Diversity of tree-infecting Botryosphaeriales on native and non-native trees in South Africa and Namibia

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Abstract

The *Botryosphaeriales* includes serious plant pathogens with a broad host and geographic distribution globally. In South Africa and Namibia, these fungi include important pathogens of native and non-native woody plants, and have consequently been studied extensively. Here we synthesize the information from the previous studies, particularly in the last decade, that report 62 species in the *Botryosphaeriales* from 66 hosts across South Africa and Namibia. Of these, 52 species have been reported from native hosts, 17 are from non-native hosts and twelve of these species occur on both native and non-native trees in the region. Much of the diversity of the *Botryosphaeriales* can be ascribed to native species that have fairly limited host and geographic ranges. *Neofusicoccum parvum* is amongst the most common species on both native and non-native hosts and it is thought to be native to the region. In contrast, *Botryosphaeria dothidea*, which is certainly an introduced species, is also widespread, and is very common on both native and non-native plants. Overall this synthesis underscores the growing understanding of the diversity of an important group of tree pathogens, their apparently common global spread as latent agents of disease, as well as their apparently common movement between commercial and native ecosystems.

Keywords

Aplosporellaceae; Botryosphaeriales; Pseudofusicoccumaceae; Saccharataceae; Host association; Fungal biogeography

Introduction

Woody plants are often colonized by *Botryosphaeriales* as endophytes, irrespective of whether they are agricultural crops, ornamental plants, plantation forestry species or plants in natural woody vegetation (Slippers and Wingfield 2007; Slippers et al. 2017). Species of the *Botryosphaeriales* include important and common pathogens of native and non-native woody plants worldwide. Consequently, these fungi have been relatively well studied. While they are equally common in native ecosystems, the majority of studies on the *Botryosphaeriales* have been on agricultural or forestry crops. The overlap between *Botryosphaeriales* occurring on native and non-native trees is an important feature of these fungi that has only recently been appreciated (Slippers et al. 2009; Sakalidis et al. 2013; Pillay et al. 2013; Marsberg et al. 2017; Slippers et al. 2017; Mehl et al. 2017a).

Advances in DNA based phylogenetic inference and its impact on the taxonomy of fungi during the past two decades has led to the description of many new species, recognition of species complexes and ongoing revisions of older taxa in the *Botryosphaeriales*. There is consequently great uncertainty regarding identifications of species in this group and particularly those for which no culture and DNA sequence data are available (Crous et al. 2016). Similar problems abound regarding the interpretations of species distributions, host associations, links of species to diseases etc. For example, up until the 1990's, *Botryosphaeria dothidea* became a repository for many species with 'Fusicoccum-like' asexual states. However, collections typically identified as this species have subsequently been described as various species and genera (Slippers et al. 2013; Phillips et al. 2013; Slippers et al. 2017). *Botryosphaeria dothidea* has also been reported from South Africa, but recent studies have shown that it is not the most common species in many areas (Jami et al. 2015; Pavlic et al. 2007). It is consequently clear that numerous previous reports recording this pathogen referred not to this species but others in *Botryosphaeria* or *Neofusicoccum.*

During the course of the past two decades, a relatively large number of studies have been conducted on the *Botryosphaeriales* on various plants in South Africa, and to a lesser extent in neighbouring, Namibia. Interestingly, this region has been one of the most intensively studied for this group of fungi anywhere in the world. But commonly, these studies have been focused on a specific disease problem or host, and the broader ecological patterns remain underexplored. In this review we synthesize the information from all reports of *Botryosphaeriales* from South Africa and Namibia with the overall aim of illustrating patterns of distribution and host association. For accuracy, we base the review only on reports for which identifications and descriptions are linked to DNA-based comparisons.

Botryosphaeriales on native and non-native hosts in South Africa and Namibia

Sixty-two species of *Botryosphaeriales* have been identified in studies undertaken in different parts of South Africa and Namibia. These studies have recorded species on 66 native and non-native hosts (Table 1, Figs. 1 and 2). The isolated species included those causing disease symptoms (Fig. 3) and others isolated from asymptomatic tissues. *Neofusicoccum* was the most diverse genus identified in these studies, with 16 species described from the region. *Neofusicoccum parvum* has been found to infect the greatest number of host species (Fig. 4) but *B. dothidea* was the most common species in the sampled sites throughout South Africa. In the following sections, we analyse these patterns of host association and distribution of *Botryosphaeriales* on native and non-native woody plants in South Africa in greater detail. Other than better understanding the patterns of

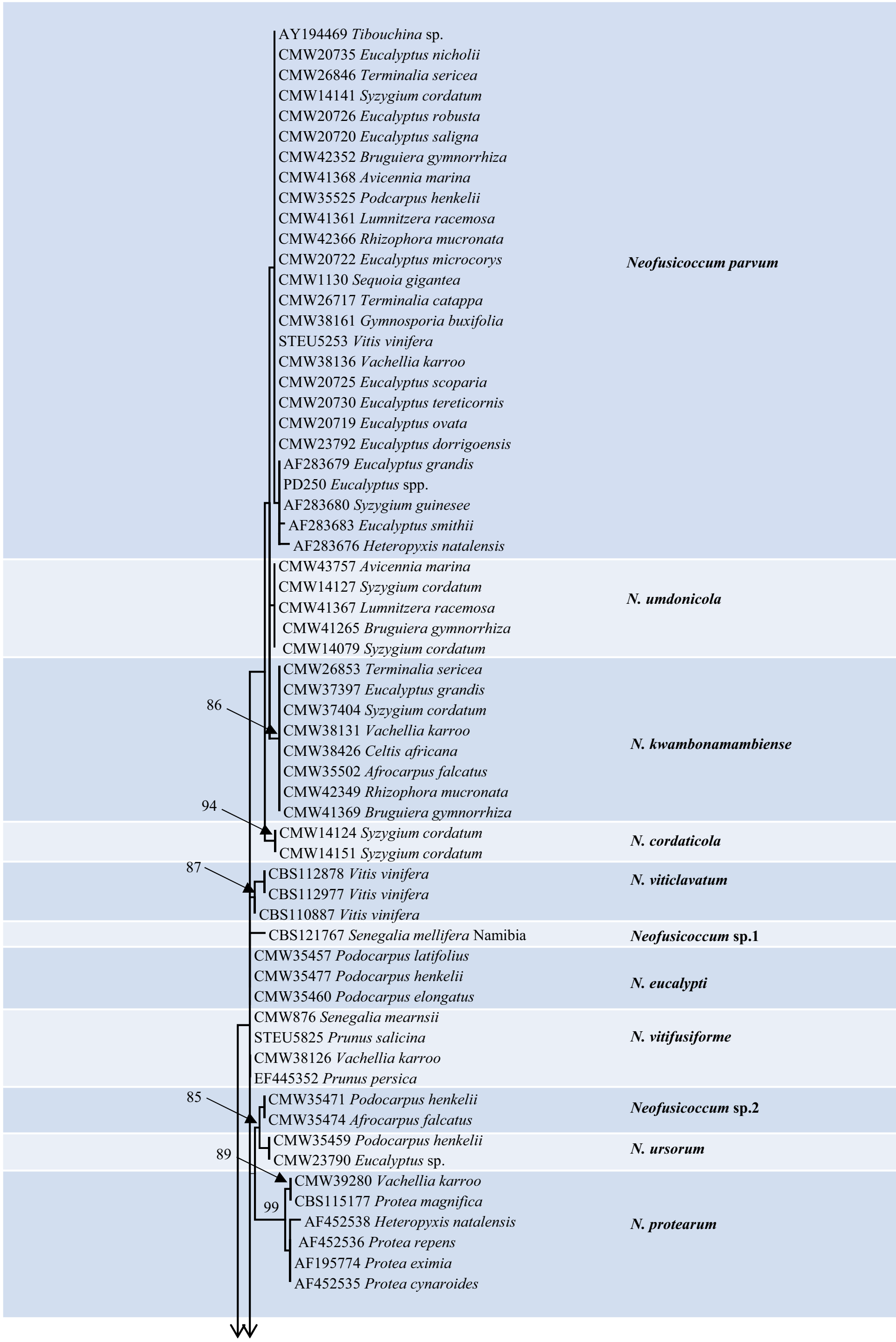
Table 1 *Botryosphaeriales* associated with southern African native and non-native trees

