

REVIEW

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# *Colletotrichum* species pathogenic to strawberry: discovery history, global diversity, prevalence in China, and the host range of top two species

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## Abstract

Anthrachnose caused by *Colletotrichum* species, is one of the most destructive diseases affecting strawberry production worldwide. Fungi of the genus *Colletotrichum*, being ancient and co-evolved with flowering plants, rank eighth among the top ten economically important fungal pathogens and have diversified to adapt to various hosts. Since it was first reported in United States in 1931, strawberry anthracnose has spread globally, resulting in devastating economic, social, and ecological consequences. In a sense, to produce organic strawberry is impracticable largely because of this disease. *Colletotrichum* species pathogenic to strawberry have been widely characterized. The review focused on providing an accurate inventory of *Colletotrichum* species pathogenic to strawberry via revisiting the discovery history scrupulously over 90 years. A total of 23 *Colletotrichum* species clustered into five species complexes and two singleton taxa were accepted as strawberry pathogens with global occurrence illustrated. The relative prevalence of distinct *Colletotrichum* species associated with strawberry was systematically analyzed in China. Finally, the host range of the prevailing *C. fructicola* and *C. siamense*, also the top two *Colletotrichum* species causing serious damages on the earth was summarized, with a goal of diagnosing accurately and improving anthracnose management in agricultural ecosystem.

**Keywords:** *Colletotrichum* species, Strawberry, Anthracnose, Global biodiversity, Prevalence, Host range

## An introduction to *Colletotrichum* spp. and strawberry anthracnose

The genus *Colletotrichum* has been considered as one of the global top 10 important genera of fungal pathogens (Dean et al. 2012). Indeed, *Colletotrichum* is an ancient fungus on the earth and has co-evolved with flowering plants. The plant microfossils of *Protocolletotrichum* preserved on an angiosperm leaf cuticle suggest

that the diversified pathogenic strategies have been well established in *Colletotrichum* spp. from the Late Cretaceous onwards (Kar et al. 2004). Different complexes in the genus *Colletotrichum* might diverge between 4.8 and 32.2 million years ago (MYA) (Bhunjun et al. 2021). The emergence of agricultural cultivation and the intensive disturbance of natural environments boosted the further diversification of *Colletotrichum* species. These fungi have diversified to adapt to thousands of hosts, occurring as endophytes, pathogens, and saprobes (Freeman et al. 1998; Dean et al. 2012; Hirayama et al. 2018; da Silva et al. 2020; Jayawardena et al. 2020). Currently, a total of 257 *Colletotrichum* species grouped into 15 complexes and 13 additional singletons have been accepted in this

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genus, with *C. gloeosporioides* sensu lato (s.l., complex, aggregate) and *C. acutatum* s.l. being the top two complexes consisting of 57 and 41 species, respectively (Talhinhas and Baroncelli 2021).

Rosaceae has been reported as the top plant family with most records of association with *Colletotrichum* genus, hosting as many as 41 *Colletotrichum* species (Talhinhas and Baroncelli 2021). Postharvest fruit rot, *Glomerella* leaf spot, and pre-mature defoliation are common symptoms caused by *Colletotrichum* fungi on apple (Zhang et al. 2021; Chen et al. 2022), pear (Fu et al. 2019), peach (Tan et al. 2022), strawberry (Eaton et al. 2021; Wang et al. 2022), and many other rosaceous plants (Dowling et al. 2020). Among these *Rosaceae* crops, strawberry is most vulnerable to fungal diseases with a short plant stature and soft berry without protective skin. One *Colletotrichum* species could infect all organs of strawberry (Adhikari et al. 2019). Anthracnose has been a limiting factor for the ecological and sustainable development of strawberry production, posing a serious and continuing threat to strawberry security (Zhang et al. 2012). In particular, anthracnose crown rot holds a destructive influence on strawberry remarkably higher than other diseases. The difficulty in controlling anthracnose crown rot is attributable to that *Colletotrichum* spp. could kill strawberry plants after aggressively invading crown tissue with a long latent period without symptom visible, no long-term effective fungicides available, and diverse origins of the causal agents unpredictable (Peres et al. 2017; Forcelini and Peres 2018; Hirayama et al. 2018). In addition, *Colletotrichum* spp. on asymptomatic plants can be dispersed by transportation over long distance, whereas relevant quarantine measures for strawberry trade are absent in China.

The prerequisite for disease control is to recognize the causal agents. Originally, identification of the causal agents largely relied on morphological observation and virulence test. Repeated subculture of microbes in vitro might alter both their morphology and virulence. The fact that morphological characteristics vary with the choice of host or environmental conditions forms a serious concern in fungal identification. Strawberry anthracnose was first reported nearly a century ago (Brooks 1931). Via using PCR and DNA sequencing techniques, scientists revealed the genetic delimitation among *Colletotrichum* spp. associated with strawberry, and sorted those pathogens of worldwide origins into *C. acutatum*, *C. fragariae*, and *C. gloeosporioides* (Martínez-Culebras et al. 2000, 2003). Still, doubtfully annotated data for *Colletotrichum* species were frequent in GenBank and full of confusions (Nilsson et al. 2006; Hyde et al. 2009). Later, the emergence of multi-locus phylogeny provides a decisive help for the identification of fungal species. Many pathologists

and biologists greatly expanded the knowledge of *Colletotrichum* systematics (Cannon et al. 2012; Damm et al. 2012a, b; Weir et al. 2012), setting solid basis for future research. A landmark work corrected many synonymous names and provided a valuable reference for understanding *Colletotrichum* pathogens (Hyde et al. 2014). The delineation of *Colletotrichum* species and description of new species keep on proceeding with the advent of novel technologies such as whole genome sequencing (Jayawardena et al. 2020, 2021; Bhunjun et al. 2021; Talhinhas and Baroncelli 2021).

To detect *Colletotrichum* pathogen, especially the asymptomatic latent infection could avoid the spread of pathogen and prevent severe outbreak of anthracnose in strawberry fields. DNA microarray (Furuta et al. 2017), loop-mediated isothermal amplification (LAMP) (Wu et al. 2019; Liu et al. 2021) and quantitative real-time PCR (qPCR) assay (Yang et al. 2022) were developed to detect *Colletotrichum* spp. for disease management in strawberry fields, although the targets of detection supposed to certain species complex were not clearly validated in those reports. A complete delineation of *Colletotrichum* spp. associated with strawberry is not only crucial for strawberry health managers and government quarantine personnels, but also provide basic information for strawberry breeders aiming to improve resistance.

Despite intensive researches already contributed to understanding *Colletotrichum* genus pathogenic to strawberry, there is as yet short of an accurate inventory of these causal agents, and the pathogen population and prevalence of strawberry-virulent *Colletotrichum* spp. have not been systematically investigated in a large producer such as China. To meet with these gaps, current review seeks to first sum up the biodiversity of *Colletotrichum* spp. pathogenic to strawberry via going through the global discovery history. Thereafter, the prevalence of *Colletotrichum* species pathogenic to strawberry in China was analyzed with data available. Finally, we sorted the host range of top two predominant species causing strawberry crown rot. Together, such knowledge has important applications for biosecurity risk management (for example, proper estimation of the risk involved in strawberry seedling trade), accurate diagnosis, and anthracnose control, further sets a basis for systematically managing *Colletotrichum* genera in agricultural ecosystems not only for strawberry industry.

