

# Novel associations between ophiostomatoid fungi, insects and tree hosts: current status—future prospects

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**Abstract** Associations between fungal tree pathogens and insects have been recognized for at least 100 years. An important group of these fungi, termed ‘ophiostomatoid fungi’ on account of their morphological similarity, are represented by genera in the families Ceratocystidaceae and Ophiostomataceae. Associations between these fungi, tree-colonizing insects, and host trees have been actively researched since their first discovery. Human activities have led to the global movement of fungi from both families, resulting in the establishment of new and sometimes

damaging associations between these fungi, insects and trees. Recent ‘black swan’ events have resulted in an unprecedented increase of ambrosia and bark beetle-associated diseases of forest and fruit trees. We revisit some of the most important emergent diseases caused by the ophiostomatoid fungi, outline the reasons behind the emergence of these diseases, and consider long-term prospects regarding the threats that they pose to forestry and agriculture.

**Keywords** Biological invasions · Fungal-insect symbiosis · Invasive forest pathogen (IFP) · Invasive fungi

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## Introduction

Associations between insects and fungi are both ubiquitous and diverse (Vega and Blackwell 2005). Amongst these associations, those involving tree-infecting fungi and their insect vectors, namely bark beetles (Scolytinae) and ambrosia beetles (Scolytinae and Platypodinae), are the best understood and have been recognized for at least 100 years (Kirisits 2013). In 1836, for example, Schmidberger discovered that ambrosia beetles cultivate fungi as a food source, and in 1907, Münch discovered that conifer-infesting bark beetles have symbiotic associations with fungi that cause sap stain (Kirisits 2004). Since their first discovery, these fungi, recognized at the time as being species in the genus *Ceratocystis*, have been the

subject of considerable study, but also great controversy. This controversy has centered on long-standing disagreements relating to their taxonomy as well as the role that they play in tree mortality.

The taxonomy of the ophiostomatoid fungi, most of which are now recognized as belonging to the fungal families Ceratocystidaceae and Ophiostomataceae, was confused virtually since their first descriptions (Halsted 1890; Sydow and Sydow 1919). This confusion stemmed largely from the fact that species in these families share very similar basic morphological features (Fig. 1a–j), especially in their sexual states (Fig. 1b, f). For example, the sexual structures (ascmata) in both families typically have round to pear-shaped bases subtending long black necks, deliquescent asci that are seldom seen, and sexually derived single-celled, hyaline ascospores that exude from the apices of long necks in sticky masses (Fig. 1a, b, f, g) (Hunt 1956; Upadhyay 1981; De Hoog and Scheffer 1984). These morphological similarities are the result of convergent evolution driven by their association with insect vectors (Malloch and Blackwell 1993). The suspended sticky spore masses provide an ideal mechanism for these fungi to reach and attach to the bodies of their vectors (Fig. 3g), ensuring effective transport to new host substrates (Malloch and Blackwell 1993). The phenotypic similarities have consequently led to a long-standing assumption that species in the Ceratocystidaceae and Ophiostomataceae were closely related or even resided in the same genus (Bakshi 1951; Moreau 1952; Upadhyay 1981; Wingfield et al. 1993). However, molecular genetic tools, especially DNA sequence comparisons, provided clear phylogenetic evidence that these fungi reside not only in different families, but different orders (Fig. 1) (Spatafora and Blackwell 1994).

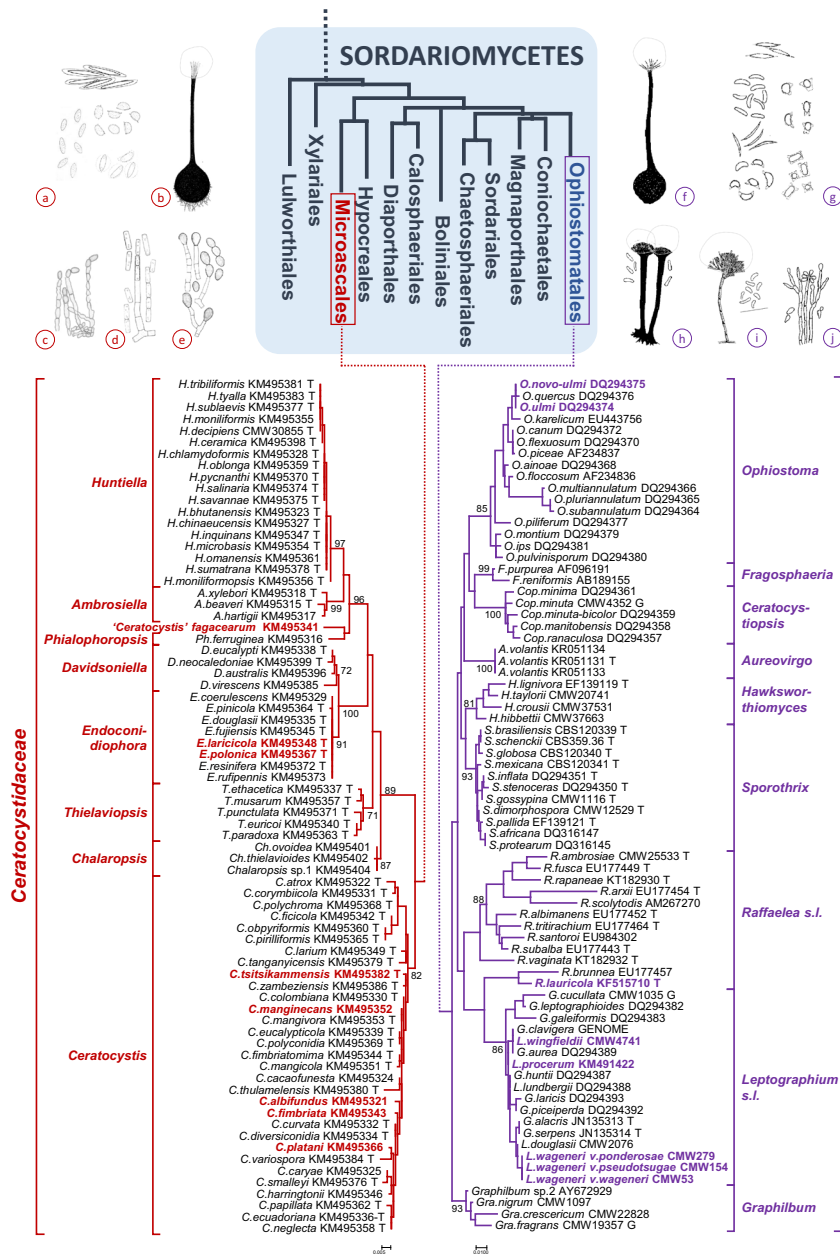
In order to facilitate communication between researchers working on fungi in the Ceratocystidaceae and Ophiostomataceae, the term “ophiostomatoid fungi” was adopted to describe these taxa (Wingfield et al. 1993; De Beer et al. 2013). The ophiostomatoid fungi are Sordariomycetes and they reside in the orders Microascales and Ophiostomatales (Fig. 1) (Hibbett et al. 2007; De Beer et al. 2013; Ploetz et al. 2013). In the Microascales, genera in the families Ceratocystidaceae, Graphiaceae and Gondwanamycetaceae are the best-known members of the ophiostomatoid fungi (Réblová et al. 2011; De Beer et al. 2013, 2014) while in the Ophiostomatales, all of the

