa et al. 2017; Gentile et al. 2019; Pelleri et al. 2020; Carella et al. 2021; Gusella et al. 2024a).

All these important species can be affected by a number of insect pests, including bark beetles (Coleoptera; Scolytinae) (González and Campos 1994; Mendel et al. 1997; Doerr et al. 2008; Masood et al. 2010; Zeiri et al. 2015; Faccoli et al. 2016; Hadj Taieb et al. 2020). There is a wide diversity of native bark beetle species in the Mediterranean regions, with some species active throughout the year (Lieutier et al. 2016). Most of them typically infest Mediterranean conifers while only a few occur in cultivated orchards (Mifsud and Knizek 2009; Lieutier et al. 2016). The orchard-inhabiting species are usually

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considered “secondary” pests, because their reproductive attacks occur on weakened trees. In addition, at low population densities, they play an important ecological role by preparing the substrate for saproxylic organisms (Brin and Bouget 2018). However, some of these beetles can also undergo population outbreaks, during which they can attack healthy trees, causing host mortality and severe economic losses (Lieutier et al. 2016).

In recent decades, the Mediterranean region has also been invaded by several bark beetle species originating from Africa, Asia, Australia and the Americas (Lieutier et al. 2016; Rassati et al. 2016; Marchioro et al. 2022). The high number of species successfully established might be explained by the distinctive conditions occurring in these areas (Rassati et al. 2016), including the wide diversity of woody plants, the varied ecosystems, and the hot and dry summers combined with the mild and rainy winters (Kirkendall and Faccoli 2010; Marini et al. 2011). The number of non-native bark beetles is also expected to increase in the next years due to climate warming and increasing global trade (Lantschner et al. 2020; Pureswaran et al. 2022). In fact, bark beetles are easily transported in all kinds of woody materials (Meurisse et al. 2019), a pathway that often enables them to evade the phytosanitary controls and preventive measures applied at both national and international levels (Brockerhoff et al. 2006; Skarpaas and Økland 2009; Haack et al. 2014).

One of the most striking features of bark beetles is the widespread association with fungi (Kirisits 2004). These typically ectosymbiotic fungi can play multiple roles, including nutrition provisioning and detoxification of plant defences. When fungal pathogens are involved, they can also facilitate host plant colonization (Paine et al. 1997; Lieutier et al. 2009; Villari et al. 2012), although this ecological role has been questioned for many years (Six and Wingfield 2011). A number of studies have been carried out around the globe in recent years to describe the fungal symbionts of bark beetles. This is because knowing them and studying their ecological role can be a first step towards providing innovative and sustainable management strategies against bark beetles and their associated (phytopathogenic) fungi (Gugliuzzo et al. 2021). While certain species have been targeted in several studies (e.g., *Ips typographus* L., *Dendroctonus* Erichson, *Pityophthorus juglandis* Blackman), the majority of bark beetle–fungus symbioses are poorly studied or unknown (Bentz and Six 2006; Newton et al. 2009; Dohet et al. 2016; Netherer et al. 2021; Schebeck et al. 2023). Some of them are of key economic importance and are therefore the focus of this review.

In the following, the terms “associated/associations” can refer to a statistical co-occurrence between a beetle and a fungus even when a functional connection is still unknown. When a proven, beneficial functional connection exists (very few cases in the present review), the terms “symbiont/symbiosis” or “mutualist/mutualism” are preferred (Vega and Biedermann 2020; Hulcr et al. 2025). In particular, we relate to fungi that have been isolated from the insect’s body, their galleries or the surrounding wood.

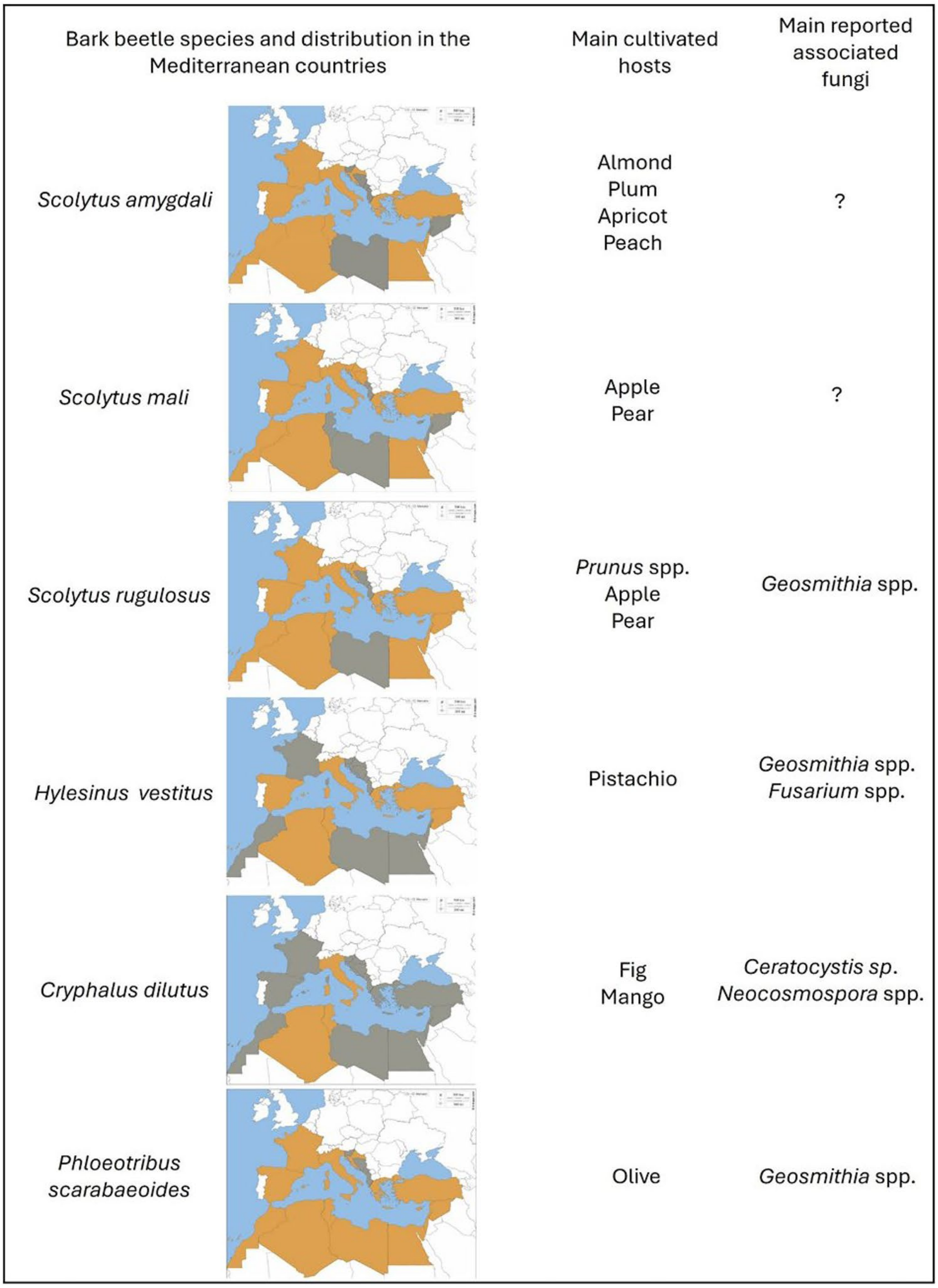
We provide an overview of important, but still under-investigated, bark beetle–fungal symbioses of the Mediterranean region. Our focus is on bark beetle species that feed on diverse plant tissues and their plant pathogenic fungal associates. We also identify key issues that should be addressed to improve early detection and risk-based responses, thereby facilitating the development of potential management strategies.

Scolytus species

Biology and ecology

Among the several species existing in the genus *Scolytus* Geoffroy, the almond bark beetle *Scolytus amygdali* Guerin-Meneville, the fruit-tree bark beetle *S. rugulosus* (= *S. mediterraneus* Eggers), and the apple bark beetle *S. mali* (= *S. sulcatus* Le Conte, Brown) are three key species of the Mediterranean region.

