Annual Review of Phytopathology

Cryphonectriaceae: Biodiverse and Threatening Tree Pathogens in the Tropics and Southern Hemisphere

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Annu. Rev. Phytopathol. 2025. 63:553–75

First published as a Review in Advance on May 28, 2025

The *Annual Review of Phytopathology* is online at phyto.annualreviews.org

https://doi.org/10.1146/annurev-phyto-121823-030316

Keywords

Cryphonectriaceae, Eucalyptus canker, invasive fungi, forest pathogens, fungal diversity, host shift

Abstract

The chestnut blight pathogen *Cryphonectria parasitica* is well-known for the devastation it caused to North American forests. It is less well recognized that numerous other fungi in the Cryphonectriaceae are emerging as threats to native and planted forests in the tropics and Southern Hemisphere. Unlike *C. parasitica*, these fungi, such as *Chrysoporthe cubensis*, initially gained attention due to a canker disease in plantations of non-native *Eucalyptus*. More than four decades of research have revealed a wide diversity of Cryphonectriaceae species that infect many other tree genera in the Myrtales. These fungi often exist as endophytes but become problematic when trees are planted outside their native range. Growing numbers of species are also undergoing host shifts from native to susceptible trees such as *Eucalyptus*, posing serious risks to both natural and planted forests. These fungi provide an example of the biodiversity of tree-infecting fungi that is understudied, despite their significant potential to harm forest ecosystems.

INTRODUCTION

Stem cankers: localized bark infection by pathogens, causing sunken or swollen areas, girdling, and death of nearby plant tissues

***Eucalyptus* plantation industry:** commercial plantations of Australian *Eucalyptus* species expanded globally for fiber production, reaching 20 million hectares by 2008

Myrtales: large plant order with nine families, notably Myrtaceae; many species host Cryphonectriaceae fungi, indicating many undiscovered, potentially pathogenic species

The Cryphonectriaceae owes its notoriety to the destructive tree pathogen *Cryphonectria parasitica* (Murrill) M.E. Barr that devastated North American chestnut [*Castanea dentata* (Marsh.) Borkh.] forests beginning in the early 1900s (3). The pathogen was first discovered on infected trees in New York in 1904, although it might have existed there as early as 1893. The disease spread rapidly throughout the eastern seaboard of the United States, virtually eliminating a dominant component of the natural forests in the area (3, 68, 86, 88). By the late 1920s, most *C. dentata* trees in the native range were dying or had died, with only coppice stems remaining (51).

The chestnut blight pathogen was first described as *Diaporthe parasitica*, residing in the Diaporthales (88). Various taxonomic treatments followed (4, 29, 108), with *Cryphonectria parasitica* most recently applied to the pathogen (7). The family Cryphonectriaceae was established by Gryzenhout et al. (59) to accommodate this fungus and numerous other related species that had been described (52, 53, 56, 58, 144). All these species are pathogens infecting the cambial tissues of trees and resulting in stem cankers. By 2009, twenty-two species had been described in the Cryphonectriaceae, and these were treated in the monograph of Gryzenhout et al. (63). They were also mostly known from the Northern Hemisphere, and only *C. parasitica*, which by that time was also causing serious disease problems on *Castanea sativa* Mill. in Europe (67), was considered a serious threat to natural forests.

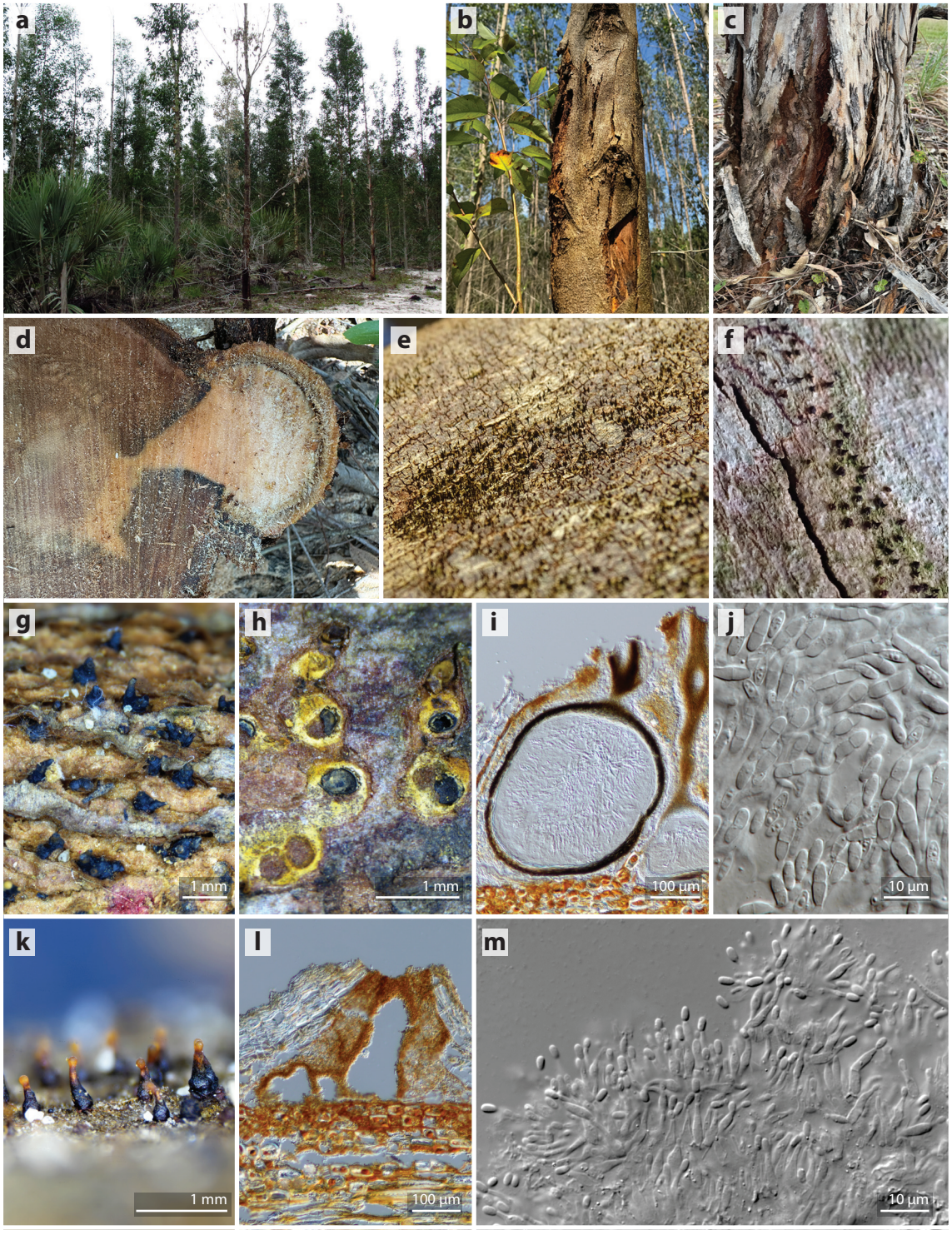
The discovery of a serious stem canker disease on *Eucalyptus* in Cuba added a fundamentally novel view of the Cryphonectriaceae as tree pathogens. This disease was first encountered and described by Bruner (13) as *Diaporthe cubensis* Bruner. As the taxonomy of the Diaporthales was revised over time (7), the fungus was recognized as a species typical of *Cryphonectria* and was transferred to that genus by Hodges (72) as *Cryphonectria cubensis* (Bruner) Hodges.

