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Ten important forest fungal pathogens: a review on their emergence and biology

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Abstract

Plant pathogenic fungi and fungus-like taxa (oomycetes) form part of the ecological makeup of healthy natural forest ecosystems. Some help to eliminate unhealthy trees, while others are essential for the conservation of plant species diversity, particularly soil-borne pathogens. However, many fungal pathogens also have devastating effects on forest ecosystems. Disease impacts are more profound when pathogens newly emerge and these can even wipe out an entire tree population. These organisms have developed a plethora of strategies to colonize and infect plants and there are several factors causing pathogens to emerge. Therefore, to prevent emerging diseases, a thorough understanding of the factors causing them is necessary. It is also important to have a comprehensive understanding of the mechanisms of disease development and propagation to design effective control measures. In this review, we describe the phenomenon of emerging and re-emerging pathogens by exemplifying ten important recently emerged forest pathogenic fungi and fungus-like taxa, namely, *Ophiostoma novo-ulmi*, *Ceratocystis fimbriata*, *Fusarium circinatum*, *Hymenoscyphus fraxineus*, *Phyllosticta citricarpa*, *Neonectria faginata*, *Sphaerulina musiva*, *Phytophthora pluvialis*, *P. agathidicida*, and *Melampsora* × *columbiana*. They have been listed in order of the most cited to the least cited species based on data obtained from the Web of Science. We provide a review for each species to document its emergence and its negative impact on the host(s). We also revise their taxonomic placement, host and country details, and provide updated phylogenetic trees for each genus. The number of accepted species based on molecular data is also provided.

Keywords – Diseases – Fungus-like pathogens – Phylogeny – Phytopathogenic fungi

Introduction

Forest plants are important in sustaining wildlife habitats and are also valued for recreational and spiritual welfare (Allen et al. 2010). Forests contribute to the industry through their harvesting value as they are primarily relied upon for timber (Allen et al. 2010, Hyde et al. 2019). A healthy natural forest ecosystem includes fungal pathogens, which are essential in removing weakened and

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unhealthy trees (Castello et al. 1995). However, they may pose threats to forest ecosystems, resulting in large forest areas being affected. For example, oak forests have experienced morbidity and mortality attributed to canker-causing taxa such as *Diplodia corticola* and *Discula quercina* (current name: *Dendrostoma leiphaemia*) (Linaldeddu et al. 2009, 2014, Maddau et al. 2011). In view of phytopathogens, fungi are considered as the most ecologically and economically important threats (Doehlemann et al. 2017, Jayawardena et al. 2021b).

Basically, upon colonization of plants, fungi exhibit pathogenic, parasitic or mutualistic lifestyles (De Silva et al. 2017). However, they can switch among the different lifestyles under favorable or unfavorable conditions (Promputtha et al. 2007, Rai & Agarkar 2016). Some endophytes, which asymptomatically colonize plants, can become pathogenic and vice versa, under certain conditions (Müller & Krauss 2005, Schulz & Boyle 2005, Delaye et al. 2013). For instance, *Sphaeropsis sapinea* can cause disease when plants are stressed under conditions such as drought, extreme temperatures or mechanical wounds (Chou 1987, Stanosz et al. 2001). Furthermore, *Diplodia mutila* is an endophyte of *Iriartea deltoidea* that may become pathogenic when there is excess light (Álvarez-Loayza et al. 2011). Similarly, certain saprobic fungi may switch to pathogens, as was the case with the opportunistic *Lasiodiplodia brasiliense* (MFLUCC 11-0414) and *L. pseudotheobromae* (MFLUCC 12-0053) (Dong et al. 2020).

Pathogenic fungi exist as biotrophs, necrotrophs or hemibiotrophs, with the impacts ranging from mild infection to host death (Doehlemann et al. 2017). *Botrytis cinerea* and *Sclerotinia sclerotiorum* are examples of necrotrophic pathogens (van Kan 2006). Some necrotrophs manifest as latent pathogens, whereby they prevail in a quiescent state until triggered by host physiological changes to re-establish growth (Brown 1998, Slippers & Wingfield 2007). Hemibiotrophs initially occur as biotrophs and later switch to a necrotrophic mode (Horbach et al. 2011, De Silva et al. 2017). Such examples include *Pyricularia oryzae* (Koeck et al. 2011) and *Phytophthora infestans* (Sowley et al. 2009, Jayawardena et al. 2020).

Some symptoms associated with fungal diseases include spots, blights, cankers, wilts, rots, and damping-off (Ray et al. 2017, Jayawardena et al. 2019). Through infection and eradication of wild plants, pathogenic fungi and fungus-like taxa threaten the vitality and viability of natural ecosystems (Fisher et al. 2020). The impacts are more profound upon the invasion and emergence of pathogens (Avila-Quezada et al. 2018). A disease is considered as "emerging" when it is newly recognized or has newly appeared in a certain region, and has the ability to spread at an increasing rate in incidence and severity (Daszak et al. 2003). Emerging pathogens are those that have a high incidence and virulence rate (Daszak et al 2000, Jones et al. 2008). Emerging pathogens can generate novel dangerous strains that threaten plant health and negatively impact biodiversity conservation (Jones et al. 2008, Avila-Quezada et al. 2018). Pathogens also emerge as a result of newly introduced taxa on native hosts (Garbelotto & Pautasso 2012). Emerging fungus-like pathogens include *Phytophthora agathidicida* (Scott & Williams 2014, Weir et al. 2015) and *P. pluvialis* (Dick et al. 2014), and emerging pathogenic fungi include *Ceratocystis platani* (Panconesi 1999, Baker et al. 2003, Engelbrecht et al. 2004, Engelbrecht & Harrington 2005), *Hymenoscyphus fraxineus* (Krauml & Kirisits 2012, Pautasso et al. 2013, Baral & Bemmann 2014, Baral et al. 2014, Fisher et al. 2020), as well as *Neonectria faginata* and *N. ditissima* (Ehrlich 1934, Lohman & Watson 1943, Houston 1994, Castlebury et al. 2006). Other examples are provided in Table 1.

Several factors prompt the emergence of pathogens (Ghelardini et al. 2016). Owing to their complex biogeography, latent and cryptic expression, phytopathogenic fungi and fungus-like taxa threaten biosecurity (Hyde et al. 2018, Scott et al. 2019). Therefore, the main objective of this review is to describe different scenarios for the occurrence of emerging pathogens by exemplifying ten important emerged or re-emerged forest pathogenic fungi and fungus-like taxa. Each entry provides details on the number of accepted species in the genus, their hosts, distributions and their negative impacts on their respective hosts. We also elucidate the taxonomic placement of each species and their relatives and provide updated phylogenetic trees based on DNA sequence analyses, concurrently revising these genera.

Table 1 Summary of emerging forest pathogenic fungi and fungus-like taxa focused in this study.

List of emerging pathogens	Invasion mechanism	Diseases caused	Main host affected	Location	References
Ophiostoma novo-ulmi (*Sordariomycetes*, *Ophiostomatales*, *Ophiostomataceae*)	-	Dutch elm disease	*Ulmus* sp. (elm trees)	Europe, western Asia and North America	Brasier (1991)
Ceratocystis fimbriata (*Sordariomycetes*, *Microascales*, *Ceratocystidaceae*)	Via wounds	Rapid `Ōhi`a death	*Metrosideros polymorpha* (`Ōhi`a lehua)	Hawaii	Baker et al. (2003), Harrington (2013), Keith et al. (2015), Mortenson et al. (2016)
Fusarium circinatum (*Sordariomycetes*, *Hypocreales*, *Nectriaceae*)	Via wounds	Pitch canker disease	*Pinus radiata* (Monterey pine)	California, USA	McCain et al. (1987), Correll et al. (1991), Gordon et al. (2001)
Hymenoscyphus fraxineus (*Leotiomycetes*, *Helotiales*, *Helotiaceae*)	-	Dieback	*Fraxinus excelsior* (European ash trees)	Europe	Krauml & Kirisits (2012), Pautasso et al. (2013), Baral & Bemmann (2014), Baral et al. (2014)
Phyllosticta citricarpa (*Dothideomycetes*, *Botryosphaeriales*, *Phyllostictaceae*)	-	Citrus black spot	*Citrus* spp.	South Africa	Kotzé (1981), Baldassari et al. (2008)
Neonectria faginata (*Sordariomycetes*, *Hypocreales*, *Nectriaceae*)	Via wounds	Beech bark disease	*Fagus grandifolia* (American beech)	USA	Ehrlich (1934)
Sphaerulina musiva (*Dothideomycetes*, *Capnodiales*, *Mycosphaerellaceae*)	Via wounds, and/or natural openings	Septoria leaf spot and stem canker	*Populus* spp. (poplars)	North America	Bier (1939), Waterman (1954), Feau et al. (2010), Quaedvlieg et al. (2006), Dhillon et al. (2015)
Phytophthora pluvialis (Peronosporomycetes, *Peronosporales*, *Peronosporaceae)*	-	Red needle cast disease	*Pinus radiata* (pine)	New Zealand	Dick et al. (2014)
Phytophthora agathidicida (*Peronosporomycetes*, *Peronosporales*, *Peronosporaceae*)	-	Kauri dieback	*Agathis australis* (kauri)	New Zealand	Scott & Williams (2014), Weir et al. (2015)
Melampsora × *columbiana* (*Pucciniomycetes*, *Pucciniales*, *Melampsoraceae*)	-	Leaf rust disease	*Populus* spp. (poplars)	USA	Newcombe et al. (2000)

Drivers of emerging fungal pathogens

Disease establishment by pathogens on their hosts depends on many factors. Much of the global increase in plant diseases are attributed to newly emerged pathogens (Rafiqi et al. 2018). When pathogens emerge, they can spread to new geographical areas and affect other hosts (Wilson 1995, Strange & Scott 2005). Among the numerous drivers of emerging phytopathogens, Morse (2004) ranked ecological changes, for example, climate change as the most significant factor leading to the emergence of diseases. Events such as floods, storms and hurricanes can generate novel virulent strains (Nnadi & Carter 2021). These events expand the geographic range of pathogens or their carriers which result in the introduction of new diseases in areas where they have not been previously reported (Tucker et al. 2011, de Crecy et al. 2009). For instance, *Phytophthora*

cinnamomi tends to migrate to warmer regions where it infects new hosts as it is sensitive to frost (Benson 1982, Bergot et al. 2004). Furthermore, climate change may enhance the virulence of pathogens and/or weaken the host defense system (Harvell et al. 2002, Eastburn et al. 2011).

Another key factor responsible for the increased occurrence of fungal pathogens is largely attributed to human-mediated activities, which alter the natural environment thus generating opportunistic situations for pathogens to emerge (Morse 2004, Fisher et al. 2012). Furthermore, perturbations due to human activities may lead to the emergence of novel hybrid species through interspecific hybridization (Brasier & Mehrotra 1995, Fisher et al. 2012, Stukenbrock 2016).

Movement of living plants across international borders has been recognized as an important invasion pathway for non-native pathogens worldwide (Brasier 2008). Such disease-causing organisms may have severe economic and ecological consequences (Brasier 2008). Pathogens that have co-existed with their hosts might have little to no adverse effects since they co-evolved and are adapted to each other (Brasier 2008, Phukhamsakda et al. 2022). However, greater risks arise when these pathogens move to other regions, where the endemic plants are endangered as they have little resistance (Brasier 2008). Such an example is *Phytophthora cinnamomi*, which can expand its geographic range and affect previously unaffected hosts (Bergot et al. 2004). *Phytophthora cinnamomi* has infected more than 3,000 plant species over the last 150 years from its presumed origin within South Asia (Hardham 2005). This root pathogen continues to infect plant ecosystems worldwide, especially forests in south-west Australia (Hardham 2005). Emerging diseases also arise as a result of a pathogen being latent (Ghelardini et al. 2016). Plants affected by latent pathogens initially do not show any visible symptoms (Migliorini et al. 2015). The pathogen perseveres and later produces signs or symptoms of diseases, perhaps triggered by changes in environmental or nutritional conditions, or if the host immune system is compromised (Photita et al. 2004).

Invasion of pathogenic fungi into plant tissues and their dispersal

Fungi have multiple ways to interact with plants (Burgess et al. 2016). Their distinct lifestyles exhibit diverse traits, such as dispersal mechanisms, types of reproduction, growth, nutrient assimilation and parasitism (Gilbert et al. 2002, García-Guzmán & Morales 2007, Dickman & de Figueiredo 2011, Porras-Alfaro & Bayman 2011). Pathogenic fungi are adapted so that they can invade plants, overcome defense mechanisms, and colonize tissues to grow, survive and reproduce (Mendgen et al. 1996, Jayawardena et al. 2021b). For a pathogen to infect a plant, it must be able to make its way into and through the tissues (Mendgen et al. 1996). As such, fungi initially target the hosts that they want to colonize and develop means for their spore dispersal (Doehlemann et al. 2017). Spore dissemination can either be independent of the host (via wind, water or insect vector) or dependent on the host (through pollen or seed dispersal) (Alfen 2001, Doehlemann et al. 2017). Some spores secrete an adhesive extracellular matrix to attach firmly to the host surface (Doehlemann et al. 2017, Chethana et al. 2021a, b). These spores adhere to the host surface to prevent them from being washed away prior to penetration (Doehlemann et al. 2017).

Following adherence to the surface, some spores penetrate the plant via phloem-feeding insect vectors (Kluth et al. 2002), via wounds or through the stomata (Dean et al. 2012, Watkinson et al. 2015). Others enter their hosts by secreting cell-wall degrading enzymes or through the formation of appressoria and pegs (Bechinger et al. 1999, Thines et al. 2000, Tonukari et al. 2000, Tonukari 2004, Dean et al. 2012, Chethana et al. 2021a, b). Prior to appressorium formation, the fungus undergoes a morphological change that results in high turgor pressure (Thines et al. 2000, Doehlemann et al. 2017). Such high pressure enables the fungus to rupture and penetrate the cuticle to enter underlying epidermal cells of the leaves (Thines et al. 2000). After entering the hosts, fungi obtain nutrients as biotrophs or necrotrophs (Eberl et al. 2019). Fig. 1 illustrates a spore germ tube that has formed an appressorium, entering the epidermis. Fig. 2 summarizes the steps of fungal invasion into its host.

Appressorial cells vary among different species, being either single-celled or multicellular, the latter termed compound appressoria (Armentrout et al. 1986, Chethana et al. 2021a, b). Most

appressoria are simple nodules that emerge at the end of spore germ tubes. However, some appressoria contain melanin pigments and are septate, such as in *Magnaporthe oryzae* (current name: *Pyricularia oryzae*) and the anthracnose disease-causing *Colletotrichum* species (Ryder & Talbot 2015, Jayawardena et al. 2021a). The biology of *P. oryzae* has been studied as a model to understand the mechanism of fungal disease formation in plants (Ebbole 2007). *Pyricularia oryzae* is a hemibiotrophic pathogen. The fungus initially invades cells, absorbs the available nutrients, but does not kill the host cells (Campos-Soriano et al. 2013). Ultimately, the fungus becomes necrotrophic, damaging and killing plant tissues (Campos-Soriano et al. 2013). The infection starts when the conidium adheres to the host surface and upon germination, an appressorium is formed to infect the plant (Wilson & Talbot 2009).

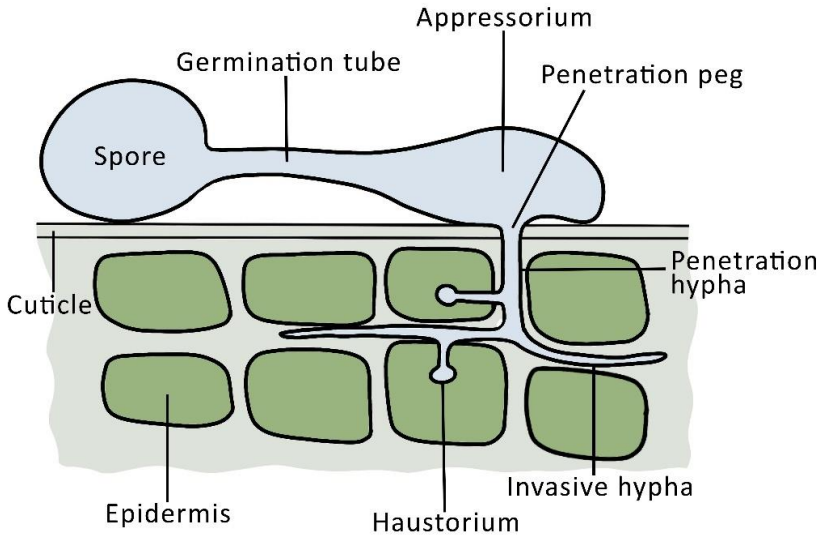

Figure 1 – Spore germ tube and appressorium entering the epidermis – process in pathogenic fungi and fungus-like taxa [Adapted and re-drawn from Meng et al. (2009)].

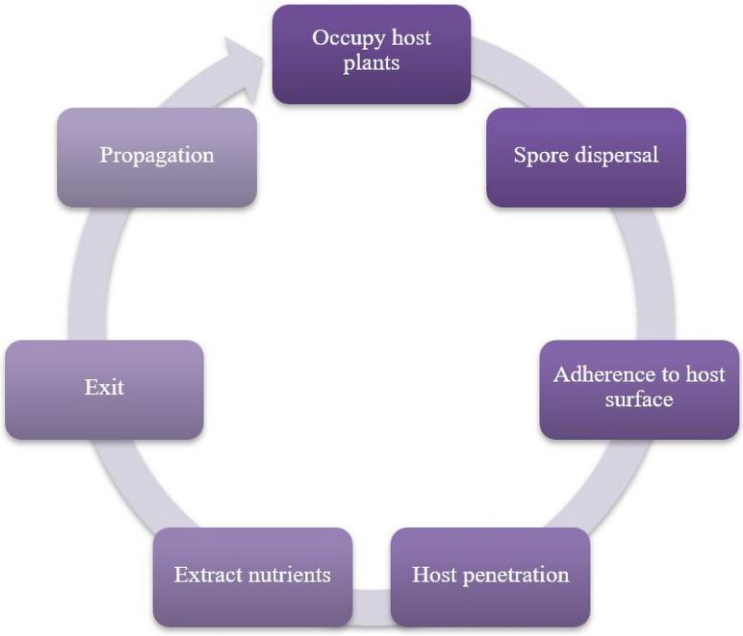

Figure 2 – Summary: fungal invasion mechanisms of the host.

Materials & Methods

Case studies

In this paper, we describe the phenomenon of emerging and re-emerging pathogens by exemplifying ten important recently emerged forest pathogenic fungi and fungus-like taxa, namely, *Ophiostoma novo-ulmi*, *Ceratocystis fimbriata*, *Fusarium circinatum*, *Hymenoscyphus fraxineus*, *Phyllosticta citricarpa*, *Neonectria faginata*, *Sphaerulina musiva*, *Phytophthora pluvialis*, *P. agathidicida*, and *Melampsora* × *columbiana*. These species have been selected in view of their degree of severity and their negative impacts on the natural ecosystems, based on a search of previous publications. Each entry highlights the emergence of the pathogens and their impacts on their respective hosts. These ten pathogens have been listed in order of the most cited to the least cited. The total number of citations per year has been obtained from the core collection of the "Web of Science" webpage. The graphs provided herein illustrate the number of times each species was cited, calculated from the years 2001 to 2021 (Figs 3, 5, 7, 8, 10, 12, 14, 16, 17, 19). This has been done by using the "advance search" option and using the species name as the query keyword. Furthermore, to estimate the number of studies carried out on fungal pathogens from forest trees, crops and ornamentals, a basic search on the Web of Science and google scholar was initiated, by using specific keywords (Table 2).

Table 2 Estimation of the number of studies carried out on fungal phytopathogens.

Types of plantation	Number of fungal pathogenic records		Keywords used
	From Web of Science	From google scholar	
Crops	3525	58,800	Fungal pathogens in/on crops
Forest trees	701	28,000	Fungal pathogens in/on forest trees
Ornamental trees	129	25,300	Fungal pathogens in/on ornamental plants

Sequence alignment and phylogenetic analyses

Phylogenetic analyses were performed using multi-locus datasets for each genus. Sequences for individual gene regions [internal transcribed spacer (ITS), large subunit (LSU), β-tubulin (*β-TUB*), translation elongation factor 1α (*TEF-1α*), RNA polymerase 1 and 2 (*RPB1* and *RPB2*), actin (*ACT*), calmodulin (*CAL*), guanine nucleotide-binding protein subunit beta (*MS204*), glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*), 60S ribosomal protein L10 (60S), enolase (*Enl*), heat shock protein 90 (*HSP90*), triosephosphate isomerase/glyceraldehyde-3-phosphate dehydrogenase gene (*TigA*)] were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/). These sequences were aligned using MAFFT v7 (https://mafft.cbrc.jp/alignment/server/) (Katoh et al. 2019). The aligned sequences were checked and trimmed using trimAl to remove uneven ends (Capella-Gutiérrez et al. 2009), and combined using BioEdit v. 7.0.5.2 (Hall 1999). Phylogenetic trees of the concatenated gene regions were reconstructed using maximum likelihood (ML), maximum parsimony (MP) and Bayesian inference (BI) method. For each genus, phylogenetic analyses were also conducted on single gene locus for verification and selection of taxon sampling for subsequent phylogenetic analyses.