Scolytus amygdali has been one of the predominant bark beetle species recorded worldwide as a pest of fruit trees since 1921 (Picard 1921; Cherif and Trigui 1990; Kinawy et al. 1991; Mendel et al. 1997). It is widespread in its native range, which includes the Mediterranean area along with some regions of North Africa, Europe and Asia (Picard 1921; Russo 1931; Benazoun 1983; Cherif and Trigui 1990; Mifsud and Knizek 2009). *S. amygdali* is mainly associated with woody species in the Rosaceae family (Benazoun and Schevester 1990; Asma et al. 2011; Zeiri et al. 2014, 2015) (Fig. 1). Among the wild and cultivated Rosaceae, common hosts are almond, peach and apricot (Bolu and Legalov 2008; Asma et al. 2011; Zeiri et al. 2014, 2015), whose suitability for the beetle appears to depend on the preference of the specific population (Zeiri et al. 2015; El-Bassiouny et al. 2017). A recent study carried out in Tunisia, for example, showed that the reproductive success of *S. amygdali* in terms of length of maternal galleries and female fecundity was higher in peach than in almond, apricot and plum (*Prunus domestica* L.) (Zeiri et al. 2015). Two early studies from the same country indicated the opposite and revealed a preference for almond (Benazoun 1983; Ben-Yenuda 2005). Even if *S. amygdali* is considered a secondary pest of fruit trees, it can kill young or mature trees that have been weakened by biotic or abiotic factors (Zeiri et al. 2018). For example, severe damage is commonly recorded in almond, apricot and plum plantations in Israel (Mendel et al. 1997), almond in Morocco and Tunisia (Cherif and Trigui 1990; Mahhou



Bark beetle species and distribution in the Mediterranean countries	Main cultivated hosts	Main reported associated fungi
Scolytus amygdali	Almond Plum Apricot Peach	?
Scolytus mali	Apple Pear	?
Scolytus rugulosus	*Prunus* spp. Apple Pear	*Geosmithia* spp.
Hylesinus vestitus	Pistachio	*Geosmithia* spp. *Fusarium* spp.
Cryphalus dilutus	Fig Mango	*Ceratocystis sp.* *Neocosmospora* spp.
Phloeotribus scarabaeoides	Olive	*Geosmithia* spp.

Fig. 1 Bark beetle species occurring in economically important cultivated trees in the Mediterranean region and their associated fungi. The orange areas represent where each beetle species is currently present, while the grey areas represent where it is not known to be present

and Dennis 1992; Zeiri 2015) and pear in Egypt (Kinawy et al. 1991).

Scolytus rugulosus is widely distributed in North Africa, the Middle East, Europe and North America. It commonly attacks apple, cherry and pear trees, especially in abandoned orchards, but also *Cydonia oblonga* Mill. and species belonging to the genera *Crataegus*, *Cotoneaster*, *Sorbus*, *Pyracantha*, *Mespilus* and *Ulmus* (Halperin and Holzschuh 1984; Mifsud and Knizek 2009; Smith and Cognato 2014). *S. mali* is present in North America, Europe, the British Isles, North Africa and Asia (Rudinsky et al. 1978; Mifsud and Knizek 2009; Sayin 2014; Smith and Cognato 2014; Isayeva 2021). Its preferred hosts are apple and pear, even though it is commonly reported also on other Rosaceae, e.g., *Pyracatha coccinea* M. Roem and *Prunus*, *Castanea*, *Cotoneaster*, *Crataegus*, *Sorbus*, *Carpinus betulus* L., *Corylus*, *Populus* and *Ulmus* (Saliba 1963; Mendel et al. 1997; Mifsud and Knizek 2009) (Fig. 1). Similar to *S. amygdali*, *S. rugulosus* and *S. mali* attack mainly weakened trees due to biotic and abiotic stressors such as soil-borne diseases, inappropriate tree maintenance and incorrect management practises, and can kill trees during population outbreaks

(Bright and Stark 1973; Rudinsky et al. 1978; Öztürk et al. 2004; Sarıkaya and Sayın 2016).

All three species are monogamous and females found the new nests (Smith and Hulcr 2015). The female burrows to the cambium-phloem layer, where excavates a nuptial chamber and one or two egg galleries. As suggested in previous studies, the females release aggregation pheromones that may attract not only males, but also other females to the same host tree (Russo 1931; Benazoun 1983; Kinawy et al. 1991; Ben-Yehuda et al. 2002). Adult females are joined by males, mating occurs near the entrance, and the eggs are laid in small niches on both sides of the egg galleries. When gallery construction is complete, the male leaves the female, which typically dies in the entrance tunnel after egg laying is finished. Larvae excavate galleries in the cambium-phloem layer perpendicular to the maternal gallery and then radiate in different directions. They pupate within the outer sapwood. The brood overwinters as pupae (or larvae) and emerges as adults in the following spring (Edson 1967; Asma et al. 2011; Smith and Hulcr 2015; Zeiri et al. 2015). In *S. amygdali*, emerging adult beetles are attracted by host-specific, stress-related chemical signals and visual stimuli, enabling them to select between resistant and non-resistant hosts before colonization (Russo 1931; Benazoun 1983; Zeiri et al. 2018). *S. amygdali* can produce three to five generations per year, depending on the location (Janjua and Samuel 1941; Benazoun 1983; Cherif and Trigui 1990; Kinawy et al. 1991). The life cycle of *S. rugulosus* is slightly different from that of *S. amygdali*. Overwintering occurs at the pupal stage, and larval galleries are firstly perpendicular to the maternal gallery and then parallel to the grain of the wood (Bright and Stark 1973; Smith and Cognato 2014). *S. rugulosus* can have one to four generations per year, depending on the location, with more generations usually occurring in warmer climates (Baker 1972; Wood 1982). Besides damage to wood tissues, *S. rugulosus* adults have also been found to feed on apricot fruits in Turkey (Özgen et al. 2012). In *S. mali,* larval galleries are initially perpendicular to the maternal gallery and then curve into a fan-shaped pattern (Smith and Cognato 2014; Smith and Hulcr 2015). Additionally, *S. mali* has only one or two generations per year, depending on the location (Pechuman 1938; Smith and Cognato 2014).

Fungal associates

Several studies have investigated the fungal communities of *Scolytus* spp. around the globe. These studies clearly show that *Geosmithia* (Hypocreales) and Ophiostomatoid fungi (Ophiostomatales and Microascales) are common associates of *Scolytus* spp. (Table 1). The current diversity of the *Geosmithia* genus includes at least 38 species formally described and several phylogenetic species named numerically without a formal taxonomic description, even though some of these have been recently identified (Hou et al. 2023; Kolařík and Hulcr 2023; Aylward et al. 2024; Liang et al. 2024; Zhao et al. 2025). *Scolytus* spp. (e.g., *S. chikisanii* Niisima, *S. japonicus* Chapuis, *S. multistriatus* Marsham, *S. scolytus* Fabricius) are also known for being vectors of *Ophiostoma ulmi* (Buismann) Nannf and *O. novo-ulmi* Brasier (Ophiostomatales), the causal agents of Dutch elm disease (Baker 1972; Brasier 1990; Webber 1990, 2000; Kirschner 1998; Kirisits 2004; Menkis et al. 2016; Pepori et al. 2025). The apple bark beetle is reported to be able to transmit the fungal pathogen causing Dutch elm disease during its maturation feeding on healthy elm twigs (Baker 1972). Additionally, *S. amygdali* and *S. rugulosus* have been reported in Turkey as potential vectors of the plant-pathogen *Verticillium dahliae* Kleb on apricot. However, their role as vectors remains unconfirmed, as Leach's postulates have not yet been fulfilled (Apak 2021). In a separate study carried out in Turkey, *Aspergillus flavus* Link. and *Fusarium oxysporum* von Schlechtendal were isolated from dead individuals of *S. amygdali*, and their entomopathogenic potential was confirmed under laboratory conditions (Asma et al. 2017). *G. flava* (= *Geosmithia* sp. 7) M. Kolařík, Kubátová & Pažoutová, *G. omnicola* (= *Geosmithia* sp. 10) Pepori, M. Kolařík, Bettini, Vettraino & Santini and *G. pulverea* (= *Geosmithia* sp. 23) R. Chang & X. Zhang have been found as associates of *S. rugulosus* in Croatia, while *G. pulverea, Geosmithia* sp. 22 and *Quambalaria cyanescens* (de Hoog & G.A. de Vries) Z.W. de Beer, Begerow & R. Bauer (formerly *Fugomyces cyanescens*) have been found as associates of *S. rugulosus* in Turkey (de Beer et al. 2006; Kolařík et al. 2006, 2007; Pepori et al. 2015; Zhang et al. 2022). The phytopathogenicity of these *Geosmithia* species still remains to be investigated, whereas *Q. cyanescens* has been confirmed to be pathogenic on grapevine (Narmani and Arzanlou 2019).