Prior to the description of *C. cubensis* from Cuba, *Cryphonectria* species were known only from temperate regions of the world and occurred on species in the Fagaceae (45, 88). This discovery also gave rise to a period when *C. cubensis* was recognized as a pathogen threatening the rapidly emerging *Eucalyptus* plantation industry in tropical regions of Brazil. This industry, also being established in various other parts of the Southern Hemisphere, was based on the rapid growth of *Eucalyptus* species, mostly native to Australia, where the genus is remarkably biodiverse. These trees include species with a wide range of climatic and edaphic characteristics as well as properties of commercial relevance such as the production of solid wood, pulp products, and charcoal. Consequently, when *C. cubensis* was first discovered as an important stem canker pathogen in Brazil, the fungus gained substantial new relevance (69–71).

In this review, we seek to emphasize the relevance of species in the Cryphonectriaceae occurring in the tropics and Southern Hemisphere. Owing to their particular importance on *Eucalyptus* species, the focus is mostly on species that occur on trees in the Myrtales, the plant order that accommodates *Eucalyptus* and its relatives. A point of emphasis is on the diversity of these fungi in the Southern Hemisphere, as new species are increasingly being discovered. Our aim is especially to emphasize the importance of fungal diversity in natural woody ecosystems, the fact that these fungi are unacceptably poorly studied, and that many also threaten the future health of forest trees globally.

CRYPHONECTRIA ON *EUCALYPTUS*: PERSPECTIVES FROM PLANTATION FORESTRY

As pathogens, the Cryphonectriaceae are best known as wound-infecting fungi that colonize cambial tissues, causing diffuse cankers that can rapidly girdle infected tree branches and stems (**Figure 1**). Asexual structures are flask-shaped pycnidia from which hyaline conidia exude in



(*Caption for* ***Figure 1*** *appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Disease symptoms associated with Cryphonectriaceae on Myrtaceae. (*a–f*) Symptoms on infected trees. (*g–j*) Characteristics of sexual structures. (*k–m*) Asexual structures.

typically yellow to orange masses. The sexual structures are perithecia, usually with long necks containing operculate asci. The ascospores are usually, but not always, two-celled, divided by a medium septum. As increasing numbers of species have been discovered, substantial diversity in these morphological characteristics has also emerged (**Figure 1**).

Hodges et al. (70) made the first formal discovery of Cryphonectria canker on *Eucalyptus* in Brazil, leading to the pathogen being identified as *Diaporthe cubensis*. This discovery set in motion numerous studies of the disease in Brazil, seeking to manage a problem that was potentially threatening to an emerging and important industry where significant pulp mills depended on timber from these trees (1, 42–44, 69). Various taxonomic studies sought to clarify the identification of the fungus where the generic names *Endothia*, *Diaporthe*, and *Cryphonectria* had been applied and remained confusing. Hodges (72) considered this problem in detail and determined that the fungus on *Eucalyptus* was best accommodated in *Cryphonectria*. The name *Endothia* applied to collections on *Syzygium aromaticum* (syn. *Eugenia aromatica*; also Myrtaceae) (99, 109) as *Endothia eugeniae* (Nutman & F.M. Roberts) J. Reid & C. Booth was resolved by Hodges et al. (73), who showed that the two fungi were the same and reduced *E. eugeniae* to synonymy with *C. cubensis*. The conspecificity was supported by Micales & Stipes (87) based on chemotaxonomic analyses and later confirmed based on DNA data (93).

The discovery of Cryphonectria canker on *Eucalyptus* gave rise to a heightened interest in this fungus. This is mainly due to the potential damage that it might cause to plantings of these trees. Surveys in plantations in various tropical areas of the world were undertaken, resulting in numerous new reports of *C. cubensis* [Cameroon (47), Florida, Hawaii, Puerto Rico (74), and India (117)]. Reports also included those on species of *Syzygium*, including the clove tree (*S. aromaticum*) in Brazil (73), Indonesia (73), and Tanzania (99). The severity of disease on clove was, however, much lower in Brazil and Indonesia (73). This led to the intriguing view of Hodges et al. (73) that the fungus might have had its origin on clove and been introduced into Brazil via the spice trade. By 1990, *C. cubensis* had been recorded on species of *Eucalyptus* and *Syzygium* (as *Eugenia*) in Brazil, Cameroon, Costa Rica, Cuba, India, Indonesia, Malaysia, Surinam, Puerto Rico, the United States (Florida, Hawaii), and Western Samoa (12, 71). An intriguing report of the fungus from the roots of naturally occurring *Eucalyptus marginata* in Western Australia by Davison & Coates (39) added some confusion regarding the possible origin of the fungus occurring outside the native range of these trees.

Wingfield et al. (157) published a first report of *C. cubensis* from South Africa, after stem cankers caused by the fungus were found on clonally propagated *Eucalyptus* in the subtropical coastal areas of the country in 1986. This was a time when *Eucalyptus* plantation industry was expanding rapidly in South Africa to provide fiber for multiple newly established pulp mills. The discovery of *C. cubensis* in that country was of particular concern because of the problems that were being reported from Brazil (30). Consequently, intensive studies were launched to better understand the pathogen as well as to establish management strategies to reduce its potential negative impact (129, 139–143). Taxonomic studies included not only isolates from South Africa but also those available from other parts of the world, including South American and Southeast Asian countries (91, 92, 134, 141)

Clove tree: *Syzygium aromaticum*, native to Indonesia, is cultivated globally for aromatic flower buds (cloves) used as a spice since the 1700s

An important breakthrough in understanding the possible origin of *C. cubensis* emerged when the fungus was discovered for the first time on a tree that did not reside in the Myrtaceae, thus not a close relative of *Eucalyptus*. In this case, the fungus was found in Colombia on native *Pleroma*