Maximum likelihood analysis was performed in the CIPRES Science Gateway v.3.3 (Miller et al. 2010). Bootstrap support was obtained by running 1000 pseudo-replicates using RAxML-HPC2 on XSEDE (8.2.12) (Stamatakis 2014). Phylogenetic Analysis Using Parsimony (PAUP) v.4.0b10 was used to perform the MP analysis using the heuristic search option with 1,000 random taxa additions (Swofford 2002). The model of evolution was estimated by using MrModeltest 2.2 (Nylander 2004) under the Akaike information criterion (AIC) implemented in PAUP v. 4.0b10.

Bayesian inference analysis was conducted using MrBayes v. 3.1.2 (Huelsenbeck et al. 2001, Ronquist & Huelsenbeck 2003) to evaluate posterior probabilities (BYPP) by Markov chain Monte Carlo sampling (BMCMC). Markov chains were run for 1,000,000 to 15,000,000 generations

depending on the genera and trees were sampled every 100th generation. The suitable burn-in phases were determined using Tracer version 1.7 (Rambaut et al. 2018) and were discarded. Phylograms were visualized using FigTree v.1.4.4 (Rambaut & Drummond 2012) and Adobe Illustrator CS5 (Version 15.0.0, Adobe, San Jose, CA).

Results

Phylogenetic analyses

From our phylogenetic analyses, all three phylogenetic trees (ML, MP and BI) resulted in similar topologies, using their respective concatenated alignments. The RAxML analysis yielded the best scoring tree, which was used as the backbone tree. The results for the ML and MP parameters are provided (Table 3).

Ten emerging forest fungal pathogens

Different circumstances whereby pathogens emerge are herein demonstrated and these include newly recognized and existing diseases. Emerging pathogenic species can develop into virulent strains that cause host morbidity and mortality in a short period of time.

Ophiostoma novo-ulmi Brasier, Mycopathologia 115(3): 155 (1991)

Dutch elm disease on *Ulmus* spp. is one of the most pernicious tree diseases across the northern Hemisphere (Brasier 1991). It is characterized by vascular wilt, and is caused by *Ophiostoma ulmi* and *O. novo-ulmi* (Brasier 2001a). Dutch elm disease-causing pathogens are vectored primarily by scolytid bark beetles (*Scolytus scolytus*) (Webber 2000). Adult beetles containing the spores infect healthy trees by transferring them into xylem vessels. The spores germinate and colonize the xylem, resulting in foliar wilting and tree death (Newbanks et al. 1983, Webber & Brasier 1984, Webber 1990, 2000, Ouellette et al. 2004). Since *O. novo-ulmi* is dimorphic, it colonizes the xylem by both budding and hyphal growth. The unicellular yeast enables vertical spread throughout the xylem of elm trees while the multicellular mycelium invades initially uninfected adjacent xylem vessels (Sarmiento-Villamil et al. 2021). Human-mediated transportation of infected elm timber further aids in the rapid expansion of the epidemic (Brasier & Webber 2019). Vascular tissues are important as they help to transport water and nutrients throughout the plant. Thus, diseases targeting these tissues have adverse effects on plant health (Perdiguero et al. 2017).

The Dutch elm disease pandemic occurred twice over two different periods. The disease, first caused by *Ophiostoma ulmi*, appeared in northwest Europe in 1910 (Brasier 1991) and spread at an increasing rate across Europe to central Asia and North America (Brasier 2000b). The pandemic declined around the 1940s since most of the trees had already died (Brasier 1979). However, the second wave of Dutch elm disease occurred in the 1950s, causing the death of elm trees in Europe, North America and western Asia. This pathogen was described as a new species named *Ophiostoma novo-ulmi*, which was grouped into two races – a Eurasian race that probably originated in the area of Moldavia and Ukraine, and a North American race (Brasier 2001a). The Eurasian race is now called *O. novo-ulmi* subsp. *novo-ulmi* and the North American race is known as *O. novo-ulmi* subsp. *americana* (Brasier 2001a).

Ophiostoma novo-ulmi and *O. ulmi* can be differentiated based on mitochondrial DNA size, mitochondrial and nuclear DNA polymorphisms, morphology and their aggressiveness, with *O. novo-ulmi* being highly aggressive in contrast to *O. ulmi* (Bates 1990, Bates et al. 1990, Brasier 1991, Brasier & Buck 2001). Even though Dutch elm disease was attributed to *O. ulmi* during the first wave, the impacts were less severe when compared with the second wave, where Dutch elm disease was caused by *O. novo-ulmi* (Brasier & Buck 2001). *Ophiostoma novo-ulmi* caused the death of approximately 30 million mature elm trees by the early twentieth century, with few remnants of elm trees in isolated or disease-controlled areas (Greig & Gibbs 1983, Brasier & Webber 2019). In due course, Dutch elm disease continued to spread around other countries

including Canada (Temple et al. 2006), Croatia (Katanić et al. 2020), Czech Republic (Dvořák et al. 2007), Estonia and north-eastern Europe (Jürisoo et al. 2019), Japan (Miyamoto et al. 2019) and Latvia (Matisone et al. 2020).

In the current Dutch elm disease epidemic, *Ophiostoma ulmi* is more likely to be replaced by the more aggressive *O. novo-ulmi* (Brasier & Webber 2019). In the first epidemic caused by *O. ulmi*, there was a decline in disease intensity (Brasier & Webber 2019). Therefore, this raised the question of whether there can be a decline in the current Dutch elm disease. A plausible explanation for the decline of the first Dutch elm disease pandemic caused by *O. ulmi* might be attributed to the increased viral infection of the fungus that led to a decreased xylem infection by the bark beetles (Mitchell & Brasier 1994, Brasier 2000c). In experiments carried out during the 1980s, both *O. ulmi* and *O. novo-ulmi* were found to carry "deleterious, cytoplasmically transmitted viruses" (Brasier 1983, Buck et al. 2003, Brasier & Webber 2019). These fungal viruses have the ability to reduce mycelial growth and conidial viability, thus resulting in low disease incidence in elm trees via the bark beetle vectors (Webber 1987, Sutherland & Brasier 1997). Unfortunately, although these viruses can be transmitted through ascospores in *O. ulmi*, they are not readily transmitted in the aggressive *O. novo-ulmi*, which explains why the current Dutch elm disease is not declining (Brasier & Webber 2019).

The optimum growth temperature of *O. ulmi* is 28°C (Brasier 1981, Brasier & Webber 2019, Et-Touil et al. 2019). Between 18–25°C, *O. ulmi* grows slower than *O. novo-ulmi* (Brasier 1981, Brasier & Webber 2019, Et-Touil et al. 2019). Therefore, the faster growth rate of *O. novo-ulmi* and its highly aggressive nature towards elm trees might explain why the current Dutch elm disease epidemic is not declining (Webber & Brasier 1984, Brasier & Webber 1987, Webber 2000, Brasier & Webber 2019). Since the optimum temperature for the growth of *O. novo-ulmi* is 22°C, it is suggested that this species is more adapted to a temperate rather than a tropical or sub-tropical environment (Brasier & Mehrotra 1995). Considering that elm trees are mostly confined to the temperate regions of the northern hemisphere (Brasier & Buck 2001), we suggest that they might be more prone to infection by the aggressive *O. novo-ulmi* rather than the less aggressive *O. ulmi*.

Considering the aggressive nature of *O. novo-ulmi*, we hypothesize that the fungus might have emerged with respect to its virulent trait. In view of its higher pathogenic ability, *O. novo-ulmi* has a tendency to acquire more of the host nutrients as compared to *O. ulmi* (Brasier & Buck 2001). A lack of prior coevolution with the pathogen might have also increased host susceptibility, leading to diminution of the mature elm trees (Brasier & Webber 2019). Environmental factors facilitating pathogen dispersal might have also led to the rapid depletion of hosts (Brasier & Webber 2019). In addition, transcriptomic analyses of the dimorphic *O. novo-ulmi* proved that a large number of homologous genes involved in pathogenicity and virulence were differentially expressed during the morphological change from yeast to hypha (Nigg & Bernier 2016).

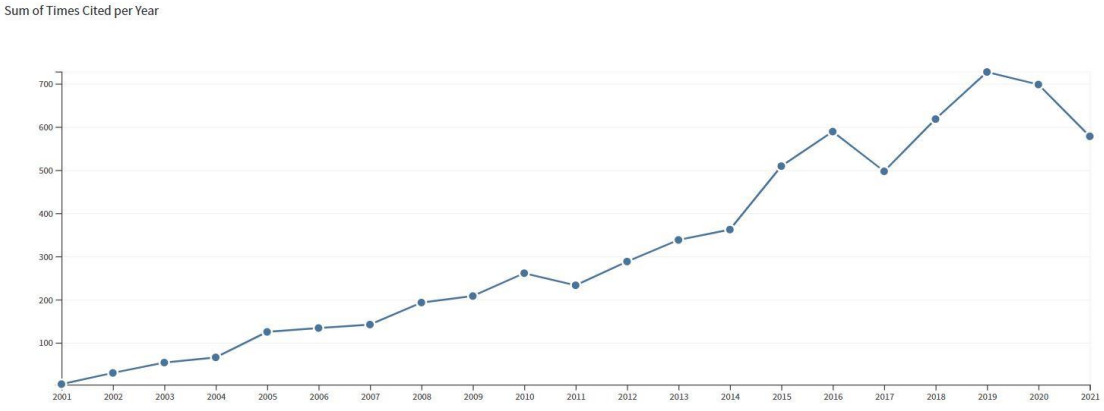

Figure 3 – Citation reports for *Ophiostoma novo-ulmi* from 2001 to 2021 (Total number of citations: 6654).

Table 3 RAxML and MP analysis parameters.

RAxML analysis parameters									
Genera		***Ophiostoma***	***Ceratocystis***	***Hymenoscyphus***	***Phyllosticta***	***Neonectria***	***Sphaerulina***	***Phytophthora***	***Melampsora***
ML optimization likelihood value		-19592.792324	-16741.202186	-17717.356778	-25922.236963	-11927.610536	-16039.415963	-104897.856414	-5275.921844
ML Tree length		10.332702	0.860209	3.170726	3.821264	0.537636	1.515705	3.838371	1.299843
Estimated base frequencies	A	0.190465	0.237055	0.234054	0.209614	0.227800	0.243219	0.214955	0.297767
	C	0.328530	0.265681	0.245832	0.291564	0.285760	0.258835	0.277278	0.167997
	G	0.259872	0.229924	0.262936	0.277288	0.257119	0.280481	0.311455	0.225362
	T	0.221133	0.267341	0.257178	0.221534	0.229321	0.217465	0.196312	0.308873
Substitution rates	AC	1.263365	1.344621	1.399620	1.272775	1.177927	1.673097	0.421605	1.239230
	AG	2.240960	4.759465	3.386606	3.486976	2.762327	3.397782	1.258017	2.594528
	AT	1.673433	1.933586	1.556380	1.452622	1.374486	0.952555	0.602518	0.667930
	CG	0.848152	1.067482	0.728797	1.356161	0.801527	1.227454	0.960377	0.282600
	CT	4.539824	6.553397	5.809631	7.371114	6.428365	7.295385	5.325356	2.986894
	GT	1.000000	1.000000	1.000000	1.000000	1.000000	1.000000	1.000000	1.000000
Gamma distribution shape parameter α		0.350163	0.234472	0.282434	0.279759	0.177784	0.176438	0.1000000000	0.317319
Distinct alignment patterns		1050	958	1074	1241	762	1012	3321	364
Undetermined characters or gaps (%)		44.54	34.76	72.56	39.80	41.95	18.84	28.84	10.18
Maximum parsimonious analysis parameters									
Genera		***Ophiostoma***	***Ceratocystis***	***Hymenoscyphus***	***Phyllosticta***	***Neonectria***	***Sphaerulina***	***Phytophthora***	***Melampsora***
MP length: Tree #1		3802	1839	2674	4446	1245	2566	17769	740
Total number of characters		1628	4521	3756	2711	4015	2994	8412	1077
Constant		671	3512	2532	1665	3174	2073	5613	676
Parsimony-informative		841	745	1073	874	741	796	2348	355
Parsimony-uninformative		116	264	151	172	100	125	451	46
Tree #1	CI	0.453	0.668	0.607	0.385	0.820	0.552	0.244	0.659
	RI	0.814	0.867	0.803	0.785	0.895	0.690	0.749	0.843
	RC	0.369	0.580	0.487	0.302	0.734	0.381	0.183	0.556
	HI	0.547	0.332	0.393	0.615	0.180	0.448	0.756	0.341

Wang et al. (2020) introduced eight new *Ophiostoma* species from hosts other than elm trees from northeastern China including *Larix* and *Pinus* spp. Since ophiostomatoid fungi are very diverse, it is possible that these taxa might emerge under certain circumstances, with similar destructive disease dynamics as exhibited by *O. novo-ulmi.*

The combined ITS, *β-TUB* and *TEF-1α* alignment of *Ophiostoma* comprised 1628 characters (ITS: 1–570, *β-TUB:* 571–779, *TEF-1α:* 780–1628), representing 155 strains of *Ophiostomataceae* (Fig. 4). There are 117 *Ophiostoma* species in Species Fungorum (2022). Based on our multigene phylogenetic analyses, we accept 93 species in *Ophiostoma*. *Ophiostoma novo-ulmi*, the emerging pathogen discussed herein, was initially isolated from *Ulmus* species (Brasier 1991). In addition, *O. ulmi* and *O. himal-ulmi*, both residing in the *O. ulmi* complex, are important tree pathogens (Brasier 1991, Gibbs 2003). Besides *Ulmus* spp., some economically significant forest trees infested by *Ophiostoma* species include *Acacia* spp., *Araucaria* spp., *Betula* spp., *Eucalyptus* spp., *Larix* spp., *Picea* spp., and *Pinus* species (Fig. 4).

Several ophiostomatoid taxa reported from Europe and Scandinavia exhibit symbiotic relationships with bark beetles (Kirisits 2007). Some examples where *Ophiostoma* infections have been vectored by bark beetles are denoted in Fig. 4. From a survey carried out in the boreal forests in Finland and Russia, 717 fungal isolates resembling *Ophiostoma* were reported, which are associated with 11 bark beetle species on *Picea abies* and *Pinus sylvestris* (Linnakoski et al. 2010). Thirty-eight ophiostomatalean isolates were reported from 16 adult wood-boring beetles (Nel et al. 2021). Furthermore, 496 ophiostomatoid strains were reported from beetle galleries infesting *Larix* spp. and *Pinus* spp. in China (Wang et al. 2020). Since spore dispersal of *Ophiostoma* species is precipitated by bark beetles (Wingfield et al. 1993, Kirisits 2007), it is important to design control strategies that target beetle galleries.

Ceratocystis fimbriata Ellis & Halst., Bull. New York Agricultural Experimental Station 76: 14 (1890)

Many saprobes and important plant pathogens are *Ceratocystis* species, ranging from weak to notorious disease-causing agents, yielding undesirable impacts (Wingfield et al. 1996). For example, *Ceratocystis platani* (≡ *Endoconidiophora fimbriata* f. *platani*), an aggressive stain-causing canker pathogen, has affected several *Platanus* spp. worldwide, including in Europe, Italy and the United States (Panconesi 1999, Baker et al. 2003, Engelbrecht et al. 2004, Engelbrecht & Harrington 2005). Diseases caused by *Ceratocystis* species include cankers and vascular wilts of trees, as well as root rot of crops such as sweet potato (Roux & Wingfield 2009).

Ceratocystis is transmitted in several ways. The tested hypotheses are that they are spread over long distances by human activity through infected wood or other plant and soil matter, equipment, tools, shoes, and by the wind, as spores embedded in tiny bits of insect frass (Loope et al. 2016). These taxa can produce a fruity aroma that attracts beetles, causing them to come into contact with spore masses that stick to their exterior and are transported to new hosts (Gibbs 1980, Appel et al. 1990, Heath et al. 2009). Moreover, spores of some *Ceratocystis* species are present in soil and can enter their hosts via roots (Hicks et al. 1980). Transmission has also been observed between trees through natural root grafts, as in the case of oak wilt (Juzwik et al. 2008).

Ceratocystis fimbriata, the type species of the genus, was first isolated from sweet potato, causing black rot of tubers (Halsted 1890). This species has a wide geographical and host range including *Acacia* spp., *Eucalyptus* spp., *Mangifera indica* (mango), *Populus* spp. (poplar), *Hevea brasiliensis* (rubber) and *Platanus* spp. (sycamore) (Barnes et al. 2001, Baker et al. 2003). *Ceratocystis fimbriata* is primarily a wound colonizer (Baker et al. 2003, Harrington 2013). The species has brown to black perithecia with long slender fimbriate necks, evanescent asci and cucullate ascospores (Halsted 1890). The perithecia are globose, either superficial or embedded in the substrate. The ascospores are hyaline, unicellular and galeate (Engelbrecht & Harrington 2005). Within the past 10 years, a native tree species of Hawaii, *Metrosideros polymorpha* (commonly known as`Ōhi`a lehua) has been dying at a very high rate (Mortenson et al. 2016). This phenomenon has been termed rapid `Ōhi`a death, induced by *Ceratocystis fimbriata* (Mortenson et

al. 2016). Affected trees display dark brown to black discoloration in the woody xylem (Keith et al. 2015). `Ōhi`a is the most abundant forest tree, occupying roughly 80% of all native forests across the Hawaiian islands (Friday & Herbert 2006, Loope et al. 2016). Ranging from sea level to 2,500 meters in elevation, `Ōhi`a can tolerate frost, volcanic vapors, and excesses or deficiencies in moisture (Loope et al. 2016).

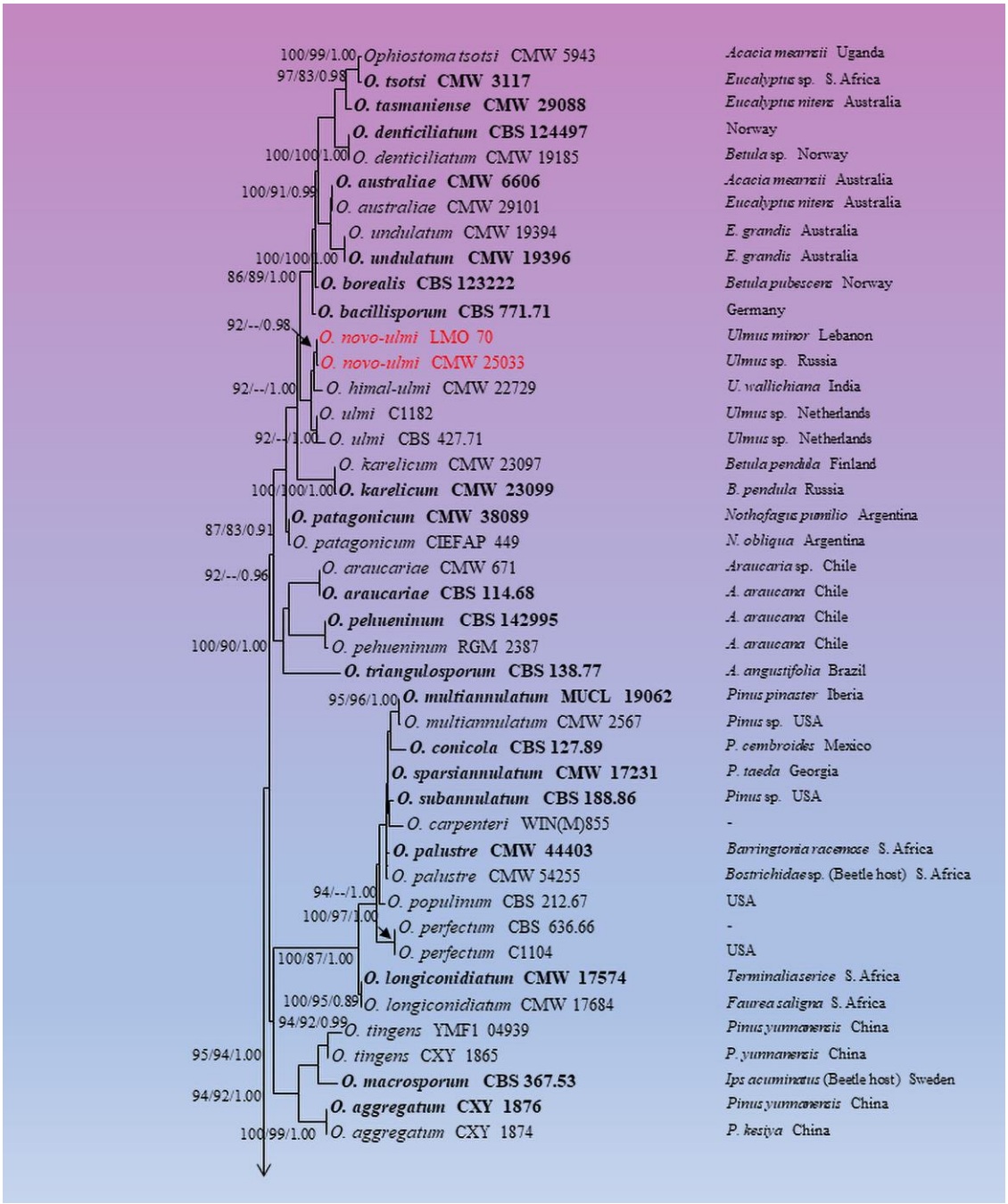

Figure 4 – Phylogram generated from maximum likelihood analysis (RAxML) based on the combined ITS, *β-TUB* and *TEF-1α* matrices of *Ophiostoma*. Maximum likelihood (ML) and maximum parsimony (MP) with bootstrap support ≥80%, and the posterior probability (PP) values (≥0.8) of Bayesian inference (BI) analyses are given at respective nodes as ML/MP/PP. The tree is rooted with *Ceratocystiopsis minima* (UM1501 and UM235) and *C. minuta* (CBS 116796 and YCC139) (*Ophiostomataceae*). Ex-type strains are indicated in bold and the emerging pathogen discussed herein is denoted in red. Hyphen (-) represents support values below 80% (ML and MP) and below 0.80 (PP). The host and country from which each species was identified are shown in the phylogram.