The pistachio bark beetle *Hylesinus vestitus*

Biology and ecology

Hylesinus (= *Chaetoptelius*) *vestitus* (Mulsant & Rey), known as the Pistachio Bark Beetle (PBB), is among the most destructive pests of pistachio in several countries of Asia (Lababidi 1998; Ziaaddini et al. 2002) and in the Mediterranean (e.g., Turkey (Kaplan et al. 2018; Sabuncu et al. 2021; Çelebi and Kaplan 2025), Algeria (Chebouti-Meziou et al. 2011), Greece (Fragoulis 2004), Tunisia (Braham and Jardak 2012; Ghrissi et al. 2019) and Italy (Russo 1925, 1926)). To date, pistachio is the only known host of PBB (Sönmez and Mamay 2022) (Fig. 1). Its life cycle has been intensively studied in Tunisia and Algeria (Braham and Jardak 2012; Meziou-Chebouti et al. 2013). Two main stages can be identified, i.e., a maturation feeding stage and

Table 1 Fungi reported to be associated with bark beetles of the genus *Scolytus* in the world

Beetle species	Reported associated fungi	Region	References
S. amygdali	*Quambalaria cyanescens*	Syria	Kolařík et al. (2006), Stodůlková et al. (2008)
	Aspergillus flavus*, *Fusarium oxysporum	**Turkey**	Asma et al. (2017)
Scolytus carpini	*Geosmithia langdonii* (=*G.* sp. 15), *Geosmithia obscura* (=*G.* sp. 17), *G. pallida* s.l. (=*G.* sp. 4), *Geosmithia* spp. (*G.* sp. 8*, 10*)	Czech Republic	Kolařík et al. (2005, 2008)
	F. cyanescens, G. obscura* (=*G.* sp. 17), *G. pallida* s.l. (=*G.* sp. 4)	Hungary	Kolařík et al. (2005, 2006, 2008)
	Geosmithia sp. 3*	USA	Kolařík et al. (2017)
S. chikisanii	*Ophiostoma novo-ulmi, O. ulmi*	Japan	Yamaki et al. (2024, 2025)
S. esuriens	*O. novo-ulmi, O. ulmi*	Japan	Masuya et al. (2010), Yamaki et al. (2025)
S. intricatus	*F. cyanescens*, G. langdonii* (=*G.* sp. 15), *Geosmithia* sp. 9, *G. pallida* s.l. (=*G.* sp. 3*, 4)	Bulgaria	Kolařík et al. (2006, 2008)
	G. fassatiae (=*G.* sp. 14), *G. langdonii* (=*G.* sp. 15), *G. lavendula*, *G. obscura* (=*G.* sp. 17), *G. pallida* s.l. (=*G.* sp. 3*, 4), *G. putterillii* (=*G.* sp. 6), *Geosmithia* spp. (*G.* sp. 8*, 9, 10*)	Czech Republic	Kolařík et al. (2004, 2005, 2008)
	G. flava, *G. langdonii*, *G. pazoutovae, Geosmithia* sp. 3, *O. quercus*, *Sporothrix eucastaneae*, *S.* cf. *foliorum*, *S. prolifera*, *Sporothrix* spp. (=*S.* sp. 4, 9)	Poland	Jankowiak et al. (2019),Strzałka et al. (2021)
	G. fassatiae (=*G.* sp. 14), *G. langdonii* (=*G.* sp. 15), *G. pallida* s.l. (=*G.* sp. 4), *G. putterillii* (=*G.* sp. 6), *Geosmithia* sp. 9	Slovakia	Kolařík et al. (2005, 2008)
	G. fassatiae (=*G.* sp. 14), *G. pallida* s.l. (=*G.* sp. 4, 5), *G. putterillii* (=*G.* sp. 6), *Geosmithia* spp. (=*G.* sp. 9, 11)	Hungary	Kolařík et al. (2005, 2008)
S. japonicus	*O. novo-ulmi, O. ulmi,*	Japan	Yamaki et al. (2024, 2025)
S. jaroschewskii	*Alternaria* sp., *Aspergillus* spp., *Beauveria bassiana*, *Cladosporium spp.*, *Clonostachys rosease*, *Dothiora sp.*, *Eutypa* sp., *Eutypella* sp., *Exophiala* sp., *Fusarium* spp., *Gliomastix tumulicola*, *Ophiostoma* sp., *Penicillium* spp., *Phaeoacremonium hungaricum*, *Phoma* spp., *Phomopsis* spp., *Stilbocrea* sp., *Trichothecium roseum*, *Wickerhamomyces* sp.	Russia	Petrov et al. (2022)
S. jiulianshanensis	*G. luteobrunnea*, *G. pulverea*, *G. radiata*	China	Zhang et al. (2022)
S. kirschii	*Paecilomyces formosus*	Iran	Alizadeh et al. (2024)
	G. pallida* s.l. (=*G.* sp. 2*), *Geosmithia* sp. 10	**Italy**	Kolařík et al. (2007)
	O. ulmi	**Portugal**	Webber (1990)
	G. lavendula* (=*G.* sp. 18), *G. pallida* s.l. (=*G.* sp. 2*), *Geosmithia* spp. (*G.* sp. 10*, 20*), *O. ulmi	**Spain**	Webber and Brasier (1984), Webber (1990), Kolařík et al. (2007)
S. laevis	*O. novo-ulmi*	Norway	Aas et al. (2018)
S. mali	*G. putterillii* (=*G.* sp. 6), *Geosmithia* spp. (*G.* sp. 8*, 10*)	Czech Republic	Kolařík et al. (2008)
	G. fagi, Geosmithia spp. (*G.* sp. 2*, 3*), *Graphilbum* sp., *Leptographium* sp. 7, *O. novo-ulmi*, *O. quercus, Ophiostoma* sp. 3	Poland	Jankowiak et al. (2019), Strzałka et al. (2021)
	G. fassiatiae (=*G.* sp. 14), *G. pallida* s.l. (=*G.* sp. 4), *Geosmithia* spp. (*G.* sp. 8*, 10*)	Hungary	Kolařík et al. (2008)
S. multistriatus	*G. pallida* s.l. (=*G.* sp. 3*, 5), *G. putterillii* (=*G.* sp. 6), *Geosmithia* spp. (*G.* sp. 8*, 10*, 13*)	Czech Republic	Kolařík et al. (2004, 2008)
	Geosmithia* spp., *O. novo-ulmi	**Italy**	Pepori et al. (2025)
	G. flava, *Geosmithia* sp. 5, *G. ulmacea*, *O. novo-ulmi*	Poland	Aas et al. (2018), Jankowiak et al. (2019), Strzałka et al. (2021)
	O. ulmi	Portugal	Webber (1990)
	O. ulmi	**Spain**	Webber and Brasier (1984), Webber (1990)
	Geosmithia sp. 23*	USA	Kolařík et al. (2017)

Table 1 (continued)

