



## Hosts of *Colletotrichum*

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Talhinhas P, Baroncelli R 2023 – Hosts of *Colletotrichum*. Mycosphere 14(2), 158–261, Doi 10.5943/mycosphere/14/si2/4

### Abstract

The taxonomy of *Colletotrichum* has undergone profound changes over the past decade, with ca. 340 species now recognised, and grouped into 20 species complexes (16 previously described and four proposed in this work). Over that period, the volatility of the taxonomic framework posed difficulties to the aetiology of anthracnose diseases along with uncertainty on cross-infection potential, quarantine rules, pesticide management and plant breeding strategies. Now that the *Colletotrichum* taxonomy is stabilising (still several new species being named, but no longer representing major pathogens), there is a point on reviewing the knowledge on the aetiology of anthracnose diseases in a global way, pointing out the relative importance of each *Colletotrichum* species for each host/crop and identifying areas/crops where information is missing (and there are several crops for which nothing is known regarding *Colletotrichum* species in modern terms). Based on 3400 host species-*Colletotrichum* species occurrence records (considering only records of *Colletotrichum* spp. identified in modern terms), we have listed over 760 host (plants) species and analysed the information available on the *Colletotrichum* species reported from them, the symptoms caused and the geographic distribution and pathological relevance. Whereas some of these hosts are wild plants, this work is mostly focused on cultivated plants and therefore on the aetiology of anthracnose diseases globally. In the context of *Colletotrichum* fungi, this compilation provides downstream users of Mycology, namely those in areas such as Plant Pathology, Plant Protection and Plant Breeding, with updated information on the main causal agents of anthracnose in each crop/plant species in each location, or alternatively with an alert on the lack of information on the identity of the species of *Colletotrichum* relevant for a given crop in a given location.

**Keywords** – anthracnose – *Colletotrichum* species complex – host specificity

### Introduction

The taxonomy of *Colletotrichum* has undergone profound changes over the past decade. In 2012, Dean et al. (2012) considered 19 major species of *Colletotrichum* (previously the number of recognised species had ranged between 29 and 700) to consider this genus as one of the most important fungal pathogens. Currently there are 344 species of *Colletotrichum* recognised (Fig. 1), grouped into 20 species complexes, and the clarification of the taxonomic framework that led to the delimitation of these species was fundamental to the increase of references to occurrences of *Colletotrichum*, now rivalling with *Fusarium* as the most referred genus in Plant Disease Notes of the journal Plant Disease (Talhinhas & Baroncelli 2021).

*Colletotrichum* fungi are more frequently necrotrophic plant pathogens, often undergoing a more or less brief initial biotrophic stage (O'Connell et al. 2012). Besides their notable importance as plant pathogens, *Colletotrichum* fungi are increasingly being recognised as epiphytes, endophytes or saprobes (Jayawardena et al. 2021), but also as insect and human opportunistic pathogens (e.g., Marcelino et al. 2008, Werbel et al. 2019, Wynns et al. 2019, Paniz-Mondolfi et al. 2021). Detailed studies conducted over the past decades on the histopathology, physiology, gene expression and genetics of host-*Colletotrichum* interactions are often challenged by the instability and the changes in the taxonomic framework. Studies conducted on plant responses to “*C. gloeosporioides*” may refer to distinct fungi depending on the year of publication. Another example is given by the prevalent olive anthracnose pathogen in Portugal, originally reported as *Gloeosporium olivarum* in 1899, and successively assigned to *C. gloeosporioides* (from 1970 to 1999), *C. acutatum* (1999-2009), *C. simmondsii* (2009-2012) and *C. nymphaeae* (2012 to present) (Talhinhas et al. 2018). Several other species of *Colletotrichum* are associated to this pathosystem depending on the geography but also varying in prevalence along time, challenging the adequate deployment of strategies for disease resistance breeding and for crop management for protection. This example can be transposed to many other crops.

As such, the objective of this work is to compile the current knowledge on the species of *Colletotrichum* occurring on each host plant species (but covering also animal hosts), depicting the diseases caused (or non-pathogenic lifestyles), the prevalence and geographic distribution, in order to enable the use of detailed information to be used in crop protection and resistance breeding. A total of 931 articles were selected and analysed, approximately half of which (435) are Plant Disease Notes from the journal Plant Disease. The selection criterion was based on the accuracy of the tools employed for *Colletotrichum* species identification. Host plant names and phylogeny was checked using the platform Plant of the World Online (<https://powo.science.kew.org/>) and the NCBI taxonomy platform (<https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi>).

### **Taxonomic issues**

Sparkled by Hyde et al. (2009), the year 2009 witnessed a thorough revision of the graminicola and spaethianum species complexes (Damm et al. 2009), followed by the year 2012 concerning the acutatum (Damm et al. 2012a), boninense (Damm et al. 2012b) and gloeosporioides (Weir et al. 2012) species complexes. To these followed the revision of the orbiculare complex in 2013 (Damm et al. 2013), those of destructivum (Damm et al. 2014) and caudatum (Crouch 2014) in 2014 and of dracaenophilum, magnum and orchidearum complexes in 2019 (Damm et al. 2019) (Table 1). In spite of a steady decrease in the number of new species across the 2012-2021 decade, the years 2022 and 2023 (up to March 2023) saw a new surge on this process, totalizing 78 new species (23% of the currently recognised species) in nearly all complexes. Most of the newly described species are placed in the phylogenetic vicinity of pre-existing species, but some are singleton species, suggesting that new complexes may be recognised in the future. Several species described in the 2009-2012 period are now widely found across numerous locations and on various hosts. Among the five most frequently reported species of *Colletotrichum*, four – *C. siamense*, *C. fructicola*, *C. karsti* and *C. fioriniae* (the remaining being *C. gloeosporioides*) – were described in that period and have now over 150 occurrences on over 70 different host plants. More recent species tend to occur less frequently and on fewer hosts. Species described in the 2000-2012 period have in average 20 occurrences and 10 hosts, whereas those described in 2013-2023 have on average 2.4 occurrences and 1.7 host species (Table 1). In spite of new species being described frequently, it seems clear that the major *Colletotrichum* pathogens of agricultural crops are identified and that newly identified species do not currently represent pathogens of global relevance.

In this work we have compiled all species currently recognised (Fig. 1), although not all were included in the phylogenetic analysis because on unavailability of nucleotide sequences (as listed in the legend of Fig. 1). Additionally, the taxa “*Colletotrichum demersi*”, “*C. philoxeroidis*”,

“*C. tengchongense*” and “*C. vulgaris*” (Zheng et al. 2022) are invalidated here because they correspond to sequence chimeras and are thus assembly artifacts, as detailed next:

- The concatenated sequence used to differentiate “*Colletotrichum tengchongense*” is chimeric between sequences related to the gloeosporioides complex (ITS, *gapdh* and *chs-1*; GenBank references OL842169, OL981264 and OL981290, respectively) and to the graminicola complex (*act*; OL981238).

- The concatenated sequence used to differentiate “*Colletotrichum philoxeroidis*” is chimeric between sequences related to the magnum complex (ITS, *gapdh* and *act*; GenBank references OL842188, OL981283 and OL981257, respectively) and to the bambusicola/graminicola/tibetense complexes (*chs-1*; OL981309).

- The concatenated sequence used to differentiate “*Colletotrichum demersi*” is chimeric between sequences related to the boninense complex (ITS and *tub2*; GenBank references OL842177 and OL981232, respectively) and to the bambusicola/graminicola/tibetense complexes (*act*, *chs-1* and *gapdh*; OL981246, OL981298 and OL981272, respectively).

- The concatenated sequence used to differentiate “*Colletotrichum vulgaris*” is chimeric between sequences related to the bambusicola/graminicola/tibetense complexes (ITS; GenBank reference OL842170) and to the gloeosporioides complex (*act*, *chs-1* and *gapdh*; OL981239, OL981291 and OL981265 and OL981265, respectively).

The taxon “*Colletotrichum ligustri*” (Zhang et al. 2023b) requires clarification, as the etymology does not correspond to the material examined (the taxon refers to *Ligustrum* but the fungal material was obtained from *Ilex chinensis*) and this taxon had already been published in 1928, based on material from *Ligustrum vulgare* in Russia.

The phylogenetic analysis using *act*, *chs-1*, *gapdh*, *ITS* and *tub2* sequence alignment of 338 reference *Colletotrichum* isolates (including *Monilochaetes infuscans* as outgroup and excluding seven *Colletotrichum* species because of insufficient nucleotide sequence information; see legend of Fig. 1) cluster the species according to species complexes, revealing four new species complexes, the citri-medicae, coccodes, tibetense and trichellum complexes (Fig. 1).

### List of hosts of *Colletotrichum*

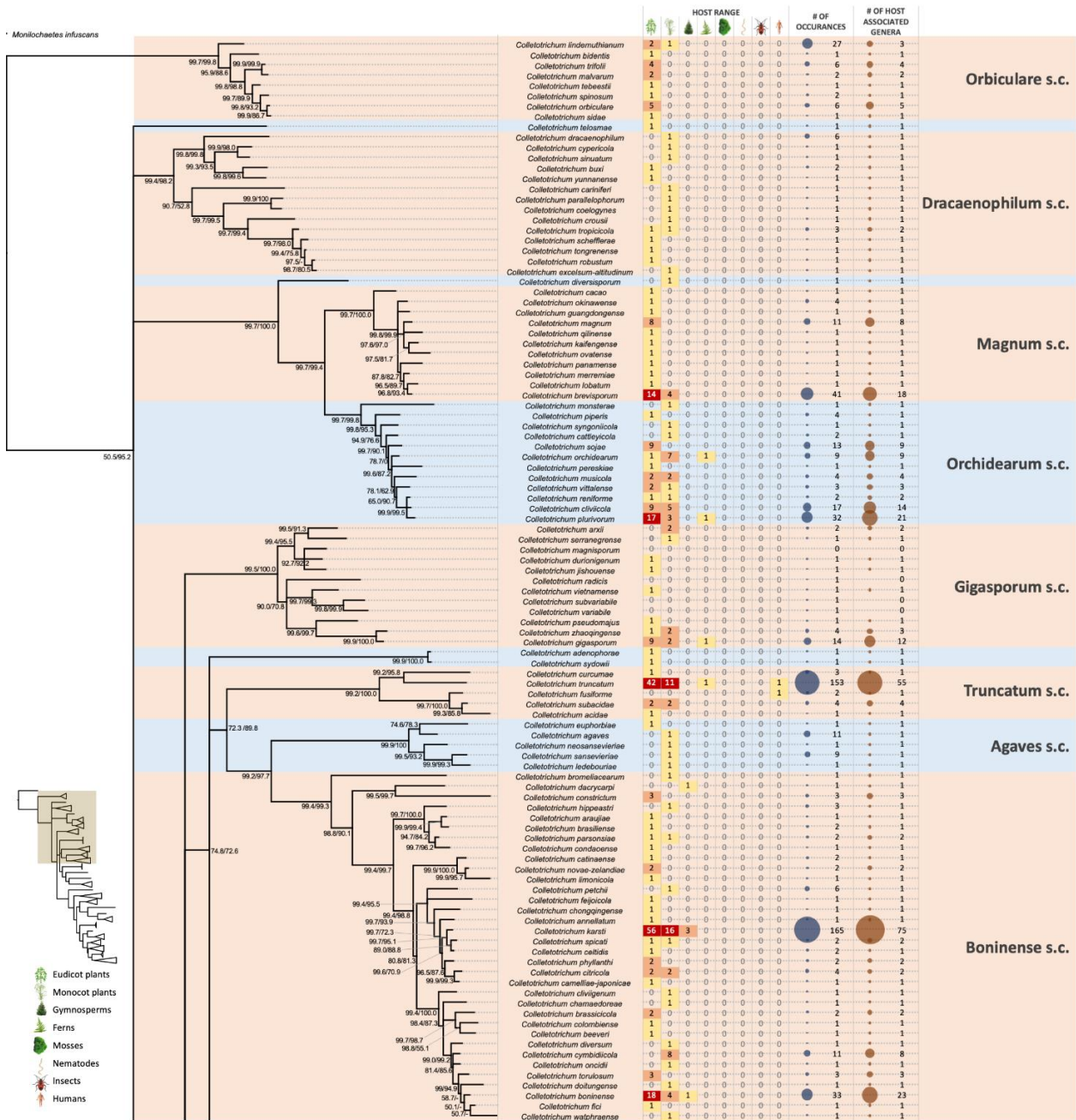
*Colletotrichum* occurs mostly on dicotyledonous plants (over 77% of all host-fungus species association records), but monocotyledonous hosts (20%) are the most common in the clade grouping the bambusicola, spaethianum, tibetense and graminicola/caudatum species complexes. *Colletotrichum* also occurs, although less frequently, on gymnosperms (1.4%), ferns, mosses and animals.

### Ferns, mosses and lycopods

Reports of *Colletotrichum* spp. in modern terms on ferns and mosses are seldom. *Colletotrichum pleopeltidis* was recently reported from leaves of *Pleopeltis* sp. in South Africa (Crous et al. 2021a) and *C. polypodiarium* (as *C. polypodialium*) was associated to leaf spots on *Nephrolepis* sp. and *Phymatosorus* sp. in Thailand (Seifollahi et al. 2023). In Thailand, leaf spots were associated to *C. fructicola* on *Nephrolepis cordifolia*, to *C. siamense* (as *C. pandanicola*; Zhang et al. 2023b) on *Thelypteris* sp. (as *Cyclosorus* sp.), *Pteris ensiformis* and *Nephrolepis cordifolia*, to *C. gigasporum* on *Nephrolepis cordifolia*, to *C. orchidearum*, *C. plurivorum* and *C. truncatum* on *Thelypteris* sp. (as *Cyclosorus* sp.) (Seifollahi et al. 2023). *Colletotrichum gloeosporioides* was reported causing leaf spots on *Pteridium aquilinum* in China (Tan et al. 2017). *Colletotrichum filicis* was reported from an unspecified fern in Costa Rica (Crous et al. 2021b) and *C. chrysophilum* was reported as an endophyte from *Terpsichore taxifolia* in Puerto Rico (Vieira et al. 2017). *Colletotrichum acutatum* sensu lato was also associated to anthracnose in the *Rumohra adiantiformis* (Norman & Strandberg 1997), but the causal agent lacks identification under current criteria.

On mosses, *Colletotrichum guizhouense* has been reported as an endophyte of the *Huperzia phlegmaria* in China (Zhang et al. 2015a), whereas a strain of *C. gloeosporioides* sensu lato was shown to be pathogenic to *Physcomitrella patens* (Reboledo et al. 2015).

Recently, “*Colletotrichum tengchongense*” was reported as an endophyte on the quillwort *Isoetes sinensis* in China (Zheng et al. 2022), but this taxon is null because of chimeric concatenated sequences.



**Figure 1** – Phylogeny of *Colletotrichum* species obtained by obtained with MrBayes 3.2.6 (Ronquist et al. 2012) and reconstructed from *act*, *chs-1*, *gapdh*, *ITS* and *tub2* sequence alignment of 338 reference isolates including *Monilochaetes infuscans* as outgroup (species not included due to unavailable or insufficient nucleotide sequence information are: in the agaves complex, *C. chinense*; in the destructivum complex, *C. quercicola*; in the gigasporum, *C. flexuosum*; in the gloeosporioides complex, *C. anhuiense*, *C. osmanthicola* and *C. polypodiarium*; in the spaethianum complex, *C. disporopsidis*). Each alignment was performed with MAFFT v7.450 (Katoh &



Standley 2013), exported to MEGAX (Kumar et al. 2016) and the best-fit substitution model calculated. The Markov chain Monte Carlo (MCMC) algorithm was performed to generate phylogenetic trees with Bayesian posterior probabilities for the alignment. Four MCMC chains were run simultaneously for random trees for 5,000,000 generations and sampled every 500 generations. The first 25% of trees were discarded as burn-in phase of each analysis and posterior probabilities were determined from the remaining trees. Bayesian posterior probability (obtained with MrBayes 3.2.6; Ronquist et al. 2012) and FastTree2 v2.1.10 (Price et al. 2010) support values above 0.50/50 are reported next of the node. Reviewer access URL: <http://purl.org/phylo/treebase/phylovs/study/TB2:S30356?x-access-code=a950a2a3b49a9dd8b15fca06ca795bff&format=html>. The scale bar represents the number of expected substitutions per site. Bubble graph represent the number of occurrences (in blue) and the number of associated genera of plants (in brown) for each *Colletotrichum* species.

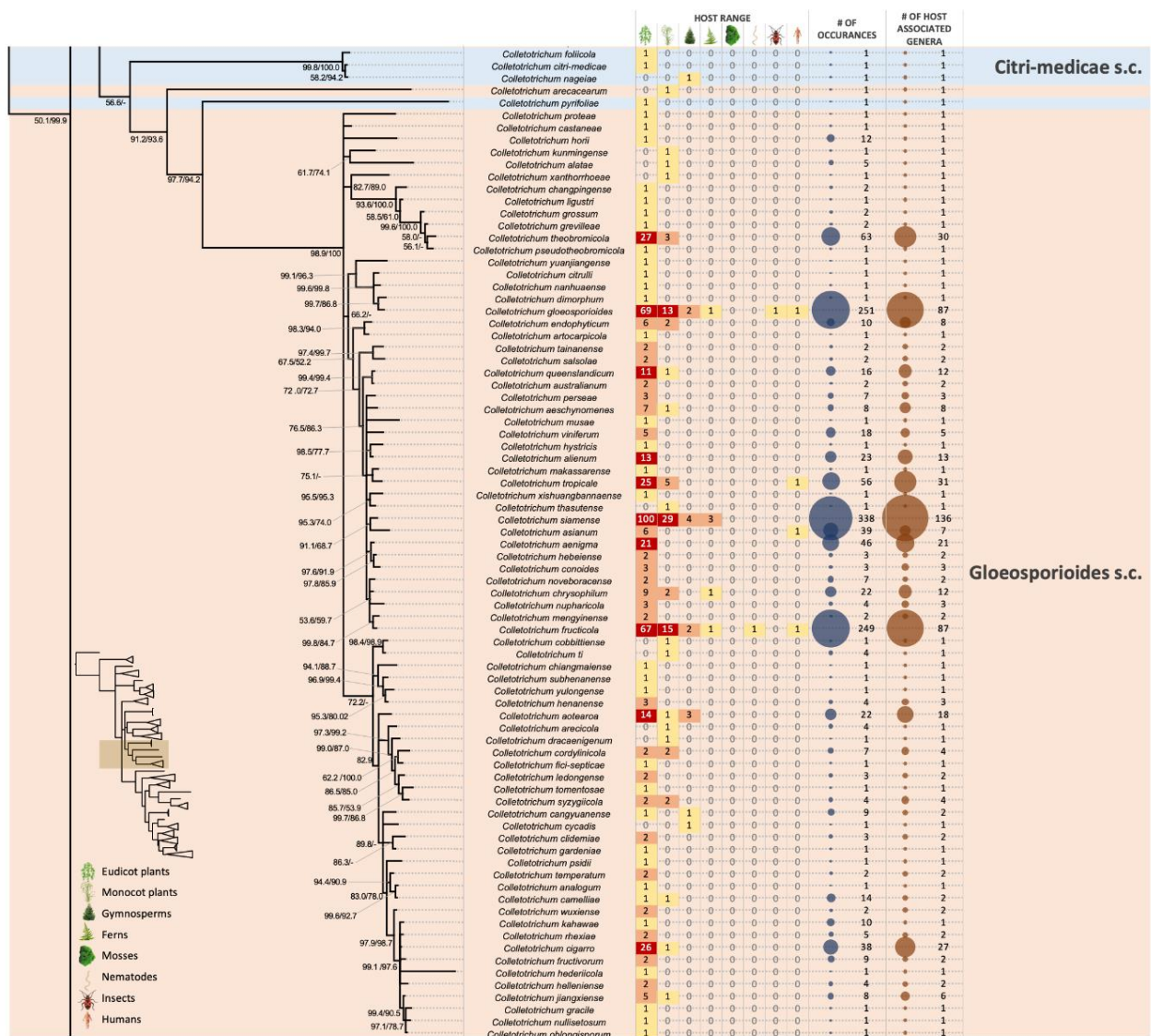


Figure 1 – Continued.

### Gymnosperms

Reports of *Colletotrichum* on gymnosperms are seldom and restricted to species in the acutatum, boninense and gloeosporioides complexes. *Colletotrichum* is reported from most gymnosperm families, with the notable exception of the Ginkgoaceae, Ephedraceae and Gnetaceae.

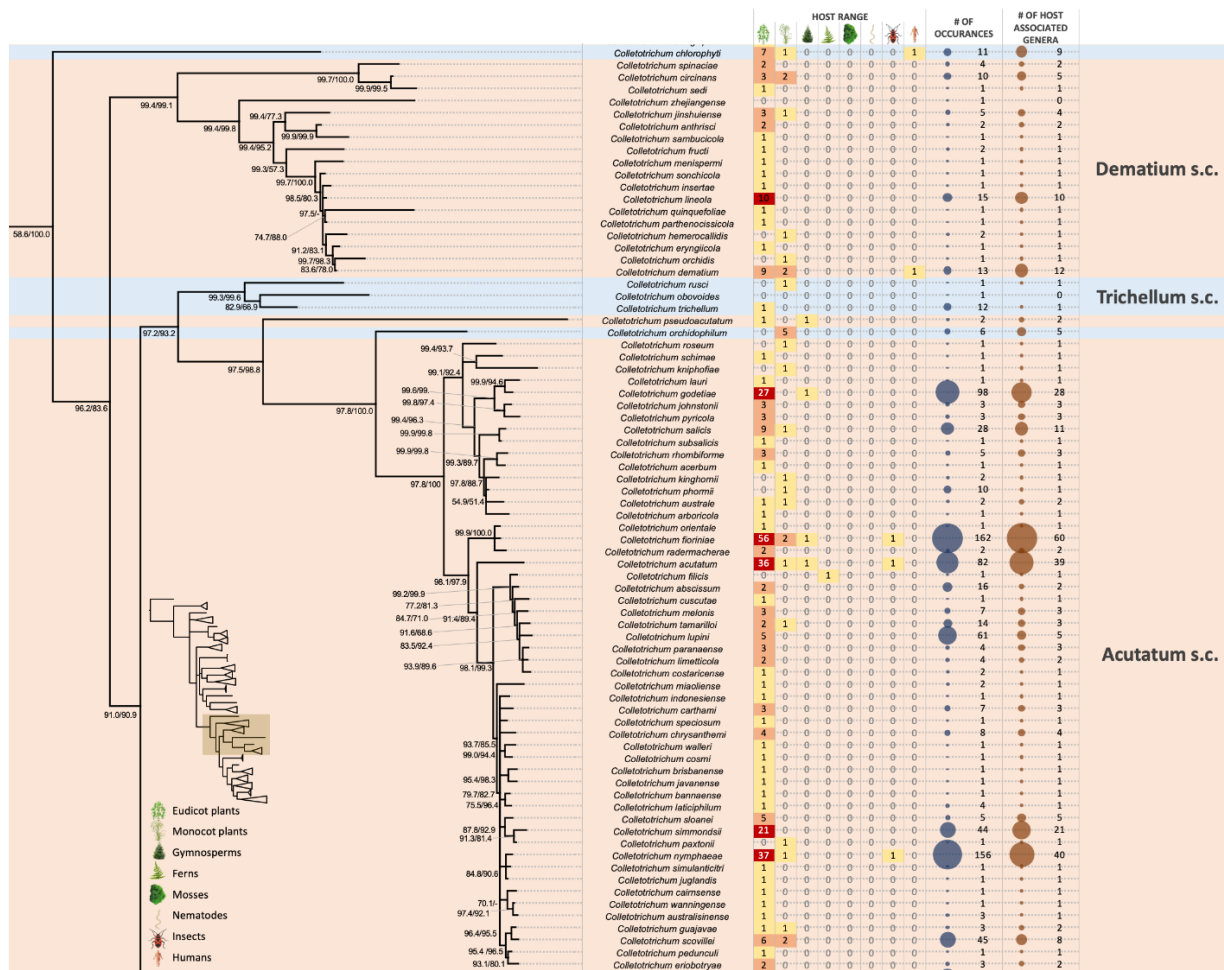


Figure 1 – Continued.

On Pinaceae, *Colletotrichum* (*C. acutatum*, *C. fioriniae* and *C. pseudoacutatum*) has been reported on *Pinus radiata* related to nursery seedling diseases, including the terminal crook disease on *Pinus*, in Chile, South Africa, Kenya, Australia and New Zealand and considered epidemic in the latter, but all records are from the 1970s or earlier (Nair and Corbin 1981, Damm et al. 2012a).

On *Araucaria columnaris* (Araucariaceae), *Colletotrichum salicis* was associated to anthracnose and dieback symptoms in the USA in 1983 (Damm et al. 2012a). A *Colletotrichum* needle necrosis disease of Norfolk Island pine (*A. heterophylla*) was also reported in 1973 in the USA (Ridings 1973).

On Chinese fir (*Cunninghamia lanceolata*, Cupressaceae), anthracnose symptoms include lesions on needles and shoots, with leaf tips showing irregular spots. Several pathogens are associated to the disease, varying according to the location, and including *Colletotrichum cangyuanense*, *C. fructicola*, *C. gloeosporioides*, *C. karsti* and *C. siamense* (Huang et al. 2019, He et al. 2022).

On *Dacrycarpus dacrydioides* (Podocarpaceae), *Colletotrichum aotearoa*, *C. boninense* and *C. dacrycarpi* were recorded as leaf endophytes from New Zealand (Damm et al. 2012b, Weir et al. 2012). *Colletotrichum aotearoa* was also recorded as an endophyte of *Podocarpus totara* in New Zealand (Weir et al. 2012), along with *C. godetiae* on *Podocarpus* sp. in South Africa (Damm et al. 2012a). *Colletotrichum siamense* was recently recorded from *P. macrophyllus* in China, causing sunken spots at the leaf tip (Liu et al. 2022d). Among the Podocarpaceae, *Colletotrichum aotearoa* was additionally recorded as an endophyte on *Prumnopitys ferruginea* in New Zealand (Weir et al. 2012). The species *C. nageiae* was named to accommodate a specimen collected from healthy



*Nageia nagi* leaves in 1993 in China (Liu et al. 2022b), whereas recently *C. siamense* was associated to leaf spots on *N. nagi* in China (Xu et al. 2023a).

On Taxaceae, *Taxus wallichiana* anthracnose was recently associated to *Colletotrichum karsti* in China, originating leaf necrosis and twig wilt (Xu et al. 2019).

*Colletotrichum karsti* was found as an endophyte in *Zamia obliqua* (Zamiaceae) (Damm et al. 2012b) and *C. fructicola* was associated to leaf spots on *Z. furfuracea* (Manawasinghe et al. 2022).

Recently, reports of anthracnose on *Cycas* (Cycadaceae) in China led to the identification of *Colletotrichum siamense* associated to brown spots on *Cycas debaoensis* (Han et al. 2021), of *Colletotrichum cycadis* associated to leaf spots on *Cycas revoluta* (Crous et al. 2020) and of *Colletotrichum gloeosporioides* associated to leaf spots on *Cycas bifida* (Zhang et al. 2023b). However, anthracnose of *Cycas* is a common disease in many parts of the world, from where *Colletotrichum* fungi are isolated, but such pathogens are pending modern taxonomic treatment.

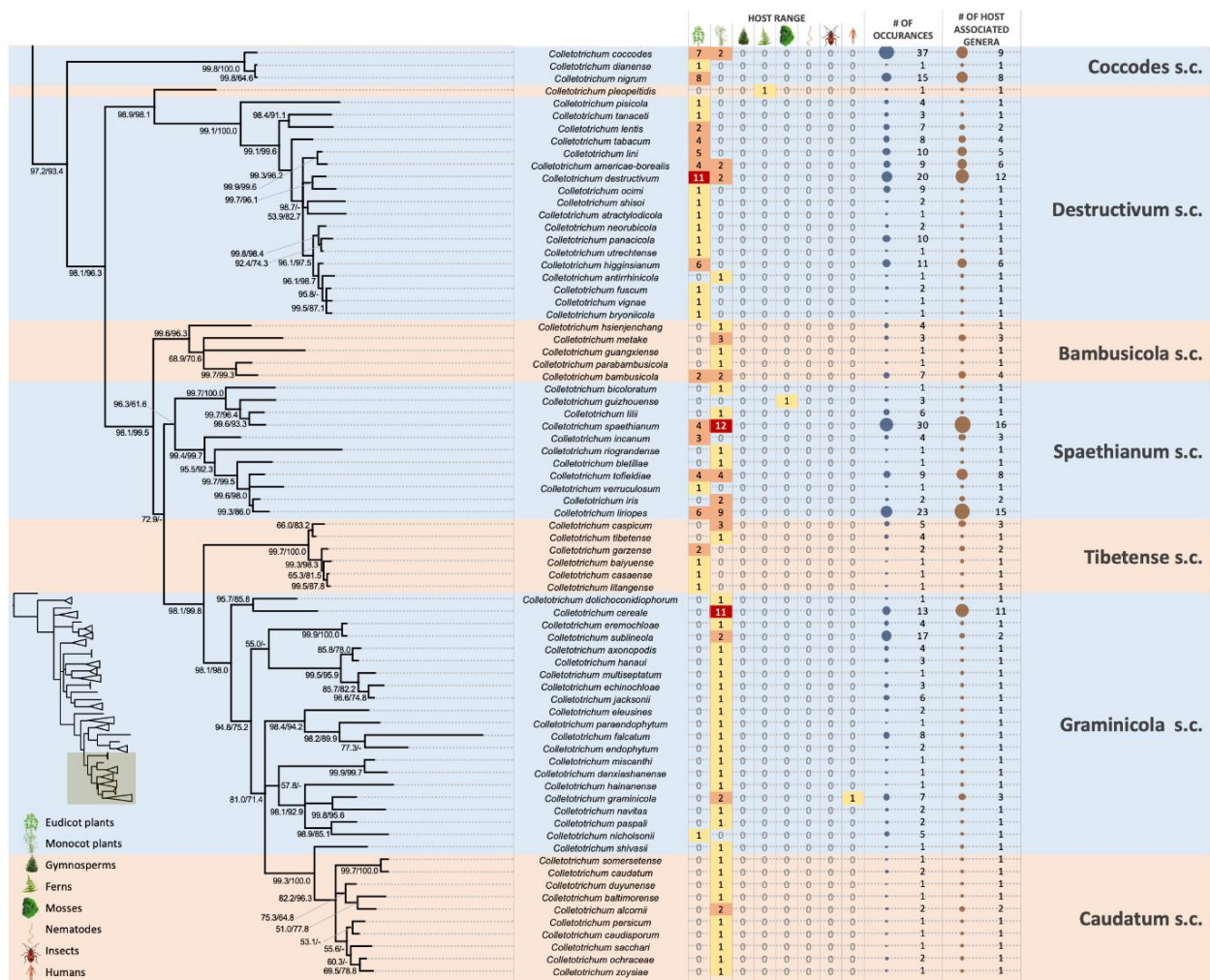


Figure 1 – Continued.