***** Vectored by beetles including *Ambrosia* sp., *Dryocoetes baikalicus*, *Ips duplicatus*, *Ips subelongatus*, *Pityogenes chalcographus*, *Polygraphus ssiori*, *Trypodendron lineatum* and some unknown beetle species
a *Pinus koraiensis* China, **b** *Pinus sylvestris* Finland, **c** *Pinus* sp. Russia, **d/d*** *Picea abies* Finland, **e*** *Picea abies* Russia

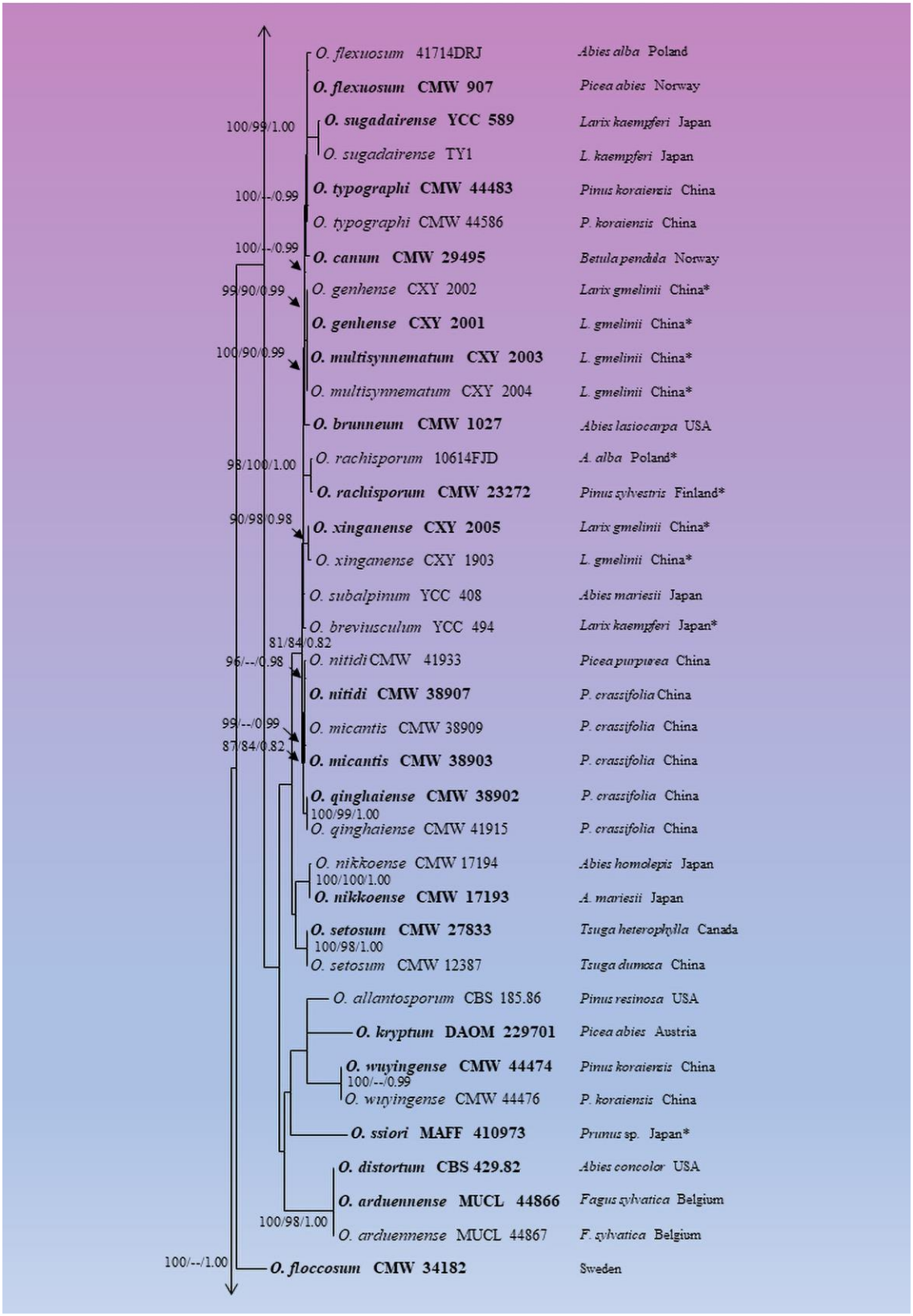

Figure 4 – Continued.

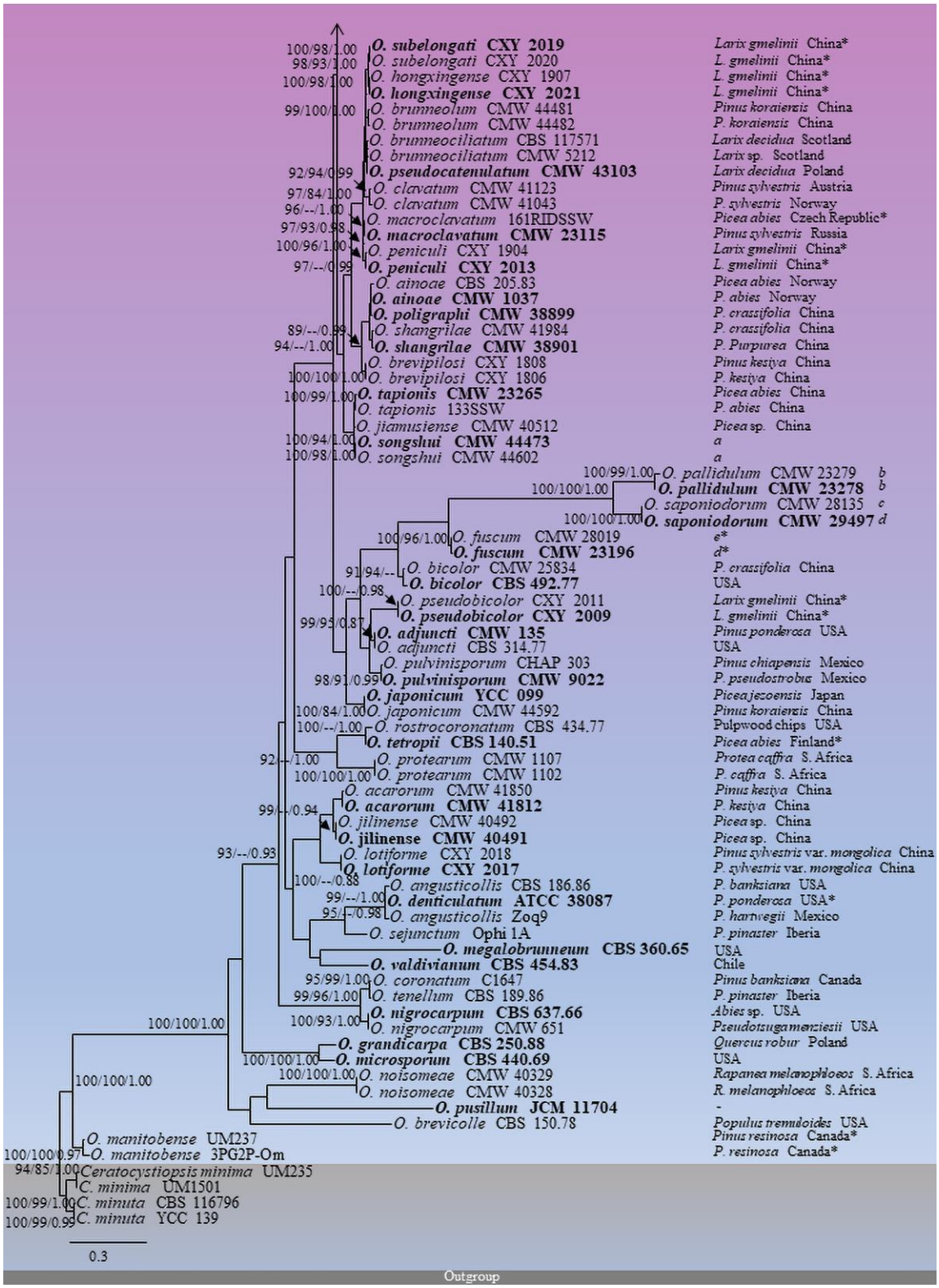

Figure 4 – Continued.

`Ōhi`a forests are important in various aspects. Firstly, they provide habitat to many endemic and endangered flora, fauna and mycota (Warshauer & Jacobi 1982, Friday & Herbert 2006). For example, the endangered *Vicia menziesii* (Hawaiian vine) exclusively inhabits the `Ōhi`a koa forests (Warshauer & Jacobi 1982). `Ōhi`a trees also have cultural and ornamental significance (Friday & Herbert 2006). Therefore, it is important to protect these trees and find ways to control the current epidemic. The absence of effective management approaches may result in the death of most `Ōhi`a trees in Hawaii (Loope et al. 2016).

A rapid increase in the death of these iconic trees was first observed in the Puna District of Hawaii island among healthy trees in undisturbed forest areas (Keith et al. 2015, Mortenson et al. 2016). By 2012, 10% or more of `Ōhi`a trees of all ages died, accounting for about 1600 hectares (ha) across Puna District, which increased to about 6400 ha by 2014 (Mortenson et al. 2016). In February 2016, approximately 15,000 ha of `Ōhi`a died and this number increased to about 20,000 ha by September 2016 (Loope et al. 2016). These statistical data characterize the malignancy and emergence of *Ceratocystis fimbriata*, whereby a single diseased `Ōhi`a leaf can ultimately spread to the entire canopy at an alarming rate (Mortenson et al. 2016).

Due to the recent discovery of this disease, research on both the pathogen and the host has only just begun. While modes of transmission, seasonality and even host resistance are understood for many species of *Ceratocystis*, only some basic biology, pathology, sanitary methods, and distribution are understood for this particular disease (Keith et al. 2015).

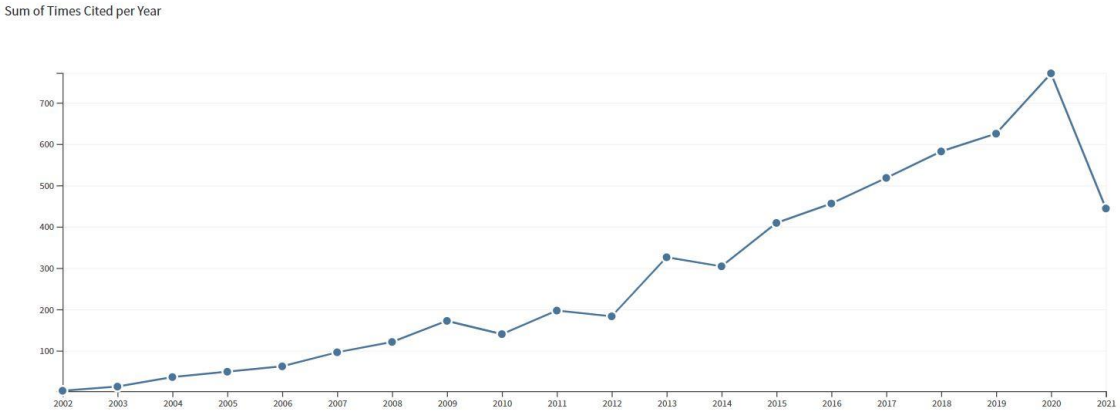

Figure 5 – Citation reports for *Ceratocystis fimbriata* from 2001 to 2021 (Total number of citations: 5507).

The combined ITS, *β-TUB*, *TEF-1α*, *MS204* and *RPB2* alignment of *Ceratocystis* comprised 4521 characters (ITS: 1–450, *β-TUB*: 451–999, *TEF-1α:* 1000–2448, *MS204:* 2449–3396, *RPB2:* 3397–4521), representing 77 strains of *Ceratocystidaceae* (Fig. 6). There are 104 *Ceratocystis* species in Species Fungorum (2022). Following previous studies carried out by Marin-Felix et al. (2017), Barnes et al. (2018), Liu et al. (2018) and Holland et al. (2019), and based on our multigene phylogenetic analyses we accept 42 species in *Ceratocystis* (Fig. 6).

Ceratocystis species comprise many undescribed and cryptic species that cause wilt and canker diseases of plants, thus, making it difficult to differentiate between morphologically identical species (Baker et al. 2003). *Ceratocystis* species have been placed in four phylogenetic lineages with respect to geographical regions namely, African clade (Heath et al. 2009, Mbenoun et al. 2014), Asian-Australian clade (Thorpe et al. 2007, Johnson et al. 2017, Liu et al. 2018, Holland et al. 2019), Latin American clade (Harrington 2000) and North American clade (Johnson et al. 2017) (Fig. 6). Based on our phylogenetic analyses and in accordance with Harrington (2000), Johnson et al. (2017), Li et al. (2017) and Holland et al. (2019), *Ceratocystis fimbriata* is located in the Latin American clade. Species residing in this clade are considered as hostile pathogens, accounting for emerging diseases (Keith et al. 2015, Barnes et al. 2018) when introduced into new locations and hosts (Al Adawi et al. 2014). From both the Latin American clade and the Asian-Australian clade strains of *Ceratocystis* identified in China, only the Latin American clade strain of *C. fimbriata* has been reported as serious pathogens (Li et al. 2016). Recently, a combination of phylogenetic, morphological and biological data by Barnes et al. (2018) revealed two new species, *Ceratocystis huliohia* and *C. lukuohia*, associated with rapid `Ōhi`a death in native `Ōhi`a forests. *Ceratocystis lukuohia* forms part of the Latin American clade (Barnes et al. 2018). Other important Latin American clade species bearing economic significance include *C. cacofunesta* causing

Ceratocystis wilt on *Theobromae cacao* and *C. platani* causing canker stain on *Platanus* spp. (Engelbrecht & Harrington 2005).

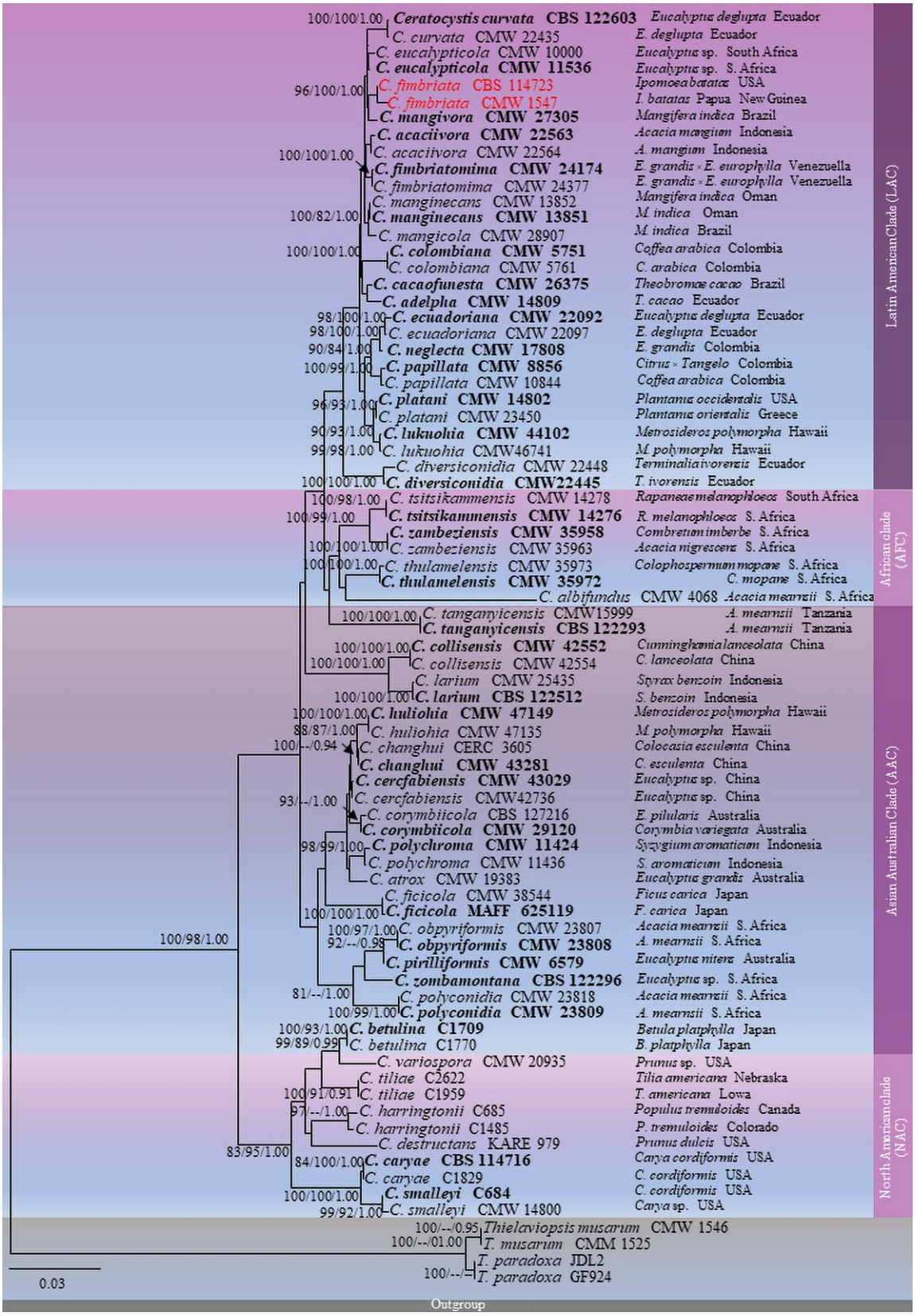

Figure 6 – Phylogram generated from maximum likelihood analysis (RAxML) based on the combined ITS, *β-TUB*, *TEF-1α*, *MS204* and *RPB2* matrices of *Ceratocystis*. Maximum likelihood (ML) and maximum parsimony (MP) with bootstrap support ≥80%, and the posterior probability (PP) values (≥0.8) of Bayesian inference (BI) analyses are given at respective nodes as ML/MP/PP.

The tree is rooted with *Thielaviopsis paradoxa* (GF924 and JDL2) and *T. musarum* (CMW1546 and CMM 1525) (*Ceratocystidaceae*). Ex-type strains are indicated in bold and the emerging pathogen discussed herein is denoted in red. Hyphen (-) represents support values below 80% (ML and MP) and below 0.80 (PP). The host and country from which each species was identified are shown in the phylogram.

Although there has been a decline in `Ōhi`a trees associated with rapid `Ōhi`a death, this is not the first time that `Ōhi`a has encountered mass death (Hodges 1986). A similar incident occurred during the late 1960s in Mauna koa and Mauna Kea in Hawaii as a result of fungal infections from *Phytophthora cinnamomi* and *Armillaria mellea*, and the `Ōhi`a borer, *Plagithmysus bilineatus* (Hodges 1986). Previously the death of `Ōhi`a trees was associated with progressive dieback and the trees were dying at a slower rate as compared to the current rapid `Ōhi`a death (Hodges 1986). Furthermore, this observation was made primarily among senescent trees in a different region (Mueller-Dombois et al. 2013). However, in the current epidemic, trees of all ages are dying (Mortenson et al. 2016). These distinct observations further indicate the emergence of *C. fimbriata.*

Some important forest trees infected by *Ceratocystis* species include *Acacia* spp., *Eucalyptus* spp., *Metrosideros* spp., *Platanus* spp. and *Populus* spp. (Fig. 6). Therefore, it is of utmost importance to study phytopathogenic fungi to protect and preserve forest ecosystems.