### **The diversity of *Colletotrichum* spp. on strawberry: a historical perspective**

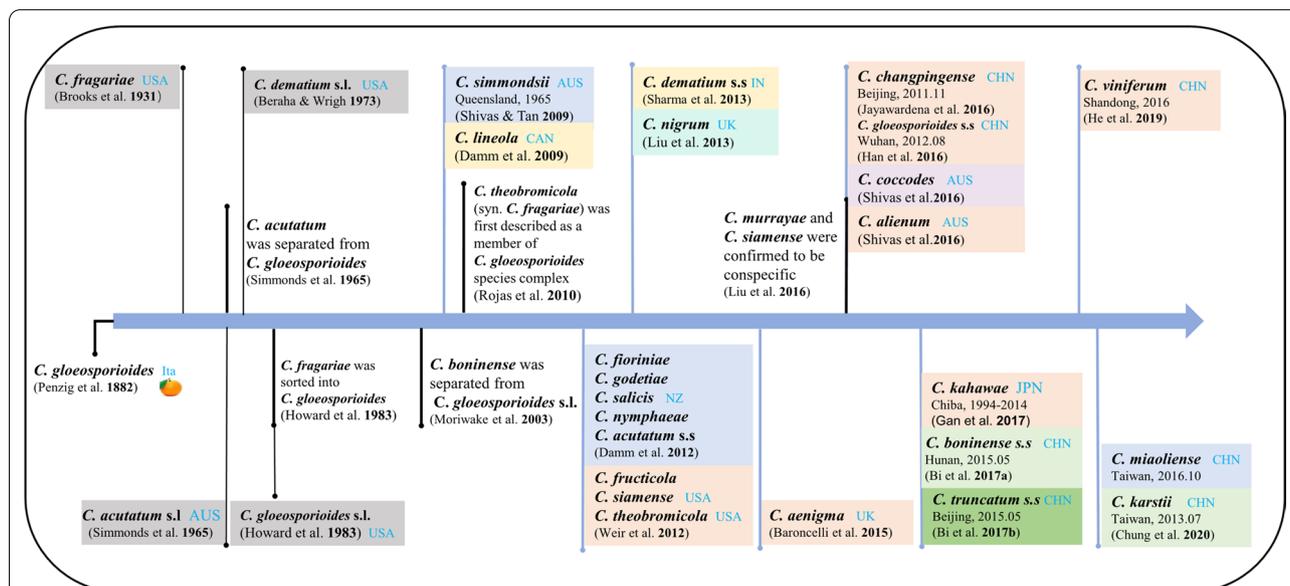
From a historic perspective, revealing the causal agents of strawberry anthracnose has gone through many confusions at the species level for a long period, gradually from a coarse estimate to fine identification along

with the taxonomic placement of some species revised and novel species revealed. As far as we know, the first report was the infection of strawberry by *C. fragariae* in southeastern USA more than 90 years ago (Brooks 1931) (Fig. 1). Based on a morphological observation, it's hard to distinguish *C. fragariae* from *C. gloeosporioides*, which had been described in the nineteenth century for the pathogen isolated from citrus in Italy (Penzig 1882). Therefore, in most cases strawberry anthracnose at early stage was believed to be caused by *C. fragariae* or *C. gloeosporioides*. A milestone occurred as the separation of *C. acutatum* from *C. gloeosporioides* when the former was described as the causal agent of strawberry fruit rot in Australia (Simmonds 1965).

In 1980s, it was suggested that *C. gloeosporioides* was the same as *C. fragariae* on strawberry (Howard 1983; Smith and Black 1987). Although many pathologists tried to draw distinctions among *C. fragariae*, *C. gloeosporioides*, and *C. acutatum* (Smith and Black 1990; Gunnell and Gubler 1992), the discrimination of causal agents of strawberry anthracnose based on morphology remained obscure. During the last decade of the twentieth century, strawberry anthracnose became a global disease. A primer CgInt targeting the internally transcribed spacer (ITS) region of the ribosomal gene was supposed to be specific to *C. gloeosporioides* (Mills et al. 1992), which

was used for a long time for strawberry anthracnose diagnosis even until 2015 (Rahman et al. 2015). At the end of the twentieth century, molecular tools were widely available. Accordingly, the highly genetic diversity was revealed within *C. acutatum* (Buddie et al. 1999; Martínez-Culebras et al. 2000, 2003; Denoyes-Rothan et al. 2003) *C. gloeosporioides* (Suzuki et al. 2010). Subsequently, *C. boninense* was separated from *C. gloeosporioides* (Moriwaki et al. 2003; Damm et al. 2012b). *C. simmondii* was re-assessed as a member of *C. acutatum* s.l. (Shivas and Tan 2009). *C. theobromicola*, synonymous with *C. fragariae*, was described as a member of the *C. gloeosporioides* complex with wide host range in tropical and subtropical regions (Rojas et al. 2010; Weir et al. 2012). In addition, strains formerly named after *C. truncatum* were re-identified as *C. lineola* (Damm et al. 2009), which were confused for their similarly curved conidia (Sato et al. 2015).

In 2012, there occurred a race to learn more about the genetic boundaries within *Colletotrichum* spp. Based on analysis of multi-locus phylogeny, previous inaccurate synonymies were distinguished and a new era boosted the understanding of *Colletotrichum*. Species within the *C. gloeosporioides* complex were reliably distinguished on the basis of multi-gene phylogenies including ITS, glyceraldehyde-3-phosphate dehydrogenase-encoding gene (*GAPDH*), calmodulin-encoding gene (*CAL*),



**Fig. 1** A timeline of reports about *Colletotrichum* species pathogenic to strawberry. Years for reports (in brackets) and original sampling (if available) were indicated, and abbreviations of geographic locations (if specific) were shown for pathogen origins. Relevant findings of mycologists (unshaded) and strawberry pathologists (shaded) were sequentially marked on the central time axis not to scale. Early reports not distinguished at the species level were indicated in gray boxes. A total of 23 *Colletotrichum* species currently accepted were illustrated in distinct colors, which include orange for nine species of *C. gloeosporioides* s.l., light blue for seven of *C. acutatum* s.l., yellow for two of *C. dematium* s.l., light green for two of *C. boninense* s.l., and dark green for one of *C. truncatum* s.l., respectively, as well as two singletons *C. nigrum* and *C. coccodes* s.l. and s.s indicate sensu lato (complex) and sensu stricto, respectively

actin-encoding gene (*ACT*), and chitin synthase-encoding gene (*CHS*) (Weir et al. 2012). Multi-loci phylogenetic analysis using ITS, *GAPDH*, *ACT*, *CHS*, histone 3 (*HIS3*), and beta-tubulin (*TUB2*) clearly delimited various species within the *C. acutatum* complex (Damm et al. 2012a). *C. fructicola* (from USA and Canada), *C. siamense* (from USA), and *C. theobromicola* (from USA) of the *C. gloeosporioides* complex were formally accepted as strawberry pathogens (Weir et al. 2012). In addition to *C. simmondsii* (from Australia) (Shivas and Tan 2009), five additional species of the *C. acutatum* complex including *C. acutatum* sensu stricto (s.s.), *C. fioriniae* (from USA, UK, and New Zealand), *C. godeiae* (widely in Europe), *C. nymphaeae* (from USA, Israel, and Europe), *C. salicis* (from New Zealand) were classified as distinct causal agents of strawberry anthracnose (Damm et al. 2012a). Furthermore, *C. miaoliense* (isolated from crown and leaf tissues) of the *C. acutatum* complex was recognized to infect strawberry in Taiwan Province, China, although with weak virulence (Chung et al. 2020). So far, a total of seven species of the *C. acutatum* complex have been known as strawberry pathogens.

*C. aenigma* of the *C. gloeosporioides* complex was reported to infect strawberry in UK (Baroncelli et al. 2015). *C. gloeosporioides* s.s. was isolated from diseased strawberry leaf, petiole, and stolon in Hubei Province, China, where *C. murrayae* was also reported as a causal agent of the disease (Han et al. 2016). In the same year, *C. murrayae* was proved to be conspecific with *C. siamense* (Liu et al. 2016). Two isolates from diseased strawberry (rhizome) in northern China were identified as a novel species named after *C. changpingense* of the *C. gloeosporioides* complex (Jayawardena et al. 2016a). Within the same species complex, *C. alienum* (from Australia) was reported as strawberry pathogen (Shivas et al. 2016). *C. kahawae* was first reported from diseased strawberry in Chiba, Japan (Gan et al. 2017). An additional species *C. viniferum* of the *C. gloeosporioides* complex was first reported to infect strawberry leaves in Shandong Province, China (He et al. 2019). Hereto, a total of nine species of the *C. gloeosporioides* complex have been reported to be pathogenic to strawberry.