ophiostomatoid fungi reside in the Ophiostomataceae (De Beer and Wingfield 2013).

Fungal genera in the Ceratocystidaceae (De Beer et al. 2014), include important tree pathogens, the majority of which reside in *Ceratocystis* and *Endoconidiophora*. There are no tree pathogenic genera in the Gondwanamycetaceae and Graphiaceae and these are not further considered in this review. The Ophiostomataceae, the taxonomy of which is currently being revised (De Beer, unpublished), accommodates important tree pathogens (Jacobs and Wingfield 2001; Harrington et al. 2010; Ploetz et al. 2013; Seifert et al. 2013), most of which are species in the genera *Leptographium*, *Ophiostoma* and *Raffaelea*.

That many ophiostomatoid fungi are intimately dependent on insects to be vectored between host trees is well established. It is now also well recognized that most ophiostomatoid fungi in the Ophiostomataceae have very different associations with their insect vectors than those in the Ceratocystidaceae. Species of *Leptographium*, *Ophiostoma* and *Raffaelea* tend to be vectored by bark or wood-boring insects (Paine et al. 1997; Jacobs and Wingfield 2001; Kirisits 2004; Harrington et al. 2010). These relationships are typically strongly co-evolved and host specific (Wingfield et al. 2016). This is broadly different to species in the genus *Ceratocystis*, most of which do not have very specific insect vectors. The latter fungi rely on strong aromas to attract their vectors, which include a range of sap-feeding beetles (Nitidulidae) and flies (Kile 1993). In addition, these fungi can readily infect a wide diversity of unrelated host plants, as single species of *Ceratocystis* can infect hosts that belong to entirely different plant orders. For example, *Ceratocystis albifundus* can infect non-native *Acacia mearnsii* (order Fabales), and trees in at least four other orders (Roux et al. 2007; Lee et al. 2016). A further distinction from the Ophiostomataceae is that species of *Ceratocystis* are less dependent on insects for their distribution than species of *Leptographium*, *Ophiostoma* and *Raffaelea*, as several species of *Ceratocystis* have spores that can be air or soil-borne (Marin et al. 2003; Ferreira et al. 2011; Luchi et al. 2013).

The rise of diseases caused by the ophiostomatoid fungi can be attributed to the ease with which the fungi and their vectors can move globally. Ophiostomatoid fungi and their arthropod vectors occur on wood and wood products (Wingfield et al. 2010), and in the case of certain *Ceratocystis*



**Fig. 1** Phylogenetic trees based on maximum likelihood analyses of ribosomal large subunit (LSU) sequences, showing the ordinal and generic placement of the ophiostomatoid fungi in the Microascales (red) and Ophiostomatales (purple). The trees were generated using MEGA6 (Tamura et al. 2013), using a GTR mutation model. Statistical support was generated for the nodes from 1000 bootstrap replicates. Names of species discussed in this review are highlighted in the phylogenetic trees. Convergent evolution is visible in sexual (a, b, f, g) and asexual (c–e, h–j) reproductive structures adapted for arthropod dispersal. A variety of sheathed and unsheathed ascospores (a,