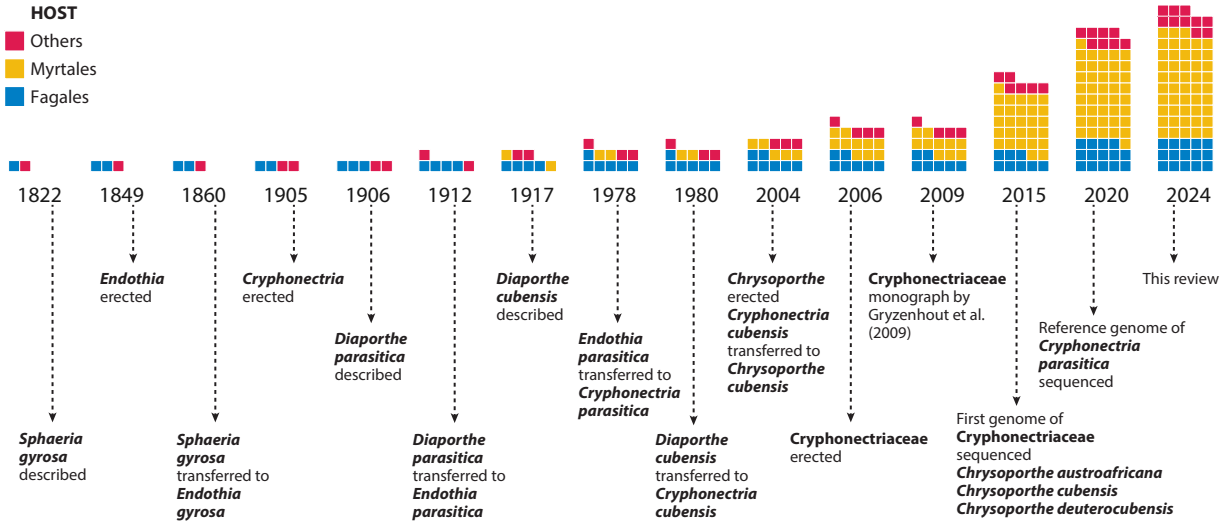


Figure 2

Historical timeline outlining the evolution of Cryphonectriaceae taxonomy. Waffle chart indicates the accumulation of formally recognized species ascribed to Cryphonectriaceae over time. Each square represents a single taxon, and different colors represent the plant order from which each species was first described.

(syn. *Tibouchina*) (156), a genus of trees and shrubs residing in the Melastomataceae (Myrtales) (31). Pathogenicity tests showed that isolates from *Pleroma* could infect both these trees as well as *Eucalyptus* (156). This discovery provided a basis for the hypothesis that *C. cubensis* on *Eucalyptus* in South America could have arisen from a host shift (121) from native Melastomataceae to infect *Eucalyptus*. It was also recognized at that time that infections on *Eucalyptus* in South America resulted in somewhat different symptoms from those found in South Africa (154). These observations began to hint at the probability that *C. cubensis* in different parts of the world might not be the same fungus. Until that time, all descriptions of this fungus and its close relatives had relied on the morphology of their fruiting structures.

DEEP IMPACT OF PHYLOGENETIC INFERENCE BASED ON DNA SEQUENCE DATA

As with most fungi, the application of DNA sequence data and phylogenetic inference had a fundamental impact on the taxonomy of these fungi, with many new genera and species being discovered (**Figure 2**). The first DNA data for the Cryphonectriaceae in the tropics and Southern Hemisphere were based only on ITS sequences (92). This study provided additional evidence that *C. cubensis* in South America and other parts of the world represented at least two different species and that these Southern Hemisphere fungi were distinct from *C. parasitica*.

Subsequent to the study of Myburg et al. (92), DNA sequence data, together with morphological characteristics, were applied to new collections of *C. cubensis* isolates from *Eucalyptus* and *Pleroma* as well as from the South African indigenous tree *Syzygium cordatum* (Myrtaceae), on which the fungus had been discovered (64, 90, 156). The occurrence of the fungus on a native tree supported the hypothesis that the pathogen known as *C. cubensis* in South Africa could have undergone a host shift from native to planted trees in the country. This and several other studies (91–93, 113) gave rise to the genus *Chrysoporthe* being established, with *Chrysoporthe cubensis*

Host shift: a situation in which a pathogen undergoes an evolutionary change to infect a new host

Table 1 Major Cryphonectriaceae species discussed in this article

Species	Previous names	Host range	Geographical distribution	Possible native range	Mode of sexual reproduction
Cryphonectria parasitica	*Diaporthe parasitica* *Endothia parasitica* *Endothia gyrosa* var. *parasitica* *Valsonectria parasitica*	Fagales (*Alnus*, *Carpinus*, *Carya*, *Castanea*, *Castanopsis*, *Fagus*, *Ostrya*, *Quercus*) Sapindales (*Acer*, *Rhus*) Magnoliales (*Liriodendron*) Rosales (*Malus*)	North America (USA, Canada) Europe Asia (China, India, Iran, Japan, Korea, Taiwan) Northern Africa (Tunisia) Oceania (Australia)	East Asia	Heterothallic
Chrysoporthe austroafricana	NA	Myrtales (*Corymbia*, *Eucalyptus*, *Eugenia*, *Dissotis*, *Pleroma*, *Psidium*, *Syzygium*)	Southern Africa (Eswatini, Malawi, Mozambique, Namibia, South Africa, Zambia)	Southern Africa	Heterothallic
Chrysoporthe cubensis	*Diaporthe cubensis* *Cryphonectria cubensis* *Cryptosporella eugeniae* *Endothia eugeniae* *Cryphonectria eugeniae*	Myrtales (*Chaetogastra*, *Corymbia*, *Eucalyptus*, *Lagerstroemia*, *Miconia*, *Pleroma*, *Plinia*, *Psidium*, *Rhynchanthera*, *Syzygium*)	North America (USA: Florida) South America (Brazil, Colombia, Suriname, Venezuela) Caribbean (Cuba) Western and Central Africa (Ghana, Democratic Republic of the Congo, Congo, Cameroon)	South America	Homothallic
Chrysoporthe deuterocubensis	NA	Myrtales (*Eucalyptus*, *Eugenia*, *Melastoma*, *Metrosideros*, *Pleroma*, *Psidium*, *Syzygium*)	Southeast and East Asia (Indonesia, Thailand, Singapore, China, Taiwan, Malaysia, Vietnam) Pacific (USA: Hawaii) East Africa (Tanzania, Kenya, Mozambique, Malawi) Oceania (Australia)	Southeast Asia	Homothallic

Abbreviation: NA, not applicable.

(Bruner) Gryzenh. & M.J. Wingf. as the type species (56). The name *Chrysoporthe austroafricana* Gryzenh. & M.J. Wingf. was then applied to the South African fungus. Furthermore, Gryzenhout et al. (59) established the Family Cryphonectriaceae for these fungi and their phylogenetic relatives, including *C. parasitica* and other Northern Hemisphere species.

Studies on the Southern African *Chr. austroafricana* and South American *Chr. cubensis* isolates, including those from Southeast Asia, provided the first evidence that the latter collections likely represented a distinct species. van der Merwe et al. (133, 134, 137) considered this question in detail, including DNA sequence data for numerous gene regions as well as the application of microsatellite markers confirming this difference, and the name *Chrysoporthe deuterocubensis* Gryzenh. & M.J. Wingf. was erected for the Southeast Asian fungus. Interestingly, isolates from areas such as Tanzania, Kenya, Mozambique, Malawi, China, Hawaii, and Australia also resolved as *Chr. deuterocubensis* (21, 91, 93, 98, 104, 133, 149) (**Table 1**).

