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REVIEW ARTICLE

# *Elsinoe* species: The rise of scab diseases

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## Abstract

The genus *Elsinoe* contains many aggressive pathogens of a wide range of plants, many of which are economically important. These fungal pathogens cause serious scab diseases affecting various plant parts, impacting plant vigour, yield and market value. While studies on *Elsinoe* species have predominantly focused on their taxonomy, there is a conspicuous gap in knowledge of these fungi from a plant pathology perspective. In this review, we draw together and critically evaluate the existing, but rather fragmented, research on the taxonomic status, phylogenetic relationships, host range, as well as the biology and epidemiology of *Elsinoe* species. Our aim is primarily to augment the existing understanding of the global significance of *Elsinoe* species, and furthermore, to shed light on the escalating prominence of scab diseases caused by species in a fungal genus that has been known for over 100 years but remains relatively poorly understood and somewhat enigmatic.

KEYWORDS

emerging diseases, globalization, invasive pathogens, plant pathogens, *Sphaceloma*, spot anthracnose

## 1 | INTRODUCTION

Species of *Elsinoe* (orthographic variant: *Elsinoë*), residing in the Elsinoaceae, Myriangiales, represent a group of highly aggressive and widely distributed plant pathogens. The genus was first erected at the end of the 19th century (Raciborski, 1900), based on the type species *E. canavaliae*, collected from sword bean (*Canavalia gladiata*) in Java, Indonesia. Fascinatingly, the genus name *Elsinoe* is derived from the name of a delicate Greek heroine, in the play *Iridion* written by the Polish poet and dramatist Zygmunt Krasiński (Saccardo & Sydow, 1902).

*Elsinoe* species are mostly necrotrophic fungi that infect various economically important agricultural, horticultural and forestry crops including grapevine, citrus, avocado, cassava and roses, to name only a few. Disease symptoms are easily recognizable by the cork-like appearance of infected tissues, commonly referred to as 'scab'. However, on some host plants, when the hyperplasia is less pronounced, the symptoms have been referred to as a form of anthracnose. To avoid confusion in the literature, Jenkins (1947) introduced the alternative term 'spot anthracnose' to differentiate infections caused by *Elsinoe* spp. from those associated with species of *Colletotrichum*.

During the last few decades, an extensive body of research has been published on *Elsinoe* spp. With respect to reviews, these have mainly been focused on taxonomic perspectives. The most recent monograph of the genus by Fan et al. (2017) provided a stable taxonomy with a well-defined species concept that has enabled contemporary plant pathologists to diagnose diseases and identify species in this genus with greater ease. However, from a plant pathology perspective, there is a distinct lack of knowledge regarding diseases caused by these fungi, their basic biology, and the underlying mechanisms that make them specialized plant pathogens. The aim of this review is to draw together and critically analyse the existing, but rather fragmented, research on the taxonomic status, phylogenetic relationships, host range as well as the biology and epidemiology of *Elsinoe* species. In this way, we hope to extend current knowledge regarding the importance of these pathogens, globally. More broadly, we highlight what appears to be a rising importance of scab diseases caused by species in a genus of fungi that has been known for over 100 years, but that remains relatively poorly understood.

## 2 | TAXONOMY, NOMENCLATURE AND PHYLOGENETIC RELATIONSHIPS

The generic name *Elsinoe* was established more than a century ago by Raciborski (1900) to accommodate species of scab-causing fungi discovered on native host plants in Bogor, Java, Indonesia (formerly Buitenzorg, Java). Raciborski (1900) assigned the binomial names to three species: *E. antidesmae* (on *Antidesma heterophyllum*), *E. menispermacearum* (on *Tinospora* spp.) and the type species *E. canavaliae* (as '*canavalliae*' on *Canavalia gladiata*). All three fungi cause scab-like lesions on host tissues with the presence of immersed, multiloculate ascostromata containing multiple bitunicate asci in each locule (Fan et al., 2017; Jenkins & Bitancourt, 1941; Marin-Felix et al., 2019).

Jenkins (1932a, 1932b) proposed the connection between the sexual morph *Elsinoe* and a previously described asexual acervular coelomycetous genus known as *Sphaceloma*. This genus was initially established in 1874, based on the description of the type species, *Sphaceloma ampelinum*, infecting *Vitis vinifera* in western Europe (de Bary, 1874). *Sphaceloma* spp. form pseudoparenchymatous acervuli, characterized by polyphialidic conidiophores that produce small ellipsoidal, hyaline and aseptate conidia (Fan et al., 2017; Jenkins & Bitancourt, 1941; Marin-Felix et al., 2019).

The taxonomy of *Elsinoe* has been the subject of considerable research but also a topic of substantial debate. During the first half of the 1900s, *Elsinoe* and its asexual state *Sphaceloma*, following their original introductions, were described independently under multiple names by various authors (Figure 1). These included *Manginia* (Viala & Pacottet, 1904), *Melanobasidium* (Maublanc, 1906), *Plectodiscella* (Woronichin, 1914); transferred to *Uleomyces* by (Arnaud, 1925), *Isotexis* (Sydow & Petrak, 1931), *Melanobasis* (Clements & Shear, 1931); *Bitancourtia* (Thirumalachar & Jenkins, 1953); *Kurasawaia* (Hara, 1954); *Uleomycina* (Petrak, 1954) and *Melanophora* (von Arx, 1957). After numerous taxonomic treatments regarding their appropriate placement, many generic names were found to be invalid, and were reduced to synonymy with either *Elsinoe*, or its asexual morph *Sphaceloma* (Jenkins, 1932a, 1971; Jenkins & Bitancourt, 1941; Sutton, 1977; von Arx, 1963; von Arx & Müller, 1975).

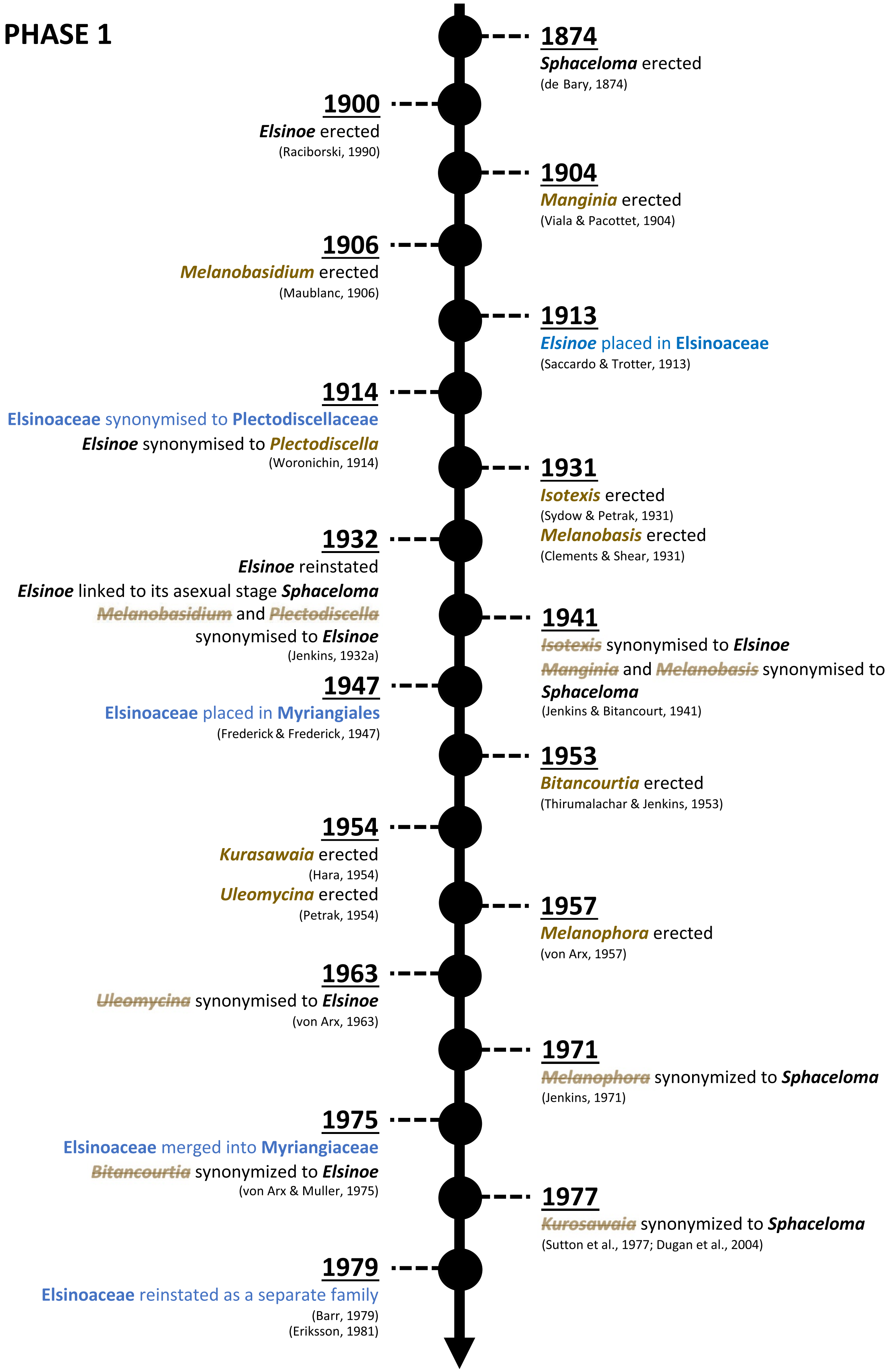
Taxonomic uncertainties for this group of fungi stemmed largely from the fact that species identification, at that time, relied heavily on the signature scab-like symptoms and characteristic morphology of fungal structures formed on the infected plant tissues. One of the challenges was the absence of fertile fruiting structures in field-collected tissues. Although the *Sphaceloma* morphs are more prevalent in nature, species characterization remains arduous due to their conserved morphology (Fan et al., 2017). Additionally, the establishment of pure cultures is notoriously challenging due to the slow growth of these fungi, being easily outcompeted by fast-growing contaminant filamentous fungi and yeasts (Fan et al., 2017; Jenkins, 1932a, 1932b; Scheper et al., 2013; Whiteside, 1986).

A general search on Index Fungorum (www.indexfungorum.org; accessed July 2024) resulted in a total of 211 and 164 name records for *Elsinoe* and *Sphaceloma*, respectively. It is worth noting that in many past studies, new species have been proposed when infections were found on plants not previously known to be hosts of *Elsinoe* species. This approach follows the famous quote by the mycologist F. C. Deighton: 'If a sparrow flies to a cherry tree, it is a cherry tree sparrow. If the same sparrow sits on an apple tree, it is an apple tree sparrow'. Furthermore, many species descriptions were solely based on symptoms and host association, and in the absence of fruiting structures or cultures (Bitancourt & Jenkins, 1949, 1950). For this reason, the validity of numerous reports remains uncertain.