Fungus	Host	Symptoms/Plant tissue	Sampled area	Reference
Aplosporella africana	*Senegalia mellifera*	Healthy branches	Dordabis, Namibia	Slippers et al. 2013
A. javeedii	*Celtis africana*	"	Gauteng, SA	Jami et al. 2014 Jami
A. javeedii	*Searsia lancea*	"	"	et al. 2014 Slippers et
A. papillata	*Vachellia tortilis*	Not available	Northern Cape, SA	al. 2013 Damm et al.
A. prunicola	*Prunnus persica*	"	Limpopo, SA	2007 Slippers et al.
A. papillata	*Vachellia erioloba*	"	Northern Cape, SA	2013 Mehl et al. 2011
Botryosphaeria atrovirens	*Pterocarpus angolensis*	Symptomless	Mpumalanga, SA	Slippers et al. 2013
B. avasmontanum	*Senegalia mellifera*	Not available	Windhoek, Namibia	Mehl et al. 2017b
B. fabiceriana	*Sclerocarya birrea*		Limpopo, SA	Mehl et al. 2017b
B. fabiceriana	*Mangifera indica*		Limpopo, SA	Jami et al. 2015
B. dothidea	*Vachellia karroo*	Healthy branches & leaves	Gauteng, SA	Slippers et al. 2013
B. dothidea	*Vachellia karroo*	Not available	Windhoek, Namibia	Roux and Wingfield
B. dothidea	*Acacia mearnsii*	Canker	KwaZulu-Natal, SA	1997
B. dothidea	*Senegalia mellifera*	Not available	Dordabis, Namibia	Slippers et al. 2013
B. dothidea	*Eucalyptus citriodora*	Symptomless	Gauteng, SA	Maleme 2009
B. dothidea	*Eucalyptus dorrigoensis*	"	"	Maleme 2009
B. dothidea	*Eucalyptus microcorvs*	"	"	Maleme 2009
B. dothidea	*Eucalyptus* spp.	"	"	Maleme 2009
B. dothidea	*Podocarpuse longatus*	Die-back	"	Ndove 2015
B. dothidea	*Podocarpus henkelii*	"	"	Ndove 2015
B. dothidea	*Syzygium cordatum*	Canker& die-back	Eastern Cape, KwaZulu-Natal, SA	Pavlic et al. 2004, 2007
Diplodia africana	*Prunnus persica*	Canker & die-back	Western Cape, SA	Damm et al. 2007
D. allocellula	*Vachellia karroo*	Healthy branches	Gauteng, SA	Jami et al. 2012
D. estuarina	*Avicennia marina*	"	KwaZulu-Natal, SA	Osorio et al. 2017
D. estuarina	*Rhizophora mucronata*	"	KwaZulu-Natal, Eastern Cape, SA	Osorio et al. 2017
D. mutila	*Prunus salicina*	Canker& die-back	Western Cape, SA	Damm et al. 2007
D. mutila	*Podocarpus henkelii*	Symptomless	"	Ndove 2015
D. pseudoseriata	*Vachellia karroo*	Healthy leaves	Gauteng, SA	Jami et al. 2015
D. pseudoseriata	*Pterocarpus angolensis*	Healthy/ Diseased tissues	Mpumalanga, SA	Mehl et al. 2011
D. sapinea	*Cupressus lusitanica*	Canker	Mpumalanga, SA	Linde et al. 1997
D. sapinea	*Prunnus persica*	Canker & die-back	Western Cape, SA	Damm et al. 2007
D. sapinea	*Pinus patula*	Diseased tissues/ Symptomless	KwaZulu-Natal, Western Cape, SA	Swart et al. 1985; Smith et al. 1996b
D. sapinea	*Pinus radiata*	"	Eastern Cape, Western Cape, SA	Swart et al. 1985; Smith et al. 1996b
D. sapinea	*Protea repens*	Symptomless	KwaZulu-Natal, SA	Smith et al. 1996b
D. scrobiculata	*Pinus patula*	Symptomless/ Die-back	KwaZulu-Natal, Mpumalanga, SA	Bihon et al. 2012a
D. seriata	*Malus* sp.	Diseased tissues	Western Cape, SA	Slippers et al. 2007
D. seriata	*Prunus sarmeniaca*	"	Limpopo, SA	Denman et al. 2003
D. seriata	*Prunnus persica*	"	Western Cape, SA	Slippers et al. 2007
D. seriata	*Prunus salicina*	"	"	Slippers et al. 2007
D. seriata	*Populus* sp.	"	"	Slippers et al. 2007
D. seriata	*Prunus magnifica*	Symptomless	"	Denman et al. 2003
D. seriata	*Pyrus communis*	Diseased tissues	"	Slippers et al. 2007
D. seriata	*Vitis vinifera*	Die-back	"	Van Niekerk et al.
Dothiorella brevicollis	*Vachellia karroo*	Healthy & die-back branches	Gauteng, SA	2004 Jami et al. 2012,
Do. capri-amissi	*Vachellia erioloba*	Not available	Gauteng, Northern Cape, SA	2015 Slippers et al.
Do. dulcispinae	*Vachellia karroo*	Die-back	"	2013 Jami et al. 2012,
Do. dulcispinae	*Senegalia mellifera*	Not available	Namibia	2015 Slippers et al.
Do. oblonga	*Senegalia mellifera*	"	Guateng Province, SA	2013 Slippers et al.
Do. pretoriensis	*Vachellia karroo*	Die-back	Gauteng, SA	2013 Jami et al. 2012,
Do. rosulata	*Vachellia karroo*	"	Northern Cape, SA, Windhoek, Namibia	2015 Slippers et al. 2013
Do. rosulata	*Senegalia mellifera*	"	Gauteng, Northern Cape, SA	Slippers et al. 2013
Do. rosulata	*Vachellia tortilis*	"	Northern Cape, SA	Slippers et al. 2013
Do. viticola	*Vachellia karroo*	Healthy leaves, branches & die-back	Gauteng, SA	Jami et al. 2014
Do. viticola	*Senegalia mellifera*	Not available	"	Slippers et al. 2013
Do. viticola	*Celtis africana*	Healthy branches	"	Jami et al. 2014
Do. viticola	*Gymnosporia buxifolia*	"	"	Jami et al. 2014
Do. viticola	*Prunus persica*	Canker & die-back	Limpopo, SA	Damm et al. 2007
Do. viticola	*Podocarpus henkelii*	Symptomless	Gauteng, SA	Ndove 2015
Do. viticola	*Vitis vinifera*	Disease tissue	Western Cape, SA	Van Niekerk et al.
Eutiarosporella urbis-rosarum	*Vachellia karroo*	Healthy branches	Gauteng, Free state, SA	2004 Jami et al. 2012
Eu. africana	*Celtis africana*	"	Gauteng, SA	Jami et al. 2014