In addition to species of the *C. acutatum* and *C. gloeosporioides* complexes, *C. dematium* was reported to be virulent to strawberry in USA nearly 50 years ago (Beraha and Wright 1973), which was again reported to infect strawberry in India (Singh et al. 2003). Later, *C. dematium* was accepted as a species complex with curved conidia, and *C. lineola* of this complex was isolated from diseased strawberry in Canada (Damm et al. 2009). *C. dematium* s.s. was again reported to be virulent to strawberry in India (Sharma et al. 2013). In addition, *C. boninense* s.s. of the *C. boninense* complex was reported

to cause strawberry fruit rot in Lou-Di, Hunan Province, China (Bi et al. 2017a). *C. karstii* of the same complex was revealed to infect strawberry leaves in Taiwan Province, China (Chung et al. 2020). Besides, *C. truncatum* s.s. was isolated from diseased strawberry in Changping District, Beijing (Bi et al. 2017b). Hitherto, at least five *Colletotrichum* species from three additional complexes beyond *C. acutatum* s.l. and *C. gloeosporioides* s.l. have been known to be associated with strawberry.

Apart from these species from distinct complexes, there are two singleton species of *Colletotrichum* genus, which were not clustered with other species of any complex (Talhinhas and Baroncelli 2021) but reported to infect strawberry. Typical strain of *C. nigrum* from *Fragaria* spp. petiole (UK) was previously reported in a work to circumscribe distinct anthracnose pathogens of several crops (Liu et al. 2013). *C. coccodes* causing strawberry fruit rot was reported in Australia (Shivas et al. 2016). Indeed, these two singletons were phylogenetically close to each other (Liu et al. 2013).

In addition, *C. paranaense* of the *C. acutatum* complex once was suggested to be associated with *Fragaria* in Australia (Moreira et al. 2019), but no additional record of *C. paranaense* virulent to strawberry is available. When examined with the barcodes of that potential *C. paranaense* strain from strawberry (Moreira et al. 2019) in GenBank, it was found to be a strain of *C. simmondsii* from Europe (data omitted). Indeed, *C. paranaense* has been considered as an endemism associated with apple, peach, and nectarine from Brazil only (Talhinhas and Baroncelli 2021). Recently, in an effort to reveal the causal agent of strawberry crown rot in USA, *C. clidemiae* was isolated from strawberry fields together with *C. siamense* (86%), *C. theobromicola*, and *C. fructicola*, but *C. clidemiae* was suggested as the only species not pathogenic to strawberry (Oliveira et al. 2022). Therefore, these two species (*C. paranaense* and *C. clidemiae*) are not included in current list of strawberry pathogens.

In sum, a total of 23 *Colletotrichum* species have been accepted as strawberry pathogens, namely, nine species of the *C. gloeosporioides* complex (*C. aenigma*, *C. alienum*, *C. changpingense*, *C. fructicola*, *C. gloeosporioides* s.s., *C. kahawae*, *C. siamense*, *C. viniferum*, and *C. theobromicola*), seven species of the *C. acutatum* complex (*C. acutatum* s.s., *C. fioriniae*, *C. godeiae*, *C. miaoliense*, *C. nymphaeae*, *C. salicis*, and *C. simmondsii*), two of the *C. boninense* complex (*C. boninense* s.s. and *C. karstii*), two of the *C. dematium* complex (*C. lineola* and *C. dematium* s.s.), and one of the *C. truncatum* complex (*C. truncatum* s.s.) as well as two singletons *C. nigrum* and *C. coccodes*. Optimal markers for identifying distinct *Colletotrichum* species could be found in recent publications (Vieira et al. 2020; Bhunjun et al. 2021; Jayawardene

et al. 2021). Undoubtedly, the archives of *Colletotrichum* species associated with strawberry will expand in the future.

**The diversity of *Colletotrichum* spp. virulent to strawberry: a geographic perspective**

So far, anthracnose epidemic has affected strawberry nursery and production fields worldwide. Reports on *Colletotrichum* spp. associated with strawberry from literature curation at PubMed and Clarivate combined with Fungal database search (Farr and Rossman 2022) were retrieved to understand the global diversity and occurrence of the causal agents of strawberry anthracnose. As far as we could reveal, since 1931 till July 9, 2022, there were over 220 citations and 310 records referring to the identification of causal agents of strawberry anthracnose at *Colletotrichum* genus level in 36 countries on six continents, of which 282 records provided pathogen identification at a species or species complex level. Moreover, following the timeline

of identification history, 189 records (Fig. 1) were supposed to delimit strawberry pathogens at a species level and included in the statistics (Table 1). It should be noted that, early reports largely provided pathogen information at a species complex level. Although only relevant reports on *C. acutatum* and *C. gloeosporioides* after the year of Weir et al. (2012) and Han et al. (2016), respectively were accepted in Table 1, the frequent use of species complex name or outdated, misleading name for *Colletotrichum* pathogen cannot be completely excluded. For example, *C. theobromicola* (syn. to *C. fragariae*) of the *C. gloeosporioides* complex has been clarified many years ago (Rojas et al. 2010), but the name *C. fragariae* was still used in some publications later (Fang et al. 2012; Rojas-Flores et al. 2019). A similar situation occurs with the use of *C. acutatum* and *C. gloeosporioides* associated with strawberry in literatures. Therefore, how many of these records are really attributable to *C. acutatum* s.s., *C. gloeosporioides* s.s., or *C. theobromicola* still remains unknown.

**Table 1** Worldwide reports on strawberry-pathogenic *Colletotrichum* spp. discriminated at species levels

Category <sup>a</sup>	Species <sup>b</sup>	Records <sup>c</sup>	Continents	Countries	Rank <sup>d</sup>	Percent (%) <sup>e</sup>
<i>C. gloeosporioides</i>	<i>C. siamense</i>	18	4	6	4	9.5
	<i>C. gloeosporioides</i> s.s.	4	1	2	9	2.1
	<i>C. fructicola</i>	23	2	5	3	12.2
	<i>C. aenigma</i>	4	2	2	9	2.1
	<i>C. viniferum</i>	1	1	1		0.5
	<i>C. changpingense</i>	3	1	1	10	1.6
	<i>C. theobromicola</i>	12	1	1	5	6.3
	<i>C. alienum</i>	1	1	1		0.5
	<i>C. kahawae</i>	1	1	1		0.5
	<i>C. acutatum</i>	<i>C. acutatum</i> s.s.	34	6	18	2
<i>C. godetiae</i>		8	1	6	7	4.2
<i>C. fiorinae</i>		7	3	5	8	3.7
<i>C. simmondsii</i>		10	3	3	6	5.3
<i>C. miaoliense</i>		1	1	1		0.5
<i>C. nymphaeae</i>		49	6	20	1	25.9
<i>C. salicis</i>		3	2	2	10	1.6
<i>C. boninense</i>		<i>C. karstii</i>	2	2	2	
	<i>C. boninense</i> s.s.	1	1	1		0.5
<i>C. dematium</i>	<i>C. dematium</i>	2	2	2		1.1
	<i>C. lineola</i>	2	1	1		1.1
<i>C. truncatum</i>	<i>C. truncatum</i> s.s.	1	1	1		0.5
Singleton	<i>C. coccodes</i>	1	1	1		0.5
	<i>C. nigrum</i>	1	1	1		0.5