Molecular investigations focusing on *Elsinoe* spp., along with their *Sphaceloma* asexual morphs, have brought about a profound change in research regarding these fungi. Application of molecular techniques, particularly DNA sequence comparisons, has been instrumental in discerning numerous cryptic species and clarifying the connections between different morphs in their life cycle. Several molecular approaches have been employed that include the use of random amplified polymorphic DNA (RAPD) (Álvarez & Molina, 2000; Hyun et al., 2001, 2009; Mchau et al., 1998; Tan et al., 1996; Wang, Liao, et al., 2009), amplified fragment length polymorphisms (AFLP) (Bagsic et al., 2016) and inter-simple sequence repeat (ISSR) markers (Hou et al., 2014; Qadri et al., 2023). Although some of these techniques have provided valuable insights into the genetic variation of the pathogens, DNA sequence comparisons and associated phylogenetic inference has had the most significant impact on the taxonomy of *Elsinoe* species.

The use of ribosomal DNA (rDNA) sequences, and in particular the 5.8S rRNA and internal transcribed spacers (ITS), to delineate *Elsinoe* and *Sphaceloma* species, commenced in the late 1990s and early 2000s (Figure 1). In 1996, sequence analysis of the ITS region was used to differentiate between different pathotypes of the citrus scab pathogens, *E. fawcettii* and *E. australis* (Tan et al., 1996). Swart et al. (2001) produced the first ITS phylogeny that confirmed the connection between the asexual morph *Sphaceloma* and *Elsinoe*.

The capacity to link sexual and asexual species and genera based on molecular evidence has profoundly impacted fungal taxonomy and nomenclature (Crous, Hawksworth, et al., 2015; Taylor, 2011; Wingfield et al., 2012). Following the 'One Fungus = One Name'



**PHASE 1**

**1874**
***Sphaceloma*** erected
(de Bary, 1874)

**1900**
***Elsinoe*** erected
(Raciborski, 1990)

**1904**
***Manginia*** erected
(Viala & Pacottet, 1904)

**1906**
***Melanobasidium*** erected
(Maublanc, 1906)

**1913**
***Elsinoe*** placed in **Elsinoaceae**
(Saccardo & Trotter, 1913)

**1914**
**Elsinoaceae** synonymised to **Plectodiscellaceae**
***Elsinoe*** synonymised to ***Plectodiscella***
(Woronichin, 1914)

**1931**
***Isotexis*** erected
(Sydow & Petrak, 1931)
***Melanobasis*** erected
(Clements & Shear, 1931)

**1932**
***Elsinoe*** reinstated
***Elsinoe*** linked to its asexual stage ***Sphaceloma***
~~***Melanobasidium***~~ and ~~***Plectodiscella***~~ synonymised to ***Elsinoe***
(Jenkins, 1932a)

**1941**
~~***Isotexis***~~ synonymised to ***Elsinoe***
~~***Manginia***~~ and ~~***Melanobasis***~~ synonymised to ***Sphaceloma***
(Jenkins & Bitancourt, 1941)

**1947**
**Elsinoaceae** placed in **Myriangiales**
(Frederick & Frederick, 1947)

**1953**
***Bitancourtia*** erected
(Thirumalachar & Jenkins, 1953)

**1954**
***Kurasawaia*** erected
(Hara, 1954)
***Uleomycina*** erected
(Petrak, 1954)

**1957**
***Melanophora*** erected
(von Arx, 1957)

**1963**
~~***Uleomycina***~~ synonymised to ***Elsinoe***
(von Arx, 1963)

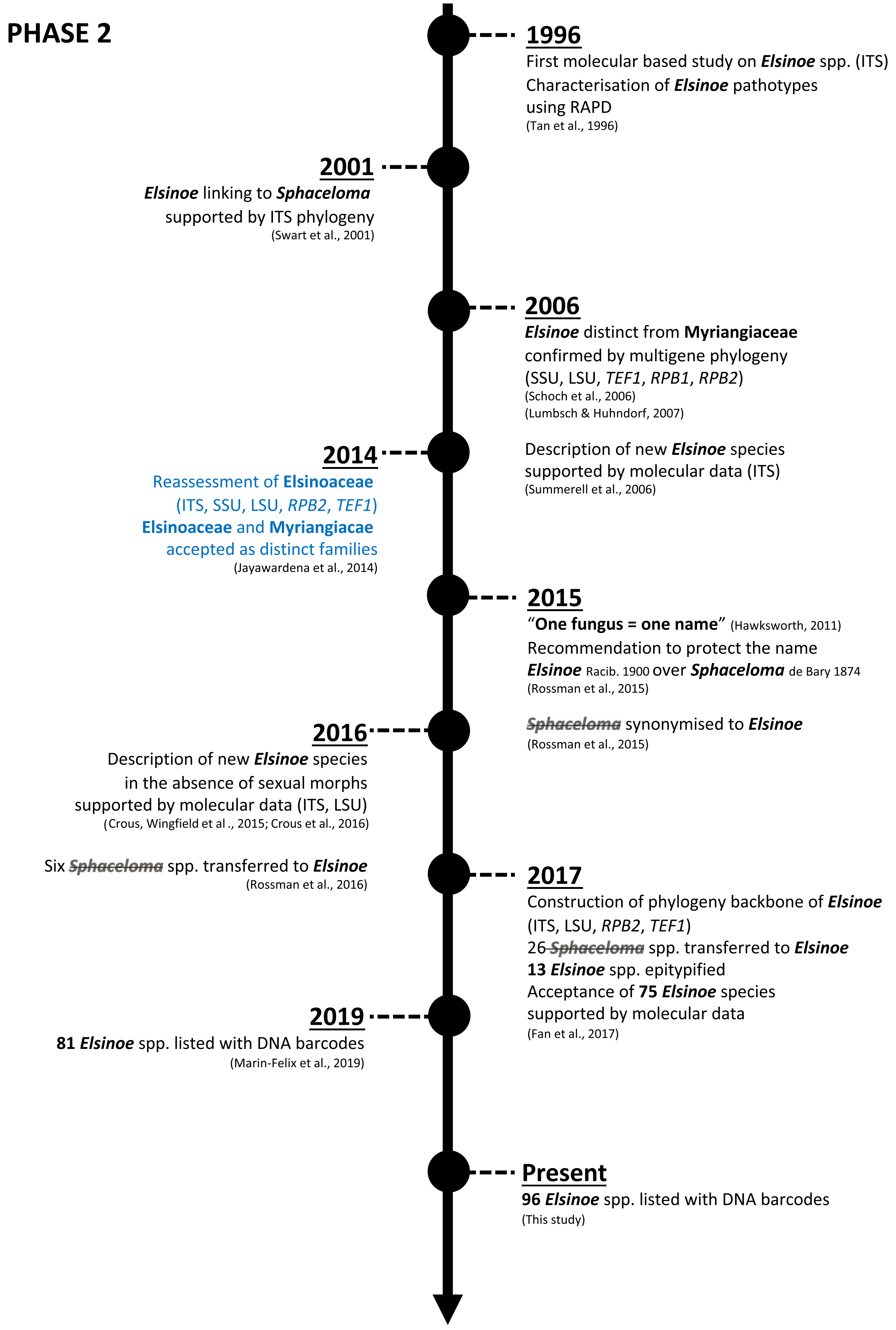
**1971**
~~***Melanophora***~~ synonymized to ***Sphaceloma***
(Jenkins, 1971)

**1975**
**Elsinoaceae** merged into **Myriangiaceae**
~~***Bitancourtia***~~ synonymized to ***Elsinoe***
(von Arx & Muller, 1975)

**1977**
~~***Kurosawaia***~~ synonymized to ***Sphaceloma***
(Sutton et al., 1977; Dugan et al., 2004)

**1979**
**Elsinoaceae** reinstated as a separate family
(Barr, 1979)
(Eriksson, 1981)

FIGURE 1 Historical timeline outlining important events in the taxonomy of *Elsinoe* species and their *Sphaceloma* asexual states. [Colour figure can be viewed at wileyonlinelibrary.com]



**PHASE 2**

**1996**

First molecular based study on ***Elsinoe*** spp. (ITS)

Characterisation of ***Elsinoe*** pathotypes using RAPD

(Tan et al., 1996)

**2001**

***Elsinoe*** linking to ***Sphaceloma*** supported by ITS phylogeny

(Swart et al., 2001)

**2006**

***Elsinoe*** distinct from **Myriangiaceae** confirmed by multigene phylogeny (SSU, LSU, *TEF1*, *RPB1*, *RPB2*)

(Schoch et al., 2006)

(Lumbsch & Huhndorf, 2007)

Description of new ***Elsinoe*** species supported by molecular data (ITS)

(Summerell et al., 2006)

**2014**

Reassessment of **Elsinoaceae** (ITS, SSU, LSU, *RPB2*, *TEF1*)

**Elsinoaceae** and **Myriangiacae** accepted as distinct families

(Jayawardena et al., 2014)

**2015**

"**One fungus = one name**" (Hawksworth, 2011)

Recommendation to protect the name ***Elsinoe*** Racib. 1900 over ***Sphaceloma*** de Bary 1874

(Rossman et al., 2015)

~~***Sphaceloma***~~ synonymised to ***Elsinoe***

(Rossman et al., 2015)

**2016**

Description of new ***Elsinoe*** species in the absence of sexual morphs supported by molecular data (ITS, LSU)

(Crous, Wingfield et al., 2015; Crous et al., 2016)

Six ~~***Sphaceloma***~~ spp. transferred to ***Elsinoe***

(Rossman et al., 2016)

**2017**

Construction of phylogeny backbone of ***Elsinoe*** (ITS, LSU, *RPB2*, *TEF1*)

26 ~~***Sphaceloma***~~ spp. transferred to ***Elsinoe***

**13 *Elsinoe*** spp. epitypified

Acceptance of **75 *Elsinoe*** species supported by molecular data

(Fan et al., 2017)

**2019**

**81 *Elsinoe*** spp. listed with DNA barcodes

(Marin-Felix et al., 2019)

**Present**

**96 *Elsinoe*** spp. listed with DNA barcodes

(This study)

FIGURE 1 (Continued)

concept (Hawksworth, 2011), a single name for polymorphic genera has generally followed the rule of assigning either the oldest name, or the most commonly used name accompanied by the largest number of species epithets (Hawksworth, 2011; Rossman et al., 2015, 2016; Taylor, 2011). Consequently, all designations for a given taxon now possess equal standing in terms of priority, irrespective of the morph that they represent (Hawksworth, 2011). In the specific case of *Elsinoe*, the more recent sexual name *Elsinoe* Racib. (1900) was chosen for conservation over the older asexual name, *Sphaceloma* de Bary (1874) (Rossman et al., 2015; Wijayawardene et al., 2012).