Following the discovery that *Chr. cubensis* represented more than a single species and fueled by a concern regarding these fungi as *Eucalyptus* pathogens, a period of intense collecting of the Cryphonectriaceae in the tropics and Southern Hemisphere ensued. These collections were focused on trees in the Myrtales, including but not exclusively *Eucalyptus* (2, 10, 22, 23, 25–27, 35, 36, 54, 55, 57–61, 65, 96, 98, 102, 106, 120, 126, 145, 147–150). When the first monographic treatment of these fungi by Gryzenhout et al. (63) appeared, five species of *Chrysoporthe* as well as several species in the novel genera, i.e., *Amphilogia*, *Aurapex*, *Celoporthe*, *Holocryphia*, *Microthia*, *Rostraureum*,

and *Ursicollum*, had been described (53–55, 58, 96). Descriptions of these new taxa were all supported by morphological characteristics and DNA sequence data for multiple informative gene regions. In most cases, those species occurring on non-*Eucalyptus* hosts were shown in pathogenicity trials to be able to infect *Eucalyptus* (55, 96, 111). This raised the possibility that the large number of Cryphonectriaceae on native trees in the tropics and Southern Hemisphere should be considered a serious threat to the health of the Myrtales in areas where these fungi are not native.

Eucalypts: a general term referring to the trees belonging to the Myrtaceae (myrtle family), including species of *Angophora*, *Corymbia*, and *Eucalyptus*

The Gryzenhout et al. (63) monograph provided a robust foundation for the collection and descriptions of new taxa in the Cryphonectriaceae (**Figure 2**). Most of these were on the Myrtales from the tropics and Southern Hemisphere, but they also included some species, specifically of those associated with Fagales, from the Northern Hemisphere (20, 33, 75–77). As of 2024, based on DNA sequence data, 28 genera and more than 70 species are known in the Cryphonectriaceae (**Figure 2**, **Figure 3**). Of these, 15 genera are known specifically in the Myrtales (**Figure 3**, **Table 2**). Among the genera known from the Southern Hemisphere, *Chrysoporthe* and *Celoporthe* include the greatest number of species (**Figure 3**). A caveat here is that this representation of species abundance more likely reflects the intensity of surveys and collections rather than the actual size of the genera.

HOST SHIFTS AND AN ENDOPHYTIC LIFESTYLE

The first discovery of a species in the Cryphonectriaceae on *Pleroma* (Melastomataceae) marked a substantial change in understanding the diversity and biology of these fungi as tree pathogens (156). Where surveys could be undertaken, they initially focused on the plants in the Melastomataceae (2, 50, 55, 57, 60, 82, 102, 120, 125). These shrubs and trees, including approximately 173 genera and 5,858 species, are mostly native to the New World tropics (132). Of these, many grow in areas where plantations of eucalypts have been established, and several species such as *Miconia crenata* (syn. *Clidemia hirta*) and *Melastoma malabathricum* are seriously problematic weeds in these environments (40). New or already known species began to be discovered on these plants, adding confidence that some of those occurring and causing canker disease on *Eucalyptus* had undergone host shifts from plants in the native environment (65, 96) (**Table 2**).

A realization that the Cryphonectriaceae on eucalypts established as exotics in plantations likely originated on native woody plants, not only the Melastomataceae and Myrtaceae but possibly trees in other families of the Myrtales, led to surveys being expanded. These, for example, included trees in the Combretaceae and Lythraceae, such as *Galpinia*, *Lagerstroemia*, *Sonneratia*, and *Terminalia*, that were subsequently also found to be hosts of these fungi (10, 23, 58, 118, 131, 145, 148, 149). Interestingly, some species such as *Aurifilum cerciana*, *Aurifilum terminali*, and *Chrysomorbus lagerstroemiae* found in China were shown, using artificial inoculations, to be able to infect and cause disease on *Eucalyptus* (148, 149) (**Table 2**).

Numerous genera and species of Cryphonectriaceae are found on native trees and shrubs residing in various genera and species of the Myrtales (**Table 2**). Most of these have also been shown to infect *Eucalyptus* in inoculation trials, although only a few have been found naturally infecting these trees (**Table 2**). There are few records of the Cryphonectriaceae on *Eucalyptus* or other Myrtaceae in Australia, the area of the world where most of these trees are native. Interestingly, *Chr. deuterocubensis* was first found on *Pleroma heteromallum* (syn. *Tibouchina heteromalla*) in the Cairns Botanic Gardens, Queensland, Australia (104). Intriguingly, DNA sequence data have shown that this is the same species that was collected many years earlier by Davison & Coates (39) on the roots of *E. marginata* in Western Australia, an area with a climate atypical for *Chr. deuterocubensis*. The only other species commonly found on *Eucalyptus* in Australia is a *Holocryphia* sp., which was once considered to be *Holocryphia eucalypti*, known from South Africa (26, 54, 62, 66), but likely