Fungus	Host	Symptoms/Plant tissue	Sampled area	Reference
Eu. graminis	*Nestlera* sp.	Disease tissue	Free State, SA	Crous et al. 2006
Eu. tritici	*Triticum* sp.	"	"	"
Lasiodiplodia avicenniae	*Avicennia marina*	Healthy branches	KwaZulu-Natal, SA	Osorio et al. 2017
L euphorbiicola	*Adansonia digitata s.l.*	Healthy/ Diseased tissues		Cruywagen et al. 2017
L. bruguierae	*Bruguiera gymnorrhiza*	Healthy branches		Osorio et al. 2017
L. crassispora	*Pterocarpus angolensis*	Diseased tissues	Mpumalanga, SA	Mehl et al. 2011
L. crassispora	*Sclerocarya birrea subsp. caffra*		KwaZulu-Natal, SA	
L. gilanensis	*Podocarpus latifolius*	Symptomless	Western Cape, SA	Ndove 2015
L. gonubiensis	*Vachellia karroo*	"	"	Jami et al. 2015
L. gonubiensis	*Syzygium cordatum*	Canker & die-back	Eastern Cape, SA	Pavlic et al. 2004, 2007
L. gonubiensis	*Bruguiera gymnorrhiza*	Healthy branches	KwaZulu-Natal, SA	Osorio et al. 2017
L. gonubiensis	*Ceriops tagal*	Healthy branches	"	Osorio et al. 2017
L. gonubiensis	*Sclerocarya birrea subsp. caffra*		KwaZulu-Natal, SA	Mehl et al. 2017b
L. iraniensis	*Sclerocarya birrea subsp. caffra*		KwaZulu-Natal, SA	Mehl et al. 2017b
L. mahajangana	*Euphorbia ingens*	Diseased tissues	Limpopo, SA	Van der Linde et al. 2011
L. mahajangana	*Adansonia digitata s.l.*	Healthy/ Diseased tissues	Limpopo, SA & Namibia	Cruywagen et al. 2017
L. mahajangana	*Sclerocarya birrea subsp. caffra*		Limpopo, SA	Mehl et al. 2017a
L. mahajangana	*Magnifera indica*		Limpopo, SA	Mehl et al. 2017a
L. plurivora	*Prunus salicina*	"	Western Cape, SA	Damm et al. 2007
L. plurivora	*Vitis vinifera*	"	"	Damm et al. 2007
L. pseudotheobromae	*Vachellia karroo*	Symptomless	Limpopo, SA	Jami et al. 2015
L. pseudotheobromae	*Senegalia mellifera*	Not available	Rundu, Namibia	Slippers et al. 2013
L. pseudotheobromae	*Pterocarpus angolensis*	Healthy/ Diseased tissues	Mpumalanga, SA	Mehl et al. 2011
L. pseudotheobromae	*Adansonia digitata s.l.*	Healthy/ Diseased tissues	Limpopo, SA	Cruywagen et al. 2017
L. pseudotheobromae	*Syzygium cordatum*	Symptomless	KwaZulu-Natal, SA	Pillay et al. 2013
L. pseudotheobromae	*Terminalia catappa*	Die-back	"	Begoude et al. 2010
L. pseudotheobromae	*Terminalia sericea*	"	Namibia	Begoude et al. 2010
L. pseudotheobromae	*Sclerocarya birrea subsp. caffra*		Limpopo, SA	Mehl et al. 2017a
L. pseudotheobromae	*Magnifera indica*		Limpopo, SA	Mehl et al. 2017a
L. pyriformis	*Senegalia mellifera*	Not available	Dordabis, Namibia	Slippers et al. 2013
L. theobromae	*Vachellia karroo*	Healthy leaves	Gauteng, SA	Jami et al. 2015
L. theobromae	*Euphorbia ingens*	Diseased tissues	Limpopo, SA	Van der Linde et al. 2011
L. theobromae	*Barringtonia racemosa*	Healthy branches	KwaZulu-Natal, SA	Osorio et al. 2017
L. theobromae	*Pterocarpus angolensis*	Symptomless	Mpumalanga, SA	Mehl et al. 2011
L. theobromae	*Syzygium cordatum*	Canker & die-back	Eastern Cape, SA	Pavlic et al. 2004, 2007
L. theobromae	*Terminalia catappa*	Die-back	KwaZulu-Natal, SA	Begoude et al. 2010
L. theobromae	*Vitis vinifera*	"	Western Cape, SA	Van Niekerk et al. 2004
L. theobromae	*Sclerocarya birrea subsp. caffra*		KwaZulu-Natal, SA	Mehl et al. 2017a
L. theobromae	*Magnifera indica*		Limpopo, SA	Mehl et al. 2017a
Neofusicoccum sp.nov1	*Senegalia mellifera*	Not available	Rundu, Namibia	Slippers et al. 2013
N. australe	*Vachellia karroo*	Healthy leaves	Gauteng, SA	Jami et al. 2015
N. australe	*Magnifera indica*		Limpopo, SA	Mehl et al. 2017a
N. australe	*Eucalyptus grandis*	Symptomless	KwaZulu-Natal, SA	Pillay et al. 2013
N. australe	*Malus domestica*	Diseased tissues	Western Cape, SA	Slippers et al. 2007
N. australe	*Prunus armeniaca*	"	Limpopo, SA	Denman et al. 2003
N. australe	*Prunus dulcis*	"	Western Cape, SA	Slippers et al. 2007
N. australe	*Prunnus persica*	Canker& die-back	"	Damm et al. 2007
N. australe	*Prunus salicina*	Diseased tissues	"	Slippers et al. 2007
N. australe	*Pyrus. communis*	"	"	Slippers et al. 2007
N. australe	*Syzygium cordatum*	Canker & die-back	Eastern Cape, SA	Pavlic et al. 2004, 2007
N. australe	*Vitis vinifera*	Die-back	Western Cape, SA	Van Niekerk et al. 2004
N. australe	*Widdringtonia nodiflora*	Diseased tissues	"	Slippers et al. 2005
N. cordaticola	*Syzygium cordatum*	Symptomless and dying branches	KwaZulu-Natal, SA	Pavlic et al. 2009
N. cryptoaustrale	*Eucalyptus* spp.	Symptomless	Gauteng, SA	Maleme 2009
N. crypto-australe	*Podocarpus henkelii*	Die-back	"	Ndove 2015
N. crypto-australe	*Podocarpus latifolius*	Symptomless	Western Cape, SA	Ndove 2015
N. crypto-australe	*Syzygium cordatum*	"	Gauteng, SA	Maleme 2009
N. crypto-australe	*Bruguiera gymnorrhiza*	Healthy branches	KwaZulu-Natal, SA	Osorio et al. 2017
N. crypto-australe	*Ceriops tagal*	"	"	Osorio et al. 2017
N. crypto-australe	*Avicennia marina*	"	KwaZulu-Natal, Eastern Cape, SA	Osorio et al. 2017
N. crypto-australe	*Rhizophora mucronata*	"	KwaZulu-Natal, SA	Osorio et al. 2017
N. crypto-australe	*Lumnitzera racemosa*	"	"	Osorio et al. 2017
N. eucalypti	*Eucalyptus* sp.	"	Gauteng, SA	Maleme 2009
N. eucalypti	*Podocarpus elongatus*	Die-back	"	Ndove 2015