Fan et al. (2017) reconstructed the most complete phylogenetic backbone for *Elsinoe*, which included sequence data from the ITS, 28S large subunit of rRNA (LSU), DNA-directed RNA polymerase II second largest subunit (*RPB2*) and the translation elongation factor 1-α (*TEF1*) regions. The study considered 119 isolates (64 ex-type strains), representing 67 host genera from 17 countries and resolved the taxonomic status of 75 *Elsinoe* species, including 26 new combinations that were originally described in *Sphaceloma*. A combination of a morphological species concept and multigene phylogenetic analyses using informative DNA barcodes provided the most robust view of species boundaries in *Elsinoe* (Fan et al., 2017).

In the recent past, several new species of *Elsinoe* have been described and others have been verified with a new epitype designation (Crous et al., 2018, 2022; Crous, Carnegie, et al., 2019; Crous, Wingfield, et al., 2019; Marin-Felix et al., 2019; Pham et al., 2021; Roux et al., 2024; Ujat et al., 2023). A combination of these new data with those available from Fan et al. (2017) is presented in Figure 2, which provides an updated phylogenetic backbone for all *Elsinoe* species currently known in culture. To date, at least 96 *Elsinoe* species have been validated based on DNA sequence data, residing in three major phylogenetic clades (Figure 2; Table S1).

## 3 | IMPORTANCE OF *ELSINOE* SPECIES

*Elsinoe* species cause diseases on a wide range of plants including agricultural crops, fruit and plantation trees, ornamental and nursery plants, and those occurring in natural ecosystems (Figure 3) (Fan et al., 2017; Marin-Felix et al., 2019). Species of *Elsinoe* can be found on a wide diversity of angiosperms, including members of at least 47 different plant families (Table S1). Upon closer inspection, the number of plant host families reaches approximately 77 if all *Elsinoe* and *Sphaceloma* epithets listed on Index Fungorum (www.indexfungorum.org) are considered (Farr et al., 2021). There are no records of *Elsinoe* infecting gymnosperms.

*Elsinoe* spp. are generally believed to have narrow host ranges or even be host specific, with single species occurring on one host genus or species. However, some *Elsinoe* species share the same host genus or species, for example, *E. genipae* and *E. genipae-americanae* on *Genipa americana* (Fan et al., 2017); *E. australis*, *E. fawcetii* and *E. citricola* on *Citrus* spp. (Fan et al., 2017); and *E. murrayae* and *E. salicina* on *Salix* sp. (Fan et al., 2017; Zhao et al., 2018), to name only a few. In contrast, some *Elsinoe* species have been reported on plants in multiple distantly related host families: *E. ampelina* on Vitaceae and Paulowniaceae (Li et al., 2021; Liu et al., 2022); *E. anacardii* on Anacardiaceae, Annonaceae and Rosaceae (Fan et al., 2017); *E. annonae* on Annonaceae and Theaceae (Bao et al., 2023; Fan et al., 2017); *E. australis* on Rutaceae, Simmondsiaceae and Salicaceae (Chung, 2011; Miles et al., 2015; Zhao et al., 2020); and *E. violae* on Violaceae and Caprifoliaceae (Fan et al., 2017).

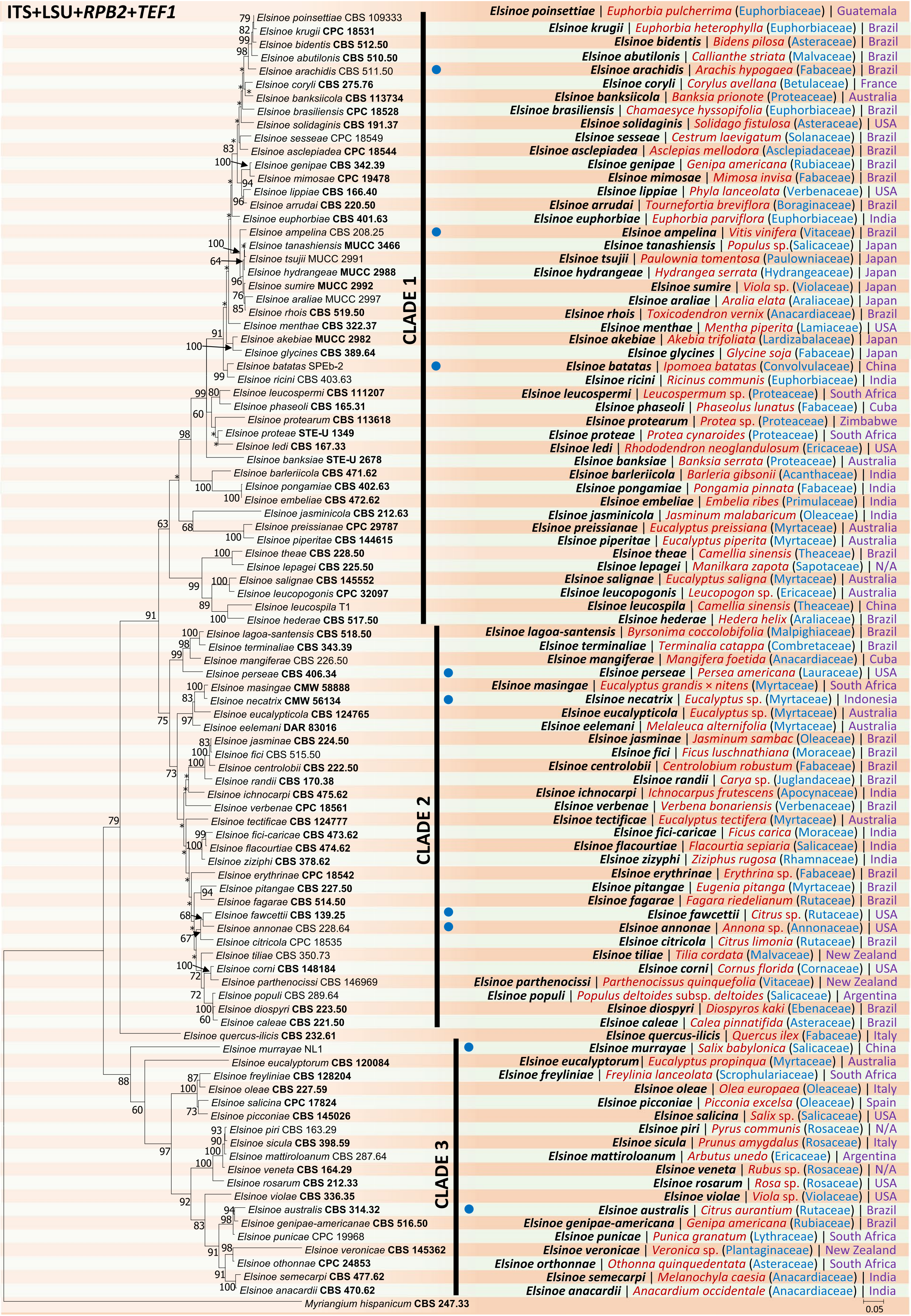
Species of *Elsinoe* can infect different parts of their host plants (leaves, shoots, petioles, young stems, flowers and fruits; Figure 3) (Alleyne, 2017; Chung, 2011; Fan et al., 2017; Li et al., 2021; Swart & Crous, 2001). Infections result in unmarketable appearance of the harvested crops, retarded growth of the infected plants, and substantial reductions in yield (Alleyne, 2017; Fan et al., 2017; Swart et al., 2001). Scab symptoms can vary depending on the host, tissue affected, and on the species of *Elsinoe*. However, in most cases, only young tissues are susceptible to infection. Initial symptoms are often small necrotic spots, which enlarge over time, becoming scab- or pustule-like as the lesions age. On some hosts, other symptoms can occur, including exaggerated internode elongation in cassava, also known as 'super-elongation disease' (SED) (Álvarez & Molina, 2000), stem elongation in poinsettia (Daughtrey & Chase, 2016) and shoot malformation or 'feathering' in planted *Eucalyptus* (Pham et al., 2021; Roux et al., 2024).

Since their first description in the 19th century, *Elsinoe* species have emerged as some of the most important fungal plant pathogens globally. In the following section, examples of various scab diseases that cause substantial economic damage on important agricultural, ornamental and forestry crops are broadly discussed.

### 3.1 | Agricultural hosts

### 3.1.1 | Scab diseases of fruit crops

Citrus scab is one of the most important and widespread diseases affecting the industry worldwide as it can cause severe losses in fruit destined for the fresh market. In addition, these fungi can cause stunting of plants and significantly lower the yields. Citrus scab is caused by three species of *Elsinoe*, namely, *E. fawcettii*, *E. australis* and *E. citricola* (Bitancourt & Jenkins, 1936a, 1936b; Chung, 2011; Fan et al., 2017; Timmer et al., 1996). *E. australis* occurs in the United States and some countries of South America, East Asia and Australia (Figure S1a). *E. citricola* represents a cryptic species discovered on *Citrus lemon*, originally identified as an isolate of '*Sphaceloma fawcettii*' but later reclassified as a separate species (Fan et al., 2017). *E. citricola* was described based on specimens from Brazil and no further information on the geographical distribution of this species is available (Fan et al., 2017). *E. fawcettii*, with a worldwide distribution, is the most common of the citrus scab pathogens, but *E. australis* can be more economically significant because it infects *Citrus* species that are more widely grown. Different pathotypes of *E. fawcettii* and *E. australis* can affect different *Citrus* species or varieties (Hyun et al., 2009; Tan et al., 1996). However, not all pathotypes occur in all