<sup>a</sup> Italic letters for species complex

<sup>b</sup> s.s., sensu stricto

<sup>c</sup> Only records for pathogens supposed to be discriminated unambiguously at a species level were included here. Until July 2022, a total of 189 records not earlier than the first report for certain species (Fig. 1) were used for analysis

<sup>d</sup> Only the top 10 frequently reported species were ranked (at least in three independent literatures)

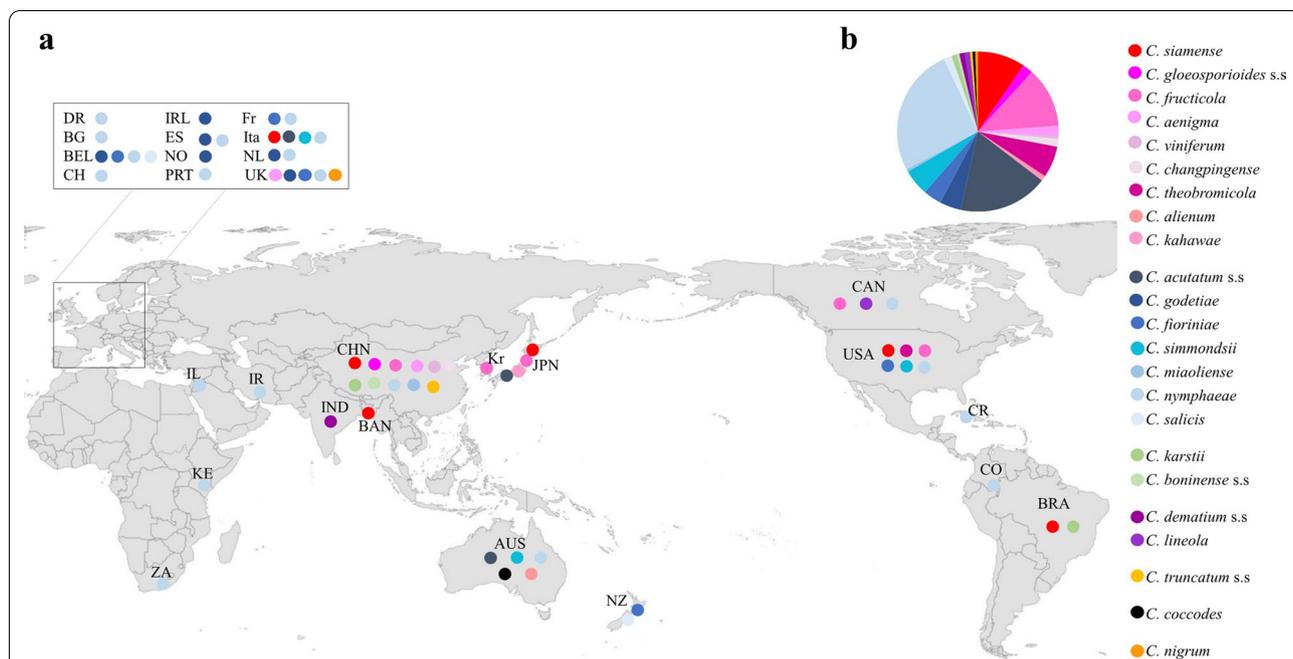
<sup>e</sup> The percentage of reported frequency (%) was calculated from report times of certain species divided by total number of 189 records

The global diversity of *Colletotrichum* spp. virulent to strawberry was illustrated with the identification records supposed at a species level (Fig. 2a, b). Those reports on the causal agents of strawberry anthracnose doubtfully at a species level were excluded. Africa produces very small amount of strawberry. In Egypt, both the *C. gloeosporioides* and *C. acutatum* complexes were reported to infect strawberry although they were not identified at a species level (Embaby et al. 2010). *C. nymphaeae* was identified as the unique *Colletotrichum* species causing strawberry anthracnose in Kenya (Martínez-Culebras et al. 2003; Baroncelli et al. 2015) and South Africa (Jayawardena et al. 2016b).

Strawberry is widely cultivated in America, where the diversity of strawberry pathogens is fostered. In Canada, three species including *C. fructicola* (Weir et al. 2012), *C. nymphaeae*, and *C. lineola* (Jayawardena et al. 2016b) were reported to be infectious to strawberry. At least six *Colletotrichum* species pathogenic to strawberry were revealed in USA, namely, *C. simmondsii* (Faedda et al. 2011), the dominant *C. nymphaeae* (Wang et al. 2019) *C. siamense* (Adhikari et al. 2019; Eaton et al. 2021; Oliveira et al. 2022), the less prevailing *C. fiorinae* (Wang et al. 2019; Eaton et al. 2021), *C. fructicola*, and *C. theobromicola* (Weir et al. 2012; Oliveira et al. 2022). In Mexico, only *Colletotrichum* spp. (genus level) from strawberry

was reported (Alvarez 1976; Rojas-Flores et al. 2019). *C. nymphaeae* infectious to strawberry was recorded in Colombia and Costa Rica (Baroncelli et al. 2015). *C. siamense* (Capobiango et al. 2016) *C. karstii* (Soares et al. 2021) were identified to infect strawberry in Brazil. In Argentina, only the *Colletotrichum* species complexes (*C. acutatum* and *C. gloeosporioides*) were reported to infect strawberry (Mónaco et al. 2000; Ramallo et al. 2000).

Strawberry anthracnose is widely prevailing in Asia. In Thailand, although both the *C. acutatum* and *C. gloeosporioides* complexes had been reported to be associated with strawberry (Photita et al. 2004; Than et al. 2008a, b; Hyde et al. 2018), the identification of *Colletotrichum* in strawberry at a species level was absent. In India, *C. dematium* was isolated from diseased strawberry (Sharma et al. 2013). In Bangladesh, *C. siamense* was shown to cause strawberry crown rot (Gupta et al. 2019). In Israel and Iran, *C. nymphaeae* was revealed to infect strawberry fruits (Jayawardena et al. 2016b; Karimi et al. 2017). In Japan, virulent *C. fructicola* (predominant) and *C. siamense*, as well as less virulent *C. aenigma* and *C. kahawae* were identified as strawberry pathogens (Gan et al. 2017; Hirayama et al. 2018). In Korea, only *C. fructicola* was confirmed virulent to strawberry (Nam et al. 2013), although *C. acutatum* (specie complex) from diseased strawberry had ever been documented before (Nam et al.



**Fig. 2** The diversity of *Colletotrichum* species pathogenic to strawberry in 28 countries based on open publications available until July 2022. **a** Global distribution of *Colletotrichum* pathogenic to strawberry. Circles of certain color represent the same *Colletotrichum* species, independent of their sizes. Data were largely retrieved from Fungal database (<https://nt.ars-grin.gov/fungaldatabases/>) (Farr and Rossman 2022) integrated with literature curation at PubMed and Clarivate. **b** Pie chart showing the relative reported frequency for each species, generated with the same data at far right in Table 1

2008). In China, a total of 11 *Colletotrichum* species have been reported as strawberry-infectious, which will be comprehensively introduced later.