Fungus	Host	Symptoms/Plant tissue	Sampled area	Reference
N. eucalypti	*Podocarpus henkelii*	"	"	Ndove 2015
N. eucalypti	*Podocarpus latifolius*	"	"	Ndove 2015
N. eucalyptorum	*Eucalyptus grandis*	Canker & die-back	Mpumalanga, SA	Smith et al. 2001
N. eucalyptorum	*Eucalyptus nitens*	"	"	Smith et al. 2001
N. eucalyptorum	*Eucalyptus* sp.	Not available	Western Cape, SA	Slippers et al. 2004
N. kwambonambiense	*Afrocarpus falcatus*	Die-back	Mpumalanga, SA	Ndove 2015
N. kwambonambiense	*Vachellia karroo*	Healthy branches & leaves	Gauteng, SA	Jami et al. 2015
N. kwambonambiense	*Celtis africana*	Healthy branches	"	Jami et al. 2014
N. kwambonambiense	*Eucalyptus grandis*	Symptomless	KwaZulu-Natal, SA	Pillay et al. 2013
N. kwambonambiense	*Podocarpus henkelii*	Die-back	Mpumalanga, SA	Ndove 2015
N. kwambonambiense	*Syzygium cordatum*	Symptomless	KwaZulu-Natal, SA	Pillay et al. 2013
N. kwambonambiense	*Terminalia sericea*	Not available	SA	Begoude et al. 2010
N. kwambonambiense	*Bruguiera gymnorrhiza*	Healthy branches	KwaZulu-Natal, SA	Osorio et al. 2017
N. kwambonambiense	*Rhizophora mucronata*	Healthy branches	"	Osorio et al. 2017
N. kwambonambiense	*Magnifera indica*		Limpopo, SA	Mehl et al., 2017a
N. luteum	*Syzygium cordatum*	Canker & die-back	Eastern Cape, SA	Pavlic et al. 2004, 2007
N. luteum	*Avicennia marina*	Healthy branches	KwaZulu-Natal, SA	Osorio et al. 2017
N. luteum	*Bruguiera gymnorrhiza*	"	"	Osorio et al. 2017
N. luteum	*Rhizophora mucronata*	"	KwaZulu-Natal, SA	Osorio et al. 2017
N. mangiferum	*Syzygium cordatum*	Canker & die-back	"	Pavlic et al. 2004, 2007
N. mangiferum	*Tibouchina urvilleana*	Healthy/ Dead tissues	KwaZulu-Natal, SA	Heath et al. 2011
N. mangroviorum	*Avicennia marina*	Healthy branches	KwaZulu-Natal, Eastern Cape, SA	
N. mangroviorum	*Bruguiera gymnorrhiza*	"	"	
N. mangroviorum	*Rhizophora mucronata*	"	Eastern Cape, SA	
N. mediterraneum	*Sclerocarya birrea subsp. caffra*		KwaZulu-Natal, Mpumalanga, SA	Mehl et al. 2017a
N. mediterraneum	*Magnifera indica*		Limpopo, SA	Mehl et al. 2017a
N. parvum	*Afrocarpus falcatus*	Die-back	Mpumalanga, SA	Ndove 2015
N. parvum	*Vachellia karroo*	Healthy leaves	Gauteng, SA	Jami et al. 2015
N. parvum	*Eucalyptus dorrigoensis*	Symptomless	"	Maleme 2009
N. parvum	*Eucalyptus grandis*	Canker &die-back	Mpumalanga, SA	Smith et al. 2001; Slippers et al. 2004
N. parvum	*Eucalyptus microcorvs*	Symptomless	Gauteng, SA	Maleme 2009
N. parvum	*Eucalyptus nicholii*	"	"	Maleme 2009
N. parvum	*Eucalyptus ovata*	"	"	Maleme 2009
N. parvum	*Eucalyptus robusta*	"	"	Maleme 2009
N. parvum	*Eucalyptus saligna*	"	"	Maleme 2009
N. parvum	*Eucalyptus scoparia*	"	"	Maleme 2009
N. parvum	*Eucalyptus smithii*	Canker & die-back	Mpumalanga, SA	Smith et al. 2001; Slippers et al. 2004
N. parvum	*Eucalyptus tereticornis*	Symptomless	Gauteng, SA	Maleme 2009
N. parvum	*Eucalyptus* spp.	"	"	Maleme 2009
N. parvum	*Gymnosporia buxifolia*	Healthy branches	"	Jami et al. 2014
N. parvum	*Heteropyxis natalensis*	Canker & die-back	KwaZulu-Natal, SA	Denman et al. 2003
N. parvum	*Podocarpus henkelii*	Symptomless	Gauteng, SA	Ndove 2015
N. parvum	*Schizolobium parahyba*	Die-back	"	Mehl et al. 2014
N. parvum	*Syzygium cordatum*	Canker & die-back	Eastern Cape, SA	Pavlic et al. 2004, 2007
N. parvum	*Sequoia gigantea*	Not available	"	Slippers et al. 2004
N. parvum	*Syzygium guineense*	Canker & die-back	"	Pavlic et al. 2004, 2007
N. parvum	*Terminalia catappa*	Die-back	KwaZulu-Natal, SA	Begoude et al. 2010
N. parvum	*Terminalia sericea*	Not available	SA	Begoude et al. 2010
N. parvum	*Tibouchina urvilleana*	Healthy/ Dead tissues	"	Heath et al. 2011
N. parvum	*Vitis vinifera*	Die-back	Western Cape, SA	Van Niekerk et al. 2004
N. parvum	*Avicennia marina*	Healthy branches	KwaZulu-Natal, Eastern Cape, SA	Osorio et al. 2017
N. parvum	*Rhizophora mucronata*	"	Eastern Cape, SA	Osorio et al. 2017
N. parvum	*Bruguiera gymnorrhiza*	"	KwaZulu-Natal, Eastern Cape, SA	Osorio et al. 2017
N. parvum	*Lumnitzera racemosa*	"	KwaZulu-Natal, SA	Osorio et al. 2017
N. parvum	*Sclerocarya birrea subsp. caffra*		Limpopo, SA	Mehl et al. 2017a
N. parvum	*Magnifera indica*		Limpopo, SA	Mehl et al. 2017a
N. protearum	*Vachellia karroo*	Symptomless	Western Cape, Eastern Cape, SA	Jami et al. 2015
N. protearum	*Heteropyxis natalensis*	Canker & die-back	Western Cape, SA	Denman et al. 2003
N. protearum	*Leucadendron laureolum X l. Salignum*	"	"	Denman et al. 2003
N. protearum	*Protea cynaroides*	Die-back	"	Denman et al. 2003
N. protearum	*Prtoea eximia*	Canker	"	Denman et al. 2003
N. protearum	*Protea magnifica*	Canker & Leaf necrosis	"	Denman et al. 2003