| | | | |
|---|---|---|---|
| | ***Elsinoe poinsettiae*** | *Euphorbia pulcherrima* (Euphorbiaceae) | Guatemala |
| | ***Elsinoe krugii*** | *Euphorbia heterophylla* (Euphorbiaceae) | Brazil |
| | ***Elsinoe bidentis*** | *Bidens pilosa* (Asteraceae) | Brazil |
| | ***Elsinoe abutilonis*** | *Callianthe striata* (Malvaceae) | Brazil |
| ● | ***Elsinoe arachidis*** | *Arachis hypogaea* (Fabaceae) | Brazil |
| | ***Elsinoe coryli*** | *Corylus avellana* (Betulaceae) | France |
| | ***Elsinoe banksiicola*** | *Banksia prionote* (Proteaceae) | Australia |
| | ***Elsinoe brasiliensis*** | *Chamaesyce hyssopifolia* (Euphorbiaceae) | Brazil |
| | ***Elsinoe solidaginis*** | *Solidago fistulosa* (Asteraceae) | USA |
| | ***Elsinoe sesseae*** | *Cestrum laevigatum* (Solanaceae) | Brazil |
| | ***Elsinoe asclepiadea*** | *Asclepias mellodora* (Asclepiadaceae) | Brazil |
| | ***Elsinoe genipae*** | *Genipa americana* (Rubiaceae) | Brazil |
| | ***Elsinoe mimosae*** | *Mimosa invisa* (Fabaceae) | Brazil |
| | ***Elsinoe lippiae*** | *Phyla lanceolata* (Verbenaceae) | USA |
| | ***Elsinoe arrudai*** | *Tournefortia breviflora* (Boraginaceae) | Brazil |
| | ***Elsinoe euphorbiae*** | *Euphorbia parviflora* (Euphorbiaceae) | India |
| ● | ***Elsinoe ampelina*** | *Vitis vinifera* (Vitaceae) | Brazil |
| | ***Elsinoe tanashiensis*** | *Populus* sp.(Salicaceae) | Japan |
| | ***Elsinoe tsujii*** | *Paulownia tomentosa* (Paulowniaceae) | Japan |
| | ***Elsinoe hydrangeae*** | *Hydrangea serrata* (Hydrangeaceae) | Japan |
| | ***Elsinoe sumire*** | *Viola* sp. (Violaceae) | Japan |
| | ***Elsinoe araliae*** | *Aralia elata* (Araliaceae) | Japan |
| | ***Elsinoe rhois*** | *Toxicodendron vernix* (Anacardiaceae) | Brazil |
| | ***Elsinoe menthae*** | *Mentha piperita* (Lamiaceae) | USA |
| | ***Elsinoe akebiae*** | *Akebia trifoliata* (Lardizabalaceae) | Japan |
| | ***Elsinoe glycines*** | *Glycine soja* (Fabaceae) | Japan |
| ● | ***Elsinoe batatas*** | *Ipomoea batatas* (Convolvulaceae) | China |
| | ***Elsinoe ricini*** | *Ricinus communis* (Euphorbiaceae) | India |
| | ***Elsinoe leucospermi*** | *Leucospermum* sp. (Proteaceae) | South Africa |
| | ***Elsinoe phaseoli*** | *Phaseolus lunatus* (Fabaceae) | Cuba |
| | ***Elsinoe protearum*** | *Protea* sp. (Proteaceae) | Zimbabwe |
| | ***Elsinoe proteae*** | *Protea cynaroides* (Proteaceae) | South Africa |
| | ***Elsinoe ledi*** | *Rhododendron neoglandulosum* (Ericaceae) | USA |
| | ***Elsinoe banksiae*** | *Banksia serrata* (Proteaceae) | Australia |
| | ***Elsinoe barleriicola*** | *Barleria gibsonii* (Acanthaceae) | India |
| | ***Elsinoe pongamiae*** | *Pongamia pinnata* (Fabaceae) | India |
| | ***Elsinoe embeliae*** | *Embelia ribes* (Primulaceae) | India |
| | ***Elsinoe jasminicola*** | *Jasminum malabaricum* (Oleaceae) | India |
| | ***Elsinoe preissianae*** | *Eucalyptus preissiana* (Myrtaceae) | Australia |
| | ***Elsinoe piperitae*** | *Eucalyptus piperita* (Myrtaceae) | Australia |
| | ***Elsinoe theae*** | *Camellia sinensis* (Theaceae) | Brazil |
| | ***Elsinoe lepagei*** | *Manilkara zapota* (Sapotaceae) | N/A |
| | ***Elsinoe salignae*** | *Eucalyptus saligna* (Myrtaceae) | Australia |
| | ***Elsinoe leucopogonis*** | *Leucopogon* sp. (Ericaceae) | Australia |
| | ***Elsinoe leucospila*** | *Camellia sinensis* (Theaceae) | China |
| | ***Elsinoe hederae*** | *Hedera helix* (Araliaceae) | Brazil |
| | ***Elsinoe lagoa-santensis*** | *Byrsonima coccolobifolia* (Malpighiaceae) | Brazil |
| | ***Elsinoe terminaliae*** | *Terminalia catappa* (Combretaceae) | Brazil |
| | ***Elsinoe mangiferae*** | *Mangifera foetida* (Anacardiaceae) | Cuba |
| ● | ***Elsinoe perseae*** | *Persea americana* (Lauraceae) | USA |
| | ***Elsinoe masingae*** | *Eucalyptus grandis × nitens* (Myrtaceae) | South Africa |
| ● | ***Elsinoe necatrix*** | *Eucalyptus* sp. (Myrtaceae) | Indonesia |
| | ***Elsinoe eucalypticola*** | *Eucalyptus* sp. (Myrtaceae) | Australia |
| | ***Elsinoe eelemani*** | *Melaleuca alternifolia* (Myrtaceae) | Australia |
| | ***Elsinoe jasminae*** | *Jasminum sambac* (Oleaceae) | Brazil |
| | ***Elsinoe fici*** | *Ficus luschnathiana* (Moraceae) | Brazil |
| | ***Elsinoe centrolobii*** | *Centrolobium robustum* (Fabaceae) | Brazil |
| | ***Elsinoe randii*** | *Carya* sp. (Juglandaceae) | Brazil |
| | ***Elsinoe ichnocarpi*** | *Ichnocarpus frutescens* (Apocynaceae) | India |
| | ***Elsinoe verbenae*** | *Verbena bonariensis* (Verbenaceae) | Brazil |
| | ***Elsinoe tectificae*** | *Eucalyptus tectifera* (Myrtaceae) | Australia |
| | ***Elsinoe fici-caricae*** | *Ficus carica* (Moraceae) | India |
| | ***Elsinoe flacourtiae*** | *Flacourtia sepiaria* (Salicaceae) | India |
| | ***Elsinoe zizyphi*** | *Ziziphus rugosa* (Rhamnaceae) | India |
| | ***Elsinoe erythrinae*** | *Erythrina* sp. (Fabaceae) | Brazil |
| | ***Elsinoe pitangae*** | *Eugenia pitanga* (Myrtaceae) | Brazil |
| | ***Elsinoe fagarae*** | *Fagara riedelianum* (Rutaceae) | Brazil |
| ● | ***Elsinoe fawcettii*** | *Citrus* sp. (Rutaceae) | USA |
| ● | ***Elsinoe annonae*** | *Annona* sp. (Annonaceae) | USA |
| | ***Elsinoe citricola*** | *Citrus limonia* (Rutaceae) | Brazil |
| | ***Elsinoe tiliae*** | *Tilia cordata* (Malvaceae) | New Zealand |
| | ***Elsinoe corni*** | *Cornus florida* (Cornaceae) | USA |
| | ***Elsinoe parthenocissi*** | *Parthenocissus quinquefolia* (Vitaceae) | New Zealand |
| | ***Elsinoe populi*** | *Populus deltoides* subsp. *deltoides* (Salicaceae) | Argentina |
| | ***Elsinoe diospyri*** | *Diospyros kaki* (Ebenaceae) | Brazil |
| | ***Elsinoe caleae*** | *Calea pinnatifida* (Asteraceae) | Brazil |
| | ***Elsinoe quercus-ilicis*** | *Quercus ilex* (Fabaceae) | Italy |
| ● | ***Elsinoe murrayae*** | *Salix babylonica* (Salicaceae) | China |
| | ***Elsinoe eucalyptorum*** | *Eucalyptus propinqua* (Myrtaceae) | Australia |
| | ***Elsinoe freyliniae*** | *Freylinia lanceolata* (Scrophulariaceae) | South Africa |
| | ***Elsinoe oleae*** | *Olea europaea* (Oleaceae) | Italy |
| | ***Elsinoe picconiae*** | *Picconia excelsa* (Oleaceae) | Spain |
| | ***Elsinoe salicina*** | *Salix* sp. (Salicaceae) | USA |
| | ***Elsinoe piri*** | *Pyrus communis* (Rosaceae) | N/A |
| | ***Elsinoe sicula*** | *Prunus amygdalus* (Rosaceae) | Italy |
| | ***Elsinoe mattiroloanum*** | *Arbutus unedo* (Ericaceae) | Argentina |
| | ***Elsinoe veneta*** | *Rubus* sp. (Rosaceae) | N/A |
| | ***Elsinoe rosarum*** | *Rosa* sp. (Rosaceae) | USA |
| | ***Elsinoe violae*** | *Viola* sp. (Violaceae) | USA |
| ● | ***Elsinoe australis*** | *Citrus aurantium* (Rutaceae) | Brazil |
| | ***Elsinoe genipae-americana*** | *Genipa americana* (Rubiaceae) | Brazil |
| | ***Elsinoe punicae*** | *Punica granatum* (Lythraceae) | South Africa |
| | ***Elsinoe veronicae*** | *Veronica* sp. (Plantaginaceae) | New Zealand |
| | ***Elsinoe orthonnae*** | *Othonna quinquedentata* (Asteraceae) | South Africa |
| | ***Elsinoe semecarpi*** | *Melanochyla caesia* (Anacardiaceae) | India |
| | ***Elsinoe anacardii*** | *Anacardium occidentale* (Anacardiaceae) | India |

**FIGURE 2** Phylogenetic tree based on maximum-likelihood (ML) analysis of a combined DNA dataset of rDNA internal transcribed spacer (ITS), large subunit (LSU), *RPB2* and *TEF1* sequences for species of *Elsinoe*. Bootstrap values ≥60% for ML analysis are indicated at the node. Isolates representing ex-type, ex-epitype and ex-isotype are indicated in bold. Host species are highlighted in red, host family in blue, and countries of origin of the isolates are in purple. Blue dots represent species with available genome sequences. *Myriangium hispanicum* (isolate CBS 247.33) represents the outgroup taxon. Table S1 contains detailed methods used to produce this tree as well as GenBank accession numbers. [Colour figure can be viewed at wileyonlinelibrary.com]

**FIGURE 3** Symptoms associated with infections by *Elsinoe* species on various plants. (a) Avocado scab; (b) mango scab; (c) bramble spot anthracnose; (d) bean scab; (e,f) *Eucalyptus* scab and shoot malformation. [Colour figure can be viewed at wileyonlinelibrary.com]

areas where these fungi occur (Hyun et al., 2009; Miles et al., 2015). Importantly, *E. australis*, *E. citricola* and *E. fawcettii* are European Union quarantine pests listed in Annex II Part A of Commission Implementing Regulation (EU) 2019/2072 (https://eur-lex.europa.eu/eli/reg_impl/2019/2072/oj).