g) are produced in slimy droplets on long-necked ascomata (b, f). Thielaviopsis-like (d, e) states of the Ceratocystidaceae produce asexual spores (conidia) in bottle-shaped phialides (d) or pigmented chlamydospores and/or aleurioconidia (e) for longer term survival. Synnematus, psotum-like (h) and mononematous, leptoglyphum-like (i) asexual structures of the Ophiostomataceae produce conidia in sticky droplets. Asexual spores of ambrosiella-(c) and raffaelea-like (j) forms are of reduced morphology and adapted for fungal feeding by ambrosia beetles

species, can also move easily on root crops and in soil (Fig. 3d, e) (Ferreira et al. 2011; Marin et al. 2003). In some cases, their means of spread and their host ranges are well recognized and well understood. However, there is growing evidence that novel vector relationships and new host-associations are emerging in the Ophiostomataceae and Ceratocystidaceae. The aim of this paper is to highlight examples of novel associations that appear to be arising and discuss the factors that have contributed to the increase in these associations (summarized in Table 1), thus considering their apparently growing importance as invasive aliens. Many of these are unexpected, emerging increasingly regularly, and clearly represent a significant threat to global forests and forestry.

### Novel associations in the Ophiostomataceae

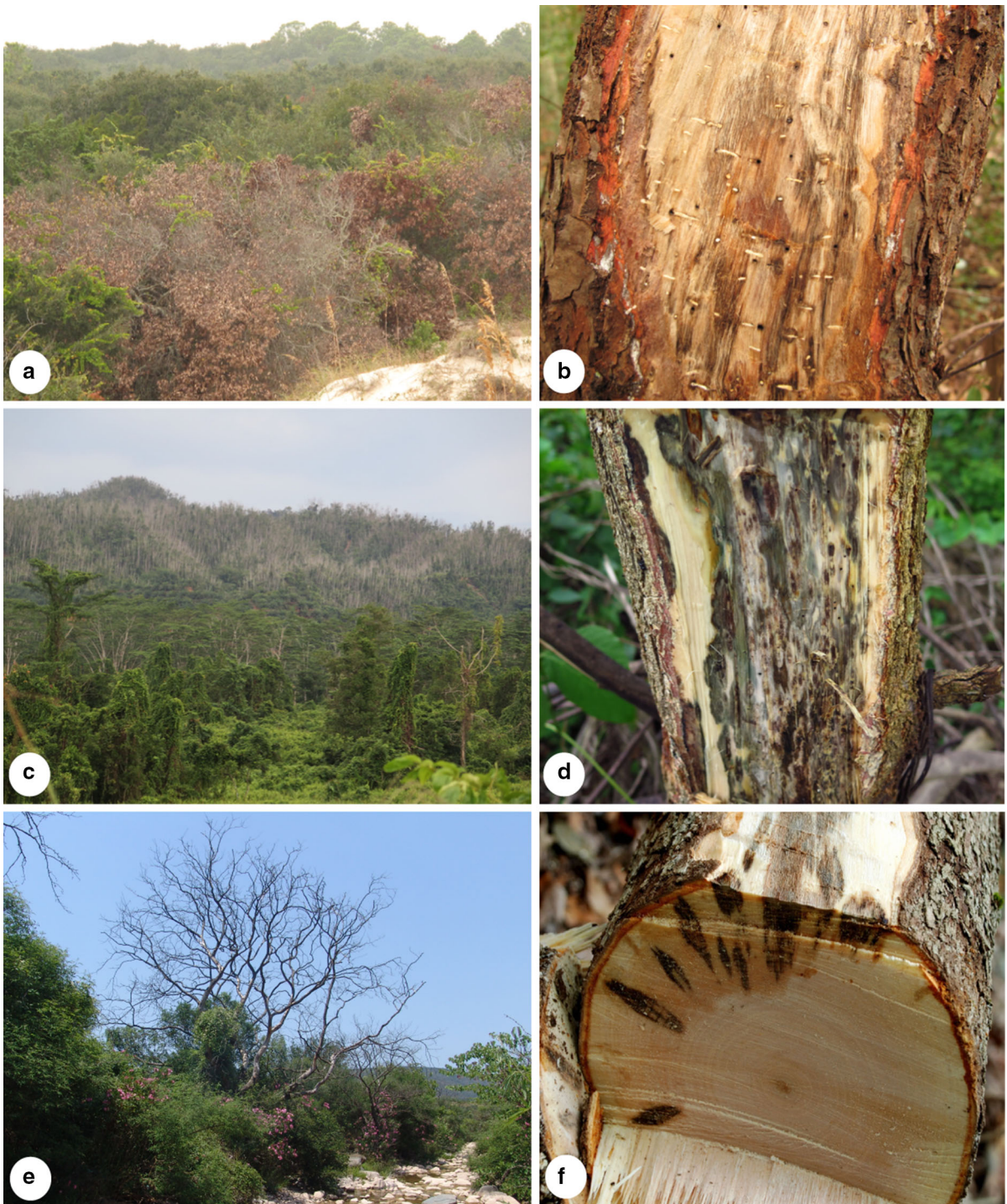
A few of the species in the Ophiostomataceae are primary pathogens, able to kill trees independently of

their insect vectors, as has been demonstrated by pathogenicity trials. The best-known examples are the Dutch elm disease (DED) fungi, *Ophiostoma ulmi* and *O. novo-ulmi* (Santini and Faccoli 2014), the more recently discovered laurel wilt pathogen *Raffaelea lauricola* (Fig. 2a) (Harrington et al. 2008) and three varieties of *Leptographium wageneri* that cause black stain root disease of conifers in the western USA (Harrington and Cobb 1986, 1987). In each case, the pathogens have very specific and reasonably strongly co-evolved bark or wood-boring insect vectors (Fig. 2b) (Webber 1990, 2004; Wingfield et al. 2016). In the case of the DED fungi and *R. lauricola*, they are invasive aliens that have been accidentally introduced into new environments where they have devastated naïve hosts, respectively in the Ulmaceae or Lauraceae (Harrington et al. 2008; Santini and Faccoli 2014).

