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Sporothrix and Sporotrichosis: A South African Perspective on a Growing Global Health Threat

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ABSTRACT

Sporotrichosis is a disease that arises from a fungal infection caused by members of the *Ascomycete* genus *Sporothrix*. The disease has a unique history in South Africa, due to an association with gold mines, where large numbers of mine workers were infected in the 1930s and 1940s. This was likely driven by hot humid conditions and timber supports used in these mine shafts. Furthermore, the disease is the most common subcutaneous fungal infection amongst the general population in South Africa, and the large number of immunocompromised individuals increases the public health risk in the country. *Sporothrix* is a genus in the *Ophiostomatales*, a fungal order primarily associated with environmental habitats. Unsurprisingly, sporotrichosis therefore has a documented history of sapronotic transmission from contaminated plant material. This review provides insights into the understanding of sporotrichosis and *Sporothrix* species, with a particular emphasis on the South African situation. We highlight knowledge gaps, particularly regarding the ecological factors influencing the occurrence and distribution of these species, which in turn affect the patterns of sporotrichosis. We also emphasise a need for ongoing proactive research and surveillance to prevent future outbreaks of sporotrichosis, an emerging disease with growing health implications worldwide.

1 | Introduction

Fungal diseases are commonly encountered occupational hazards in several industries [1]. This is certainly the case for sporotrichosis, caused by members of the fungal genus *Sporothrix*. Historically, the disease has regularly been reported in horticulture, agriculture and other related fields worldwide. In South Africa, a unique disease epidemiology has persisted, with recurrent reports of gold miners contracting the mycosis [2–4]. It is thought that the climatic conditions and mining timber facilitate the success of *Sporothrix* species in mineshafts [5]. Despite this, difficulties in isolating the pathogen from environmental sources make understanding its ecology and hence identifying sources of infection challenging.

Sporotrichosis is an emerging disease anticipated to grow in significance in the future. This escalation is fuelled by increasingly favourable weather conditions, heightened virulence and the emergence of drug-resistant strains [6–8]. This rising significance extends beyond sporotrichosis and is acknowledged for numerous other fungal infections, underscoring the urgency of swiftly adopting a One Health approach to their management. This review focuses on understanding the ecological determinants of *Sporothrix* species, particularly in the context of South Africa's unique disease epidemiology. Broadly, our aim is to provide insights into the environmental ecology of disease-causing *Sporothrix* species.

2 | Sporotrichosis

Sporotrichosis is a granulomatous mycosis of humans and other mammals, caused by the traumatic inoculation of *Sporothrix* mitospores (conidia) [9]. The disease usually affects the subcutaneous layers of the skin, where granulomas form at the site of infection to prevent the spread of yeast cells [10, 11]. Lymphocutaneous infections are the most common disseminated form, where the cutaneous infection is spread through the lymphatic system. Cutaneous infections are generally considered benign forms of the disease and are most often treated successfully [12]. However, in rare cases of extracutaneous infection, immunocompromised individuals are at risk of systemic sporotrichosis. These extracutaneous forms can be significantly more severe and are capable of affecting every organ in the body, with the worst cases being fatal [13–15].

Sporotrichosis is an emerging disease, with more serious outbreaks anticipated in the future. One of the major concerns lies in the development of antifungal resistance in *Sporothrix* species residing in the pathogenic clade of the genus (Figure 1). Resistance to itraconazole, the first-choice treatment for sporotrichosis, is more frequently being reported, and these reports include strains from all three of the major etiological agents (*S. schenckii*, *S. brasiliensis* and *S. globosa*) [6–8, 16]. Furthermore, *S. schenckii* strains with reduced susceptibility to Amphotericin B and posaconazole, and *S. brasiliensis* to terbinafine and voriconazole [17–19], highlight growing records of resistance to multiple antifungals amongst *Sporothrix*. Genetic diversity, melanin production and cytochrome P450 mutations are thought to contribute to this increasing fungicide resistance [16], and consequently, this continues to complicate sporotrichosis treatment regimens.

Sporotrichosis is an endemic disease that occurs predominantly in tropical and subtropical regions of the world [20, 21]. Due to the effects of climate change, the epidemiology of infectious diseases such as sporothricosis is also expected to change. In this regard, projections of higher average global temperatures and precipitation levels [22] are likely to provide optimal conditions for fungal proliferation in the future. For *Sporothrix* species, this could imply a broader ecological range, with some regions becoming more tropical and allowing these fungi to establish and spread.

3 | The Genus *Sporothrix*

The order *Ophiostomatales* (*Ascomycota*) includes fungi known to cause plant and human disease, and many species are associated with bark and ambrosia beetles [23–25]. While several species are notable tree pathogens [26], and most cause sap stain of timber [27], a few result in animal disease [9]. Several new genera have been described in the *Ophiostomatales* in recent years [25, 28–31], supported by multigene phylogenetic data [31]. De Beer et al. [31] showed that in most cases, species with similar morphology, ecology and/or geographic origin grouped together phylogenetically within their respective genera. Within *Sporothrix*, this also held true, with the clinically relevant species forming a distinct lineage, separate from those that occur on plants, mainly as saprotrophs (Figure 1).

Based on this contemporary taxonomy, species accommodated in *Sporothrix* cause sporotrichosis. Like other members of the *Ophiostomatales*, pathogenic *Sporothrix* species are dimorphic in nature. Thermal conditions dictate their state, with 25°C–27°C promoting mycelial growth in the environment and at 37°C+ the yeast form dominates [32]. This thermal dimorphism is considered one of the necessary criteria for these fungi to cause disease in mammals [33].