Fusarium circinatum Nirenberg & O'Donnell, Mycologia 90(3): 442 (1998)

Fusarium species are among the most significant phytopathogens known to cause diseases on a myriad of crops and forest trees (Summerell 2019). *Fusarium circinatum* (≡ *Gibberella circinata*) causes pitch canker disease of pine trees (McCain et al. 1987). The disease was first reported in California in 1986 and was found to affect *Pinus radiata* (Monterey pine) (McCain et al. 1987, Correll et al. 1991). *Fusarium circinatum* possibly originates from Mexico and/or southern Florida (Correll et al. 1991, Gordon et al. 2001). It is among the major pathogens affecting pine globally (Wingfield et al. 2008). Following its initial outbreak, the pathogen was later recorded from Europe (Landeras et al. 2005, Pérez-Sierra et al. 2007), Italy (Carlucci et al. 2007), Portugal (Bragança et al. 2009) and Spain (Landeras et al. 2005, Pérez-Sierra et al. 2007). In addition, the pathogen is present in Chile, Haiti, Korea, South Africa and south-east USA (Watt et al. 2011). *Fusarium circinatum* is found in most of the pine plantation areas, with a higher incidence in the Mediterranean and sub-tropical rather than temperate regions (Ganley et al. 2009). Since its dispersal depends largely on climatic conditions, *F. circinatum* is unlikely to spread to cooler northern latitudes despite the presence of susceptible hosts (Ganley et al. 2009, Baker et al. 2010, Möykkynen et al. 2015, Drenkhan et al. 2020).

Fusarium circinatum is in the European and Mediterranean Plant Protection Organization (EPPO) A2 quarantine list and is regulated by the European Union (Vettraino et al. 2018, Drenkhan et al. 2020, EPPO 2022b). It is an invasive necrotroph, which can be airborne and seed-borne (Aloi et al. 2021). *Fusarium circinatum* has both endophytic and pathogenic lifestyles (Elvira-Recuenco et al. 2020). Accounting for both life modes, we hypothesize that *F. circinatum* can switch from endophytic to pathogenic lifestyles and vice versa when conditions are favorable. As a consequence, it is probably more threatening to plants if its pathogenic lifestyle is predominant. We speculate that these lifestyle changes may result in increased virulent genotypes of the fungus. We further hypothesize that the pathogenesis of *F. circinatum* depends largely on its intrusive nature, implying that it can easily spread and infect certain hosts. Collectively, in view of these characteristics, it is unlikely to predict how the fungus will emerge.

Wounding is a prerequisite for *F. circinatum* to invade the plant tissues (Gordon et al. 2001). Wounds are generated by insects, weather-related events (including wind and hail) or mechanical damage (Gordon et al. 2001). Symptoms exhibited by the pitch canker disease include pitch-soaked cankers in trunks that can girdle trees and branches, and lead to tree death (Gordon et al. 2001, Wingfield et al. 2008, Bezos et al. 2017). Branch dieback, exudation of excessive resin leading to

cankers, canopy defoliation, reduced tree growth and decreased survival capacity also occur (Wingfield et al. 2008).

Pinus spp. are native to Europe and North America, and are economically important as their wood is used for timber and pulp, and their resins for the production of varnishes (Elvira-Recuenco et al. 2020). *Pinus radiata* is mainly used for commercial purposes (Mead 2013). Twelve native pine species occur in Europe (Richardson 2000). Considering the importance of pine trees, it is essential to protect them from fungal infections. *Pinus radiata* is the main *Pinus* species being affected by *Fusarium circinatum*. However, other pine such as *P. pinaster* in Spain is also affected (Landeras et al. 2005, Pérez-Sierra et al. 2007). However, a Mesoamerican pine (*P. oocarpa*), perhaps co-evolved with *Fusarium circinatum* and is therefore resistant to pitch canker disease (Dvorak et al. 2009).

Several studies have focused on the infection mechanism of *Fusarium circinatum*. For example, five candidate genes involved in pathogenicity were detected in the genome of *F. circinatum* (Muñoz-Adalia et al. 2018). Moreover, dual RNA-seq analysis of *F. circinatum* showed that ergosterol might be needed to cause diseases in pine (Visser et al. 2019). Therefore, a reduction in the *F. circinatum* ergosterol biosynthetic gene expression might reduce virulence of the fungus and contribute to host resistance (Visser et al. 2019). Another study aiming to investigate the effect of secondary metabolites in the pathogenicity of *F. circinatum* found that fusaric acid plays a significant role in the pathogenesis of *F. circinatum* (Phasha et al. 2021). Fusaric acid is a phytotoxin produced by the enzyme polyketide synthases (PKS6) encoded by the *FUB1* gene (Wiemann et al. 2013, Brown et al. 2015). These characteristics exhibited by *F. circinatum* account for some probable infection mechanisms and its pathogenicity.

There are 380 *Fusarium* species listed in Species Fungorum (2022), but many species lack molecular data. Based on the concatenated alignment of ITS, LSU, *CAM*, *RPB1*, *RPB2*, *TEF-1α*, *β-TUB*, Crous et al. (2021) provided an updated phylogenetic tree for *Fusarium* and accepted 220 species in this genus.

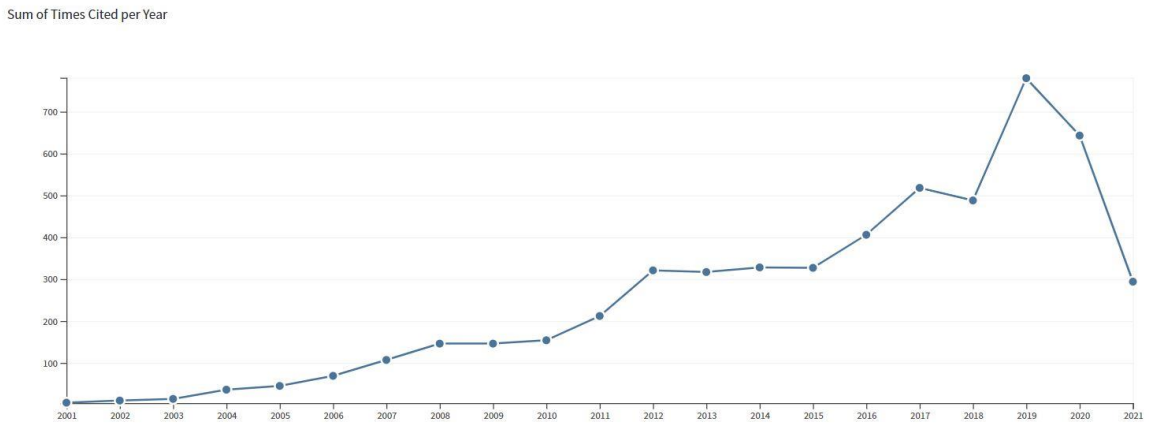

Figure 7 – Citation reports for *Fusarium circinatum* from 2001 to 2021 (Total number of citations: 5366).

Hymenoscyphus fraxineus (T. Kowalski) Baral, Queloz & Hosoya, IMA Fungus5(1): 79 (2014)

Hymenoscyphus was established in 1821 (Dennis 1964) and comprises 236 species (Species Fungorum 2022). It has a cosmopolitan distribution with most of its members being saprobes (Gross et al. 2015). Along with multi-locus phylogenetic analyses and morphological characteristics (apothecial colour, shape and size, guttulation, septation, and presence of cilia), habitats are considered for species recognition (Queloz et al. 2011, Zheng & Zhuang 2014, 2015, Gross & Han 2015, Gross et al. 2015). A decade ago, *Hymenoscyphus fraxineus* became a subject of interest since it was linked to the novel European ash dieback (Kowalski & Holdenrieder 2009).

Hymenoscyphus fraxineus (≡ *Chalara fraxinea*, = *Hymenoscyphus pseudoalbidus*) is a pleiomorphic invasive emerging discomycete that causes dieback of *Fraxinus excelsior* (European ash trees) (Queloz et al. 2011, Krauml & Kirisits 2012, Pautasso et al. 2013, Baral & Bemmann 2014, Baral et al. 2014, Fones et al. 2016). Ash trees occur in both tropical and temperate regions, distributed over Asia, Central America, Europe, North America and Northwest Africa (Kowalski 2006), and *Hymenoscyphus fraxineus* is distributed in East Asia and Europe (Farr & Rossman 2022). *Hymenoscyphus fraxineus* probably originates from Eastern Asia (Zhao et al. 2013) and was initially reported on petioles of decaying leaves of *Fraxinus mandshurica* (Mandshurian ash) (Hosoya et al. 1993). However, the causal agent was misidentified as *Lambertella albida* (≡ *Hymenoscyphus albidus*). *Hymenoscyphus albidus* is a sister species of *H. fraxineus* and is not virulent on ash (Husson et al. 2011, Gross et al. 2014). On the other hand, *H. fraxineus* has catastrophic effects, displaying dieback symptoms among ash trees of all age groups (Kowalski 2006, Kowalski & Holdenrieder 2009, Kowalski et al. 2015, Gross & Sieber 2015).

Ash dieback was initially detected in north-western Poland in 1992 without identifying the real cause of the disease (Przybył 2002, Kowalski & Holdenrieder 2009, Timmermann et al. 2011). In due course, the disease spread to more than 25 European countries (Pautasso et al. 2013, Mckinney et al. 2014). Subsequent events of ash dieback in Europe are listed in chronological order in Table 4. *Hymenoscyphus fraxineus* has also been reported on leaves of *Fraxinus mandshurica* (Mandshurian ash) from Eastern China (Zheng & Zhuang 2014) and Russia (Baral & Bemmann 2014, Cleary et al. 2016), and on rachises and petioles of fallen leaves of *Fraxinus rhynchophylla* (Korean ash) from Korea (Han et al. 2018).

Hymenoscyphus fraxineus is an aggressive pathogen, displaying symptoms of bark cankers and crown dieback, leaf necrosis, premature leaf fall, shoot and xylem wilt, ultimately causing tree mortality (Timmermann et al. 2011). Ascospores of *H. fraxineus* are commonly produced on fallen leaf petioles of ash. The ascospores are dispersed by wind and are easily spread to other ash trees (Timmermann et al. 2011, Krauml & Kirisits 2012). *Hymenoscyphus fraxineus* proliferates from infected leaves into twigs and stems via petioles, inducing necrotic bark lesions, subsequently leading to dieback (Gross et al. 2014).

Ash dieback jeopardizes stands of ash and increases its overall death rate (Gross et al. 2014). Infected seedlings are at higher risks of dying. However, aged trees develop long-term lethal infection (Hietala et al. 2013). Barely a fraction of European ash trees exhibit resistance against *Hymenoscyphus fraxineus*. Since *H. fraxineus* has emerged and has affected European ash for only around two decades, it is unlikely that natural adaptation has occurred (Mckinney et al. 2014). The harmless saprotroph *H. albidus* has been replaced by the invasive pathogenic *H. fraxineus*. This was confirmed through the "2010 Danish collection" that reported no *H. albidus* from sites previously known as *H. albidus* habitat (McKinney et al. 2012). Early colonization of *H. albidus* and *H. fraxineus* on 1-year-old ash-petioles is essential for spore dispersal during the early summer-autumn (McKinney et al. 2012). Therefore, a plausible explanation for the substitution of *H. albidus* by *H. fraxineus* could be due to competition between them for colonizing ash petioles, eliminating the native decomposer *H. albidus* from its natural ecological niche (McKinney et al. 2012). Even though the invasion mechanism of *H. fraxineus* is unclear, we hypothesize that the intrusive pathogenic nature of *H. fraxineus* is key to the replacement of *H. albidus*. Owing to the pathogenic nature of *H. fraxineus*, we further hypothesize that it can also generate appressoria to invade ash trees, which the saprobic *H. albidus* is unable to do. These explain the emergence of *H. fraxineus* as a forest pathogen.

The combined ITS, LSU, *TEF-1α*, *CAL*, *ACT* and *β-TUB* alignment of *Hymenoscyphus* comprised 3756 characters (ITS: 1–513, LSU: 514–1341, *TEF-1α*: 1342–2379, *CAL*: 2380–2745, *ACT*: 2746–2988, *β-TUB*: 2989–3756), representing 79 strains of *Helotiaceae* (Fig. 9). There are 235 *Hymenoscyphus* species in Species Fungorum (2022). Based on our multigene phylogenetic analyses, we accept 49 species in *Hymenoscyphus*.

Ash trees have great ecological and economic importance as they are usually grown for timber (Chavez et al. 2015, Mitchell et al. 2016). A reduction in ash trees yields huge economic

losses (Chavez et al. 2015, Mitchell et al. 2016). For better management approaches, forest pathologists should collaborate with conservation biologists, forest and landscape managers, plant breeders, restoration ecologists, social scientists and tree geneticists (Pautasso et al. 2013, Tallmon et al. 2004, McKay et al. 2005, Waring & O'Hara 2005, Laine et al. 2011, McRoberts et al. 2011, Pliura et al. 2011, Brukas & Sallnäs 2012). A breeding program to generate resistance and simultaneously conserve the genetic diversity of ash trees could be helpful (Pautasso et al. 2013).

Table 4 Events of sequential ash dieback in Europe.

Year	Countries	References
1996	Lithuania	Timmermann et al. (2011)
late 1990s	Czech Republic	Jankovský & Holdenrieder (2009)
2000	Latvia	Timmermann et al. (2011)
2002	Sweden	Barklund (2005)
2002	Denmark	Thomsen & Skovsgaard (2012)
2003	Estonia	Drenkhan & Hanso (2009), Timmermann et al. (2011)
2003	Belarus	Timmermann et al. (2011)
2004	Slovenia	Ogris et al. (2009)
2005	Austria	Halmschlager & Kirisits (2008)
2006	Norway	Timmermann et al. (2011)
2007	Finland	Rytkönen et al. (2011)
2007	Switzerland	Pautasso et al. (2013)
2008	Hungary	Szabó (2009)
2009	Italy	Ogris et al. (2010)
2009	Croatia	Barić et al. (2012)
2010	Belgium	Chandelier et al. (2011)
2010	Ukraine	Davydenko et al. (2013)

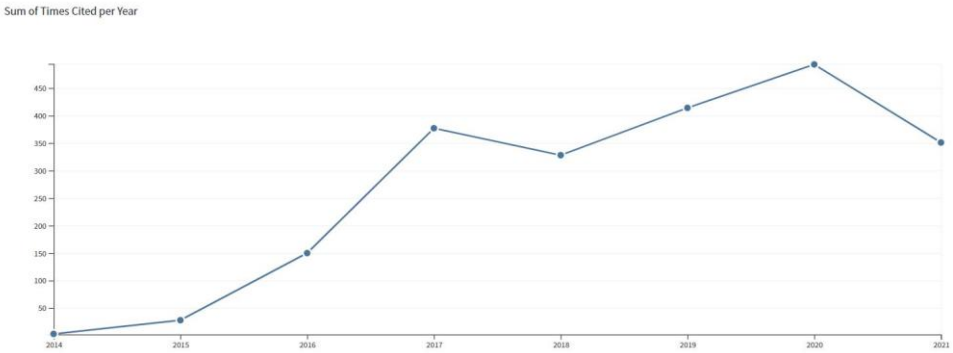

Figure 8 – Citation reports for *Hymenoscyphus fraxineus* from 2001 to 2021 (Total number of citations: 2144).

Phyllosticta citricarpa (McAlpine) Aa, Stud. Mycol. 5: 40 (1973)

Phyllosticta species exist mainly as pathogens, as well as endophytes and saprobes (Okane et al. 2001, 2003, Baayen et al. 2002, Thongkantha et al. 2008, Glienke et al. 2011, Rashmi et al. 2019, Norphanphoun et al. 2020, Bhunjun et al. 2021). They have a ubiquitous and worldwide distribution and occur on a broad range of hosts (Glienke et al. 2011, Rashmi et al. 2019). Pathogenic *Phyllosticta* species are mostly associated with leaf and fruit spots (Wang et al. 2012, Wikee et al. 2013a). Economically important plants such as *Citrus* spp. (*Rutaceae*) are greatly affected by *Phyllosticta* and one of the major diseases is Citrus black spot (Baayen et al. 2002, Glienke-Blanco et al. 2002, Everett & Rees-George 2006, Baldassari et al. 2008, Glienke et al.

2011, Brentu et al. 2012, Wikee et al. 2013b, Guarnaccia et al. 2017, 2019, Petters-Vandresen et al. 2020).

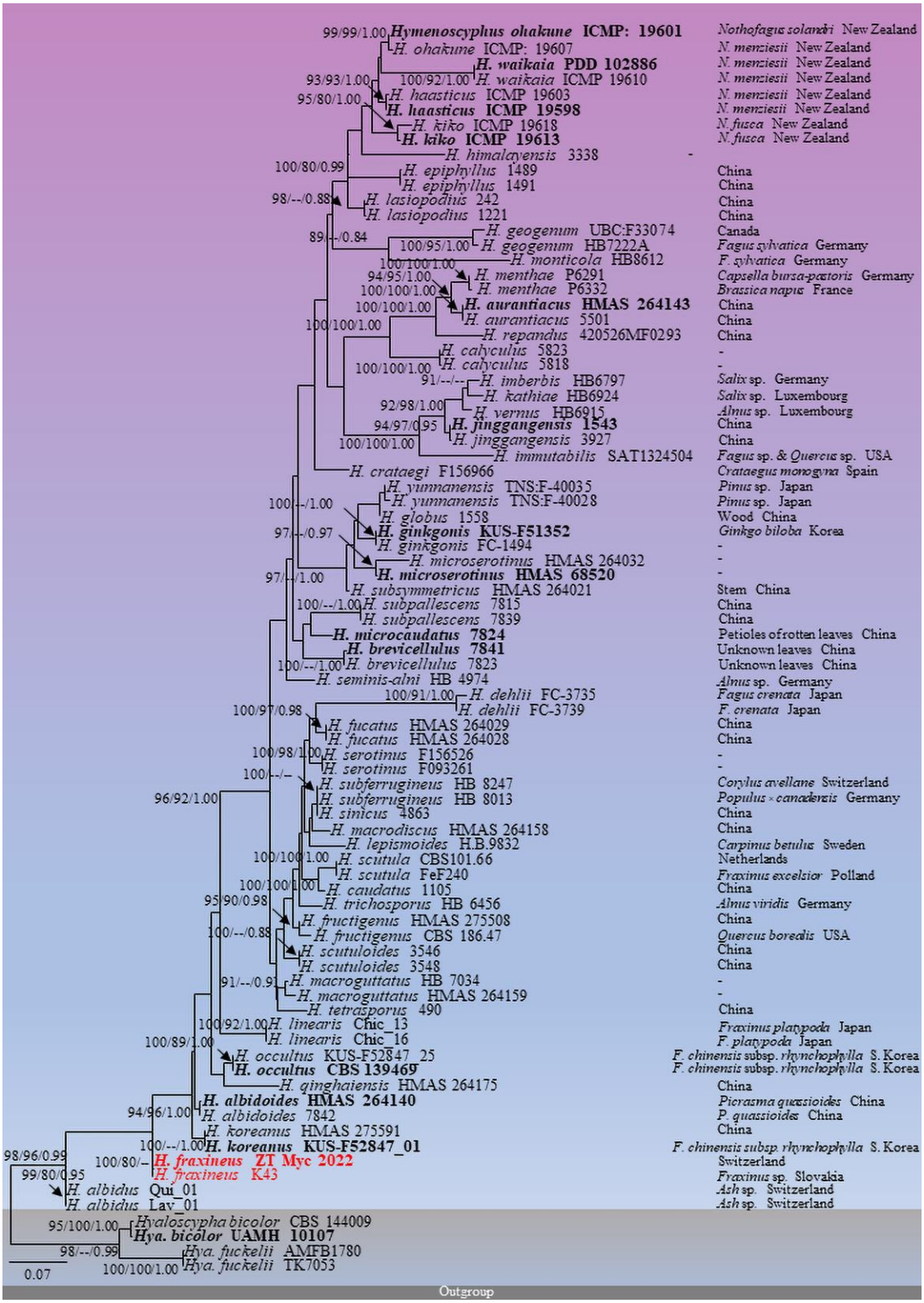

Figure 9 – Phylogram generated from maximum likelihood analysis (RAxML) based on the combined ITS, LSU, *TEF-1α*, *CAL*, *ACT* and *β-TUB* matrices of *Hymenoscyphus*. Maximum likelihood (ML) and maximum parsimony (MP) with bootstrap support ≥80%, and the posterior probability (PP) values (≥0.8) of Bayesian inference (BI) analyses are given at respective nodes as ML/MP/PP. The tree is rooted with *Hyaloscypha Bicolor* (UAMH 10107 and CBS 144009) and

Hya. fuckelii (AMFB1780 and TK7053) (*Hyaloscyphaceae*). Ex-type strains are indicated in bold and the emerging pathogen discussed herein is denoted in red. Hyphen (-) represents support values below 80% (ML and MP) and below 0.80 (PP). The host and country from which each species was identified are shown in the phylogram.