### Monocots

*Colletotrichum* spp. are seldom or not reported from key monocot families such as the Bromeliaceae, Cyperaceae, Juncaceae, Liliaceae and Pandanaceae, but common in many others as listed next.

**Table 1** Number of currently recognised species of *Colletotrichum* according to the year of publication and their species complex, including information on the number of occurrences and number of host species per species of *Colletotrichum* per complex and per year of species description.

Complex	<1900	1900-1949	1950-1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022	2023	total	Nr occurrences/ species (average)	Nr hosts/ species (average)	
singleton spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	0	0	4	0	<b>9</b>	2.8	2.3	
orbiculare	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	<b>8</b>	5.8	2.5	
magnum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	5	0	0	0	3	1	<b>11</b>	5.8	3.4	
orchidearum	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	1	3	0	<b>12</b>	7.3	5.9	
dracaenophilum	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	3	1	0	0	4	2	<b>14</b>	1.6	1.1	
gigasporum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5	0	0	0	1	1	0	0	3	2	<b>13</b>	2.3	2.0	
truncatum	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	<b>5</b>	32.4	14.8	
agaves	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	<b>6</b>	4.0	1.7	
boninense	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	14	1	0	0	1	2	3	1	0	4	5	0	<b>34</b>	7.6	5.1	
citri-medicae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	<b>3</b>	1.0	1.0	
gloeosporioides	3	2	4	0	0	0	0	0	0	0	0	0	3	2	1	10	7	0	3	2	6	1	5	4	7	12	7	<b>79</b>	17.7	8.8	
dematium	2	3	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	3	3	1	0	2	0	1	0	<b>18</b>	3.5	2.7	
coccodes	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	<b>3</b>	17.7	7.0	
destructivum	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	0	0	1	0	1	1	1	1	0	<b>20</b>	5.5	3.1	
bambusicola	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	<b>5</b>	3.2	2.6	
spaethianum	0	0	1	0	0	0	0	0	0	0	0	0	4	0	0	0	2	1	0	1	0	0	0	1	0	2	0	<b>12</b>	6.9	5.2	
tibetense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	<b>6</b>	1.8	1.5
graminicola	1	3	1	0	0	0	0	0	0	0	0	0	8	0	0	1	1	0	0	0	0	0	0	1	0	4	0	<b>20</b>	4.3	2.0	
caudatum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	4	0	0	0	0	0	0	0	3	0	<b>11</b>	1.3	1.1	
trichellum	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	<b>3</b>	4.7	1.3	
acutatum	0	1	3	0	0	0	0	0	0	1	0	0	2	0	0	23	0	0	1	2	1	3	2	2	3	7	1	<b>52</b>	15.5	6.3	
<b>total</b>	<b>10</b>	<b>24</b>	<b>11</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>3</b>	<b>1</b>	<b>0</b>	<b>19</b>	<b>2</b>	<b>2</b>	<b>53</b>	<b>22</b>	<b>18</b>	<b>7</b>	<b>11</b>	<b>15</b>	<b>25</b>	<b>11</b>	<b>13</b>	<b>18</b>	<b>65</b>	<b>13</b>	<b>344</b>	9.8	5.1	
Nr occurrences/ spp. (average)	35	16	39							8.3			46			8.8	3.6	2.8	5.0	2.4	3.3	3.8	1.4	2.1	1.8	1.4	1.2				
Nr hosts/ spp. (average)	15	8.6	14							2			22			5.0	2.2	1.5	2.6	1.9	2.4	3.0	1.1	1.2	1.6	1.2	1.2				



## Amaryllidaceae

*Colletotrichum* on *Allium* spp. is most noticeable as the causal agent of onion anthracnose, also known as onion twister disease, along with anthracnose on garlic and leek. Typical symptoms on onion are twisting and discolouration of the leaves, leading to elongated necks and slender bulbs (Alberto et al. 2019). Several species of *Colletotrichum* are associated with the disease: *C. circinans* and *C. coccodes* are most common in temperate regions (Damm et al. 2009, Rodriguez-Salamanca et al. 2012, Baysal-Gurel et al. 2014, Sato et al. 2015, Chen et al. 2022c), whereas *C. spaethianum*, *C. truncatum* and *C. siamense* seem to be more common in tropical areas (Chowdappa et al. 2015, Santana et al. 2016, Matos et al. 2017, Salunkhe et al. 2018a, 2018b, Herath et al. 2021). Any of these fungi infect multiple hosts, potentially connecting this disease with anthracnose on other hosts. Nevertheless, comprehensive studies focusing on the disease are scarce, as stressed by Chowdappa et al. (2015). To this end, a study on onion anthracnose across Brazilian onion-growing areas has revealed *C. theobromicola* as the most prevalent pathogen (Lopes et al. 2021) and a recent review on the disease has compiled an array of genetic, cultural, biological and chemical control measures (Dutta et al. 2022).

Several species of *Colletotrichum* occur on ornamental Amaryllidaceae such as *Clivia* (Damm et al. 2019, Crous et al. 2021b), *Crinum* (Damm et al. 2012b, Sato et al. 2015, Khoo et al. 2022b), *Hippeastrum* (Damm et al. 2012b, Sato et al. 2015) and *Hymenocallis* (Yang et al. 2012b, Weir et al. 2012, Ariyawansa et al. 2015, Zhao et al. 2019, Huang et al. 2021c, Zhang et al. 2023b), namely *Colletotrichum boninense*, *C. cliviicola*, *C. cliviigenum*, *C. gloeosporioides*, *C. hippeastri*, *C. karsti*, *C. orchidearum*, *C. siamense*, *C. spaethianum* and *C. truncatum*, associated to anthracnose symptoms, namely red-brown lesions on leaves and scapes (Yang et al. 2009, Khoo et al. 2022b, Zhang et al. 2023b), although their global pathological relevance remains to be dissected.

## Araceae

Although much used as ornamental indoor plants, the plants of the arum family from which *Colletotrichum* was recorded occur mostly in outdoor tropical to sub-tropical environments. Host-pathogen combinations include: on *Alocasia*, *C. karsti*, *C. gigasporum*, *C. siamense* and *C. truncatum* (He et al. 2014, Liu et al. 2014, Ben et al. 2020, Huang et al. 2021b, Zhang et al. 2023b); on *Amorphophallus*, *C. camelliae*, *C. gloeosporioides* and *C. siamense* (Prasad et al. 2017, Cheng 2021, Sun et al. 2023b); on *Anthurium*, *C. brevisporum* and *C. karsti* (Damm et al. 2012b, 2019) and, associated to spathe rot, to spadix rot and to leaf spots, *C. fructicola* and *C. orchidearum* (Vithanage et al. 2021); on taro (*Colocasia esculenta*), *Colletotrichum brevisporum* and *C. musicola* (Vásquez-López et al. 2019); on *Dieffenbachia*, *C. siamense* and *C. truncatum* (Sato et al. 2015, Sharma et al. 2015a); on *Epipremnum aureum*, *C. orchidearum* (Damm et al. 2019); on *Monstera deliciosa*, *C. monsterae* (Liu et al. 2022b), *C. orchidearum* (Hou et al. 2016) and *C. siamense* (Liu et al. 2021c); on *Philodendron*, *C. orchidearum* (Hou et al. 2016, Xue et al. 2020) and *C. siamense* (Ning et al. 2022); on *Rhaphidophora* sp., *C. crousii* (Liu et al. 2022b); on *Spathiphyllum wallisii*, *C. plurivorum* (Damm et al. 2019); on *Syngonium*, *C. plurivorum* (Zhang et al. 2023b), *C. syngoniicola* (Liu et al. 2022b), *C. thasutense* (Jayawardena et al. 2023) and *C. truncatum* (Sato et al. 2015); on *Zamioculcas*, *C. cliviicola* (Zhou & Li 2017). Symptoms usually begin with water-soaked yellow or green spots, progressing to form brown, round to oval lesions with yellow halos.

## Arecaceae

Among the palm family, species of *Colletotrichum* are recorded: on *Areca catechu*, *C. arecicola*, *C. cigarro*, *C. cordylinicola*, *C. fructicola*, *C. gloeosporioides*, *C. karsti*, *C. siamense* and *C. tropicale*, causing expanding brown spots that, under severe conditions, can lead to plant death (Cao et al. 2020, Zhang et al. 2020d); on *Chamaedorea elegans*, *Colletotrichum siamense* associated to leaf spots, and on *Chamaedorea seifrizii* (as *C. erumpens*), *Colletotrichum chamaedoreae* (Liu et al. 2022b); on *Cocos nucifera*, *Colletotrichum siamense* (Sharma et al. 2015a); on *Copernicia prunifera*, *Colletotrichum theobromicola* and *C. tropicale* (Araújo et al.

2018), affecting fruits at maturity; on *Dypsis lutescens*, *C. siamense* (Chou et al. 2019), initially originating small dark spots with a distinct yellow halo that subsequently coalesce, leading to leaf yellowing and fall; on *Euterpe oleracea* (açai palm), *C. chrysophilum* causing leaf spots (Santos et al. 2022); on *Philodendron bipinnatifidum*, *C. diversum* (Liu et al. 2022b), *C. orchidearum* (Hou et al. 2016), *C. siamense* (Ning et al. 2022), *C. karsti* and *C. endophyticum* (Zhang et al. 2023c) causing leaf spots; on *Trachycarpus fortunei*, *C. australe* (Damm et al. 2012a); on an unknown *Areaceae*, *C. areacearum* and *C. zhaoqingense* (Liu et al. 2022b).

### Asparagaceae

Anthraxnose on Asparagaceae is a disease of ornamental and also of agricultural relevance.

On *Agave* spp., anthracnose can affect ornamental species as well as cultivated sisal (*A. sisalana*), with *Colletotrichum agaves* originating sunken lesions on leaves and exhibiting a high degree of host specificity (Farr et al. 2006).

On *Cordyline* spp., anthracnose is associated to *Colletotrichum cobbittiense*, *C. cordylinicola* and *C. ti* (Weir et al. 2012, Sharma et al. 2014, Crous et al. 2018c, Zhang et al. 2023b).

On *Dracaena* spp., anthracnose is associated to *Colletotrichum diversiporum*, *C. dracaenophilum*, *C. dracaenigenum*, *C. karsti*, *C. petchii*, *C. queenslandicum*, *C. sansevieriae* and *C. truncatum* (Damm et al. 2012a, 2012b, 2019, Macedo & Barreto 2016, Morsy & Elshahawy 2016, Shivas et al. 2016, Li et al. 2018a, Liu et al. 2019b, 2022b, Chaiwan et al. 2021, Wang et al. 2022j, David et al. 2023). Typical symptoms include sunken necrotic spots, leading to leaf and shoot dieback.

On *Hosta* spp., anthracnose (brown necrotic lesions) is associated to *Colletotrichum spaethianum* (Damm et al. 2009, Sato et al. 2015, Cheon & Jeon 2016, Sun et al. 2020a). Recently, *C. subacidiae* was isolated from diseased *Hosta* sp. leaves (Liu et al. 2022b).

On *Liriope* spp., anthracnose is associated to *Colletotrichum gloeosporioides* and *C. liriopes* (Damm et al. 2009, Oo & Oh 2017b, Chen et al. 2019c, Yang et al. 2020a, Liu et al. 2022b). Typical symptoms are leaf spots, often with dark brown edges and yellow halos.

On *Dracaena trifasciata* (syn. *Sansevieria trifasciata*), anthracnose is associated to *Colletotrichum neosansevieriae*, *C. sansevieriae* and *C. truncatum* (Nakamura et al. 2006, Aldaoud et al. 2011, Palmateer et al. 2012, Park et al. 2013, Crous et al. 2015, Sato et al. 2015, Karimi et al. 2017a, Kee et al. 2020, Brand & Wichura 2023, Li et al. 2023a). Symptoms start as small water-soaked lesions that rapidly enlarge and coalesce. In the centre of the lesions, concentric rings of numerous brownish black acervuli are formed.

Other host-pathogen combinations in the Asparagaceae include: on *Anemarrhena asphodeloides*, *Colletotrichum gloeosporioides*, *C. liriopes* and *C. spaethianum*, originating slightly sunken lesions with distinct reddish-black rims, contained acervuli (Okorley et al. 2019, Wei et al. 2022b); on *Asparagus officinalis*, *C. subacidiae* from diseased stems (Liu et al. 2022b); on *A. racemosus*, *C. dematium* and *C. lindemuthianum* as endophytes (Rather et al. 2018); on *Aspidistra elatior*, *C. iris* associated to leaf spots (Zhang et al. 2023b); on *Chlorophytum*, *Colletotrichum chlorophyti* (Damm et al. 2009); on *Convallaria keiskei*, *Colletotrichum spaethianum* (Ran et al. 2017); on *Disporopsis fuscipicta*, *C. disporopsidis* (Zhang & Wang, 2021; as *C. disporopsis*); on *Ledebouria floridunda*, *C. ledebouriae* (Crous et al. 2016); on *Ophiopogon japonicus*, *C. kunmingense* associated to leaf spots (Zhang et al. 2023b), *C. bicoloratum* and *C. sinuatum* from dead tissue (Liu et al. 2022b) and *C. liriopes* originating necrotic leaf spots (Wang & Wang 2021), the latter also on *O. jaburan* (Yi et al. 2022); on *Ornithogalum umbellatum*, *C. tofieldiae* (Sato et al. 2015); on *Polianthes tuberosa*, *C. truncatum* originating circular sunken lesions with abundant black acervuli on leaves and peduncles (Mahadevakumar et al. 2019); on *Polygonatum* spp., *C. circinans*, *C. dematium* and *C. spaethianum* causing brown to reddish leaf spots (Sato et al. 2015, Karimi et al. 2016, Liu et al. 2020b; Ma et al. 2021, Zhao et al. 2023); on *Reineckea carnea*, *C. siamense* (as *C. pandanicola*; Zhang et al. 2023b) associated to leaf spots (Manawasinghe et al. 2022); on *Rohdea japonica*, *C. liriopes* causing brown to reddish leaf spots

(Kwon & Kim 2013, Sato et al. 2015, Trigiano et al. 2018, Zhu et al. 2023b); on *Ruscus* sp., *C. rusci* (Damm et al. 2009); on *Yucca gloriosa*, *C. chinense* (Wang et al. 2022i).

### Bromeliaceae

Records of *Colletotrichum* on Bromeliaceae are scarce. Leaf anthracnose was recorded on *Vriesea imperialis* (as *Alcantarea imperialis*) in Brazil associated to *C. boninense* (Meneses et al. 2019) and on *Neoregelia* sp. in Thailand associated to *C. brevisporum* (Noireung et al. 2012). Symptoms include circular to elliptical, sunken and light brown leaf spots. *Colletotrichum bromeliacearum* was recorded from an unspecified Bromeliaceae in China (Liu et al. 2022a).

### Cannaceae

Anthracnose of *Canna indica* (as *C. edulis*) has been reported from China, associated to leaf spots and attributed to *Colletotrichum gloeosporioides* (Sun et al. 2021). Symptoms are characterised by oval-shaped lesions, initially pale to yellow then turning brown and increasing in size in a circular pattern.

### Commelinaceae

Records of *Colletotrichum* on Commelinaceae are known only on *Commelina* sp. from Nigeria, associated to *Colletotrichum siamense* (Weir et al. 2012), and on *Tradescantia fluminensis* from Brazil, associated to *C. riograndense*, causing circular pale-yellow to brown leaf spots surrounded by a chlorotical halo (Macedo et al. 2016).

### Cyperaceae

*Colletotrichum caspicum* was recently isolated from *Cyperus* sp. leaves in Iran (Alizadeh et al. 2022), but the authors note previous records of *Colletotrichum* spp. from *Cyperus* that pend treatment under current taxonomic framework. More recently, *Colletotrichum cypericola* was recorded as a saprobe of *Cyperus rotundus* leaves in China (Zhang et al. 2023b).

### Dioscoreaceae

Water yam (*Dioscorea alata*) anthracnose is an important disease, recorded throughout the areas where the crop is grown. The disease can lead up to 90% tuber yield losses in severe situations, with all plant parts being affected. Symptoms on leaves, petioles and stems begin as dark brown or black lesions surrounded by a chlorotic halo, which coalesce to originate leaf necrosis and stem dieback (Ntui et al. 2021). The causal agent is *Colletotrichum alatae* (Weir et al. 2012, Lin et al. 2018b), although *C. fructicola* and *C. siamense* have also been recorded from *Dioscorea* spp. (Weir et al. 2012, Souza Junior & Assunção 2021, Qiu et al. 2023) and *C. karsti* from *D. cayenensis* (Amaral et al. 2023). Disease resistance breeding, including the deployment of interspecific hybrids, is an important disease control measure (Lebot et al. 2019). The diversity of the pathogen has been studied using microsatellite markers (Penet et al. 2017) and the fungus was shown to be able to adapt to new cultivars (Frézal et al. 2018) and to survive in the wild (Dentika et al. 2023). A thorough review on this disease was recently published (Ntui et al. 2021). Additionally, *C. jinshuiense* has been recently recorded from the pharmaceutical plant *D. zingiberensis* in China (Liu et al. 2022b).

### Iridaceae

Records of *Colletotrichum* in the Iridaceae are restricted to *Iris* in Australasia, with *Iris* anthracnose associated to *C. coccodes* and *C. tofieldiae* in Australia (Shivas et al. 2016), to *C. spaethianum* in Japan (Sato et al. 2015) and to *C. iris* (Liu et al. 2022b), *C. siamense* (Liu et al. 2017a) and *C. truncatum* (Wang et al. 2022g) in China. Symptoms on leaves include chlorotic spots that coalesce to form irregular lesions with a grey centre, a brown border and surrounded by a yellow halo (Liu et al. 2017a).

## Liliaceae

Reports of *Colletotrichum* on Liliaceae are scarce. *Colletotrichum spaethianum* was reported to cause leaf blight on *Lilium lancifolium* in China, with brown necrotic spots on the outer edge of the leaf progressing to irregular dark brown lesions surrounded by a pale-yellow halo extending along the entire leaf (Zhao et al. 2016b). *Colletotrichum lilii* is associated to black scale disease of *Lilium* sp. in Japan, the Netherlands and the USA, with dark brown to black lesions eventually enlarging to cover the entire scale (Damm et al. 2009, Chastagner et al. 2018). *Colletotrichum fioriniae* was associated to anthracnose symptoms in tulip bulbs (*Tulipa* sp.) in the UK (Talhinhas et al. 2005, Damm et al. 2012a).

## Melanthiaceae

Anthracnose has been recently recorded as leaf spots on *Paris polyphylla* in China and attributed to *Colletotrichum spaethianum* and to *C. fructicola* (Zhong et al. 2020, Zhou et al. 2020). Symptoms begin as light-brown chlorotic spots, becoming elliptical or irregular brown lesions.

## Musaceae

Banana anthracnose, causing black sunken lesions on fruits, occurs throughout the crop cultivation range and is mostly a post-harvest disease, as infection starts during the development of the fruit but remains quiescent until the fruit ripens, with symptoms often manifesting during storage and marketing following wounding due to handling and transportation (Zakaria et al. 2009). Controlling the disease requires the employment of chemicals to prolong the shelf life of fresh bananas (Vilaplana et al. 2018, Madjouko et al. 2019). The main causal agent is *Colletotrichum musae*. As reviewed by Damm et al. (2019) and Zakaria (2021), other species in the gloeosporioides complex are associated with banana anthracnose, including *C. aotearoa* in India (Sharma et al. 2015a), *C. chrysophilum* in Brazil (Vieira et al. 2017) and Mexico (Fuentes-Aragón et al. 2020c), *C. fructicola* in China (Huang et al. 2021d), *C. gloeosporioides* in Ecuador (Riera et al. 2019) and Pakistan (Alam et al. 2021), *C. siamense* in Brazil (Vieira et al. 2017), China (Huang et al. 2021d), Malaysia (as endophyte; Zakaria & Aziz 2018) and India (on *Ensete superbum*; Kumar et al. 2017) and *C. theobromicola* and *C. tropicale* in Brazil (Vieira et al. 2017). Species from other complexes are also associated to banana anthracnose: in the boninense complex, *C. citricola* has been recorded from China (Huang et al. 2022a) and *C. karsti* from Australia, China, Colombia, Mexico and Italy (Damm et al. 2012b, Schena et al. 2014, Shivas et al. 2016, Huang et al. 2021d); in the acutatum complex, *C. paxtonii* from Saint Lucia and *C. scovillei* from China (Damm et al. 2012a, Zhou et al. 2017); in the gigasporum complex, *C. gigasporum* from Mexico (Liu et al. 2014) and *C. zhaoqingense* from China (Liu et al. 2022b); in the orchidearum complex, *C. cliviicola* from China (Huang et al. 2021d) and *C. musicola* from Mexico (Damm et al. 2019). Vieira et al. (2017) analysed the diversity of banana anthracnose pathogens across 11 states in Brazil and found *C. musae* as the most prevalent species, corroborating the findings by Udayanga et al. (2013). On the contrary, Huang et al. (2021d) depicted *C. fructicola* as the prevalent pathogen in Guangxi, China, discussing whether geographical location, climate, cultivar, planting method, biotic and abiotic environment, and collection time may have influenced this difference. These contradictory reports show that the pathological relevance and geographic distribution of the banana anthracnose causal agents remain to be dissected, which is of utmost importance for the adequate deployment of appropriate protection measures.

## Orchidaceae

There are 37 species of *Colletotrichum* inhabiting Orchidaceae plants, representing the vast majority of species complexes. Many of these species inhabit simultaneously the same host plants and few appear to be host specific, although 12 of these species have been recorded only once and from a single host.

On *Bletilla ochracea* there are 15 species of *Colletotrichum* recorded as leaf endophytes, all from China (Tao et al. 2013): *C. boninense*, *C. karsti* and *C. parsonsiae* in the boninense complex;



*C. caudisporum*, *C. duyunense* and *C. ochraceae* in the caudatum complex; *C. destructivum* in the destructivum complex; *C. excelsum-altitudinum* in the dracaenophilum complex; *C. cereale*, *C. endophytum* and *C. miscanthi* in the graminicola complex; and *C. bletillae*, *C. guizhouense*, *C. liriopes* and *C. tofieldiae* in the spaethianum complex. However, recently *C. fructicola* and *C. orchidophilum* were reported, also from China, as the causal agent of anthracnose on *B. striata*, with symptoms on leaves beginning as round light-brown spots, progressing to larger oval brown-black, sunken lesions (Wang et al. 2022b, Yang et al. 2022).

On *Cattleya* spp. the *Colletotrichum* species recorded are *C. cattleyicola* in the orchidearum complex (Damm et al. 2019), *C. fructicola* and *C. tropicale* in the gloeosporioides complex, causing small circular to elliptical necrotic lesions with irregular margins on leaves (Silva-Cabral et al. 2019b), *C. karsti* in the boninense complex, causing circular to elliptic or irregular necrotic sunken lesions (Silva et al. 2021a), and *C. serranegrense* in the gigasporum complex, as an endophyte (Silva et al. 2018).

On *Cymbidium* spp. the *Colletotrichum* species recorded associated to anthracnose symptoms, from diverse locations, are *C. cymbidiicola* in the boninense complex (Damm et al. 2012b), *C. gloeosporioides* (Park & Seo 2013) and *C. syzygiicola* (Manawasinghe et al. 2022) in the gloeosporioides complex and *C. cliviicola* in the orchidearum complex (Chowdappa et al. 2014). Symptoms typically start at the leaf tip or margins, as multiple brownish lesions, coalescing and progressing towards the base of the leaf.

On *Dendrobium* spp. there are 13 species of *Colletotrichum* recorded from diverse locations: in the boninense complex, *C. boninense*, *C. citricola*, *C. doitungense* and *C. watphraense* as endophytes in Thailand (Ma et al. 2018), *C. cymbidiicola* associated to anthracnose symptoms in India, affecting leaves, petioles and blooms causing necrosis of leaf tips that proceed to the base, scattered black sunken spots, and dark brown or light grey patches with concentric rings (Chowdappa et al. 2014), *C. karsti* associated to anthracnose symptoms in Mexico, originating leaf spots that expanded rapidly into large necrotic areas ranging in colour from light tan to brown (Fernández-Herrera et al. 2020); *C. cariniferi* as endophyte in Thailand (Ma et al. 2018) and *C. parallelophorum* (Ma et al. 2018) in the dracaenophilum complex; in the gloeosporioides complex, *C. fructicola* (Ma et al. 2018, 2020a), *C. gloeosporioides*, associated to anthracnose symptoms (initially as small, slightly sunken, water-soaked, circular to semicircular spots progressing to lesions that are dark greyish in the centre with dark-brown margins and bordered by a tan halo; Lan et al. 2016), and *C. jiangxiense*, as endophyte (Ma et al. 2018); *C. orchidearum* (orchidearum complex) associated to anthracnose symptoms (Damm et al. 2019); the singleton species *C. orchidophilum* (Damm et al. 2012a).

On *Oncidium* spp. the *Colletotrichum* species recorded associated with anthracnose symptoms are *C. cymbidiicola* (Chowdappa et al. 2014) and *C. oncidii* (Damm et al. 2012b) in the boninense complex, and *C. arxii* (Liu et al. 2014) in the gigasporum complex.

On *Phalaenopsis* sp., *Colletotrichum* species are *C. fructicola* (Silva-Cabral et al. 2019b), *C. karsti* (Jadrane et al. 2012) and *C. orchidophilum* (Damm et al. 2012a), originating symptoms on leaves (small circular to elliptical necrotic lesions with irregular margins) and petals (with necrotic tissue surrounded by a ring of green tissue).

Other plant-fungus associations in the Orchidaceae include: on *Anoectochilus roxburghii*, *Colletotrichum gloeosporioides* causing leaf spots (Chen et al. 2016b); on *×Ascocenda* sp., *C. orchidophilum* (Damm et al. 2012a); on *Bulbophyllum hirtum* and *Callostylis bambusifolia*, *Colletotrichum cymbidiicola* associated to anthracnose symptoms (Chowdappa et al. 2014); on *Coelogyne*, *Colletotrichum cymbidiicola* (Chowdappa et al. 2014) and *C. coelogyne* (Damm et al. 2019); on *Cynoches aureum*, *Colletotrichum orchidophilum* (Damm et al. 2012a); on *Eria*, *C. liriopes* (Yang et al. 2012b) and *C. orchidearum* (Damm et al. 2019); on *Liparis viridiflora*, *C. cymbidiicola* associated to anthracnose symptoms (Chowdappa et al. 2014); on *Orchis* sp., *C. orchidis* (Hyde et al. 2020b); on *Paphiopedilum*, *C. arxii* (Liu et al. 2014) and *C. tropicicola* (Noireung et al. 2012); on *Pinalia amica*, *C. cymbidiicola* associated to anthracnose symptoms

(Chowdappa et al. 2014); on *Pleione bulbocodioides*, *C. liriopes* (Yang et al. 2012b); *C. vittalense* on an unspecified orchid (Damm et al. 2019).

It seems likely that new species of *Colletotrichum* are to be found on orchids. Much is to be known yet on the ecological role of *Colletotrichum* on orchids, and some of these interactions may provide exquisite cases for studying switching processes between endophytism and parasitism.

### Pandanaceae

*Colletotrichum* is known from *Pandanus pygmaeus* in Thailand, with *C. brevisporum* associated to anthracnose symptoms (Noireung et al. 2012) and *C. siamense* (as *C. pandanicola*; Zhang et al. 2023b) identified as an endophyte (Tibpromma et al. 2018). Previous reports of fungi associated to a leaf disease on *P. utilis* and *P. veitchii* (Noireung et al. 2012) require identification of the pathogens in modern terms.

### Philesiaceae

*Colletotrichum roseum* was described to accommodate fungi isolated from anthracnose symptoms on leaves of *Lapageria rosea* in Chile (Crous et al. 2019a), although the authors refer previous reports of other species of *Colletotrichum* on this host in Chile. Additional research may provide information on the diversity of the pathogen and on the relevance of the disease.

### Poaceae

Maize (*Zea mays*) anthracnose, caused by *Colletotrichum graminicola*, is a widespread disease, causing leaf blight, top dieback and stalk rot (Munkvold & White 2016) and is considered one of the most important diseases of the crop (Mueller et al. 2016). Although the development and use of resistant cultivars alleviated the severe outbreaks recorded in the end of the 20<sup>th</sup> century (Crouch & Beirn 2009), environmental stresses may aggravate disease severity (Belisário et al. 2022). Diversity among *C. graminicola* populations is insufficiently documented and races have not been identified (Crouch & Beirn 2009), although two distinct clades have been noted, corresponding to New and Old-World populations (Crouch & Beirn 2009). High but geographically unstructured diversity has been recorded among Brazilian populations (Parreira et al. 2016). The pathogen has been recurrently detected in new locations recently, including China, Bosnia and Herzegovina, Portugal and Switzerland (Sukno et al. 2014, Sanz-Martín et al. 2016, Cuevas-Fernández et al. 2019, Duan et al. 2019), suggesting that a global comparison of populations may shed additional light over the diversity and host adaptation of the pathogen.