The genus *Sporothrix* was first described based on the type species, *S. schenckii*, and morphological characteristics were primarily utilised to identify the species. In their filamentous state, *S. schenckii* colonies are initially white to orange-grey in colour, with older cultures becoming moist and wrinkled, and occasionally turning a darker brown-black colour. Conidiophores of *S. schenckii* are mostly unbranched, with hyaline and sympodial conidiogenous cells producing small hyaline ovoid conidia found in rosette-like clusters. Conidia are also found on conspicuous denticles (intercalary), each producing a slightly larger dematiaceous conidium [9, 34, 35]. In the yeast phase, *S. schenckii* colonies are typically smooth, cream to tan in colour, with yeast cells of various sizes and shapes. Round and oval yeast cells between 2 and 6 μm in diameter are accompanied by characteristic oval, tapered yeast cells, often referred to as cigar bodies [34].

These characteristic features, alongside the successful conversion from mycelial to a yeast form, have traditionally been used to diagnose sporotrichosis in patients. Also, these characteristics are mainly shared across the genus; however, nuanced differences between species have been noted. These include for example, more pigmented condia in *S. brasiliensis*, and more spherical conidia in *S. globosa*. Despite this, similarities in morphology often make it difficult to distinguish species in the *Sporothrix* pathogenic clade from the environmental species.

The inability to distinguish *Sporothrix* members morphologically makes the use of molecular techniques necessary for species identification. These molecular methods have shown that environmentally collected isolates previously morphologically identified as *S. schenckii*, to belong to species from the environmental clades [31, 36, 37]. This may contribute to the current knowledge gaps regarding the ecology of *Sporothrix* species in the pathogenic clade, with historical inferences on the ecology of *S. schenckii senso lato*, referring to other species in the genus. It is therefore necessary to carefully navigate the literature where *S. schenckii* has been recorded from environmental sources, at a time when modern molecular tools used to confirm species level identification were not available. To this end, Zhang et al. used genic data and historical records in an attempt to clarify previous inferences regarding environmental sources of infection [38]. They highlighted the clear lack of environmentally collected strains from the pathogenic clade, a situation that is also evident in more recent research on species in this clade [39, 40].

Molecular identification methods have resulted in a substantially revised taxonomy and the description of many cryptic species of *Sporothrix*. The genus currently includes at least 68 species (Table 1 [31, 41–49]) with a global geographic distribution [31, 41]. Based on multigene sequence data, De Beer et al. proposed six species complexes including the pathogenic clade as well as the *S. pallida, S. candida, S. inflata, S. gossypina* and *S. stenoceras* complexes [42]. The four species making up the pathogenic clade (*S. schenckii sensu stricto, S. globosa, S. brasiliensis* and *S. luriei*) have all been isolated from diseased patients and show differences in virulence, prevalence and geographic distribution (Figure 2 [21, 50–93]) [20, 94, 95].

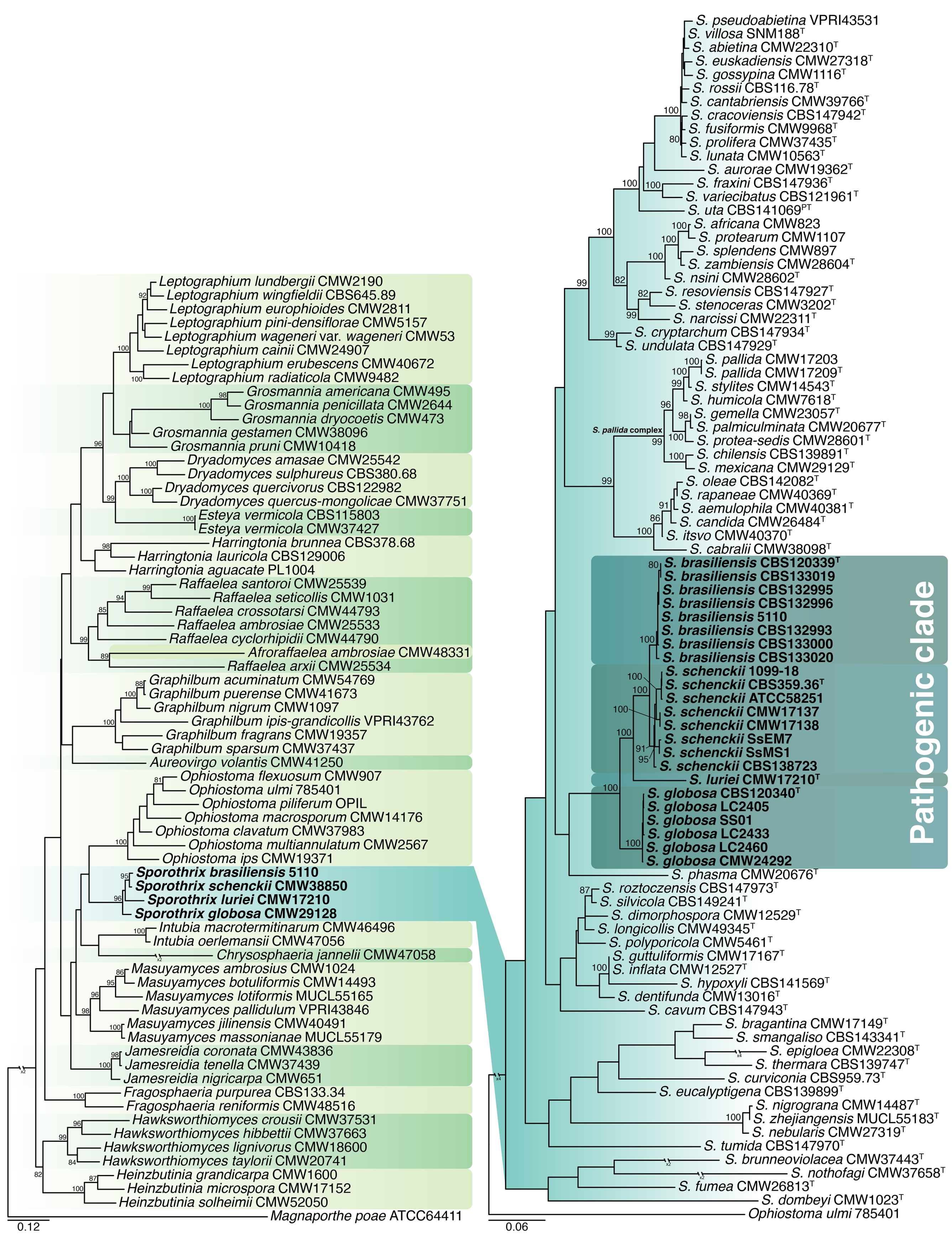

FIGURE 1 | Legend on next page.