In the tropics and Southern Hemisphere, mango scab, caused by *E. mangiferae* (Bitancourt & Jenkins, 1946), can be a significant problem on seedlings in nurseries because young host tissues are most susceptible to infection (Conde et al., 2007; Ploetz & Prakash, 1997; Prakash, 2004; Ruehle & Ledin, 1955). The disease was first observed in Cuba, Chile and the United States (Florida) in the 1940s (Bitancourt & Jenkins, 1946). Currently, it is found in most mango-growing regions of the world, including Central and South America, the Pacific, Australia, South and South-east

Asia, and Africa (Figure S1a). Avocado scab caused by *E. perseae* was first reported on leaves and fruit of avocado in the United States (Florida) (Jenkins, 1934; Stevens, 1918). Even though there are multiple informal accounts of its presence in many avocado-growing areas in the Americas and the Caribbean, this disease has only been confirmed in the United States (with restricted distribution in Florida), Brazil and Mexico (Figure S1a). Scab infection results in severe losses from fruit drop, and superficial cosmetic defects that reduce fruit value and export opportunities (Belizaire et al., 2024; Manicom, 2001; Marais, 2004; Pernezny & Marlatt, 2007; Pohronezny & Simone, 1998).

In temperate regions, spot anthracnose of raspberries, blackberries and other brambles or cane fruits (*Rubus* spp.) is caused by *E. veneta* (Jenkins, 1932a). *E. veneta*, originally reported in the United States (Burkholder, 1917), is widespread in all cane fruit-growing regions, especially in North and South America, western Europe, southern Africa, East Asia and Australia (Figure S1a). Cane fruit spot anthracnose was regarded as one of the most aggressive diseases of raspberry and blackberry in North America early in the 20th century (Jones, 1924). The infected fruits are severely disfigured and unmarketable (Burkholder, 1917; Harris, 1931, 1933; Jones, 1924; Labruyère, 1957). Wild *Rubus* spp. growing in the proximity of the cane fruit fields can also become infected and act as inoculum reservoirs (Jones, 1924). In organic orchards located in cooler temperate areas where fungicides are not sprayed, spot anthracnose in apples and pears caused by *E. piri* (Jenkins, 1932a) can be economically important (Glazowska et al., 2013; Scheper et al., 2013). Severely infected fruits lose market value and can thus only be used for juice or by-product production (Scheper et al., 2013).

Grape spot anthracnose or bird's eye spot caused by *E. ampelina* (de Bary, 1874; Shear, 1929) is one of the most important diseases affecting wine and table grapes. The disease was first described in western Europe (de Bary, 1874). *E. ampelina* is now found wherever grapes are grown (Figure S1a). Although the disease may not directly kill the vines, it can diminish photosynthetic capacity, resulting in reduced carbohydrate reserves. Eventually, as these reserves are depleted, vines can succumb to winter conditions (Brook, 1973; Li et al., 2021). In addition to the direct effects on yield, infections also alter the biochemical components of berries and lower the quality of the fruit (Magarey et al., 1993; Thind et al., 1998, 2004). In some regions, yield losses can reach 50%–100% in susceptible cultivars (Anderson, 1956; Bedi et al., 1969).

### 3.1.2 | Scab diseases of root and tuber crops

*Elsinoe* species can infect the above-ground parts of root and tuber crops, including leaves, shoots, stems and flowers, but not the below-ground parts. However, infection in the phyllosphere results in yield reduction and reduced quality of the roots and tubers. Scab disease of cassava was first described by Bitancourt and Jenkins (1950) in Central America. The causal agent was described as *E. brasiliensis* (Bitancourt & Jenkins, 1950), and the disease has since become widespread in the neighbouring regions of Central and South America and the Caribbean (Figure S1b). The disease is unknown in Africa, despite this being one of the main cassava-growing regions. Infection by *E. brasiliensis* results in reduced root size, and thus tuber quality. In some countries, it can lead to up to 80% crop loss (Álvarez et al., 2012; Álvarez & Molina, 2000; Reeder et al., 2009; Zeigler et al., 1983). The advanced symptoms of this disease are excessive lengthening of the stem internodes, thus the name SED, resulting in thin and frail stems (Zeigler et al., 1980). Diseased plants are much taller than those that are healthy but are weaker; symptoms progress to dieback and extensive defoliation (Zeigler et al., 1983). Cross-inoculation trials demonstrated that *Elsinoe* spp. isolated from wild Euphorbiaceae can cause infections on cassava (Zeigler & Lozano, 1983). Pathotypes of *E. brasiliensis* have high levels of genetic variability in some regions (Álvarez et al., 2003; Álvarez & Molina, 2000).

Sweet potato scab was first reported from Taiwan in 1931, and later described from Brazil in the 1940s (Jenkins & Viegas, 1943). Other than Brazil, it is not widespread in tropical regions of America as it is known only in Mexico (McGuire Jr. & Crandall, 1967) and Puerto Rico (Watson, 1971). The disease is more prevalent in Southeast Asia, East Asia and the Pacific (Figure S1B). Severe disease incidence can result in low tuber production (up to 50% yield loss) or plant death (Clark et al., 2009; Divinagracia & Mailum, 1976; Goodbody, 1983; Lenné, 1991). Other susceptible Convolvulaceae species, including multiple wild *Ipomoea* spp. frequently found growing adjacent to sweet potato fields, can potentially act as an inoculum source (Hanson, 1963; Lenné, 1991).

### 3.1.3 | Scab diseases of leguminous crops

Scab diseases of cultivated legumes are caused by three species of *Elsinoe* including *E. arachidis* on peanut (Bitancourt & Jenkins, 1940), *E. glycines* on soybean (Kurata & Kuribayashi, 1954) and *E. phaseoli* on common and Lima bean (Bruner & Jenkins, 1933). While *E. glycines* is confined to East Asian countries, *E. arachidis* and *E. phaseoli* are found in America, Asia and Africa (Figure S1c). *E. phaseoli* appears to be the most widespread of these fungi (Figure S1c). In China, *E. arachidis* can cause yield losses of up to 50% in susceptible peanut varieties (Fang et al., 2007; Zhou et al., 2014). In some regions of Africa, epidemics caused by *E. phaseoli* can result in 100% infection and yield losses of 40%–70% (Phillips, 1994; Schwartz, 1991). Very little is known regarding the impact of *E. glycines* in East Asian countries. Cross-inoculation trials of *E. glycines* on other leguminous hosts have shown that it is not pathogenic on common and Lima bean (Kurata & Kuribayashi, 1954).

## 3.2 | Ornamental plants

*Elsinoe* species can infect ornamental plants in field and nursery settings, leading to significant aesthetic damage and reduced market value. Spot anthracnose on roses is most serious on field-cultivated roses, with an increasing incidence in recent years occurring in all regions where roses are grown (Bagsic et al., 2016; Horst & Cloyd, 2007). The disease, caused by *E. rosarum* (Jenkins, 1932b), is widespread mostly in temperate regions (Figure S1e). Spot anthracnose on roses can lead to reduced vigour, inferior blooms and elevated susceptibility to frost damage (Pscheidt & Rodriguez, 2018). Different pathotypes of the fungus have been identified in Germany (Bagsic et al., 2016).

Poinsettia scab, caused by *E. poinsettiae* (Jenkins & Ruehle, 1942), can result in serious economic losses in ornamental poinsettia nurseries (Benson et al., 2002; Daughtrey & Chase, 2016; Wehlburg, 1968). *E. poinsettiae* was originally detected on leaves and branches of poinsettia (*Euphorbia pulcherrima* var. *plenissima*) in Florida and Hawaii, United States (Jenkins & Ruehle, 1942; Ruehle, 1941). This scab disease has subsequently been recorded from countries in subtropical and tropical America, southern Africa and the South Pacific (Figure S1e). de Lima Nechet et al. (2014) studied the potential use of *E. poinsettiae* as a mycoherbicide to control wild poinsettia (*Euphorbia heterophylla*) in Brazil. However, phylogenetic analysis showed that all isolates infecting *E. heterophylla* in that study were not *E. poinsettiae*, but rather the closely related species, *E. krugii* (Fan et al., 2017). Fan et al. (2017) showed that *E. krugii* was also a pathogen of *E. pulcherrima*, hinting at the possibility that scab disease of poinsettia in some Central and South American countries could be caused by a complex of different species.

Several *Elsinoe* species are associated with scab diseases of cultivated Proteaceae, the more important of which are *E. leucospermi*, *E. proteae* and *E. protearum* (Swart et al., 2001). Scab diseases are present on Proteaceae crops in the United States, Spain, Australia and some African countries including South Africa, Malawi and Zimbabwe (Crous et al., 2004; Swart et al., 2001; Figure S1e). *E. leucospermi* is the most widespread (United States, Spain, Australia and African countries), while *E. protearum* is present only in South Africa and Zimbabwe (Figure S1e). In some common commercially planted cultivars of *Protea*, *Leucospermum* and *Leucodendron*, the disease can cause significant damage and economic losses (Swart & Crous, 2001), often up to 40%–80% loss in total revenue (Ziehrl et al., 1995). The scab-like lesions reduce the aesthetics of the cut flowers, thus affecting their market value (Swart & Crous, 2001). Severely infected plants may die in the absence of adequate disease control measures (Benić & Knox-Davies, 1983; Ziehrl et al., 2000). Importantly, Ziehrl et al. (2000) showed the cross-infection potential of *Elsinoe* spp. from South African Proteaceae onto those native to Australia, including species of *Banksia* and *Dryandra*.

### 3.3 | Plantation-grown forestry crops

Until very recently, scab diseases caused by *Elsinoe* spp. were not known to affect trees grown for plantation forestry. This situation changed in the early 2010s when a seriously damaging leaf and shoot disease of unknown aetiology was discovered in *Eucalyptus* plantations of North Sumatra, Indonesia. The symptoms were unlike any other leaf or shoot diseases known on these trees elsewhere in the world. After a decade of intensive research, the causal agent was identified and described as the novel species, *E. necatrix* (Pham et al., 2021). Interestingly, after this discovery, a similar *Eucalyptus* disease caused by a different *Elsinoe* species was encountered in South Africa for the first time (Roux et al., 2024).