Sorghum (*Sorghum bicolor* and its wild relative *S. halepense*) anthracnose, caused by *Colletotrichum sublineola*, is a relevant disease in warm and humid regions of Africa, Asia and America, affecting the stalk, leaves, the panicle and grains (Frederiksen & Odvody 2000, Tesso et al. 2012, Tsedaley et al. 2016). The use of resistant cultivars is considered the preferred control measure (Tesso et al. 2012). Nevertheless, there are at least 40 physiological races of the pathogen recognised worldwide and the fungus is considered to be very heterogeneous, posing difficulties to the adequate use of resistant cultivars. Race characterisation studies are mainly conducted on regional or national scales (e.g., Valério et al. 2005, Chala et al. 2011, Xavier et al. 2018, Tsedaley et al. 2021) and global studies are lacking. Recently, *C. americae-borealis* was recorded from *S. halepense* in Iran (Khodaei et al. 2019), but its pathological relevance remains to be analysed.

Sugarcane (*Saccharum officinarum*) anthracnose, also known as red rot, is an important disease, caused by *Colletotrichum falcatum* (Crouch et al. 2009a). The most effective control strategy is the use of resistant cultivars (Singh et al. 2017), but breakdown of resistant due to pathogen evolution poses difficulties, although genetic diversity of the pathogen remains elusive (Scindiya et al. 2019). Biological control, namely using *Trichoderma*, has been addressed as a possible alternative control measure (Viswanathan & Malathi 2019). Recently *C. cereale*, *C. sacchari* and *C. sublineola* were reported from *S. spontaneum* in Iran (Alizadeh et al. 2022) and *C. siamense* and *C. plurivorum* from *S. officinarum* in Brazil (Marins et al. 2022).

*Colletotrichum* spp. on bamboos occur mostly asymptotically (Wang et al. 2021b) and are directly associated to the bambusicola species complex (Liu et al. 2022b): on *Chimonobambusa quadrangularis*, *Colletotrichum metake* is known as a seed endophyte (Wang et al. 2021b); on *Pleioblastus simonii*, *C. metake* (Sato et al. 2012); on *Phyllostachys* spp., *C. bambusicola*, *C. guangxiense* and *C. hsienjenchang* (Sato et al. 2012, Wang et al. 2021b, Liu et al. 2022b); on *Semiarundinaria densiflora* (as *Brachystachyum densiflorum*), *C. bambusicola* (Wang et al. 2021b); on the dead culm of an unidentified bamboo, *C. parabambusicola* (Liu et al. 2022b).

Other host-pathogen combinations in the Poaceae include (fungi in the graminicola complex, unless otherwise stated): on *Arrhenatherum elatius*, *Colletotrichum cereale* (Crouch et al. 2009a); on *Avena sativa*, *C. cereale* (Crouch et al. 2009a, Zhao et al. 2021b) and *C. americanae-borealis* (destructivum complex), the latter causing leaf spots (Wang et al. 2022c); on *Axonopus compressus* and *A. fissifolius*, *C. axonopodis* in diverse regions (Crouch et al. 2009a) and *C. hainanense* in China, originating elongated lesions with reddish brown margins containing numerous acervuli with abundant setae, often in long rows parallel to the veins (Zhang et al. 2020c); on *Bothriochloa bladhii*, *C. alcornii* (caudatum complex; Crouch 2014); on *Calamagrostis inexpansa*, *Colletotrichum cereale* (Crouch et al. 2009a); on *Cymbopogon citratus*, *Colletotrichum fructicola* and *C. siamense* (gloeosporioides complex; Manamgoda et al. 2013, Hyde et al. 2018); on *Cynodon dactylon*, *Colletotrichum caspicum* (tibetense complex; Alizadeh et al. 2022); on *Dactylis glomerata*, *C. cereale* (Crouch et al. 2009a); on *Digitaria ciliaris* and *D. sanguinalis*, *C. hanau* (Crouch et al. 2009a); on *Echinochloa crus-galli* and *E. esculenta*, *C. jacksonii* (Crouch et al. 2009a), and on *E. crus-galli* and *E. utilis*, *C. echinochloae*, regarded as a potential bioherbicide (Moriwaki & Tsukiboshi 2009, Gu et al. 2023); on *Eleusine indica*, *C. eleusines* (Crouch et al. 2009a); on *Eremochloa ophiuroides*, *C. eremochloae* (Crouch & Tomaso-Peterson 2012); on *Imperata cylindrica* var. *major*, *C. alcornii* (caudatum complex; Crouch 2014); on *Lolium* sp., *C. cereale* (Alizadeh et al. 2022); on *Miscanthus sinensis*, *C. miscanthi* (Crouch et al. 2009a), and on *Miscanthus* sp., *C. danxiashanense* (Liu et al. 2022b); on *Pennisetum purpureum*, *C. cliviicola*, originating small, reddish brown spots that develop into larger, sunken, necrotic, dark brown, ellipsoid lesions (orchiderarum complex; Han et al. 2019), and, as endophytes, *C. endophyticum*, *C. fructicola*, *C. siamense* and *C. tropicale* (Manamgoda et al. 2013); on *Panicum hemitomom* and *P. virgatum*, *C. navitas*, causing tan coloured and elongated lesions, with sharply tapered ends and reddish brown borders (Crouch et al. 2009b); on *Paspalum dilatatum*, *C. nicholsonii*, and on *P. notatum*, *C. paspali* (Crouch et al. 2009a, Alizadeh et al. 2022); on *Phragmites australis*, *C. persicum* (Alizadeh et al. 2022) and on *Phragmites* sp., *C. destructivum* (destructivum complex; Damm et al. 2014); on *Poa annua*, *C. cereale* (Crouch et al. 2009a); on *Polypogon fugax*, *C. cereale* (Crouch et al. 2009a); on *Rottboellia cochinchinensis*, *C. graminicola* (Hyde et al. 2018); on *Setaria viridis*, *C. truncatum* (truncatum complex; Yu et al. 2023); on *Sorghastrum nutans*, *C. baltimoreense*, *C. caudatum* and *C. somersetense* (caudatum complex; Crouch 2014); on *Themeda triandra*, *C. shivasii* (caudatum complex; Liu et al. 2022b); on *Triticum* sp., *C. karsti* (boninense complex) and *C. cereale* (Crouch et al. 2009a, Damm et al. 2012b); on *Zoysia tenuifolia*, *C. zoysiae* (caudatum complex; Crouch 2014); on unspecified Poaceae, *C. caspicum* (tibetense complex), *C. dolichoconidiophorum* (as *C. dolichoconidiophori*), *C. liriopes*, *C. multiseptatum*, *C. tibetense* (tibetense complex) and *C. paraendophytum* (Alizadeh et al. 2022, Liu et al. 2022b).

There are 27 species of *Colletotrichum* inhabiting Poaceae hosts, mostly from the bambusicola, graminicola and caudatum complexes, and 12 of these species are known from a single host, whereas a few (like *C. cereale*) are known from several host species. This suggests a higher degree of host specialisation as compared to other groups of *Colletotrichum* and it is likely that new species of *Colletotrichum* are revealed as analyses of Poaceae hosts in less surveyed areas (namely the tropics) are performed.

### Pontederiaceae

Anthraco-nose on water hyacinth (*Eichhornia crassipes*) was recently attributed to *Colletotrichum fructicola* in China, causing irregular necrotic lesions on leaves, stems, and crown and petiole rot symptoms, with the fungus being regarded as a potential bioherbicide (Huang et al. 2021a).

### Potamogetonaceae

Recently, *Colletotrichum* spp. were isolated from the aquatic plants *Potamogeton* spp. as endophytes, namely *C. spicati* on *P. wrightii* and *C. karsti* (as *C. wuxuhaiense*; Zhang et al. 2023b) on *P. crispus* and *P. pectinatus* from China (Zheng et al. 2022).

### Saururaceae

Among the Saururaceae, *Colletotrichum* has been recorded only on *Houttuynia cordata*, as *C. truncatum* in Japan and China (Sato et al. 2015, Zhang et al. 2023b) and as *C. siamense* in China (Zhang et al. 2023b).

### Smilacaceae

*Colletotrichum gloeosporioides* was recorded on *Smilax sieboldii* in China causing leaf spots (Zhang et al. 2017), whereas *C. reniforme* was reported from China on *S. cocculoides* (Liu et al. 2022b).

### Tofieldiaceae

On *Tofieldia calyculata*, *Colletotrichum tofieldiae* was recorded in Switzerland (Damm et al. 2019).

### Velloziaceae

On *Vellozia gigantea*, both *Colletotrichum aeshynomenes* and *C. karsti* were recorded as endophytes in Brazil (Ferreira et al. 2017).

### Xanthorrhoeaceae

Daylily (*Hemerocallis* spp.) anthracnose causes leaf spots that begin as reddish-brown lesions with a yellow halo, rapidly expanded down the leaves, resulting in severe blight (Vieira et al. 2014). The disease has been recorded associated with different *Colletotrichum* pathogens: in the dematium complex, *C. hemerocallidis*; in the gloeosporioides complex, *C. gloeosporioides* and *C. siamense*; in the spaethianum complex, *C. liriopes* and *C. spaethianum* (Yang et al. 2012b, Vieira et al. 2014, Chen et al. 2022a).

On *Kniphofia*, *Colletotrichum spaethianum* has been recorded from *K. northiae* in Japan (Sato et al. 2015) and *C. kniphofiae* from *K. uvaria* in the UK (Crous et al. 2018b).

Anthraco-nose of New Zealand flax (*Phormium tenax*) has been documented from various locations and attributed to *Colletotrichum phormii* (Damm et al. 2012a, Serdani et al. 2013). *Colletotrichum kinghornii* was also identified from *Ph. tenax* in 1935 in the UK (Damm et al. 2012a) and from *Ph. cookianum* in 2019 in New Zealand (Crous et al. 2021a).

On *Aloe vera*, leaf spots were recorded in Bangladesh and attributed to *Colletotrichum siamense* (Azad et al. 2020).

On *Xanthorrhoea preissii*, *Colletotrichum xanthorrhoeae* is reported from Australia (Shivas et al. 1998, Weir et al. 2012).

### Zingiberaceae

Anthraco-nose on *Alpinia purpurata* flowers was recently reported from Brazil, caused by *Colletotrichum siamense* (Chaves et al. 2019).

Anthraco-nose of turmeric (*Curcuma longa*) is caused by *Colletotrichum curcumae* and is known from India (Damm et al. 2009). The pathogen was also identified on *Curcuma wenyujin* in



China (Li et al. 2016d). On *C. phaeocaulis*, *Colletotrichum fructicola* and *C. siamense* were associated to leaf spots in China (Zhang et al. 2023b).

Anthrachnose of small cardamom (*Elettaria cardamomum*), causing yellow lesions which elongate to form necrotic streaks that run parallel to the veins, has been reported from India and attributed to several species of *Colletotrichum*: *C. guajavae* in the acutatum complex; *C. karsti* in the boninense complex; *C. gloeosporioides*, *C. siamense* and *C. syzygiicola* in the gloeosporioides complex (Chethana et al. 2016).

Anthrachnose of the medicinal *Amomum villosum* has recently been attributed to *Colletotrichum fructicola* in China, causing leaf spots that start at the tips or edges of the leaves, leading to lesions that are slightly sunken, with a grey-white centre, brown edges, and irregular or round shapes (Song et al. 2021a).

Anthrachnose on torch ginger (*Etilingera elatior*) was recently reported in Brazil causing spots in bracts that evolve to dark brown, depressed, water-soaked lesions, and was attributed to *Colletotrichum siamense* (Duarte et al. 2022).

On *Zingiber officinale*, *Colletotrichum fructicola* was associated to leaf spots in China (Zhang et al. 2023b).

### **Eudicots**

*Colletotrichum* spp. occur across the most emblematic eudicot families, but are notably absent from families such as the Aizoaceae, Capparaceae, Cistaceae, Clusiaceae, Combretaceae, Gesneriaceae, Loranthaceae, Orobanchaceae, Papaveraceae, Saxifragaceae, Scrophulariaceae and Verbenaceae.

### Actinidiaceae

Anthrachnose of kiwi (*Actinidia chinensis*) and of kiwiberry (*A. arguta*) is associated to leaf spots and fruit rot symptoms. On leaves, symptoms begin as irregularly shaped watery lesions, developing into necroses with grey centres and dark brown edges. On fruits, symptoms begin as light brown round spots that develop into slightly sunken brown lesions. Several species of *Colletotrichum* have been associated with the disease: in the acutatum complex, *C. fioriniae* in New Zealand (Damm et al. 2012a) and Japan (Poti et al. 2023), *C. nymphaeae* in Korea (Kim et al. 2018a) and *C. simmondsii* in Australia (Shivas et al. 2016); in the gloeosporioides complex, *C. aenigma*, *C. fructicola* and *C. gloeosporioides* all in China (Deng et al. 2017, Li et al. 2017a, Wang et al. 2019a, Huang et al. 2022d) and *C. gloeosporioides*, *C. fructicola* and *C. siamense* in Japan (Poti et al. 2023); in the boninense complex, *C. karsti* from Japan (Poti et al. 2023). The relative importance of each pathogen to the disease remains to be elucidated, as well as the prevalence and incidence of the disease worldwide. Most of these species of *Colletotrichum* are found throughout the world affecting different fruit crops, suggesting a risk of cross-infection from such crops to kiwi crops.

### Altingiaceae

On American sweetgum (*Liquidambar styraciflua*), *Colletotrichum cigarro* and *C. fructicola* were identified in Italy associated to leaf spots with purple margins, often intersecting the margin of the leaf (Garibaldi et al. 2016b, Guarnaccia et al. 2021).

### Amaranthaceae

Spinach (*Spinacia oleracea*) anthracnose is an important disease worldwide (Uysal & Kurt 2017, Awika et al. 2020), caused by *Colletotrichum spinaciae* (Damm et al. 2009, Kurt et al. 2016, Shivas et al. 2016). Symptoms include small, circular, water-soaked, tan-coloured lesions, with dark acervuli and setae developing under wet conditions.

On beet (*Beta vulgaris*), *Colletotrichum circinans* was reported from New Zealand in 1972 (Damm et al. 2009). Previous reports from Japan, mainly from stems and fruits, attributed to *C. dematium* f. *spinaciae* (Chikuo et al. 1984), pend modern treatment of the pathogen.

On *Salsola*, *Colletotrichum salsolae* is known from Hungary on *S. kali* subsp. *tragus* (Weir et al. 2012) and *C. truncatum* is known from Japan on *S. komarovii* (Sato et al. 2015).

On *Achyranthes bidentata*, *Colletotrichum gloeosporioides* was associated to leaf spots in China (Zhang et al. 2023b).

On the aquatic plant *Alternanthera philoxeroides*, *Colletotrichum dianense* and “*C. philoxeroidis*” have been recently reported as endophytes from China (Zheng et al. 2022), but the latter taxon is null because of concatenated sequences.

### Anacardiaceae

Anthraxnose is one of the most important diseases of cashew (*Anacardium occidentale*) in Africa and America, resulting in defoliation, death of inflorescences and necrosis and falling of immature nuts (Uaciquete et al. 2013). Symptoms include water-soaked lesions on leaves that become orange-reddish prior to defoliation, dark depressed lesions on fruits, necroses on branches and abortion and desiccation of inflorescences (Veloso et al. 2021). The disease has been attributed to *Colletotrichum gloeosporioides*, but recent studies on the diversity of the pathogen in Brazil revealed several species in the gloeosporioides complex associated to the disease in cashew but also on the wild relatives *A. humile* and *A. othonianum*. These include *C. siamense* as the prevalent species, along with *C. chrysophilum*, *C. fructicola*, *C. gloeosporioides*, *C. queenslandicum*, *C. theobromicola* and *C. tropicale* (Veloso et al. 2018, 2021). Comparative virulence analysis and the characterisation of pathogen diversity in other parts of the world are needed to ascertain the pathological status of each of these species and their cross-infection potential to and from other hosts. Such information may prove useful for the adequate identification and deployment of resistant cultivars (Uaciquete et al. 2013).

Anthraxnose is the most important disease of mango (*Mangifera indica*) in several countries, with symptoms occurring on twigs and branches, leaves and especially on fruits, limiting productivity and reducing fruit quality and marketability (Arauz 2000). There are 26 species of *Colletotrichum* associated to mango anthracnose. In the acutatum complex, *C. acutatum* (Shivas et al. 2016), *C. fioriniae* (Damm et al. 2012a) and *C. simmondsii* (Damm et al. 2012a) are known from Australia, *C. pedunculi*, *C. scovillei* and *C. sloanei* from China (Qin et al. 2019, Lin et al. 2023a) and *C. tamarilloi* from Colombia (Pardo-De La Hoz et al. 2016). In the boninense complex, *C. karsti* is known from Brazil, Italy, China and Australia (Damm et al. 2012b, Lima et al. 2013a, 2013b, Ismail et al. 2015, Li et al. 2019b). In the gigasporum complex, *C. gigasporum* is known from China (Li et al. 2019b). In the gloeosporioides complex, *C. alienum* is known from Mexico and China (Tovar-Pedraza et al. 2020, Ahmad et al. 2021, Lin et al. 2023a), *C. asianum* from Brazil, Peru, Colombia, Panama, Mexico, South Africa, China, India, Thailand, Malaysia, Indonesia, the Philippines and Australia (Weir et al. 2012, Lima et al. 2013a, 2015, Sharma et al. 2013, 2015b, Gañán et al. 2015, Shivas et al. 2016, Liu et al. 2017d, Li et al. 2019a, 2019b, Tovar-Pedraza et al. 2020, Wu et al. 2020, Benatar et al. 2021, Lin et al. 2023a, Vilcarromero-Ramos et al. 2023), *C. chrysophilum* from Mexico (Fuentes-Aragón et al. 2020a), *C. cigarro* from Italy (Ismail et al. 2015), *C. cordylinicola* from China (Li et al. 2019b), *C. endophyticum* from China (Li et al. 2019b), *C. fructicola* from Brazil, Mexico, Egypt, China, Korea and India (Lima et al. 2013a, 2015, Sharma et al. 2013, Joa et al. 2016, Li et al. 2019b, Tovar-Pedraza et al. 2020, Wu et al. 2020, Ismail & El-Ganainy 2022, Lin et al. 2023a), *C. gloeosporioides* from Italy, South Africa and China (Weir et al. 2012, Ismail et al. 2015, Li et al. 2019b), *C. musae* from China (Li et al. 2019b), *C. nullisetosum* from China (Yu et al. 2022b), *C. queenslandicum* from Mexico and Australia (Shivas et al. 2016, Fuentes-Aragón et al. 2020b), *C. siamense* from Brazil, Mexico, China, India, Thailand and Malaysia (Lima et al. 2013a, 2015, Sharma et al. 2013, Udayanga et al. 2013, Li et al. 2019a, 2019b, Tovar-Pedraza et al. 2020, Wu et al. 2020, Jayawardena et al. 2023, Lin et al. 2023a, Zhang et al. 2023b), *C. theobromicola* from India (Sharma et al. 2013) and *C. tropicale* from Brazil, Mexico and China (Lima et al. 2013a, 2015, Li et al. 2019b, Tovar-Pedraza et al. 2020, Wu et al. 2020, Lin et al. 2023a). In the magnum complex, *C. magnum* (as *C. liaoningense*; Liu et al. 2022b) is known from China (Li et al. 2019b). In the orchidearum complex, *C. clivicola* (Li et al.

2019b) and *C. plurivorum* (Lu et al. 2022) are known from China. *Colletotrichum asianum*, *C. fructicola* and *C. siamense* are thus the most ubiquitous pathogens worldwide, and *C. asianum* has recently been used for a large-scale germplasm screening for anthracnose tolerance (Grice et al. 2023), but a global study on mango anthracnose etiology and pathology is needed.

Anthracnose on pistachio (*Pistacia vera*) is not a very common disease. Under favourable conditions, however, the disease may be severe, affecting fruit, leaves, and rachises (Lichtemberg et al. 2017). Several causal agents have been recorded, namely *Colletotrichum acutatum* (Damm et al. 2012a, Shivas et al. 2016) and *C. siamense* (Weir et al. 2012, Shivas et al. 2016) in Australia, *C. gloeosporioides* in Italy (Schena et al. 2014), *C. fioriniae* in the USA (Lichtemberg et al. 2017) and *C. karsti* in Italy and the USA (Schena et al. 2014, Lichtemberg et al. 2017). Further surveys on pistachio orchards may help anticipate possible future outbreaks of the disease, since these fungi are common pathogens of other fruit crops.

Additional host-fungus associations in the Anacardiaceae are: on *Choerospondias axillaris*, *Colletotrichum gloeosporioides* occurring in China affecting fruits causing irregular yellow-brown lesions with sunken centres (Li et al. 2017b); on *Pistacia terebinthus*, *C. godetiae* occurring in Spain (Moral et al. 2021); on *Schinus molle*, *C. godetiae* occurring in Mexico (Damm et al. 2012a); on *Toxicodendron radicans*, *C. fioriniae* occurring in the USA causing seedling blight (Kasson et al. 2014).

### Annonaceae

Anthracnose is considered the most important disease of annonaceous fruit crops (soursop - *Annona muricata*, sugar apple - *A. squamosa*, cherimoya - *A. cherimola* and hybrids) due to the effect on blossoms and fruits, on which it originates round, dark-coloured, sunken lesions often of a quiescent nature (Guardado-Valdivia et al. 2018). There are 10 *Colletotrichum* species associated to the disease: in the boninense complex, *C. karsti* from Brazil, Colombia, Mexico and New Zealand (Damm et al. 2012b, Álvarez et al. 2014, Belisário et al. 2018, Costa et al. 2019); in the gigasporum complex, *C. gigasporum* from Brazil (Costa et al. 2019); in the gloeosporioides complex, *C. fructicola* from Brazil (Costa et al. 2017, 2019), *C. gloeosporioides* from Brazil, Colombia and Italy (Álvarez et al. 2014, Schena et al. 2014, Costa et al. 2019), *C. siamense* from Brazil, Colombia and Mexico (Álvarez et al. 2014, Costa et al. 2019, Salinas-Castro et al. 2020, Borges et al. 2021), *C. theobromicola* from Brazil, Colombia and Mexico (Weir et al. 2012, Álvarez et al. 2014, Costa et al. 2019) and *C. tropicale* from Brazil, Colombia, Panama and Cuba (Rojas et al. 2010, Álvarez et al. 2014, García & Manzano 2017, Costa et al. 2019); in the magnum complex, *C. brevisporum* from Brazil (Costa et al. 2019); in the orchidearum complex, *C. cliviicola* from Brazil (Costa et al. 2019); in the acutatum complex, *C. fioriniae* from New Zealand (Liu et al. 2021b). A comparison among the pathogens occurring in Colombia depicted *C. theobromicola* as the most virulent one (Álvarez et al. 2014). In Brazil, *C. theobromicola* is the prevalent pathogen, followed by *C. karsti* (Costa et al. 2019). The occurrence of the other species of *Colletotrichum* on *Annona* spp. and on other tropical fruit crops may cause shifts in the population structure of the pathogen.

### Apiaceae

*Colletotrichum* occur seldomly on Apiaceae and anthracnose on cultivated Apiaceae is notably absent. As such, celery (*Apium graveolens*) stunt anthracnose is an exception. This disease is severe, causing twisted petioles and curled leaves rendering the crop unmarketable, but apparently geographically confined. In Japan the disease is caused by *Colletotrichum nymphaeae* (Yamagishi et al. 2015, Yamagishi 2017), whereas in the USA the disease is caused by *C. fioriniae* (Liu et al. 2021b). The disease has also been observed in Canada and Australia (Liu et al. 2021b), but the pathogens pend modern taxonomic treatment.

Anthracnose (leaf spots with a dark brown margin) on the Chinese medicinal herb *Peucedanum praeruptorum* is caused by *Colletotrichum spaethianum* (Guo et al. 2013) and *C. fructicola* (Ma et al. 2020b).

Other fungus-host combinations in the Apiaceae are: on *Anthriscus sylvestris* stems, *Colletotrichum anthrisci* in the Netherlands and *C. circinans* in Germany (Damm et al. 2009); on *Centella asiatica* healthy leaves, *Colletotrichum gigasporum* (Rakotoniriana et al. 2013) and *C. tabacum* (Damm et al. 2014) in Madagascar; on *Eryngium campestre* dead leaves, *C. dematium* in France (Damm et al. 2009) and *C. eryngiicola* in Russia (Buyck et al. 2017); on *Heracleum persicum*, *C. americanae-borealis* in Iran (Khodaei et al. 2019); on *Heracleum* sp. dead stems, *C. fuscum* in the Netherlands (Damm et al. 2014).

### Apocynaceae

Records of *Colletotrichum* on the Apocynaceae are scarce, except for the ornamentals *Mandevilla* sp. and *Nerium oleander*.

On *Mandevilla* sp., leaf spots are attributed to *Colletotrichum siamense* and *C. truncatum* in Japan (Watanabe et al. 2016) and to *C. simmondsii* in Australia (Shivas et al. 2016). Symptoms include pale brown lesions surrounded by a dark red ring, with dark acervuli in the centre of the lesion.

On *Nerium oleander*, leaf spots are attributed to *Colletotrichum alienum* in Australia (Schena et al. 2014) and to *C. acutatum* in New Zealand and Italy (Damm et al. 2012a, Mosca et al. 2014). Developed lesions are pale grey with black acervuli and a dark border.

Other fungus-host combinations in the Apocynaceae are: on *Allamanda cathartica*, *Colletotrichum siamense* causing leaf spots in China (Huang et al. 2022c); on *Alstonia scholaris*, *C. siamense* (as *C. pandanicola*; Zhang et al. 2023b) in India (Jayawardena et al. 2023); on *Araujia hortorum*, *C. araujiae* associated to purple leaf spots in Argentina (Tan et al. 2022a); on *Carissa macrocarpa* (= *C. grandiflora*), *Colletotrichum karsti*, causing anthracnose on fruits in Spain (García-Lopez et al. 2021); on *Cynanchum atratum*, *Colletotrichum destructivum* causing leaf spots in China (Miao et al. 2017); on *Hemidesmus indicus*, *C. dematium* as an endophyte in India (Rather et al. 2018); on *Hoodia* sp., *C. acutatum* in South Africa (Damm et al. 2012a); on *Parsonsia capsularis*, *C. parsonsiae* as a leaf endophyte in New Zealand (Damm et al. 2012b); on *Plumeria alba*, *C. siamense* in Malaysia (Ismail et al. 2021b) and on *P. rubra*, *C. truncatum* in Japan (Sato et al. 2015); on *Telosma cordata* (as *T. cordarum*), *C. telosmae* (Liu et al. 2022b).

### Aquifoliaceae

Rot of holly (*Ilex* spp.) berries has been reported as causing significant losses, with *Colletotrichum fioriniae* and *C. nymphaeae* identified as minor pathogens (Lin et al. 2018a). *Colletotrichum fioriniae* is also associated to brown spots on *I. integra* leaves in Korea (Woo et al. 2021) and *C. boninense*, *C. karsti*, *C. fructicola*, *C. gloeosporioides*, *C. siamense* and “*C. ligustri*” to leaf spots on *I. chinensis* in China (Zhang et al. 2023b).

### Araliaceae

Ivy (*Hedera* spp.) anthracnose, causing leaf spots, is found in several parts of the world and is caused by *Colletotrichum trichellum* (Damm et al. 2009, Sato et al. 2015). Lesions are pale yellow, surrounded by a dark border. Additionally, *C. hedericola* was described as a saprobe on dead *H. helix* stems (Hyde et al. 2020a) and *C. godetiae* was associated to spots on *H. nepalensis* leaves (Zhang et al. 2023b), but the pathological status of these fungi on ivies remains to be elucidated.

Other fungus-host combinations in the Araliaceae are: on *Fatsia japonica*, *Colletotrichum boninense*, *C. karsti*, *C. fructicola*, *C. gloeosporioides*, *C. jiangxiense* and *C. siamense* associated to leaf spots in China (Shi et al. 2017, Xu et al. 2021, Zhang et al. 2023b); on *Heptapleurum heptaphyllum* (= *Schefflera heptaphylla*), *C. schefflerae* as a saprobe from China (Zhang et al. 2023b); on *Heteropanax fragrans*, *C. siamense* associated to leaf spots in China (Zhang et al. 2023b); on *Meryta sinclairii*, *C. aotearoa* causing leaf spots in New Zealand (Weir et al. 2012); on *Panax ginseng*, *C. lineola* and *C. panacicola* causing leaf and fruit anthracnose in Korea (Choi et al. 2011, Liu et al. 2020c); on *P. quinquefolium*, *C. sojae* causing leaf necroses in China (Guan et



al. 2021); on *Tetrapanax papyrifer*, *C. fructicola* causing leaf spots in China (Tang et al. 2023); on *Schefflera actinophylla*, *C. gloeosporioides* causing leaf spots in China (Huang 2013).

### Asteraceae

Anthraco-nose of safflower (*Carthamus tinctorius*) is an important seed-borne disease-causing seedling wilting, stem blight and leaf spots. The disease is attributed to *Colletotrichum carthami* in Japan (Uematsu et al. 2012) and to *C. chrysanthemi* in Italy and the Czech Republic (Baroncelli et al. 2015a).