FIGURE 1 | Multigene phylogenies showing the placement of *Sporothrix* in *Ophiostomatales* (left) and the placement of the pathogenic clade in *Sporothrix* (right). The *Ophiostomales* tree was based on a concatenated alignment of the internal transcribed spacer (ITS1-5.8S-ITS2) rDNA region (ITS), large subunit (LSU), partial beta-tubulin (*tub2*), partial translation elongation factor 1-alpha (*tef1*) and partial RNA polymerase II second largest subunit (*RPB2*) gene regions (see Table S1). The *Sporothrix* tree was based on a concatenated alignment of the ITS, *tub2*, *tef1*, *RPB2* and partial calmodulin (cmdA) gene regions (see Table S2). Datasets were aligned using MAFFT v. 7.520 [201], and a Maximum Likelihood tree was calculated in IQtree v. 2.2.2.6 [202]. Each region was treated as separate partitions, and the most appropriate nucleotide substitution model was selected for and applied in IQtree. Branch support in nodes was calculated using bootstrapping with 1000 repeats, with >80% support indicated on branches (^{T} = ex-type, ^{PT} = ex-paratype).

Sporothrix brasiliensis has received significant attention in recent years, due to the ongoing human and feline sporotrichosis outbreaks in South America [13, 65, 83, 96–99]. The epidemic in South America has seen unprecedented levels of zoonotic transmission of the pathogen from cats to humans (zoonotically) and sporotrichosis [83, 100]. The success of *S. brasiliensis* spreading zoonotically is thought to be attributed to the elevated levels of virulence in the fungus [94, 101–103]. However, it is also believed that cats are particularly effective at spreading the pathogen, with their saliva providing a stable environment for fungal propagules and hence accumulation of a larger source of fungal inoculum. Feline cleaning habits move the fungus from their saliva to their claws, allowing for effective transmission through scratch and bite wounds [104].

The type species, *S. schenckii*, is the major etiological agent in most countries where sporotrichosis is endemic, encompassing regions from all inhabited continents. *Sporothrix schenckii* is best known for sapronotic transmission, by means of contaminated plant material and soil [38]. In addition to sapronotic transmission, it is of considerable concern that there are growing numbers of records of feline–human transmission of this species [83, 91, 105–108]. This zoonotic aspect of transmission adds complexity to managing *S. schenckii*, as even asymptomatic cats can be carriers, further facilitating the spread of the pathogen [109].

Sporothrix globosa, another species in the pathogenic clade of *Sporothrix* [110], shares sapronotic transmission routes with *S. schenckii*. The species remains most prevalent in Asia where it recurrently drives sporotrichosis sapronoses [75, 111, 112]. While the most endemic areas for the species may differ from that of *S. schenckii*, *S. globosa* also has a near global distribution (Figure 2). This suggests that both of these species are adapted to survive in a wide range of environmental conditions, facilitating their wide distribution, and making them a persistent public health issue in both rural and urban settings.

Sporothrix luriei, also a member of the pathogenic clade, is very rare but appears to have a wide global distribution. To the best of our knowledge, there are only three reports of *S. luriei*, each of these from South Africa, Italy and India [113–115]. The rarity of this species may be due to specific ecological niche or host interactions. However, the historical lack of molecular tools used to identify sporotrichosis agents may also have resulted in an inaccurate perception regarding its true prevalence.

Outside the *Sporothrix* pathogenic clade, several species found in the *Sporothrix pallida* complex have also been reported to cause opportunistic infections in mammals [74, 116, 117]. These species are less virulent than members of the *Sporothrix* pathogenic clade and are most commonly isolated from soil and plant material [118, 119]. The remaining species of *Sporothrix* are known only as saprotrophs and have never been associated with disease of mammals (Table 1) [31].

4 | *Sporothrix* in the Genomic Era

Next-generation sequencing technologies have made full genome sequencing more common than ever before. The availability of the resulting genomes allows for species to be compared and has proven to be an invaluable tool in the study of fungal pathogens [120–122]. In the case of *Sporothrix*, several genomes have been sequenced and used in phylogenomic analyses [31] and species comparisons [123–126]. This will continue to rapidly expand our understanding of the genetic factors associated with pathogenicity in mammal hosts and also provide insights into the ecological niches associated with these fungi.

A comparison of the genome data of species in the *Sporothrix* pathogenic clade with those in the environmental clades has revealed a significant reduction in the genome size of the mammal pathogens [123]. Huang et al. suggested that this genome size reduction is in part due to the absence of CAZyme and peptidase encoding genes in pathogenic species, which are present in the environmental counterparts [123]. Additionally, a lack of polysaccharide lyase (PL) genes also associated with the decay of plant material was reported [125]. However, these comparisons did not exclusively compare *Sporothrix* species. When only comparing species in the pathogenic clade with environmental *Sporothrix* species known to degrade plant material, no significant differences in the abundance of CAZymes were observed, although some CAZyme families were not present in the pathogenic *Sporothrix* species [127]. Furthermore, Du et al. found a novel PL family in several *Sporothrix* species in their comparisons. The authors therefore suggested a need for further gene screening to enhance understanding of the genomic evolution of these fungi [127].