Currently, Eucalyptus scab and shoot malformation caused by *E. necatrix* is known only in North Sumatra, and *E. masingae* only in South Africa (Figure S1e). In North Sumatra, *E. necatrix* has emerged as an aggressive pathogen infecting approximately 40,000 ha of planted *Eucalyptus* (Pham et al., 2021). In South Africa, the disease is widespread and has already resulted in a significant negative impact to the local forestry industry (Roux et al., 2024).

Six other species of *Elsinoe*, namely, *E. eucalypticola*, *E. eucalyptorum*, *E. piperitae*, *E. preissianae*, *E. salignae* and *E. tectificae*, have been described from *Eucalyptus* species, all from Australia, the native range of *Eucalyptus* spp. (Crous et al., 2016; Crous, Carnegie, et al., 2019; Crous, Wingfield, et al., 2019; Fan et al., 2017). None of these species have been experimentally tested for pathogenicity and only *E. necatrix* and *E. masingae* are known to cause serious disease problems in plantation forestry settings using non-native *Eucalyptus*. It is believed that Eucalyptus scab caused by *Elsinoe* spp. could be an important constraint to plantation-grown *Eucalyptus* in the future (Pham et al., 2021, 2024; Roux et al., 2024).

## 4 | REPRODUCTIVE BIOLOGY AND INFECTION CYCLE

### 4.1 | Reproductive biology

The studies by Zhao et al. (2020) and Pham et al. (2023) have shown that species of *Elsinoe* have a typical heterothallic mating system. This is characterized by the presence of a single mating-type idiomorph (either *MAT1-1* or *MAT1-2*) in individual isolates and the need for two compatible partners with opposite mating-type idiomorphs for sexual reproduction (Ni et al., 2011; Turgeon & Yoder, 2000). Based on comparisons of genome sequences, *MAT1-1* and *MAT1-2* idiomorphs in *Elsinoe* were defined by the *MAT1-1-1* or the *MAT1-2-1* gene, respectively (Figure S2; Pham et al., 2023). The availability of a set of universal mating-type primers developed for *Elsinoe* spp., targeting the *MAT1-1-1* and *MAT1-2-1* genes (Pham et al., 2023), has made it possible to characterize the mating type distribution in natural populations of these important fungi. Such knowledge will facilitate an understanding of the mode of reproduction occurring in particular regions, and consequently an understanding of the population dynamics and adaptation potential of these pathogens (Debuchy & Turgeon, 2006; Ni et al., 2011). This PCR-based mating type diagnostic assay is effective on more than 20 species of *Elsinoe*, including some of the most important pathogens in the genus (Pham et al., 2023).

## 4.2 | Putative infection cycle

Most *Elsinoe* species are known based on their asexual states but in some cases the sexual states have been found (Fan et al., 2017). Under favourable environmental conditions (wet and rainy periods), abundant conidia are readily produced asexually on wet scab lesions on leaves, petioles, fruits or plant debris (Brook, 1973; Chung, 2011; Kearney et al., 2002; Whiteside, 1975). Because conidia are dispersed by rain splash, heavy dew or overhead irrigation over short distances (Brook, 1973; Whiteside, 1975), they are mainly responsible for localized vertical spread of the pathogen (Brook, 1973; Chung, 2011; Kearney et al., 2002; Whiteside, 1975). Some species produce spindle-shaped conidia, which facilitates longer distance dispersal by rain splash or by wind (Benson et al., 2002; Chung, 2011; Whiteside, 1975; Zeigler & Lozano, 1983).

The sexual state of *Elsinoe* species, characterized by multiloculate ascostromata, is usually found on older tissues infected in the previous season, or on leaf litter and plant debris (Gabel & Tiffany, 1987; Jones, 1924). Wind-dispersed ascospores are released from asci within eroded ascostromata and can initiate new infections (Gabel & Tiffany, 1987; Jones, 1924). Depending on the species of *Elsinoe*, both conidia and ascospores can be the primary source of inoculum during new growing seasons (Anderson, 1956; Brook, 1973; Gabel & Tiffany, 1987; Jones, 1924).

*Elsinoe* spp. are polycyclic and thus capable of several infection cycles in a single season (Figure 4). Once the disease is established, the pathogen produces lesions on which acervuli form and produce conidia. These are dispersed by water splash and serve as a secondary source of inoculum for the remainder of the growing season, assuming that susceptible young tissues are available for infection (Brook, 1973; Gabel & Tiffany, 1987; Kearney et al., 2002). During periods of humid weather, conidia can be released throughout the entire rainy season, providing continuous infections. *Elsinoe* species overwinter as ascostromata or sclerotia on infected tissues or plant debris, some with a survival period of up to 5 years (Brook, 1992; Suhag & Grover, 1972).

## 5 | PHYTOTOXIN AND PHYTOHORMONE PRODUCTION

Specialized metabolites produced by plant-pathogenic fungi can act as important virulence factors during the infection of plant tissues (Möbius & Hertweck, 2009). *Elsinoe* species produce a group of nonhost-selective specialized metabolites that are light-activated, polyketide-derived phytotoxins known as elsinochromes (Chung & Liao, 2008; Jiao et al., 2021; Liao & Chung, 2008). Production of elsinochromes in these fungi results in the characteristic red

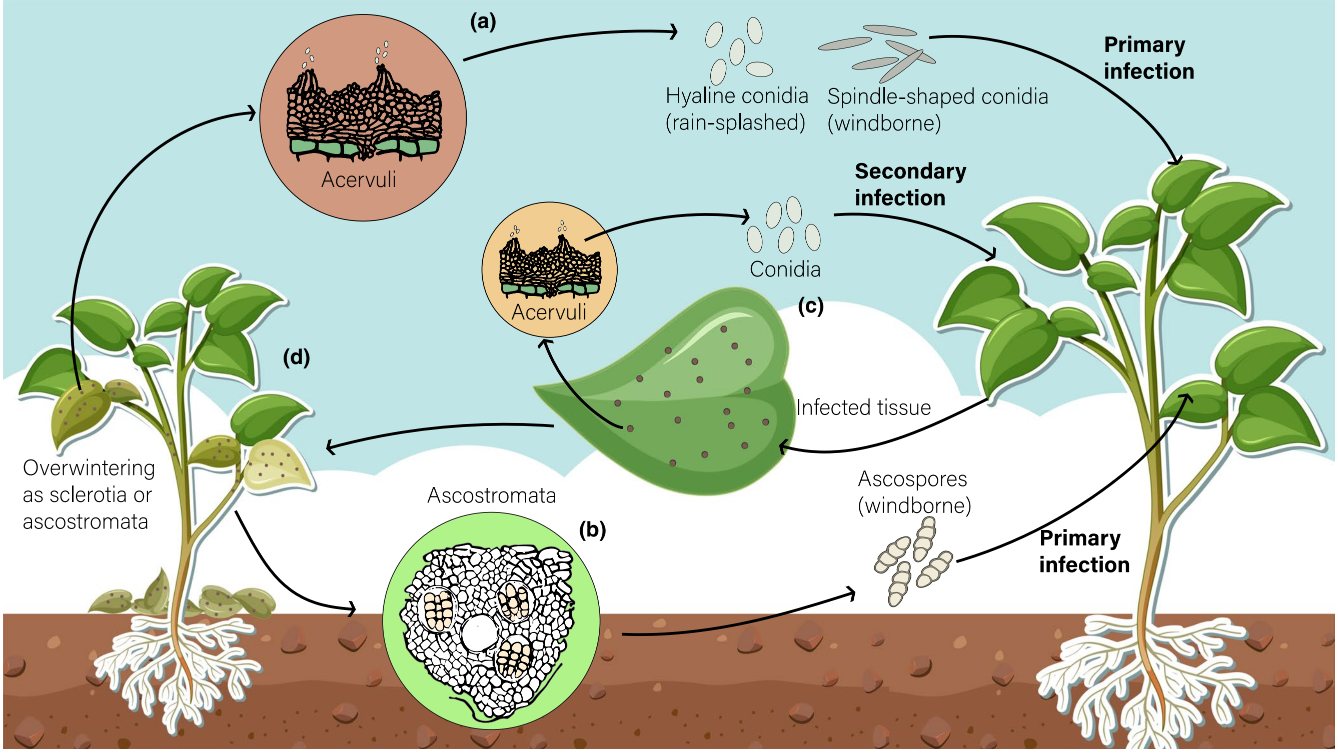


FIGURE 4 Putative generalized infection cycle for *Elsinoe* species. (a) Abundant conidia produced in acervuli on infected plant tissues in previous season (or infection cycle), (b) or ascospores released from ascostromata, can act as primary inoculum and infect young host tissues. (c) Acervuli develop on the newly formed lesions, disseminate conidia that become the source of secondary inoculum, providing continuous infections for the remainder of the growing season. (d) The fungus overwinters by forming either sclerotia or ascostromata on infected materials or plant debris. A sexual state is not known and may not occur in all *Elsinoe* species, in the absence of which infections would depend only on asexual reproduction of the pathogen. [Colour figure can be viewed at wileyonlinelibrary.com]

(elsinochromes A–C) to orange (elsinochrome D) pigments in cultures (Chung, 2011; Weiss et al., 1957). Elsinochromes are structurally related to some perylenequinones produced by other fungi such as species of *Cercospora* and *Cladosporium*. They react with oxygen molecules after light activation to produce highly toxic reactive oxygen species (Chung, 2011; Daub et al., 2005). This chemical reaction results in necrosis of host cell membranes at the point of infection and is vital to the infection process in these fungi (Jiao et al., 2021; Liao & Chung, 2008; Wang, Bau, et al., 2009).

Chung and Liao (2008) predicted a biosynthetic gene cluster (BGC) responsible for elsinochrome biosynthesis, with a core gene, *EfPKS1*, encoding a polypeptide containing all of the functional domains characteristic of a fungal non-reducing polyketide synthase (PKS). Ebert et al. (2019) showed that *EfPKS1* and the above-mentioned BGC containing that gene were involved in DHN-melanin biosynthesis, which consequently resulted in some confusion in subsequent studies (So et al., 2015). Using a genomic mining and comparison method, Ebert et al. (2019) identified the emended elsinochrome BGC, containing the core gene *EfETB1*. This perylenequione gene was proven legitimate in a gene knockout study, which confirmed its role in toxin production (Ebert et al., 2019).