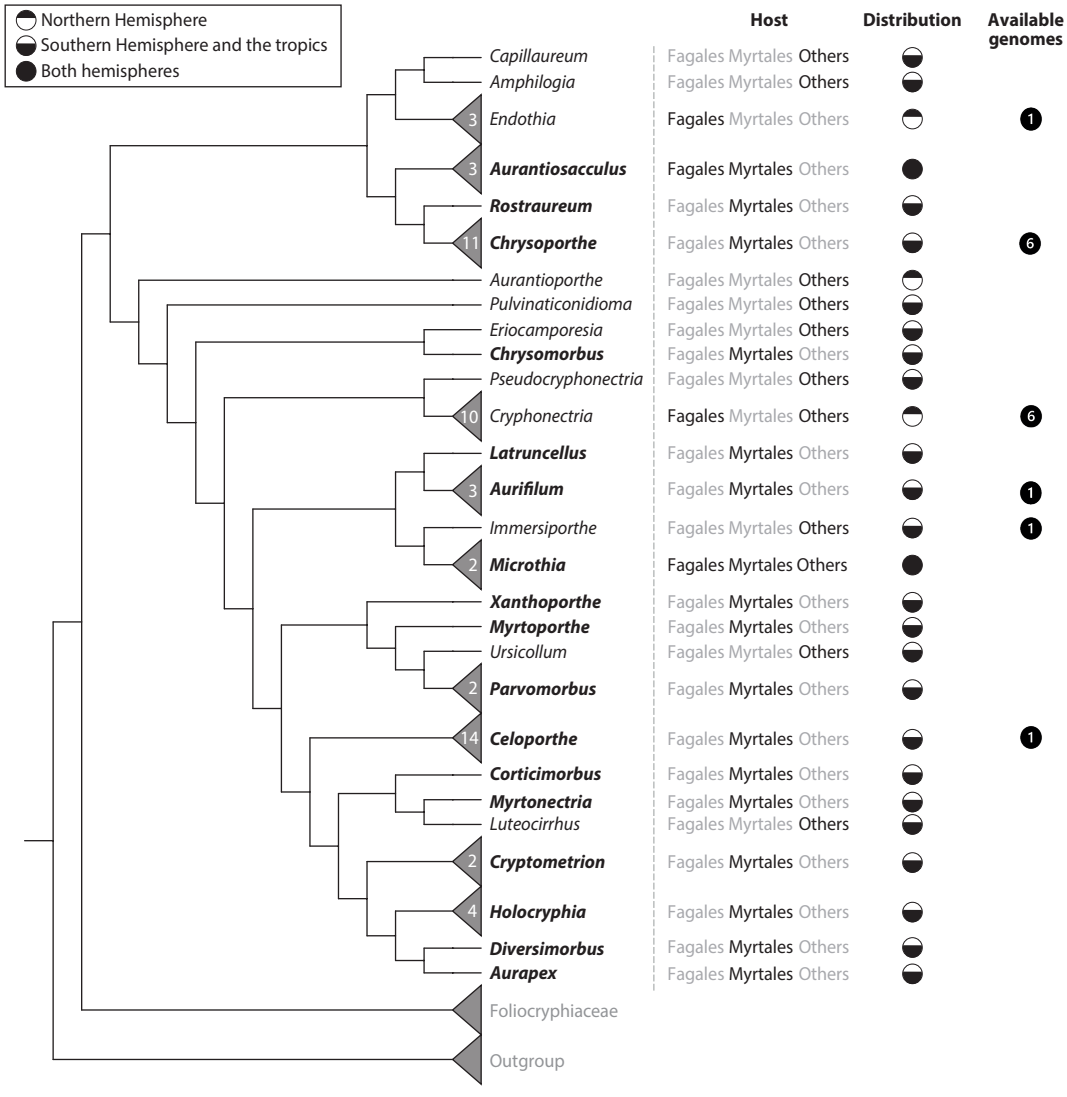


Figure 3

Schematic overview of the phylogeny of Cryphonectriaceae species known in culture. Numbers in triangles represent species number in each genus. Genera occurring on Myrtales in the tropics and Southern Hemisphere are indicated in bold. Where genome sequences are available, the list reflects the number of species sequenced but not strains, which in some cases, such as *Cryphonectria parasitica*, is at least 90.

represents a cryptic and distinct species (26). This fungus appears to have a relatively wide host range and to occur on trees in regions that have temperate or subtropical environments (16, 17, 54). It is thought to be native to Australia (16, 17, 39, 62, 100, 151, 158) and has also been found on *Pleroma urvilleanum* (syn. *Tibouchina urvilleana*), presumably having undergone a host shift to that non-native tree, commonly planted as an ornamental (66).

A survey of native *Metrosideros angustifolia* in the Western Cape Province of South Africa, which has a Mediterranean climate, led to the discovery of numerous new species of *Holocryphia* and a single species in a new genus *Diversimorbus*, causing cankers on these trees (26). A population

Table 2 Species of Cryphonectriaceae found on native Myrtales hosts and *Eucalyptus* hosts in the tropics and Southern Hemisphere

Genus	Species	Distribution	*Eucalyptus* hosts	Other Myrtales hosts	Reference(s)
Aurantiosacculus	*Aurantiosacculus acutatus*	Australia	*Eucalyptus viminalis*	NA	36
	Aurantiosacculus eucalyptorum	Australia	*Eucalyptus globulus*	NA	36
Aurapex	*Aurapex penicillata*	Colombia	*Eucalyptus grandis*	*Miconia theaezans*, *Miconia lineatum* *Andesanthus lepidotus* (syn. *Tibouchina lepidota*) *Pleroma urvilleanum* (syn. *Tibouchina urvilleana*)	50, 55
Aurifilum	*Aurifilum cerciana*	China	*E. grandis* hybrids[a]	*Terminalia neotaliala*	148
	Aurifilum marmelostoma	Cameroon Taiwan	NA	*Terminalia mantaly*, *Terminalia ivorensis*	10, 118
	Aurifilum terminali	China	*E. grandis* hybrids[a]	*T. neotaliala*	149
Celoporthe	*Celoporthe borbonica*	La Réunion	*E. grandis*[a]	*Pleroma heteromallum* (syn. *Tibouchina grandifolia*)	2
	Celoporthe cerciana	China	*E. grandis* hybrids	NA	150
	Celoporthe dispersa	South Africa Zambia	*E. grandis*[a]	*Syzygium cordatum*, *Syzygium guineense*, *Syzygium legatii* *Pleroma granulosum* (syn. *Tibouchina granulosa*) *Heteropyxis canescens*	96, 145
	Celoporthe eucalypti	China	*Eucalyptus* sp.	*Syzygium jambos*	22, 149
	Celoporthe foliorum	Indonesia	NA	*Syzygium* sp.	20
	Celoporthe fontana	Zambia	*E. grandis*[a]	*S. guineense*	147
	Celoporthe guangdongensis	China	*Eucalyptus* sp.	*S. jambos* *Sonneratia apetala*	22, 131
	Celoporthe hauoliensis	USA (Hawaii)	NA	*Psidium cattleianum* *S. jambos*	114
	Celoporthe hawaiiensis	USA (Hawaii)	NA	*P. cattleianum* *Syzygium* sp., *S. jambos*	114
	Celoporthe indonesiensis	Indonesia	NA	*Syzygium aromaticum*	22
	Celoporthe paradisiaca	USA (Hawaii)	NA	*P. cattleianum* *S. jambos*	114

(*Continued*)

Table 2 (*Continued*)

Genus	Species	Distribution	*Eucalyptus* hosts	Other Myrtales hosts	Reference(s)
	Celoporthe syzygii	China	*E. grandis* hybrids[a], *Eucalyptus urophylla* hybrids	*Psidium guajava* *Syzygium cumini*, *Syzygium hancei*, *S. jambos*, *Syzygium samarangense*	22, 149
	Celoporthe tibouchinae	La Réunion	*E. grandis*[a]	*P. heteromallum* (syn. *T. grandifolia*)	2
	Celoporthe woodiana	South Africa Mozambique	*E. grandis*[a]	*P. granulosum* (syn. *T. granulosa*) *S. cordatum*	82, 147
Chrysomorbus	*Chrysomorbus lagerstroemiae*	China	*E. urophylla* × *E. grandis*[a]	*Lagerstroemia speciosa*	23
Chrysoporthe	*Chrysoporthe austroafricana*	South Africa Mozambique Malawi Zambia Namibia Eswatini	*E. grandis*	*Corymbia henryi* *S. cordatum*, *S. guineense*, *Syzygium apiculatum* *P. granulosum* (syn. *T. granulosa*) *Dissotis* sp. *Eugenia capensis* *P. guajava*	65, 82, 90, 98, 112, 127, 145, 157
	Chrysoporthe brasiliensis	Brazil	NA	*Rhynchanthera grandiflora* *Miconia theaezans*, *Miconia ibaguensis*	120
	Chrysoporthe colombiana	Colombia	*E. grandis*[a]	*Henriettea seemannii*	125
	Chrysoporthe cubensis	USA (Florida) Colombia Brazil Venezuela Cuba Suriname Ghana Democratic Republic of Congo Congo Cameroon	*Eucalyptus angulosa*, *Eucalyptus botryoides*, *Eucalyptus camaldulensis*, *Eucalyptus dagambae*, *Eucalyptus deglupta*, *E. grandis*, *Eucalyptus microcorys*, *Eucalyptus paniculata*, *Eucalyptus pilularis*, *Eucalyptus propinqua*, *Eucalyptus robusta*, *Eucalyptus saligna*, *Eucalyptus tereticornis*, *Eucalyptus trabutii*, *E. urophylla*	*S. aromaticum* *M. theaezans*, *Miconia rubiginosa*, *Miconia sericea* (syn. *Clidemia sericea*) *Lagerstroemia indica* *Rhynchanthera mexicana* *Corymbia citriodora*, *Corymbia maculata* *P. granulosum* (syn. *T. granulosa*), *P. heteromallum* (syn. *Tibouchina heteromalla*), *P. urvilleanum* (syn. *T. urvilleana*) *Chaetogastra mollis* (syn. *Tibouchina mollis*) *Plinia edulis* (syn. *Marlierea edulis*) *P. cattleianum*	6, 8, 50, 56, 60, 63, 98, 101, 111, 115, 122, 133