Genomic analysis of four clinically relevant *Sporothrix* species (*S. brasiliensis, S. globosa*, *S. schenckii* and *S. pallida*) revealed that of the predicted protein encoding genes, 5% were predicted as CAZymes [124]. This compared to 3% found in other dimorphic fungal pathogens. These genomes were also compared with those of several other *Ascomycete* genera and revealed an expansion of CAZymes belonging to the glycoside hydrolase (GH), carbohydrate esterase (CE) and auxiliary activity (AAs) classes in *Sporothrix* [124]. The authors hypothesised that these carbohydrate-active enzymes may allow the

TABLE 1 | The species complexes within *Sporothrix* following De Beer et al. The species comprising each clade, their known hosts, report of pathogenicity in mammals, whether or not they have been isolated from soil, their vectors and whether or not a sexual state has been observed, is shown [31, 41–49].

Complex	Species	Host/ substrate	Pathogenicity in mammals	Soil inhabiting	Vectors	Sexual state known
Pathogenic clade	*S. brasiliensis*	M	Yes	—	—	No
	S. globosa	M	Yes	Yes	—	No
	S. luriei	M	Yes	—	—	No
	S. schenckii	M	Yes	Yes	—	No
S. inflata complex	*S. dentifunda*	H	No	—	—	Yes
	S. dimorphospora	H, P	No	Yes	—	No
	S. guttiliformis	H	No	Yes	—	No
	S. inflata	H, P	No	Yes	—	No
	S. silvicola	C	No	Yes	—	No
	S. roztoczensis	C	No	Yes	—	No
S. gossypina & *S. stenoceras* complex	*S. abietina*	C	No	Yes	AB	Yes
	S. africana	H	No	—	—	Yes
	S. aurorae	C	No	Yes	BB	Yes
	S. cantabriensis	C	No	Yes	BB	No
	S. cracoviensis	H	No	—	W	Yes
	S. eucastanea	H	No	—	—	Yes
	S. euskadiensis	C	No	Yes	BB	Yes
	S. fusiformis	H	No	—	—	Yes
	S. fraxini	H	No	—	BB	Yes
	S. gossypina	C	No	—	BB	Yes
	S. lunata	H	No	—	—	Yes
	S. narcissi	H	No	Yes	—	Yes
	S. nsini	P	No	—	—	No
	S. prolifera	H	No	—	—	Yes
	S. protearum	H	No	—	—	Yes
	S. resoviensis	H	No	—	—	Yes
	S. rossii	C	No	—	BB	Yes
	S. splendens	H	No	—	M	Yes
	S. stenoceras	H	No	Yes	—	Yes
	S. uta	H	No	—	—	Yes
	S. variecibata	P	No	—	M	No
	S. villosa	C	No	—	BB	No
	S. zambiensis	H	No	—	M	Yes
S. candida complex	*S. aemulophila*	H	No	—	AB	Yes
	S. cabralii	H	No	—	AB	No
	S. candida	H	No	—	—	Yes

(Continues)

TABLE 1 | (Continued)

Complex	Species	Host/ substrate	Pathogenicity in mammals	Soil inhabiting	Vectors	Sexual state known
	S. itsvo	H	No	—	—	Yes
	S. oleae	H	No	—	—	Yes
	S. rapaneae	H	No	—	—	Yes
S. pallida complex	*S. chilensis*	M, H	Yes	Yes	—	No
	S. gemella	P	No	—	M	Yes
	S. humicola	—	Yes	Yes	—	No
	S. mexicana	M, H	Yes	Yes	—	No
	S. pallida	M, H	Yes	Yes	—	No
	S. palmiculminata	P	No	—	M	Yes
	S. protea-sedis	P	No	—	M	Yes
	S. stylites	C, H	No	Yes	—	No
Group D	*S. cavum*	H	No	—	WP	No
	S. polyporicola	H	No	—	—	Yes
Group E	*S. phasma*	P	No	—	M	Yes
Group F	*S. bragantina*	H, P	No	Yes	—	Yes
	S. curviconia	H	No	—	—	No
	S. epigloea	F	No	—	—	Yes
	S. eucalyptigena	H	No	—	—	Yes
	S. nebularis	H	No	Yes	BB	Yes
	S. nigrograna	C	No	—	BB	Yes
	S. smagaliso	P	No	—	—	Yes
	S. thermara	H	No	—	AB	No
	S. zhenjangensis	C	No	—	—	Yes
Group G	*S. dombeyi*	H	No	—	—	Yes
Lineage XVI	*S. fumea*	H	No	—	C	Yes
Lineage XIX	*S. brunneoviolacea*	H	No	Yes	—	No
Sporothrix incertae sedis	*S. cryptarchum*	H	No	—	—	Yes
	S. hypoxyli	H	No	—	—	No
	S. undulata	H	No	—	SB	Yes
	S. tumida	C	No	Yes	—	No
	S. macroconidia	C	No	—	BB	No
	S. pseudoabietina	H	No	—	BB	Yes

Note: **Host/substrate:** C, Conifer; H, Hardwood; M, Mammal; P, *Protea*. **Vectors:** AB, Ambrosia beetles; BB, Bark beetles; C, Cerambycid; M, Mites; SB, Sap beetles; W, Weevils; WP, Woodpeckers.

fungi to survive in their natural environments. The changing CAZyme profiles in the pathogenic clade could be due to specific ecological and host adaptation. However, these studies are relatively few in number and additional genomes, as well as more comprehensive comparisons will be needed to better understand the differences and evolutionary histories of *Sporothrix* species.