Fungus	Host	Symptoms/Plant tissue	Sampled area	Reference
N. protearum	*Protea repens*	Canker	“	Denman et al. 2003
N. umdonicola	*Syzygium cordatum*	Canker & die-back	Eastern Cape, SA	Pavlic et al. 2004, 2007
N. umdonicola	*Avicennia marina*	Healthy branches	KwaZulu-Natal, SA	Osorio et al. 2017
N. umdonicola	*Bruguiera gymnorrhiza*	“	KwaZulu-Natal, Eastern Cape, SA	Osorio et al. 2017
N. umdonicola	*Lumnitzera racemosa*	“	KwaZulu-Natal, SA	Osorio et al. 2017
N. umdonicola	*Magnifera indica*		Limpopo, SA	Mehl et al. 2017a
N. ursorum	*Eucalyptus* spp.	Symptomless	Gauteng, SA	Maleme 2009
N. ursorum	*Podocarpus henkelii*	“	“	Ndove 2015
N. viticlavatum	*Vitis vinifera*	Die-back	Western Cape, SA	Van Niekerk et al.
N. vitifusiforme	*Vachellia karroo*	Healthy branches & leaves	Gauteng, SA	2004 Jami et al. 2015
N. vitifusiforme	*Acacia mearnsii*	Not available	SA	Van der Linde 2010
N. vitifusiforme	*Prunnus persica*	Canker & die-back	Western Cape, SA	Damm et al. 2007
N. vitifusiforme	*Prunus salicina*	“	“	Damm et al. 2007 Mehl
N. vitifusiforme	*Schizolobium parahyba*	Die-back	Gauteng, Mpumalanga, SA	et al. 2014
N. vitifusiforme	*Vitis vinifera*	“	Western Cape, SA	Van Niekerk et al.
N. vitifusiforme	*Sclerocarya birrea subsp. caffra*		KwaZulu-Natal, Mpumalanga, SA	2004 Mehl et al. 2017a
Neofusicoccum sp.nov2	*Afrocarpus falcatus*	Die-back	Gauteng, SA	Ndove 2015
Neofusicoccum sp.nov2	*Podocarpus henkelii*	“	Mpumalanga, SA	Ndove 2015
Oblongocollomyces variabilis	*Vachellia hebeclada*	Not available	Windhoek, Namibia	Slippers et al. 2013
Oblongocollomyces variabilis	*Vachellia karroo*	Healthy branches	Gauteng, SA	Jami et al. 2015
Oblongocollomyces variabilis	*Senegalia mellifera*	Not available	Northern Cape, SA	Slippers et al. 2013
Pseudofusicoccum olivaceum	*Magnifera indica*		Limpopo, SA	Mehl et al. 2017a
Ps. violaceum	*Pterocarpus angolensis*	“	“	Mehl et al. 2011
Ps. olivaceum	*Pterocarpus angolensis*	Symptomless	Mpumalanga, SA	Mehl et al. 2011
Saccharata proteae	*Protea cynaroides*	“	Western Cape, SA	Denman et al. 2003
Sa. proteae	*Protea repens*	Leaf necrosis	“	Denman et al. 2003 Van
Sphaeropsis porosa	*Vitis vinifera*	“	“	Niekerk et al. 2004


AY194469 Tibouchina sp.
CMW20735 Eucalyptus nicholii
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CMW20720 Eucalyptus saligna
CMW42352 Bruguiera gymnorrhiza
CMW41368 Avicennia marina
CMW35525 Podcarpus henkelii
CMW41361 Lumnitzera racemosa
CMW42366 Rhizophora mucronata
CMW20722 Eucalyptus microcorys
CMW1130 Sequoia gigantea
CMW26717 Terminalia catappa
CMW38161 Gymnosporia buxifolia
STEU5253 Vitis vinifera
CMW38136 Vachellia karroo
CMW20725 Eucalyptus scoparia
CMW20730 Eucalyptus tereticornis
CMW20719 Eucalyptus ovata
CMW23792 Eucalyptus dorrigoensis
AF283679 Eucalyptus grandis
PD250 Eucalyptus spp.
AF283680 Syzygium guinesee
AF283683 Eucalyptus smithii
AF283676 Heteropyxis natalensis
Neofusicoccum parvum
CMW43757 Avicennia marina
CMW14127 Syzygium cordatum
CMW41367 Lumnitzera racemosa
CMW41265 Bruguiera gymnorrhiza
CMW14079 Syzygium cordatum
N. umdonicola
CMW26853 Terminalia sericea
CMW37397 Eucalyptus grandis
CMW37404 Syzygium cordatum
86
CMW38131 Vachellia karroo
CMW38426 Celtis africana
CMW35502 Afrocarpus falcatus
CMW42349 Rhizophora mucronata
CMW41369 Bruguiera gymnorrhiza
N. kwambonamambiense
94
CMW14124 Syzygium cordatum
CMW14151 Syzygium cordatum
N. cordaticola
87
CBS112878 Vitis vinifera
CBS112977 Vitis vinifera
CBS110887 Vitis vinifera
N. viticlavatum
CBS121767 Senegalia mellifera Namibia
Neofusicoccum sp.1
CMW35457 Podocarpus latifolius
CMW35477 Podocarpus henkelii
CMW35460 Podocarpus elongatus
N. eucalypti
CMW876 Senegalia mearnsii
STEU5825 Prunus salicina
CMW38126 Vachellia karroo
EF445352 Prunus persica
N. vitifusiforme
85
CMW35471 Podocarpus henkelii
CMW35474 Afrocarpus falcatus
Neofusicoccum sp.2
CMW35459 Podocarpus henkelii
CMW23790 Eucalyptus sp.
N. ursorum
89
CMW39280 Vachellia karroo
CBS115177 Protea magnifica
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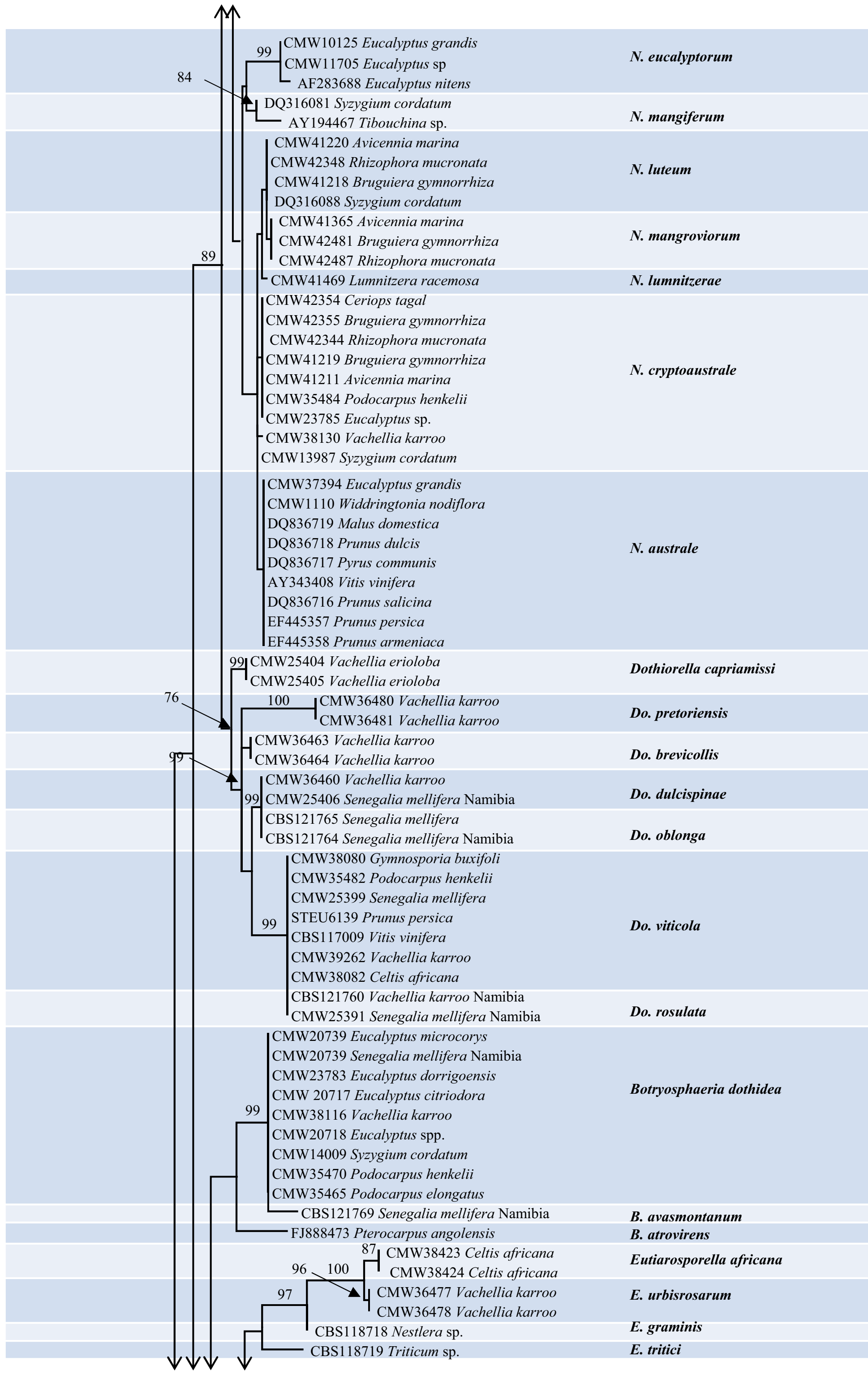
AF452538 Heteropyxis natalensis
AF452536 Protea repens
AF195774 Protea eximia
AF452535 Protea cynaroides
N. protearum