The novel relationships between the Ophiostomataceae and insects are likely due to the fact that the fungi cause disease on tree species that are apparently related to those in the areas from which the fungi

**Table 1** Factors impacting the increase in tree diseases caused by ophiostomatoid fungi

Factor	Impact of the factor		
<i>Anthropogenic factors</i>			
Increased global movement of wood/wood products, soil	Increased establishment of exotic ophiostomatoid fungi and insect vectors		
Establishment of exotic plantations	Facilitates establishment of new exotic fungi and insect vectors through movement of plant and wood products and via the 'bridgehead' effect		
Pollution, climate change	Expands ranges of fungi and vectors; makes tree hosts increasingly susceptible		
Factor	Impact of the factor	Ceratocystidaceae versus Ophiostomatales	
<i>Biological factors</i>			
Phylogenetic/ecological similarity between hosts and vectors in the native and exotic ranges of fungi	Easier for fungi to make host and vector shifts between closely related/ecologically similar hosts/vectors	Phylogenetic similarity frequently important, but some species can readily shift onto distantly related hosts	Typically infects closely related hosts, and are vectored by closely related insects
Vector breadth	Vector breadth can influence ability of fungi to be transmitted and make host jumps	Broad vector range, including bark beetles, ambrosia beetles, nitidulids, flies, mites	Almost all vectored by bark or ambrosia beetles, mites
Pathogenicity factors of fungi (e.g. toxin production, impact of fungi on host vascular tissue)	Influences ability of a fungus to cause disease in a host	Several known to produce toxins, block vascular tissues	Some known to produce toxins, block vascular tissues
Transmission methods	Can influence the ways by which a fungal species is moved from one location to another	Most vectored by insects, but several can be transmitted via soil or air-borne spores	Almost entirely dependent on insect vectors, occasionally tree-to-tree contact, only a few species soil-borne



**Fig. 2** Symptoms associated with diseases caused by pathogens in the Ophiostomataceae and Ceratocystidaceae. **a** Dead and dying Red Bay Laurel (*Persea borbonia*) trees due to infection by *Raffaelea lauricola*. **b** Streaked discoloration in the wood of *P. borbonia* caused by *R. lauricola* as well as tunnels made by the wood-boring beetle *Xyleborus glabratus*. Frass tubes are

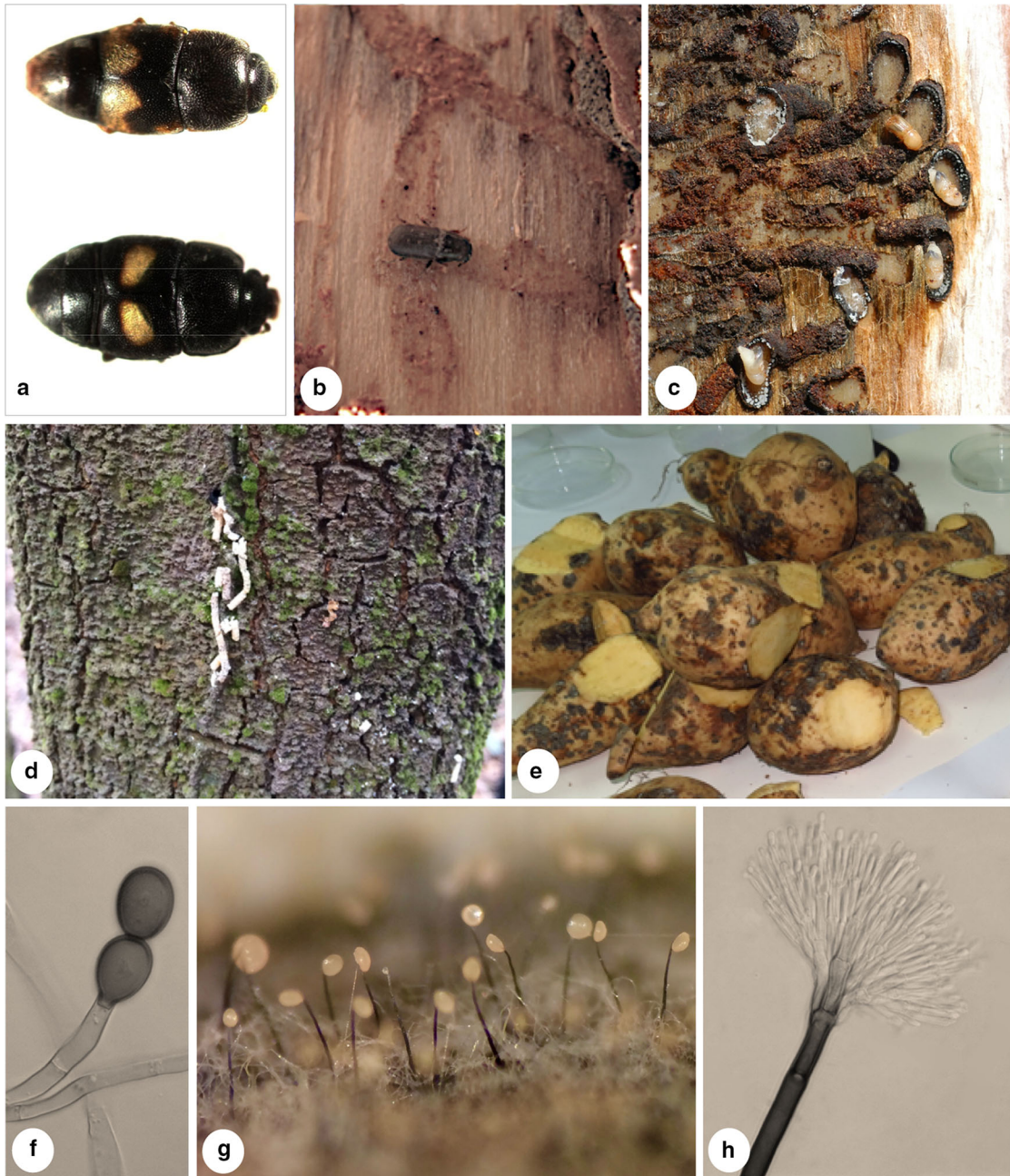
typically associated with borer ingress. **c** Large areas of dying *Acacia mangium* resulting from infection by *Ceratocystis manginecans*. **d** Lesions in *A. mangium* wood caused by *C. manginecans*. **e** Death of *Platanus orientalis* trees along a river in Greece caused by *Ceratocystis platani*. **f** Streaked discoloration in the wood of *P. orientalis* typical of infection by *C. platani*