Beetle species	Reported associated fungi	Region	References
S. oregoni	*G. flava* (=*G.* sp. 7), *Geosmithia* spp. (*G.* sp. 35, 37, 21*)	USA	Kolařík et al. (2017)
S. praeceps	*Geosmithia* spp. (*G.* sp. 33, 34, 40, 41)	USA	Kolařík et al. (2017)
S. pygmaeus	*G. pallida* s.l. (=*G.* sp. 3*), *G. putterillii* (=*G.* sp. 6), *Geosmithia* sp. 10*	Czech Republic	Kolařík et al. (2008)
S. ratzeburgi	*O. katzeburgi*	Finland	Linnakoski et al. (2008)
	O. borealis, O, denticiliatum, O. karelicum, O. quercus	Norway	Linnakoski et al. (2009), Aas et al. (2018)
	L. betulae, O. karelicum, O. quercus	Poland	Aas et al. (2018), Jankowiak et al. (2019)
	O. katzeburgi	Russia	Linnakoski et al. (2008)
S. rugulosus	***G. flava* (=*G.* sp. 7), *Geosmithia* spp. (*G.* sp. 10*, 23*)**	**Croatia**	Kolařík et al. (2007)
	G. fassatiae (=*G.* sp. 14), *G. flava* (*G.* sp. 7), *G. langdonii* (=*G.* sp. 15), *G. pallida* s.l. (=*G.* sp. 3*), *G. putterillii* (*G.* sp. 6), *Geosmithia* spp. (*G.* sp. 8*, 10*)	Czech Republic	Kolařík et al. (2005, 2008)
	G. flava, *G. langdonii*, *G. omnicola*, *Geosmithia* spp. (*G.* sp. 2*, 5*), *O. piceae*	Poland	Jankowiak et al. (2019), Strzałka et al. (2021)
	G. putterillii (=*G.* sp. 6), *Geosmithia* sp. 8*	Slovakia	Kolařík et al. (2008)
	***F. cyanescens**, *G. pallida* s.l. (=*G.* sp. 23*), *Geosmithia* sp. 22**	**Turkey**	Kolařík et al. (2006, 2007)
	G. pallida s.l. (=*G.* sp. 3*, 4), *Geosmithia* spp. (*G.* sp. 8*, 10*)	Hungary	Kolařík et al. (2008)
	G. lavendula (=*G.* sp. 18), *Geosmithia* spp. (*G.* sp. 2*, 21*, 42)	USA	Kolařík et al. (2017)
S. schevyrewi	*Byssochlamys* sp., *Cladosporium* sp., *Geosmithia* spp., *G. pallida*, *Gibellulopsis* sp., *Pleosporales* sp., Saccharomycetales, *Wickerhamomyces* spp.	China	Zhu et al. (2022)
	G. ulmacea	Czech Republic	Pepori et al. (2015)
	Geosmithia sp. 20*, *G. ulmacea* (=*G.* sp. 13), *O. novo-ulmi*	USA	Jacobi et al. (2007), Kolařík et al. (2017)
S. scolytus	*G. flava*, *Graphium* sp. 3, *O. novo-ulmi*	Poland	Aas et al. (2018), Jankowiak et al. (2019), Strzałka et al. (2021)
	O. ulmi	Portugal	Webber (1990)
	O. ulmi	**Spain**	Webber (1990), Webber and Brasier (1984)
S. semenovi	*G. granulata*, *G. pulverea*, *G. pumila*	China	Zhang et al. (2022)
S. ventralis	*O. symbioticum*	California	Six and Livingston (2023)
		Canada	
		Mexico	
		USA	

Bold text indicates reports referred to the Mediterranean area

Indicates species that have undergone taxonomic revision. The names reported in the table follow the original reference cited therein; updated valid names and references are as follows: *F. cyanescens* = *Quambalaria cyanescens* (de Beer et al. 2006), *Geosmithia* sp. 2 = *G. pumila* (Zhang et al. 2022), *Geosmithia* sp. 3, 23 = *G. pulverea* (Zhang et al. 2022), *Geosmithia* sp. 8 = *G. multisociorum* (Aylward et al. 2024), *Geosmithia* sp. 10 = *G. omnicola* (Pepori et al. 2015), *Geosmithia* sp. 13 = *G. ulmacea* (Pepori et al. 2015), *Geosmithia* sp. 20 = *G. granulata* (Zhang et al. 2022), *Geosmithia* sp. 21 = *G. xerotolerans* (Crous et al. 2018)

a reproductive stage. During the feeding stage, which begins in early spring and ends in autumn, adults attack tree buds and bore tunnels through the twigs of healthy trees. This causes buds and the fruit to dry out and fall off (Ghrissi et al. 2018). Since a single adult can destroy 8–10 fruit buds, a high population can lead to serious economic losses (Sönmez and Mamay 2022). At the beginning of October, adults leave the feeding tunnels and search for oviposition sites. During the reproductive stage, they prefer to colonize pruned or unhealthy pistachio branches or damaged trunks. After mating at the entrance of the maternal gallery and oviposition, the eggs hatch and the young larvae begin to dig tunnels under the bark. After pupation, the adults emerge and cause further tissue damage, thus causing the branches to dry out. Newly emerged adults are found between April and May (Mehrnejad 2001; Sönmez and Mamay 2022). Although the number of generations per year still needs to be investigated in the invaded Mediterranean countries, in Iran, *H. vestitus* has only one generation per year (Fariwar-Mehin 1983; Mehrnejad 2001).

Fungal associates

Studies carried out in temperate regions of Europe, the Mediterranean regions and the USA report *Geosmithia* spp. and Ophiostomatoid fungi as the most frequent fungal associates of *Hylesinus* bark beetles (Table 2). For PBB, the genera *Geosmithia*, *Alternaria*, *Aspergillus, Fusarium* and *Penicillium* were isolated in Tunisia from living and dead beetles, and galleries were found on pistachio plants showing dieback symptoms associated with a high level of bark beetle infestations (Hadj Taieb et al. 2019). The genera *Curvularia* and *Nothophoma* were isolated from both living beetles and galleries, whereas the genus *Talaromyces* was isolated from both living and dead beetles. Finally, the genera *Paecilomyces*, *Parengyodontium* and *Trichothecium* were isolated only from dead beetles (Hadj Taieb et al. 2019). Each of the 28 isolated species was tested for phytopathogenic activity on pistachio stems. The highest virulence was found for seven of them (i.e., *Fusarium equiseti* (Corda) Sacc., *F. graminearum* Schwabe, *Nothophoma quercina* (Syd.) Q. Chen & L. Cai, *F. solani* (Mart.) Sacc., *Trichothecium roseum* (Pers.) Link, *Alternaria alternata* (Fr.) Keissl., and *F. verticilloides* (Sacc.) Nirenberg), followed by *F. brachygibbosum* Padwick, *Geosmithia* sp. 20*,* *Penicillium sumatrense* Svilv. and *Paecilomyces variotii* Bainier (Hadj Taieb et al. 2019). These results are supported by previous studies showing that *F. equiseti*, *F. solani*, *A. alternata*, *P. variotii* and *N. quercina* are pathogenic on pistachio plants (Ash and Lanoiselet 2001; Eskalen et al. 2001; Triki et al. 2009; Venturini et al. 2012; Hamid et al. 2014; Mirhosseini et al. 2014; Sabbagh and Khosravi Moghaddam 2016; Mahdian

Table 2 Fungi reported to be associated with bark beetles of the genus *Hylesinus* in the world