Genomic data have allowed molecular tools to be designed for the study of *Sporothrix* genetic diversity and population structure. Population genetic studies utilising microsatellite markers, chromosomal polymorphism, restriction fragment polymorphisms (RFLPs) and amplified fragment length polymorphisms (AFLP's) all support a high genetic diversity in *S. schenckii* [39, 128–132]. The diversity within the species is also reflected

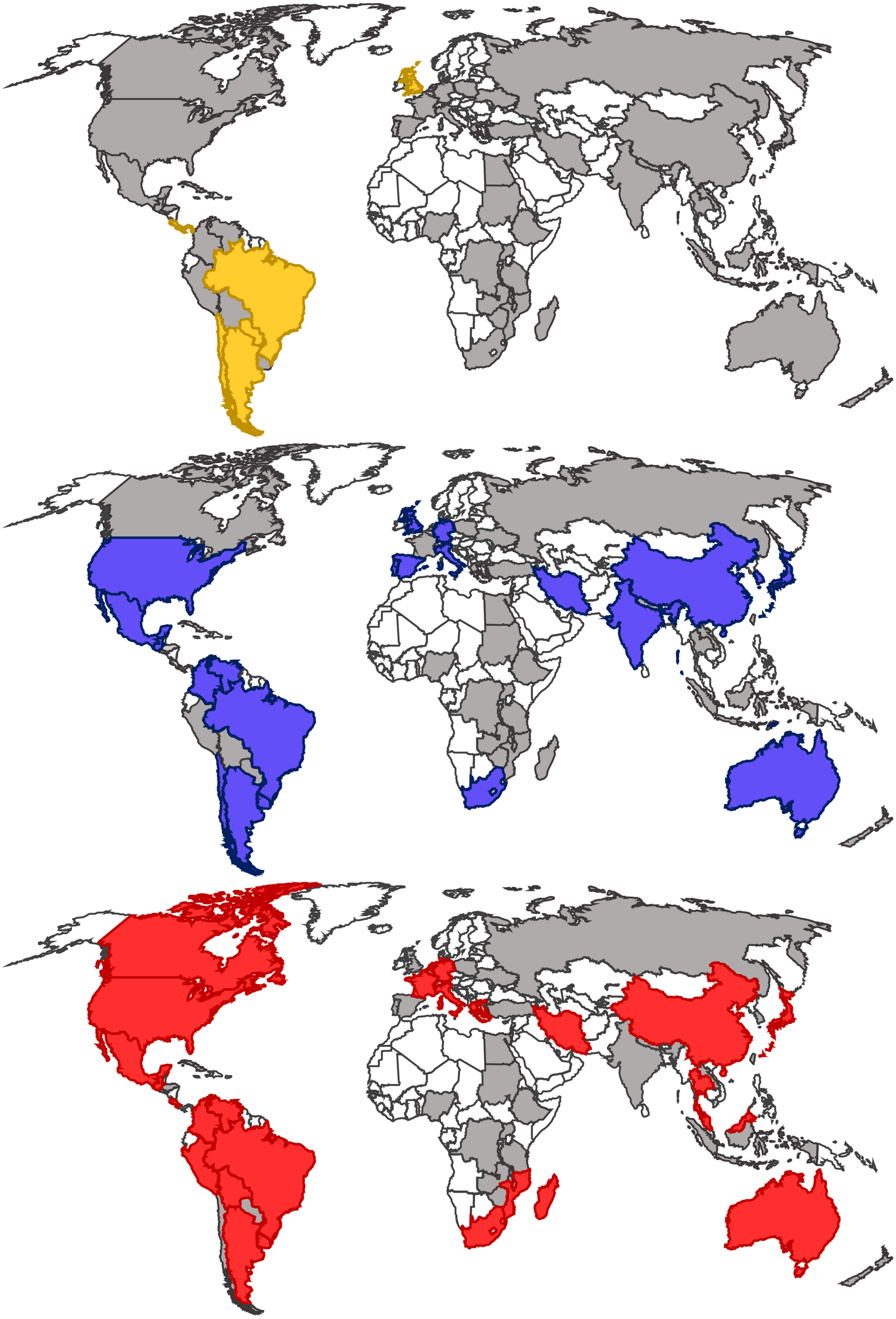

FIGURE 2 | Global distribution maps depicting the geographic spread of the three major agents of sporotrichosis: *Sporothrix brasiliensis* (yellow), *S. globosa* (blue) and *S. schenckii* (red). Only strains identified with molecular tools are included. Countries where sporotrichosis has been reported, but the specific species has not been identified, are represented in grey.

in the differences in morphology, antifungal susceptibility and virulence between strains [35, 101]. Similarly, *S. brasiliensis* appears to be genetically diverse, with clonal complexes being attributed to temporal variability in sample collection [39]. Losada et al. also identified putative hybrids in the pathogenic clade, with *S. schenckii* thought to be able to hybridise with both *S. brasiliensis* and *S. globosa* [39].

Species in the *Sporothrix* pathogenic clade are heterothallic, and *S. schenckii* populations have been reported to have a near 50:50 MAT-idiomorph distribution [39, 60]. This suggests that cryptic sexual reproduction is occurring in *S. schenckii*, and possibly between the species of the pathogenic clade. Sexual reproduction has been observed in several environmental *Sporothrix* species, including both heterothallic and homothallic representatives [60, 133]; however, sexual structures have never been observed in the pathogenic clade species.

5 | Ecology

The species in the *Sporothrix* environmental clades are readily isolated from plant tissues and soil. Their ecology is therefore significantly better understood than the members of the pathogenic clade. These environmental species are for example found associated with the flower heads of *Protea* spp. and their associated mites [134–136]; wood of many different forest tree species [46, 48, 137]; bark, ambrosia and pine shoot beetles [41, 48, 138]; and many species occur in the soil [37, 41, 139, 140]. These associations are summarised in Table 1. The presence of multiple *Sporothrix* species in soils worldwide suggests that these fungi may be widespread in that environment [37, 41, 116, 140–142]. Wood and other decomposing plant materials likely serve as nutrient sources, facilitating their survival [140].

Since the first discovery of sporotrichosis, sapronotic transmission of the pathogens has remained a significant route of infection, and this is apparently more prevalent in tropical and subtropical regions of the world. This is illustrated by a common incidence of the disease reported in individuals associated with floriculture, horticulture, gardening and other related fields [4, 38, 75, 143, 144]. An association of infections by *S. schenckii* with gardening gave rise to the common name 'rose gardeners' disease' being adopted, due to rose thorns providing entry wounds for sapronotic transmission [144]. This association clearly illustrates a public and occupational health risk to those working with plant material and where tissue wounding might occur. However, the specific roles of environmental determinants, vectors or reservoir hosts in facilitating the presence of pathogenic *Sporothrix* species in the environment remain largely unknown.