CMW10125 *Eucalyptus grandis*
CMW11705 *Eucalyptus* sp
AF283688 *Eucalyptus nitens*
N. eucalyptorum
DQ316081 *Syzygium cordatum*
AY194467 *Tibouchina* sp.
N. mangiferum
CMW41220 *Avicennia marina*
CMW42348 *Rhizophora mucronata*
CMW41218 *Bruguiera gymnorrhiza*
DQ316088 *Syzygium cordatum*
N. luteum
CMW41365 *Avicennia marina*
CMW42481 *Bruguiera gymnorrhiza*
CMW42487 *Rhizophora mucronata*
N. mangroviorum
CMW41469 *Lumnitzera racemosa*
N. lumnitzerae
CMW42354 *Ceriops tagal*
CMW42355 *Bruguiera gymnorrhiza*
CMW42344 *Rhizophora mucronata*
CMW41219 *Bruguiera gymnorrhiza*
CMW41211 *Avicennia marina*
CMW35484 *Podocarpus henkelii*
CMW23785 *Eucalyptus* sp.
CMW38130 *Vachellia karroo*
CMW13987 *Syzygium cordatum*
N. cryptoaustrale
CMW37394 *Eucalyptus grandis*
CMW1110 *Widdringtonia nodiflora*
DQ836719 *Malus domestica*
DQ836718 *Prunus dulcis*
DQ836717 *Pyrus communis*
AY343408 *Vitis vinifera*
DQ836716 *Prunus salicina*
EF445357 *Prunus persica*
EF445358 *Prunus armeniaca*
N. australe
CMW25404 *Vachellia erioloba*
CMW25405 *Vachellia erioloba*
Dothiorella capriamissi
CMW36480 *Vachellia karroo*
CMW36481 *Vachellia karroo*
Do. pretoriensis
CMW36463 *Vachellia karroo*
CMW36464 *Vachellia karroo*
Do. brevicollis
CMW36460 *Vachellia karroo*
CMW25406 *Senegalia mellifera* Namibia
Do. dulcispinae
CBS121765 *Senegalia mellifera*
CBS121764 *Senegalia mellifera* Namibia
Do. oblonga
CMW38080 *Gymnosporia buxifoli*
CMW35482 *Podocarpus henkelii*
CMW25399 *Senegalia mellifera*
STEU6139 *Prunus persica*
CBS117009 *Vitis vinifera*
CMW39262 *Vachellia karroo*
CMW38082 *Celtis africana*
CBS121760 *Vachellia karroo* Namibia
Do. viticola
CMW25391 *Senegalia mellifera* Namibia
Do. rosulata
CMW20739 *Eucalyptus microcorys*
CMW20739 *Senegalia mellifera* Namibia
CMW23783 *Eucalyptus dorrigoensis*
CMW 20717 *Eucalyptus citriodora*
CMW38116 *Vachellia karroo*
CMW20718 *Eucalyptus* spp.
CMW14009 *Syzygium cordatum*
CMW35470 *Podocarpus henkelii*
CMW35465 *Podocarpus elongatus*
Botryosphaeria dothidea
CBS121769 *Senegalia mellifera* Namibia
B. avasmontanum
FJ888473 *Pterocarpus angolensis*
B. atrovirens
CMW38423 *Celtis africana*
CMW38424 *Celtis africana*
Eutiarosporella africana
CMW36477 *Vachellia karroo*
CMW36478 *Vachellia karroo*
E. urbisrosarum
CBS118718 *Nestlera* sp.
E. graminis
CBS118719 *Triticum* sp.
E. tritici

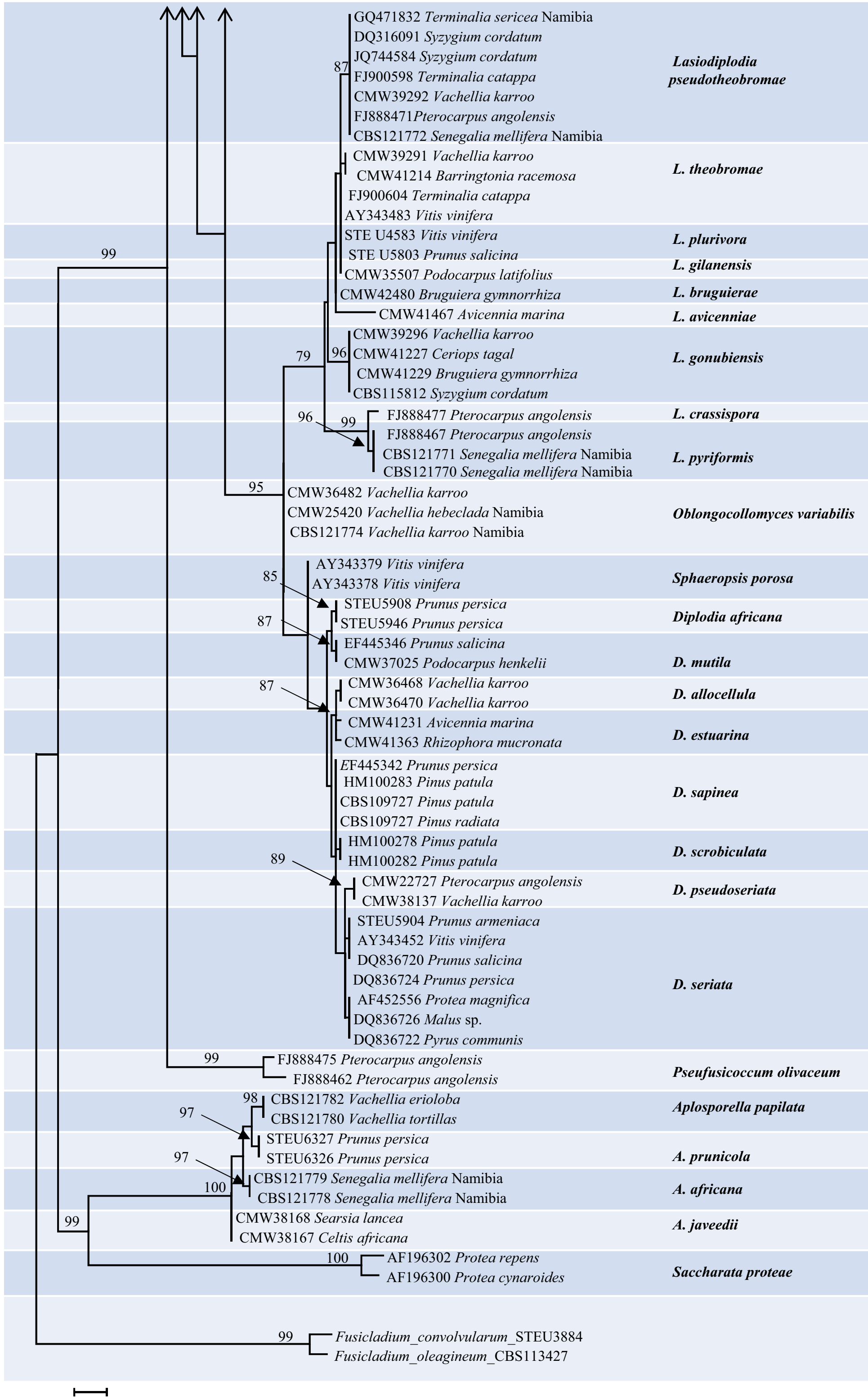


Fig. 1 Maximum Likelihood (ML) tree of ITS ribosomal DNA of Botryosphaeriales. Bootstrap values above 70% are given at the nodes. The tree was rooted to Fusicladium convolvularum and F. oleagineum (STEU3884 and CBS113427)