Beetle species	Reported associated fungi	Region	References
H. crenatus	*Geosmithia* spp., *O. catonianum*-like, *O. hylesinum*, *O. karelicum*	Norway	Aas (2017), Aas et al. (2018)
	G. flava, *O. hylesinum*, *O. novo-ulmi*, *O. quercus*, *Sporothrix* sp. 8	Poland	Aas et al. (2018), Jankowiak et al. (2019), Strzałka et al. (2021)
H. oregonus	*Geosmithia* sp. 12	USA	Kolařík et al. (2017)
H. orni	*G. flava* (= *G.* sp. 7), *Geosmithia* spp. (*G.* sp. 10*, 12)	Bulgaria	Kolařík et al. (2008)
	G. flava (= *G.* sp. 7)*,* *G. pallida* s.l. (= *G.* sp. 2*, 5), *Geosmithia* spp. (*G.* sp. 10*, 12)	Hungary	Kolařík et al. (2008)
H. toranio	*G. pallida* s.l. (= *G.* sp. 3*), *G. putterillii* (= *G.* sp. 6), *Geosmithia* spp. (*G.* sp. 8*, 12)	Czech Republic	Kolařík et al. (2008)
H. varius	*G. pallida* s.l. (= *G.* sp. 3*), *G. putterillii* (= *G.* sp. 6), *Geosmithia* spp. (*G.* sp. 8*, 12)	Czech Republic	Kolařík et al. (2008)
	Geosmithia spp., *O. catonianum*-like, *O. quercus*, *Sporothrix* sp. 8	Norway	Aas (2017), Aas et al. (2018)
	G. flava, *Geosmithia* sp. 12, *O. quercus*, *Sporothrix* sp. 8	Poland	Jankowiak et al. (2019), Strzałka et al. (2021)
	Geosmithia spp. (*G.* sp. 8*, 12)	Slovakia	Kolařík et al. (2008)
Hylesinus* (= *Chaetoptelius*) *vestitus	***F. cyanescens**, *Geosmithia* sp. 10***	**Croatia**	Kolařík et al. (2006, 2007)
	Alternaria alternata*, *Aspergillus* spp., *Curvularia spicifera*, *Fusarium* spp., *G. lavendula*, *G. omnicola*, *G. pallida*, *Geosmithia* sp. 20*, *Nothophoma quercina*, *Paecilomyces variotii*, *Parengyodontium album*, *Penicillium* spp., *Talaromyces* spp., *Thielavia microspora*, *Trichothecium roseum	**Tunisia**	Hadj Taieb et al. (2019)
	F. cyanescens**, *G. langdonii* (= *G.* sp. 15), *Geosmithia* sp. 10	**Turkey**	Kolařík et al. (2006, 2007)

Bold text indicates reports referred to the Mediterranean area

Indicates species that have undergone taxonomic revision. The names reported in the table follow the original reference cited therein; updated valid names and references are as follows: *F. cyanescens* = *Quambalaria cyanescens* (de Beer et al. 2006), *Geosmithia* sp. 2 = *G. pumila* (Zhang et al. 2022), *Geosmithia* sp. 3 = *G. pulverea* (Zhang et al. 2022), *Geosmithia* sp. 8 = *G. multisociorum* (Aylward et al. 2024), *Geosmithia* sp. 10 = *G. omnicola* (Pepori et al. 2015), *Geosmithia* sp. 20 = *G. granulata* (Zhang et al. 2022) and Zafari 2017). On the contrary, several species belonging to the genera *Aspergillus*, *Penicillium* and *Talaromyces* showed no phytopathogenicity (Hadj Taieb et al. 2019). Some of the tested species belonging to these genera are reported to be plant endophytes (Meng et al. 2011; Zhang et al. 2012; Vinale et al. 2017). Since one relevant role of fungal endophytes is to provide plant protection against phytopathogens, the in vitro fungal antagonistic activity of *Talaromyces pinophilus* (Hedgc.) Samson, N. Yilmaz, Frisvad & Seifert, *Penicillium bilaiae* Chalab. and *Aspergillus sclerotiorum* G.A. Huber have been tested and positively demonstrated against many of the phytopathogenic fungal isolates mentioned above (Dingle and Mcgee 2003; Hadj Taieb et al. 2019). If the beetles are absolutely dependent on some of the latter phytopathogenic fungi, then antagonism by some plant endosymbionts could negatively affect the PBB population (Klepzig and Six 2004). Furthermore, some of the species isolated by Hadj Taieb et al. (2019), i.e., *Aspergillus tamarii* Kita, *F. verticillioides*, *Penicillium chrysogenum* Thom, *P. variotii*, *T. pinophilus*, *T. roseum* and *A. alternata,* were shown to potentially act as entomopathogens on several pests (Mohi-ud-Din et al. 2006; Francis et al. 2011; Pelizza et al. 2011; Sharma et al. 2012; Moorthi et al. 2015; Yang et al. 2015; Vinale et al. 2017). However, their entomopathogenic role needs specific evaluation under field conditions in different contexts. All the above-listed fungi, together with *P. bilaiae* and *Parengyodontium album* (Limber) C.C. Tsang, J.F.W. Chan et al., were tested in vitro for their entomopathogenic activity against PBB and found to be highly pathogenic to adults and larvae (Hadj Taieb et al. 2020). Given that some fungi show both pathogenicity and potential entomopathogenic activity in vitro, and that the insect could act as a vector for all the fungi listed above, further studies are needed to better understand their ecological role. This is essential in order to develop a potential biological control strategy for the PBB in the Mediterranean regions (Hadj Taieb et al. 2020).

Cryphalus dilutus

Biology and ecology

Cryphalus dilutus Eichhoff (formerly *Hypocryphalus dilutus,* ex *Hypocryphalus scabricollis*), is a bark beetle native to the Indian subcontinent and now found throughout the Asian continent, North Africa and Southern Europe (Wood and Bright 1992; Faccoli et al. 2016; Barnouin et al. 2020; Johnson et al. 2020; EPPO 2025). Unlike most species belonging to the genus *Cryphalus*, *C. dilutus* is polyphagous. In its native range, it can develop under the bark of various tropical trees such as *Buchanania lanzan* Spreng., *Canarium euphyllum* Kurz., *Garuga pinnata* Roxb., *Ficus* spp. and others (Wood and Bright 1992; Faccoli et al. 2016). However, outside its native range, it can reproduce on Moraceae (including fig species, i.e., *F. retusa* L. and *F. carica*) and Anacardiaceae (including mango) (Wood and Bright 1992; Johnson et al. 2017; Gugliuzzo et al. 2023) (Fig. 1). Recent accidental introductions have led to infestations in the Mediterranean, where *C. dilutus* is currently emerging as a pest. It has been reported on fig trees in Algeria, Tunisia and Malta, and on both fig and mango trees in Italy (Mifsud and Knizek 2009; Mifsud et al. 2012; Faccoli et al. 2016; Gaaliche et al. 2018; Gugliuzzo et al. 2023; Mellal et al. 2023). On fig trees, adults of *C. dilutus* usually attack the trunk. Females bore galleries where they lay eggs under the outer bark. Larvae develop in the phloem-cambial region, where they pupate. New adults commonly emerge in late spring, and once again in late summer to early fall. However, if they are fully developed and the temperatures are suitable, they can emerge at any time. In the Mediterranean, this bark beetle can have at least two generations per year, as reported in Malta (Cutajar and Mifsud 2017).

Fungal associates

Several fungal species are commonly associated with bark beetles in the genus *Cryphalus*, particularly members of the family Ceratocystidaceae, as well as species of *Geosmithia* spp. and *Lasiodiplodia* sp. (Table 3). Outside the Mediterranean area, in Oman, Pakistan, Bangladesh, Mexico and Brasil, *Cryphalus mangiferae* Stebbing (formerly *Hypocryphalus mangiferae* Stebbing) has been reported as the primary vector of lethal mango pathogens belonging to the *Ceratocystis fimbriata* Ellis & Halst species complex (Johnson et al. 2020). Notably, *Cryphalus mangiferae* has been the only Scolytinae found in both diseased and healthy trees (Ribeiro 1980; Al Adawi et al. 2006, 2013; van Wyk et al. 2007; Masood et al. 2010, 2011; Masood and Saeed 2012; Oliveira et al. 2015; Galdino et al. 2016, 2017). The *C. fimbriata* species complex was supposed to include not only the mango pathogen described in Oman (i.e., *C. manginecans* M. van Wyk, A. Adawi & M.J. Wingf.), but also *C. mangivora* and *C. mangicola* M. van Wyk & M.J. Wingf. (van Wyk et al. 2011). However, the identification of these *Ceratocystis* species was based only on one marker (ITS). More recently, phylogenetic analyses using TEF-1α and β-tubulin microsatellite markers in addition to ITS, coupled with morphological and sexual compatibility tests, have demonstrated that the species collected in Oman, Pakistan and Brazil are synonyms of *C. fimbriata* (Oliveira et al. 2015). The precise identification of the *Cryphalus* species infesting mango in some regions needs to be re-evaluated (Johnson et al. 2020). *C. mangiferae* is a specific pest of *Mangifera* spp. that mainly colonises dead or heavily stressed mango trees and is not known to cause severe damage or to transmit lethal fungal plant pathogens (van Wyk et al. 2007; Johnson et al.