Gibberellins (GAs) are tetracyclic diterpenoid phytohormones that were first identified as one of the specialized metabolites of the rice-pathogenic fungus *Fusarium fujikuroi* (MacMillan & Suter, 1958). Surprisingly, they were also found in *E. brasiliensis*, the causal agent of SED in cassava (Rademacher & Graebe, 1979). *F. fujikuroi* causes infected plants to develop abnormally, resulting in hyperelongated internodes, yellowish leaves and sterile or empty grains, all of which significantly reduce grain production (Leslie & Summerell, 2006). The ability to cause a similar abnormal increase in longitudinal growth of infected plants led to the discovery of these phytohormones in *E. brasiliensis* (Rademacher & Graebe, 1979; Zeigler et al., 1980). Later, Rademacher (1992) showed that other *Elsinoe* spp. also produce $GA_4$ in culture filtrates. The gibberellin BGC from *E. brasiliensis* has been identified and functionally characterized by Bömke et al. (2008). The similarity in gene structure and organization, and conserved intron positions compared to that of *F. fujikuroi* gibberellin BGC suggest a common evolutionary origin of these specialized metabolite clusters, despite the distant relatedness of the two organisms (Bömke et al., 2008).

## 6 | DETECTION ASSAYS FOR *ELSINOE* SPECIES

Scab diseases cannot be identified with confidence using only symptoms. This is because the initial symptoms of infection by *Elsinoe* spp. can be confused with damage by other pathogens or insect pests (Barreto, 1997; Belizaire et al., 2024; Conde et al., 2007; Everett et al., 2011; Fan et al., 2017; McCoy, 1996). Early detection and diagnostic tools relied on isolating the pathogen from symptomatic plant tissues. Semiselective media containing antibiotics and fungicides were developed (Whiteside, 1986); however, the slow growth of *Elsinoe* spp. remained a challenge (Fan et al., 2017). Even when a culture is obtained, the lack of diagnostic characters makes isolate identification difficult and unreliable (Fan et al., 2017; Timmer et al., 2000).

The availability of various molecular techniques has prompted the development of several methods to detect *Elsinoe* spp. in infected plant tissues. For example, Hyun et al. (2007) developed a conventional PCR assay based on a RAPD fragment to distinguish between the citrus pathogens *E. fawcettii* and *E. australis*. Everett et al. (2011) designed species-specific primers from the ITS region to detect *E. perseae* infecting avocado. Similarly, Alleyne et al. (2015) designed specific PCR primers to target a fragment of the *Smp450-2* gene, belonging to the gibberellin BGC, to detect *E. brasiliensis* in cassava plants affected by SED. Ahmed et al. (2019) developed a multiplex real-time (quantitative) PCR protocol, targeting the nuclear single-copy gene *MS204*, to detect *E. fawcettii* and *E. australis* on *Citrus*. Later, Elliott et al. (2023) introduced an assay targeting the ITS region for the diagnosis of all *Elsinoe* spp. occurring on *Citrus*, including *E. citricola*. Chandelier et al. (2022) developed a quantitative PCR test to detect and quantify *E. piri*. In terms of point-of-care diagnosis, Shin et al. (2021) developed a recombinase polymerase amplification (RPA)-clustered regularly interspaced short palindromic repeats (CRISPR)/associated (Cas) system with a lateral flow assay (RPA-CRISPR/CAS12a-LFA) to detect *E. fawcettii* on *Citrus*. More recently, a rapid and sensitive loop-mediated isothermal amplification (LAMP) assay for *E. necatrix* was developed by van Heerden et al. (2024) to facilitate the management of disease outbreaks and implementation of quarantine measures for the *Eucalyptus* plantation forestry.

## 7 | DISEASE MANAGEMENT

Chemical control is commonly used to reduce the impact of *Elsinoe* infections. Contact fungicides used for this purpose include captafol (Ziehrl et al., 2000), captan (Barros et al., 2015), copper-based (oxychloride, hydroxide, oxide; Daughtrey & Chase, 2016; du Plessis, 1940; Rao, 1983), chlorothalonil (Barros et al., 2015; Daughtrey & Chase, 2016; Lopes et al., 1997; Ramsey et al., 1988), mancozeb (Barros et al., 2015; Daughtrey & Chase, 2016; Ziehrl et al., 2000) and prochloraz (Ziehrl et al., 2000). In the case of systemic fungicides, azoles (imidazole, benzimidazole, tebuconazole, propiconazole, difenoconazole; Barreto, 1997; Daughtrey & Chase, 2016), barbendazim (Reddy et al., 1983), benomyl (Daughtrey & Chase, 2016; Floyd, 1988; Ramsey et al., 1988), boscalid (Daughtrey & Chase, 2016), strobilurins (azoxystrobin, pyraclostrobin; Daughtrey & Chase, 2016) and thiophanate-methyl (Barros et al., 2015) have been effective for the control of scab diseases. Their efficacy relies on spraying young active growth or fruits when conditions are favourable for infection. However, persistent use of chemicals sharing the same mode of action can induce a selective pressure on these pathogens, leading to chemical resistance (Brent & Hollomon, 2007). For example, strains resistant to benomyl have been reported in *E. fawcettii* (Whiteside, 1980) and *E. batatas*

(Lenné, 1991), and methyl benzimidazole carbamate (MBC) resistance has been observed in *E. veneta* (Munro et al., 1988).

Efficient and accurate fungicide applications can be streamlined by establishing data-driven forecasting approaches. These can also improve disease management while moderating negative environmental effects, reducing costs and reducing the risk of fungicide resistance. In this regard, models to estimate the amount of primary inoculum in the field (Carisse & Lefebvre, 2011), to predict environmental conditions triggering the development of epidemics (Carisse et al., 2020) or to forecast infection occurrence throughout the whole growing season (Ji et al., 2021), have been applied to develop scab disease management schemes for *E. ampelina*.

A small number of infected plants amongst newly established planting stock can be sufficient to result in the rapid spread of *Elsinoe* spp., and once established, the disease becomes difficult to manage (Jones, 1924; Kearney et al., 2002). Therefore, cultural practices can be useful to reduce the impact of diseases caused by *Elsinoe* spp. These include sanitary methods such as removal of primary sources of inoculum including infected plants, or plant residues from previous season's infections, before planting (Jones, 1924; Timmer et al., 2004). Because scab symptoms are visible on young growth, it is possible to select disease-free plants before establishment (Li et al., 2021; Swart & Crous, 2001). Biennial cropping can also reduce the inoculum levels (Waister et al., 1977; Wright & Waister, 1982). Planting locations that favour the retention of moisture on plants, or overuse of overhead irrigation should be avoided. Sanitation pruning of infected materials, as well as weeding, should be conducted frequently because this facilitates optimal airflow around and between plants (Chung, 2011; Jones, 1924; Summerell, 2018; Swart & Crous, 2001).

Many crops such as cassava, sweet potato and legumes sustain the livelihoods of mainly low-income farmers in developing economy countries. In these situations, deployment of disease tolerant or resistant varieties is considered one of the main solutions to control scab diseases. This is also true for commercial forestry plantations, which are usually established over large areas and where chemical applications, or removal of diseased trees, is not feasible.

Selection for resistance to *Elsinoe* infections has been successfully used to reduce the impact of the disease on many crops. For instance, tolerant grape genotypes have been identified in greenhouse trials (Hopkins & Harris, 2000; Poolsawat et al., 2012) and using field screening (Goyal et al., 1971; Prasad & Nirvan, 1965; Suhag et al., 1982). Phillips (1995) evaluated some cultivars of common bean in the greenhouse and field for resistance to *E. phaseoli*. There were considerable differences in the susceptibility of the tested bean cultivars, ranging from very susceptible to apparently immune (Phillips, 1995). In a period of over 10 years, 6400 genotypes of cassava were screened in Colombia and resistance to SED was found in 4% (Álvarez et al., 2012). In regions with widespread and severe scab disease, sweet potato breeding lines and genetic materials are routinely examined in the field and under glasshouse conditions (Mariscal & Carpena, 1988; Ramsey et al., 1988; Smit et al., 1991). In the United States, an evaluation of over 100 cultivars of poinsettia showed that all cultivars tested were susceptible to *E. poinsettiae* (Daughtrey & Chase, 2016). In the case of plantation-grown trees, field observations have shown that *Eucalyptus* genotypes differ in their susceptibility to infection by *E. necatrix* and *E. masingae*, with some genotypes showing evidence of tolerance (Pham et al., 2021; Roux et al., 2024).

## 8 | DRIVERS OF SCAB DISEASE EMERGENCE

Major drivers of infectious plant disease emergence have been intensively reviewed previously (Anderson et al., 2004; Corredor-Moreno & Saunders, 2020; Ghelardini et al., 2016; Ramsfield et al., 2016; Richardson et al., 2016; Stukenbrock & McDonald, 2008; Wingfield et al., 2015). These determinants can include anthropogenic introduction of alien plant pathogens, changes in climatic conditions as a result of climate change, changes in genetics of the pathogens by means of recombination, hybridization or mutation, host shifts or expansion of host range, or influence of cropping systems and practices. For diseases caused by *Elsinoe* species, there is good evidence for the involvement of some of the above-mentioned drivers. These are discussed in the following sections.

### 8.1 | Movement of host plants and their pathogens

The movement of plant material around the world, resulting in the accidental introduction of pests and pathogens, is one of the main factors leading to the emergence of new plant disease outbreaks (Anderson et al., 2004; Brasier, 2008; Liebhold et al., 2012; Santini et al., 2018). Such movement is facilitated by anthropogenic activities, also referred to as pathogen pollution, resulting in pathogen introductions into new regions outside their natural geographical boundaries or their natural host range (Anderson et al., 2004; Cunningham et al., 2003). These accidental introductions pose a significant threat to endemic plant species that are especially vulnerable because the host plants have not co-evolved with the pathogens (Cunningham et al., 2003).

*E. fawcetii*, the causal agent of citrus scab, has a worldwide distribution and provides a good example of global spread linked to anthropogenic activity. Hyun et al. (2009) examined the genetic relationships of a worldwide collection of *E. fawcettii* isolates and found that some regions harboured many pathotypes. They also showed that outcrossing might occur at a relatively high frequency in some groups of pathotypes. This result was surprising because the sexual state of *E. fawcettii* has only been found in Brazil (Bitancourt & Jenkins, 1936a; EFSA et al., 2022). Hyun et al. (2009) suggested that *E. fawcettii* could have originated in Asia where *Citrus* originated, and that *E. fawcettii* was introduced multiple times in areas including the United States (Florida) and New Zealand (Hyun et al., 2009). Given that *E. fawcettii* is spread mostly by rain splash and that conidia are dispersed very locally (Chung, 2011), it is believed that introduced scab pathotypes have been distributed globally via infected plant germplasm, that is, rootstocks, grafted plants, scions and fruit (EFSA et al., 2022; Hyun et al., 2009). Efforts should thus focus on reducing the possibility of new pathogen genotypes emerging due to the accidental introduction of new pathotypes having outcrossing potential into new areas.