(*Continued*)

Table 2 (*Continued*)

Genus	Species	Distribution	*Eucalyptus* hosts	Other Myrtales hosts	Reference(s)
	Chrysoporthe deuterocubensis	Indonesia Thailand Singapore Australia China Taiwan Malaysia Vietnam USA (Hawaii) Tanzania Kenya Mozambique Malawi	*Eucalyptus marginata*, *E. grandis*, *E. grandis* × *Eucalyptus pellita*, *E. urophylla* × *E. grandis*, *E. camaldulensis*	*Melastoma malabathricum*, *Melastoma candidum*, *Melastoma sanguineum* *S. aromaticum*, *S. cumini*, *S. jambos*, *S. samarangense* *P. urvilleanum* (syn. *T. urvilleana*), *P. heteromallum* (syn. *T. heteromalla*) *Eugenia* sp. *P. guajava*, *P. cattleianum* *Metrosideros polymorpha*	21, 41, 56, 60, 63, 98, 104, 106, 114, 128, 130, 133, 149
	Chrysoporthe doradensis	Ecuador Colombia Brazil	*E. grandis*, *E. deglupta*, *E. grandis* × *E. urophylla*	*R. grandiflora* *P. granulosum* (syn. *T. granulosa*) *H. seemannii*	57, 119, 122, 125
	Chrysoporthe hodgesiana	Colombia	*E. grandis*[a]	*Pleroma semidecandrum* (syn. *Tibouchina semidecandra*), *P. urvilleanum* (syn. *T. urvilleana*) *A. lepidotus* (syn. *T. lepidota*) *M. theaezans*	56, 111
	Chrysoporthe inopina	Colombia	*E. grandis*[a]	*P. semidecandrum* (syn. *T. semidecandra*), *P. urvilleanum* (syn. *T. urvilleana*) *A. lepidotus* (syn. *T. lepidota*)	50, 60
	Chrysoporthe puriensis	Brazil	*E. grandis* × *E. urophylla*[a]	*Pleroma candolleanum* (syn. *Tibouchina candolleana*), *P. granulosum* (syn. *T. granulosa*), *P. heteromallum* (syn. *T. heteromalla*), *Pleroma mutabile* (syn. *Tibouchina mutabilis*) *Tibouchina* sp. *R. grandiflora* *M. theaezans*	102, 107, 119
	Chrysoporthe syzygiicola	Zambia	*E. grandis*[a]	*S. guineense*	27
	Chrysoporthe zambiensis	Zambia Zimbabwe	*E. grandis*	*S. guineense*	27, 78
Corticimorbus	*Corticimorbus sinomyrti*	China	*E. urophylla* × *E. grandis*[a]	*Rhodomyrtus tomentosa*	25

(*Continued*)

Table 2 (*Continued*)

Genus	Species	Distribution	*Eucalyptus* hosts	Other Myrtales hosts	Reference(s)
Cryptometrion	*Cryptometrion aestuescens*	Indonesia	*E. grandis*	NA	61
	Cryptometrion metrosideri	New Zealand	NA	*Metrosideros* sp., *Metrosideros excelsa*	35
Diversimorbus	*Diversimorbus metrosideri*	South Africa	*E. grandis*[a]	*Metrosideros angustifolia*	26
Holocryphia	*Holocryphia capensis*	South Africa	*E. grandis*[a]	*M. angustifolia*	26
	Holocryphia eucalypti	South Africa Eswatini Uganda	*Eucalyptus* sp., *E. grandis*, *E. saligna*	NA	26, 145
	Holocryphia gleniana	South Africa	*E. grandis*[a]	*M. angustifolia*	26
	Holocryphia mzansi	South Africa	*E. grandis*[a]	*M. angustifolia*	26
Latruncellus	*Latruncellus aurorae*	Eswatini	*E. grandis*[a]	*Galpinia transvaalica*	145
Microthia	*Microthia havanensis*	USA (Hawaii, Florida) Cuba Mexico Portugal (Azores, Madeira) Puerto Rico	*Eucalyptus* sp.; *Eucalyptus botryoides*, *E. camaldulensis*, *E. grandis*, *Eucalyptus microphylla*, *Eucalyptus occidentalis*, *E. robusta*, *E. saligna*	*S. jambos*, *S. cumini* *P. cattleianum*	54, 63, 114
Myrtonectria	*Myrtonectria myrtacearum*	South Africa	*E. grandis*[a]	*Heteropyxis natalensis* *S. cordatum*	2
Myrtoporthe	*Myrtoporthe bodenii*	Malaysia	*E. grandis*	NA	106
Parvomorbus	*Parvomorbus eucalypti*	China	*E. urophylla* × *E. grandis*, *E. urophylla* hybrids	NA	149
	Parvomorbus guangdongensis	China	*E. urophylla* hybrids, *E. grandis* hybrids	NA	149
Rostraureum	*Rostraureum tropicale*	Ecuador	NA	*T. ivorensis*, *Terminalia superba*	58
Xanthoporthe	*Xanthoporthe myrticola*	South Africa	*E. urophylla* × *E. grandis*, *E. grandis*	*C. henryi*	126

[a]Artificial inoculation.
Abbreviation: NA, not available.

Endophytes: fungi that live in healthy plant tissues without causing visible disease for part of their life cycle

genetics study on *Holocryphia capensis* surprisingly suggested that it was likely introduced from an as yet unknown origin (24). All these fungi were shown to be able to infect and cause disease on *Eucalyptus* in a pathogenicity trial (24).

As new species of Cryphonectriaceae from many native trees and shrubs in the Myrtales have been discovered, it has become increasingly clear that they exist mostly as asymptomatic endophytes on their natural hosts. This has been most obvious for collections of these fungi on the Melastomataceae in Colombia, where damaged or fallen branches of asymptomatic plants have

been examined and found to bear fruiting structures (**Figure 1**) of these fungi (60). Mausse-Sitoe et al. (82) tested this hypothesis by incubating fully asymptomatic stem tissue excised from various species of *Syzygium*, *Eugenia*, *Psidium* (Myrtaceae), and *Dissotis* (Melastomataceae) collected in Mozambique under continuously humid conditions. Fruiting structures of *Chr. austroafricana* developed on the majority of these samples after two months (82). A metagenomic study on *Eucalyptus* has also confirmed that many fungi, including those in groups such as the Diaporthales, which accommodates pathogens such as the Cryphonectriaceae, occur as asymptomatic endophytes in healthy trees (81). This is likely true for many of the woody plants in the Myrtales considered in this review.