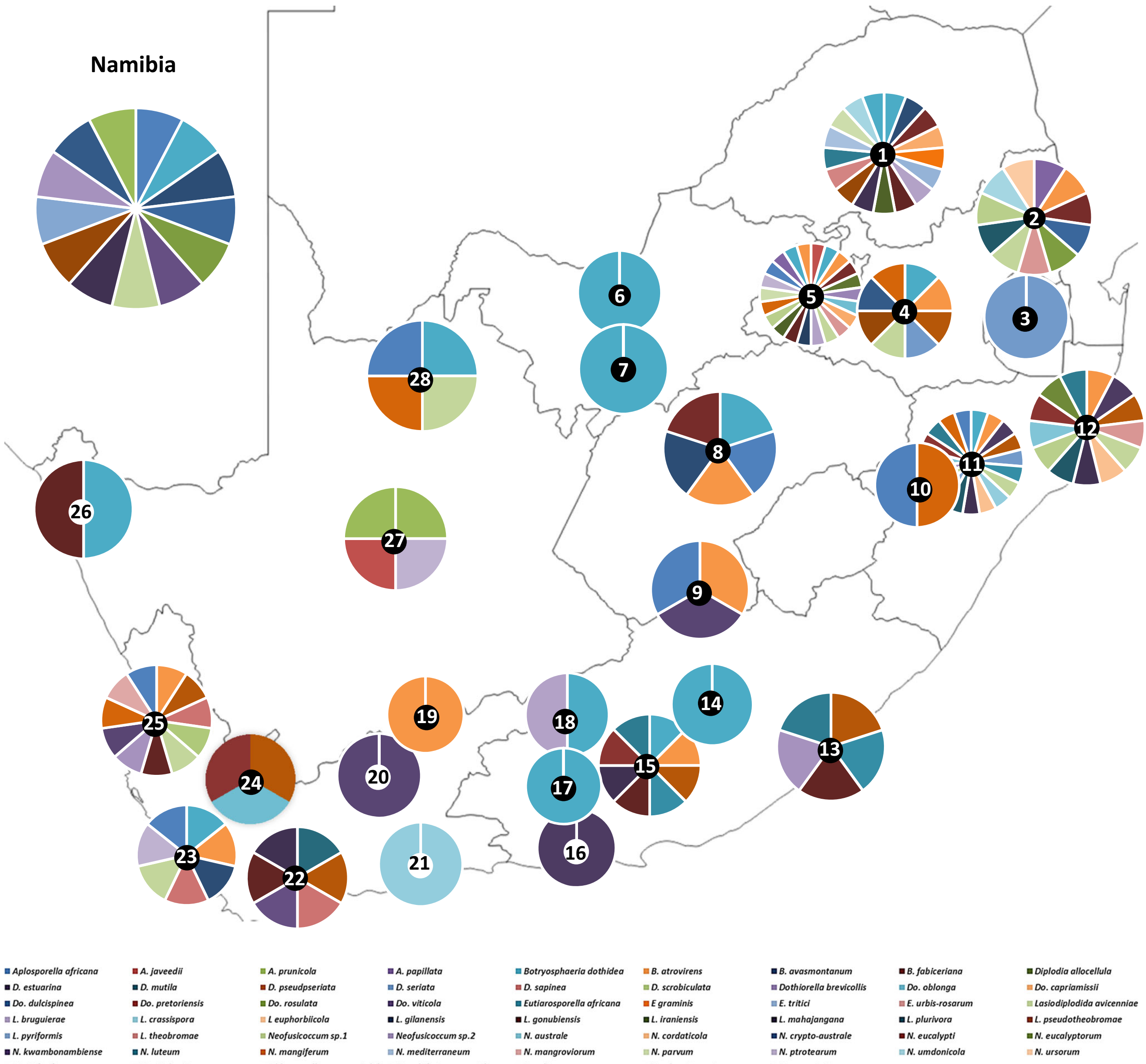


Fig. 2 Diversity of Botryosphaeriales species in each published site in South Africa and Namibia. *South African sites in the map: 1 = Limpopo, Mokopane, Tzaneen (Limpopo Province); 2 = Sabie, Pretoriuskop (Mpumalanga Province), Phalaborwa (Limpopo Province); 3 = Bracken Hill (Swaziland); 4 = Mpumalanga, Piet Retief (Mpumalanga Province); 5 = Pretoria (Gauteng Province), Tweefontein (Mpumalanga Province), Modimolle (Limpopo Province); 6 = Delareyville (North West Province); 7 = Bloemhof (North West Province); 8 = Bloemfontein (Free State Provincce); 9 = Aliwal North (Eastern Cape Province); 10 = Wasbank (KwaZulu-Natal Province); 11 = KwaZulu-Natal Province; 12 = R i c h a r d s Bay, Mkuze, Kwambonambi, Kosi Bay, Sodwana Bay (KwaZulu-Natal Province); 13 = Haga Haga, East London (Eastern Cape Province); 14 = Queenstown (Eastern Cape Province); 15 = Eastern Cape Province; 16 = Humansdorp (Eastern Cape Province); 17 = Jansenville (Eastern Cape Province); 18 = Graaff-Reinet (Eastern Cape Province); 19 = Beaufort West (Western Cape Province); 20 = Calitzdorp, Buffelskloof (Western Cape Province); 21 = George (Western Cape Province); 22 = Hermanus, Elgine, Jonkershoek (Western Cape Province); 23 = Cape Town (Western Cape Province); 24 = Western Cape Province; 25 = Ceres, Swellendam, Robertson (Western Cape Province); 26 = Hondeklip Bay (Northern Cape Province); 27 = Prieska (Northern Cape Province); 28 = Kuruman, Augrabies, Upington (Northern Cape Province)

richness and distribution, an important objective was to consider knowledge gaps, particularly those relating to geographical distribution and host range.

Fig. 3. Symptoms causes by *Botryosphaeriales* species, A. Dieback on *Podocarpus* sp. (Ndove 2015). B, C. Canker and pith discoloration on a *Eucalyptus* stem and branches (Slippers et al. 2009). D. Die-back on *Vachellia* (*Acacia*) *karroo* (Jami et al. 2013)