Citrus black spot is caused by *Phyllosticta citricarpa* (≡ *Guignardia citricarpa*) and is a foliar and fruit disease affecting citrus hosts (Kotzé 1981, Baldassari et al. 2008). Commercially grown citrus varieties comprising grapefruit, lemon, mandarin and sweet orange are greatly affected by this disease (Kotzé 1981, Baldassari et al. 2008). Five pathogenic *Phyllosticta* species (*P. citriasiana*, *P. citricarpa*, *P. citrichinaensis*, *P. citrimaxima* and *P. paracitricarpa*) and three endophytic species (*P. capitalensis*, *P. citribraziliensis* and *P. paracapitalensis*) are associated with *Citrus* spp. (Glienke et al. 2011, Wang et al. 2012, Wikee et al. 2013b, Guarnaccia et al. 2017). It has been observed that *P. citricarpa* occurs mainly in subtropical citrus-growing regions (Kotzé 1981, 1996).

The conidia of *Phyllosticta* species are aseptate and hyaline, usually bearing an apical appendage and covered by a mucoid layer (Van Der Aa 1973). Symptoms associated with Citrus black spot occur primarily in three stages, namely: "hard spot, freckle spot and virulent spot" (Kiely 1948). Hard spot is characterized by "sunken lesions with brick red to black margins", while virulent spot is characterized by "sunken necrotic lesions" without any defined borders (Brentu et al. 2012). The disease was first detected in Australia (Benson 1895), and later described by Kiely (1948). Citrus black spot has emerged in Florida (USA) and was initially found on sweet oranges in April 2010 (Chiyaka et al. 2012, Dewdney et al. 2011, Schubert et al. 2012, Shen et al. 2013, Wang et al. 2016). Events of Citrus black spot are listed in chronological order from different countries (Table 5).

Table 5 First records of Citrus black spots from different countries.

Year	Countries	References
2009	Uganda	Reeder et al. (2009)
2010	Brazil, Cuba	Góngora & Pérez (2010)
2010	Florida	Schubert et al. (2012)
2012	Ghana	Brentu et al. (2012)
2017	Italy, Malta, Portugal	Guarnaccia et al. (2017)

Infections caused by *P. citricarpa* can be initiated by both ascospores and conidia (Tran et al. 2017, Hendricks et al. 2017). Epidemiological studies demonstrate that the primary inoculum for the spread of Citrus black spot are ascospores produced in decomposing leaf litter (Kotzé 1981, Reis et al. 2006, Spósito et al. 2008). Ascospores are released during wet environmental conditions and dispersed via wind, while conidia are dispersed by rain splash (Huang & Chang 1972, Kotzé 1981). It has been observed that the emergence of *P. citricarpa* is mainly attributed to changes in environmental conditions, mostly favored within tropical citrus cultivars areas, in warm and humid climatic conditions (Hendricks et al. 2020).

The combined ITS, LSU, *TEF-1α*, *ACT*, *RPB1* and *β-TUB* alignment of *Phyllosticta* comprised 2711 characters (ITS: 1–627, LSU: 628–1390, *TEF-1α*: 1391–1873, *ACT:* 1874–2093, *GAPDH:* 2094–2711), representing 142 strains of *Phyllostictaceae* (Fig. 11). There are 1488 *Phyllosticta* species in Species Fungorum (2022). Based on our multigene phylogenetic analyses, we accept 103 species in *Phyllosticta* (Fig. 11). *Phyllosticta citricarpa* is found in the *P. concentrica* species complex, primarily affecting citrus hosts (Kotzé 1981, Baldassari et al. 2008).

Other species located in the *Phyllosticta concentrica* species complex include *P. aspidistricola*, *P. aucubae-japonicae*, *P. bifrenariae*, *P. catimbauensis*, *P. citriasiana*, *P. citribrasiliensis*, *P. citricarpa*, *P. citrichinaensis*, *P. citrimaxima*, *P. concentrica*, *P. cussonia*, *P. domestica*, *P. elongata*, *P. ericarum*, *P. gardeniicola*, *P. harai*, *P. hostae*, *P. hymenocallidicola*,

P. hypoglossi, *P. iridigena*, *P. kerriae*, *P. kobus*, *P. mate*, *P. ophiopogonis*, *P. paracitricarpa*, *P. pilospora*, *P. religiosa*, *P. rhaphiolepidis*, *P. speewahensis*, *P. spinarum*, accounting for a total of 29 *Phyllosticta* species (Fig. 11).

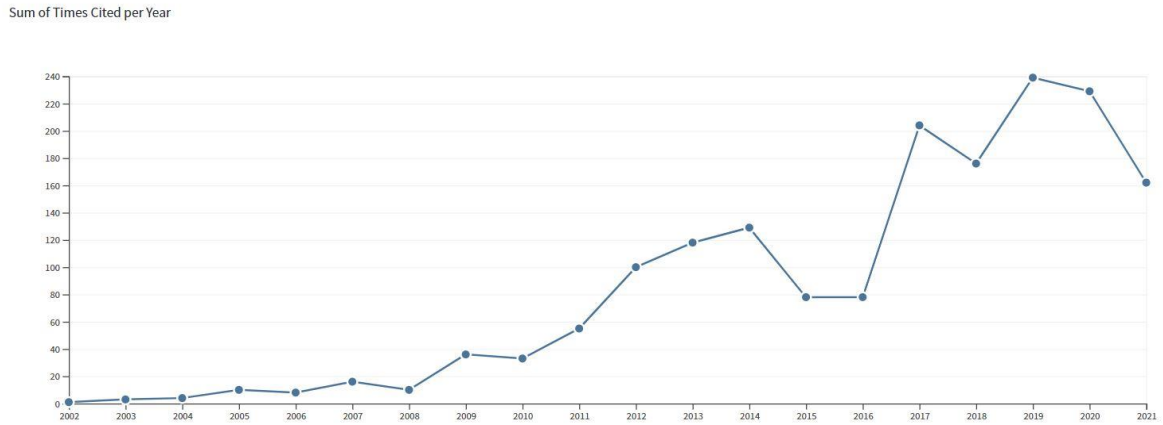

Figure 10 – Citation reports for *Phyllosticta citricarpa* from 2001 to 2021 (Total number of citations: 1689).

Considerable impacts related to Citrus black spot include a downfall in the economy as injured fruits are prone to fruit drops in the orchards, which jeopardizes international trade (Everett & Rees-George 2006, Dewdney et al. 2011, Gabriela et al. 2014). Essentially, *P. citricarpa* is regarded as a quarantine pest in Europe and the USA (Baayen et al. 2002, Glienke et al. 2011, EPPO 2022a). This pathogen has been reported from more than 12 *Citrus* species (Guarnaccia et al. 2019). Notwithstanding the importance of Citrus black spot, the origin of *P. citricarpa* is not well-documented. The pathogen is presumed to be native to a *Citrus*-rich zone such as South and Southeast Asia (Scora 1975, Malik et al. 2013, Hynniewta et al. 2014). Since citrus is of great economic importance, it necessitates extreme control and management strategies. Great care must be taken when handling citrus fruits with leaves and debris from Citrus black spot quarantined areas. This may prevent the introduction of Citrus black spot into other citrus-grown regions. Fungicide applications are regarded as major control measures globally (Hincapie et al. 2014).

Neonectria faginata (M.L. Lohman, A.M.J. Watson & Ayers) Castl. & Rossman, in Castlebury, Rossman & Hyten, Can. J. Bot. 84(9): 1425 (2006)

Fagus grandifolia (American beech), a temperate deciduous tree (Tubbs & Houston 1990), has been suffering from beech bark disease for over 100 years (Hewitt 1914, Houston 1994, Morin et al. 2005). Beech bark disease is principally associated with *Neonectria ditissima* and *N. faginata* (Lohman & Watson 1943, Houston 1994, Castlebury et al. 2006). However, the disease is also attributed to the introduced European felted beech scale insect, *Cryptococcus fagisuga* (Ehrlich 1934). The insect was accidentally brought into Halifax, Nova Scotia, Canada, from Europe in the 1890s (Morin et al. 2005, 2007, Garnas et al. 2011). Beech bark disease is an insect-fungus complex that comprises the scale insect and both species of *Neonectria* (Ehrlich 1934). Prior to colonization by *Neonectria* species, *Cryptococcus fagisuga* infests beech trees by feeding on their boles, thus creating a wound and weakening the trees (Ehrlich 1934). This generates a point of entry for pathogenic fungi to invade the cambium, leading to beech bark disease (Houston 1994).

Neonectria species are distributed in both tropical and temperate regions (Chaverri et al. 2011). Beech bark disease usually occurs in three phases (Shigo 1972); the “advancing front”, the “killing front” and the “aftermath”. Canker disease caused by the insect-fungus interaction leads to apertures in the bark, resulting in reduced tree growth, leaf chlorosis and subsequently death. Excessive *Neonectria* infection girdles the vascular cambium and causes crown dieback (Ehrlich

1934, Gavin & Peart 1993, Houston 1994, Gove & Houston 1996). In addition, *Xylococculus betulae*, a secondary scale insect, occasionally infests beech trees, which also facilitates *Neonectria* colonization (Morin et al. 2007).

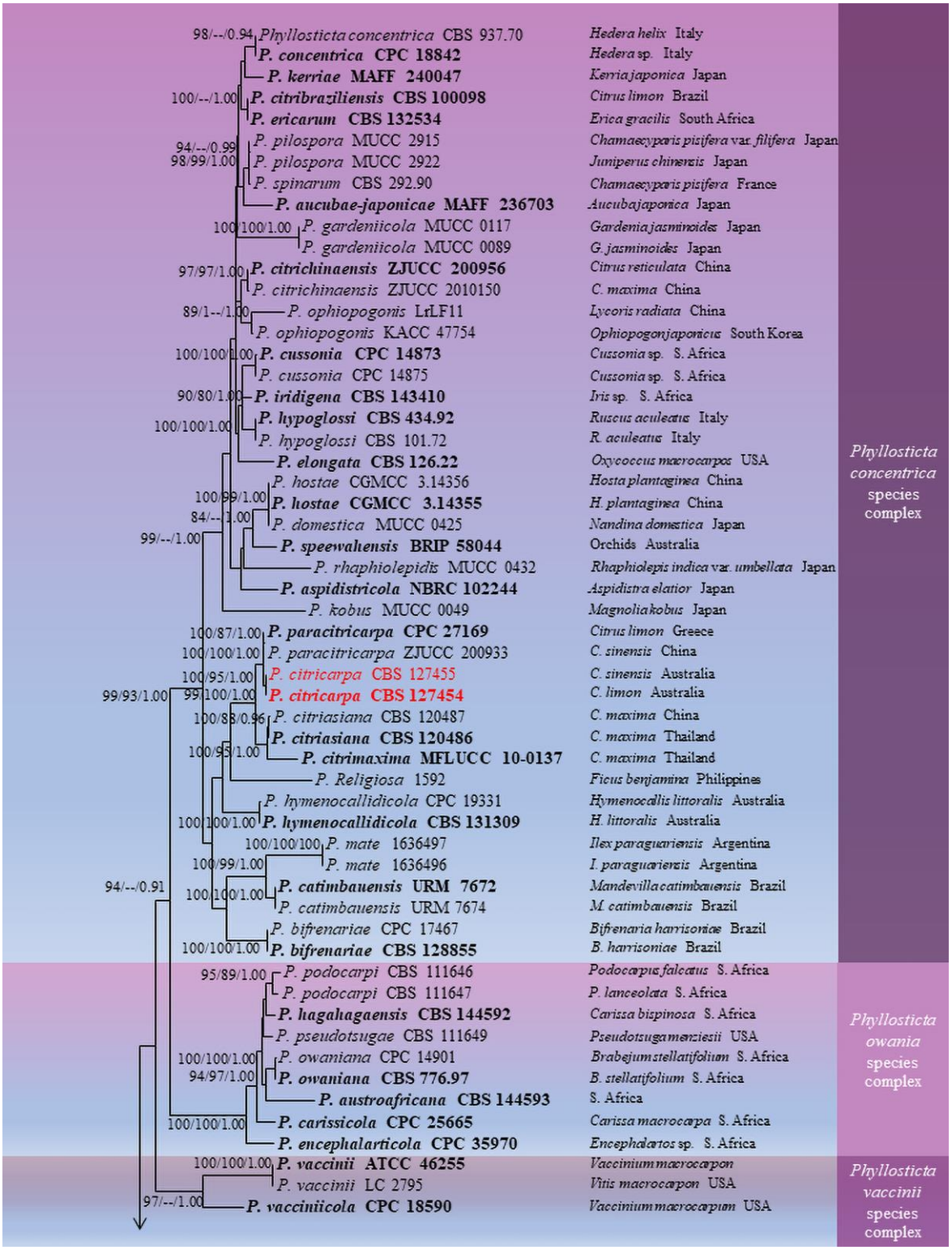

Figure 11 – Phylogram generated from maximum likelihood analysis (RAxML) based on the combined ITS, LSU, *TEF-1α*, *ACT* and *GAPDH* matrices of *Phyllosticta*. Maximum likelihood (ML) and maximum parsimony (MP) with bootstrap support ≥80%, and the posterior probability (PP) values (≥0.8) of Bayesian inference (BI) analyses are given at respective nodes as ML/MP/PP. The tree is rooted with *Botryosphaeria obtusa* (CMW 8232 and CMW 7775) and *B. stevensii* (CBS112553 and CMW7060) (*Botryosphaeriaceae*). Ex-type strains are indicated in bold and the

emerging pathogen discussed herein is denoted in red. Hyphen (-) represents support values below 80% (ML and MP) and below 0.80 (PP). The host and country from which each species was identified are shown in the phylogram.

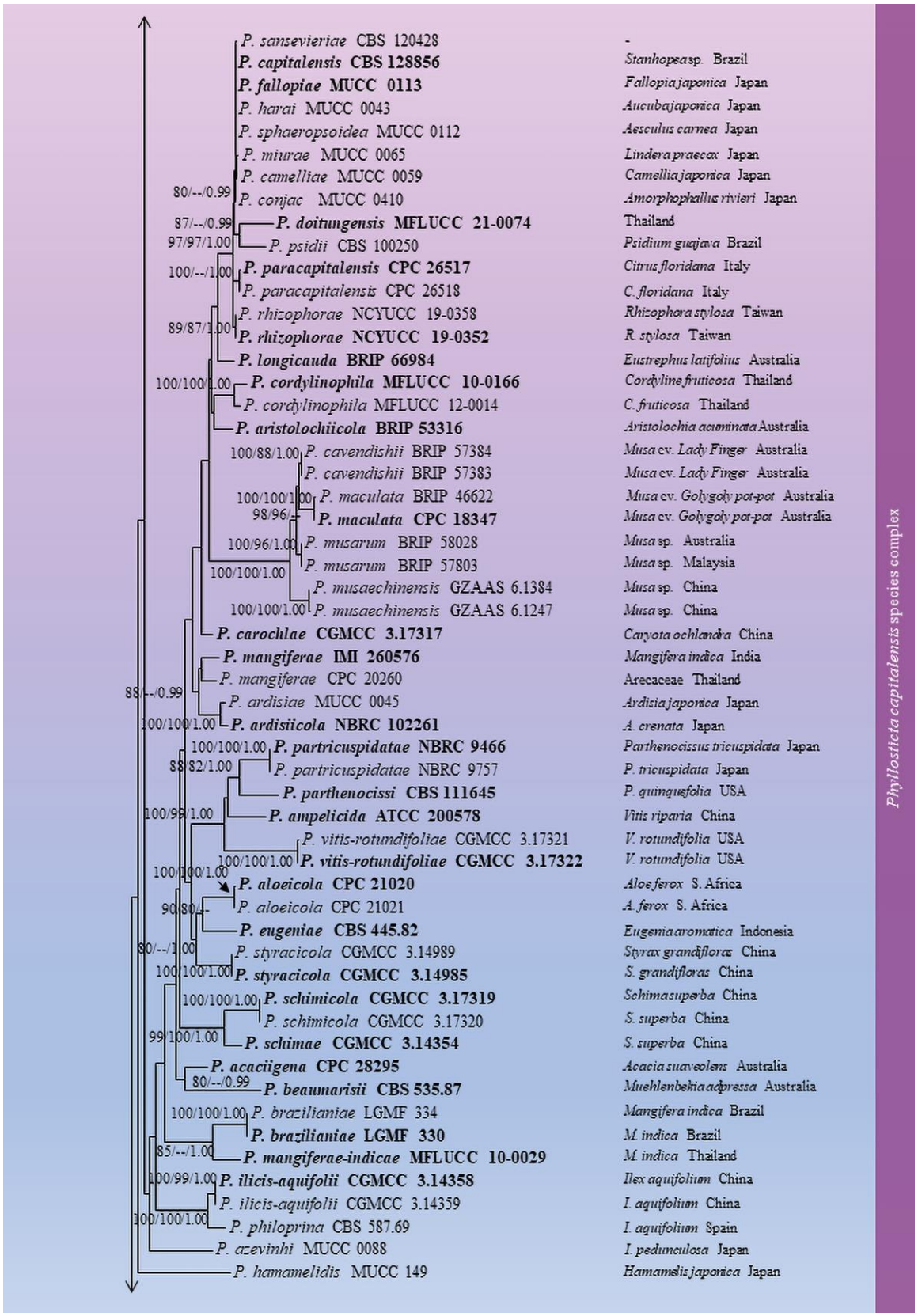

Figure 11 – Continued.

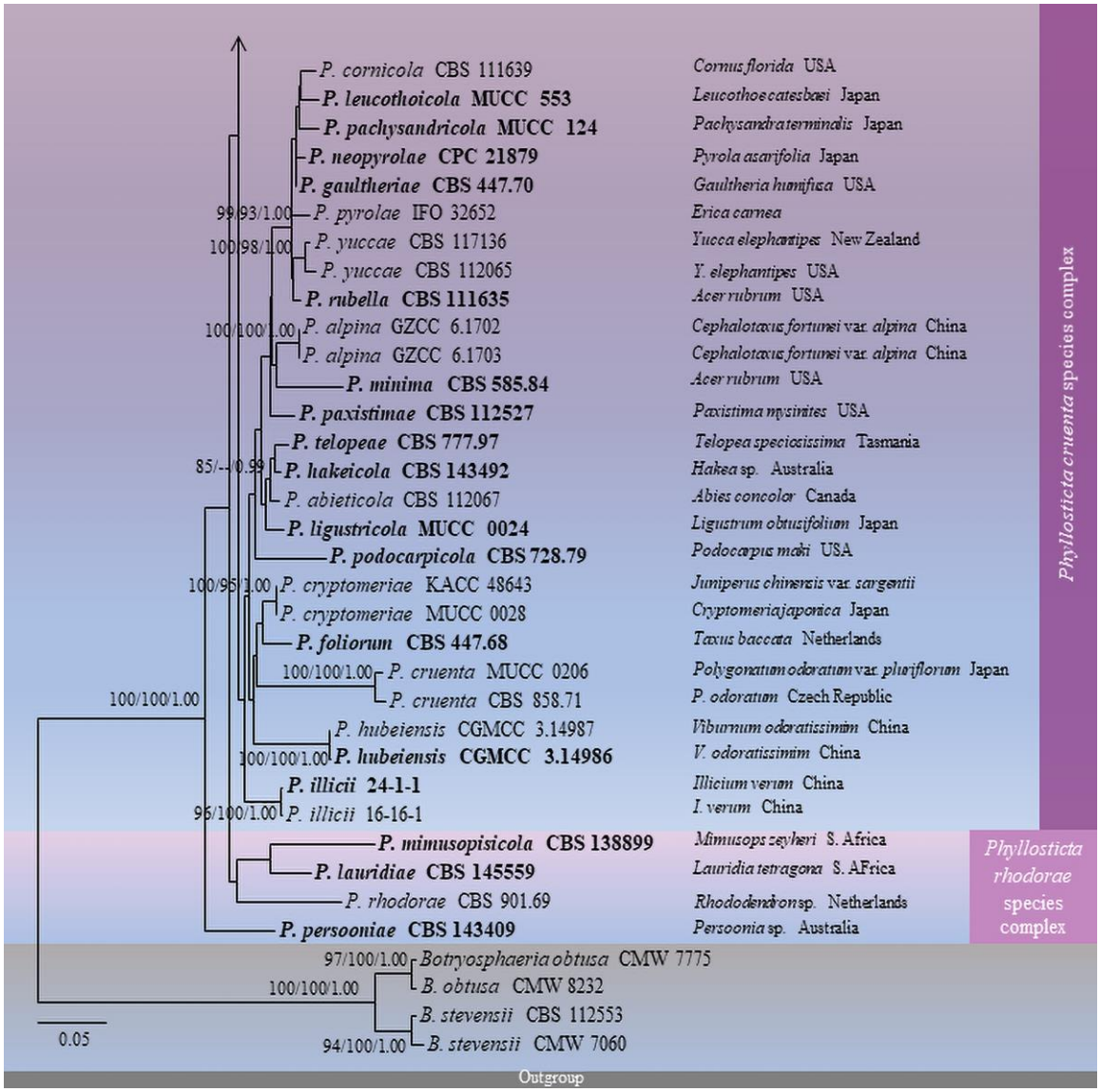

Figure 11 – Continued.