Assuming that the Cryphonectriaceae would be present as endophytes in healthy trees and likely fruit under conditions of stress, Roux et al. (114) collected samples from the non-native Myrtaceae, showing dieback due to rust (*Austropuccinia psidii*) infection in Hawaii. This study resulted in a remarkably diverse collection of Cryphonectriaceae, including two known pathogens of *Eucalyptus*, *Chr. deuterocubensis* and *Microthia havanensis*, and three undescribed species of *Celoporthe*. The origin of these fungi is unknown, but they probably include some that have been accidentally introduced into Hawaii and others that are native. But evidence suggests that they are asymptomatic endophytes on the host trees and have probably originated from other trees in the environment (114).

Owing to their importance as pathogens of eucalypts, surveys focused on understanding the global occurrence and relevance of the Cryphonectriaceae have focused on plantations of these trees. Consequently, these have been mostly in the tropics and subtropics where non-native eucalypts have been established in intensively managed plantations. Under these situations, the three species *Chr. cubensis*, *Chr. deuterocubensis*, and *Chr. austroafricana* in South America, Southeast Asia, and Southern Africa, respectively, are most commonly associated with obvious canker diseases. However, as new areas have increasingly been investigated, several other species, known only on native Myrtales or of unknown origin, have been found causing cankers on eucalypts. For example, *Chrysoporthe doradensis* was first described on *Eucalyptus grandis* and *Eucalyptus deglupta* in Ecuador (57) and subsequently found on *Eucalyptus* and native *Rhynchanthera grandiflora* and *Pleroma granulosum* (syn. *Tibouchina granulosa*) (Melastomataceae) in Brazil (119, 122) and most recently on *Eucalyptus* as well as *Henriettea seemannii* (Melastomataceae) in Colombia (125). Likewise, various newly described genera and species have been found causing stem cankers on *Eucalyptus*, but their origins remain to be determined. Examples include *Myrtoporthe* in Malaysia (Sabah) (106), *Parvomorbus* in south China (149), and *Xanthoporthe* in South Africa (126).

POPULATION GENETICS AND PATHWAYS OF MOVEMENT

Observational evidence and patterns of occurrence of the Cryphonectriaceae on the Myrtales have provided strong evidence for many examples of these fungi moving from native trees to infect planted trees. As discussed above, most examples involve these fungi becoming pathogens of eucalypts in established plantations (65, 98, 111). However, there are a few cases in which the Cryphonectriaceae have apparently moved from eucalypts to non-native ornamental trees such as *Pleroma* (syn. *Tibouchina*) (115, 136).

Genetic diversity studies have been conducted on various species of Cryphonectriaceae in an effort to determine the areas of origin of some of these fungi. The first of these studies was conducted on populations of *Chr. cubensis* in Brazil (143) and *Chr. austroafricana* in Southern Africa (141, 146), utilizing vegetative compatibility groups as markers. They provided evidence that populations of these fungi were relatively diverse, but they were not sufficiently informative to provide evidence of origin. Once it became recognized that these fungi occur on native plants, and when

powerful tools such as microsatellite markers became more readily available, various studies were undertaken to consider the population diversity of other species (24, 94, 95, 97, 101, 136).

To better understand the relationships between Cryphonectriaceae on native and closely associated planted trees, population genetic studies have continued to be undertaken. The most important constraint underpinning these studies remains the difficulty involved in establishing collections of these fungi on native hosts. These trees and shrubs mostly occur naturally in inaccessible areas, such as tropical jungles, mountainous areas, and regions of the world where security issues can be problematic. Yet some such collections have been made, notably for *Chrysoporthe cubensis* and *Chr. puriensis* in South America (101, 136), *Chr. austroafricana* (127) and *Holocryphia* spp. in Southern Africa (24, 94), and *Chr. deuterocubensis* in Southeast Asia (128). Results of all these studies have provided robust evidence of the Cryphonectriaceae occurring naturally on native Myrtales and undergoing host shifts to related planted trees.

The increasing availability of whole-genome sequences for fungi and, in this case, the Cryphonectriaceae from the tropics and Southern Hemisphere will provide many opportunities to better understand their biology, native origins, and pathways of movement. Genomes are currently available for most species of *Chrysoporthe* (80, 135, 138, 152, 153), and projects are well advanced to sequence species in all the genera (**Figure 3**). From those sequence data already available, it has been possible to determine that *Chrysoporthe* includes heterothallic species having the *MAT1-1* and *MAT1-2* idiomorphs as well as homothallic species with both idiomorphs in single haplotypes. This knowledge of mating type distribution adds information regarding the structure of populations and whether they represent native or introduced lineages (83).

Heterothallic: fungi that require the presence of a compatible individual for sexual reproduction

***MAT1-1* and *MAT1-2* idiomorphs:** mating in ascomycete fungi is controlled by the *MAT1* locus, with *MAT1-1* and *MAT1-2* variants determining sexual reproduction mode

Homothallic: fungal species able to undergo sexual reproduction in the absence of a partner of opposite mating type

EMERGING PATHOGENS AND DISEASE THREATS

Species of the Cryphonectriaceae occurring on trees in the Myrtales include highly aggressive pathogens that have the capacity to kill trees. Owing to their importance as canker pathogens of eucalypts, the best known of these are species of *Chrysoporthe*. Most of these species have been found causing cankers on eucalypts that have been established in plantations in the tropics and Southern Hemisphere. And many of these have now been shown to have originated on native Myrtales growing in close proximity to the plantations of non-native eucalypts. Beyond natural infections, most species of the Cryphonectriaceae residing in various genera and currently known only from native Myrtales have been shown in artificial inoculations to be pathogens of eucalypts.

The only example of serious tree diseases caused by the Cryphonectriaceae arising from host shifts from native Myrtales is the canker disease on eucalypts. There is no evidence of other species of the Cryphonectriaceae having emerged as disease agents on trees in natural ecosystems. Given the fact that those trees mostly occur in remote areas, it seems reasonable to assume that any emerging pathogen would probably not be recorded until it had begun to cause serious damage and undergone substantial spread. This raises the interesting question as to how fast a new disease caused by one of these fungi as a novel pathogen on a naïve host might emerge and spread.

A fundamental difference between woody ecosystems in the Northern and Southern Hemispheres is the diversity of plants in the south. Whereas the Northern Hemisphere mostly includes only the single Boreal floral Kingdom with relatively few tree genera, the remaining five floral kingdoms occur mostly in the Southern Hemisphere and include a much greater diversity of woody plants (32). It would be reasonable to assume that rapidly emerging epidemics would occur in areas where a single species covers large areas. If this is a major defining factor, then epidemic levels of disease caused by accidentally introduced Cryphonectriaceae in the Myrtales might not

occur as dramatically as in the case with various invasive pathogens in the Northern Hemisphere, such as chestnut blight (110) and Dutch elm disease (46).