In Europe, strawberry anthracnose was largely attributable to the *C. acutatum* complex. *C. godetiae* strains infectious to strawberry were present in Ireland and Norway (Baroncelli et al. 2015; Chethana et al. 2016). *C. nymphaeae* was the only *Colletotrichum* species reported as strawberry pathogen in Denmark (Braganca et al. 2016), Bulgaria (Bobev et al. 2002; Jelev et al. 2008; Jayawardena et al. 2016b), Switzerland, and Portugal (Baroncelli et al. 2015). Both *C. godetiae* and *C. nymphaeae* were identified as strawberry pathogens in Netherlands (Baroncelli et al. 2015; Jayawardena et al. 2016b) and Spain (Damm et al. 2012; Baroncelli et al. 2015). In United Kingdom, five species including *C. nigrum* (Liu et al. 2013), more aggressive *C. nymphaeae* and *C. fioriniae* as well as less aggressive *C. godetiae* and *C. aenigma* (Baroncelli et al. 2015) had been reported as strawberry pathogens, of which *C. nigrum* and *C. aenigma* were beyond the *C. acutatum* complex. In Belgium, four species of the *C. acutatum* complex: *C. fioriniae*, *C. godetiae*, *C. nymphaeae*, and *C. salicis* were identified as strawberry pathogens (Grammen et al. 2019). Both *C. fioriniae* (Baroncelli et al. 2015) *C. nymphaeae* (Jayawardena et al. 2016b) were also isolated from diseased strawberry in France. In Italy, pathogens causing strawberry anthracnose were identified as *C. simmondsii* (Faedda et al. 2011), *C. nymphaeae* (Damm et al. 2012), *C. acutatum* s.s. (Vitale and Infantino 2014), and *C. siamense* (Jayawardena et al. 2016b). Besides, there were reports of *C. acutatum* (complex) causing strawberry anthracnose rot, although not delimited at a species level in four additional countries of Europe: Germany (Nirenberg et al. 2002), Czech Republic (Novotný et al. 2007), Finland (Lilja et al. 2011), and Montenegro (Latinovic et al. 2012). Generally speaking, *Colletotrichum* spp. infectious to strawberry beyond the *C. acutatum* complex was only reported in United Kingdom and Italy of Europe.

In Australia of Oceania, at least five *Colletotrichum* species including *C. simmondsii* (Damm et al. 2012), *C. acutatum* s.s., *C. nymphaeae*, *C. alienum*, and *C. coccodes* (Shivas et al. 2016) were reported to cause strawberry diseases. In New Zealand, distinct species including *C. salicis* (Jayawardena et al. 2016b) *C. fioriniae* (Baroncelli et al. 2015; Braganca et al. 2016) were recorded as strawberry pathogens.

An overview on the global distribution of strawberry-pathogenic *Colletotrichum* spp. showed that the number of common species frequently found worldwide and those of potential endemism reported only in one region are roughly the same (Table 1). Generally, *Colletotrichum* spp. of the *C. acutatum* complex pathogenic

to strawberry are epidemic in Europe, Africa, and Oceania, whereas species of the *C. gloeosporioides* complex are prevailing in strawberry fields in East Asia and North America. *C. nymphaeae* and *C. acutatum* s.s. of the *C. acutatum* complex are cosmopolitan pathogens of strawberry reported in six continents. *C. fructicola*, *C. siamense*, and *C. theobromicola* of the *C. gloeosporioides* complex are among the top five species threatening strawberry. In Africa, Europe and western Asia, *C. nymphaeae* is more prevailing in strawberry fields than other species. In northern China, Korea, and Japan of eastern Asia-Pacific region, *C. fructicola* is prevailing. Recently, *C. siamense* is increasingly prevailing in USA (Adhikari et al. 2019; Oliveira et al. 2022) and China (Wang et al. 2022), which is in accordance with the tolerance of *C. siamense* to high temperature observed in several labs (Han et al. 2016; Chung et al. 2020; Zhang et al. 2020). It is expected that the diversity and global distribution of *Colletotrichum* pathogens of strawberry are undergoing plentiful changes with the gradual shift of agricultural system under a global warming context.

### The prevalence of *Colletotrichum* spp. pathogenic to strawberry in China

China has become the largest strawberry producer in the world since 2010 (annual statistic data of the Strawberry Division, Chinese Society for Horticultural Science). Strawberry growers in Chinese mainland planted 173,333 hectares and produced fruits of five million tons in 2021 (Zhang 2021). Diversified cultivation and climate conditions in China favored a high biodiversity of various pathogens for strawberry. The first formal report of strawberry anthracnose in China (Jiangsu Province) was by Hu (1990) on the fifth annual conference of Chinese Society of Plant Pathology. In Shanghai, *C. fragariae* and *C. acutatum* were identified as strawberry pathogens (Shao 1992; Ye et al. 1997). Later, fruit rot caused by *C. acutatum* was reported in Shanghai based on morphology identification (Dai et al. 2006). Molecular analysis with ITS sequences facilitated the identification of 16 *C. gloeosporioides* isolates and one *C. acutatum* isolate sampled during 1996–2006 in Shanghai (Ren et al. 2008). Based on ITS sequences and restriction enzyme digestion, 31 *Colletotrichum* isolates isolated from diseased strawberry during 2006–2007 in Shanghai and Zhejiang were identified as *C. acutatum*, *C. gloeosporioides*, and *C. fragariae* (Xie et al. 2010). Afterwards, *C. gloeosporioides* and *C. fragariae* were again reported as pathogens for strawberry in Zhejiang (Ren et al. 2011). There were 114 fungal isolates of the *C. gloeosporioides* complex collected from diseased strawberry during 2010–2013 in Zhejiang Province, although not distinguished at a species level (Lin et al. 2016).

The first use of multi-locus phylogenetic analysis integrated with morphological characterization by Han et al. (2016) created a new situation for understanding strawberry anthracnose in China. Based on 11 published works (Han et al. 2016; Jayawardena et al. 2016a; Bi et al. 2017a, b; He et al. 2019; Chen et al. 2020; Chung et al. 2020; Zhang et al. 2020; Jian et al. 2021; Zhong et al. 2021; Wang et al. 2022) and current work distinguished at a species level, we provided a glimpse of the overall population structure and relative prevalence of *Colletotrichum* spp. in strawberry fields in China (Fig. 3). Since 2016, a total of 492 isolates belonging to 11 *Colletotrichum* species of four complexes *C. gloeosporioides*, *C. acutatum*, *C. boninense*, and *C. truncatum* have been identified as causal agents of strawberry anthracnose in China.

Analyzing the prevalence of *Colletotrichum* species revealed that the *C. gloeosporioides* complex was most widely reported. Currently, *C. siamense* (226 isolates, 45.9% of the total) is the most predominantly reported species in strawberry fields of China across a wide range of latitudes and is distributed in nearly all provinces except for Liaoning, followed by *C. fructicola* (189 isolates, 38.4%) similarly distributed across whole China. We acknowledge limitations in above illustration (Fig. 3) due to the availability of data sources. But the broad prevalence of the *C. gloeosporioides* complex on strawberry is not limited in China. *C. fructicola* has been identified as the predominant fungus causing strawberry anthracnose in both South Korea (Nam et al. 2013) and Japan (Gan et al. 2017).

Actually, the occurrence of *C. acutatum* s.l., *C. boninense* s.l., and *C. truncatum* s.l. species was essentially random in China. Notably, *C. nymphphaeae* and *C. miaoliense* were only identified in temperate zones including Hebei and Beijing or from subtropical regions with an elevation approximately 1000 m (1100 m in Enshi, Hubei; 1300 m in Renai or 960 m in Shitan Nantou, Taiwan) (Han et al. 2016; Chung et al. 2020).