Sapronotic transmission of pathogenic *Sporothrix* species has been linked to material from several different plant species. Studies have implicated *Sporothrix* contamination of spagnum moss [145, 146], hay [147], reeds [148] and mining timber [149], suggesting these substrates as sources of infection. The extent of fungal colonisation, persistence and the likelihood of outbreaks associated with these plants remain areas deserving further investigation. Additionally, understanding the mechanisms by which *Sporothrix spp.* colonise and survive on diverse plant materials could inform strategies aimed at mitigating environmental exposure.

Despite a documented history of sapronotic sporotrichosis, isolating pathogenic *Sporothrix* species from environmental sources has proven challenging [40]. However, while relatively rarely so, these species have been successfully isolated from environmental samples [58, 140, 142]. The species in the pathogenic clade also have the ability to grow on timber sources [150] and can survive in that environment for extended time periods [151]. The fact that the pathogenic *Sporothrix* species occur in an Order of fungi primarily associated with environmental habitats [31] suggests a likelihood that the environmental component has been retained within their ecology.

Zhang et al. hypothesised that very specific conditions within the plant material, such as those during fermentation, are required to facilitate growth of the pathogenic *Sporothrix* species [38], thereby making it difficult to find these clinically relevant species in the environment. Lopes-Bezerra et al. also suggested that under these conditions of decay and fermentation, excessive growth of these pathogens may be facilitated. Historical association and circumstantial evidence suggests the pathogenic *Sporothrix* species are able to establish and proliferate in the environment. Increased environmental sampling efforts and the application of new approaches are however needed to expand our understanding of the ecological niche of clinically relevant *Sporothrix*.

6 | Global Epidemiology

The animal pathogenic species of *Sporothrix* possess the ability to cause disease in a variety of mammal hosts. They include cats [152], dogs [153, 154], rats [155], guinea pigs [156], armadillos [157, 158], horses and mules [159, 160]. Hosts act as reservoirs increasing the presence of the pathogens in environmental sources [142, 158] and may result in direct transmission to humans [158, 161, 162]. However, until the onset of the current South American epidemic, zoonotic transmission of these fungi has generally not been considered as significant a risk factor as the sapronotic transmission routes. However, the threat of zoonotic transmission is now being more widely recognised [163, 164]. While the effects of feline transmission in South America are clear [43], feline–human transmission remains rare in other regions where these fungi are thought to be endemic. Cases have nonetheless been reported in North America and Asia on multiple occasions [152, 163]. This mode of transmission is growing in importance and needs to be carefully monitored to implement effective public health intervention.

The colloquial name Rose Gardeners' Disease reflects the historical significance of sapronotic transmission of sporotrichosis infections. These sapronoses continue today most prominently in Asia, where *S. globosa* drives recurrent and sporadic sapronotic outbreaks [75, 155, 165]. The species has also been found in the Americas and Europe, where it is less frequent but also associated with transmission from plant material [20, 165]. Similarly, *S. schenckii* is most commonly associated with sapronotic modes of infection with these cases reported in Asia, the Americas, Australia, Europe and Africa [20, 143, 166]. Although sapronotic transmission is common, the absence of transmission between humans prevents outbreaks from spreading further. This is unlike situations where the pathogens are sustained within animal populations and transmitted through zoonotic means.

Sporotrichosis in Africa represents a varied epidemiological landscape. Sporadic cases of the disease have been reported in countries spanning the African continent [55, 63, 64, 70, 72]. However, limited data on the disease on the continent impede our understanding of the distribution and prevelance [55, 167]. It is likely that the disease exists sporadically across the continent, but that disparities in healthcare and surveillance infrastructure result in a paucity of case reports. Despite these challenges, Madagascar and South Africa stand out as focal points for sporotrichosis cases in Africa, with recurrent outbreaks and well-established documentation of the disease [79, 168, 169].

7 | Epidemiology in South Africa

Sporotrichosis in South Africa has a unique epidemiological history, with the most common outbreaks associated with gold miners contracting the disease [2–4, 168, 170, 171]. The most significant of these outbreaks were between 1941 and 1943, where more than 2500 cases were reported in mining operations on the West Rand of the Transvaal (now Gauteng) [149, 168, 171]. It is not clear how long sporotrichosis has persisted in South African gold mines, but it is known that dermatological issues were persisting in the mines after Dr. Davidine Pullinger, who had previous experience with the disease, identified sporotrichosis in South Africa for the first time in 1927 [3, 169].

The link between mining operations and sporotrichosis is thought to be due to optimal conditions for growth of the pathogen and an association with the timber used for mine shaft support [5]. To evaluate this hypothesis, Vismer and Eicker showed that clinical *S. schenckii* isolates grew on timber species used by the mining industry [150]. Of the species tested, *Eucalyptus* (amongst others) facilitated the best growth of clinical strains. At that time, *Eucalyptus* timber was used extensively for mineshaft support, and this remains true today. Despite this, the causal agent of the disease had never been isolated from the timber and neither from dirt in affected mine shafts. Consequently, the source of infections leading to sporotrichosis remains a mystery.

In 2015, South Africa was reported to be amongst the regions of the world where sporotrichosis is most endemic. Literature searches reported 3451 cases in South Africa, compared to China and Brazil with 3299 and 5418 cases, respectively [38]. However, the number of reported cases of sporotrichosis in South Africa is most likely not a true reflection of the incidence of the disease. A retrospective study investigated the laboratory diagnosed mycoses in South Africa between 2010 and 2020 and found that the majority of cases were unspecified endemic mycoses (30.1%). However, of the diagnosed cases, sporotrichosis was the most prevalent (24.9%) [172]. The large number of undiagnosed cases makes attaining an accurate measure of incidence of the disease difficult, and it highlights the general lack of data in this regard.