In North America, the first beech bark disease epidemic was reported in Halifax, Nova Scotia around 1920. Eighty-five percent of deaths were observed in the basal area of beech in Nova Scotia (Ehrlich 1934). Following the first outbreak, the disease had spread throughout Nova Scotia and southward to Maine over the next decade. Beech bark disease was later reported in Michigan (O'Brien et al. 2001) and Ohio in the United States (MacKenzie & Iskra 2005). Following screening against the phi-base, predicted genes associated with virulence and pathogenicity were high in *Neonectria ditissima* and *N. faginata*. The highest number of effectors were seen in *N. ditissima*, followed by *N. faginata* among other *Neonectria* species (Salgado-Salazar et al. 2021).

The combined ITS, LSU, *TEF-1α*, *ACT*, *RPB1* and *β-TUB* alignment of *Neonectria* comprised 4015 characters (ITS: 1–444, LSU: 445–1341, *TEF-1α*: 1342–2221, *ACT:* 2222–2811, *RPB1:* 2812–3425, *β-TUB:* 3426–4015), representing 30 strains of *Nectriaceae* (Fig. 13). There are 22 *Neonectria* species in Species Fungorum (2022). Based on multigene our phylogenetic analyses, we accept 15 species in *Neonectria* (Fig. 13).

Neonectria faginata was initially isolated from *Fagus* spp. (beech) (Lohman & Watson 1943, Houston 1994, Castlebury et al. 2006). Beech can normally attain a height of approximately 37 meters and may live up to 300 to 400 years (Tubbs & Houston 1990). Beech wood is used for furniture, flooring and containers (Tubbs & Houston 1990). Even though beech timber has low value, it is important to manage beech bark disease because it affects primary productivity,

biodiversity and structural sustainability, and disturbs forest ecosystems (Cale et al. 2013, 2014, 2017). However, management of beech bark disease is challenging because the scale insects and *Neonectria* spores are easily spread via wind (McCullough et al. 2001). Attempts to control the scale insect were made. However, the use of pesticides was not effective in decreasing the number of scale insects due to their ability to form a waxy protective layer (McCullough et al. 2001). Furthermore, the requirement of extensive labor and finance makes it impracticable to use pesticide or to remove infected trees over large forest areas (Wiggins et al. 2004). Therefore, further investigations are required.

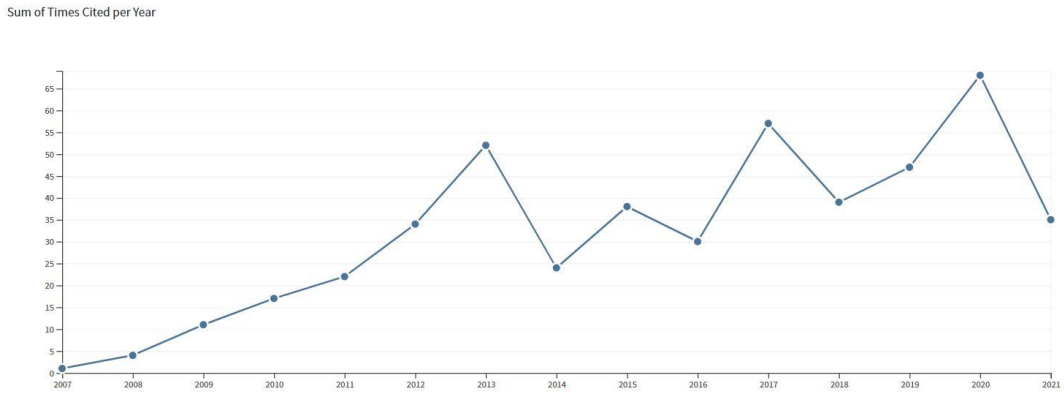

Figure 12 – Citation reports for *Neonectria faginata* from 2001 to 2021 (Total number of citations: 479).

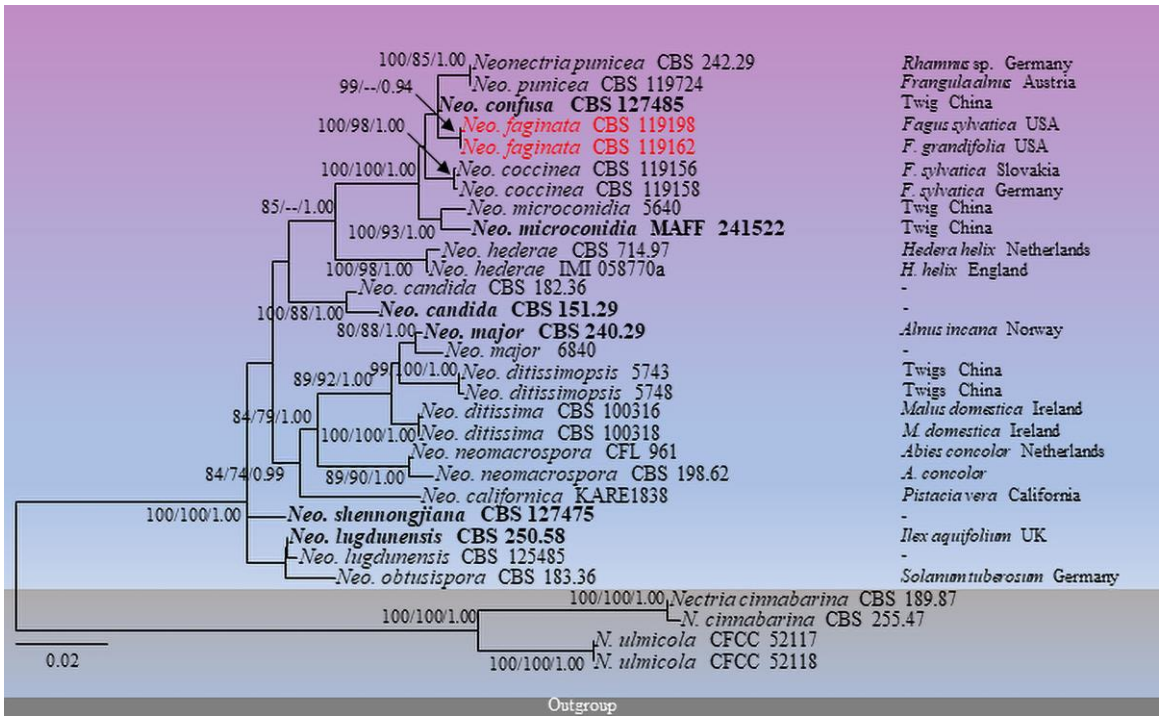

Figure 13 – Phylogram generated from maximum likelihood analysis (RAxML) based on the combined ITS, LSU, *TEF-1α*, *ACT*, *RPB1* and *β-TUB* matrices of *Neonectria*. Maximum likelihood (ML) and maximum parsimony (MP) with bootstrap support ≥80%, and the posterior probability (PP) values (≥0.8) of Bayesian inference (BI) analyses are given at respective nodes as ML/MP/PP. The tree is rooted with *Nectria cinnabarina* (CBS 189.87 and CBS 255.47) and *N. ulmicola* (CFCC 52117 and CFCC 52118) (*Nectriaceae*). Ex-type strains are indicated in bold and the emerging pathogen discussed herein is denoted in red. Hyphen (-) represents support values below 80% (ML

and MP) and below 0.80 (PP). The host and country from which each species was identified are shown in the phylogram.

Sphaerulina musiva (Peck) Quaedvl., Verkley & Crous, Stud. Mycol. 75: 345 (2013)

Sphaerulina musiva (≡ *Septoria musiva*; asexual morph = *Mycosphaerella populorum*) is a heterothallic ascomycete that exhibits both asexual and sexual morphs (Tabima et al. 2020). The latter causes Septoria leaf spot and stem canker of *Populus* spp. (poplars) (Bier 1939, Waterman 1954, Quaedvlieg et al. 2006, Feau et al. 2010, Dhillon et al. 2015). Natural *Populus deltoides* (eastern cottonwood) were exclusively affected by leaf spots in North America. However, interspecific hybrids such as *Populus deltoides* × *P. trichocarpa* and *P. deltoides* × *P. nigra* were affected by both, Septoria leaf spots and stem canker disease (Newcombe et al. 2001a, Feau et al. 2010). *Sphaerulina musiva* was initially identified among a hybrid poplar plantation in British Columbia, Canada in 2006 (Callan et al. 2007). The emergence of *S. musiva* in British Columbia perhaps occurred as a result of the cultivation of hybrid poplars, subsequently leading to an increased proliferation across nearby poplars (Herath et al. 2016).

Severe Septoria leaf spot causes premature defoliation of trees while canker disease results in weak stands of branches and stems that causes breakage, stunted growth and mortality (Bier 1939, Waterman 1954, Long et al. 1986, Spielman et al. 1986, Feau et al. 2010). Canker disease can cause tree death through a single infection, which alters the gross pulp and bioenergy plantation (Weiland et al. 2003). Therefore, it is regarded as the most devastating disease in hybrid poplars of North America (Bier 1939, Feau et al. 2010). *Sphaerulina musiva* is cited in the quarantine list of pathogens in Europe and is of primary concern because of its invasive nature (Niemczyk & Thomas 2020).

Sphaerulina musiva enters its host via wounds and through natural openings (Bier 1939, Waterman 1954, Long et al. 1986, Krupinsky 1989, Feau et al. 2010). Stems of highly susceptible hybrid poplars are prone to direct infection (Krupinsky 1989). Since *S. musiva* can occur in sexual and asexual morphs, both ascospores and conidia are accountable to infect its host. Generally, ascospores serve as the primary inoculum (Tabima et al. 2020). Hereby, we hypothesize that the easy penetration and the different morphs of *S. musiva* are responsible for its emerging trait. Owing to the different morphs of *S. musiva*, we speculate that it can spread and cause diseases throughout the year, instead of a specific period. Furthermore, it does not require any specialized structure such as appressoria to infect its host. Therefore, we hypothesize that it can easily multiply and colonize a large number of hosts.

Poplars are among the fast-growing temperate trees (Abraham 2017). In North America, endemic poplars and their interspecific hybrids are fast-growing and are widely distributed across the country. They have huge ecological and industrial significance and are ideally used for fiber and biomass due to the ease of replication and adaptation to various environmental conditions. Furthermore, poplars can be grown effortlessly on marginal lands (Tabima et al. 2020). Over the last century, Septoria leaf spot and stem canker disease have emanated in such a way that they threatened poplar populations in the north-eastern and north-central regions of North America (Feau et al. 2010, Dhillon et al. 2015). An estimated 44,128 hectares and 45,000 hectares of poplars were endangered by *S. musiva* in Canada and the USA, respectively (Derbowka et al. 2012, FAO 2012). Following the initial outbreak, *S. musiva* has also been reported from areas beyond its endemic range such as Argentina (Sarasola 1944), Asia (Maxwell et al. 1997) and Brazil (Santos et al. 2010).

The combined ITS, LSU, *RPB2*, *TEF-1α*, *ACT*, *CAL* and *β-TUB* alignment of *Sphaerulina* comprised 2994 characters (ITS: 1–493, LSU: 494–1315, *RPB2:* 1316–1661, *TEF-1α:* 1662–2037, *ACT*: 2038–2249, *CAL:* 2250–2685, *β-TUB:* 2686–2994), representing 42 strains of *Mycosphaerellaceae* (Fig. 15). There are 72 *Sphaerulina* species in Species Fungorum (2022). Based on our multigene phylogenetic analyses, we accept 29 species in *Sphaerulina*.

Sphaerulina (Fig. 15, Clade 1) mainly includes species infecting forest trees; *S. aceris* and *S. neoaceris* from *Acer* spp., *S. musiva*, *S. populicola*, *S. populi* from *Populus* spp., and

S. quercicola from *Quercus* spp. (Fig. 15). Apart from poplars, *S. musiva* has also been reported from *Salix lucida* (Feau & Bernier 2004). Therefore, it is of utmost importance to control the proliferation of *S. musiva.*

The most effective control strategy of *S. musiva* is to use disease-resistant hybrid poplars (LeBoldus et al. 2007, 2008, Qin & LeBoldus 2014, Dunnell et al. 2016, Niemczyk & Thomas 2020). Several management strategies have been adopted to mitigate the effect of Septoria leaf spots and canker diseases, including cultural and biological control (Ostry 1989, Feau et al. 2010). However, these methods are not feasible as they are either inefficient or expensive (Tabima et al. 2020).

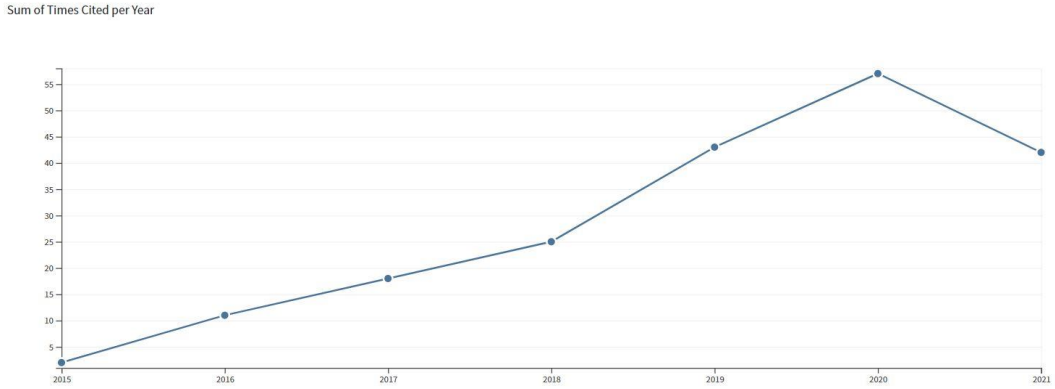

Figure 14 – Citation reports for *Sphaerulina musiva* from 2001 to 2021 (Total number of citations: 198).

Phytophthora pluvialis Reeser, W. Sutton & E.M. Hansen, N. Amer. Fung. 8(7): 2 (2013)

Phytophthora is an economically significant fungus-like genus (oomycetes) in *Peronosporaceae* (Thines & Choi 2016, Cavalier-Smith 2018, Ho 2018). *Phytophthora* species are prominent in the list of plant pathogens that epitomize international biosecurity challenges (Scott et al. 2019), causing damage to a diverse range of hosts (Bollmann et al. 2016, Jayawardena et al. 2020). Some *Phytophthora* species have co-evolved with their hosts, leaving the ecosystem undisturbed. Others have profound effects as invasive pathogens. *Phytophthora cinnamomi*, a soil-borne oomycete, is a notable example. It is among the most destructive and invasive of pathogens affecting a wide range of hosts worldwide, including cork and holm oaks (Hardham 2005, Camilo-Alves et al. 2013). Other significant species include *P. nicotianae* and *P. sojae* (Erwin & Ribeiro 1996). The impact caused by *Phytophthora* species has continued to increase, with the emergence of new pathogens and diseases (Yang et al. 2017).

Phytophthora pluvialis has recently emerged as a significant pathogen of *Pinus radiata* (Monterey pine), causing red needle cast disease in New Zealand (Dick et al. 2014). *Pinus radiata* originates from California (USA) and is largely grown in the southern hemisphere, especially in Australia, Chile, New Zealand and South Africa (Dick et al. 2014). Exotic plantation in New Zealand accounts for 1.7 million hectares, constituting 90% of *P. radiata* (NEFD 2016). Planted *P. radiata* has notable economic importance within the southern hemisphere (Watt et al. 2017). Forty-seven percent of *P. radiata* in the New Zealand forest industry is cultivated for timber (Li 2017). The wood of *P. radiata* is used to manufacture several products including boards, panel products, papers, pulp and veneers (Li 2017). However, wood quality decreases in the case of external resin bleeding, thus lowering the value of appearance-grade timber (Li 2017). Due to its high economic value, these plantations require great care to prevent pest and pathogen infestation. Globally, over 400 pests and pathogens have been reported from *Pinus radiata* (Flux et al. 1993).

The emergence of *Phytophthora pluvialis* causing foliar disease and red needle cast disease of *Pinus radiata*, and the subsequent identification of the same pathogen from Douglas-fir in New

Zealand highlights the dire need to study this pathogen (Dick et al. 2014, Hansen et al. 2015). Symptoms include olive discoloration of needles, usually bearing resin-like dark bands (Dick et al. 2014). Reeser et al. (2013) isolated *Phytophthora pluvialis* from streams, soil and canopy drip in mixed tanoak-Douglas-fir forest in Oregon. Pine needles are easily infected by *P. pluvialis* because the latter is aerial (Reeser et al. 2013). Furthermore, *P. pluvialis* is homothallic, implying that it can easily produce oogonia (Reeser et al. 2013). *Phytophthora pluvialis* also has caducous sporangia, which makes it easier to release zoospores that can reach needle surfaces by water splash (Reeser et al. 2013, Dick et al. 2014, Hansen et al. 2017). Following this event, zoospores enter the intercellular spaces. Sporangia develop from the stomata so that *P. pluvialis* can start its cycle over again (Gómez-Gallego et al. 2019).

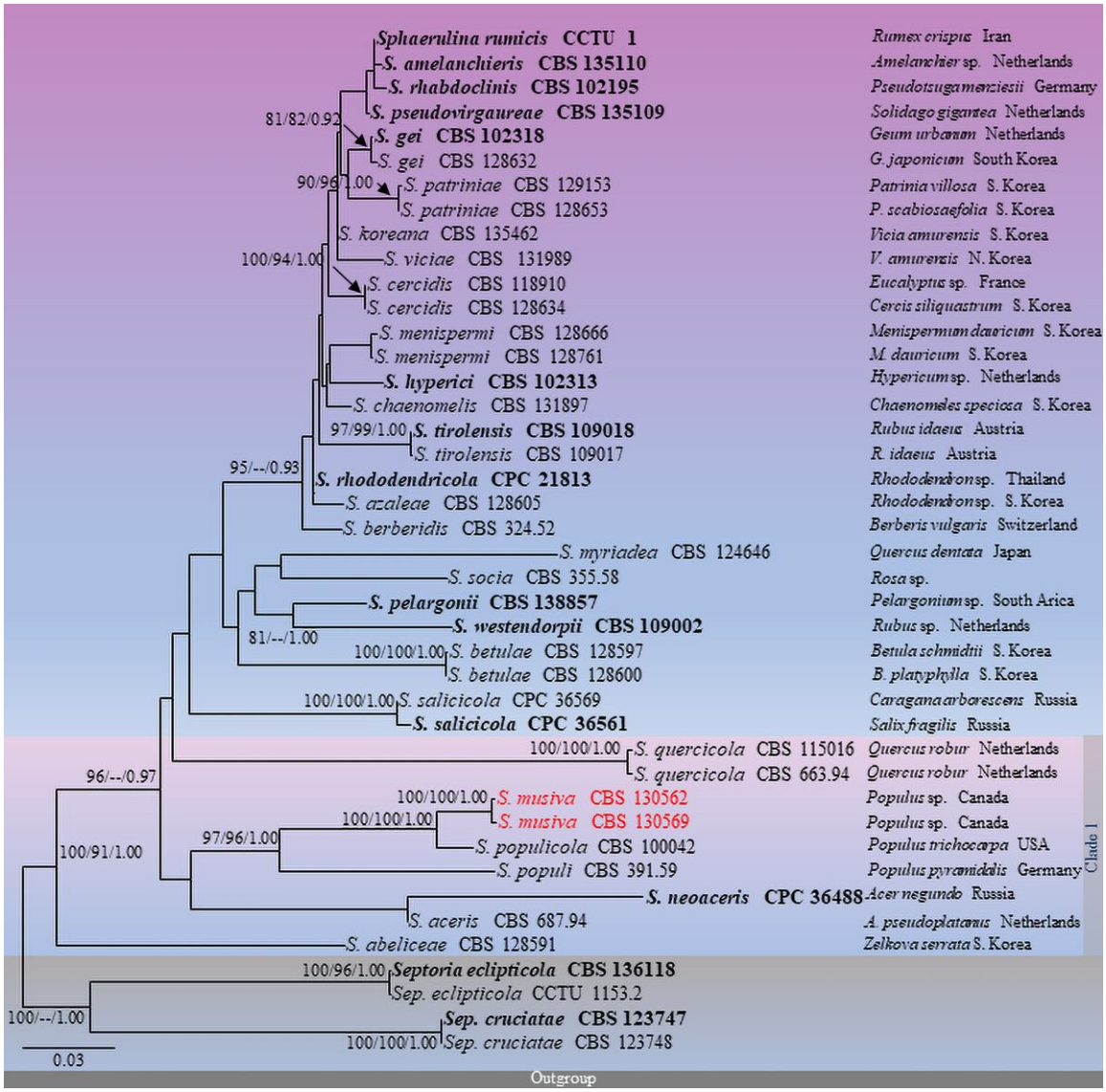

Figure 15 – Phylogram generated from maximum likelihood analysis (RAxML) based on the combined ITS, LSU, *RPB2*, *TEF-1α*, *ACT*, *CAL* and *β-TUB* matrices of *Sphaerulina*. Maximum likelihood (ML) and maximum parsimony (MP) with bootstrap support ≥80%, and the posterior probability (PP) values (≥0.8) of Bayesian inference (BI) analyses are given at respective nodes as ML/MP/PP. The tree is rooted with *Septoria cruciatae* (CBS 123747 and CBS 123748) and *Sep. eclipticola* (CBS 136118 and CCTU 1153.2) (*Mycosphaerellaceae*). Ex-type strains are indicated in bold and the emerging pathogen discussed herein is denoted in red. Hyphen (-) represents support values below 80% (ML and MP) and below 0.80 (PP). The host and country from which each species was identified are shown in the phylogram.