Even if extensive disease epidemics caused by accidentally introduced Cryphonectriaceae would not occur in native populations of trees in the Myrtales, serious losses to plants and associated plant diversity might still occur. An apt example is found in the case of myrtle rust caused by *Austropuccinia psidii* (9). This pathogen is believed to be native to South America (34, 48, 49), and at least two genotypes have been accidentally moved across countries of the Southern Hemisphere (38, 84, 124). After many years of anticipating its arrival in Australia, the pandemic strain of *A. psidii* reached Australia in 2010 (18, 103). This pathogen has a very wide host range, which might be similar to some species of Cryphonectriaceae, and it has rapidly emerged to infect a large number of hosts (34, 123). But there are only some cases in which species of trees are sufficiently susceptible to be considered as highly threatened (19). The example of myrtle rust might provide a reasonable view of what to expect from possible accidental introductions of species of Cryphonectriaceae across the Southern Hemisphere.

Host–pathogen arms race: a coevolutionary race in which plants and pathogens adapt to each other, requiring continual development of resistant cultivars and clones

Plantation forestry using non-native eucalypts, including species of *Eucalyptus* and *Corymbia*, gave rise to the first concern that Cryphonectria canker might emerge as a serious limiting factor. From a commercial perspective, the disease has been very effectively managed by establishing planting stock known to be tolerant to infection by the Cryphonectriaceae, which for the present include mostly species of *Chrysoporthe*. One of the most important approaches in this case has been to utilize clonal hybrids between different species of *Eucalyptus* and, in many cases, test these in greenhouse and field screening trials. Such trials have been conducted in South America, South Africa, and Southeast Asia for *Chr. cubensis* (1, 79, 111, 122), *Chr. austroafricana* (139), and *Chr. deuterocubensis* (21, 106, 130). These have also included tests using different genotypes of the pathogens and considering issues such as clone-by-genotype interactions (1, 139).

The fact that the Cryphonectriaceae infecting *Eucalyptus* originate in the natural environment where these trees are being planted implies that disease-resistant clones will continuously be challenged by genetically diverse populations of the pathogens. Consequently, clones currently resistant to the pathogens might not be so after relatively short periods of time. A recent example can be found in the first example of a *Chrysoporthe* sp., in this case, *Chr. austroafricana*, infecting a species of *Corymbia* (127). This exemplifies the so-called host–pathogen arms race (28) and the need for forestry companies to introduce new genetic stock that will not be damaged by disease (14). Ultimately, technologies such as genetic modification of the planting stock will likely be required to maintain the sustainability of *Eucalyptus* forestry operations**.** The availability of a full sequence of the *E. grandis* genome (89), as well as of the pathogen genome, will provide the tools to ensure that disease-tolerant planting stock remains available.

Although new genotypes of known Cryphonectriaceae will continuously emerge to challenge eucalypts in plantations, new genera and species of these genera are likely to also emerge, adding greater challenges to plantation forestry. This has already been clear in recent outbreaks of Cryphonectria canker on *Eucalyptus* clonal hybrids in Indonesia, Malaysia, and South Africa. In these cases, species residing in the new genera *Cryptometrion*, *Myrtoporthe*, and *Xanthoporthe* have emerged to cause serious disease problems (61, 106, 126). Others will surely follow in the future.

FUTURE PROSPECTS

The Cryphonectriaceae on trees in the tropics and Southern Hemisphere provide a vivid example of the huge biodiversity of fungi in an area of the world that has been relatively poorly sampled. As important and emerging pathogens, they also illustrate the risks of serious tree disease problems

emerging in the future. This is especially true as the movement of people and products continues to increase globally, thus facilitating increasing risks of accidental introductions into new areas (15, 105). This also argues for much greater attention being given to documenting and understanding the very poorly explored global fungal biodiversity.

It is relevant that many of these Cryphonectriaceae give rise to cankers on trees that are biologically similar to the disease caused by the chestnut blight fungus, *C. parasitica*. They infect their hosts easily through naturally occurring wounds and on susceptible hosts develop rapidly in the cambial tissues to girdle stems (**Figure 1**). Consequently, they have the capacity to cause diseases as serious as chestnut blight. Thus, if a species naturally occurring on a particular tree genus were to be accidentally introduced into a new area where a susceptible native congener occurs as a naïve host, a very serious epidemic could easily arise (5, 37, 155). This view is based on many similar situations in the Northern Hemisphere, and the only limiting factor might be a greater host diversity in the tropics and Southern Hemisphere.

The discovery of the Cryphonectriaceae and their importance as tree pathogens on the Myrtales first emerged from planting *Eucalyptus* spp. outside their native range. These trees have now been established in plantations over very large areas, particularly in South America, Africa, and Southeast Asia. This area is currently estimated to be approximately 22 million hectares, making eucalypts the most widely planted genus of trees in the world (116). Most of the areas where these plantations occur are also areas of a rich biodiversity of trees and shrubs in the Myrtales. Fungi in the Cryphonectriaceae and likely others represent significant future threats to planted eucalypts via host shifts that are already evident in the case of numerous species.

Species of the Cryphonectriaceae that have undergone host shifts to infect eucalypts have effectively emerged as novel pathogens of those trees. The intensive nature of plantation forestry results in the pathogen populations building up such that the chance of their being moved to new areas increases markedly. This represents a situation known as a bridgehead effect (11), where pathogens or pests, once introduced into new areas, are most likely to be moved again. In effect, planting trees that typically have very long lifespans provides land bridges for tree pathogens to move globally (155).

All currently available information suggests that tree diseases caused by the Cryphonectriaceae will become increasingly important in the future. Consequently, efforts to reduce this threat must be vigorously pursued. This should include a better understanding of the possible pathways of movement of these fungi and identifying means to reduce new invasions. Surveys of diseases on Myrtales in their natural environment should also be supported and pursued. Tools such as those relying on data from genomes to identify and understand the biology and ecology of these fungi are also becoming increasingly powerful and can be utilized, for example, in improving diagnostics and quarantine procedures (85). Importantly, companies involved in commercially exploiting trees in the Myrtales should be made aware of the risks of accidentally moving pathogens and pests such as those in the Cryphonectriaceae. This would bear advantages not only to their business ventures but also to the health of forests and forestry globally.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We are grateful to many colleagues and students who have participated in our studies on the Cryphonectriaceae, a period that has extended over approximately 40 years. These studies have

had the benefit of financial and in-kind support from companies pursuing plantation forestry, particularly with eucalypts in many countries of the tropics and Southern Hemisphere. The forestry companies that have been members of the Tree Protection Co-Operative Program in South Africa, a relationship that has lasted more than 35 years, deserve special thanks. We also thank the National Research Foundation, the Department of Science and Innovation, South Africa, and the University of Pretoria for long-term financial support.

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