A similar situation to that of safflower occurs for garland chrysanthemum (*Glebionis coronaria*, = *Chrysanthemum coronarium*), with *Colletotrichum carthami* recognised as the pathogen in Japan (Uematsu et al. 2012) and *C. chrysanthemi* in China and the Netherlands (Damm et al. 2012a). On *Cichorium intybus*, *Colletotrichum nigrum* has been reported from Chile (Liu et al. 2013b). On *Cirsium japonicum*, *Colletotrichum henanense* is known from China (Liu et al. 2015a). On *Cosmos* sp. seeds, *Colletotrichum cosmi* is known from the the Netherlands (Damm et al. 2012a). On *Dendranthema grandiflorum*, *C. truncatum* was reported in Japan (Sato et al. 2015). On *Erigeron philadelphicus*, *C. liriopes* is known also from Japan (Sato et al. 2015).

Sunflower (*Helianthus annuus*) anthracnose was reported recently in China, with symptoms characterised by elongated stem lesions leading to wilting at flowering time under severe infection conditions (Sun & Liang 2018, Sun et al. 2020d). The pathogen was assigned to *Colletotrichum destructivum*, although *C. truncatum* had also been isolated for sunflower in Australia previously (Shivas et al. 2016). Additionally, *C. nigrum* was also reported as a pathogen of *H. tuberosus* in Serbia (Liu et al. 2013b) and a member of the acutatum complex (presumably *C. nymphaeae*) was reported from the USA associated to anthracnose of sunflower sprouts (French et al. 2013). Irregularly shaped spots on mature *H. verticillatus* leaves, expanding to become dark brown surrounded by chlorotic halos, were reported from the USA and associated to *C. fioriniae* (Odoi et al. 2023).

Pyrethrum (*Tanacetum cinerariifolium*) anthracnose is caused by *C. tanacetii* throughout the crop cultivation range in Australia (Barimani et al. 2013, Damm et al. 2014, Lelwala et al. 2019). Symptoms on leaves include scattered dark-brown sunken spots.

Recently several species of *Colletotrichum* were designated based on fungi isolated from leaf spots on *Ageratina adenophora*, namely *C. adenophorae* (singleton species), *C. robustum* (dracaenophilum complex), *C. analogum*, *C. dimorphum*, *C. gracile*, *C. nanhuaense*, *C. siamense* (as *C. parvisporum*; Zhang et al. 2023b), *C. subhenanense* and *C. yuanjiangense* (gloeosporioides complex), along with other fungi treated as endophytes, namely *C. adenophorae*, *C. cangyuanense*, *C. oblongisporum* (gloeosporioides complex) and *C. speciosum* (acutatum complex) (Yu et al. 2022b).

Other fungus-host combinations in the Asteraceae include: on *Arctium lappa*, *Colletotrichum orchidearum* causing leaf spots in China (Xu et al. 2016); on *Aster tataricus*, *C. destructivum* causing leaf spots in China (Cong et al. 2018); on *Atractylodes japonica* and *A. lancea*, *C. atractylodicola* (Xu et al. 2018b), *C. chlorophyti* (Sun et al. 2019a) and *C. spaethianum* (Guan et al. 2018) causing leaf symptoms in China, whereas on *A. ovata*, *C. cigarro*, *C. fructicola*, *C. ovatense*, *C. plurivorum*, *C. siamense* and *C. sojiae* are associated to leaf lesions in Korea (Hassan et al. 2022); on *Bidens subalternans*, *C. bidentis* causing anthracnose on stems in Brazil (Damm et al. 2013); on *Brachyglottis repanda*, *C. beeveri* causing leaf lesions in New Zealand (Damm et al. 2012b); on *Calendula officinalis*, *Colletotrichum carthami* causing anthracnose on leaves and stems in Japan (Sato et al. 2013); on *Coreopsis lanceolata*, *Colletotrichum fuscum* in Italy (Guarnaccia et al. 2021); on *Laphangium affine*, *C. liriopes* in Japan (Sato et al. 2015); on *Mikania micrantha*, *C. gloeosporioides* causing leaf and stem anthracnose symptoms in China (Zhu et al. 2019b); on *Petasites hybridus*, *C. bambusicola* in China (Liu et al. 2022b); on *Sonchus* sp., *C. sonchicola* as a saprobe on dead stems in Italy (Jayawardena et al. 2017); on *Taraxacum campylodes*, *C. lineola* in Japan (Sato et al. 2015); on *Tragopogon graminifolius*, *C. americanae-borealis* in Iran (Khodaei et al. 2019); on *Xanthium spinosum*, *C. spinosum* (Damm et al. 2013),

and on *X. strumarium*, *C. truncatum* (Shivas et al. 2016), both in Australia; on *Zinnia elegans*, *C. siamense* in China (Li et al. 2021d).

#### Basellaceae

Anthrachnose on *Basella alba* leaves is caused by *Colletotrichum truncatum* in China (Yang et al. 2018). Symptoms include semicircular or irregular-shaped lesions with greyish centres surrounded by deep red borders, leading to leaf wither and death.

#### Begoniaceae

Anthrachnose of begonia (*Begonia* × *semperflorens* and *B. lanternaria*), causing stem and leaf lesions with large brown sunken necroses, is attributed to *Colletotrichum truncatum* and *C. karsti* and is known from China (Zhai et al. 2018, Wu et al. 2022b).

#### Berberidaceae

Anthrachnose of *Berberis* spp., including *B. aquifolium* (= *Mahonia aquifolium*) and *B. glaucocarpa*, causing leaf blight, has been reported from New Zealand, attributed to *Colletotrichum aotearoa* (Weir et al. 2012) and from Italy, Germany and the Netherlands, attributed to *C. fiorinae*, *C. godetiae* and *C. nymphaeae* (Damm et al. 2012a, Garibaldi et al. 2020, Guarnaccia et al. 2021). *Colletotrichum godetiae* and *C. karsti* were also associated to leaf spots on *B. fortunei* (= *M. fortunei*) in China (Zhang et al. 2023b). An additional fungal taxon has been associated to leaf spots on *B. aquifolium*, named “*C. japonicum*” (Bedlan 2012, Świdarska-Burek 2021), but this taxon is pending modern taxonomic treatment. Symptoms include circular, brown, slightly sunken, necrotic lesions with a well-defined border, surrounded by a chlorotic halo.

On *Nandina domestica*, leaf blight is caused by *Colletotrichum karsti* in China (Li et al. 2018b).

#### Betulaceae

Hazelnut (*Corylus avellana*) anthracnose is recorded sporadically, causing lesions at the bottom end of the hazelnut cluster. The disease has been recorded from Turkey, Iran and Italy (Mirhosseini-Moghaddam et al. 2007, Belisario & Santori 2009, Sezer et al. 2017), but the pathogen has been identified in modern terms only from Turkey, as *Colletotrichum fiorinae* (Sezer et al. 2017).

*Colletotrichum simulanticitri* was recently recorded from *Betula* sp. in China, associated to leaf spots (Yu et al. 2022b).

#### Bignoniaceae

Host-fungus combinations in the Bignoniaceae include: on *Catalpa fargesii* f. *duciouxii*, *Colletotrichum gloeosporioides* causing leaf spots in China (Fu et al. 2013a); on *Jacaranda mimosifolia*, *C. karsti* causing brown leaf spots in China (Dai et al. 2022); on *Radermachera sinica* (china doll), *C. siamense* in China associated leaf anthracnose symptoms, although *C. fructicola* and *C. karsti* were also isolated but pathogenicity was not confirmed (Yu et al. 2022a) and *C. radermacherae* was isolated as a saprobe (Zhang et al. 2023b); on *Tecomanthe speciosa*, *C. boninense* in New Zealand (Damm et al. 2012).

#### Boraginaceae

Host-fungus combinations in the Boraginaceae include: on *Cordia alliodora*, *Colletotrichum tropicale* as an endophyte in Panama (Rojas et al. 2010); on *Echium italicum*, *C. destructivum* in Iran (Khodaei et al. 2019).

#### Brassicaceae

Anthrachnose of *Brassica* spp. (and other Brassicaceae) crops is a disease reported recurrently (e.g., Mahmodi et al. 2013c, Lee & Hong 2015), and traditionally associated to *Colletotrichum*

*higginsianum* (Damm et al. 2014). Besides *C. higginsianum*, other species associated to anthracnose of *Brassica* spp. are *C. brassicicola* (Damm et al. 2012b), *C. truncatum* (Sato et al. 2015, He et al. 2016) and *C. fructicola* (Yu et al. 2022c).

*Colletotrichum* occurrence on *Arabidopsis thaliana* has provided important research models, both concerning fungus-leaf pathogenic interactions (O'Connell et al. 2004) and fungus (*C. tofieldiae*)-root mutualistic interactions (Hacquard et al. 2016).

Rocket (*Eruca vesicaria*; = *E. sativa*) anthracnose symptoms are leaf spots and have been attributed to *Colletotrichum higginsianum* in the USA (Patel et al. 2014) and to *C. cigarro* in Italy (Garibaldi et al. 2016a). Symptoms appear as small pale or water-soaked circular spots, surrounded by dark brown or black borders, expanding to round or irregular shapes, to form extensive dead areas.

Other host-fungus combinations in the Brassicaceae include: on *Raphanus raphanistrum*, *Colletotrichum lini* reported from Tunisia, and on *Raphanus sativus*, *C. higginsianum*, reported from Japan (Damm et al. 2014); on *Matthiola incana*, *C. higginsianum*, reported from Japan and Romania (Damm et al. 2014).

### Burseraceae

On *Tetragastris panamensis*, *Colletotrichum fructicola* was reported as a leaf endophyte in Panama (Weir et al. 2012).

### Buxaceae

Boxwood (*Buxus* spp.) shoot dieback is considered a new disease (Singh & Doyle 2017), reported from the USA, with the causal agent identified as *Colletotrichum theobromicola* (Singh et al. 2015). Diseased plants shown black discolouration beneath the bark and extending along the affected stems and branches. Variability in disease response among cultivars has been reported (Kaur et al. 2022) Additionally, *C. yunnanense* has been reported as an endophyte (Liu et al. 2007, Damm et al. 2019) and *C. buxi* from healthy leaves (Liu et al. 2022b), both from China.

### Cactaceae

Anthracnose is an important disease of pitaya/dragon fruit (*Selenicereus undatus*; syn. *Hylocereus undatus*), with symptoms occurring on stems and fruits. Symptoms are characterised by reddish-orange spots with chlorotic halos. Fruit lesions develop at maturity and during storage and are attributed to *Colletotrichum truncatum* and reported from Asia (Guo et al. 2014b, Sato et al. 2015, Ngoc et al. 2018, Salunkhe et al. 2023). Stem lesions are originated by *C. aenigma* (Meetum et al. 2015), *C. siamense* (Meetum et al. 2015, Zhao et al. 2018, Abirami et al. 2019), *C. fructicola* (Udayanga et al. 2013) and *C. karsti* (Nascimento et al. 2019b), reported from Asia and South America. Recently, *C. tropicale* was reported causing anthracnose on *S. monacanthus* in the Philippines (Evallo et al. 2023) and Mexico (Nuñez-García et al. 2023).

On *Nopalea cochenillifera*, brown sunken spots on cladodes are caused by *Colletotrichum fructicola* and *C. siamense* and are known from Brazil (Conforto et al. 2017).

On Barbados gooseberry/ora-pro-nóbis (*Pereskia aculeata*), leaf spots were recorded in Brazil and attributed to *Colletotrichum pereskiae* (Custódio et al. 2021).

### Calycanthaceae

On *Chimonanthus praecox*, *Colletotrichum karsti* was associated to leaf spots in China (Zhang et al. 2023b).

### Campanulaceae

Host-fungus combinations in the Campanulaceae include: on *Campanula* sp., *Colletotrichum higginsianum* in Iran (Khodaei et al. 2019); on *Campanula rapunculoides* and *C. trachelium*, *Colletotrichum nymphaeae* and *C. lineola* respectively, in Italy (Guarnaccia et al. 2021); on

*Isotoma axillaris*, *C. lineola* in Japan (Sato et al. 2015); on *Lobelia* sp., *C. acutatum* in the Netherlands (Damm et al. 2012a), and on *Lobelia chinensis*, *C. magnum* in China (Li et al. 2013a).

#### Cannabaceae

On Japanese hop (*Humulus scandens*), *Colletotrichum fioriniae* was reported in the USA associated to severe chlorotic and necrotic leaf lesions (Frederick et al. 2021).

*Colletotrichum celtidis* was reported from leaf litter of *Celtis formosana* in China (Tennakoon et al. 2021).

#### Caprifoliaceae

On *Patrinia villosa*, *Colletotrichum bambusicola* was recorded in China (Liu et al. 2022b).

#### Caricaceae

Papaya (*Carica papaya*) anthracnose affects fruits at maturity and during storage, originating sunken dark brown lesions, often covered by orange spore masses, and is thus subject of extensive research regarding chemical and biological control, coating, and selection of storage conditions (Oliveira et al. 2016b, Silva-Jara et al. 2019, Vilaplana et al. 2020). Symptoms also occur on leaves as dark brown lesions with black margins and surrounded by a yellow halo. Seventeen species of *Colletotrichum* have been associated with the disease: in the acutatum complex, *C. acutatum* is known from Australia (Damm et al. 2012a, Shivas et al. 2016) and *C. simmondsii* from Australia (Damm et al. 2012a, Shivas et al. 2016) and Costa Rica (Ruiz-Campos et al. 2022); in the boninense complex, *C. karsti* is known from Brazil (Damm et al. 2012a, Vieira et al. 2022); in the gigasporum complex, *C. zhaoqingense* is known from China (Liu et al. 2022b); in the gloeosporioides complex, *C. chrysophilum* is known from Mexico (Pacheco-Esteve et al. 2022a) and Brazil (Vieira et al. 2022); *C. fructicola* from Mexico (Marquez-Zequera et al. 2018), Costa Rica (Ruiz-Campos et al. 2022) and Brazil (Vieira et al. 2022), *C. gloeosporioides* from Brazil (Vieira et al. 2022), *C. queenslandicum* from Australia (Weir et al. 2012) and Brazil (Vieira et al. 2022), *C. salsolae* from India (Saini et al. 2017a), *C. siamense* from South Africa, China, Brazil and Mexico (Weir et al. 2012, Zhang et al. 2021a, Pacheco-Esteve et al. 2022b, Vieira et al. 2022), *C. theobromicola* from Costa Rica (Ruiz-Campos et al. 2022) and Brazil (Vieira et al. 2022) and *C. tropicale* from Costa Rica (Ruiz-Campos et al. 2022); in the magnum complex, *C. brevisporum* is known from Australia, the Philippines, China and Brazil (Vieira et al. 2013, Shivas et al. 2016, Duan et al. 2018b, Damm et al. 2019, Liu et al. 2019c, Laurel et al. 2021), *C. magnum* from Costa Rica (Ruiz-Campos et al. 2022) and Brazil (Tapia-Tussell et al. 2016) and *C. okinawense* from Brazil and Japan (Damm et al. 2019, Dias et al. 2020, Vieira et al. 2022); in the orchidearum complex, *C. plurivorum* is known from China, Brazil and Mexico (Sun et al. 2019b, García-Estrada et al. 2020, Vieira et al. 2022); in the truncatum complex, *C. truncatum* is known from Brazil, Costa Rica, the Philippines, Korea and Japan (Sato et al. 2015, Aktaruzzaman et al. 2018, Vieira et al. 2020, 2022, Laurel et al. 2021, Ruiz-Campos et al. 2022). Global studies are needed to shed additional light on the relative importance of these species to papaya anthracnose worldwide. To this end, Vieira et al. (2022) have shown *C. okinawense* as the prevalent species in Brazil as well as the most virulent, along *C. truncatum*.

#### Caryocaraceae

On *Caryocar brasiliense*, *Colletotrichum paranaense* was reported from Brazil (Bragança et al. 2016a).

#### Caryophyllaceae

On *Dianthus* spp., three species of *Colletotrichum* have been reported: *C. tofieldiae* in the UK (Damm et al. 2009) and *C. lineola* and *C. spaethianum* in Japan (Sato et al. 2015).

On *Saponaria officinalis*, *Colletotrichum lineola* has been reported from Japan (Sato et al. 2015).

### Celastraceae

Anthracnose of *Euonymus japonicus* is characterised by the occurrence of leaf spots, often at the leaf margin, with grey-white, brown borders, surrounded by a yellow halo. It has been reported from China and the causal agents assigned to *Colletotrichum aenigma* (Tan et al. 2023), *C. gloeosporioides* (Huang et al. 2016, Li et al. 2017c), *C. siamense* (Wu 2020, Tan et al. 2023) and *C. theobromicola* (Qin et al. 2023), although a fungus presumably from the boninense complex has been reported from Korea (Lee et al. 2005).

### Ceratophyllaceae

On the aquatic plant *Ceratophyllum demersum*, “*Colletotrichum demersi*” has been recently reported as an endophyte from China (Zheng et al. 2022), but this taxon is null because of chimeric concatenated sequences.

### Chenopodiaceae

Anthracnose of quinoa (*Chenopodium quinoa*) was recently reported in the USA associated to slightly sunken, oval to linear stem lesions containing setose acervuli and attributed to *Colletotrichum nigrum* and *C. truncatum* (Pal & Testen 2021), although this appears to be a minor disease (Colque-Little et al. 2021).

### Chloranthaceae

On *Sarcandra glabra*, *Colletotrichum siamense* was recorded as the causal agent of leaf and stem spots in China (Ye et al. 2016).

### Chrysobalanaceae

On *Licania tomentosa* in Brazil, anthracnose affects stems and fruits, with the causal agents identified as *Colletotrichum siamense* and *C. tropicale* (Lisboa et al. 2018). Additionally, *C. queenslandicum* and *C. fructicola* were also found to occur as endophytes on *L. tomentosa* (Lisboa et al. 2018).

### Convolvulaceae

Host-fungus combinations in the Convolvulaceae include: on *Convolvulus arvensis*, *Colletotrichum americae-borealis* from Iran (Khodaei et al. 2019); on *Cuscuta* sp., *Colletotrichum cuscutae* from Dominica (Damm et al. 2012a) and *C. fiorinae* from the USA (Liu et al. 2021b); on *Ipomoea batatas*, *C. chlorophyti* from Japan (Sato et al. 2015), on *I. pes-caprae*, *C. condaoense* from Vietnam (Crous et al. 2018c) and on *I. purpurea* (as *Pharbitis purpurea*), *C. siamense* (Dai et al. 2023b); on *Merremia umbellata*, *C. merremiae* and *C. panamense* both as endophytes from Panama (Damm et al. 2019).

### Cornaceae

Anthracnose of Cornelian cherry (*Cornus mas*) affects fruits at maturity, causing brown sunken spots covered with orange masses of conidia. In Hungary, the causal agent has been identified as *Colletotrichum godetiae* (Tóth et al. 2017). Marginal leaf lesions (grey centre and reddish-brown edges) on *Cornus hongkongensis* in China were recently attributed to *Colletotrichum gloeosporioides* and *C. siamense* (Wang et al. 2021d, Zhang et al. 2022c).

### Crassulaceae

Anthracnose of *Sedum kamtschaticum* is known to affect leaves and stems, causing necrotic lesions. It has been recorded from Korea and assigned to *Colletotrichum gloeosporioides* and *C. aenigma* (Jeon & Kwak 2016, Choi et al. 2017). Additionally, *C. sedi* was also found as a saprobe on dead *Sedum* sp. stems in Russia (Liu et al. 2015b).

## Cucurbitaceae

Watermelon (*Citrullus lanatus*) anthracnose, causing necrotic spots on leaves and sunken lesions on fruits, is a disease that lost relevance during the 20th century because of the use of resistant cultivars (Maynard & Hopkins 1999). Fungi associated to the disease include *Colletotrichum orbiculare* and *C. magnum* reported from the USA (Rennberger et al. 2018, Damm et al. 2019), *C. karsti* reported from New Zealand (Damm et al. 2012b) and *C. scovillei* reported from Malaysia (Goh et al. 2022), but the pathological importance and geographical distribution of these fungi on watermelon needs to be established and compared. To this end, a recent study (Guo et al. 2022) revealed *C. orbiculare* as the most prevalent pathogen in the major watermelon growing provinces in China, but another 14 species of *Colletotrichum* were identified associated to watermelon anthracnose.

Anthracnose in melon (*Cucumis melo*) is a minor disease in global terms, with effective control being usually achieved with adequate agricultural practices and selection of cultivars (Ge et al. 2013). Species of *Colletotrichum* recognised as associated to the disease are *C. karsti* in Japan (Damm et al. 2012b), *C. melonis* in Brazil (Damm et al. 2012a) and *C. orbiculare* in Japan (Damm et al. 2013), but the pathological importance and geographical distribution of these fungi on melon needs to be established and compared. Anthracnose on Luffa sponge gourd (*Luffa cylindrica*; syn. *Cucumis melo*) was recently associated to *Colletotrichum fructicola* and *C. siamense* in China, causing oval to irregular chlorotic leaf lesions surrounded by yellow halos (Li et al. 2022f).

The cucumber (*Cucumis sativus*) anthracnose pathosystem is often used to study the induction of resistance by chemicals as alternative to control using fungicides (Eskandari et al. 2020). The disease is caused by *Colletotrichum orbiculare* (the synonym *C. lagenarium* is still commonly found in the literature), but *C. truncatum* has also been reported associated to cucumber (Sato et al. 2015).

Anthracnose of squash and pumpkins (*Cucurbita* spp.) is a common disease causing necrotic lesions on fruits, but usually of low severity. Fungi associated have been identified as *Colletotrichum orbiculare* (Damm et al. 2013), *C. coccodes* (Liu et al. 2013b), *C. brevisporum* (Liu et al. 2018c) and *C. fioriniae* (Liu et al. 2021b).

Other fungus-host combinations in the Cucurbitaceae include: on *Benincasa hispida*, *Colletotrichum orbiculare* in Australia (Shivas et al. 2016); on *Bryonia cretica* subsp. *dioica*, *C. bryoniicola* in the Netherlands (Damm et al. 2014); on *Lagenaria siceraria*, *C. orbiculare* in Portugal (Damm et al. 2013); on *Momordica cochinchinensis*, *C. brevisporum* in China (Chai et al. 2018); on *Sechium edule*, *C. brevisporum* in Brazil (Bezerra et al. 2016, Damm et al. 2019); on *Trichosanthes kirilowii*, *C. magnum* (as *C. liaoningense*; Liu et al. 2022b) in China causing fruit lesions developing from small off-white necrotic spots to larger, irregular grey necrotic lesions on green fruits leading to fruit rot and fruit drop (Zhang et al. 2022a).

## Dipterocarpaceae

A leaf spot disease on *Hopea odorata* was recently reported from Bangladesh and attributed to *Colletotrichum viniferum* (Rashid et al. 2020). Similarly, leaf spots on *Shorea siamensis* in Thailand were attributed to *C. aeshynomenes* (Jayawardena et al. 2023).

## Droseraceae

On the Venus flytrap (*Dionaea muscipula*), leaf blight is attributed to *Colletotrichum siamense* in Australia (Shivas et al. 2016).

## Ebenaceae

Persimmon (*Diospyros kaki*) anthracnose has become increasingly important over the last few decades. The disease affects the fruits, causing sunken necrotic lesions, and may be a post-harvest disease in certain circumstances (Palou et al. 2015). It can also affect twigs and leaves, causing severe defoliation and even death of the entire tree (Xie et al. 2010, Blood et al. 2015, Dolinski et al. 2022). There are ten species of *Colletotrichum* recorded from persimmon: in the acutatum



complex, *C. melonis* is known from Brazil (Carraro et al. 2019) and *C. nymphaeae* from Brazil (Carraro et al. 2019) and Korea (Hassan et al. 2019a); in the boninense complex, *C. karsti* is known from Australia (Damm et al. 2012b, Shivas et al. 2016) and China (Wang et al. 2016b, Zhang et al. 2023e); in the dematium complex, *C. jinshuiense* (as *C. kakiivorum*; Liu et al. 2022b) is known from Korea (Lee & Jung 2018); in the gloeosporioides complex, *C. alienum* is known from New Zealand (Weir et al. 2012), *C. fructicola* from Brazil (Carraro et al. 2019), China (Zhang et al. 2023e) and from fruits imported from an unknown location into the Philippines (Evallo et al. 2022), *C. gloeosporioides* from Spain (Palou et al. 2015), *C. horii* from Brazil (Blood et al. 2015, Mio et al. 2015), China (Weir et al. 2012, Zhang et al. 2023e), Korea (Kwon et al. 2013, Jeon et al. 2017, An et al. 2018), Japan (Weir et al. 2012) and New Zealand (Weir et al. 2012) and *C. siamense* from Korea (Chang et al. 2018a) and China (Zhang et al. 2023e); in the orchidearum complex, *C. cliviicola* is known from China (Zhang et al. 2023e). Whereas *C. horii* is the most widespread persimmon anthracnose pathogen, the pathological relevance and geographic distribution of these ten species should be further dissected, in order to improve control measures and to foresee possible future changes in the disease and fungal population structure. For instance, in São Paulo and Paraná states in Brazil, *C. horii*, *C. fructicola* and *C. nymphaeae* were found at similar frequencies and showing little differences in virulence (Carraro et al. 2022), whereas in Guangxi (China) *C. fructicola* showed to be the most virulent in a study comparing five *Colletotrichum* species (Zhang et al. 2023e).

#### Elaeocarpaceae

Anthracnose of *Elaeocarpus sylvestris* causes leaf spots with light brown centre and deep red borders. The disease is known from China and caused by *Colletotrichum gloeosporioides* (Li et al. 2016b).

#### Ericaceae

Blueberry (*Vaccinium* spp.) anthracnose is an important disease in humid areas, affecting fruits at maturity as necrotic lesions covered in orange spore masses, although leaves and stems can also be affected. The disease is generally managed with fungicides and cultural practices (Miles et al. 2013). There are 12 species of *Colletotrichum* known from *Vaccinium* spp. In the acutatum complex, *C. fioriniae* is known from the USA (Damm et al. 2012a, Eaton et al. 2021, Liu et al. 2021b), Chile (Castro et al. 2023), the Netherlands (Damm et al. 2012a), Italy (Mosca et al. 2014), Poland (Pszczółkowska et al. 2016) and New Zealand (Damm et al. 2012a), *C. rhombiforme* is known from China (Wang et al. 2019b) and the USA (Damm et al. 2012a), *C. salicis* is known from Norway (Baroncelli et al. 2015b) and *C. simmondsii* is known from Australia (Shivas et al. 2016). In the boninense complex, *C. karsti* is known from Brazil (Rios et al. 2015). In the gloeosporioides complex, *C. chrysophilum* is known from Brazil (Soares et al. 2022), *C. cigarro* is known from the USA (Weir et al. 2012), *C. fructivorum*, *C. rhexiae*, *C. siamense* and *C. temperatum* are known from the USA (Doyle et al. 2013), *C. helleniense* is known from Italy (Guarnaccia et al. 2022) and *C. yulongense* is known from China (Wang et al. 2019b). A global analysis is needed to ascertain the etiology of blueberry anthracnose.

Other host-fungus combinations in the Ericaceae include: on *Kalmia* sp., *Colletotrichum fioriniae* from the USA (Damm et al. 2012a); on *Rhododendron* spp., *C. celtidis* from China (Zhang et al. 2023b), *C. fioriniae* from the USA (Damm et al. 2012a), Korea (Sultana et al. 2018) and China (Hu et al. 2022) and *C. gloeosporioides* from China (Zhang et al. 2023b), all associated to leaf spots, and *C. salicis* from Latvia (Damm et al. 2012a).

#### Euphorbiaceae

*Colletotrichum* leaf disease of rubber tree (*Hevea brasiliensis*), originating leaf necroses, causes relevant yield losses throughout the world (Liu et al. 2018a), providing an important model to study resistance and pathogenicity mechanisms (Lin et al. 2018c, Yang et al. 2020b). The identity of the pathogen has been subject of diverse studies and for a long time it has been

recognised the occurrence of genetically distinct fungi associated to the disease (Sreenivasaprasad et al. 1994, Liu et al. 2018a), which is critical for the selection of the most appropriate fungi for studies dissecting plant-fungus interactions. There are 13 species of *Colletotrichum* associated to the disease. In the acutatum complex: *C. acutatum* is known from Sri Lanka (Hunupolagama et al. 2017); *C. australisinese* and *C. bannaense* from China (Liu et al. 2018a); *C. laticiphilum* from China (Shi et al. 2019a), Sri Lanka (Hunupolagama et al. 2017), India and Colombia (Damm et al. 2012a); *C. nymphaeae* (as *C. citri*) from Sri Lanka (Hunupolagama et al. 2017); *C. simmondsii* from Sri Lanka (Hunupolagama et al. 2017); *C. wanningense* from China (Cao et al. 2019b). In the boninense complex, *C. annellatum* is known from Colombia (Damm et al. 2012b) and *C. karsti* from China (Cai et al. 2016a). In the gloeosporioides complex, *C. fructicola* (Cao et al. 2019b), *C. ledongense* (Liu et al. 2018a) and *C. siamense* (Cao et al. 2019b) are known from China. In the orchidearum complex, *C. cliviicola* (as *C. cliviae*) is known from China (Zhang et al. 2021e). Population analysis studies have shown that *C. simmondsii* is the major pathogen in Sri Lanka (Hunupolagama et al. 2017) and that *C. siamense* and *C. australisinese* are the most prevalent pathogens in China (Liu et al. 2018a, Cao et al. 2019b). Studies of this kind, focusing on the American continent, may shed additional light on the diversity of the pathogen and prevalence of each species.