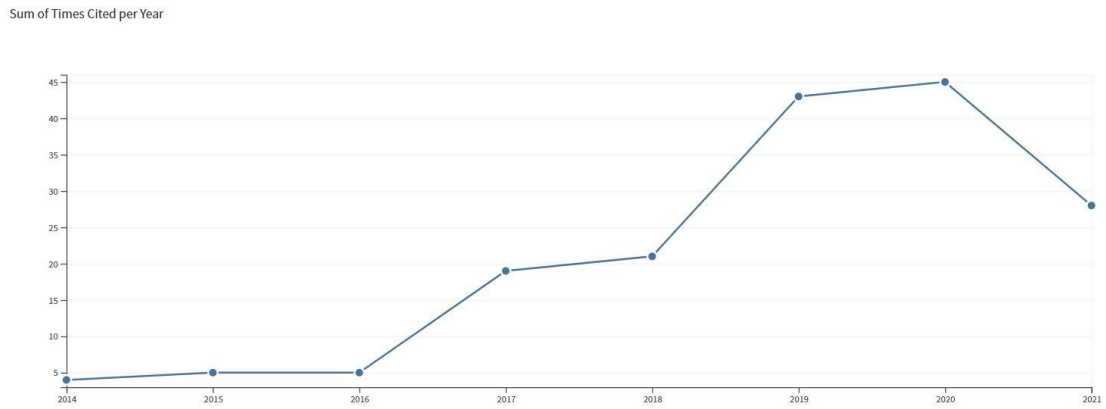

Figure 16 – Citation reports for *Phytophthora pluvialis* from 2001 to 2021 (Total number of citations: 170).

Little is known about red needle cast disease. Therefore, it is challenging to analyze its potential impacts on forest ecosystems and develop control measures (Ganley et al. 2014). To protect *P. radiata* forestry productivity, active management strategies are required. A decline in disease severity was observed after applying stem injections and aerial phosphite in *P. radiata* (Rolando et al. 2014). Understanding the epidemiology of infectious diseases and the combined use of chemical and biological control can be effective in minimizing disease occurrence and severity in New Zealand forests (Ganley et al. 2014).

Phytophthora agathidicida B.S. Weir, Beever, Pennycook & Bellgard, in Weir, Paderes, Anand, Uchida, Pennycook, Bellgard & Beever, Phytotaxa 205(1): 29 (2015)

The native host *Agathis australis* (kauri), in New Zealand, has been under threat from the newly emerged soil-borne dieback pathogen *Phytophthora agathidicida* (Scott & Williams 2014, Weir et al. 2015). The pathogen has emerged in such a way that it can kill different stages of kauri, including seedlings and large mature trees (Beever et al. 2009). Kauri is endemic to New Zealand and forms part of the coniferous *Araucariaceae* (Wilf et al. 2014). The carbon-rich kauri, storing up to 670 Mg of carbon per hectare in wood biomass (Keith et al. 2009), is one of the largest and longest-lived tree species in New Zealand (Ahmed & Ogden 2011). The trunk height can reach 30–50 m with an average lifespan of 600 years, sometimes exceeding 1500 years (Steward & Beveridge 2010, Ahmed & Ogden 2011). Kauri has ecological and immense cultural significance (Black et al. 2018). Kauri is also capable of growing on low nutrients in infertile soil (Wyse et al. 2014, Padamsee et al. 2016, Byers et al. 2020).

Following colonization by European settlers, kauri was extensively logged. Therefore, its distribution was altered in New Zealand. Additionally, huge populations of kauri were cleared for pastoral farming and this led to the depletion of kauri forests (Steward & Beveridge 2010). An estimated 1% of the original remnant kauri remains (Steward & Beveridge 2010). Unfortunately, the 60,000 ha of kauri forest regenerated is now under threat of extinction from dieback disease caused by *P. agathidicida* (Halkett 1983, Beever et al. 2009, Weir et al. 2015). Thus, it is important to study this lethal pathogen and develop control strategies.

Kauri dieback is not a newly described disease as it was initially reported by Gadgil (1974) on Great Barrier Island. However, based on morphology, the pathogen responsible was misidentified as *Phytophthora heveae* at that time (Gadgil 1974). Consequently, kauri morbidity and mortality were observed in the Waitākere Ranges in 2006, which prompted surveys that identified the same pathogen from unhealthy kauri (Waipara et al. 2013). Kauri dieback was confirmed in other forests in Auckland and Northland from 2005 to 2010 (Beever et al. 2009, Waipara et al. 2013). In 2008, the pathogen was identified as *Phytophthora* taxon *Agathis* (Beever et al. 2009) and was classified as an unwanted organism under the Biosecurity Act (Waipara et al.

2010). In 2015, the pathogen was formally described as *Phytophthora agathidicida* (Weir et al. 2015).

Phytophthora agathidicida is a hemibiotrophic pathogen that is dependent on the root tissues of the host for completion of its life cycle (Bellgard et al. 2019). After the death of kauri, *P. agathidicida* continues to reside in the root tissues (Bellgard et al. 2019). *Phytophthora agathidicida* is a notable example of an invasive pathogen (Waipara et al. 2013). It causes root rot that gives rise to canker bleeding of the lower trunk, foliage yellowing, and uncontrolled resin (gummosis) at the collar and lower trunk (Seyfullah et al. 2018). The pathogen also causes tree death eventually resulting in a decrease in tree density (Winkworth et al. 2020). These symptoms are solely notable during the chronic phase of the disease. The time-lapse between disease symptom manifestation and tree death usually takes one to ten years. It is suggested that even trees >1000 years old are not immune (Bradshaw et al. 2020).

Little is known about kauri dieback because the latter has recently emerged (Guo et al. 2020). Schwendenmann & Michalzik (2019) suggested that interactions between multiple *Phytophthora* species may increase the susceptibility of kauri to *P. agathidicida*. At present, there is no known cure for kauri dieback (Bradshaw et al. 2020). However, several disease management strategies have been proposed, focusing on attempts to control the spread of *P. agathidicida* (Bradshaw et al. 2020). One strategy involves biological control, which refers to the "purposeful use of introduced or resident micro-organisms" (Bellgard et al. 2019). Arbuscular mycorrhizal fungi can be used as biocontrol agents as they have antagonistic effects on soil-borne pathogens (Bellgard & Williams 2011). Furthermore, chemical control using phosphite to manage kauri dieback was effective by suppressing the activity of *P. agathidicida* in glasshouse seedlings and trees, ranging from 30–50 years in the field (Horner & Hough 2013).

Phytophthora agathidicida can easily be dispersed through infected root materials contained in soil adhered to footwear, tools, machinery and logs (Bellgard et al. 2013). Improved management measures are required for kauri dieback. Further surveillance may ameliorate understanding of the biology of *P. agathidicida*, such as latency period. Advanced research can reveal whether *P. agathidicida* affects hosts other than kauri (Bradshaw et al. 2020). Since the infection occurs at the root-pathogen interface, control strategies towards kauri dieback need to be targeted in the rhizosphere (Bellgard et al. 2019). Currently, there are few options for controlling or treating *P. agathidicida*. The main method for reducing pathogen spread is physical barriers such as walking track closures and shoe cleaning stations. In 2020, three new *Phytophthora* species were introduced, namely *P. acaciivora*, *P. aysenensis* and *P. personensis* (Burgess et al. 2020, Crous et al. 2020). Since many *Phytophthora* species are destructive pathogens (Scott et al. 2019), the emergence, severity and dispersal of these novel species are unpredictable. We hypothesize that the newly introduced species might emerge with co-existed pathogens and affect new hosts.

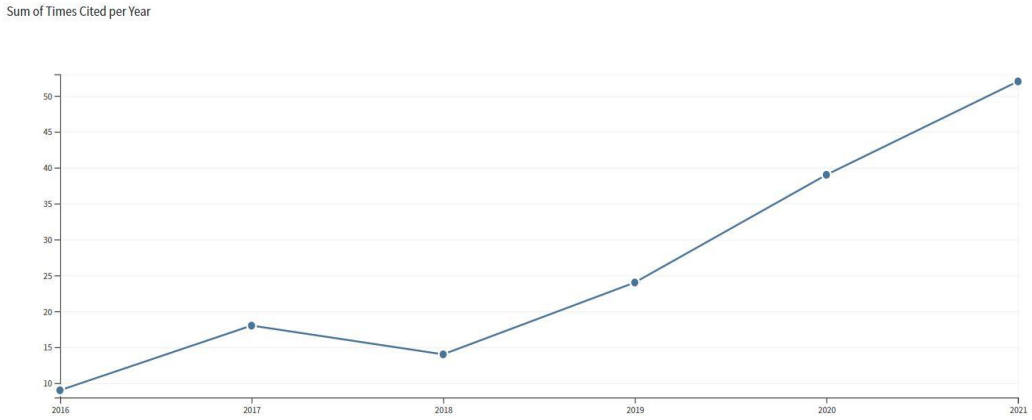

Figure 17 – Citation reports for *Phytophthora agathidicida* from 2001 to 2021 (Total number of citations: 156).

The combined LSU, *60S*, *β-TUB*, *TEF-1α*, *Enl*, *HSP90* and *TigA* alignment of *Phytophthora* comprised 8412 characters (LSU: 1–1241, *60S*: 1242–1703, *β-TUB:* 1704–2841, *TEF-1α:* 2842–3856, *Enl*: 3857–5025, *HSP90:* 5026–6772, *TigA:* 6773–8412), representing 217 strains of *Peronosporaceae* (Fig.18). In the case of *Phytophthora*, only Maximum likelihood and Maximum parsimony analyses were performed. There are 186 *Phytophthora* species in Species Fungorum (2022). Based on our multigene phylogenetic analyses, we accept 180 species in *Phytophthora*.

Melampsora* × *columbiana G. Newc., in Newcombe, Stirling, McDonald & Bradshaw, Mycol. Res. 104(3): 271 (2000)

Melampsora × *columbiana* is a natural hybrid of *M. medusae* and *M. occidentalis* (Newcombe et al. 2000). Hybridization is considered as a major reason for the emergence of fungal diseases, especially if the hybrid taxon has the ability to infect a wide range of hosts (Brasier 2000a, 2001b, Schardl & Craven 2003, Inderbitzin et al. 2011). Natural hybridization is the mating between individuals of two distinct populations in nature (Arnold 1997). The offspring generated via genetic crosses of two non-conspecific individuals may be defined as a hybrid (Mallet 2007, Stukenbrock 2016). Hybrids may be formed through both, sexual mating and asexual fusion of the vegetative hyphae (Schardl & Craven 2003, Kohn 2005, Stukenbrock 2016). Intermediate clades with incongruence in phylogenetic topologies may be recognized as hybrid species in a phylogenetic tree (Schardl & Craven 2003).

Melampsora species cause foliar rust disease (Newcombe et al. 2000). Severe infection by these taxa may result in early leaf drop, reduced photosynthetic ability, reduced growth and decreased biomass (Steenackers et al. 1996). *Melampsora* species affect trees worldwide, including *Populus* spp. (poplars) (Steenackers et al. 1996). Some examples of *Melampsora* leaf rust are caused by *M. medusae*, *M. occidentalis*, *M. allii-populina* and *M. laricis-populina* (Newcombe et al. 2000, Albornoz et al. 2018). Leaf rust disease has spread throughout Asia, Europe, North America, Oceania and South America (Albornoz et al. 2018).

The telial hosts of *Melampsora* are *Populus* sections *Aigeiros* and *Tacamahaca*. *Populus* section *Aigeiros* has two native species in North America, *Populus deltoides* and *P. fremontii*. *Populus* section *Tacamahaca* has three native species, namely *P. angustifolia*, *P. balsamifera* and *P. trichocarpa* (Eckenwalder 1984). Newcombe et al. (2000) determined that natural hybridization occurs between *Melampsora medusae* and *M. occidentalis* in hybrid poplars, thus giving rise to the hybrid *Melampsora* × *columbiana*. This poplar rust hybrid has had huge impacts on poplars in the USA (Dickmann 2001). It has the ability to generate novel virulent traits on *Populus trichocarpa* × *P. deltoides* hybrid poplar (Newcombe et al. 2001b). In North America, *Melampsora* ×*columbiana* has exhibited diverse pathogenic traits (La Mantia et al. 2013).

Melampsora × *columbiana* probably occurred due to the introduction of *M. medusae* in the Pacific Northwest in 1991 (Newcombe 1996, 1998). Prior to the establishment of *M. medusae*, *Populus trichocarpa* × *P. deltoides* was not infected by leaf rust disease even in the presence of *M. occidentalis* due to its non-pathogenic nature on *Populus trichocarpa* × *P. deltoides* (Hsiang & Van Der Kamp 1985). *Melampsora medusae* has been identified beyond its native range of *Populus deltoides* (Thümen 1878), from Australia (Galović et al. 2010), China (Zheng et al. 2019), India (Vialle et al. 2011), Japan (Hiratsuka 1939), Portugal (Pinon 1986, 1991), Russia (Farr & Rossman 2022) and South Africa (Galović et al. 2010). Since *M. medusa* undergoes natural hybridization with other species (Spiers & Hopcroft 1994, Newcombe et al. 2000), it is important to develop management strategies for poplar rust disease to prevent the formation of *Melampsora* hybrids which have the potential to develop novel pathogenic traits.

The combined ITS and LSU alignment of *Melampsora* comprised 1077 characters (ITS: 1–527, LSU: 528–1077), representing 70 strains of *Melampsoraceae* (Fig. 20). There are 114 *Melampsora* species in Species Fungorum (2022). Based on our multigene phylogenetic analyses, we accept 42 species in *Melampsora*.

Melampsora was established by Castagne, with *M. euphorbiae* as the type species (Cummins & Hiratsuka 2003). *Melampsora* species are obligate biotrophic pathogens infecting a wide range

of plants (Vialle et al. 2011, Zheng et al. 2019), including *Populus* spp. (poplars) and *Salix* spp. (willows) (Fig. 20). Of the 74 strains and 42 *Melampsora* species, 50 strains and 28 species were isolated from willows (Fig. 20). Willows are great sources of renewable energy and bioproducts (Kuzovkina & Quigley 2005, González-García et al. 2012). Furthermore, they are widely used for ornamentation and production of fibers (Verwijst et al. 2008). Willow rust disease caused by *Melampsora* species is emerging, thus limiting willow cultivation (Zhao et al. 2015).

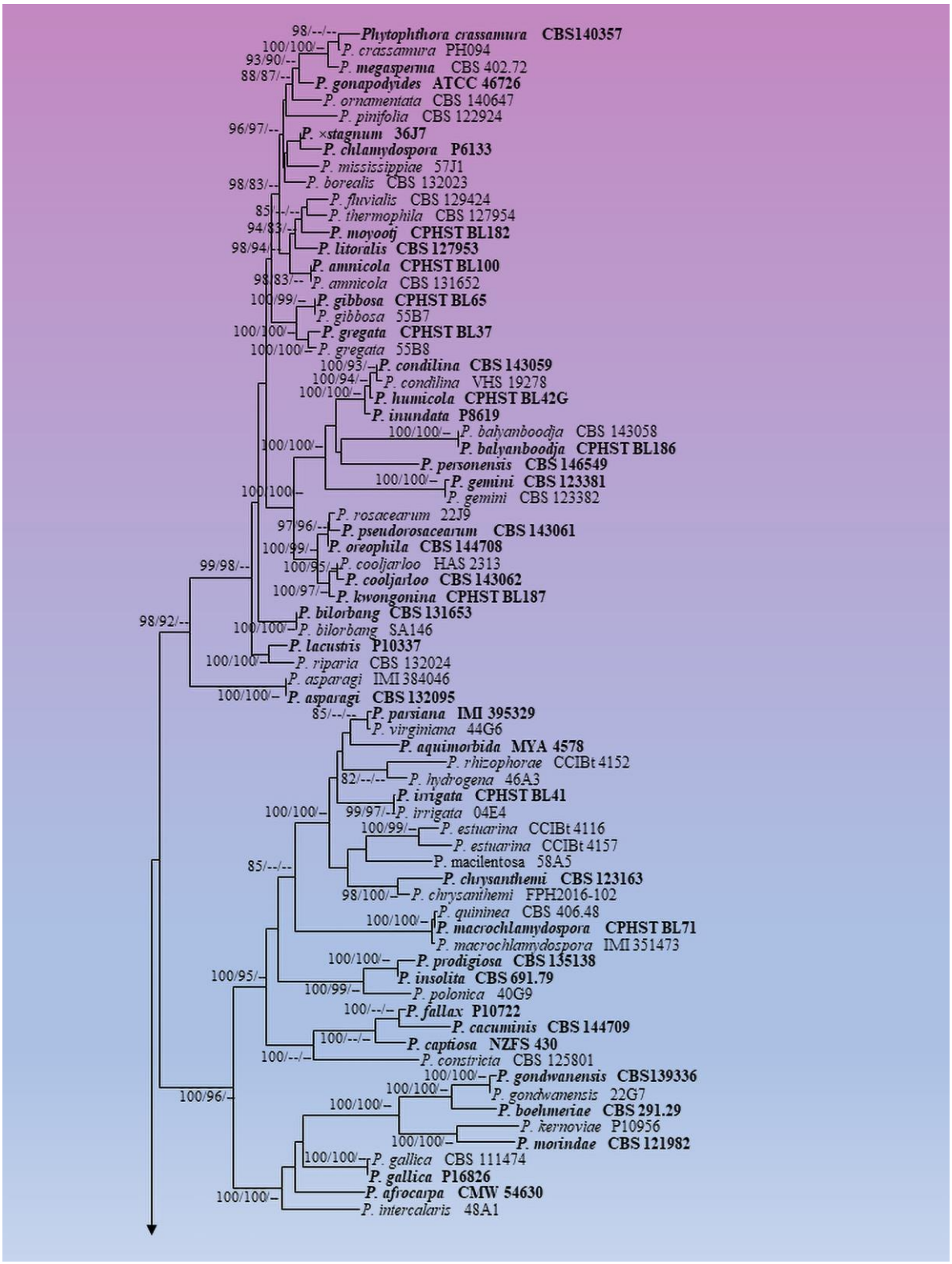

Figure 18 – Phylogram generated from maximum likelihood analysis (RAxML) based on the combined LSU, *60S*, *β-TUB*, *TEF-1α*, *Enl*, *HSP90* and *TigA* matrices of *Phytophthora*. Maximum

likelihood (ML) and maximum parsimony (MP) with bootstrap support ≥80% are given at respective nodes as ML/MP. The tree is rooted with *Pythium longipapillum* (NRh8 and NS05) and *Py. oryzicollum* (Ts3 and Kr7) (*Pythiaceae*). Ex-type strains are indicated in bold and the emerging pathogen discussed herein is denoted in red. Hyphen (-) represents support values below 80% (ML and MP).