Introduction of emerging pathogens can also occur naturally, largely via aerial dispersal mechanisms (Aylor, 1990; Mukherjee et al., 2021). Favourable environments at the time of arrival and access to susceptible hosts is essential for successful establishment (Corredor-Moreno & Saunders, 2020). Although windborne ascospores can be involved in the life cycle of some *Elsinoe* species (Gabel & Tiffany, 1987; Jones, 1924; Minutolo et al., 2016), very little is known regarding the possible distances that these spores can be dispersed. Jones (1924) showed that ascospores of *E. veneta* carried by wind from diseased plants could infect plants up to 0.8 km away. But it is also relevant to consider that severe weather conditions such as hurricanes could substantially increase long-distance dissemination of these propagules (Stokstad, 2004).

### 8.2 | Influence of cropping systems and management practices

Modern cropping systems and management practices are typified by high-density monocultures of fast-growing and high-yielding crops. In these situations, fields or plantations are typically planted to a single genotype, or a population of half-sib individuals that have very little genetic diversity (van de Wouw et al., 2010). These genetically uniform landscapes reduce spatial constraints on dispersal and provide easy access to susceptible host material, and thus increase the potential for epidemics to emerge (Corredor-Moreno & Saunders, 2020; Drenth et al., 2019). For example, in North Sumatra, Indonesia, relatively low host genetic diversity and low resistance levels in clonal *Eucalyptus* plantations has resulted in a rapid build-up of the *E. necatrix* population, facilitating considerable gene flow across *E. necatrix* strains (Pham et al., 2024). In addition, unhindered sexual outcrossing could generate considerable genetic variation, and a capacity to rapidly overcome narrow host genetic resistance in a genetically uniform setting (Pham et al., 2024).

### 8.3 | Shifts in an existing host range of pathogens

A pathogen can emerge as a result of adaptation to a new host following a host-range expansion, host shift or host jump (Giraud et al., 2010; Morris & Moury, 2019; Slippers et al., 2005; Stukenbrock & McDonald, 2008). Host shifts, involving a novel host that is closely related to the original host, could occur from wild species to a crop plant, especially when the two are growing in adjacent areas (Stukenbrock & McDonald, 2008). A probable example of host shifts in *Elsinoe* is in the case of sweet potato scab caused by *E. batatas*. The pathogen is most likely native to South-east Asia and the Pacific where it infects wild species of Convolvulaceae. *Elsinoe* species infecting *Ipomoea* species, including water spinach (*Ipomoea aquatica*), often grown near sweet potato fields in much of the range of this disease, could have undergone a host shift to infect sweet potato (Clark et al., 2009). Another example could be the species complex including *E. poinsettiae* affecting poinsettia, *E. krugii* affecting wild poinsettia and *E. brasiliensis* affecting cassava. The disease on domesticated plants could have originated from various native Euphorbiaceae in Central and South America (de Lima Nechet et al., 2004; Fan et al., 2017; Zeigler & Lozano, 1983). These host shift hypotheses need to be addressed using molecular tools.

The current view that most *Elsinoe* species are host specific should be considered carefully. This is because most sampling of these pathogens has been restricted to populations affecting cultivated crops, leading to an underestimation of the gene pool being sampled. Advances in DNA sequencing technology and the ability to accurately identify organisms to the species level have revealed a much broader host range than has been assumed for some *Elsinoe* species. For example, species such as *E. ampelina*, *E. anacardia*, *E. annonae*, *E. australis* and *E. violae* have been shown to cause infection on alternative hosts residing in different and even distantly related plant families (Bao et al., 2023; Chung, 2011; Fan et al., 2017; Li et al., 2021; Liu et al., 2022; Miles et al., 2015; Zhao et al., 2020). More focused sampling strategies will need to be used to estimate pathogen prevalence in the wild and thus to assess the risks of spillover effects (Plowright et al., 2019).

### 8.4 | Climate change

Sudden and substantial changes in climatic conditions associated with climate change can, and in some cases are already resulting in new or more serious plant disease problems (Anderson et al., 2004; Cacciola & Gullino, 2019; Corredor-Moreno & Saunders, 2020; Laine, 2023; Nnadi & Carter, 2021). These can be a consequence of enhanced plant pathogen fitness where altered climatic conditions can contribute to the re-emergence of pre-existing pathogens (Anderson et al., 2004; Harvell et al., 2002; Nnadi & Carter, 2021). In the case of the recently described *E. masingae* on *Eucalyptus* in South Africa, the emergence of the disease is probably associated with abnormal climate conditions. These include, amongst others, higher-than-average rainfall, lower levels of evaporation and extended periods of leaf wetness, all of which could be the result of climate change (Roux et al., 2024). Likewise, an increase in frequency of rainfall, higher humidity and temperature during flowering and fruiting of hazelnut in southern Italy, has also catalysed the re-emergence of *E. coryli*, 30 years after it was first reported in that area (Minutolo et al., 2016).

## 9 | FUTURE PROSPECTS

Scab diseases caused by *Elsinoe* species are amongst the most serious threats to the world's crops, and they appear to be rising in importance. There is little doubt that these fungi will continue to be of significant social, biological and economic importance in the coming years and beyond. As a result of globalization and climate change, scab diseases appear to be on the rise. These fungi have an immense capacity to move and adapt to new ecosystems, as well as to rapidly evolve and overcome existing host resistance, or to colonize naive crops. Despite representing one of the most important groups of plant pathogens, the biology of *Elsinoe* pathogens is surprisingly poorly understood.

The majority of investigations on *Elsinoe* have focused on species identification and geographical distribution. Phylogenies based on DNA sequence inference have substantially improved our understanding of the taxonomy of these fungi. However, knowledge regarding the population biology of *Elsinoe* spp. remains notably scarce, and in many cases is nonexistent. This represents a significant gap in research on *Elsinoe* species and the diseases they cause. A comprehensive understanding of the population dynamics of *Elsinoe* spp. would not only provide an ability to trace the origins and pathways of invasion of these fungi, but also play a pivotal role in developing phytosanitary and quarantine regulations for them. Additionally, a better comprehension of *Elsinoe* population biology holds significance for plant breeding and selection programmes. Incorporating knowledge from population genomics into disease modelling should also improve our ability to predict the evolutionary and adaptation potential of the causal agents. This would augment efforts to develop suitable management strategies against diseases associated with these important pathogens.

Recent advances in next-generation sequencing technology have made it possible to sequence many high-quality reference genomes. From the beginning of the 2020s alone, 27 genomes representing nine *Elsinoe* species have been sequenced (Table 1), and it is reasonable to anticipate that more will become publicly available in the relatively near future. These will allow for the development of tools for population genetic studies and thus to better understand the complex

**TABLE 1** Details of all *Elsinoe* species for which genomes have been sequenced.

| Species | Strain | Accession number[a] | Genome size (Mb) | Reference |
|---|---|---|---|---|
| *Elsinoe ampelina* | YL-1 | SMYM00000000 | 28.30 | Li et al. (2020) |
| | CECT 20119 | JAAEIW000000000 | 28.27 | Haridas et al. (2020) |
| *E. annonae* | SM-YC-2 | GWHBKHL00000000[b] | 25.93 | Bao et al. (2023) |
| *E. arachidis* | LNFT-H01 | JAAPAX000000000 | 33.18 | Jiao et al. (2021) |
| | LY-HS-1 | GWHBFXO00000000[b] | 32.44 | Su et al. (2022) |
| *E. australis* | Ea-1 | SWCS00000000 | 23.79 | Shanmugam et al. (2020) |
| | NL1 | NHZQ00000000 | 23.34 | Zhao et al. (2020) |
| | BRIP 52616a | WLZB00000000 | 23.87 | Jeffress (2021) |
| | Wagga_1 | QGII00000000 | 26.28 | Jeffress (2021) |
| | Wagga_2 | PTQP00000000 | 26.60 | Jeffress (2021) |
| | Wagga_3 | QGIH00000000 | 26.29 | Jeffress (2021) |
| | Hillstone_1 | QGIJ00000000 | 24.98 | Jeffress (2021) |
| | Hillstone_2 | PTQR00000000 | 26.63 | Jeffress (2021) |
| | Hillstone_3 | QGIG00000000 | 27.12 | Jeffress (2021) |
| | Forbes_1 | PTQO00000000 | 26.62 | Jeffress (2021) |
| | Forbes_2 | PTQQ00000000 | 26.62 | Jeffress (2021) |
| *E. batatas* | CRI-CJ2 | JAESVG000000000 | 26.49 | Zhang et al. (2022) |
| *E. fawcettii* | SM16-1 | VAAB00000000 | 26.65 | Shanmugam et al. (2020) |
| | DAR-70024 | SWCR00000000 | 26.32 | Shanmugam et al. (2020) |
| | BRIP 53147a | SDJM00000000 | 26.01 | Jeffress et al. (2020) |
| | BRIP 54245a | WLYY00000000 | 26.48 | Jeffress (2021) |
| | BRIP 54425a | WLYZ00000000 | 25.86 | Jeffress (2021) |
| | BRIP 54434a | WLZA00000000 | 25.87 | Jeffress (2021) |
| *E. murrayae* | CQ-2017a | NKHZ00000000 | 20.72 | Cheng and Zhao (2022) |
| *E. necatrix* | CMW 56134 | JANZYH000000000 | 24.07 | Wingfield et al. (2022) |
| | CMW 56129 | JANZYI000000000 | 25.64 | Pham et al. (2023) |
| *E. perseae* | TREC-ASLL3 | JARDAA010000000 | 23.49 | Gañán-Betancur and Gazis (2023) |

[a] GenBank database accession number, National Centre for Biotechnology Information (NCBI; https://www.ncbi.nlm.nih.gov).

[b] Genome warehouse (GWH), National Genomics Data Center (NGDC), part of the China National Center for Bioinformation (CNCB; https://ngdc.cncb.ac.cn).

biology of these pathogens as well as the drivers of their emergence. The availability of these genomes will also provide opportunities to investigate the genomic basis of host specificity; to characterize BGCs involved in the production of important specialized metabolites; to develop efficient early detection tools; and to have a substantially enhanced understanding of the mechanisms underlying the pathogenicity of these economically important pathogens.

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## CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were generated.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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