On cassava (*Manihot esculenta*), anthracnose affects the crop throughout the world, causing lesions on stems, leaves, and fruits, and tip dieback (Fokunang et al. 2001) and the selection of resistant genotypes can convey disease control (Owolade et al. 2005). Twelve species of *Colletotrichum* have been associated to the disease: in the acutatum complex, *C. lupini* is known from Rwanda (Damm et al. 2012a); in the gloeosporioides complex, *C. aeshynomenes* is known from Thailand (Sangpueak et al. 2018), *C. chrysophilum* from Brazil (Machado et al. 2021a), *C. fructicola* from China (Liu et al. 2019a) and Brazil (Bragança et al. 2016b, Oliveira et al. 2020), *C. siamense* from China (Liu et al. 2019a) and Brazil (Oliveira et al. 2018, 2020), *C. theobromicola* from Brazil (Oliveira et al. 2018, 2020) and *C. tropicale* from Brazil on wild cassava species *M. dichotoma* and *M. epruinosa* (Oliveira et al. 2016a); in the boninense complex, *C. boninense* is known from Thailand (Hyde et al. 2018) and *C. karsti* from China (Liu et al. 2019a); in the orchidearum complex, *C. musicola* is known from Brazil (Machado et al. 2022) and *C. plurivorum* from China (Liu et al. 2019a); in the truncatum complex, *C. truncatum* is known from Thailand (Hyde et al. 2018) and Brazil (Machado et al. 2021b). A survey conducted in the Recôncavo of Bahia area of the Bahia state in Brazil suggested *C. fructicola* as the main causal agent of cassava anthracnose in the area (Oliveira et al. 2020) and this fungus also proved as the most virulent in a study conducted in China (Liu et al. 2019a), but the relative importance of these *Colletotrichum* species to cassava anthracnose in global terms remains to be elucidated.

Anthracnose on physic nut (*Jatropha curcas*) causes lesions on stems, leaves and fruits, with diversity on disease response being recognised among ecotypes (Ferreira-Pinto et al. 2011). The causal agent has been assigned to *Colletotrichum truncatum* in Burkina Faso (Ellison et al. 2015).

Other host-fungus combinations in the Euphorbiaceae include: on *Euphorbia pulcherrima*, *Colletotrichum truncatum* known from Japan (Sato et al. 2015); on an unspecified species of *Euphorbia*, the rare *C. euphorbiae* from South Africa (Crous et al. 2013); on *Plukenetia volubilis*, *C. siamense* from China (Wang et al. 2020c); on *Ricinus communis*, *C. siamense* from China (Tang et al. 2021); on *Sclerocroton integerrimus*, *C. karsti* from Australia (Damm et al. 2012b); on *Vernicia montana*, *C. fioriniae* from China (Zhang et al. 2021c).

## Fabaceae

Anthracnose of soybean (*Glycine max*) is an important disease in tropical areas, causing severe yield losses associated to disease symptoms on seedlings, leaves, pods, stems and petioles, presenting typical necrotic patterns on the abaxial leaf veins (Sharma et al. 2011, Dias et al. 2019, Bouffleur et al. 2021). The pathogen microsclerotia can survive in soil until a subsequent cultivation cycle (Tikami et al. 2023). Control is achieved by the employment of fungicides, but resistance sources have been recently highlighted in India, using local pathogen populations, assigned to

*Colletotrichum truncatum* based on morphological characters (Nataraj et al. 2020). However, there are 10 species of *Colletotrichum* associated to soybean anthracnose: *C. chlorophyti* (singleton species) known from the USA (Yang et al. 2012a, Yang et al. 2013) and India (Bhatt et al. 2022); in the gloeosporioides complex, *C. fructicola* from China (Xu et al. 2023b) and *C. gloeosporioides* from Malaysia (Mahmodi et al. 2013b); in the magnum complex, *C. brevisporum* from China (Shi et al. 2021); in the orchidearum complex, *C. cliviicola* from Brazil (Barbieri et al. 2017) and India (Bhatt et al. 2022), *C. musicola* from Brazil (Bouffleur et al. 2020), *C. plurivorum* from Myanmar (Zaw et al. 2020) and *C. sojae* from Iran, Serbia, Italy and the USA (Damm et al. 2019); in the spaethianum complex, *C. incanum* from the USA (Yang et al. 2014); *C. truncatum* from the USA (Yang et al. 2014), Brazil (Rogério et al. 2019), India (Bhatt et al. 2022, Kavanashree et al. 2022), Myanmar (Zaw et al. 2020), Thailand (Hyde et al. 2018), China (Hu et al. 2015), Japan (Sato et al. 2015) and Australia (Shivas et al. 2016). Whereas *C. truncatum* appears to be the most prevalent pathogen of soybean anthracnose (Dias et al. 2019), the analysis by Damm et al. (2019) shows that *C. sojae* was detected along with *C. truncatum* and that this species also occurs in diverse locations, drawing attention on the need for global studies on soybean anthracnose pathogen prevalence and distribution.

Lentil (*Lens culinaris*) anthracnose is a major disease worldwide. Lesions affect leaves, stems, flowers and pods and the disease is caused by *Colletotrichum lentis* (Altaf et al. 2018). There are two known races of the pathogen (Banniza et al. 2018), with virulence assigned to a mini-chromosome (Bhadauria et al. 2019). Breeding for disease resistance is thus guided by knowledge of pathogen diversity (Buchwaldt et al. 2018). An additional fungal species, *C. nigrum*, was also associated to the disease (Liu et al. 2013b), but its pathological relevance in this pathosystem remains to be evaluated.

Lupin (*Lupinus* spp.) anthracnose is an important disease of lupins cultivated for grain, forage and as ornamentals, that spread throughout the world in the last 40 years. The disease is seed-borne and can thus affect seedlings, as well as stems and pods (Talhinhas et al. 2016). The disease is globally caused by a rather homogeneous fungal population belonging to *Colletotrichum lupini* (Nirenberg et al. 2002, Talhinhas et al. 2002, Dubrulle et al. 2020), although variability among South American populations has recently been disclosed (Alkemade et al. 2021).

Anthracnose of common bean (*Phaseolus vulgaris*) can cause up to 100% yield losses in cool and humid environments (Mohammed 2013, Padder et al. 2017). Typical symptoms include black-red sunken necroses in pods, often developing also on seeds, and red to purple discolouration of leaf veins. Agricultural practices and the use of fungicides may convey protection to the crop, but disease resistance breeding is the most sustainable control measure (Singh & Schwartz 2010). However, the bean anthracnose pathosystem is characterised by a unique profusion of pathogen races within the species *Colletotrichum lindemuthianum* (Pastor-Corrales 1991, Kelly & Vallejo 2004, Nabi et al. 2022), hampering the selection of cultivars depending on the evolving local pathogen populations (Conner et al. 2020, Kamfwa et al. 2021, Xavier et al. 2021).

Anthracnose is considered the most important disease of cowpea (*Vigna* spp.), originating tan to brown sunken spots on leaves and branches, causing up to 100% yield losses under favourable conditions (Siqueira et al. 2019). Although the infection process has been subject of detailed research (Latunde-Dada et al. 1996, Silva et al. 2019), the variability of the pathogen is considered a factor hampering the deployment of adequate control measures (Siqueira et al. 2019). In fact, there are seven species of *Colletotrichum* associated to the disease: *C. chlorophyti* (singleton species) is known from Japan on *V. radiata* (Sato et al. 2015); in the dematium complex, *C. lineola* from Japan on *V. angularis* (Sato et al. 2015); in the destructivum complex, *C. vignae* from Nigeria on *V. unguiculata* (Damm et al. 2014); in the orchidearum complex, *C. cliviicola* from Nigeria (Adenike et al. 2023) and *C. sojae* from Iran (Damm et al. 2019) both on *V. unguiculata*; *C. truncatum* from Thailand and Japan on *V. unguiculata* (Sato et al. 2015, Hyde et al. 2018); *C. plurivorum* from China on *V. unguiculata* (Liu et al. 2022b).

Anthraco-nose of chickpea (*Cicer arietinum*) has been recently reported from Malaysia, causing leaf spots and premature leaf drop, and associated to *Colletotrichum truncatum* (Mahmodi et al. 2013a).

Anthraco-nose of peanut (*Arachis hypogaea*) is seldom referred. The disease causes leaf spots and is attributed to *Colletotrichum truncatum*, which has been reported from the Gambia (Damm et al. 2009), Australia (Shivas et al. 2016) and China (Yu et al. 2020), but also to *C. fructicola* in China (Gong et al. 2023).

Anthraco-nose reports on pea (*Pisum sativum*) associated to *Colletotrichum pisicola* are known from Ecuador, Mexico and the USA, but records are ancient (Damm et al. 2014). However, recently the disease was reported from Brazil associated to *C. coccodes*, causing leaf spots (Bellé et al. 2020).

Anthraco-nose of northern jointvetch (*Aeschynomene indica*, an aquatic weed of rice fields, frequently referred in the literature as *A. virginica*), led to the development of a mycoherbicide based on the fungus *Colletotrichum aeschynomenes* in the USA (Damm et al. 2012a, Weir et al. 2012). Additionally, *C. godetiae* is also known from this host in that country (Damm et al. 2012a). On the other hand, anthraco-nose on the forage plant Australian jointvetch (*A. falcata*) is caused by *C. theobromicola* (Shivas et al. 2016).

Anthraco-nose of alfalfa/lucerne (*Medicago sativa*) is an important disease in some areas, causing loss of total biomass due to stem death, and reduction of stand life and winter survival, due to crown rot (Samac et al. 2014). The disease is assigned to several *Colletotrichum* species: in the destructivum complex, *C. americae-borealis* from the USA, Argentina and China (Damm et al. 2014, Kemei et al. 2021, Lima et al. 2021), *C. destructivum* from Canada (Damm et al. 2014) and Australia (Shivas et al. 2016) and *C. lini* from Serbia (Vasić et al. 2014); in the orbiculare complex, *C. trifolii* from the USA (Damm et al. 2013, Samac et al. 2014); in the orchidearum complex, *C. sojajae* from the USA (Damm et al. 2019).

Anthraco-nose of stylo (*Stylosanthes* spp.) is a major disease of these forage crops, causing lesions with light-brown centres and dark margins, that expand to cover the entire leaf surface, affecting stems and causing terminal shoot blight resulting in plant death. Classically associated to *Colletotrichum gloeosporioides*, in fact several species of *Colletotrichum* are known from *Stylosanthes* spp.: *C. chlorophyti* (singleton species) is known from Australia on *S. hamata* (Shivas et al. 2016); in the boninense complex, *C. karsti* from Australia on *S. sympodialis* (Damm et al. 2012b) and from China on *S. guianensis* (Jia et al. 2017); *C. gigasporum* from Mexico on *S. guianensis* (Rakotoniriana et al. 2013); in the gloeosporioides complex, *C. theobromicola* from Australia on *S. viscosa* (Weir et al. 2012); *C. truncatum* from Thailand on *S. hamata* (Hyde et al. 2018). It is unclear which of these fungi prevail on *Stylosanthes*, which may hamper disease resistance breeding efforts (Falco et al. 2016).

Anthraco-nose of clover (*Trifolium* spp.) lost relevance over the last decades, with most cultivars showing elevated levels of resistance (Jacob et al. 2015, 2016, Hartmann et al. 2022). Several species of *Colletotrichum* have been associated to the disease. *Colletotrichum trifolii* (orbiculare complex), in modern terms, has not been recorded from clover for over one century (Damm et al. 2013). Other *Colletotrichum* species, from the destructivum complex, are: *C. destructivum* known from the USA, the Netherlands (Damm et al. 2014) and China (Xue et al. 2018b); *C. lini* from the USA, Germany and New Zealand (Damm et al. 2014); *C. utrechtense* from the Netherlands (Damm et al. 2014).

Anthraco-nose of common vetch (*Vicia sativa*) is responsible for severe losses in Gansu, China, although the causal agent was identified as *Colletotrichum lentis* in the 2012 and 2013 outbreaks (Xu & Li 2015, Xu et al. 2017a) and as *C. spinaciae* in the 2018 outbreak (Wang et al. 2019c).

Anthraco-nose of orchid tree (*Bauhinia* spp.) is characterised by leaf lesions with reddish-brown centres and black borders, surrounded by a yellow halo. The disease is attributed to *Colletotrichum siamense* in Argentina and India (Larran et al. 2015, Sharma et al. 2015a) and to *C. endophyticum* and *C. gloeosporioides* in China (Li et al. 2016a, Liang et al. 2023).

Anthraco-nose of golden tree (*Cassia fistula*) is characterised by light brown circular lesions with a dark border on leaves and precocious leaflet fall (Rabuske et al. 2018). The disease has been assigned to *Colletotrichum gloeosporioides* in Brazil (Rabuske et al. 2018) and to *C. siamense* in India (Sharma et al. 2015a).

Anthraco-nose of black locust (*Robinia pseudoacacia*) is characterised by black spots on leaves. The disease was associated to *Colletotrichum nymphaeae* in Japan (Yamagishi et al. 2016) and to *C. gloeosporioides* in China (Xue et al. 2018a).

Recently anthracnose of sword bean (*Canavalia gladiata*) was described in China as causing stem, petiole and leaf blade lesions, and attributed to *Colletotrichum truncatum* (Shi et al. 2022b).

Other host-fungus combinations in the Fabaceae include: on *Acacia acuminata*, *Colletotrichum fioriniae* known from Australia (Shivas et al. 2016), on *A. confusa*, *C. endophyticum* from China (Manawasinghe et al. 2022) and on *A. melanoxylon*, *C. siamense* from China (Yuan et al. 2023); on *Aspalathus linearis*, *C. acutatum* from South Africa (Damm et al. 2012a); on *Cercis chinensis*, *Colletotrichum siamense* from China (Ji et al. 2019); on *Crotalaria juncea*, *Colletotrichum verruculosum* from Zimbabwe (Damm et al. 2009); on *Cyamopsis tetragonoloba*, *Colletotrichum truncatum* from Mexico causing lesions on leaves and pods (García-León et al. 2022); on *Dalbergia hupeana*, *C. fructicola* (Zhou et al. 2022b), and on *D. odorifera*, *C. gigasporum* (Wan et al. 2018), both from China; on *Erythrina crista-galli*, *C. siamense* causing leaf spots in China (Li et al. 2021c); on *Falcataria moluccana*, *C. gloeosporioides* causing twig anthracnose in China (Chen et al. 2019b); on *Lablab purpureus*, *C. karsti* causing leaf spots (Luo & Jiang 2022); on *Leucaena* sp., *C. nymphaeae* from Mexico (Damm et al. 2012a); on *Ornithopus compressus*, *C. destructivum* from Australia (Shivas et al. 2016); on *Phanera championii* (= *Bauhinia championii*), *C. siamense* from China associated to leaf spots (Zhang et al. 2023b), on *Pongamia pinnata*, *C. siamense* from India (Dwarka et al. 2016); on kudzu (*Pueraria montana*), *C. gloeosporioides* from the USA (Weir et al. 2012); on *Samanea tubulosa*, *C. karsti* from Brazil causing black spots on seedlings (Almeida et al. 2022); on *Saraca indica*, *C. siamense* from India (Sharma et al. 2015a); on *Sophora tonkinensis*, *C. siamense* from China (Song et al. 2021b); on *Spatholobus suberectus*, *C. gloeosporioides* from China associated to leaf spots (Zhang et al. 2023b); on *Uraria picta*, *C. siamense* from India (Srivastava et al. 2017); on faba bean (*Vicia faba*), *C. acutatum* from Australia (Shivas et al. 2016).

### Fagaceae

There are few records of *Colletotrichum* associated to Fagaceae hosts. Pink-rot of chestnut (*Castanea sativa*) nuts, i.e., a clear and sometimes intense pink colouration of the endosperm, was reported from Italy and attributed to *Colletotrichum acutatum* (Gaffuri et al. 2017). On Chinese chestnut (*Castanea mollissima*), *Colletotrichum henanense* was recently found in the USA associated to blossom end rot, including black spots on the chestnut shell and blackening of the kernels, and sunken brown/black cankers on twigs of one-year old seedlings (Miller & Lewis Ivey 2022) and *C. castaneae* was recorded in China associated to leaf spots (Zhang et al. 2023b). On beech (*Fagus sylvatica*) nurseries, leaf spots were recorded from Poland and associated to *C. fioriniae* (Pszczółkowska et al. 2017). On oaks (*Quercus* spp.), leaf spots were reported from China associated to *C. gloeosporioides* on *Q. glauca* (as *Cyclobalanopsis glauca*; Liu et al. 2021d) and to *C. quercicola* on *Q. variabilis* (Wang et al. 2022i), *Colletotrichum karsti* was recorded on *Q. salicifolia* from Panama as an endophyte (Damm et al. 2012b) and *C. theobromicola* was recorded from an unspecified species of *Quercus* in the USA (Weir et al. 2012). On *Lithocarpus litseifolius*, *C. nymphaeae* was recorded from China associated to leaf spots (Du et al. 2022).

### Garryaceae

On *Aucuba japonica*, red-brown leaf spots evolving to grey-white lesions with purple-brown borders, surrounded by a yellowish green halo, were associated to *Colletotrichum fructicola* (Li et al. 2016e), whereas faded leaf spots progressing to black-brown lesions with irregular edges were associated to *C. boninense* and *C. siamense* (Liu et al. 2022e, 2023c, Zhang et al. 2023b), reported

from China. *Colletotrichum fructicola* has also recently been reported from Korea (Hassan et al. 2023).

#### Geraniaceae

On *Pelargonium graveolens*, *Colletotrichum nymphaeae* was isolated from lesions on petioles, leaves and twigs in India (Damm et al. 2012a).

On *Geranium wilfordii*, *Colletotrichum dematium* in China was associated to brown necrotic leaf spots with a grey-white centre, expanding to necrotic concentric rings (Ding et al. 2023).

#### Haloragaceae

On *Myriophyllum spicatum*, *Colletotrichum fioriniae* was recorded on a submerged stem in the USA (Damm et al. 2012a) and *C. garzense* and *C. spicati* were recently reported as endophytes in China (Zheng et al. 2022).

#### Hamamelidaceae

On *Loropetalum chinense*, *Colletotrichum fructicola* was recorded associated to leaf spots in China (Qiu et al. 2022).

#### Hydrangeaceae

On *Hydrangea paniculata*, *Colletotrichum fructicola* was found associated to leaf spots in Italy (Guarnaccia et al. 2021).

#### Hypericaceae

There is a single, ancient record of *Colletotrichum* on *Hypericum perforatum*, attributed to *C. cigarro* in Germany (Weir et al. 2012).

#### Icacinaceae

Two species of *Colletotrichum* were recorded to occur as endophytes in *Nothapodytes pittosporoides* in China, *C. jishouense* and *C. tongrenense* (Zhou et al. 2019).

#### Juglandaceae

Walnut (*Juglans regia*) anthracnose has been increasingly recorded over the last decade, causing brown spots on leaves and fruits, often leading to relevant yield losses. The disease has been attributed to *Colletotrichum acutatum* in China (He et al. 2019), *C. fioriniae* in China (Zhu et al. 2015), Hungary (Varjas et al. 2019), France (Da Lio et al. 2018) and Italy (Luongo et al. 2022), *C. godetiae* in Hungary (Varjas et al. 2021), France (Da Lio et al. 2018), Austria (Damm et al. 2012a) and China (Wang et al. 2023b), *C. juglandis* in China (Wei et al. 2022c) and *C. nymphaeae* in Brazil (Savian et al. 2019), France (Da Lio et al. 2018), Italy (Luongo et al. 2022) and China (Wang et al. 2022h) in the acutatum complex, to *C. aenigma* (Wang et al. 2021e, Li et al. 2023c), *C. cigarro* (as *C. kahawae*; Wei et al. 2022c), *C. fructicola* (Wang et al. 2018, Li et al. 2023c), *C. gloeosporioides* (Wang et al. 2020b, Mu et al. 2021, Yang et al. 2021a, Li et al. 2023c), *C. mengyinense* (Mu et al. 2021), *C. siamense* (Wang et al. 2017, Li et al. 2023c, Zhang et al. 2023b) and *C. viniferum* (He et al. 2019) in China and *C. siamense* in Korea (Cho et al. 2023), in the gloeosporioides complex, to *C. sojae* in the orchidearum complex in China (Li et al. 2023c) and to *C. magnum* in China (Li et al. 2023c). Although anthracnose resistance sources have been identified in *J. regia* × *J. sigillata* hybrids (Yang et al. 2021a), the elucidation of the identity of the causal agent in each region may be relevant for the correct deployment of such resistances in breeding programmes.

Pecan (*Carya illinoensis*) anthracnose can be a disease of concern, causing lesions on leaves (irregularly shaped lesions with a chlorotic halo) and fruits (dark sunken expanding lesions leading to fruit drop or mummification). The disease has been attributed to *Colletotrichum gloeosporioides* in Australia (Shivas et al. 2016), to *C. siamense* in Korea (Oh et al. 2021) and



China (Zhuo et al. 2023), to *C. nymphaeae* in China (Zhang et al. 2019a) and Brazil (Poletto et al. 2019) and to *C. fioriniae*, *C. fructicola* and *C. plurivorum* in China (Chang et al. 2022, Zhang et al. 2023a). On the forest tree species *Carya cathayensis*, *Colletotrichum fructicola* was recently reported from China causing irregular brown leaf spots (Ma et al. 2023).

Anthraco-nose on the pharmaceutical plant *Cyclocarya paliurus* was recently attributed to a mixture of pathogens identified as *Colletotrichum aenigma*, *C. fructicola* and *C. gloeosporioides* (Zheng et al. 2021b).

### Lamiaceae

Black spot is a major foliar disease of basil (*Ocimum basilicum*) in northern Italy (Guarnaccia et al. 2019, Cacciola et al. 2020). The disease is caused by *Colletotrichum ocimi* and *C. destritivum* (Damm et al. 2014, Mosca et al. 2014, Guarnaccia et al. 2019, Cacciola et al. 2020). *Colletotrichum siamense* was recently identified as the causal agent of blossom blight in Malaysia (Ismail et al. 2021a).

On Autumn sage (*Salvia greggii*), leaf spots can hamper productivity under greenhouse conditions (Garibaldi et al. 2015, Guarnaccia et al. 2019). The disease has been associated to *Colletotrichum coccodes*, *C. fructicola* and *C. nigrum* in Italy (Garibaldi et al. 2015, Guarnaccia et al. 2019). Anthracnose was also associated to *C. fioriniae* on *S. leucantha* (Garibaldi et al. 2016c) and to *C. bryoniicola* on *S. nemerosa* (Guarnaccia et al. 2019).

Other host-fungus combinations in the Lamiaceae include: on *Lycopus lucidus*, *Colletotrichum dematium* from China originating black spots on leaves and stems (Guan et al. 2016); on *Mentha* spp., *C. siamense* from Australia (Shivas et al. 2016) and *C. karsti* from Mexico (Solano-Báez et al. 2023); on oregano (*Origanum vulgare*), *C. fioriniae* from Italy (Guarnaccia et al. 2019) and *C. tropicale* from Mexico (Ayvar-Serna et al. 2020); on *Perilla frutescens*, *C. shiso* from Japan (Gan et al. 2019) and the USA (Fulcher & Owen-Smith 2023); on *Platostoma palustre*, *C. karsti* from China (Hsieh et al. 2020); on *Rosmarinus officinalis*, *C. siamense* as an endophyte from Australia (Shivas et al. 2016); on *Teucrium scorodonia*, *C. lini* from the Netherlands (Damm et al. 2014); on *Thymus vulgaris*, *C. destritivum* from the USA (Fu et al. 2015); on *Vitex*, *C. aotearoa* from New Zealand on *V. lucens* (Weir et al. 2012) and *C. aenigma* from Korea on *V. angustifolia* (Park et al. 2023).

### Lardizabalaceae

On *Akebia trifoliata*, anthracnose symptoms, associated to leaf spots and round or needle-shaped dark brown spots formed on fruit peel, were reported from China and attributed to *Colletotrichum gloeosporioides* (Pan et al. 2021).

### Lauraceae

Anthraco-nose is a serious post-harvest disease on avocado (*Persea americana*) fruits, besides also affecting vegetative organs (Sharma et al. 2017, Uysal & Kurt 2020). Symptoms start on leaves as yellow spots turning brown and coalescing, with necrosis occurring between leaf veins and most often at leaf tips. Severe conditions may lead to purple lesions on shoots and to shoot and flower head dieback. Infections on fruits develop around lenticels as small brown to black lesions. After harvest and ripening, lesions become blacker, larger, and increasingly sunken, often exhibiting a hemispherical pattern in transversal cut. The disease has been associated to 20 species of *Colletotrichum* mostly in the gloeosporioides complex. In the acutatum complex, *C. eryobotriae* is known from China (Wu et al. 2023c), *C. fioriniae* from Australia (Damm et al. 2012a) and New Zealand (Hofer et al. 2021) and *C. godetiae* from Mexico (Hernández-Lauzardo et al. 2015). In the boninense complex, *C. karsti* is known from Mexico (Hernández-Lauzardo et al. 2015, Velázquez-del Valle et al. 2016), Israel (Sharma et al. 2017), Turkey (Uysal & Kurt 2020) and New Zealand (Hofer et al. 2021). In the dematium complex, *C. anthrisci* is known from Chile (Bustamante et al. 2022). In the gloeosporioides complex: *C. aenigma* is known from Israel (Weir et al. 2012, Sharma et al. 2017); *C. alienum* from Israel (Sharma et al. 2017), Australia and New Zealand (Weir et al.

2012); *C. aotearoa* from New Zealand (Hofer et al. 2021); *C. asianum* from Indonesia (Zhafarina et al. 2021); *C. chrysophilum* from Mexico (Fuentes-Aragón et al. 2020b); *C. cigarro* from New Zealand (Weir et al. 2012) and Korea (Kwon et al. 2020); *C. fructicola* from New Zealand (Hofer et al. 2021), Australia (Weir et al. 2012), China (Li et al. 2022c), Israel (Sharma et al. 2017), Colombia (Gañán et al. 2015) and Mexico (Fuentes-Aragón et al. 2018); *C. gloeosporioides* from Israel (Sharma et al. 2017) and Turkey (Akgül et al. 2016); *C. jiangxiense* from Mexico (Ayvar-Serna et al. 2021); *C. nupharicola* from Israel (Sharma et al. 2017); *C. perseae* from Israel (Sharma et al. 2017) and New Zealand (Hofer et al. 2021); *C. queenslandicum* from Australia (Weir et al. 2012, Shivas et al. 2016); *C. siamense* from New Zealand (Hofer et al. 2021), Australia (Weir et al. 2012, Shivas et al. 2016), China (Li et al. 2022e), Israel (Sharma et al. 2017) and South Africa (Weir et al. 2012); *C. theobromicola* from Israel (Sharma et al. 2017); *C. tropicale* from Mexico (Fuentes-Aragón et al. 2020b). Studies on the etiology of avocado anthracnose suggest that multiple fungi are responsible for the disease, but few studies have compared the prevalence of the multiple fungal species in a given area. In Israel, *C. perseae* was reported as the prevalent fungus and one of the most virulent (Sharma et al. 2017). In New Zealand, eight *Colletotrichum* species were associated to “tannin stain” fruit symptoms, but the individual contribution of each species to the disease was not established (Hofer et al. 2021).

Other host-fungus combinations in the Lauraceae include: on *Cinnamomum* spp., *Colletotrichum siamense* (Zhou et al. 2016, Liu et al. 2022a), *C. fioriniae* (Sun et al. 2012, Chen et al. 2022d, Liu et al. 2022a), *C. jiangxiense*, *C. karsti*, *C. radermacherae* (Zhang et al. 2023b) and *C. scovillei* (Li et al. 2022b) from China, *C. siamense* from Malaysia (Khoo et al. 2023) and *C. lupini* from Portugal (Damm et al. 2012a); on *Phoebe sheareri*, *C. fructicola* causing leaf tip necrosis and twig wilt (Huang et al. 2022b); saprophytically on laurel (*Laurus nobilis*), *C. godetiae* from the UK (Damm et al. 2012a) and *C. lauri* from Italy (Hyde et al. 2017); on *Machilus ichangensis* (Cheng et al. 2019) and on *M. pauhoi* (Lv et al. 2023), *C. siamense* from China.

#### Lecythidaceae

On *Barringtonia edulis*, *Colletotrichum gloeosporioides* is associated to anthracnose in Papua-New Guinea, with symptoms gradually progressing from an angular, asymmetrical yellow discoloration to an ulcer-like necrosis causing death to the whole leaf (Buyoyu et al. 2017).

On *Cariniana legalis*, *Colletotrichum tropicale* is associated to anthracnose in Brazil, causing light to dark brown necrotic leaf lesions, coalescing to cause death of the leaves and weakening of the trees (Souza et al. 2023).

#### Linaceae

Flax (*Linum usitatissimum*) anthracnose is a seed- and soil-borne disease, causing damping-off of seedlings, and attributed to *Colletotrichum lini* (Damm et al. 2014).

#### Loganiaceae

On *Geniostoma rupestre* var. *ligustrifolium*, *Colletotrichum aotearoa* was reported as an endophyte in New Zealand (Weir et al. 2012).

#### Lythraceae

Anthracnose on pomegranate (*Punica granatum*) affects ripe fruits, constituting a post-harvest disease, but also affects young fruits, flowers and leaves as small black spots developing to dark brown depressed lesions. The disease is associated to eight species of *Colletotrichum*: in the acutatum complex, *C. acutatum* is known from Brazil (Bellé et al. 2018) and Italy (Mincuzzi et al. 2017), and *C. fioriniae*, *C. nymphaeae* and *C. simmondsii* from the USA (Xavier et al. 2019); in the gloeosporioides complex, *C. gloeosporioides* is known from Albania and the USA (Xavier et al. 2019, Cara et al. 2020), *C. siamense* from the USA (Xavier et al. 2019), *C. theobromicola* from the USA (Xavier et al. 2019), India (Sharma et al. 2015a) and Australia (Shivas et al. 2016), and *C. tropicale* from Brazil (Silva-Cabral et al. 2019a). It is unclear if any of these fungi are

specifically associated to each of the disease symptoms reported and few studies have addressed the relative frequency of the pathogen populations. In a study conducted in the USA, *C. theobromicola* was shown to be the most prevalent species, although species in the acutatum complex were more virulent (Xavier et al. 2019).

### Magnoliaceae

Anthraco-nose of tulip tree (*Liriodendron tulipifera* and *L. chinense* × *tulipifera*) is associated to leaf spot symptoms that progress to elongated or irregularly shaped lesions. It is caused by *Colletotrichum fioriniae* in the UK (Damm et al. 2012a) and by *C. fructicola*, *C. siamense* and *C. gloeosporioides* in China (Zhu et al. 2019a, Dou et al. 2022, Wan et al. 2022a).