Table 3 Fungi reported to be associated with bark beetles of the genus *Cryphalus* in the world

Beetle species	Reported associated fungi	Region	References
Cryphalus abietis	*Geosmithia* sp. 2*	Czech Republic	Kolařík and Jankowiak (2013)
C. dilutus	***Botryosphaeriaceae*, *Ceratocystis ficicola*, *Neocosmospora* spp.**	**Italy**	Gugliuzzo et al. (2023), Gusella et al. (2024a, b)
C. dilutus/*C. mangiferae* (*ex Hypocryphalus mangiferae*)[b]	*C. fimbriata*, *C. mangicola*[a], *G. mangivora*[a]	Brazil	van Wyk et al. (2011), Galdino et al. (2016, 2017), Pereira et al. (2021)[a]
	C. fimbriata, *C. manginecans*[a], *Lasiodiplodia theobromae*	Oman	Al Adawi et al. (2006, 2013)[a], van Wyk et al. (2007)[a]
	C. fimbriata, *C. manginecans*[a], *L. theobromae*, *Phomopsis* sp.	Pakistan	van Wyk et al. (2007), Masood et al. (2010, 2011), Masood and Saeed (2012)[a]
C. eriobotryae	*G. bombycina, G. pulverea*	China	Zhang et al. (2022)
C. kyotoensis	*G. pulverea, G. subfulva*	China	Zhang et al. (2022)
C. piceae	*Geosmithia* sp. 25	Czech Republic	Kolařík and Jankowiak (2013)
	Geosmithia spp. (*G.* sp. 9, 16, 29)	Poland	Jankowiak and Kolařík (2010), Kolařík and Jankowiak (2013), Jankowiak and Bilański (2018)
C. pubescens	*G. flava* (=*G.* sp. 7), *G. langdonii* (=*G.* sp. 15), *G. putterilii* (=*G.* sp. 6), *Geosmithia* spp. (*G.* sp. 21*, 40)	USA	Kolařík et al. (2017)
C. rhusi	*Fusarium* sp., *Penicillium pinophilum*, *Yamadazyma* sp.	Japan	Masuya et al. (2019)

Bold text indicates reports referred to the Mediterranean area

[a] Synonyms of C. *fimbriata* according to Oliveira et al. (2015)

[b] Supposed to be *C. dilutus* instead of *C. mangiferae*

[*] Indicates species that have undergone taxonomic revision. The names reported in the table follow the original reference cited therein; updated valid names and references are as follows*: *Geosmithia* sp. 2 = *G. pumila* (Zhang et al. 2022), *Geosmithia* sp. 21 = *G. xerotolerans* (Crous et al. 2018)

2017). For these reasons, it is supposed that the actual bark beetle species infesting mango trees in the above-mentioned regions and acting as the fungal disease vector is not *C. mangiferae*, but rather *C. dilutus*, formerly *H. dilutus* (Hassan and Nazami 2017; Johnson et al. 2017, 2020; Gugliuzzo et al. 2023).

In Sicily (Italy), infestations on mango trees and fig trees observed in 2022 were confirmed to be caused by *C. dilutus* (Gugliuzzo et al. 2023; Gusella et al. 2024b). Investigations concerning the potential of *C. dilutus* to act as a vector of phytopathogenic fungi require further attention. It has been suggested that while feeding on diseased trees, fungal propagules may contaminate their bodies and thus be spread to healthy trees (Ploetz et al. 2013). Furthermore, little is known about the role of fungal associates in the life cycle of the *C. dilutus* insect. Preliminary observation in Pakistan suggests that, like other bark beetles, *Cryphalus* spp. may feed on fungi to enhance their nutrition and reproduction or to help themselves survive in unsuitable environmental conditions (Iqbal and Saeed 2012). In Sicily, fungi belonging to the Botryosphaeriaceae family and the *Neocosmospora* genus have been isolated from both symptomatic mango-wood samples and emerging beetle individuals (Gugliuzzo et al. 2023). In the same geographical area, previous surveys on mango woody canker and shoot blight revealed the presence of Botryosphaeriaceae, including *Botryosphaeria dothidea* (Moug. ex Fr.) Ces. & De Not., *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl. and *Neofusicoccum parvum* (Pennycook & Samuels) Crous, Slippers & A.J.L. Phillips (Aiello et al. 2022). Botryosphaeriaceae and *Neocosmospora* spp. were also found in association with *C. dilutus* individuals and necrotic woody tissues near the beetle galleries, together with *C. ficicola* Kajitani & Masuya, fungal species that were all found to be pathogenic to fig (Crous et al. 2023; Gugliuzzo et al. 2023; Gusella et al. 2024b). The results obtained in Sicily on the association of relevant phytopathogenic fungal species with *C. dilutus* on mango and common fig should also be tested in other Mediterranean populations of the beetle. In addition, Leach's postulates still need to be tested to understand the relative importance of *C. dilutus* as a vector of Botryosphaeriaceae, *Neocosmospora* spp. and *Ceratocystis* spp. in comparison to other means of dissemination.

The olive bark beetle *Phloeotribus scarabaeoides*

Biology and ecology

Phloeotribus scarabaeoides Bernand is generally considered a secondary pest in olive groves because it preferentially attacks young branches of damaged, weakened or diseased olive trees. However, it can become a serious pest of olive trees when pruned branches are left on the ground, posing a high risk for infesting nearby healthy trees (González and Campos 1994; Alvarado et al. 2010; Vizzarri and Tosi 2015). *P. scarabaeoides* is widespread in several Mediterranean countries. In Europe, it is found in Croatia, Cyprus, France, Greece, Italy, Malta, Portugal and Spain. In North Africa it is present in Algeria, Egypt, Libya, Morocco and Tunisia. In Asia, it has been reported in Israel, Lebanon, Libya and Turkey. Its preferred host is the olive tree, although it has also been recorded on other tree species such as *Phillyrea*, *Fraxinus*, *Ligustrum* and *Syringa* (Arambourg 1986) (Fig. 1).

In mid-spring, from April to May, depending on the local climate, newly emerging adults leave their galleries and move to new plants where they dig maturation feeding tunnels. Finally, in late summer, adults leave these tunnels and dig holes in vegetative buds, where they overwinter until the following spring (Alvarado et al. 2010). These attacks lead to the death of small shoots, inflorescences and young fruiting shoots, which results in reduced production (Vizzarri and Tosi 2015). In Southern Spain, after an incubation period of 8 to 13 days, larvae are known to bore solitary tunnels perpendicular to the maternal gallery. It can have 4 generations per year in warmer regions such as Algeria, while fewer generations are expected to occur in the cooler areas of the Mediterranean (Campos and González 1991; Lozano et al. 1996; Mimoun and Doumandji 2014).

Fungal associates

Although only a few studies have investigated fungal associates of *Phloeotribus* spp., *Geosmithia* spp. (Hypocreales) appear to be common associates of this bark beetle genus (Table 4). *P. scarabeoides* is specifically associated with *G. xerotolerans* Rodr.-Andr., Cano & Stchigel (*Geosmithia* sp. 21) in Spain (Crous et al. 2018), with *Geosmithia* sp. 11 in Spain and Croatia, with *G. granulata* (*Geosmithia* sp. 20) R. Chang and X. Zhang in Spain, Croatia and Italy, and with *Geosmithia* sp. 22 in Jordan and Croatia (Kolařík et al. 2008; Zhang et al. 2022). In addition, it has been found to be associated with *Q. cyanescens* in Syria, Croatia and Spain (de Beer et al. 2006; Kolařík et al. 2006). The role of these *Geosmithia* spp. and *Quambalaria* sp. for *P. scarabaeoides* is still unclear and requires further investigation. Moreover, a recent study conducted in Spain (ElDesouki-Arafat et al. 2021) showed that *P. scarabaeoides* is not a vector of the serious olive tree pathogen, *Verticillium dahliae,* contrary to the hypothesis of Alvarado et al. (2010).