Concerning the regional biodiversity in *Colletotrichum* spp. pathogenic to strawberry, a higher diversity could be observed in Beijing (Jayawardena et al. 2016a; Bi et al. 2017a, b; Zhong et al. 2021), Hubei (Han et al. 2016) and Taiwan (Chung et al. 2020) than other regions, which might be partially interpreted from the diversified geographic conditions and subclimates in these regions. Actually, *C. fructicola* was most prevalent in Sichuan Province (Jian et al. 2021). In Shanghai, Shandong, and Anhui Provinces, *C. fructicola* and *C. siamense* exhibited a matched occurrence in strawberry fields (Jayawardena et al. 2016; He et al. 2019; Zhang et al. 2020; Zhong et al. 2021). However, *C. siamense* took the predominant position in strawberry fields of Hubei and Taiwan, where the climate

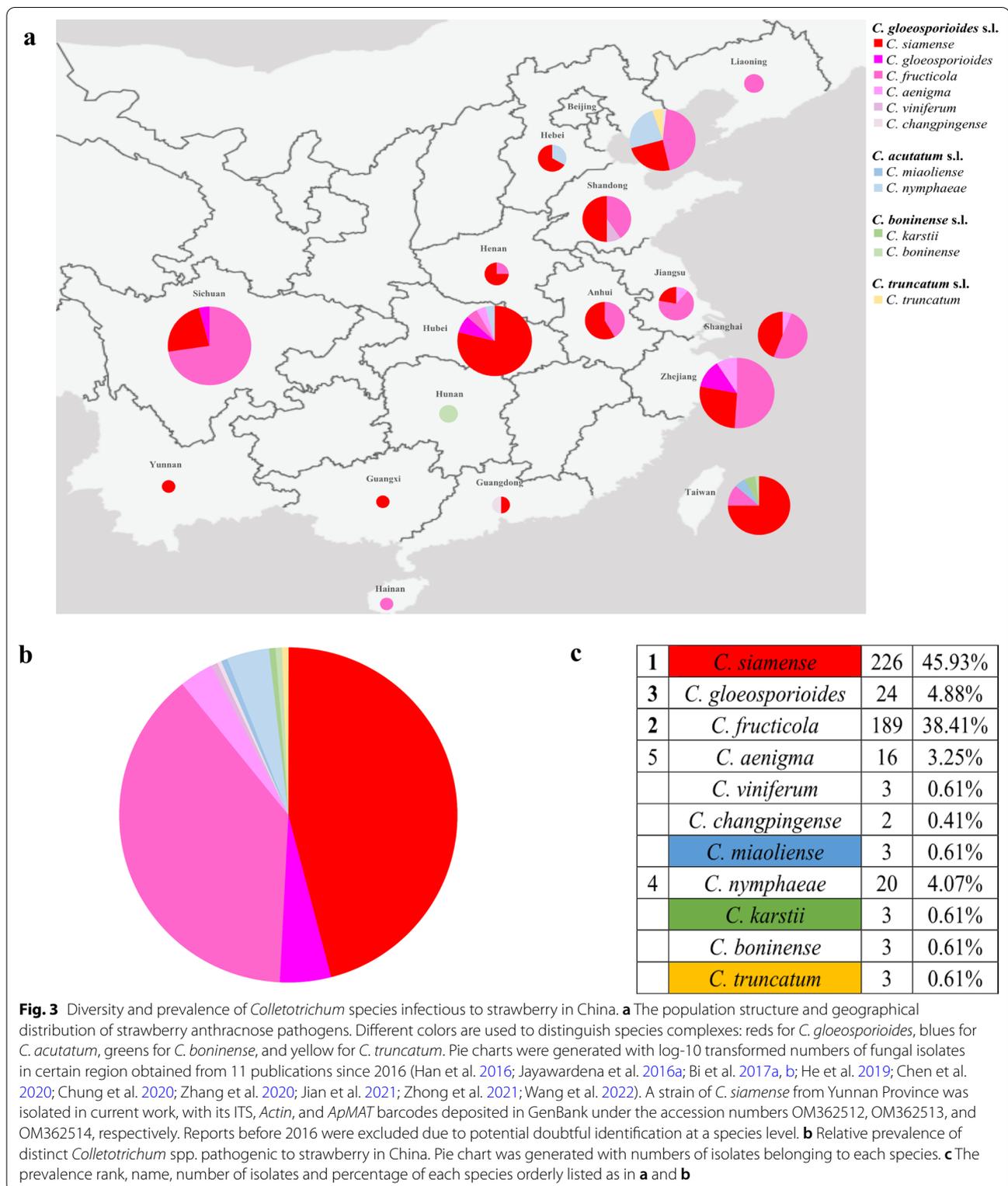
is subtropical with higher annual average temperature. Latitude and elevation in relation to temperature variations might play some roles in affecting the geographic distribution of *Colletotrichum* pathogen (Han et al. 2016).

### Host ranges of *C. siamense* and *C. fructicola*, the most prevailing causal agents of strawberry crown rot

The vast majority of *Colletotrichum* fungi are not host-specific but adapt to a wide range of hosts. This is one of the main difficulties in managing *Colletotrichum* spp. and reducing their destructive effects in agricultural production. Comparative analysis of host range might partially reflect the prevalence of distinct *Colletotrichum* spp. in strawberry fields. Of the five *Colletotrichum* complexes associated with strawberry, the number of *Colletotrichum* species–host species combinations by complex was 516, 295, 129, 58, and 37 for the *C. gloeosporioides*, *C. acutatum*, *C. boninense*, *C. truncatum*, and *C. dematiatum* complex, respectively (Talhinhas and Baroncelli 2021). Obviously, the host range of *Colletotrichum* species complex is positively correlated with their prevalence in strawberry fields (Fig. 2).

As the most prevailing pathogens causing strawberry anthracnose crown rot in Asia-Pacific region (Nam et al. 2013; Han et al. 2016; Jayawardena et al. 2016a; Gan et al. 2017; Hirayama et al. 2018; Gupta et al. 2019; Chen et al. 2020; Chung et al. 2020; Zhang et al. 2020; Jian et al. 2021; Zhong et al. 2021; Oliveira et al. 2022; Wang et al. 2022), *C. siamense* and *C. fructicola* are actually the top two *Colletotrichum* species most frequently occurred worldwide (Talhinhas and Baroncelli 2021). Both two species are cosmopolitan fungi adapting to a wide range of host plants, most reported in tropical and sub-tropical regions but with significantly higher occurrences in Asia than in other continents. In vitro mating of fungal isolates demonstrated that *C. fructicola* is homothallic whereas *C. siamense* is heterothallic (Oliveira et al. 2022), hinting the latter with a relatively higher capability of genetic mutations and flexibility, partially congruent with a wider host spectrum than *C. fructicola*.

To provide practical information for strawberry anthracnose management, we updated the host ranges of *C. fructicola* and *C. siamense* through website search at Fungal database (on July 8, 2022 at <https://nt.ars-grin.gov/fungalatabases/>) and determined the taxonomy of these hosts (on July 15–16, 2022 at <https://www.iplant.cn/>). This analysis resulted in a significantly wider range of hosts for *C. siamense* and *C. fructicola*. than ever suggested in previous publications (da Silva et al. 2020; Bhunjun et al. 2021; Talhinhas and Baroncelli 2021).



Accordingly, the host ranges of these two predominant pathogens were sorted based on their taxonomy (Table 2 and Additional file 1: Table S1).

A total of 314 and 358 plant host records were obtained for *C. fructicola* and *C. siamense* at Fungal Database (July 8, 2022), respectively. Four additional host records of *C.*

**Table 2** Host range of the predominant *Colletotrichum* spp. causing strawberry anthracnose crown rot

<i>Colletotrichum</i> hosts	Host range <sup>c</sup>			Host composition (%) <sup>d</sup>			
	Order	Family	Genus	Gymnosperm	Basal angiosperm	Monocot	Dicot
<i>C. fructicola</i>	31	49	75	0	5.3	24	70.7
<i>C. siamense</i>	36	57	111	0.9	9	23.4	66.7
Common hosts <sup>a</sup>	19	25	34	0	5.9	17.6	76.5
Joint hosts <sup>b</sup>	39	71	152	0.7	7.9	25	66.4

<sup>a</sup> Genera of plants commonly hosting both *C. fructicola* and *C. siamense*

<sup>b</sup> Genera of plants hosting *C. fructicola* and/or those hosting *C. siamense* were combined

<sup>c</sup> Host range was retrieved on July 8, 2022 at <https://nt.ars-grin.gov/fungalatabases/> (Far and Rossman 2022). The taxonomy of each host was determined at <https://www.iplant.cn/>

<sup>d</sup> Host composition is expressed as the percentage (%) of hosts belonging to distinct phylogenetic clades at genus level

*siamense* including *Datura metel*, *Dieffenbachia* spp. (Araceae), *Pongamia pinnata* (Fabaceae), and *Viola odorata* (Violaceae) (Talhinhas and Baroncelli 2021) which were missed in Fungal Database, were recruited into current analysis. Since some host records were not determined at a species level, we sorted these hosts at a genus level based on taxonomic analysis at <https://www.iplant.cn/>. *C. siamense* is associated with hosts of 111 genera including one genus of gymnosperm (*Cycas*), 10 genera of basal angiosperms, 26 genera of monocots, and 74 genera of dicots. Rosales and Malpighiales are the top two orders of plants containing nine genera, followed by Fabales (8), Sapindales (8), Lamiales (6), Malvales (6), Asparagales (6), and Alismatales (6) hosting *C. siamense*. By contrast, *C. fructicola* is associated with hosts of 75 genera, a relatively smaller spectrum than that of *C. siamense*. No gymnosperm was recorded as *C. fructicola* host, and the top three plant orders hosting this species are Rosales (9 genera), Sapindales (7), and Caryophyllales (6).