On *Magnolia* spp. (including *Magnolia champaca* syn. *Michelia champaca*, *Magnolia decidua* syn. *Manglietia decidua*, *Magnolia denudata* syn. *Yulania denudata* and *Magnolia maclurei* syn. *Michelia macclurei*), leaf spots are associated to *Colletotrichum boninense* and *C. celtidis* in China (Zhang et al. 2023b), to *C. fioriniae* in China (Zhang et al. 2018a), New Zealand (Liu et al. 2021b) and the UK (Damm et al. 2012a) and to *C. fructicola* and *C. siamense* in China (Yin et al. 2022, Zhou et al. 2022a, 2023b, Wang et al. 2023a). As endophytes, *C. Chiangmaiense* has been reported on *Magnolia garrettii* in Thailand, and *C. fructicola*, *C. gloeosporioides* and *C. xishuangbannaense* on *M. candolli* in China (De Silva et al. 2021b).

On *Michelia alba*, marginal leaf spots are associated to *Colletotrichum siamense* in China (Qin et al. 2021).

### Malpighiaceae

On acerola or Barbados cherry (*Malpighia emarginata*), anthracnose is an important fruit disease, causing necrotic and sunken spots (Bragança et al. 2014). The disease is associated to *Colletotrichum theobromicola* in Brazil (Bragança et al. 2014) and to *C. tropicale* in Japan (Takushi et al. 2018).

### Malvaceae

Anthraco-nose of jute (*Corchorus capsularis*) is an important disease, affecting stems and reducing fibre value. On leaves, lesions progress from small circular spots to dark brown expanded necroses. On stems, lesions appear on the leaf scar as fusiform, sunken, water soaked and dark necroses. Reports from China have assigned it to *Colletotrichum fructicola*, *C. siamense* and “*C. corchori-capsularis*” (nom. invalid.), the latter presenting higher virulence and prevalence than the others (Niu et al. 2016a, 2016b).

There are two *Colletotrichum*-related diseases known from cotton (*Gossypium hirsutum*), cotton anthracnose, causing damping-off of seedlings, and ramulosis, causing abnormal over-sprouting and branching of adult plants, found in South America (Weir et al. 2012, Moreno-Moran & Burbano-Figueroa 2017, PLH et al. 2018). These diseases are associated respectively to “*C. gossypii*” and “*C. gossypii* var. *cephalosporioides*”, but Weir et al. (2012) has treated these taxa as belonging to the gloeosporioides complex but pending modern description and delimitation. Although cotton anthracnose is one of the most ancient diseases caused by *Colletotrichum* in the scientific literature, “*C. gossypii*” is absent from modern *Colletotrichum* checklists, leaving Plant Pathology applications to use the names “*C. gossypii*” and “*C. gossypii* var. *cephalosporioides*” without modern taxonomic support. For instance, “*C. gossypii*” is known from Bulgaria and Romania (PLH et al. 2018) and “*C. gossypii* var. *cephalosporioides*” has recently been reported from Colombia (Moreno-Moran & Burbano-Figueroa 2017), while both have been recorded from Brazil (Oliveira et al. 2022). rDNA-ITS sequences deposited in the NCBI database labelled as “*C. gossypii*” and “*C. gossypii* var. *cephalosporioides*”, arising from the works by Nawaz et al. (2019) and Salustiano et al. (2014) respectively, show 100% similarity to the *C. theobromicola* type strain sequence (JX010294; Weir et al. 2014) whereas exhibiting a 3-bp difference to the closest species, *C. grossum* (KP890165; Diao et al. 2017). The analysis of *tub2* sequences labelled as “*C. gossypii*” and “*C. gossypii* var. *cephalosporioides*” reveals a 10 bp-difference to *C. grossum*

(KP890171; Diao et al. 2017) whereas only a 3 bp-difference to *C. theobromicola* (JX010447), suggesting that the cotton anthracnose pathogens may belong to *C. theobromicola*. Other species of *Colletotrichum* recorded from cotton are: *C. karsti* from Germany (Damm et al. 2012b); *C. plurivorum* from Brazil (Damm et al. 2019); *C. siamense* from India associated to symptoms on leaves (Salunkhe et al. 2020); *C. truncatum* from Thailand (Hyde et al. 2018).

Anthracnose on cocoa (*Theobroma cacao*) can cause leaf spots and pod rot, leading to yield losses (Nascimento et al. 2019a, Serrato-Díaz et al. 2020). There are 10 species of *Colletotrichum* recorded from cocoa, but only three are reportedly pathogenic, all belonging to the gloeosporioides complex: *C. aeshynomenes* is known from Brazil, causing leaf spots (Nascimento et al. 2019a); *C. siamense* from Puerto Rico, causing pod rot (Serrato-Díaz et al. 2020); *C. theobromicola* from Panama, associated to leaf and pod lesions (Rojas et al. 2010). Species reported as endophytes are: *C. cacao* from Costa Rica (Damm et al. 2019); *C. chrysophilum* from Panama (Vieira et al. 2017); *C. fructicola* (Weir et al. 2012); *C. karsti* from Panama (Damm et al. 2012b); *C. sloanei* from Malaysia (Damm et al. 2012a); *C. tropicale* from Panama (Rojas et al. 2010); *C. vittalense* from India (Damm et al. 2019).

Other host-fungus combinations in the Malvaceae include: on *Abelmoschus esculentus*, *Colletotrichum gloeosporioides* known from China causing leaf blight (Shi et al. 2019b); on *Abutilon theophrasti*, *C. truncatum* from China causing leaf lesions (Cong et al. 2020); on *Durio zibethinus*, *C. durionigenum*, *C. gigasporum*, *C. siamense* (as *C. pandanicola*; Zhang et al. 2023b) and *C. truncatum* associated to fruit rot in Thailand (Armand et al. 2023); on *Gossypium indicum*, *C. theobromicola* associated to leaf spots in Korea (Kang et al. 2022); on *Hibiscus* spp., *C. gigasporum* from Thailand (Liu et al. 2014) and *C. siamense* from Australia (Schena et al. 2014) and Brazil (Rocha et al. 2022); on *Lavatera trimestris*, *C. malvarum* from the UK (Damm et al. 2013); on *Malva* spp., *C. malvarum* from Germany on *Malva* sp. (Damm et al. 2013), *C. tebeestii* from Canada on *M. pusilla* (Damm et al. 2013) and *C. trifolii* from China on *M. crispa* (Liu et al. 2017c) and *M. sylvestris* (Zhou et al. 2014); on *Pachira* spp., *C. karsti* from China and Brazil (Damm et al. 2012b) and *C. siamense* from China (Wu et al. 2023a); on *Sida spinosa*, *C. sidae* from the USA (Damm et al. 2013); on *Sterculia* spp., *C. siamense* from China on *S. lanceolata* (Zhang et al. 2020b) and *S. nobilis* (Zhang et al. 2020a).

#### Melastomataceae

Host-fungus combinations in the Melastomataceae include: on *Clidemia hirta*, *Colletotrichum clidemiae* known from Panama and the USA (Weir et al. 2012); on *Miconia* sp., *C. cigarro* from Brazil (Weir et al. 2012); on *Rhexia virginica*, *C. fructivorum* and *C. rhexiae* from the USA (Doyle et al. 2013).

#### Meliaceae

Host-fungus combinations in the Meliaceae include: on *Azadirachta indica*, *Colletotrichum siamense* known from Thailand (Udayanga et al. 2013) and India (Sharma et al. 2015a); on *Dysoxylum spectabile*, *C. aotearoa* from New Zealand (Weir et al. 2012); on *Trichilia tuberculata*, *C. tropicale* from Panama as an endophyte (Rojas et al. 2010).

#### Menispermaceae

On *Menispermum dauricum*, *Colletotrichum menispermii* was reported as a saprobe from Russia (Li et al. 2016c).

#### Monimiaceae

On *Hedycarya angustifolia*, *Colletotrichum aotearoa* is known from Australia (Shivas et al. 2016).

#### Moraceae

Mulberry (*Morus alba*) anthracnose causes necrotic spots or streaks in leaves, resulting in

significant loss of leaves for silkworm feeding (Xue et al. 2019, Zhu et al. 2023a). In a study conducted in China, *Colletotrichum fioriniae* was found to be the most important causal agent of mulberry anthracnose, followed by *C. brevisporum*, *C. karsti* and *C. cigarro*, whereas *C. fructicola* and *C. cliviicola* (as *C. cliviae*) were isolated from the host but did not show to be pathogenic (Xue et al. 2019).

There are several reports of *Colletotrichum* on *Ficus* spp. Fruit rot on fig (*F. carica*) has been reported from Korea on unripe fruits, and attributed to *C. gloeosporioides* (Choi et al. 2013), whereas in China fruit rot was observed throughout fruit development and specially in ripe fruits, and attributed to *C. tropicale* (Duan & Chen 2022b). *Colletotrichum siamense* was also reported from *F. carica*, as an endophyte (Shivas et al. 2016). Other host-fungus combinations include: on *F. ampela* leaf litter, *C. fici* from China (Tennakoon et al. 2021); on *F. binnendijkii* var. *variegata*, *C. tropicale* causing leaf spots in China (Kong et al. 2020); on *F. edulis*, *C. fructicola* from Germany (Weir et al. 2012); on *F. elastica*, *C. siamense* (as *C. communis*) from India (Sharma et al. 2015a); on *F. septica* leaf litter, *C. fici-septicae* from China (Tennakoon et al. 2021); on *F. virens*, *C. fioriniae* from China causing leaf spots (Xue et al. 2017).

Other host-fungus combinations in the Moraceae include: on jackfruit (*Artocarpus heterophyllus*), *Colletotrichum artocarpicola* as a saprobe in Thailand (Bhunjun et al. 2019) and *C. siamense* as an endophyte in Australia (Shivas et al. 2016) and associated to leaf spots in Brazil (Borges et al. 2023); on *A. sericarpus*, *C. siamense* as an endophyte in Australia (Shivas et al. 2016).

#### Moringaceae

Leaf spots and stem lesions were reported on *Moringa oleifera* in China, caused by *Colletotrichum chlorophyti* (Cai et al. 2016b).

#### Myricaceae

Leaf spots, leading to chlorosis and wilting, were reported on *Myrica rubra* in China, caused by *Colletotrichum fructicola* (Li et al. 2022a).

#### Myrtaceae

Anthracnose on feijoa (*Acca sellowiana*) has been recorded from Brazil, with irregularly shaped well defined dark spots on fruits becoming depressed and coalescing, associated to *Colletotrichum gloeosporioides* (Fantinel et al. 2017), from Italy, with dark sunken lesions on mature fruits and leaves associated to *C. acutatum* (Camele et al. 2018), from Portugal (Azores islands), with symptoms on leaves associated to *C. feijoicola* (Crous et al. 2019b), and from New Zealand, associated to *C. theobromicola* (Weir et al. 2012).

Anthracnose on eucalypts (*Eucalyptus* spp.) cause leaf spot and twig die-back. The disease is attributed to *Colletotrichum cigarro* on *E. grandis* (Mangwende et al. 2020), to *C. cigarro* and *C. fructicola* on *E. dunnii*, *E. nitens* and *E. macarthurii* (Mangwende et al. 2021) and to *C. theobromicola* on *E. grandis* × *E. urophylla* (Solis et al. 2022) in South Africa, and to *C. boninense* on *E. robusta* in China (Zhang & Zhu 2018). *Colletotrichum karsti* and *C. indonesiense* have been reported from South Africa and Indonesia respectively, but with unconfirmed pathogenicity (Damm et al. 2012b, Weir et al. 2012).

Guava (*Psidium guajava*) anthracnose is a common disease worldwide affecting fruit production and storage, originating circular to irregular sunken lesions. The disease has been attributed to *Colletotrichum abscissum* and *C. nymphaeae* in Brazil (Bragança et al. 2016a), to *C. siamense* in India (Sharma et al. 2015a) and Mexico (Rodríguez-Palafox et al. 2021), to *C. sloanei* in Indonesia (Zhafarina et al. 2021) and to *C. acutatum* in New Zealand (Liu et al. 2021b). Additional fungi with unconfirmed pathogenicity are *C. guajavae* and *C. psidii* (Damm et al. 2012a, Weir et al. 2012).

Other host-fungus combinations in the Myrtaceae include: on *Calothamnus quadrifidus*, *Colletotrichum simmondsii* known from Australia (Shivas et al. 2016); on cambuci (*Campomanesia*

*phaea*), *Colletotrichum theobromicola* from Brazil causing lesions on leaves and branches (Santos et al. 2017); on *Eugenia* sp., *C. karsti* from Brazil (Damm et al. 2012b) and *C. cordylinicola* from Laos (Weir et al. 2012); on *Kunzea ericoides*, *C. aotearoa*, *C. cigarro* and *C. torulosum* from New Zealand (Joshee et al. 2009, Weir et al. 2012); on *Myrciaria dubia*, *C. aeschynomenes* and *C. tropicale* from Brazil (Matos et al. 2020); on jabuticaba (*Plinia cauliflora*), *C. tropicale* from Japan (Taba et al. 2020); on *Syzygium* spp., *C. aotearoa* from New Zealand on *S. smithii* (Weir et al. 2012), *C. gloeosporioides* from Malaysia (Al-Obaidi et al. 2017), *C. siamense* from Thailand (Khuna et al. 2023) and *C. syzygiicola* from Thailand (Udayanga et al. 2013) on *S. samarangense*, and *C. pseudoacutatum* from Brazil (Soares et al. 2017) on *S. jambos*; on *Ugni molinae*, *C. godetiae* from Chile (Damm et al. 2012a).

#### Nelumbonaceae

On *Nelumbo nucifera*, *Colletotrichum siamense* and *C. tropicale* occur as endophytes in China (Chen & Kirschner 2018).

#### Nymphaeaceae

Anthracoze of waterlilies (*Nuphar* spp. and *Nymphaea* spp.), affecting leaves and petioles, is caused by *C. nupharicola* and *C. nymphaeae*, recorded from the USA, Italy and the Netherlands (Johnson et al. 1997, Damm et al. 2012a, Weir et al. 2012).

#### Oleaceae

Olive (*Olea europaea*) anthracnose affects fruits at maturity with dark sunken necroses covered in orange spore masses, causing fruit drop and depreciation of oil quality (Talhinhas et al. 2018). The disease is caused by several species of *Colletotrichum*, with *C. acutatum*, *C. nymphaeae* and *C. theobromicola* reported as the most virulent (Schena et al. 2014, Talhinhas et al. 2015, Peres et al. 2021, Riolo et al. 2023). *Colletotrichum acutatum* is known from South Africa and Australia (Damm et al. 2012a, Shivas et al. 2016) and is expanding recently in the Mediterranean region, where it has been reported from Portugal, Spain, Italy, Tunisia, Albania and Greece (Talhinhas et al. 2005, 2011, Mosca et al. 2014, Chattaoui et al. 2016, Iliadi et al. 2018, Cara et al. 2021, Licciardello et al. 2022), as well as in Uruguay, where it was recently reported as the prevalent pathogen (Moreira et al. 2021), in Brazil (Filoda et al. 2021) and in Pakistan (Nawaz et al. 2022, 2023). *Colletotrichum nymphaeae* is mostly restricted to southwestern Iberia (Talhinhas et al. 2005, 2011, López-Moral et al. 2017, Materatski et al. 2018), but has been recently reported from northeastern Italy (Antelmi et al. 2019), Uruguay (Moreira et al. 2021) and Brazil (Filoda et al. 2021). *Colletotrichum theobromicola* is known from Australia (Weir et al. 2012, Schena et al. 2014) and has been recently reported from Argentina (Lima et al. 2020) and Uruguay (Moreira et al. 2021). Although less virulent than those three species, *C. godetiae* is common across the Mediterranean region, being known from Portugal, Spain, Italy, Montenegro and Greece (Talhinhas et al. 2005, 2011, Mosca et al. 2014, Baroncelli et al. 2015b, López-Moral et al. 2017), often as the most prevalent pathogen (Talhinhas et al. 2018, Moral et al. 2021). *Colletotrichum gloeosporioides* is known from Portugal, Spain, Italy, Tunisia and China, but mostly with low prevalence (Talhinhas et al. 2005, 2011, Schena et al. 2014, Chattaoui et al. 2016, Moral et al. 2021, Licciardello et al. 2022). Sporadic pathogens are: *C. alienum*, known from Uruguay and Australia (Moral et al. 2021, Moreira et al. 2021); *C. boninense*, from Australia (Moral et al. 2021); *C. fioriniae*, from Portugal, Italy, Turkey, the USA and Australia (Talhinhas et al. 2005, 2011, Mosca et al. 2014, Moral et al. 2021, Riolo & Cacciola 2023); *C. lupini*, from Morocco (Msairi et al. 2020); *C. perseae*, from Australia (Moral et al. 2021); *C. rhombiforme*, from Portugal (Talhinhas et al. 2005). Several other fungi were isolated from diseased olive fruits, but pathogenicity has not been confirmed: *C. aenigma* from Italy (Schena et al. 2014); *C. cigarro* from Italy and Australia (Weir et al. 2012, Schena et al. 2014, Licciardello et al. 2022); *C. karsti* from Italy (Mosca et al. 2014, Schena et al. 2014); *C. queenslandicum* from Montenegro (Schena et al. 2014); *C. siamense* from Australia (Schena et al. 2014). The recent report of the most virulent



species in new regions, namely the spread of *C. acutatum* in the Mediterranean region and in South America, the report of *C. nymphaeae* in Italy and that of *C. theobromicola* in Argentina and Uruguay, may lead to more severe olive anthracnose outbreaks and pose additional challenges to crop protection.

Other host-fungus combinations in the Oleaceae include: on *Fraxinus excelsior*, *Colletotrichum truncatum* was detected among other fungi in the Ukraine (Davydenko et al. 2013); on *Jasminum* spp., *C. siamense* is known on *J. mesnyi* from China (Zhang et al. 2019b) and on *J. sambac* from Vietnam (Wikee et al. 2011, Weir et al. 2012) and China (Sun et al. 2023a); on *Ligustrum* spp., *C. aotearoa* and *C. fructicola* are known on *L. lucidum* from New Zealand (Weir et al. 2012) and China (Zhang et al. 2023b) respectively, and *C. gloeosporioides* and *C. siamense* on *L. japonicum* from China (Shen et al. 2017, Li et al. 2022g); on *Osmanthus fragrans*, *C. karsti*, *C. gloeosporioides*, *C. fructicola*, *C. siamense*, *C. anhuiense* and *C. osmanthicola* causing leaf spots (Tang et al. 2018, Liu et al. 2022c, He et al. 2023, Zhang et al. 2023b) and *C. liriopes* (Liu et al. 2022b), all from China.

### Onagraceae

Host-fungus combinations in the Onagraceae include: on *Clarkia hybrida*, *Colletotrichum godetiae* known from Denmark found on seeds (Damm et al. 2012a); on *Fuchsia magellanica*, *C. arboricola* from Chile (Crous et al. 2018a); on *Oenothera* sp., *C. nymphaeae* from the Netherlands (Damm et al. 2012a).

### Oxalidaceae

Host-fungus combinations in the Oxalidaceae include: on *Averrhoa carambola*, *Colletotrichum simmondsii* known from Australia (Shivas et al. 2016) and *C. fructicola* from China (Li & Zhang 2023); on *Oxalis corniculata*, *C. gloeosporioides* from Brazil (Bellé et al. 2019) and *C. truncatum* from China (Wang et al. 2022d) causing circular to oval brown leaf spots.

### Paeoniaceae

On *Paeonia suffruticosa* (tree peony), anthracnose symptoms develop from small purple leaf spots, evolving to brown scorch, and are caused by *Colletotrichum aenigma* in China (Wang et al. 2023d), whereas on *P. lactiflora* *C. gloeosporioides* is associated to reddish-brown lesions on stems and leaves in China (Zhang & Dai 2017) and *C. fioriniae* has been reported from the USA on *Paeonia* sp. (Liu et al. 2021b).

### Passifloraceae

Anthracnose of passion fruit (*Passiflora edulis*) affects vegetative and floral organs, and is also a post-harvest disease of fruits, causing sunken circular to irregular lesions (Dutra & Blum 2019). The disease has been assigned to *Colletotrichum brasiliense* in Brazil and China (Damm et al. 2012b, Shi et al. 2022a), to *C. brevisporum* in China (Du et al. 2017, Qiu et al. 2021) and Australia (Shivas et al. 2016), to *C. constrictum* in China (Wang et al. 2021f), to *C. siamense* in China (Zhang et al. 2022b), to *C. truncatum* (as *C. capsici*) in China (Chen & Huang 2018) and Japan (Sato et al. 2015) and to *C. tropicale* in Brazil (Silva et al. 2021b). Additional species recorded from passion fruit, but with unconfirmed pathogenicity, are: *C. colombiense*, from Colombia (Damm et al. 2012b); *C. karsti*, from Colombia and Japan (Damm et al. 2012b); *C. queenslandicum*, from Australia (Shivas et al. 2016); *C. torulosum* from New Zealand (Damm et al. 2012b).

### Phyllanthaceae

Anthracnose on Otaheite gooseberry (*Phyllanthus acidus*) has been recorded in the past, as revised by Samarakoon et al. (2018), and the pathogen recognised as *Colletotrichum phyllanthi* associated to symptoms on leaves in India, but there are no records since 1966 (Damm et al.

2012b). Additionally, *C. acidae* was identified as a saprobe from dead *Ph. acidus* rachises (Samarakoon et al. 2018).

On *Sauropus androgynus*, *Colletotrichum tropicale* is responsible for stem and leaf lesions recorded in China (Liu et al. 2018b).

#### Piperaceae

Records of anthracnose on pepper are seldom, but they are scattered over time and in different longitudes. Nevertheless, there are nine species of *Colletotrichum* recognised from *Piper*: in the acutatum complex, *C. fioriniae* recorded on *Piper nigrum* at an unknown location (Damm et al. 2012a); in the boninense complex, *C. karsti* on *P. nigrum* from China (Lin et al. 2022); in the destructivum complex, *C. tabacum* on *P. sarmentosum* from China (Zhang et al. 2023b); in the gloeosporioides complex, *C. siamense* on *P. nigrum* from Australia (Shivas et al. 2016) and India (Verma et al. 2023) and on *P. sarmentosum* from China (Zhang et al. 2023b); in the magnum complex, *C. lobatum* on *P. catalpaefolium* from Trinidad and Tobago (Damm et al. 2019); in the orchidearum complex, *C. piperis* on *P. nigrum*, *P. betle* and *P. umbellatum* from Asia and the Caribbean (Damm et al. 2019) and *C. plurivorum* and *C. vittalense* on *P. sarmentosum* from China (Zhang et al. 2023b); *C. truncatum* from China on *P. betle* (Sun et al. 2020b) and on *P. sarmentosum* (Zhang et al. 2023b).

#### Plantaginaceae

Snapdragon (*Antirrhinum majus*) anthracnose is characterised by spotting and blight of leaves (Tomioka et al. 2011), being *Colletotrichum antirrhinicola* reported from New Zealand (Damm et al. 2014).

Other host-fungus combinations in the Plantaginaceae include: from *Digitalis lutea*, *D. obscura* and *D. purpurea*, *C. fuscum* from Germany and the Netherlands (Damm et al. 2014); from *Hippuris vulgaris*, *C. baiyuense*, *C. casaense*, *C. litangense* and “*C. vulgaris*” (invalid taxon due to chimeric concatenated sequence) as endophytes from China (Li et al. 2022d, Zheng et al. 2022); from *Penstemon* sp., *C. fioriniae* from the Netherlands (Damm et al. 2012a).

#### Plumbaginaceae

Host-fungus combinations in the Plumbaginaceae include: on *Armeria maritima*, *Colletotrichum dematium* reported from Japan (Sato et al. 2015); on *Limonium* sp., *C. acutatum* from the UK (Baroncelli et al. 2015b) and *C. fructicola* and *C. theobromicola* from Israel (Weir et al. 2012).

#### Polemoniaceae

On *Phlox* sp., *Colletotrichum acutatum* has been reported from the UK (Damm et al. 2012a).

#### Polygalaceae

On *Xanthophyllum sylvestri*, *Colletotrichum flexuosum* has been reported from Vietnam associated to leaf spots (Jayawardena et al. 2023).

#### Polygonaceae

Host-fungus combinations in the Polygonaceae include: on *Fagopyrum esculentum*, *Colletotrichum truncatum* recorded from Japan (Sato et al. 2015) and *C. liriopes* from China (Chen et al. 2021); on *Polygonum aviculare*, *C. dematium* from China (Liu et al. 2016d); on *Rumex* spp., *C. destructivum* on *Rumex* sp. from China (Liu et al. 2017b) and Korea (Damm et al. 2014), *C. higginsianum* on *R. acetosa* from China (Zhang et al. 2018b) and *C. liriopes* on *R. acetosa* from Japan (Sato et al. 2015).

#### Primulaceae

Anthracnose on *Cyclamen* sp. affects foliage (Sharma et al. 2016), and has been attributed to

*Colletotrichum theobromicola* in Israel (Sharma et al. 2016), *C. fructicola* and *C. fioriniae* in Italy (Damm et al. 2012a, Guarnaccia et al. 2021) and *C. simmondsii* in the Netherlands (Damm et al. 2012a). On *Ardisia japonica*, *C. siamense* was associated to leaf spots in China (Zhang et al. 2023b). On *Primula* sp., *C. fioriniae* is known from the Netherlands (Damm et al. 2012a).

### Proteaceae

There are 15 species of *Colletotrichum*, representing the *acutatum*, *boninense*, *gloeosporioides* and *spaethianum* complexes, occurring on 13 genera within the Proteaceae, in general associated to leaf spots.

On *Banksia* sp., anthracnose is associated to *Colletotrichum aotearoa* in Australia and to *C. cigarro* in Portugal (Madeira Island) and Spain (Liu et al. 2013a). The latter species is also associated to *Dryandra* sp. in Madeira (Weir et al. 2012).

On *Leucadendron* sp., *Colletotrichum alienum* is known from South Africa and Portugal (Liu et al. 2013a), whereas *C. acutatum* is known from South Africa (Damm et al. 2012a).

On *Leucospermum* sp., anthracnose is associated to *Colletotrichum acutatum* in South Africa (Damm et al. 2012a), to *C. boninense* and *C. karsti* in Australia (Damm et al. 2012b) and to *C. cigarro* (Liu et al. 2013a) and *C. karsti* in the USA (Hawaii) (Damm et al. 2012b, Liu et al. 2013a).

On *Protea* spp., *Colletotrichum acutatum* is known from South Africa on *P. cynaroides* (Damm et al. 2012a), *C. alienum* from South Africa and Portugal (Madeira) on *P. cynaroides* (Liu et al. 2013a), *C. karsti* from Portugal (Madeira) on *P. obtusifolia* and from Zimbabwe on *P. cynaroides* (Damm et al. 2012b), *C. nymphaeae* from South Africa on *P. cynaroides* and *P. magnifica* and from Australia on *Protea* sp. (Damm et al. 2012a), *C. proteae* from South Africa on *Protea* sp. (Liu et al. 2013a), *C. siamense* from Zimbabwe on *P. cynaroides* (Liu et al. 2013a) and *C. simmondsii* from the USA (Hawaii) on *P. cynaroides* (Damm et al. 2012a).

Recently, irregular dark brown leaf spots were reported from *Macadamia integrifolia* in Australia, caused by *Colletotrichum siamense* (Prasannath et al. 2020), and from *M. ternifolia* in China, caused by *C. fructicola* (Li et al. 2023b).

Anthracnose on ornamental trees and shrubs include: on *Embothrium coccineum*, *Colletotrichum pyricola* associated to leaf spots in urban trees in Chile (Zapata & Opazo 2017); on *Grevillea* sp., *C. acutatum* (Damm et al. 2012a), *C. alienum* (Liu et al. 2013a) and *C. tofieldiae* (Shivas et al. 2016) known from Australia, *C. fioriniae* from Germany (Damm et al. 2012a) and *C. grevilleae* from Italy (Liu et al. 2013a); on *Hakea* sp., *C. acutatum* known from South Africa and *C. australe* from Australia (Damm et al. 2012a); on *Knightia* sp., *C. aotearoa* known from New Zealand (Liu et al. 2013a); on *Mimetes* sp., *C. acutatum* known from South Africa (Damm et al. 2012a); on *Serruria* sp., *C. alienum* from South Africa (Liu et al. 2013a); on *Toronia toru*, *C. cigarro* from New Zealand (Weir et al. 2012).

### Ranunculaceae

Anthracnose, or leaf-curl disease, of anemone (*Anemone coronaria*) causes corm rot, leaf crinkles and twisting of floral peduncles (Freeman et al. 2000). The causal agents are assigned to *Colletotrichum acutatum*, known from Australia and the Netherlands, and to *C. nymphaeae*, from the Netherlands, Italy and Israel (Damm et al. 2012a).

On goldthread (*Coptis chinensis*), a leaf spot disease was recently reported in China caused by *Colletotrichum boninense* (Ding et al. 2020) and by *C. jinshuiense* (Wang et al. 2023c).

On *Helleborus niger*, *Colletotrichum godetiae* is known from Australia (Shivas et al. 2016) and *C. lineola* and *C. liriopes* from Japan (Sato et al. 2015).

### Rhamnaceae

Host-fungus combinations in the Rhamnaceae include: on *Ceanothus thyrsiflorus*, *Colletotrichum fructicola* known from Italy (Guarnaccia et al. 2021); on *Ceanothus* sp., *Colletotrichum godetiae* from the UK (Damm et al. 2012a); on *Ziziphus jujuba* (= *Z. mauritiana*),

*C. fructicola* and *C. siamense* from China (Shu et al. 2021, Duan & Chen 2022c, Fan et al. 2022, Han et al. 2023b) and *C. gloeosporioides* and *C. nymphaeae* from Korea (Kang et al. 2023); on *Ziziphus* sp., *C. fructicola* and *C. gloeosporioides* from Thailand (Udayanga et al. 2013).