originated (Wingfield et al. 2016). For instance, *O. ulmi* and *O. novo-ulmi* most likely originated from Asia (Brasier 1990), where native elm trees are more resistant to the fungi (Santini and Faccoli 2014). However, the fungi are strongly pathogenic on elm trees that are native to Europe and North America, and have dramatically altered the forest structures in both continents. Similarly, *R. lauricola*, relatively non-pathogenic in its native range in Asia, is highly aggressive on trees in the Lauraceae in its invaded range in North America (Fraedrich et al. 2008; Harrington et al. 2011). The three varieties of *L. wagneri* are host-specialized on conifers (Harrington and Cobb 1986, 1987) and while there is no evidence that they have moved out of their area of origin, there is significant potential that they could do so if their vectors should be introduced into new areas where susceptible conifers are growing.

The DED fungi emerged as devastating pathogens during the early and mid-twentieth century, while *R. lauricola* emerged as a disease-causing organism much more recently (Harrington et al. 2008; Santini and Faccoli 2014). *Raffaelea lauricola* in many respects resembles the fungi that cause DED. However, one intriguing difference is the fact that the pathogenic fungi utilize beetles with dramatically different colonization behaviours as the primary vector of *R. lauricola*, *Xyleborus glabratus*, is a wood-boring insect as opposed to the phloem-feeding bark beetles (*Scolytus* spp.) that vector the DED fungi. The vectors of DED undergo maturation feeding in the branch crotches of *Ulmus* spp. resulting in a rapid wilt disease after which the insects infest the stems of these trees for brood development. In the case of laurel wilt, the beetles penetrate the stems of healthy trees directly, carrying the pathogen with them. Wood-boring beetles tend to be less host-specific than bark beetles, and *R. lauricola* has already been found on wood boring beetles other than its original vector (Carillo et al. 2014). The fungus also colonizes other trees in the Lauraceae (Hughes et al. 2011; Bates et al. 2013), including commercially propagated avocado trees (Ploetz et al. 2013). Overall, the laurel wilt disease system suggests that novel insect and host associations may be more likely to emerge in Ophiostomataceae associated with wood boring than with bark-infesting beetles because of the colonization behaviour of the insects. Further investigations are needed to test this hypothesis.

Recently, the fungus *Leptographium procerum* has been implicated as an invasive pathogen of trees. This fungus is associated with the red turpentine beetle (*Dendroctonus valens*) (Fig. 3b, h), a bark beetle species that is native to North America. *Dendroctonus valens* typically infests stressed or dying *Pinus* spp. in its native range, and rarely is the primary cause of tree mortality (Owen et al. 2010). However, this beetle was accidentally introduced into China, resulting in the death of millions of native pine trees, especially *Pinus tabulaeformis* (Yan et al. 2005). The reason for this change in behavior is unknown but it has been suggested that *L. procerum*, which is the most closely associated fungus with *D. valens* in the beetle's native and invasive ranges, has altered the chemical ecology of *P. tabulaeformis*, resulting in an altered and more aggressive behavior of the insect in China (Sun et al. 2013). In addition, it has been suggested that certain haplotypes of *L. procerum* are pathogenic on *P. tabulaeformis* (Sun et al. 2013), possibly because the fungus and pine species might not share a coevolutionary history. The assumption has been that *L. procerum* was introduced into China from North America along with *D. valens*, but more recent population genetic studies on the fungus suggest that *L. procerum* is more likely of Eurasian origin (Taerum et al. 2017) and may in fact be native to China. It is therefore possible that *L. procerum* has coevolved with pine-infesting beetle species that are native to China. Consequently, the damage caused by the insect fungus complex would be due to novel interactions between an introduced insect and a native fungus. The historical movement of this association is not yet fully understood, but this example does illustrate the well-known fact that insect-fungus associations that are relatively benign in one part of the world can create serious tree health issues elsewhere.