Records of plant hosts cross-infected or co-infected by multiple *Colletotrichum* species were not scarcely (Dean et al. 2012; Hirayama et al. 2018; da Silva et al. 2020). Indeed, the co-occurrence of *C. fructicola* and *C. siamense* has been simultaneously identified in a same strawberry production field in Shanghai (Liu et al. 2021). The combined host range of the top two *Colletotrichum* species was expanded to 152 genera, including one of gymnosperm, 12 of angiosperms (six orders), 38 of monocots (10 orders), and 101 of dicots (22 orders). Among the combined hosts of *C. fructicola* and *C. siamense*, Fabales, Sapindales, Rosales, and Asparagales are the top four orders each consisting of 12, 12, 11, and 11 genera, respectively. Furthermore, there were plants of 34 genera in 19 orders recorded as shared hosts of *C. fructicola* and *C. siamense*, including two genera of basal angiosperms (*Annona* and *Persea*), six of monocots (*Anthurium*, *Areca*, *Cymbopogon*, *Dioscorea*, *Musa*, and *Pennisetum*) and 26 of dicots. Notably, the common

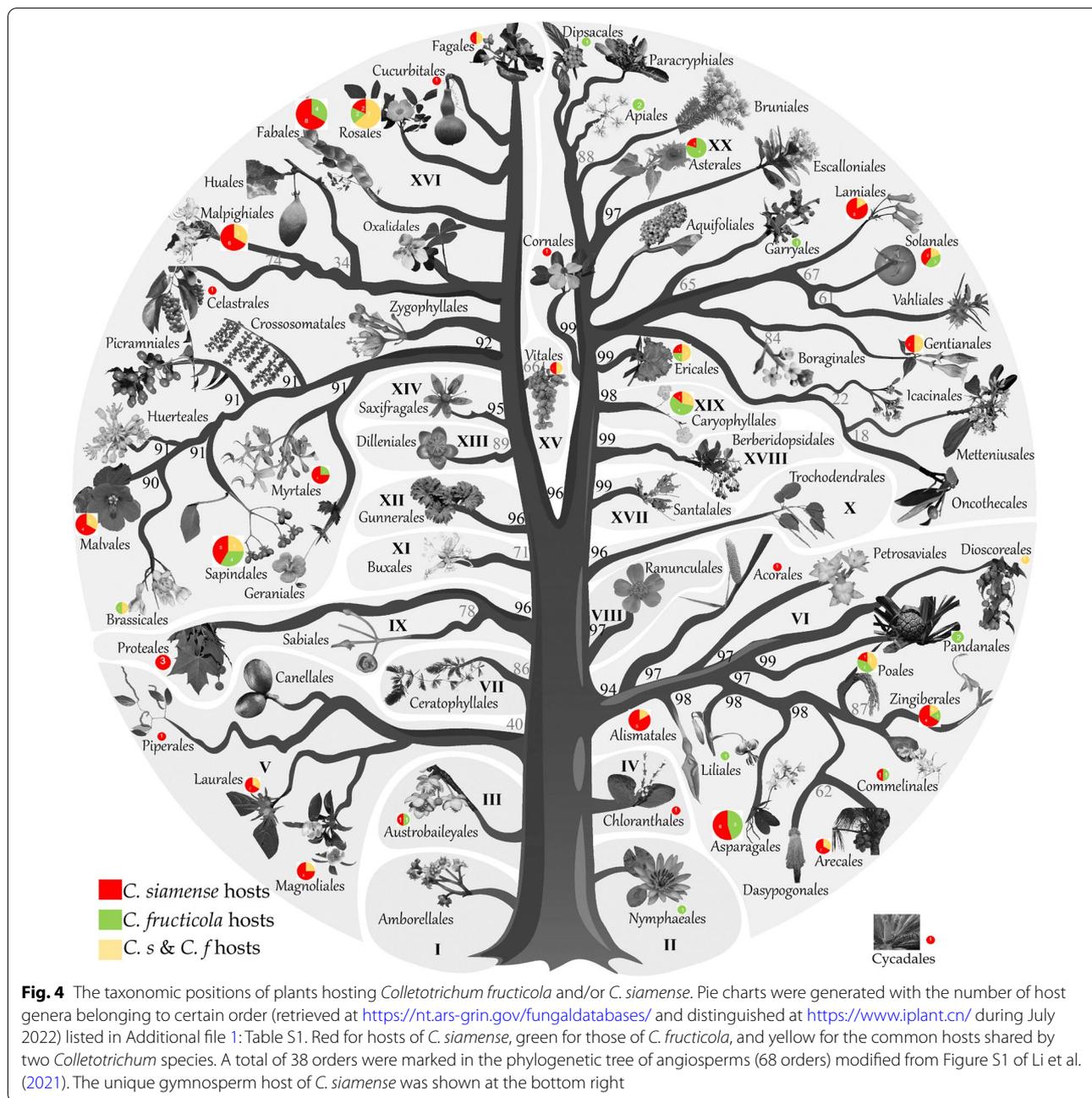
hosts of *C. fructicola* and *C. siamense* are composed of seven genera of Rosales order, namely, *Fragaria*, *Malus*, *Pyrus*, *Prunus* of Rosaceae, as well as *Artocarpus*, *Ficus*, and *Ziziphus*.

The taxonomic positions of all hosts of *C. siamense* and *C. fructicola* were illustrated in Fig. 4, which provides a global evolutionary picture of all the plants (by genus) hosting the top two *Colletotrichum* species on the earth. The wide diffusion of *C. siamense*/*C. fructicola* hosts in whole phylogenetic tree of angiosperms reinforced that they diverged very early, reasonably maintaining pathogenic strategies well established during coevolution with flowering plants (Kar et al. 2004; Bhunjun et al. 2021).

### Conclusions, implications, and perspectives

In this work we revisited the discovery history of the causal agents of strawberry anthracnose and provided a global glimpse of the genetic diversity of *Colletotrichum* species pathogenic to strawberry. Under the current knowledge, 23 species of *Colletotrichum*, clustering in five species complexes as well as two singleton taxa have been listed as the causal agents of strawberry anthracnose. Two species have been rejected as they turned out to be a confused citation (*C. paranaense*) or not pathogenic to strawberry (*C. clidemiae*). Notably, it has been suggested that about 30% ITS sequences in open databases including GenBank are relevant to wrong taxon of fungi such as *Colletotrichum* genus (Hofstetter et al. 2019; Bouffleur et al. 2021). Thus, future identification and acceptance of novel species as causal agents of crop anthracnose should be performed rigorously following the rules of both taxonomy and plant pathology, relying on not only multiple barcode genes but whole genome sequencing suggested.