### Rosaceae

There are 42 species of *Colletotrichum* known from the Rosaceae, mostly in the acutatum and gloeosporioides complexes, causing anthracnose on several fruit crops.

Strawberry (*Fragaria* × *ananassa*) anthracnose is one of the most studied diseases caused by *Colletotrichum*, and is considered one of the most important fungal diseases of this fruit crop, after grey mold. As revised by Baroncelli et al. (2015b), the most common symptoms in the field are flower blight and fruit rot, whereas in nurseries are lesions on stolons, petioles and leaves, with crown and root necrosis also occurring. The causal agents cluster mostly in the acutatum and gloeosporioides species complexes. In the acutatum complex: *Colletotrichum acutatum* has been reported from Australia (Damm et al. 2012a); *C. fioriniae* from New Zealand (Damm et al. 2012a), Belgium (Grammen et al. 2019), the UK (Baroncelli et al. 2015b) and the USA (Wang et al. 2019d); *C. godetiae* from Spain, France, the UK, Ireland, Belgium, the Netherlands and Norway (Damm et al. 2012a, Baroncelli et al. 2015b, Grammen et al. 2019); *C. miaoliense* from China (Chung et al. 2020); *C. nymphaeae* from the UK, the Netherlands, Belgium, France, Switzerland, Austria, Bulgaria, Italy, Spain and Portugal in Europe (Damm et al. 2012a, Mosca et al. 2014; Baroncelli et al. 2015b, Grammen et al. 2019), Canada, the USA, Costa Rica and Colombia in America (Damm et al. 2012a, Baroncelli et al. 2015b, Wang et al. 2019d), Kenya and South Africa in Africa (Damm et al. 2012a, Baroncelli et al. 2015b), Israel, Iran and China in Asia (Damm et al. 2012a, Han et al. 2016, Karimi et al. 2017b) and Australia (Shivas et al. 2016); *C. salicis* from New Zealand and Belgium (Damm et al. 2012a, Grammen et al. 2019); *C. simmondsii* from Australia (Damm et al. 2012a, Baroncelli et al. 2015b, Shivas et al. 2016). In the gloeosporioides complex: *C. aenigma* has been reported from China (Han et al. 2016, Chen et al. 2020); *C. alienum* from Australia (Shivas et al. 2016); *C. changpingense* from China (Jayawardena et al. 2016b); *C. fructicola* from China (Han et al. 2016, Jayawardena et al. 2016b, He et al. 2019, Chen et al. 2020, Jiang et al. 2021), Canada and the USA (Weir et al. 2012); *C. gloeosporioides* from China (Han et al. 2016, Shu et al. 2018, Chen et al. 2020; Jiang et al. 2021); *C. siamense* from China (Han et al. 2016, Chung et al. 2019, Chen et al. 2020, Jiang et al. 2021, Wang et al. 2022f, Zhang et al. 2023b), Bangladesh (Gupta et al. 2019), Brazil (Capobianco et al. 2016) and the USA (Weir et al. 2012, Adhikari et al. 2019); *C. theobromicola* from the USA (Weir et al. 2012); *C. viniferum* from China (He et al. 2019). Additional species are: *C. coccodes*, known from Australia (Shivas et al. 2016); *C. boninense* from China (Bi et al. 2017b); *C. karsti* from Brazil (Soares et al. 2021); *C. truncatum* from China (Bi et al. 2017a); *C. nigrum* from Argentina (Liu et al. 2013b). Among these 21 species associated to strawberry anthracnose, *C. nymphaeae* is the most widespread. This fungus represents 98% of the isolates collected from strawberry anthracnose over a 23-year period in the USA (Wang et al. 2019d) and also proved the most common species in the UK (Baroncelli et al. 2015b). *Colletotrichum nymphaeae* was also the sole species identified in Iran, where the disease is recent (Karimi et al. 2017b). On the other hand, *C. siamense* is the most prevalent pathogen in Brazil (Capobianco et al. 2016), Bangladesh (Gupta et al. 2019) and China (along *C. fructicola*; Han et al. 2016, Chung et al. 2019, Chen et al. 2020, Jiang et al. 2021), although *C. siamense* has also been recently reported from the USA (Adhikari et al. 2019) and *C. pandanicola* was recently associated to a severe crown rot disease in China (Yan et al. 2023). In a study covering diverse latitudes and climatic zones in China, Ji et al. (2022) point out *C. siamense* and *C. fructicola* as the prevalent pathogens in sub-tropical areas, whereas fungi from the acutatum and the boninense complexes are more common in temperate regions. Worldwide differences and dynamics of the prevalent pathogen populations may hamper the deployment of accurate crop protection measures in such a highly profitable crop but with a very short growth period. The analysis of the interaction between pathogen species and alternative fungicide substances (Rebello et al. 2022) is an example of such approaches.

Apple (*Malus domestica*) bitter rot is an important disease in areas with warm and humid summer conditions, with small brown lesions on young fruits, expanding rapidly into round sunken lesions developing spore masses, often in concentric circles (Turechek 2004). Glomerella leaf spot of apple is an additional and relatively recent disease associated to *Colletotrichum* spp., resulting on severe defoliation in humid sub-tropical climates (Velho et al. 2019, Wang et al. 2020d). The causal agents cluster mostly in the acutatum and gloeosporioides species complexes. In the acutatum complex: *Colletotrichum acerbum* is known from New Zealand (Damm et al. 2012a); *C. acutatum* from Australia (Shivas et al. 2016); *C. fioriniae* from New Zealand (Damm et al. 2012a), Korea (Oo et al. 2018, Kim et al. 2020), the USA (Damm et al. 2012a, Kou et al. 2014, Munir et al. 2016), Portugal (Azores islands) (Damm et al. 2012a), France (Nodet et al. 2016), Belgium (Grammen et al. 2019), the Netherlands (Damm et al. 2012a), Italy (Damm et al. 2012a, Carneiro & Baric 2021) and Slovenia (Munda 2014); *C. godetiae* from Slovenia (Munda 2014), Italy (Carneiro & Baric 2021), Belgium (Grammen et al. 2019), the Netherlands (Damm et al. 2012a, Wenneker et al. 2016), the UK (Baroncelli et al. 2014) and Australia (Shivas et al. 2016); *C. limeticola* from Brazil (Moreira et al. 2019a); *C. melonis* from Brazil (Bragança et al. 2016a, Moreira et al. 2019a, Gelain et al. 2023) and Uruguay (Alaniz et al. 2015); *C. nymphaeae* from Brazil (Damm et al. 2012a, Velho et al. 2014b, 2015, 2019, Bragança et al. 2016a, Moreira et al. 2019a, Gelain et al. 2023), the USA (Munir et al. 2016, Liu et al. 2021b), China (Chen et al. 2022f) and Korea (Oo et al. 2018, Kim et al. 2020); *C. orientale* from China (Chen et al. 2022f); *C. paranaense* from Brazil (Bragança et al. 2016a, Moreira et al. 2019a); *C. rhombiforme* from Belgium (Grammen et al. 2019) and China (Wu et al. 2017); *C. salicis* from Belgium (Grammen et al. 2019), Italy (Carneiro et al. 2021), New Zealand and Germany (Damm et al. 2012a); *C. sloanei* from Indonesia (Zhafarina et al. 2021). In the gloeosporioides complex: *C. aenigma* is known from China (Zhang et al. 2021b, Chen et al. 2022f); *C. alienum* from New Zealand (Damm et al. 2012a) and China (Chen et al. 2022f); *C. asianum* from China (Wang et al. 2020d); *C. chrysophilum* from Spain (Cabrefiga et al. 2022), Italy (Deltedesco & Oetl 2023) and Brazil and Uruguay (Astolfi et al. 2022); *C. cigarro* from Belgium (Grammen et al. 2019) and the USA (McCulloch et al. 2020); *C. fructicola* from the USA (Weir et al. 2012, Munir et al. 2016), Brazil (Weir et al. 2012, Velho et al. 2015, 2018, 2019, Moreira et al. 2019a), Uruguay (Alaniz et al. 2015, 2019, Velho et al. 2015, Casanova et al. 2017), China (Fu et al. 2013b, Chen et al. 2022f), Korea (Kim et al. 2018b, 2020, Oo et al. 2018, Park et al. 2018), Japan (Yokosawa et al. 2017), Italy (Wenneker et al. 2021) and France (Nodet et al. 2019); *C. gloeosporioides* from China (Chen et al. 2022f) and Korea (on *M. pumila*; Cheon et al. 2016); *C. noveboracense* from the USA (Khodadadi et al. 2020); *C. siamense* from Japan (Yokosawa et al. 2017), Korea (Oo et al. 2018, Park et al. 2018, Kim et al. 2020), China (Chen et al. 2022f; also on red-fleshed apple, *M. niedzwetzkyana*; Han et al. 2022), Pakistan (Abid et al. 2019), the USA (Weir et al. 2012, Munir et al. 2016) and Argentina (Fernandez et al. 2018, 2022); *C. theobromicola* from Uruguay (Alaniz et al. 2015, Velho et al. 2015). *Colletotrichum karsti* is known from Uruguay (Alaniz et al. 2019), Brazil (Velho et al. 2014a, 2015) and the USA (Damm et al. 2012b). There are 20 species of *Colletotrichum* identified from apple, varying in distribution and prevalence. *Colletotrichum fructicola* was shown to be prevalent in a study conducted in Japan (Yokosawa et al. 2017). This fungus, along with *C. siamense*, was the prevalent and most virulent pathogen in Korea (Oo et al. 2018) and was recently recorded in France (Nodet et al. 2019). Still, *C. godetiae* seems to be the prevalent pathogen in Europe, according to studies from the UK (Baroncelli et al. 2014), Belgium (Grammen et al. 2019), the Netherlands (Wenneker et al. 2016) and Slovenia (Munda 2014). Several studies conducted in Brazil and Uruguay reveal *C. fructicola* as the prevalent pathogen (Alaniz et al. 2015, 2019, Velho et al. 2015, 2019, Casanova et al. 2017, Moreira et al. 2019a), although *C. nymphaeae* is also pointed as the prevalent species in a different study (Bragança et al. 2016a) and a recent study has shown that isolates from Brazil and Uruguay, previously assigned to *C. fructicola*, in fact belong to *C. chrysophilum* (Astolfi et al. 2022). However, Fernandez et al. (2022) reported *C. siamense* as the sole pathogen associated to bitter rot in central Argentina. In a study conducted in the USA, *C. fioriniae* was the prevalent pathogen (Munir et al. 2016). The prevalent apple bitter rot pathogen varies across the globe. Similarly, the

causal agent of Glomerella leaf spot varies across the globe. Global analyses of these pathosystems are needed in order to promote control measures and to anticipate future dynamics of the pathogen populations (PLH et al. 2022). To this end, data compiled in the present work suggest concern regarding the recent identification of *C. chrysophilum* in different parts of the world.

Anthraxnose of pear (*Pyrus* × *bretschneideri*, *P. communis* and *P. pyrifolia*) causes fruit rot (bitter rot) as well as leaf lesions (leaf black spot), leading to yield losses and loss of vigour (Fu et al. 2019). There are 16 species of *Colletotrichum* associated to pear anthracnose, mostly in the gloeosporioides complex: *C. aenigma* is known from Italy (Scheda et al. 2014), China (Fu et al. 2019) and Japan (Weir et al. 2012); *C. conoides* from China (Fu et al. 2019); *C. fructicola* from China (Weir et al. 2012, Li et al. 2013b, Zhang et al. 2015b, Fu et al. 2019) and Korea (Choi & Park 2021); *C. gloeosporioides* from China (Fu et al. 2019); *C. siamense* from China (Fu et al. 2019); *C. wuxiense* from China (Fu et al. 2019). In the acutatum complex: *C. acutatum* from New Zealand (Damm et al. 2012a); *C. fioriniae* from France (Da Lio et al. 2017), Serbia (Živković et al. 2023), the USA (Damm et al. 2012a, Pavlović et al. 2019), China (Fu et al. 2019) and New Zealand (Liu et al. 2021b); *C. nymphaeae* from Brazil (Moreira et al. 2019b); *C. pyricola* and *C. salicis* from New Zealand (Damm et al. 2012a). In the boninense complex: *C. citricola* and *C. karsti* from China (Fu et al. 2019). Other species are: *C. jinshuiense* (dematium complex), *C. plurivorum* (orchidearum complex) and *C. pyrifoliae* (singleton species). As for other fruit crops, *C. fioriniae* appears to be the most common pathogen associated to pear anthracnose in Europe and North America and *C. nymphaeae* in South America. In China, a recent and detailed study (Fu et al. 2019) revealed *C. fructicola* as the most prevalent pathogen in *P. pyrifolia* and *P. bretschneideri*, followed by *C. siamense*, but *C. fioriniae* (followed by *C. siamense*) prevailed on *P. communis*. The complex pathogen population structure of pear anthracnose must be taken in consideration when deploying precise crop protection measures, including disease resistance breeding and fungicide development and optimisation of use conditions.

Peach (*Prunus persica*) anthracnose affects vegetative and reproductive organs and can also develop into a post-harvest fruit disease. Symptoms on fruits include sunken lesions with circular rings and the disease can be highly damaging under wet and warm summer conditions (Hu et al. 2015). The disease has been assigned to several species of *Colletotrichum*, including *C. fioriniae* from the USA (Chen et al. 2018), Korea (Lee et al. 2018) and China (Tan et al. 2022b), *C. godetiae* from China (Tan et al. 2022b), *C. nymphaeae* from China (Tan et al. 2022b) and Brazil (Moreira et al. 2020) and *C. paranaense* (Bragança et al. 2016a) from Brazil in the acutatum complex, *C. fructicola* from the USA (Hu et al. 2015, Chen et al. 2018), China (Tan et al. 2022b) and Korea (Lee et al. 2020) and *C. siamense* from the USA (Chen et al. 2018, Eaton et al. 2021), Uruguay (Carbone et al. 2021), China (Tan et al. 2022b) and Korea (Lee et al. 2020) in the gloeosporioides complex, and *C. truncatum* from the USA (Grabke et al. 2014, Chen et al. 2018) and *C. foliicola* from China (as *C. folicola*; Tan et al. 2022b). It is unclear which species prevails in each region, and the few studies conducted to ascertain this aspect have not conveyed a clear response (Hu et al. 2015, Moreira et al. 2020).

Almond (*Prunus dulcis*) anthracnose is an important disease occurring throughout the world, with important outbreaks following the intensification of the crop in recent years. Symptoms occur on fruits, beginning on the hull and progressing into the kernel, leading to mummification. Other symptoms include blossom blight and lesions on leaves and twigs (Förster & Adaskaveg 1999). Etiology studies in modern terms have shown *Colletotrichum godetiae* as the most common pathogen in Spain and Israel, with *C. acutatum* (Damm et al. 2012a, López-Moral et al. 2017) and *C. nymphaeae* (Varjas et al. 2022) also reported. Conversely, *C. acutatum* was the most frequent pathogen associated with almond anthracnose in Australia, with *C. fioriniae* and *C. simmondsii* also being detected, but not *C. godetiae* (De Silva et al. 2021c).

Anthraxnose of pearl plum (*Prunus salicina*) causes leaf blight and has been reported from China associated to *Colletotrichum fructicola* and to a lesser extent to *C. aeshynomenes*, *C. gloeosporioides*, *C. cigarro* and *C. siamense* (Huang et al. 2022e, Lu et al. 2023) and to *C. nymphaeae* in Korea (Chang et al. 2018b). Anthracnose on sweet and sour cherry (*P. avium* and



*P. cerasus*) is relatively uncommon and has been associated to fruit rot and shoot dieback (Damm et al. 2012a) and to leaf spot disease (Chethana et al. 2019). *Colletotrichum godetiae* is the pathogen more frequently reported in Europe (Damm et al. 2012a, Baroncelli et al. 2015b, Grammen et al. 2019), but *C. gloeosporioides* has also been reported from Italy (Scheda et al. 2014). *Colletotrichum aenigma*, *C. fructicola* and *C. pseudotheobromicola* have been associated to leaf spot disease in China as minor pathogens (Chethana et al. 2019, Tang et al. 2022), but recently the disease became of major concern (Zhou et al. 2023a), the main pathogens being *C. aenigma*, *C. gloeosporioides*, *C. fructicola*, *C. conoides* and *C. dematium*, but being also found *C. siamense*, *C. temperatum*, *C. hebeiense*, *C. sojiae*, *C. plurivorum*, *C. karsti*, *C. truncatum* and *C. incanum*. Additionally, *C. chlorophyti* has been reported from Yoshino cherry tree (*Prunus* × *yedoensis*) in Japan (Sato et al. 2015), *C. fioriniae* from apricot (*P. armeniaca*) in the USA (Eaton et al. 2021), *C. godetiae* from *P. pseudocerasus* in China (Wu et al. 2023b), *C. fioriniae* from *P. serrulata* in China (Dai et al. 2023a) and *C. fructicola* from *P. sibirica* in China (Han et al. 2023a).

Anthracnose of loquat (*Eriobotrya japonica*) causes circular to irregular necrotic lesions on leaves as well as fruit infections that can cause post-harvest fruit depreciation (Naz et al. 2017). The disease has been reported from several countries, and associated to diverse fungi: *Colletotrichum siamense* in Australia and China (Shivas et al. 2016, Kuang et al. 2023, Zhang et al. 2023b); *C. godetiae* in Mexico (Juárez-Vázquez et al. 2019) and China (Zhang et al. 2023b); *C. gloeosporioides* in Pakistan (Naz et al. 2017); *C. nymphaeae*, *C. fructicola*, *C. eriobotryae* and *C. scovillei* in China (Wu et al. 2018, 2022a, Damm et al. 2020, Kuang et al. 2021).

Quince (*Cydonia oblonga*) anthracnose has been recorded as a post-harvest disease in Serbia, attaining high severity but low incidence, and attributed to *Colletotrichum godetiae* (Živković et al. 2014). *Colletotrichum fioriniae* has also been reported associated to *Cydonia oblonga* in New Zealand (Liu et al. 2021b).

Anthracnose on *Rubus* spp. (*R. glaucus* and *R. idaeus*) affects fruits as well as vegetative organs (Afanador-Kafuri et al. 2014, Schoeneberg & Hu 2020). The fungi associated to the disease are: *Colletotrichum fioriniae* in the USA (Damm et al. 2012a, Schoeneberg & Hu 2020); *C. godetiae* in Turkey (Damm et al. 2012a) and Colombia (Afanador-Kafuri et al. 2014); *C. cigarro*, *C. fructicola*, *C. brassicicola* and *C. karsti* in Colombia (Afanador-Kafuri et al. 2014); *C. neorubicola* in China (Liu et al. 2020d). A survey conducted in Colombia on the Andean blackberry (*R. glaucus*) anthracnose pathogens revealed complex patterns of geographic distribution according to host type and neighbouring crops (Afanador-Kafuri et al. 2014). Recently, anthracnose on *R. rosaefolius* was attributed to *C. boninense* (Zheng et al. 2021a) and on *R. corchorifolius* to *C. nymphaeae* and *C. fructicola* (Wu et al. 2021), in China.

Other host-fungus combinations in the Rosaceae include: on *Agrimonia eupatoria*, *Colletotrichum godetiae* known from Austria (Damm et al. 2012a); on *Chaenomeles sinensis*, *Colletotrichum gloeosporioides* causing brown leaf spots from China (Ni et al. 2021); on *Crataegus gracilior*, *Colletotrichum gloeosporioides* on fruits from Mexico (Nieto-López et al. 2018); on *Dryas octopetala*, *C. cigarro* from Switzerland (Weir et al. 2012); on *Photinia* spp., *C. nymphaeae* from the UK (Damm et al. 2012a) and *C. karsti* and *C. siamense* from China (Mao et al. 2021, Zhang et al. 2023b); on *Rosa* spp., *C. boninense*, *C. gloeosporioides*, *C. mengyinense* and *C. siamense* from China (Feng et al. 2019, Hassan et al. 2019b, Ding et al. 2021, Mu et al. 2021); on *Sanguisorba officinalis*, *C. lineola* from Japan (Sato et al. 2015); on *Sorbaria sorbifolia*, *C. gloeosporioides* from China (Li et al. 2019c, Wang et al. 2021a).

## Rubiaceae

Coffee (*Coffea arabica*) berry disease affects green coffee berries, rotting the fruit pulp and the seed, thus causing severe yield losses (Silva et al. 2006). The disease is a major constraint to sustainable production of Arabica coffee in Africa, to where it is restricted, and is of quarantine concern in America and Asia, where it has not been recorded (Batista et al. 2017). The causal agent is *Colletotrichum kahawae*, a fungus that has the unique capacity of infecting green coffee berries, as opposed to other species of *Colletotrichum* that occur in the ecosystem, and which are only

capable of infecting ripe berries (and thus not affecting the seed) or that live on leaves (Waller et al. 1993). *Colletotrichum kahawae* has recently undergone speciation via host-jump from a polyphagous and widespread group of fungi, *C. cigarro*, to the coffee green berry ecological niche (Silva et al. 2012). Whereas *C. kahawae* and *C. cigarro* are phylogenetically closely related (Weir et al. 2012), host specialization, cytogenomic, molecular and biochemical evidences support the distinction of these two species (Cabral et al. 2020). Besides *C. kahawae*, there is a plethora of species of *Colletotrichum* occurring on *Coffea* spp., found mainly on leaves and ripe fruits, most of them from the gloeosporioides complex. In this complex are: *C. asianum* from Thailand (Weir et al. 2012); *C. endophyticum* from China (Cao et al. 2019a), *C. fructicola* from Thailand (Weir et al. 2012, Numponsak et al. 2018) and China (Cao et al. 2019a); *C. gloeosporioides* from Mexico (Cristóbal-Martínez et al. 2017); *C. queenslandicum* from the Fiji (Weir et al. 2012); *C. siamense* from Mexico (Cristóbal-Martínez et al. 2017), Thailand (Weir et al. 2012, Liu et al. 2013a, Udayanga et al. 2013), China (Cao et al. 2019a) and Australia (Shivas et al. 2016); *C. theobromicola* from Australia (Shivas et al. 2016) and Mexico (Cristóbal-Martínez et al. 2017); *C. tropicale* from China (Cao et al. 2019a). In the acutatum complex, *C. acutatum* from Kenya, *C. costaricense* from Costa Rica, *C. fioriniae* from Angola and *C. walleri* from Vietnam (Damm et al. 2012a). In the boninense complex, *C. boninense* from Brazil (Freitas et al. 2013) and *C. karsti* from Vietnam (Damm et al. 2012b), China (Cao et al. 2019a) and Mexico (Cristóbal-Martínez et al. 2017). In the gigasporum complex, *C. gigasporum* from Mexico (Cristóbal-Martínez et al. 2017), Colombia (Rakotoniriana et al. 2013) and China (Cao et al. 2019a), and *C. vietnamense* from Vietnam (Liu et al. 2014). In the magnum complex, *C. brevisporum* from China (Cao et al. 2019a). In the orchidearum complex, *C. plurivorum* from Vietnam (Damm et al. 2019). The control of coffee berry disease requires the use of fungicides, although resistance breeding is a promising crop protection alternative measure against *C. kahawae* (Silva et al. 2006). Other anthracnose diseases affecting coffee leaves can also be of relevance (Freitas et al. 2013, Cao et al. 2019a), but these are caused by multiple fungi, prompting for studies comparing those pathosystems.

Other host-fungus combinations in the Rubiaceae include: on *Carapichea ipecacuanha*, *Colletotrichum brevisporum*, *C. gigasporum*, *C. phyllanthi* and *C. theobromicola* as epiphytes from Brazil (Ferreira et al. 2020); on *Coprosma* sp., *Colletotrichum aotearoa* from New Zealand (Weir et al. 2012); on *Gardenia jasminoides*, *C. gardeniae* associated to leaf spots in China (Zhang et al. 2023b); on *Genipa americana*, *C. chrysophilum* as an endophyte from Panama (Vieira et al. 2017); on *Paederia foetida*, *C. plurivorum* and *C. reniforme* (Liu et al. 2022b); on *Rubia cordifolia*, *C. gloeosporioides* causing leaf lesions in China (Tang & Tan 2020).

## Rutaceae

*Colletotrichum*-related diseases occurring on citrus (oranges, lemons, limes, mandarins and others), namely anthracnose (wither-tip, leaf spot, shoot dieback, pre- and post-harvest anthracnose), post-bloom fruit drop and Key lime anthracnose, have long been studied and the identification and distinction of their causal agents has played an important role in such studies (Peres et al. 2008). Many studies have been conducted recently on these pathosystems in different parts of the world, in part providing fungal specimens relevant to the establishment of the current taxonomic delimitation within *Colletotrichum*. Under the current understanding, and as revised by Guarnaccia et al. (2017), *C. abscissum* and *C. gloeosporioides* are the causal agents of post-bloom fruit drop in Brazil (Crous et al. 2015) and *C. limetticola* is the causal agent of Key lime anthracnose (Damm et al. 2012a). Additionally, *C. gloeosporioides* and *C. karsti* are the causal agents of twig and shoot dieback (Riolo et al. 2021). Anthracnose on fruits (pre- and post-harvest), leaves and twigs, however, are caused by diverse fungi, with varied prevalence according to host and location. There are 34 species of *Colletotrichum* identified from citrus, mostly in the acutatum, boninense and gloeosporioides complexes. In the acutatum complex, *C. abscissum* is recorded from Brazil (Crous et al. 2015, Bragança et al. 2016a, Silva et al. 2017a) and the USA (Guarnaccia et al. 2017), *C. acutatum* from Italy (Guarnaccia et al. 2017), *C. godetiae* from as unknown location (Damm et al. 2012a), *C. johnstonii* from New Zealand (Damm et al. 2012a), *C. limetticola* from

Cuba and the USA (Damm et al. 2012a, Guarnaccia et al. 2017), *C. limonicola* from Malta (Guarnaccia et al. 2017), *C. nymphaeae* from China (as *C. citri*; Huang et al. 2013) and Australia (Shivas et al. 2016), *C. scovillei* on wampi (*Clausena lansium*) from China (Lin et al. 2020) and *C. simmondsii* from China (Guarnaccia et al. 2017). In the boninense complex, *C. boninense* is recorded from China (Guarnaccia et al. 2017), *C. catinaense* from Italy and Portugal (Guarnaccia et al. 2017), *C. citricola* as an endophyte from China (Huang et al. 2013), *C. constrictum* from New Zealand (Damm et al. 2012b), *C. karsti* from New Zealand (Damm et al. 2012b), Australia (Wang et al. 2021c), South Africa (Damm et al. 2012b), the USA (Mayorquin et al. 2019, Camiletti et al. 2022), China (Huang et al. 2013), Turkey (Uysal & Kurt 2019, Uysal et al. 2022), Italy (Mosca et al. 2014, Aiello et al. 2015, Guarnaccia et al. 2017, Riolo et al. 2021) and Portugal (Ramos et al. 2016), and *C. novae-zelandiae* from New Zealand (Damm et al. 2012b). In the gloeosporioides complex, *C. australianum* is recorded from Australia (Wang et al. 2021c), *C. aenigma* from Italy (Schena et al. 2014), *C. cigarro* from Italy (Perrone et al. 2016), *C. fructicola* from China (Huang et al. 2013, Hu et al. 2019), *C. gloeosporioides* from all continents (Weir et al. 2012, Huang et al. 2013, Udayanga et al. 2013, Schena et al. 2014, Aiello et al. 2015, Ramos et al. 2016, Rhaiem & Taylor 2016, Shivas et al. 2016, Douanla-Meli & Unger 2017, Guarnaccia et al. 2017, Silva et al. 2017a, Waculicz-Andrade et al. 2017, Mayorquin et al. 2019, Wang et al. 2019e, Pérez-Mora et al. 2021, Camiletti et al. 2022, Uysal et al. 2022), *C. helleniense* from Greece (Guarnaccia et al. 2017), *C. hystricis* from Italy (Guarnaccia et al. 2017), *C. queenslandicum* from the USA (Kunta et al. 2018), *C. siamense* from Mexico (Pérez-Mora et al. 2021), Egypt (Guarnaccia et al. 2017), Pakistan (Fayyaz et al. 2018), India (Sharma et al. 2015a), Bangladesh (Guarnaccia et al. 2017), Vietnam (Guarnaccia et al. 2017) and China (Cheng et al. 2013, Liu et al. 2023d), *C. syzygiicola* from Thailand (Udayanga et al. 2013) and *C. theobromicola* from Australia (Wang et al. 2021c), as well as *C. asianum*, *C. tainanense* and *C. tomentosae* from China as endophytes (Liu et al. 2023d). Other species are: in the dracaenophilum complex, *C. tropicicola* from Thailand (Noireung et al. 2012) and Mexico (Damm et al. 2019); in the magnum complex, *C. brevisporum* (Guarnaccia et al. 2017, Damm et al. 2019) and *C. guangdongense* (as endophyte; Liu et al. 2023d) from China; in the orchidearum complex, *C. plurivorum* from Vietnam (Damm et al. 2019) and China (as endophyte; Liu et al. 2023d); in the truncatum complex, *C. truncatum* from China (Huang et al. 2013, Cheng et al. 2014); *C. citri-medicae* from China (Hyde et al. 2020c; as *C. citrus-medicae*). Further, intra-specific variability has been recently revealed among *C. gloeosporioides* strains associated with citrus anthracnose in China, but no correlation has been established to geography or host (Liu et al. 2023a). The citrus anthracnose pathosystems offer complex research areas, for which the elucidation of disease etiology and prevalent pathogen populations are fundamental to devise accurate crop protection measures.

Other host-fungus combinations in the Rutaceae include: on *Boronia megastigma*, *Colletotrichum acutatum* from Australia (Shivas et al. 2016); on *Murraya* sp., *C. simmondsii* (Guarnaccia et al. 2017).