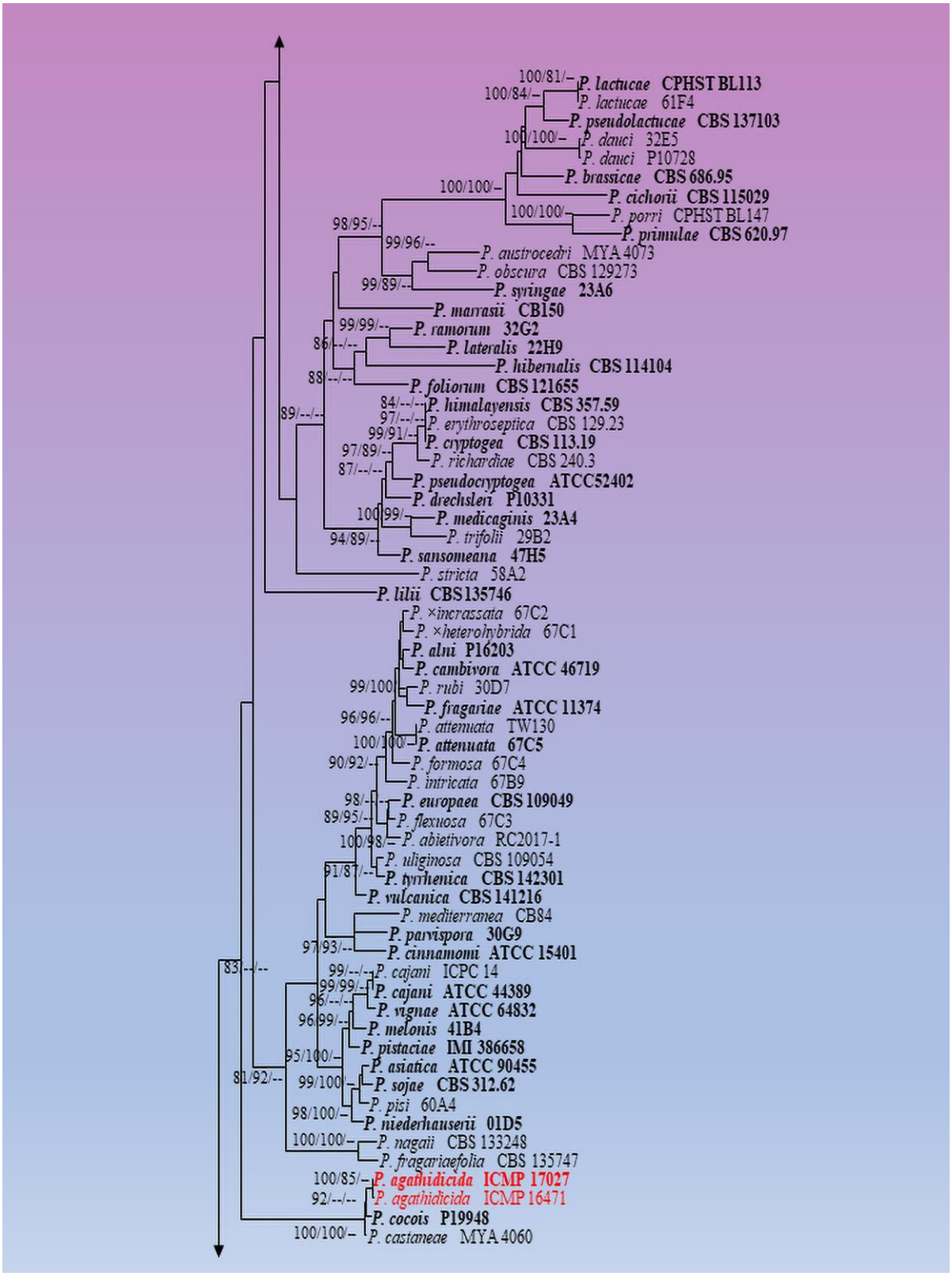

Figure 18 – Continued.

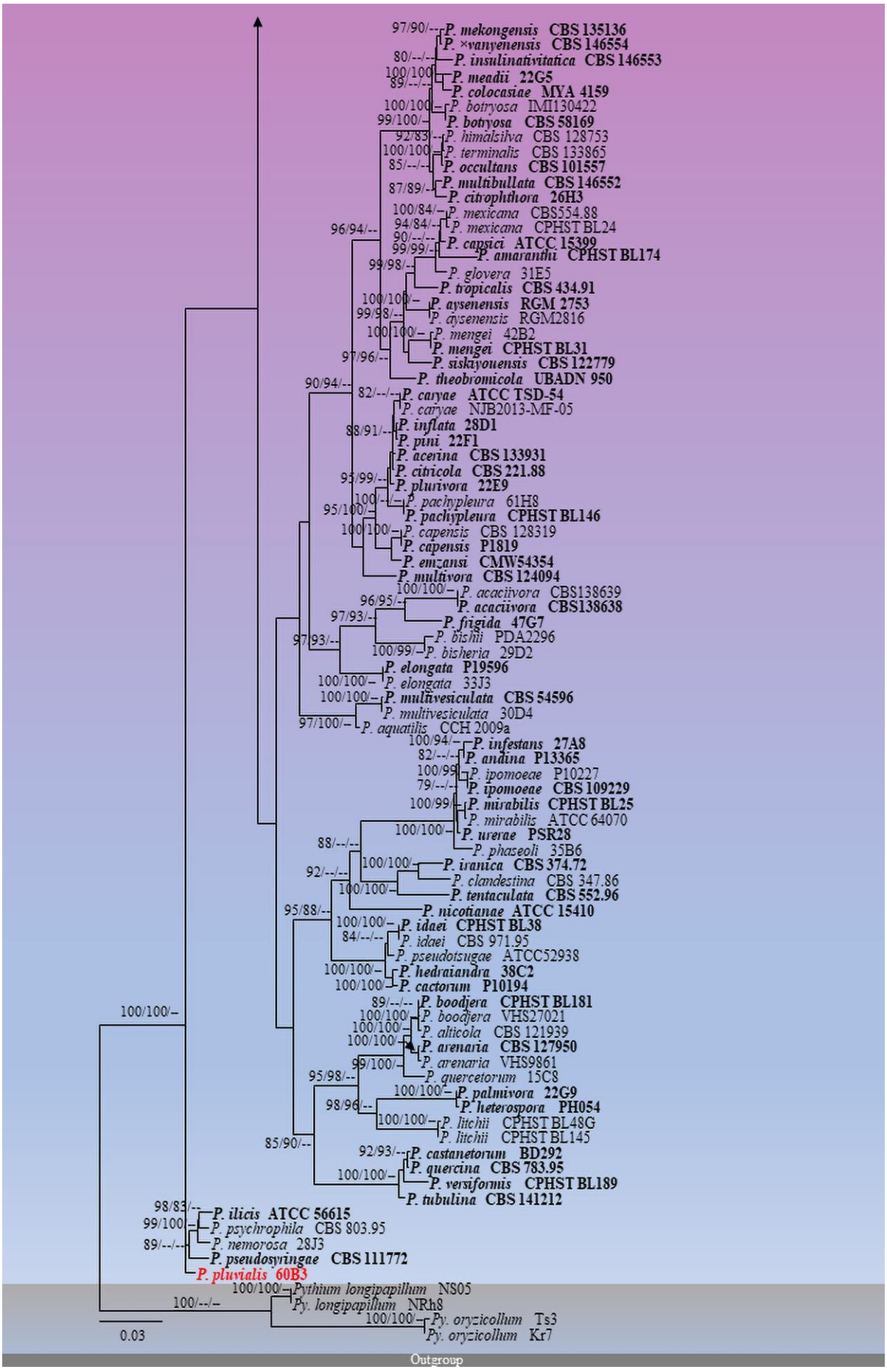

Figure 18 – Continued.

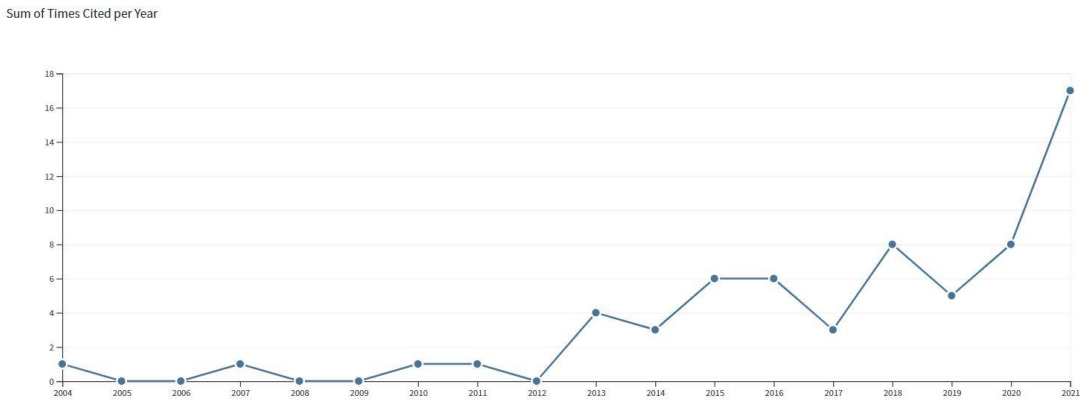

Figure 19 – Citation reports for *Melampsora* × *columbiana* from 2001 to 2021 (Total number of citations: 64).

Melampsora × *columbiana* is an emerging pathogen that has been isolated from *Populus angustifolia* (Newcombe et al. 2000). Other *Melampsora* species obtained from poplars include *M. abietis-populi*, *M. laricis-populina*, *M. magnusiana*, *M. medusae*, *M. microspora*, *M. occidentalis*, *M. populnea* and *M. pruinosae*. They have mainly been collected in China, Iraq and North America (Fig. 20). Rust disease on poplars is considered as one of the most important diseases in China (Tian et al. 2004) and are important worldwide (Frey et al. 2005). Therefore, to control diseases it is important to study the biology of disease formation of these taxa.

Discussion

Forest pathogens have continued to emerge, thus affecting plant health (Jones et al. 2008, Avila-Quezada et al. 2018). There are several explanations for disease emergence. Firstly, the transfer of genetic information among species via hybridization and horizontal gene transfer can cause disease (Calo et al. 2013). A mutation in genes that confer virulence may also result in the emergence of pathogenic strains (Ahmed et al. 2012, Stukenbrock 2013, Fones et al. 2017). Furthermore, some fungal pathogens have "two-speed" genomes, implying that genes responsible for pathogenicity and virulence may occupy genomic regions that emerge at a higher rate as compared to other fundamental gene regions (Dong et al. 2015, Rafiqi et al. 2018).

Other possible causes for pathogens to emerge include the introduction of pathogenic taxa into new geographical areas, or introduction of hosts in areas where the pathogens are already present (Manning & Tiedemann 1995, Bebber et al. 2013, Fones et al. 2017). Several biotic and abiotic factors may also contribute to the occurrence of new disease (Bebber et al. 2013, Fones et al. 2017). Fungi also emerge as a result of lifestyle switching, particularly from mutualistic to a parasitic lifestyle (Promputtha et al. 2007, Rai & Agarkar 2016). A plausible explanation for lifestyle switching is a mutation in the NADPH oxidase gene NoxA produced from reactive oxygen species (ROS) (Tanaka et al. 2006). Other factors include host age and changes in climatic conditions (Saikkonen et al. 1998, Rai & Agarkar 2016, Bhunjun et al. 2021). Another cause for the emergence of pathogens may be host-jumping, whereby pathogens colonize new host groups, resulting in increased genetic separation from the parent population (Thines 2019). Host jumps are induced by several factors.

Fungal phytopathogens yield significant economic losses in both tropical and temperate forest ecosystems. A huge number of fungi have been reported in tropical rainforests, suggesting that fungal diversity is higher in these regions as compared to temperate forests (Arnold & Lutzoni 2007, Tedersoo et al. 2014). A decline in fungal species richness was observed when moving towards the poles (Tedersoo et al. 2014). The probability of finding a huge number of fungi in the tropics is higher than in temperate regions because three quarters of known plant genera are confined to the tropics (Lücking et al. 2017). Even though tropical forests have high fungal species

richness, they are poorly studied. Thus, continuous research is needed whereby all fungal groups in each ecological habitat are surveyed in depth, which is a strenuous procedure requiring the contribution of several experts and mycologists.

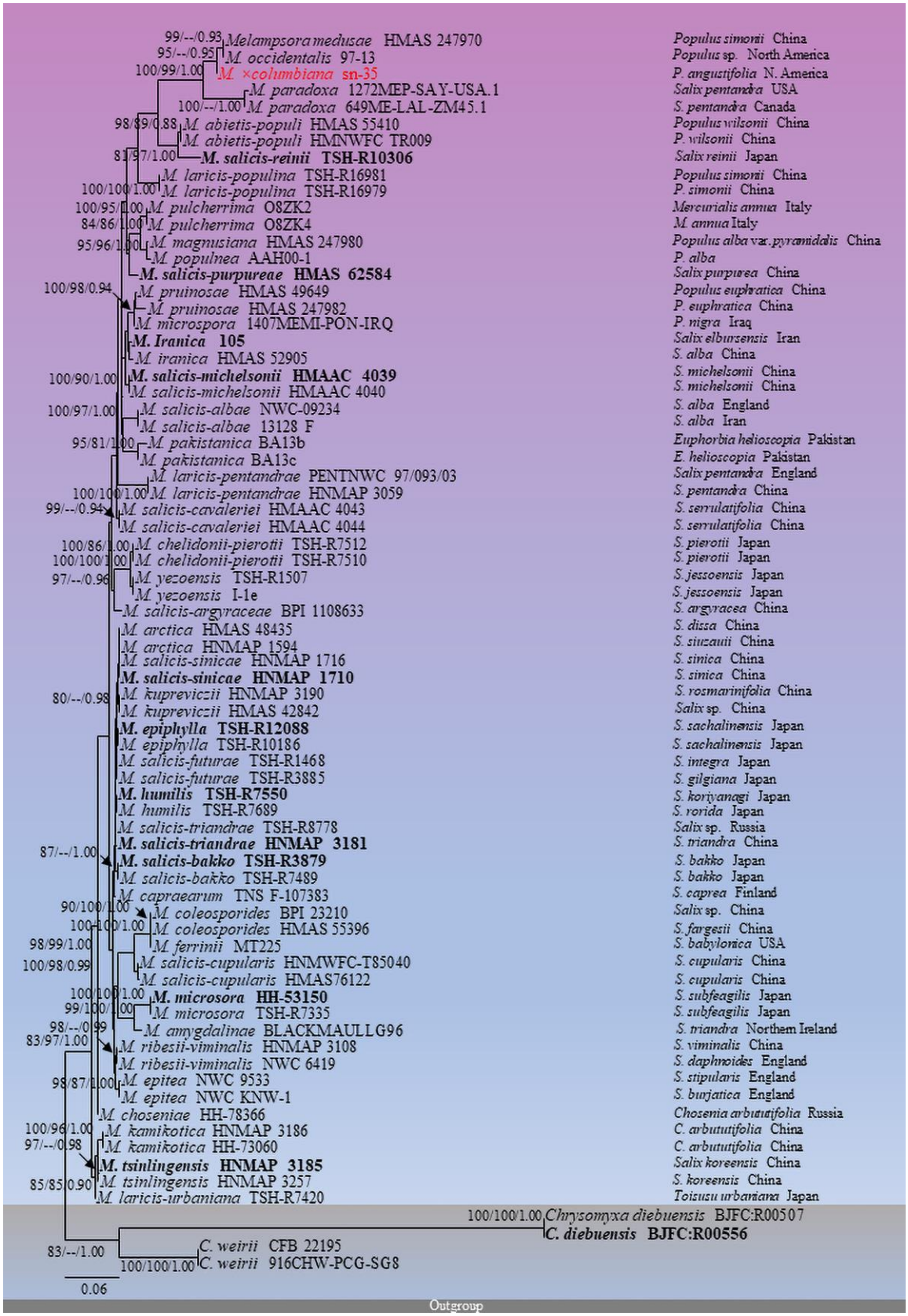

Figure 20 – Phylogram generated from maximum likelihood analysis (RAxML) based on the combined ITS and LSU matrices of *Melampsora*. Maximum likelihood (ML) and maximum

parsimony (MP) with bootstrap support ≥80%, and the posterior probability (PP) values (≥0.8) of Bayesian inference (BI) analyses are given at respective nodes as ML/MP/PP. The tree is rooted with *Chrysomyxa diebuensis* (BJFC: R00556 and BJFC: R00507) and *C. weirii* (CFB 22195 and 916CHW-PCG-SG8) (*Coleosporiaceae*). Ex-type strains are indicated in bold and the emerging pathogen discussed herein is denoted in red. Hyphen (-) represents support values below 80% (ML and MP) and below 0.80 (PP). The host and country from which each species was identified are shown in the phylogram.

In this paper, ten important emerging and re-emerging forest pathogenic species have been reviewed. Each entry provides examples of different scenarios whereby a pathogen can emerge. Firstly, the invasive nature of certain pathogens can cause the emergence of new virulent strains, which can be more aggressive than other closely related taxa. This was the case for the pathogenic *Hymenoscyphus fraxineus*, which replaced the harmless saprobic *H. albidus* (McKinney et al. 2012). The emergence of *Fusarium circinatum* was also attributed to its invasive nature. In view of the lifestyles of *F. circinatum*, we hypothesize that when conditions are favorable, its pathogenic lifestyle may predominate as compared to its endophytic lifestyle. Therefore, it may affect hosts in other geographical areas. In the case of *Ophiostoma novo-ulmi*, it mutated into a more aggressive species that caused the death of a huge number of elm trees in contrast to its closely related *O. ulmi*.

Ceratocystis fimbriata, responsible for rapid `Ōhi`a death, targets and kills `Ōhi`a trees of all ages. In the current epidemic, *C. fimbriata* has emerged in such a way that there was a rapid increase in the number of host deaths in a short period of time. Other fungi may emerge as a result of close association with insects, as in the case of *Neonectria faginata*. Another scenario for the emergence of a pathogen is through natural hybridization, as suggested for *Melampsora* × *columbiana*.

To predict the emergence of phytopathogenic fungi and fungus-like taxa, a proper understanding of the biology and mechanisms of pathogenesis is important. However, along with these data, morphological illustration and phylogenetic analyses are fundamental. In addition, quantifying the number of existing pathogenic fungi is significant in determining their emergence, owing to the fact that some fungal species have different lifestyles. Prior to the advent of molecular tools, fungal species were introduced primarily based on morphological examination. Nevertheless, with the advent of molecular tools, it might be possible that the same species has been introduced and described more than once. Thus, these details should be taken into account when determining the number of described species, including pathogenic strains.

The estimated number of fungal species has increased from 2.2–3.8 to 11.7–13.2 million (Hawksworth & Lücking 2017, Wu et al. 2019), but with only around 150,000 described species (Hyde et al. 2020, Bhunjun et al. 2022, Phukhamsakda et al. 2022). However, the number of pathogenic fungi, their diversity and re-occurrence is still unknown. Thus, there is a dire need to estimate the number of pathogenic fungi that have hitherto been described for the several reasons aforementioned. Eventually, an estimated number of pathogenic species will not solely help plant pathologists to study the biology of pathogenesis but also help farmers with biocontrol and management strategies.

Quantifying the number of pathogenic fungi is strenuous because they are constantly emerging. Their emergence generates novel virulent traits which can annihilate an entire tree population and destroy forest ecosystems, as in the case of *Ceratocystis fimbriata*. Quarantine lists of pathogens could be used to estimate the number of pathogenic fungi. Quarantine regulations have been executed based on existing plant pathogens that have affected specific hosts globally (McTaggart et al. 2016). Nonetheless, quarantine lists are rarely updated and therefore, not reliable. Besides, each country has its list, and while some countries recorded the sexual morph name of a species, others have listed the asexual morphs (Wingfield et al. 2011, Jayawardena et al. 2021b, Manawasinghe et al. 2021). This leads to confusion where the same species might be considered different. Another hindrance in identifying and quantifying the number of pathogenic strains is the restriction to conduct pathogenicity tests in vivo, especially in natural forests. Also, farmers might

not allow plant pathologists to carry out these tests in plantation areas. Some fungi are host-specific. Therefore, in order to carry out pathogenicity tests on certain hosts, we need to grow them, which is an arduous and time-consuming process. Thus, it is difficult to confirm whether certain described pathogens are actually pathogenic on their respective hosts.

Also, the number of pathogenic fungi reported from forest trees and crops is not classified per se. Remarkably, very few studies have been carried out on fungal pathogens affecting forest trees as compared to crops and to a lesser extent on ornamentals. As it happens, the very few studies carried out on forest trees stipulate huge economic consequences as a result of invasive pathogens (Pimentel 2011, Lovett et al. 2016). From Table 2, we can decipher that more research is required in view of forest diseases. Furthermore, pathogens have a tendency to cause diseases on specific hosts due to the limited host range (Van Der Does & Rep 2007). However, from the phylogenetic trees provided herein, it is evident that each species is not host-specific.

From Figs 3, 5, 7, 8, 10, 12, 14, and 16, it is observed that the total number of citations have decreased between the years 2020 to 2021. A probable explanation for this decline might be attributed to the Covid-19 crisis period, during which research was hindered. Therefore, we speculate that there might be other emerging fungal strains, probably more virulent in nature. Continuous long-term studies are required to monitor existing fungal diseases to properly control and manage them, thus preserving natural ecosystems. Given their ruinous effect, it is critically essential for the genera discussed herein to have a stable taxonomy that allows plant pathologists to study and identify these fungi. This will help to develop effective management strategies against the diseases.

Conclusions and future prospects

Emerging pathogenic fungi and fungus-like taxa pose a significant risk to forest ecosystems. They are capable of causing complete host eradication. The reasons these pathogens emerge are unpredictable. Therefore, a complete understanding of the mechanisms of host invasion and disease formation is fundamental for disease control. This will help to better understand their biology and lifestyles. As such, we can predict pathogenicity and virulence of certain pathogenic fungi and fungus-like taxa and thus design control measures. What are the different life modes and lifestyles of these pathogens? Why do some species become virulent and aggressive? What are the mechanisms of pathogenesis? Are pathogens host-specific or can they expand their host range? These questions need to be addressed to understand the several mechanisms of disease formation and emergence.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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