A potentially interesting example of an ophiostomatoid fungus that was introduced into a new environment along with its insect vector is that of *Leptographium wingfieldii*. This fungus was introduced into eastern North America from Europe along with the invasive and damaging pine shoot-infesting beetle *Tomicus piniperda* (Jacobs et al. 2004). Unlike most conifer-infesting bark beetles, this insect is a primary pest while it undergoes maturation feeding in the shoots of pines, after which it becomes a secondary pest while it infests the stems of stressed *Pinus* spp. for brood development (Poland and Haack 2000). During



**Fig. 3** Ophiostomatoid fungi are highly adapted to dispersal by insects but they can also be wind dispersed or spread in soil or with root vectors. **a** Nitidulid beetles (*Carpophilus* sp.) that are common vectors of *Ceratocystis* spp. **b** The bark beetle *Dendroctonus valens* is a vector of numerous Ophiostomatoid fungi including *Leptographium procerum*. **c** Pupal chambers of *Ips typographus* showing profuse sporulation of Ophiostomatoid fungi at their margins. **d** Frass emerging from wood borer infestation where the frass carrying Ceratocystidaceae

propagules can be wind-borne. **e** Sweet potato tuber heavily infected by *Ceratocystis fimbriata*. **f** Chlamydospores with thick walls in some species of *Ceratocystis* facilitate survival and dispersal in soil. **g** Sticky spore masses of *Ceratocystis* spp. form at the apices of sexual fruiting structures and are easily picked up by insect vectors. **h** The apex of the asexual state of *Leptographium procerum* (and related fungi) produce sticky spores that are well-adapted to dispersal by insects

colonization, a wide variety of ophiostomatoid fungi that are loosely associated with *T. piniperda* are inoculated into the pine hosts. *Leptographium wingfieldii* is the most pathogenic of these fungi (Solheim et al. 1993) and the fungus has, subsequent to its introduction, become associated with various native north American bark beetle species. The implications of this new and pathogenic fungal species in a new environment associated with novel vectors and hosts are unknown but they should be monitored through regular surveys.

Although the main focus of this review is associations where a fungus is clearly pathogenic, there are many examples of non or mildly pathogenic exotic fungi from the Ophiostomataceae that have been introduced to new environments along with their bark beetle vectors. Most of these are known from countries where *Pinus* spp. are propagated as non-natives in plantations. For example, the pine stem infesting bark beetle *Orthotomicus erosus* of European origin has been accidentally introduced into southern Africa (Tribe 1990a), while *Ips grandicollis* of North American origin has been introduced into Australia (Yousuf et al. 2014). Likewise, species of *Hylastes* and *Hylurgus*, of European origin, have been introduced into New Zealand, southern Africa and Chile (Tribe 1990b, 1991; Billings 1993; Brockerhoff et al. 2006). In all cases, these insects have carried *Ophiostoma* spp. with them (Zhou et al. 2001, 2004; Reay et al. 2005, 2006; Yousuf et al. 2014), although it is usually unknown what proportion of the fungi associated with the beetles in the insect's native ranges were successfully introduced. Aside from the fact that they stain timber, it is unknown whether these exotic fungi could have more serious impacts than those currently recognized. Most of these fungi do not appear to pose an immediate threat, however, they may become serious pests in the future and they should be monitored by forest researchers.

### Associations in the Ceratocystidaceae

Forest tree pathogens in the Ceratocystidaceae reside in the genera *Ceratocystis* and *Endoconidiophora* (De Beer et al. 2014). *Ceratocystis* spp. do not have close associations with any specific insect and generally are not reliant on them for survival. Insects do, however, play an important role in the dispersal and

transmission of these fungi (Moller and DeVay 1968; Upadhyay 1981) and they are vectored non-specifically by insects such as flies (Diptera) and nitidulid beetles (Fig. 3a) (Coleoptera: Nitidulidae) (Crone 1962; Moller and DeVay 1968; Hinds 1972; Juzwik and French 1983).

Species in *Endoconidiophora*, such as *E. laricicola*, *E. rufipennis* and *E. polonica* (all previously called *Ceratocystis*) are specifically associated with bark beetles (Siemaszko 1938; Jewell 1956; Redfern et al. 1987; Wingfield et al. 1997). One of the best known beetle-fungal associations in *Endoconidiophora* is *E. polonica*, that is vectored by *Ips typographus* (Fig. 3c) (Solheim 1986). This blue-stain fungus has a high level of pathogenicity, and is able to kill trees in mass inoculations (Yamaoka et al. 1997; Krokene and Solheim 1998; Repe et al. 2015). The fungus has also been suggested to contribute to the detoxification of phenolic compounds produced by the tree in response to attacks by the beetle and fungus (Hammerbacher et al. 2015). However, whether the presence of the fungus is required for the beetles to kill trees is still a matter of debate (Lieutier et al. 2009; Six and Wingfield 2011).