### Salicaceae

Anthracnose on poplar (*Populus* spp.) can be an important disease, causing circular to irregular brown spots, leading to premature leaf abscission and loss of tree vigour (Li et al. 2012). *Colletotrichum salicis* (from the acutatum complex) has been associated to the disease in the Netherlands (Damm et al. 2012a) and Iran (Khodaei et al. 2019), whereas *C. aenigma* (as *C. populi*; from the gloeosporioides complex) is associated to this disease in China (Li et al. 2012), from where *C. subsalicis* has also been reported (Liu et al. 2022b).

Anthracnose of willows (*Salix* spp.) is due to diverse pathogens. Those belonging to *Colletotrichum* are assigned to *C. salicis*, and have been reported from New Zealand (Damm et al. 2012a), Australia (Shivas et al. 2016), Japan (Damm et al. 2012a), Poland (Okorski et al. 2018), Germany (Damm et al. 2012a), the Netherlands (Damm et al. 2012a) and the UK (Damm et al. 2012a), although recently in China *C. siamense* was also associated to anthracnose on *S. matsudana*

(Zhang et al. 2021d) and *C. siamense* and *C. gloeosporioides* on *S. babylonica* (Zhang et al. 2023g).

### Santalaceae

Anthracnose of sandalwood (*Santalum album*) seedlings was recently reported in India as causing pale yellow leaf lesions surrounded by a purple halo and attributed to *Colletotrichum siamense* (Purushotham et al. 2022). This is the single record across all families in the Santalales.

### Sapindaceae

Lychee (*Litchi chinensis*) anthracnose is characterised by small black lesions on leaves, petioles, pedicels and fruits, where it can also become a post-harvest disease (Anderson et al. 2013). Reports from Australia have associated the species *Colletotrichum simmondsii*, *C. sloanei* and *C. queenslandicum* to the disease (Anderson et al. 2013, Shivas et al. 2016), while in China the disease is attributed to *C. siamense* (Ni et al. 2017), *C. fioriniae* (Ling et al. 2021) and *C. karsti* (Zhao et al. 2021c) and in Japan to *C. tropicale* (Weir et al. 2012).

Rambutan (*Nephelium lappaceum*) anthracnose is a pre- and post-harvest disease, causing fruit rot (Sivakumar et al. 1997). The disease has been attributed to *Colletotrichum fructicola* and *C. queenslandicum* in Puerto Rico (Serrato-Diaz et al. 2017) and to *C. simmondsii* in Australia (Shivas et al. 2016).

Leaf blotch on *Acer coriaceifolium* was recently reported from China, and attributed to *Colletotrichum gloeosporioides* (Zhu et al. 2020), whereas leaf spots on *A. fabri* were attributed to *C. siamense* (Zhang et al. 2023d). *Colletotrichum salicis* has also been reported on *A. platanoides* in the USA (Damm et al. 2012a), whereas *C. fioriniae* has been reported on *A. negundo* in the same country (Liu et al. 2021b).

Leaf blotch on *Aesculus chinensis* was recently reported from China, and attributed to *Colletotrichum fructicola* and *C. gloeosporioides* (Sun et al. 2020c).

On *Dimocarpus longan*, *Colletotrichum fructicola* had been reported from Thailand (Hyde et al. 2018).

### Sapotaceae

Anthracnose on sapota (*Manilkara zapota*) was recently reported as necrotic leaf spots on seedlings in a nursery in Brazil and the causal agent identified as *Colletotrichum theobromicola* (Martins et al. 2018).

Anthracnose on abiu (*Pouteria caimito*) was recently reported as leaf spots on seedlings in a nursery in China and the causal agent identified as *Colletotrichum gloeosporioides* (Duan et al. 2018a). Leaf spots on *P. campechiana* are also attributed to *C. fructicola* in China (Yang et al. 2021b).

On miracle berry (*Synsepalum dulcificum*), *Colletotrichum karsti* has been recorded from China (Damm et al. 2012b).

### Sarraceniaceae

Anthracnose was recently described on leaves of the insectivorous plant *Sarracenia purpurea* subsp. *purpurea* f. *heterophylla* and associated to *Colletotrichum cigarro* (Taba et al. 2022).

### Schisandraceae

Anthracnose is one of the important diseases of star anise (*Illicium verum*), affecting twigs, pedicels, fruit stalks and fruits. The disease was recently attributed to *Colletotrichum fructicola* and *C. siamense* in China (Zhao et al. 2022, Liao et al. 2023). On *I. simonsii*, *C. jiangxiense* was associated to leaf spots in China (Zhang et al. 2023b).

On *Kadsura coccinea*, *Colletotrichum siamense* is known from China associated to circular brown leaf spots (Jiang et al. 2022).

On *Schisandra chinensis*, *Colletotrichum fioriniae* was recently reported from Korea causing small sunken lesions on fruits (Kim et al. 2022).

#### Simaroubaceae

On *Ailanthus altissima*, *Colletotrichum fioriniae* was recorded from a dead branch in Italy (Hyde et al. 2017) and *C. subacidiae* from a dead petiole in China (Liu et al. 2022b).

#### Solanaceae

Chilli (*Capsicum* spp.) anthracnose is a major disease of these crops, mostly affecting fruits. Symptoms include sunken round coalescing lesions, with rings of acervuli. This pathosystem has provided a ground for many studies under diverse perspectives, including epidemiology, crop protection and fungal taxonomy (Than et al. 2008, Oo & Oh 2016, Saxena et al. 2016, Mongkolporn & Taylor 2018, Saini et al. 2021). In fact, there are 35 species of *Colletotrichum* recorded from *Capsicum*, four of which are only known from *Capsicum* spp., namely *Colletotrichum cairnsense*, *C. grossum*, *C. javanense* and *C. makassarensense*. The prevalent pathogen populations vary across the globe, with differences in virulence and temporal dynamics (De Silva et al. 2019), hampering the deployment of accurate control measures such as the selection of resistant cultivars based on resistance genes identified in *Capsicum baccatum* (Mahasuk et al. 2016). Most of the 36 species are from the gloeosporioides and acutatum complexes. In the gloeosporioides complex: *Colletotrichum aenigma* has been reported from Israel (Sharma et al. 2022); *C. australianum* from Australia (Wang et al. 2021c); *C. cigarro* from Bulgaria (Manova et al. 2022); *C. conoides* from China (Diao et al. 2017); *C. endophyticum* from China (Diao et al. 2017) and Thailand (De Silva et al. 2019); *C. fructicola* from China (Liu et al. 2016c, Diao et al. 2017) and Thailand (De Silva et al. 2019); *C. gloeosporioides* from China (Liu et al. 2016c, Diao et al. 2017, Li et al. 2021b) and Italy (Scheda et al. 2014); *C. grossum* from Italy (Guarnaccia et al. 2021) and China (Diao et al. 2017); *C. makassarensense* from Indonesia (De Silva et al. 2019); *C. perseae* from Israel (Sharma et al. 2022); *C. siamense* from Australia (De Silva et al. 2017), Sri Lanka (De Silva et al. 2019), Indonesia (De Silva et al. 2019), Thailand (Weir et al. 2012, Hyde et al. 2018, De Silva et al. 2019), China (Liu et al. 2016c, Diao et al. 2017; also as *C. hymenocallidis*), Korea (Oo et al. 2021) and Brazil (Oliveira et al. 2017, Silva et al. 2017c); *C. tainanense* from China (De Silva et al. 2019); *C. tropicale* from Indonesia (De Silva et al. 2019) and Brazil (Silva et al. 2017c); *C. viniferum* from China (Diao et al. 2017). In the acutatum complex: *C. acutatum* from Sri Lanka (Damm et al. 2012a); *C. brisbanense* from Australia (Damm et al. 2012a); *C. cairnsense* from Australia (Damm et al. 2012a); *C. fioriniae* from China (Diao et al. 2017); *C. javanense* from Indonesia (De Silva et al. 2019); *C. nymphaeae* from Indonesia (Damm et al. 2012a), Malaysia (Nasehi et al. 2016), Zimbabwe (Damm et al. 2012a) and Bulgaria (Manova et al. 2022); *C. scovillei* from the USA (Toporek & Keinath 2021), Brazil (Caires et al. 2014, Oliveira et al. 2017, Silva et al. 2017b), Indonesia (Damm et al. 2012a, De Silva et al. 2019), Thailand (Damm et al. 2012a), China (Zhao et al. 2016a, Liu et al. 2016c, Diao et al. 2017, Huo et al. 2021), Korea (Oo et al. 2017) and Japan (Kanto et al. 2014); *C. simmondsii* from Australia (De Silva et al. 2017). In the boninense complex: *C. boninense* from China (Diao et al. 2013); *C. karsti* from China (Diao et al. 2017, Zhang et al. 2023b), Indonesia (De Silva et al. 2019) and New Zealand (Damm et al. 2012b); *C. novae-zelandiae* from New Zealand (Damm et al. 2012b). Other species are: *C. tabacum* from China in the destructivum complex (Wei et al. 2022a); *C. brevisporum* from Trinidad and Tobago (Villafana et al. 2019), Brazil (Almeida et al. 2017, Oliveira et al. 2017, Silva et al. 2017c, Damm et al. 2019) and China (Liu et al. 2016c, Damm et al. 2019) and *C. magnum* (also as *C. liaoningense*; Diao et al. 2017, Liu et al. 2022b) from China in the magnum complex; *C. lindemuthianum* from China (Gao et al. 2018) in the orbiculare complex; *C. plurivorum* from and Thailand (De Silva et al. 2019) and *C. sojae* (Zhang et al. 2023f) from China in the orchidearum complex; *C. incanum* (Diao et al. 2017) in the spaethianum complex; *C. coccodes* from Italy (Mosca et al. 2014), Poland (Jamiołkowska et al. 2018), Bulgaria and North Macedonia (Manova et al. 2022) and China (Sheu et al. 2020); *C. nigrum* from the USA, Argentina, Indonesia

and New Zealand (Liu et al. 2013b); *C. truncatum* (syn. *C. capsici*) from Brazil (Silva et al. 2017c), Australia (De Silva et al. 2017), Pakistan (Tariq et al. 2017), India (Damm et al. 2009, Gowtham et al. 2018), Malaysia (Mokhtar et al. 2018), Thailand (Boukaew et al. 2018, Srikhong et al. 2018), China (Liu et al. 2016c, Diao et al. 2017), Korea (Oo & Oh 2020) and Japan (Sato et al. 2015). *Colletotrichum truncatum*, *C. siamense* and *C. scovillei* are reported as the prevalent pathogens in Asia, but *C. javanense* and *C. scovillei* were considered the most virulent to *Capsicum annuum* and *C. chinense* among pathogens representing 10 species of *Colletotrichum* from diverse Asian countries (De Silva et al. 2019, 2021a). Nevertheless, regional variations and the occurrence of less frequent but highly virulent fungal species illustrates the dynamic nature of this pathosystem.

Tomato (*Solanum lycopersicum*) anthracnose (black dot) is an important disease, causing fruit rot, but affecting also leaves and roots, forming microsclerotia in senescent tissues (Dillard 1992). Liu et al. (2013b) described *Colletotrichum coccodes* and *C. nigrum* as the prevalent pathogens associated to tomato anthracnose, but recently several additional species were associated to the disease. In the acutatum complex: *Colletotrichum acutatum* has been reported from New Zealand (Liu et al. 2021b); *C. fioriniae* from New Zealand (Damm et al. 2012a) and the USA (Damm et al. 2012a, Chechi et al. 2019); *C. godetiae* from Bulgaria (Manova et al. 2022); *C. johnstonii* from New Zealand (Damm et al. 2012a); *C. nymphaeae* from the USA (Chechi et al. 2019); *C. salicis* from Germany (Damm et al. 2012a) and Bulgaria (Manova et al. 2022); *C. simmondsii* from Australia (Shivas et al. 2016). In the boninense complex: *C. boninense* from New Zealand (Damm et al. 2012a) and Malaysia (Rashid et al. 2015); *C. karsti* from New Zealand (Damm et al. 2012a). In the truncatum complex: *C. truncatum* from China (Diao et al. 2014), Malaysia (Shahriar et al. 2023), India (Saini et al. 2017b) and Mexico (Almaraz-Sánchez et al. 2019). In the gloeosporioides complex: *C. cigarro* from Bulgaria (Manova et al. 2022). The pathological relevance of these recently reported species remains to be established.

Potato (*Solanum tuberosum*) black dot is an important disease, causing silvery lesions on the tuber surface and tuber blemish symptoms, along with symptoms on stems and leaves (Lees & Hilton 2003). Taxonomic analyses confirmed *Colletotrichum coccodes* as the potato black dot pathogen (Liu et al. 2011, 2013b) and the pathogen has been recently reported from Mexico (Pérez-Mora et al. 2020), Turkey (Çakır et al. 2019), Russia (Nikitin et al. 2018) and China (Tian et al. 2019, Zhong et al. 2022).

Tamarillo (*Solanum betaceum*) anthracnose affects fruits throughout their development and often attains high incidence, besides affecting leaves and flowers (Afanador-Kafuri et al. 2003). The disease is caused by *Colletotrichum tamarilloi* (Damm et al. 2012a), which has been reported from Colombia (Pardo-De La Hoz et al. 2016) and Ecuador (Caicedo et al. 2017). Additional species of *Colletotrichum* recorded from tamarillo are: *C. cigarro* (Rojas et al. 2018), *C. godetiae* (Damm et al. 2012a) and *C. karsti* (Damm et al. 2012b) from Colombia, the latter also from Brazil (Rosado et al. 2022); *C. simmondsii* from Australia (Shivas et al. 2016); *C. boninense* and *C. constrictum* from New Zealand (Damm et al. 2012b). The pathological relevance of these species for tamarillo anthracnose remains to be dissected.

Aubergine/eggplant/brinjal (*Solanum melongena*) anthracnose is a relatively uncommon disease, responsible for sunken lesions on fruits (Xu et al. 2018a). The causal agents have been assigned to *Colletotrichum truncatum* in Japan (Sato et al. 2015) and Thailand (Hyde et al. 2018), to *C. siamense* in Malaysia (Khoo et al. 2022a), to *C. torulosum* in New Zealand (Damm et al. 2012b), to *C. fioriniae* in Korea (Xu et al. 2018a) and to *C. coccodes* in Bulgaria (Manova et al. 2022).

Anthracnose is a fruit disease of Chinese wolfberries (*Lycium barbarum* and *L. chinense*) (Han-Mo 2008). The disease has been attributed to *Colletotrichum fioriniae* in China (Liu et al. 2016a, Xu et al. 2022) and Korea (Oo et al. 2016), although *C. brevisporum* has been reported from Korea as an endophyte (Paul et al. 2014).

Anthracnose of tobacco (*Nicotiana tabacum*) affects seedlings under cool and wet conditions (Shen et al. 2001). The causal agent has been assigned to *Colletotrichum tabacum*, known from Germany, France, Zambia and India (Damm et al. 2014), but recent reports of this fungus are

scarce. Nevertheless, strains of this fungus from culture collections have been used to dissect histopathological processes in tobacco anthracnose (Shen et al. 2001). Recently, however, chlorotic and necrotic spots on tobacco leaves recorded in China were attributed to *C. fructicola* (Wang et al. 2016c), to *C. cliviicola* (Wang et al. 2022a), to *C. nymphaeae* (Liu et al. 2023b) but also to *C. tabacum* (Wan et al. 2022b), suggesting that the etiology and prevalence of the current tobacco anthracnose pathogens require further elucidation.

On Jerusalem cherry (*Solanum pseudocapsicum*), anthracnose has been attributed to *Colletotrichum magnum* (as *C. liaoningense*; Liu et al. 2022b) in China, causing large irregular white spots on leaves, with a pale grey edge (Liu et al. 2021a).

On *Datura metel*, *Colletotrichum siamense* was reported as an endophyte from India (Naik et al. 2018).

### Theaceae

There are 20 species of *Colletotrichum* recorded from *Camellia* spp. plants, three of which are only known from these hosts (*C. camelliae-japonicae*, *C. chongqingense* and *C. pseudomajus*).

Anthracnose of tea plant (*Camellia sinensis*) causes water-soaked leaf lesions that progress to necrosis, leading to yield losses (Wang et al. 2016a). At least 17 species of *Colletotrichum* have been retrieved from the plant. In the acutatum complex, *C. acutatum* (Chen et al. 2016a) and *C. fioriniae* (Liu et al. 2015a, Wang et al. 2016a) are known from China. In the boninense complex, *C. boninense* (Liu et al. 2015a), *C. chongqingense* and *C. karsti* (Liu et al. 2015a, Wang et al. 2016a, Wan et al. 2021) are known from China. In the gigasporum complex, *C. pseudomajus* is known from China (Liu et al. 2014). In the truncatum complex, *C. truncatum* is known from China (Wang et al. 2016a). In the gloeosporioides complex, there are 10 species: *C. aenigma*, from China (Wang et al. 2016a, Lin et al. 2023b); *C. alienum*, from China (Liu et al. 2015a); *C. camelliae*, from China (Liu et al. 2015a, Wang et al. 2016a, Lu et al. 2018, He et al. 2019, Lin et al. 2023b) and Japan (Win et al. 2018); *C. endophyticum*, from China (Wang et al. 2016a); *C. fructicola*, from China (Liu et al. 2015a, Wang et al. 2016a, Lu et al. 2018, Shi et al. 2018, Lin et al. 2021, 2023b, Zhang et al. 2023b) and Indonesia (Weir et al. 2012, Liu et al. 2015a); *C. gloeosporioides* from China (Guo et al. 2014a, Liu et al. 2015a); *C. henanense* from China (Liu et al. 2015a); *C. jiangxiense* from China (Liu et al. 2015a); *C. siamense* from China (Wang et al. 2016a); *C. wuxiense* from China (Wang et al. 2016a).

Anthracnose on tea-oil tree (*Camellia oleifera*) causes symptoms on leaves, designated brown spot disease (Xu et al. 2017b). Various surveys conducted recently in diverse regions in China have identified different causal agents: in the acutatum complex, *Colletotrichum nymphaeae* (Li & Li 2020); in the boninense complex, *C. karsti* (Jiang & Li 2018); in the gloeosporioides complex, *C. aenigma*, *C. camelliae*, *C. fructicola* (Wang et al. 2020a), *C. gloeosporioides* (Xu et al. 2017b, Wang et al. 2020a), *C. henanense* (Li et al. 2018c) and *C. siamense* (Liu et al. 2015a, Wang et al. 2020a). Pathogen population analyses have revealed *C. fructicola* as the prevalent pathogen (Wang et al. 2020a). *Colletotrichum camelliae*, *C. fructicola* and *C. siamense* were recently recorded to cause anthracnose on *Camellia grijsii* (synonym *C. yuhsienensis*) leaves, raising concern as this tea-oil tree wild relative was considered anthracnose-resistant and used as resistance-donor in breeding programmes (Chen et al. 2022b, 2022e).

On camellia (*Camellia japonica*), anthracnose symptoms (leaf spots) were attributed to *Colletotrichum aenigma*, *C. karsti* and *C. siamense* in China (Yang et al. 2019, Peng et al. 2022, Zhang et al. 2023b) and to *C. camelliae-japonicae* in Japan (Hou et al. 2016).

Other host-fungus combinations in the Theaceae include: on *Camellia chrysantha*, *Colletotrichum fructicola* and *C. siamense* from China (Zhao et al. 2021a); on *Camellia reticulata*, *Colletotrichum fioriniae* from China (Damm et al. 2012a); on *Camellia sasanqua*, *Colletotrichum aenigma* from China (Chen et al. 2019a) and *C. camelliae* from the USA (Liu et al. 2015a); on *Camellia* sp., *Colletotrichum lupini* from the UK (Damm et al. 2012a); on *Schima* sp., *C. schimae* from China (Liu et al. 2022b); on *S. superba*, *C. fioriniae* from China (Wang et al. 2022e).



### Thymelaeaceae

Anthracnose on *Aquilaria sinensis* is characterised by necrotic spots on mature leaves (Liu et al. 2020a). The causal agents have been identified as *Colletotrichum aenigma* (Li et al. 2021a) and *C. alienum* (Liu et al. 2020a) in China.

On *Daphne odora*, *Colletotrichum pyricola* was recorded from Australia (Shivas et al. 2016).

### Urticaceae

*Colletotrichum asianum* was recorded from *Boehmeria nivea* (Weir et al. 2012).

On *Myrianthus arboreus*, *Colletotrichum plurivorum* (as *C. sichuanensis*) was recorded from Cameroon (Damm et al. 2019).

### Viburnaceae

There are three species of *Colletotrichum* known from *Sambucus* spp.: in the dematium complex, *C. sambucicola*, recorded in Italy associated to dead branches of *S. ebulus* (Tibpromma et al. 2017); in the acutatum complex, *C. godetiae*, recorded in the Netherlands from *S. nigra* fruits (Damm et al. 2012a); and *C. sydowii* (singleton species), recorded in China from *Sambucus* sp. leaves (Marín-Felix et al. 2017).

On *Viburnum odoratissimum*, *Colletotrichum gloeosporioides* was identified in China as causing leaf lesions. Symptoms start in the leaf margins as yellow-green spots, progressing into lesions with desiccated and light-brown and deep-red borders, surrounded by a yellowish-green halo (Yang et al. 2015). This fungus was also associated to leaf spots on *V. dilatatum* in China (Zhang et al. 2023b).

### Violaceae

Leaf spot was recorded on *Viola tricolor* in Iran, associated to *Colletotrichum coccodes* (Karamnejadi et al. 2017). Additional species recorded as endophytes on *Viola* spp. are: *C. circinans* on *V. hirta* from the Czech Republic (Damm et al. 2009); *C. destructivum*, *C. siamense*, *C. trifolii* and *C. truncatum* on *V. odorata* from India (Katoch et al. 2017); *C. tropicale* on *V. surinamensis* from Panama (Rojas et al. 2010).

On *Melicytus ramiflorus*, *Colletotrichum aotearoa* was recorded as an endophyte from New Zealand (Weir et al. 2012).

### Vitaceae

*Colletotrichum*-related anthracnose of grapevine (*Vitis vinifera* and other *Vitis* spp.) causes sunken water soaked necrotic lesions on leaves and affect fruits at maturity, giving rise to brown sunken lesions with concentric rings (Yan et al. 2015, Lim et al. 2020), some times producing symptoms similar to those attributed to *Elsinöe ampelina* (Nigar et al. 2023). The disease is more common in areas with warm and humid summer conditions. There are 12 species of *Colletotrichum* recorded from grapevine, most of them from the gloeosporioides complex. In the truncatum complex, *C. truncatum* has been recorded from China (Zhang et al. 2018c). In the acutatum complex: *C. fiorinae*, from Portugal (Damm et al. 2012a) and the USA (Nigar et al. 2023); *C. godetiae*, from the UK (Damm et al. 2012a, Baroncelli et al. 2015b) and Italy (Zapparata et al. 2017); *C. nymphaeae*, from China (Liu et al. 2016b) and Brazil (Echeverrigaray et al. 2020). In the gloeosporioides complex: *C. aenigma*, from China (Yan et al. 2015) and Korea (Kim et al. 2021); *C. cigarro*, from Brazil (Echeverrigaray et al. 2020); *C. clidemiae*, from the USA (Weir et al. 2012); *C. fructicola*, from Korea (Lim et al. 2020) and Brazil (Echeverrigaray et al. 2020); *C. gloeosporioides*, from the USA (Weir et al. 2012) and China (He et al. 2019, Fan et al. 2023); *C. hebeiense*, from China (Yan et al. 2015); *C. siamense*, from the USA (Weir et al. 2012); *C. viniferum*, from Brazil (Echeverrigaray et al. 2020), Korea (Oo & Oh 2017a) and China (Peng et al. 2013, Yan et al. 2015, Lei et al. 2016, Duan & Chen 2022a). Pathogen population studies conducted in China revealed *C. viniferum* as the most prevalent anthracnose pathogen on grapevine (Yan et al. 2015, Lei et al. 2016).

Anthraco-nose on *Parthenocissus tricuspidata* was recently recorded as leaf spots from China, with the causal agent assigned to *Colletotrichum siamense* (Zhao et al. 2020). Additional species of *Colletotrichum* have been isolated as saprobes from *Parthenocissus* spp.: *C. fioriniae* and *C. godetiae* from the Netherlands (Damm et al. 2012a); *C. insertae*, *C. parthenocissicola* and *C. quinquefoliae* from Russia (Li et al. 2016c, Yuan et al. 2020).

On *Cissus hexangularis*, *Colletotrichum truncatum* is known from China (Zhang et al. 2023b). On *Tetrastigma obovatum*, *C. subacidae* is known from China (Liu et al. 2022b).

### Zygophyllaceae

On *Tribulus terrestris*, necrotic leaf spots were recently recorded from China and attributed to *C. truncatum* (Guan et al. 2023).

## **Animals**

### Insects

*Fiorinia externa* (Hemiptera: Coccoidea), elongate hemlock scale (a pest of *Tsuga canadensis*), is infected by *Colletotrichum fioriniae*, producing profuse sclerotial masses enclosing in the insect body as recorded in the USA (Marcelino et al. 2008, Damm et al. 2012a).

*Praelongorthezia praelonga* (Hemiptera: Ortheziidae), citrus scale insect (a major pest of citrus, coffee and figs), is infected by *Colletotrichum nymphaeae* var. *entomophilum*, as recorded from Brazil (Mascarin et al. 2016). The fungus causes high levels of mortality and is regarded as a biological control agent (Wynns et al. 2019).

*Colletotrichum acutatum* and *C. gloeosporioides* were recorded to occur in the olive fruit fly, *Bactrocera oleae* (Diptera: Tephritidae), in Italy, but without causing disease to the insect (Malacrino et al. 2017).

*Colletotrichum godetiae* has been recorded on an asymptomatic scale insect belonging to the Coccoidea superfamily (order Hemiptera) (Da Lio et al. 2018).

As all insect hosts of *Colletotrichum* are phytophagous insects, we can speculate that insects can be vectors of these fungi.

### Nematodes

Recently, *Colletotrichum fructicola* was recorded in China infecting horsehair worms (*Chordodes formosanus*), a parasite of praying mantis (Vivo et al. 2021).

### Human

Several species of *Colletotrichum* have been recorded to occur as opportunists on humans, causing, among others, rare but important ophthalmological diseases (Valenzuela-Lopez et al. 2018, Buchta et al. 2019, Hung et al. 2020). The species recorded are: *C. graminicola* and *C. truncatum* (Valenzuela-Lopez et al. 2018); *C. dematium* (Buchta et al. 2019); *C. siamense* (Werbel et al. 2019); *C. fructicola*, *C. fusiforme* and *C. tropicale* (Hung et al. 2020); *C. gloeosporioides* (Izadi et al. 2021); *C. chlorophyti* (Paniz-Mondolfi et al. 2021); *C. asianum* (Ghorpade et al. 2022).

## **Unknown hosts and environmental samples**

Conidia of “*Colletotrichum menglaense*” were collected from an air sample in a tropical environmental in southern China and the fungus was subsequently shown to be pathogenic to several crops, including strawberry, orange, grape, tomato, and blueberry (Qiao et al. 2021), but this taxon was recently synonymized to *C. siamense* (Zhang et al. 2023b). The species *C. obovoides*, *C. subvariabile* and *C. zhejiangense* were recently named to accommodate fungi collected from leaves of unidentified host plants (Liu et al. 2022b).

## Final notes

The taxonomy of *Colletotrichum* was undergone profound changes during the past decade, with a two-tier structure (species and species complexes) that enables the organisation of the biological diversity recognised among these organisms, mostly using nucleotide sequence information. This taxonomic clarification has enabled the recognition of some taxa exhibiting high host specificity, such as the common bean anthracnose pathogen (*C. lindemuthianum*) or the causal agent of Coffee Berry Disease (*C. kahawae*). Most taxa, however, are found in multiple hosts, suggesting that they are polyphagous and many host plant species harbour several species of *Colletotrichum*. Host plants such as papaya, tea, avocado and strawberry host between 15 and 19 species of *Colletotrichum*, and apple, mango and chillies (*Capsicum* spp.) host respectively 22, 26 and 36 species of *Colletotrichum*. Many other agricultural crops host various species of *Colletotrichum*, with varied geographic distribution, prevalence and virulence. In many cases little is known on the pathological relevance of such species of *Colletotrichum* to their hosts, posing difficulties to the selection of the most relevant pathosystems for plant pathology analyses, namely for plant breeding and crop protection applications. In this work we have reviewed and updated the current knowledge on species of *Colletotrichum* recognised, their species complexes and their host plants, and we provide a commented list of *Colletotrichum* fungi occurring on each host, with emphasis on agricultural crops and on the major causal agents of anthracnose diseases, but also with reference to seemingly emergent pathogens/diseases. In many cases this review points out the need to clarify the pathological relevance of the diverse species of *Colletotrichum* recognised from given hosts, promoting more efficient deployment of accurate plant protection measures and helping to anticipate future shifts in pathogen populations across geographical areas. Plant Pathology has provided a multitude of case studies in *Colletotrichum* that enabled Mycology to dissect in detail the diversity of the fungi involved, in many cases enabling the clarification of such pathosystems, as in citrus anthracnose pathosystems. This analysis shows that much is yet to be discovered in other diverse systems, such as the cotton anthracnose pathosystems or endophytic communities on bamboos or orchids, among several others.

## Acknowledgements

This research was financially supported by the R&D unit LEAF (FCT/UIDB/04129/2020; Fundação para a Ciência e a Tecnologia I.P., Portugal). This study was also carried out within the Agritech National Research Center and received funding from the European Union Next-GenerationEU (PIANO NAZIONALE DI RIPRESA E RESILIENZA (PNRR) – MISSIONE 4 COMPONENTE 2, INVESTIMENTO 1.4 – D.D. 1032 17/06/2022, CN00000022). This manuscript reflects only the authors' views and opinions, neither the European Union nor the European Commission can be considered responsible for them.

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