Table 4 Fungi reported to be associated with bark beetles of the genus *Phloeotribus* in the world

Beetle species	Reported associated fungi	Region	References
P. cristatus latus + P. rhododactylus	***Geosmithia* sp. 10*, *G. lavendula* (=*G.* sp. 18)**	**Italy**	Kolařík et al. (2007)
	***Geosmithia* spp. (*G.* sp. 10*, 20*, 21*)**	**Spain**	Kolařík et al. (2007)
P. frontalis	*G. proliferans*	USA	Huang et al. (2017)
P. liminaris	*Geosmithia* sp. 27	USA	Huang et al. (2017)
P. scarabaeoides	***Geosmithia* spp. (*G.* sp. 11, 20*, 22)** ***Quambalaria cyanescens***	**Croatia**	Kolařík et al. (2006, 2007), Stodůlková et al. (2008)
	Geosmithia* sp. 20	**Italy**	Kolařík et al. (2007)
	***Geosmithia* sp. 22**	**Jordan**	Kolařík et al. (2007)
	Geosmithia* spp. (*G.* sp. 11, 20*), *G. xerotolerans* (=*G.* sp. 21), *F. cyanescens*	**Spain**	Kolařík et al. (2006, 2007), Crous et al. (2018)
	*F. cyanescens**	Syria	Kolařík et al. (2006)
P. texanus	*G. pallida* (=G. sp. 2*)	USA	Huang et al. (2017)

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Future directions to reveal bark beetle–fungus associations in the Mediterranean

The overview presented above on the fungal associates of *S. amygdali, S. rugulosus, S. mali, C. dilutus, H. vestitus* and *P. scarabeoides* highlights that the mycobiome of these economically important bark beetle species is still largely understudied. To address this knowledge gap, we propose the following research questions that should guide future investigations: (i) what is the core mycobiome of these bark beetles, and how variable is it within and between different populations across the Mediterranean regions? (ii) what are the ecological roles of the core fungi for each bark beetle species? (iii) do any of the associated fungi act as plant pathogens, thus posing a threat to infested plants?

To answer these questions in a comprehensive and scientifically rigorous manner, it is necessary to take into account some recent and key conceptual advances from bark beetle microbiome research (Hulcr et al. 2020, 2025; Cambronero-Heinrichs et al. 2025).

The first aspect regards the methodology used to collect bark beetles and/or infested wood samples. Adult individuals can be collected by using traps baited with attractive lures (Dodds et al. 2024), by dissecting wood samples showing signs of colonization, or by collecting the latter wood samples, caging them and waiting for adult emergence (Hulcr et al. 2025). A key factor to consider when using traps is whether adult beetles are collected in wet conditions (i.e., traps or collection cups containing liquid) or dry conditions (i.e., traps or cups without liquid). The use of liquid in the collection cup should be avoided, as it can increase the risk of cross-contamination among captured specimens. As an alternative, placing crumpled paper moistened with sterile water inside the collection cup helps keep the beetles alive for a few days while minimizing potential cross-contamination (Preiswerk et al. 2018; Cambronero-Heinrichs et al. 2025). Sampling adult beetles directly from their galleries or with emergence traps at their gallery entrances reduces the likelihood of cross-contamination among individuals. In this regard, it is important to consider that adults collected directly out of the wood may not have the representative fungal community due to the fact that in many bark beetle species the emerging adults actively select their vectored microbiome shortly before emergence (e.g., by mycetangia or selective feeding; Mayers et al. 2022).

The second key aspect regards the identification of fungal associates, ideally using both culture-dependent and culture-independent methods. Traditional culturing is typically followed by morphological and multigene molecular identification methods (Kolařík et al. 2008; Biedermann et al. 2013; Cruz et al. 2018, 2019; Saucedo-Carabez et al. 2018; Hadj Taieb et al. 2019; Gugliuzzo et al. 2023; Gusella et al. 2024b). However, these methods have some limitations. They often fail to detect non-culturable microorganisms and to under- or over-represent specific species on general growth media (Kirk et al. 2004; Hulcr et al. 2020; Wijayawardene et al. 2021). In order to overcome these limitations imposed by culturing, culture-independent techniques, such as metabarcoding, can be used (Kostovčík et al. 2015; Ibarra-Juarez et al. 2018; Diehl et al. 2022). This technique, however, can have drawbacks, including incomplete sequence databases, amplification biases and incorrect quantitative representations of communities (Wijayawardene et al. 2021; Hulcr et al. 2025). For these reasons, both approaches should be used jointly to gain an accurate description of the diversity of fungal symbionts associated with bark beetles. In Table 5, a more detailed overview of these identification diagnostic options is provided.

The correct identification of both beetles and fungi is made complicated by the continuous taxonomic renaming of these organisms, which can provide wrong information about the evolutionary classification of bark-beetle associations (Johnson et al. 2017; Hulcr et al. 2020). In addition, confirmation of species identity is crucial because the use of an outdated taxonomic classification can spread incorrect data, compromising the reliability of DNA sequence databases (Hulcr et al. 2015, 2020; Crous et al. 2021). To ensure accurate fungal identification, it is essential to rely on well-curated key repositories. Among the most trusted resources for fungal reference sequences, UNITE (synchronized with the INSDC (International Nucleotide Seqeunce Database Collaboration) and/or integrated with NCBI RefSeq-Targeted Loci (RTL)) provides an operational taxonomic units (OTUs) system based on ITS sequence data obtained via Sanger technology, organized into Species Hypotheses (SHs) (Lücking et al. 2020; Abarenkov et al. 2024; Goldfarb et al. 2025). Additionally, MycoBank and Index Fungorum provide resources for taxonomic and nomenclature validation (Robert et al. 2013), while the Barcode of Life Database (BOLD), which typically offers COI barcode sequences, is limited in fungal applications and more suitable for Animalia (Meiklejohn et al. 2019).

The isolation, identification and frequent presence of a fungus from an insect or from its galleries are not sufficient to deduce the type of interaction occurring. As suggested by Hulcr et al. (2020, 2025), experimental set-up and characterization methods must be vigorous, but unfortunately, some recent studies reporting co-occurring bark-beetle/fungi associations have sometimes been based on weak methodology. Claiming that a symbiosis is mutualistic, commensalistic or antagonistic requires several replications of factorial experiments that clearly demonstrate the effects of the presence or absence of the fungus. When carried out and documented in detail, such experiments are undoubtedly of great value for

Table 5 Diagnostic at a glance: overview of the main potential approaches and relative advantages and limitations for the identification of bark beetle fungal associates

Fungal identification approach	Microbial source	Potential advantages	Potential limitations
Culture-based techniques + morphology + Sanger sequencing	Adult insects*: identification of culturable fungi carried by the insect	Morphological description of fungi	No detection of unculturable taxa or non-sporulating fungi
		High-resolution molecular identification based on specific markers (ITS, tef, tub and others), including species complexes and pleomorphism	Under/over representation of fungi depending on the artificial media
	Wood/galleries: identification of culturable fungi directly from the environment	Preservation of strains for future studies about their ecological roles and pathogenicity	Overgrowth of fast-growing fungi and suppression of slower-growing fungi
		Detection of viable and growing fungal tissues (spores and hyphae)	DNA amplification from viable and non-viable fungal material, if the sample is well preserved and DNA is not degraded
Metabarcoding [(High-Throughput Sequencing) HTS]	Adult insects*: microbial community profiling	Detection of greater taxonomic diversity, including the unculturable ones	Inaccurate data due to incomplete reference databases
		Opportunity to process samples with low biomass (e.g., insect gut)	Poor quantification of relative abundance
	Wood/galleries: surrounding environment's fungal community	Fast and broad comparison between fungal communities across host species, beetle stages and locations	Overestimation of some taxa and failure to detect others due to amplification biases
Combination of both the above methods	All of the mentioned-above	Detection of method-specific biases	Longer processing time, higher costs, and more manual and bioinformatic work
		Addition of Sanger sequences to databases to improve OTU identification accuracy	

*It is recommended to collect beetles during their dispersal flight using emergence traps or pheromone traps to identify their specific fungal community and exclude non-associated species subsequent research (French and Roeper 1972; Bracewell and Six 2015; Saucedo et al. 2018; Carrillo et al. 2020).