While there are relatively few known species of *Endoconidiophora* that are pathogenic to trees, there are numerous examples of pathogenic *Ceratocystis* species. Many of these species are primary pathogens of angiosperm trees grown in orchards for fruit production as well as trees in natural forests and plantations. Important and well-known primary pathogens include the oak-wilt pathogen *C. fagacearum* (Jacobi and MacDonald 1980; Juzwik et al. 2008) and the causal agent of canker wilt disease of *Platanus* spp., *Ceratocystis platani* (Tsopelas et al. 2017). In non-native plantation forestry, *Ceratocystis albifundus* and *Ceratocystis manginecans* are important pathogens of *Acacia mearnsii* in South Africa and *Acacia mangium* in various countries of southeast Asia respectively (Roux et al. 2007; Tarigan et al. 2011; Thu et al. 2012; Brawner et al. 2015; Fourie et al. 2016). A serious disease of plantation-grown *Eucalyptus* in countries of Africa and South America is caused by a species of *Ceratocystis*, the taxonomy of which remains to be resolved and that is generally treated as *Ceratocystis fimbriata sensu lato* (Roux et al. 1999; Barnes et al. 2003; Roux and Wingfield 2009; Van Wyk et al. 2010; Ferreira et al. 2011; Van Wyk et al. 2013).



The complex taxonomy of these fungi continues to frustrate our understanding of the biology and global movement of *Ceratocystis* species. This also makes it difficult to understand or correctly assess what appear to be novel host and vector relationships for these fungi. Until very recently, ecologically and phylogenetically different groups of these fungi were treated collectively in the single genus, *Ceratocystis* (Wingfield et al. 2013). This problem has been largely resolved through the establishment of discrete genera for these groups (De Beer et al. 2014). However, the taxonomy of some fungi including the important and well-studied agent of oak wilt, *C. fagacearum*, remains to be resolved. Likewise, there is contention regarding the species boundaries in *Ceratocystis sensu stricto* with some species being treated either as *C. fimbriata*, which is the type species for the genus, or discrete taxa in the genus (Fourie et al. 2015; Oliveira et al. 2015; da Silva Galdino et al. 2016). Arguments are based on the delimitation of species boundaries using a variety of different species concepts. However, an important consideration is that proper classification and identification of these fungi is needed to understand their pathways of movement globally. Likewise, it is necessary to be able to apply meaningful quarantine measures to limit the movement of these fungi.

*Ceratocystis platani* in Greece provides an excellent example of a pathogen-vector shift that is increasing the distribution of the pathogen (Ploetz et al. 2013; Soulioti et al. 2015). *Ceratocystis platani* is native to North America where *Platanus* spp. are native and thus relatively resistant to infection (Anselmi et al. 1994; Vigoroux and Olivier 2004; Engelbrecht and Harrington 2005) and where nitidulid beetles have been shown to transmit the pathogen (Crone 1962). The pathogen is believed to have been accidentally introduced into Europe (Italy) on crating material during World War II (Panconesi 1999) and is now causing a devastating disease of the highly susceptible *Platanus orientalis* in France, Switzerland, Albania and Greece (Fig. 2e, f) (Panconesi 1999; Santini and Capretti 2000; Ocasio-Morales et al. 2007; Tsopelas et al. 2015). Spread of the disease is driven primarily by infections of natural and artificially induced wounds, particularly pruning wounds (Walter et al. 1952; Ocasio-Morales et al. 2007), anastomosis via root grafting between infected and healthy roots, and air or water-borne inoculum (Ocasio-Morales

et al. 2007). In Greece, the ambrosia beetle, *Platypus cylindrus* is a vector of the pathogen (Soulioti et al. 2015). These native wood-boring insects are attracted to dying trees and the frass produced by these insects also provides an active source of air and waterborne inoculum (Fig. 3d). This new insect-pathogen relationship is clearly driving the incidence of the disease in Greece and it threatens to ultimately destroy native populations of *Platanus* spp. (Soulioti et al. 2015).

In terms of novel host relationships, *C. albifundus* provides an interesting example. This fungus has been shown as native to Africa where it occurs on native trees in natural woody ecosystems (Roux et al. 2001; Barnes et al. 2005; Roux et al. 2007). It clearly has a wide host range and has undergone what appears to be a host range expansion to infect non-native *Acacia mearnsii* grown in South African plantations (Lee et al. 2016). As with all *Ceratocystis* spp., infections occur through wounds (natural or artificially induced) on trees and nitidulid beetles (Fig. 3a) appear to be the most common vectors of this pathogen (Heath et al. 2009). Its potential spread to Australia, where *A. mearnsii* is native, is of considerable concern.

In recent years, an unprecedented occurrence of a very serious *Ceratocystis* canker and wilt disease problem has emerged, killing thousands of *Acacia mangium* trees in countries of southeast Asia (Fig. 2c, d) (Tarigan et al. 2011; Thu et al. 2012; Brawner et al. 2015; Fourie et al. 2016). The causal agent of this disease (initially described as the new species *Ceratocystis acaciivora*) is *C. manginecans* (Fourie et al. 2015) which also causes a devastating wilt disease of mango in Oman and Pakistan (van Wyk et al. 2007). The rapid spread of the fungus can most likely be attributed to insect vectors, as the fungus is effectively vectored by the wood boring beetle *Hypocryphalus mangiferae* in Oman (Al Adawi et al. 2012). Because mango is unrelated to *Acacia*, which is a legume, it is interesting that *C. manginecans* can infect and kill both hosts. Recently, *C. manginecans* has been found killing the legume trees *Prosopis cineraria* and *Dalbergia sisoo* in Oman and Pakistan respectively (Al Adawi et al. 2013), suggesting that host shifts by the fungus present a major threat for legume trees around the world.