Sporothrix schenckii is the major etiological agent of sporotrichosis found in South Africa, with a single report of *S. luriei* being the only exception [115]. A high genetic diversity within *S. schenckii* is recurrently reported in the fungus in other parts of the world, demonstrated by significant chromosomal polymorphism [129], highly polymorphic microsatellites [39] and AFLPs [128, 173]. This high level of diversity likewise results in highly variable virulence within the species [95, 101].

The genetic diversity of *S. schenckii sensu lato* in South Africa was investigated, when 62 clinical isolates were analysed by mitochondrial DNA RFLPs [130]. Five different genotypic patterns were found in the South African isolates, demonstrating diversity in the population. However, considering the updated taxonomy of the genus, genetic and species diversity of sporotrichosis agents in the country needs to be re-evaluated. These analyses also suggested that the South African strains were most closely related to the populations in North, Central and South America [130, 174], and more distantly related to those in Australia, Asia and Europe [131, 132, 175].

South Africa has one of the most significant HIV epidemics in the world [176]. While the country has had a 1.3% reduction in incidence from 2017 to 2022, this still leaves at least 7.8 million individuals in the country living with HIV [177]. This large number of immunocompromised individuals increases the threat of serious fungal epidemics and makes controlling diseases such as sporotrichosis of great importance. While sporotrichosis is most often associated with a cutaneous manifestation, individuals with compromised immunities are at higher risk of disseminated infections that pose significantly greater health risks [13, 178–180].

Pathogenic *Sporothrix* species can cause pulmonary sporotrichosis, typically in immunosuppressed individuals [181]. This disease expression is significantly more rare than cutaneous forms of the disease [182]. Clinical similarities with more common pulmonary conditions such as tuberculosis can complicate diagnoses, potentially leading to under-reporting of this clinical form of sporotrichosis [183, 184]. Primary pulmonary cases have seldom been reported in South Africa and appear not to be a driving force of the disease [185–187]. Furthermore, a true reflection of pulmonary sporotrichosis is obscured by the fact that data regarding this clinical form are usually limited to historical records that are sporadic and inconclusive.

No large outbreaks of sporotrichosis have been reported in the mining industry in recent years; however, sporadic cases have continued in South Africa [2, 4, 188–190]. Furthermore, since the disease in not considered reportable, dealing with infections at a local level can mean that cases remain oblivious to the medical profession and the general public. For example, neglect in controlling a disease that may have seemed unimportant has made control of sporotrichosis extremely difficult in South America [43]. The misfortunes faced by that continent in this regard provide a vicarious learning opportunity for countries such as South Africa. Highlighting the fact that proactive surveillance strategies should be considered as a first line of defence to prevent disease outbreaks that have potentially devastating public health implications.

8 | *Sporothrix brasiliensis*: A New Global Threat

Brazil has a long history of sporotrichosis, with the disease first reported in rats in 1907 that had contracted the fungus from the sewer systems [32]. Several human cases, unrelated to feline transmission, were then reported in 1920 [191]. Sporadic cases were reported amongst humans, cats, dogs and horses in the 1950s, and these included the first case report of feline–human transmission [51]. However, it took until the mid 1990s for the current feline sporotrichosis epidemic to be identified as a major public health concern [39].

Feline transmission of *S. brasiliensis* has resulted in unprecedented levels of sporotrichosis in Brazil, with the disease incidence being significantly higher than that reported elsewhere in the world [96, 97]. Since sporotrichosis is generally not considered reportable, neglect in dealing with the disease has resulted in its spread throughout the continent [13, 65, 80, 96, 98, 192]. This reflects the general nature of the disease in endemic areas; ever present and carrying the risk of more severe future outbreaks, especially when not swiftly acted on. The seriousness of the outbreaks in South America has led to increased efforts to understand the pathogens, which is clearly reflected in the increasing number of publications on the topic over time (Figure 3).

Increasing levels of feline transmission of *S. schenckii* have also been reported in Asia and North America [163, 193–196]. These cases have been sporadic and significantly less common, but they nevertheless highlight the growing risk of transmission by infected felines and the need to monitor the disease in cat populations. In South America, feline–feline transmission has led to large populations of domestic and feral cats harbouring *S. brasiliensis* and this has allowed for repeated reintroduction of the pathogen into the human population. How these felines initially contracted the fungal infection is not clear; however, transmission through ingestion of naturally infected rats is hypothesised [155, 197]. This underscores a lack of understanding of the role that reservoir hosts may play in the already complicated epidemiology of *Sporothrix* pathogens.

Recently, the first case of *S. brasiliensis* causing feline and human sporotrichosis was reported in the United Kingdom, a first from outside South America [53, 198]. The report highlights the effects that modern travel can play in the distribution of diseases, akin to that seen during the COVID-19 pandemic. This also highlights the urgency with which medical and veterinary clinicians should be made aware of disease, and it argues for more effective surveillance systems to be implemented to prevent further disease spread and outbreaks in new regions.

9 | Future Prospects

The increase in sporotrichosis outbreaks, particularly in South America, has re-invigorated research into *Sporothrix* species residing in the pathogenic clade. These studies have focused on gaining a better understanding of the genetic diversity, spread and increasing levels of drug resistance of fungi. This will provide researchers with a better understanding of the epidemiology of sporotrichosis outbreaks and improved means to manage the disease.