Based on published data available we discussed the prevalence of *Colletotrichum* species in strawberry fields in China. *C. siamense* and *C. fructicola* of *C. gloeosporioides* s.l. are currently most prevailing. The prevalence of



certain *Colletotrichum* species in strawberry fields in one region is influenced by the whole agricultural ecosystem and especially interconnected with neighboring plants and climate changes. The relative prevalence of different *Colletotrichum* species varied with geographic region and dynamically changed in certain region. In Shanghai, *C. acutatum* was identified before 2005 (Dai et al. 2006) but has not been detected since 2016 (Zhang et al. 2020). Similarly, an early report showed that strawberry anthracnose caused by *C. gloeosporioides* was incidental

while *C. acutatum* was frequently detected (Kikuchi et al. 2010), but a later study identified *C. fructicola* as the dominant virulent species on strawberry in Japan (Gan et al. 2017). Such shift also occurred in Korea (Nam et al. 2008, 2013). This shift of prevailing *Colletotrichum* species related to strawberry in several regions might be associated with global warming, changes in cultivation pattern from open field to protected cultivation or soil-less elevated cultivation, and substitution of strawberry varieties. The wide application of raised plastic-mulched

beds in a protected cultivation significantly increased the temperature for strawberry production. It has been revealed that *Colletotrichum* species of *C. gloeosporioides* s.l. displayed an advantageous tolerance to high temperature than those of *C. acutatum* s.l. (Han et al. 2016; Chung et al. 2020). Besides, the prevalence of *C. siamense* and *C. fructicola* in China might be closely correlated with the wide cultivation of a highly susceptible cv. Benihoppe, since a susceptible host imposes a strong and direct selection on pathogen populations (Chen et al. 2017). It is expected that the biodiversity of *Colletotrichum* associated with strawberry in China would change in the future following the gradually expanded cultivation of resistant or partially resistant cultivars such as ‘Kantoseika’, ‘HongYu’, ‘YueXin’, ‘Tongzhou Princess’, and ‘Shanghai Fragrance’ in several provinces and regions.

There exists a high genome plasticity in *Colletotrichum* species enabling them a powerful adaptation capability (Gan et al. 2021). In the genus *Colletotrichum*, *C. gloeosporioides* s.l. is the most diversified complex composed of as many as 57 species, which has been considered as a heterogeneous species aggregate affecting more than 700 plant species (O’Connell et al. 2012; Talhinas and Baroncelli 2021; Farr and Rossman 2022). The most prevailing *C. siamense* and *C. fructicola* in Chinese strawberry fields belong to *C. gloeosporioides* s.l., actually the top two *Colletotrichum* species most frequently occurred on the earth, although with remarkably more records in Asia than in other continents. Both *C. siamense* and *C. fructicola* could affect more than 70 genera of hosts widely distributed in the phylogenetic tree of angiosperms. As compared to *C. fructicola*, *C. siamense* infects significantly more plants including one gymnosperm. Notably, some *Colletotrichum* species pathogenic to strawberry even infect members of other kingdoms beyond plant hosts. For example, the prevalent *C. siamense* in strawberry fields had been reported as a human pathogen resulting in skin lesions in the immune compromised host (Werbel et al. 2019). *C. truncatum* was reported as an opportunistic human pathogen (Valenzuela-Lopez et al. 2018). *C. dematium* has also been reported to be capable of infecting human tissues such as cornea (Talhinas and Baroncelli 2021). These associations of strawberry pathogens with human invite our special attention to biosecurity during scientific research and agricultural practices.

The longest summer ever in Shanghai lasted 162 days in 2021 till middle Oct., with 52 days more than the summer 60 years ago, which evidenced the broad outbreak of several diseases including anthracnose crown rot-caused mortality after transplanting in strawberry production fields. It is tempting to speculate that global

warming will exacerbate the threat of anthracnose to strawberry production. However, the change in temperature and other climate factors can have positive, neutral, or negative effects on disease development, depending on the response of the specific “disease triangle” to these variations (Velásquez et al. 2018). In an era of anthropogenic habitat modification and climate change, how can we mitigate the impacts of global warming on strawberry sustainable development? To meet with this challenge, it is urgent to investigate the temperature adaptation of *Colletotrichum* species pathogenic to strawberry, especially those prevailing ones such as *C. siamense* and *C. fructicola* in life cycle and pathogenesis. For a better control of anthracnose crown rot, it is essential to produce disease-resistant strawberry varieties. Resistance to crown anthracnose rot integrated with enhanced tolerance to high temperature would be one of the most important aims for strawberry breeders. Under global warming, apparent latitudinal range shifts of plant pathogens have been observed, indicating that migration rather than adaptation to new climates in situ is the dominant response of pathogen populations to changing climates, and host jumps and transitions occur frequently (Bebber et al. 2013; Chaloner et al. 2020). In turn, shifts in host range also facilitate the emergence of new fungal pathogens (Corredor-Moreno and Saunders 2020). The evolution and hence flexibility of both temperature responses and host ranges of the destructive *Colletotrichum* spp. would simultaneously contribute to their spread, invasion, and threat to strawberry production. Therefore, much attentions should be ongoingly paid to changes in the biodiversity of fungal causal agents and their host ranges.

The present study provided a comprehensive list of *Colletotrichum* species virulent to strawberry and the global diversity of these fungi with their occurrence data, which will help to establish an improved disease management and to design appropriate quarantine monitoring in trade for strawberry. The relative prevalence of distinct *Colletotrichum* species will guide the studies on fungicide sensitivity of pathogens and strain- or species-specific susceptibility of strawberry varieties. Knowledge of pathogen host range can further help to manage plant disease in choice of crop rotation, intercropping, elimination of reservoirs such as weeds, quarantine, forecasting disease emergence, and risk assessment (Morris and Moury 2019). Since the most prevailing *C. siamense* and *C. fructicola* causing strawberry crown rot infect many economically important crops, such knowledge will hold implications in agricultural practices not confined to strawberry.

## Abbreviations

ACT: Actin-encoding gene; AUS: Australia; BAN: Bangladesh; BEL: Belgium; BG: Bulgaria; BRA: Brazil; C: *Colletotrichum*; CAL: Calmodulin-encoding gene; CAN: Canada; Cf: *Colletotrichum fructicola*; CH: Switzerland; CHN: China; CHS: Chitin synthase-encoding gene; CO: Colombia; CR: Costa Rica; Cs: *Colletotrichum siamense*; DR: Denmark; ES: Spain; Fr: France; GAPDH: Glyceraldehyde-3-phosphate dehydrogenase-encoding gene; HIS3: Histone 3; IL: Israel; IN(IND): India; IR: Iran; IRL: the Republic of Ireland; Ita: Italy; ITS: Internally transcribed spacer; JPN: Japan; KE: Kenya; Kr: Korea; LAMP: Loop-mediated isothermal amplification; MYA: Million years ago; NL: Netherlands; NO: Norway; NZ: New Zealand; PCR: Polymerase chain reaction; PRT: Portugal; qPCR: Quantitative real-time PCR; s.l.: Sensu lato; s.s.: Sensu stricto; TUB2: beta-tubulin; UK: the United Kingdom; USA: the United States of America; ZA: South Africa.

## Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42483-022-00147-9>.

**Additional file 1: Table S1.** The host range of the global top two most occurred *Colletotrichum* species. Data were largely retrieved on July 8, 2022 via website search at <https://nt.ars-grin.gov/fungalatabases/> and analyzed at <https://www.iplant.cn/>. Y for hosted. Gray for common hosts shared by *C. siamense* and *C. fructicola*, orange for hosts of *C. siamense* only, light blue for those of *C. fructicola*. Letters in red for records from previous publication (Talhinhas and Baroncelli 2021).

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## Authors' contribution

YJ: data curation, visualization, review, and editing. XL: data curation, review, and editing. QHG: funding, review, and editing. CG: review and editing. KD: funding, conceptualization, visualization, writing (original draft, review, and editing). All authors read and approved the final manuscript.

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## Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

### Ethical approval and consent to participate

Not applicable.

### Consent for publication

Not applicable.

### Competing interests

The authors declare that they have no competing interests.

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