Finally, a common approach used in the field of bark beetle–fungal research is to infer causality from observations (Faccoli et al. 2016; Tarno et al. 2016). However, to prove that a beetle is a vector of a particular fungus, and that this fungus has a phytopathogenic effect on the host plant, standards such as Leach's rules and Koch's postulates must be applied consistently. If these criteria are met, the conceptual model of the disease triangle used in the field of plant pathology, consisting of parasite/pathogen, host and environment, is no longer sufficient to explain infectious disease. Thus, the beetle vector itself must also be considered to effectively predict and treat such diseases (Agrios 2005).

All the above-mentioned aspects need to be translated into operational steps that can be adapted to the specific context of Mediterranean orchards. Implementing surveillance protocols during the pre-inoculation or early colonization stages helps to prevent the spread of the pathogen or facilitates early detection. In this regard, highly sensitive and reliable molecular methods such as the use of qPCR for the early detection of wood pathogens (Luchi et al. 2013; 2020) or real-time PCR based on probe technology for the early tracking of insect vectors, can be useful (Rizzo et al. 2024a, b). These methods can also contribute to analysing the multi-temporal and multi-zonal spread of pathogens and their bark beetle vectors, which can facilitate the understanding of any microhabitat preferences, if existing (Luchi et al. 2020). Surveillance must be accompanied by diagnostic workflows that can accurately confirm the presence of the pathogen or its vector. When scientifically justified, decision thresholds can contribute to the development of operational standards in line with the European and Mediterranean Plant Protection Organization (EPPO) and provide useful evidence for the European Food Safety Authority (EFSA) risk assessment processes. For instance, trees showing multiple entry holes and frass accumulation on the outer bark as consequence of bark beetle infestation can contextually show symptoms of fungal infection. The subsequent detection of propagules of the fungal pathogen in this frass can represent an operational indication for the activation of disease containment measures, such as the removal of affected plants, the disinfection of tools or the blocking of the movement of wood material (Hughes et al. 2023).

Many countries in the Mediterranean basin are experiencing an increasing frequency of extreme climatic conditions, such as heatwaves and severe drought (Zittis et al. 2022). These affect host tree health, accelerating their susceptibility to attacks by bark beetles (Jaime et al. 2024). Climate change can thus facilitate the establishment and spread of alien bark beetles that have been accidentally introduced to new areas (Brockerhoff and Liebhold 2017; Pureswaran et al. 2022). In such a context, the lack of co-evolution between alien beetle species and endemic plants can lead to the loss of a large number of trees, as a consequence of their susceptibility to the insects and/or associated fungi. This can occur even when these beetles and fungi are not known to cause host mortality in their native range (Yan et al. 2005; Poland and McCullough 2006). Furthermore, new associations may develop between alien bark beetles and native phytopathogens or between native bark beetles and alien phytopathogens (Raffa et al. 2014). Fungal pathogens can have a much more devastating impact in non-native areas, where co-evolution with host tree species has not occurred. This results in a lower level of resistance, making bark beetle infestations even more difficult to contain (Loo 2008).

Several important questions remain unresolved in the study of these beetle–fungus relationships, such as the evolution of pathogenicity among some symbiotic fungi. Consequently, future research efforts should be directed at understanding why and how some beetle symbionts act as plant pathogens and why others do not, especially in non-native regions (Hulcr and Dunn 2011). Some species apparently invade the sapwood only after the host tissue has died and show little capability of naturally colonizing living trees (Harrington 2005). Although not all these fungi are considered to be pathogenic, a few of the species in the Ophiostomataceae and Ceratocystidaceae are primary plant pathogens, including the genera *Leptographium*, *Ophiostoma*, *Raffaelea*, *Ceratocystis* and *Endoconidiophora* (Jacobs and Wingfield 2001; Harrington et al. 2010; de Beer and Wingfield 2013; Ploetz et al. 2013; Seifert et al. 2013; Linnakoski and Forbes 2019).

In addition, fungal associates may or may not depend on insect vectors. Fungal species in the family Ophiostomataceae (e.g., the genera *Leptographium*, *Ophiostoma* and *Raffaelea*) have closer associations with insect vectors as compared to those belonging to the Ceratocystidaceae (Wingfield et al. 2017). Only a few of these fungi are considered primary phytopathogens capable of killing trees without the aid of their insect vectors (Wingfield et al. 2017). Examples are the laurel wilt pathogen *Harringtonia lauricola* (T.C. Harr., Fraedrich & Aghayeva) Z.W. de Beer & M. Procter (formerly *Raffaelea lauricola*) (Harrington et al. 2008; de Beer et al. 2021; Araújo et al. 2022; Mayfield et al. 2023) and the black-stain root pathogen *Leptographium wageneri* (W.B. Kendr.) M.J. Wingf., which can be introduced to the hosts also via root or by grafting (Harrington and Cobb 1987; Choi et al. 2023). Similarly, the tree infection by the pathogen *Ophiostoma ulmi*, involved in Dutch elm disease, can infect trees through root anastomoses (Webber and Brasier 1984; Santini and Faccoli 2014). In contrast, most *Ceratocystis* spp. do not have a specific insect vector and are less dependent on insects for their dissemination. Their spores, both airborne or soilborne, can infect hosts belonging to a broad range of plants (Marin et al. 2003; Ferreira et al. 2011;

Luchi et al. 2013; Lee et al. 2016). This less specific association with bark beetles also suggests a potentially lower value for beetles (Hulcr and Cognato 2010). However, some fungi and bark beetles may be unable to colonize a tree host without their partner (van Wyk et al. 2007). For example, despite the weak pathogenicity of *Ceratocystis* spp., some isolates have been considered responsible for tree deaths when associated with *Cryphalus mangiferae* on non-native hosts (Hulcr and Dunn 2011).

Finally, understanding how bark beetle associations with phytopathogenic fungi spread and persist in specific contexts is of crucial importance in order to develop sustainable and efficient management strategies that target insects, vectored fungi, or ideally both.

Author contributions

All authors conceived and designed the study. MBC performed the bibliographic search and wrote the first draft of the manuscript. PHWB, DR, AR, GP and AG commented on and edited earlier versions of the manuscript. All authors read and approved the final version of the manuscript.

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Data Availability No datasets were generated or analyzed during the current study.

Declarations

Ethics approval This study does not contain any studies with human participants or vertebrate animals and no ethical approval is required.

Competing interests The authors declare no competing interests.

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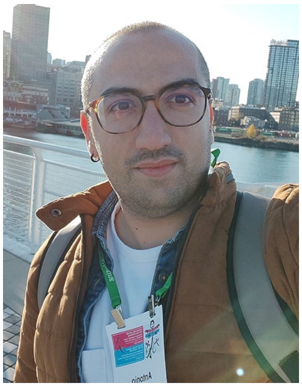

Antonio Gugliuzzo is currently a postdoctoral researcher at the University of Catania in Italy, where his research mainly focuses on evaluating innovative and sustainable pest management approaches. He earned his PhD in 2022 with a thesis entitled 'Development of new tools for the sustainable management of non-native ambrosia beetles', which was awarded the 'Michele Stanca 2024 Award' by the Italian Association of Scientific Societies in Agriculture (AISSA) as the best national PhD thesis in Entomology for 2022–23. Antonio's primary research interest is the biology, ecology, multi-trophic interactions and mutualistic relationships of different invasive agricultural and forest insect pests and their natural enemies. This forms the basis of his work on multidisciplinary research activities, which he undertakes as part of his collaborations in scientific projects with national and international scientific groups.