Sampling efforts focussed on isolating the disease-causing *Sporothrix* species from environmental sources, particularly

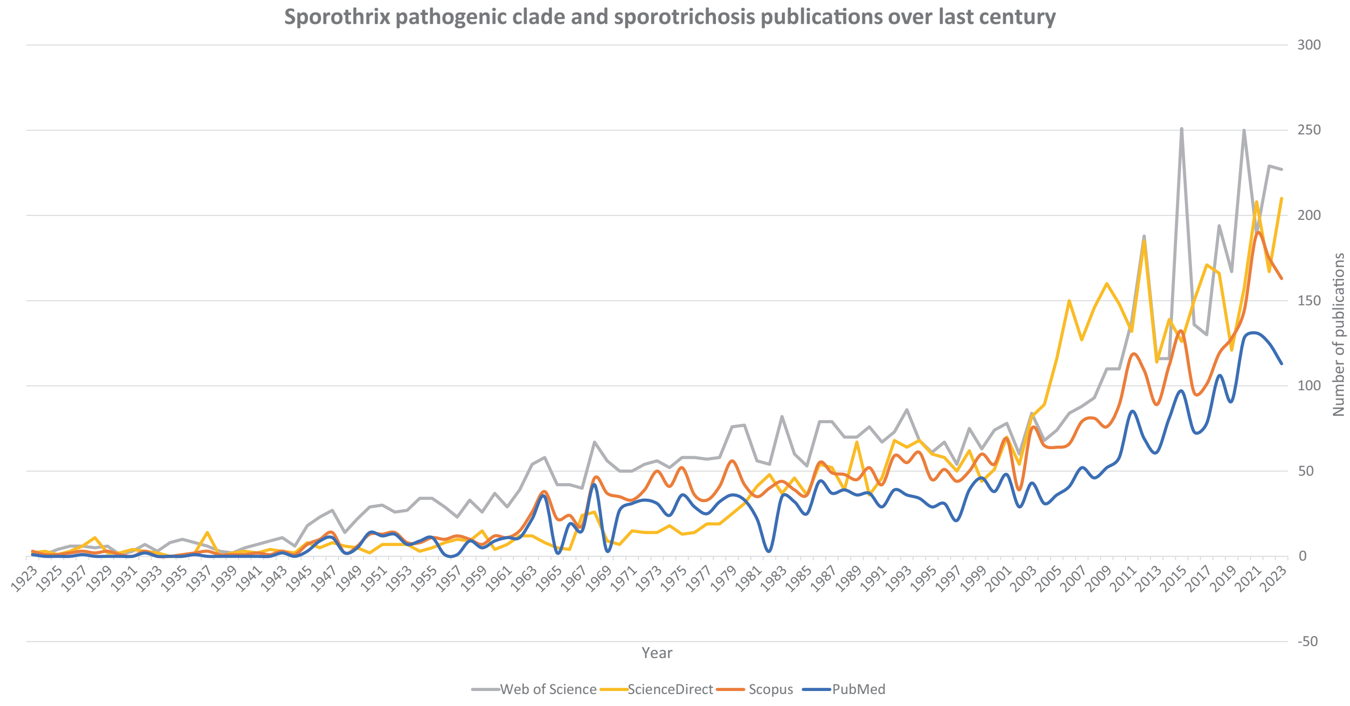

FIGURE 3 | Line graph reflecting the number of publications on sporotrichosis and the *Sporothrix* pathogenic clade. Data were collected from Web of Science, ScienceDirect, Scopus and PubMed databases using the following search query: (Sporotrichosis) OR (Lymphocutaneous sporotrichosis) OR (Systemic sporotrichosis) OR (Sporothrix schenckii) OR (Sporothrix brasiliensis) OR (Sporothrix globosa) OR (Sporothrix pathogenic clade).

where sporotrichosis cases are reported, are critically important. The difficulty in isolating these pathogens from the environment has meant that there are many unanswered questions regarding their environmental ecology. Optimisation of molecular and culturing techniques will continue to provide means to more readily isolate the pathogens from environmental sources. These will include the use of selective media and a dilution to extinction approach, which resulted in *S. brasiliensis* being isolated from environmental sources [151]. Increased sampling efforts to isolate the *Sporothrix* species in the pathogenic clade from the environment should provide a more comprehensive understanding of epidemiology of these fungi and help identify new sources of infection.

While prevention should be considered the first line of defence for any disease, it is also imperative to have effective means of treatment. The emergence of multidrug resistance in several *Sporothrix* strains [16, 199] highlights a need for the etiological agents to be molecularly identified and in this way anticipate disease and treatment outcomes. For this reason, medical practitioners should be made aware of the disease and its symptoms, as well as taught the skills to implement MALDI-TOF (Matrix-Assisted Laser Desorption/Ionisation-Time of Flight) for rapid diagnosis in clinical laboratories [200]. Additionally, the ability to isolate the fungi for molecular characterisation would contribute to the implementation of more successful treatments and allow for more rapid responses to disease outbreaks or spread to new regions.

The sequencing of whole genomes for greater numbers of *Sporothrix* species, both from environmental clades as well as for those in the pathogenic clade, will allow for genome comparisons and concomitant functional studies. These have the potential for the genetic components associated with increased virulence and antifungal resistance to be further elucidated. Furthermore, data from these genomes make it possible to identify novel therapeutic and vaccine targets that are vitally important to increase options for sporotrichosis treatment and prevention. Sporotrichosis is emerging as an important disease worldwide with highly variable disease presentation and outcomes. Maintaining active research on the disease, its causal agents and promoting interdisciplinary collaboration will allow for informed decision making in the battle against sporotrichosis.

Author Contributions

Taygen Fuchs: conceptualization, data curation, formal analysis, visualization, writing – original draft, methodology, investigation, writing – review and editing, software, validation. **Cobus M. Visagie:** conceptualization, data curation, formal analysis, writing – original draft, methodology, investigation, supervision, project administration, writing – review and editing. **Brenda D. Wingfield:** conceptualization, visualization, writing – original draft, investigation, methodology, supervision, project administration, writing – review and editing, funding acquisition, resources, software. **Michael J. Wingfield:** conceptualization, writing – original draft, methodology, supervision, investigation, project administration, writing – review and editing, funding acquisition, resources.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The manuscript is a review and all articles used are referenced. No new data is generated in the manuscript.

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Supporting Information

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