The insect vectors of most *Ceratocystis* spp. are casual and their relationship with these fungi is strongly driven by the fruity aromas produced by these fungi (Moller and De Vay 1968; Kile 1993;

Juzwik et al. 2008). This wide and non-specific vector assemblage provides opportunities for these fungi to reach wounds on a wide variety of tree hosts and for novel host relationships to emerge. For example, *C. tsitsikammensis*, considered native to parts of South Africa (Kamgan et al. 2008; Misse et al. 2017) was recently recovered from non-indigenous and invasive host species in the Cape floristic region (Van der Colff 2014; Misse et al. 2017). Population genetic studies suggest that nitidulid and staphylinid beetles play an important role in spreading *C. tsitsikammensis*, with similar haplotypes of the pathogen recovered from these insects as well as from native and non-native hosts over large distances (Misse et al. 2017).

It is likely that, at least in some cases, the assumed lack of vector specificity for *Ceratocystis* species represents an over-simplification. *Ceratocystis facaecearum* for example, appears to have a close association with the nitidulid species *Colopterus truncates*, and Juzwik et al. (2008) suggested that there is some specificity in nitidulids that vector *Ceratocystis* species. Similarly, the wattle wilt pathogen, *C. albifundus*, has also been shown to be associated with nitidulid beetles that visit wounds on *Acacia mearnsii* in South Africa (Heath et al. 2009). Insect-*Ceratocystis* interactions need to be further investigated to determine which insect and fungal species have tight vector-fungus associations, and why these associations exist.

## Conclusions and future prospects

The ophiostomatoid fungi include some of the most devastating tree pathogens to have emerged during the past century. These include causal agents of DED, which is one of the earliest examples of a globally important tree disease. It is also one that has strongly influenced the field of forest pathology and our knowledge of the taxonomy, ecology and genetics of tree pathogens. The DED pandemic has provided examples of how a tree pathogen can spread globally via the movement of wood products (Brasier 2008; Santini and Faccoli 2014). It has also provided knowledge regarding novel host associations as well as how naïve, and non-co-evolved hosts, can be devastated by an alien tree-infecting fungus. Furthermore, studies on DED have also contributed to our understanding of tree pathogen insect relationships,

and, in this case, how insects presumably related to the natural vectors, but novel in the introduced environments, can become effective vectors driving a devastating tree disease problem.

In contrast to most *Ophiostoma* spp., the majority of *Ceratocystis* spp. tend to have relatively broad host ranges. This would presumably provide enhanced opportunities for these fungi to succeed in new environments where serious tree disease problems could emerge. In this regard, there appear to be growing numbers of tree diseases, both in natural woody ecosystems as well as planted forests and orchards caused by species of *Ceratocystis*. We consequently expect many more serious *Ceratocystis* diseases to emerge in the future. This group of fungi deserve much greater attention by forest pathologists than is currently the case.

Confused taxonomy has substantially frustrated progress relating to our understanding of tree diseases caused by the ophiostomatoid fungi. This is a situation that has improved in recent years, especially due to the availability of phylogenetic inference based on DNA sequence data. As mentioned earlier in this review, molecular techniques have helped scientists differentiate between fungi in the Ophiostomataceae and Ceratocystidaceae. However, there remain many taxonomic questions, especially at the species level that need to be resolved. For the Ophiostomataceae, species complexes are gradually emerging and species boundaries are becoming more obvious as sampling of these fungi from new and previously unexplored environments improve (De Beer and Wingfield 2013). In the case of the Ceratocystidaceae, species boundaries remain much more confused (De Beer et al. 2014). There is an urgent need to more clearly define species boundaries in a manner that is practical yet meaningful. Importantly, these boundaries need to be defined in a way that can also be understood and applied by agencies responsible for quarantine and those seeking to reduce the global movement of these threatening pathogens.

The ophiostomatoid fungi include a multiplicity of modes of spread. Many species of Ceratocystidaceae infect the sapwood of trees. Where this wood is moved, and not treated, these fungi can sporulate on the wood surfaces where they produce fruity aromas attractive to sap feeding insects. These insects can then be transported to new locations and have the opportunity to infect new tree hosts, simultaneously

transmitting the fungi. Some *Ceratocystis* spp. and especially those related to *Ceratocystis fimbriata sensu stricto* are also soil-borne (Ferreira et al. 2011; Marin et al. 2003) and infested soil can very easily be moved to new environments where new host associations could emerge (Fig. 3e, f). In contrast, most ophiostomatoid fungi in the Ophiostomataceae have more specialized modes of spread via specific insect vectors. It has thus been possible to limit their spread via regulations regarding the treatment of wood and wood products moved globally. Further efforts to reduce the spread of fungi from both families, as well as their vectors, are required.

Tree diseases caused by the ophiostomatoid fungi have increased in number as well as in incidence in recent decades. This group of fungal pathogens represents a large number of new tree disease problems relative to other groups of fungi. This appears to be a trend that is increasing and it is perhaps due to the many different modes of spread including insect vectors, soil and air-borne inoculum as well as wood and wood products. However, the number of researchers studying these fungi is relatively limited. One of the reasons is that unlike many other groups of fungi, the ophiostomatoid fungi are almost exclusively relevant to tree crops. In this regard, plant pathology funding tends to be strongly biased to agriculture and plant products perceived as more relevant to food security. This is a situation that is naïve and unfortunate. It also illustrates a poor recognition of trees and forests and the essential role that they play in human well being, including not only in our need for wood and wood products but for water and food security.

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