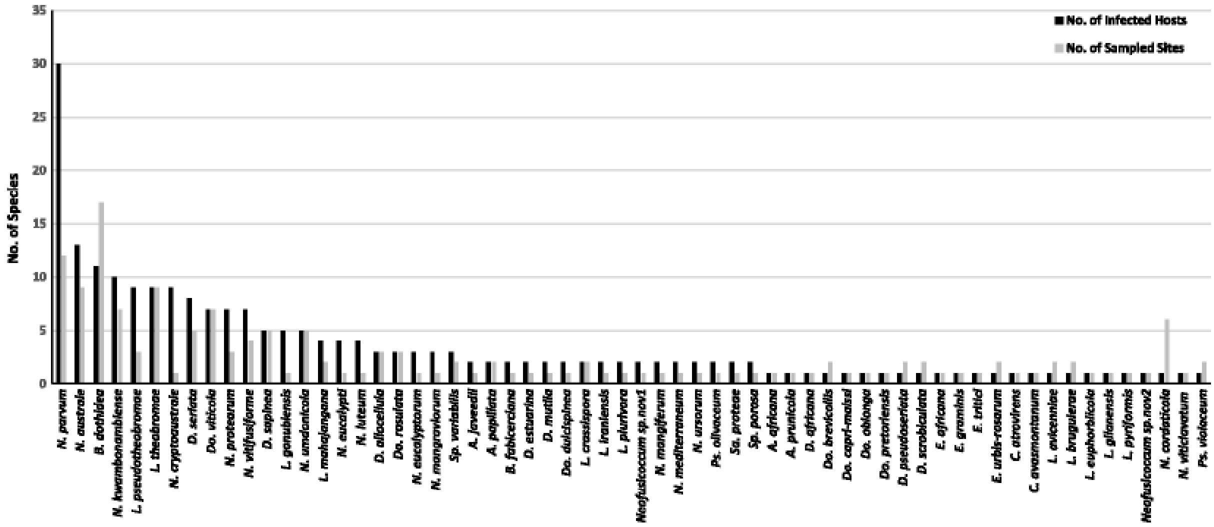


Fig. 4. Frequency of *Botryosphaeriales* species and number of sampled sites (per species) from all previous published studies across South Africa and Namibia on various hosts. Pie charts illustrate the species diversity in each sampled site

Botryosphaeriales associated with native trees

A number of relatively intensive studies have been completed on *Botryosphaeriales* on native trees in South Africa and Namibia. In total, 52 *Botryosphaeriales* species have been characterised from both symptomatic and asymptomatic tissues on 32 native tree species studied in these two countries (Marincowitz et al. 2008; Denman et al. 2003; Begoude et al. 2010; Mehl et al. 2011; Van der Linde et al. 2011; Ndove 2015; Jami et al. 2012, 2013, 2014, 2015; Swart 1986; Osorio et al. 2017; Mehl et al. 2017a; Cruywagen et al. 2017). Of these, 18 species were isolated from *Vachellia* (*Acacia*) species (Jami et al. 2012, 2013, 2014, 2015; Slippers et al. 2014), 14 species were from mangrove trees (Osorio et al. 2017), 12 species from *Syzygium cordatum* (Pavlic et al. 2007), 12 species from *Sclerocarya birrea* subsp. *caffra* (Mehl et al. 2017a), 11 species from *A. mellifera* (Slippers et al. 2014), and nine species from *Adansonia digitata s.l* (Cruywagen et al. 2017) and *Podocarpus* spp. (Ndove 2015) (Table 1).

Canker and die-back are typical symptoms of diseases caused by *Botryosphaeriales* that have commonly been reported from native trees in South Africa. These, however, received little attention until 2004 when the South African government funded an initiative (Centre of Excellence in Tree Health Biotechnology) to specifically study the health of native trees (Steenkamp and Wingfield 2013). Nineteen species of the *Botryosphaeriales* have been reported from diseased tissue taken from native trees in South Africa and Namibia (Table 1), although some might have been associated as secondary pathogens or as saprophytic colonists of the dead tissue. Some species such as *Neofusicoccum parvum* are common and well-known pathogens on numerous hosts, but are also common endophytes existing asymptomatically in many of these studies. Six species on native and non-native hosts that are important include *B. dothidea, Lasiodiplodia theobromae, N. australe, N. parvum, N. kwambonambiense* and *Dothiorella viticola*. These species were particularly common in studies and have been found in both healthy and diseased tissues.

The role of many of *Botryosphaeriales* species in causing diseases is not known. In those cases where inoculation studies have been conducted, species vary in their pathogenicity (Slippers et al. 2017). Given this uncertainty, we consider all the species described from native plants in this section as potential pathogens. On native hosts, inoculation studies with *Botryosphaeriales* have been conducted only on *Avicennia marina, Bruguiera gymnorrhiza, Euphorbia ingens, Pterocarpus angolensis, Podocarpus henkelii, S. cordatum* and *Vachellia* (*Acacia*) *karroo* (Pavlic et al. 2007; Mehl et al. 2011; Jami et al. 2013, 2015; Ndove 2015; Osorio et al. 2017; Van der Linde et al. 2011). These studies have shown all the inoculated species were capable of causing lesions. Although they might be considered as potential pathogens, their epidemiology, particularly under natural conditions remains to be understood. Some produced very small lesions and could play a minor or no role in disease development. The most aggressive species across these studies were *N. mangiferae* on *S. cordatum* (Pavlic et al. 2007), *Lasiodiplodia pseudotheobromae* on *Pterocarpus* (Mehl et al. 2011), *L. theobromae*, *N. australe*, *N. parvum*, *Sphaeropsis variabilis* on *V. karroo* (Jami et al. 2015) and *Neofusicoccum* sp. nov. 2 on *Pt. henkelii* (Ndove 2015) and *L. avicenniae* on *A. marina* (Osorio et al. 2017).

Botryosphaeriales associated with plantation-grown trees

The *Botryosphaeriales* pose an important threat to the productivity of South African forestry. The commercial forestry area in the country includes approximately 1.3 million ha, of which 671,000 ha is planted with pine species (mainly *Pinus patula*, *P. elliottii, P. taeda*), 516,407 ha with eucalypts (mostly *Eucalyptus grandis* or derived hybrids and clones) and 100,606 ha with wattle (*Acacia mearnsii*) (Geldenhuys 1997; Http://www.forestry.co.za/statistical-data/ 2011). These plantations are important sources of structural timber, fuel wood, pulpwood and resin as well as providing employment for large numbers of South Africans. Diseases associated with *Botryosphaeriales* are prominent on all the genera deployed by the South African forestry industry and in some cases have contributed significantly to shaping the industry (Swart and Wingfield 1991). There is no significant forestry industry in Namibia and consequently, these fungi are not relevant in terms of commercial tree planting.

Diplodia sapinea is one of the most important die-back and canker pathogens on pine species worldwide, and this is especially true in South Africa (Swart and Wingfield 1991). The pathogen is particularly important due to its common occurrence, and latent, opportunistic nature of infection (Flowers et al. 2003; Stanosz and Carlson 1996). In infected areas, which include most of South Africa were *Pinus* spp. are planted, this pathogen exists almost ubiquitously within healthy *Pinus* trees as an endophyte (Bihon et al. 2011). When the trees are weakened through wounding by hail, or due to drought or other forms of stress, die-back can be very rapid and dramatic (Swart and Wingfield 1991; Zwolinski et al. 1995; Zwolinski et al. 1990). For example, *P. radiata* is a preferred forestry species, but is also one of the most susceptible *Pinus* species to *D. sapinea,* and it is consequently no longer planted in large areas in South Africa where hail is common (Swart and Wingfield 1991; Smith et al. 1996b).

Diplodia sapinea was introduced into South Africa together with its pine hosts (Swart et al. 1985; Burgess and Wingfield 2002). A number of studies have shown that *D. sapinea* populations are highly diverse and must have been introduced many times (Bihon et al. 2012a; Bihon et al. 2012b; Burgess et al. 2004b; Smith et al. 2000). Bihon et al. (2012b) showed this introduction is unlikely to have been predominantly by seed, and it must consequently have been through seedling imports or other routes. Subsequent spread within the country has been horizontal between established plants, and mostly via rain-splash and wind over relatively short distances (Úrbez-Torres et al. 2010; Epstein et al. 2008; Swart et al. 1987). A cryptic sister species, *D. scrobiculata*, has been reported only once from South Africa, but appears to be rare in comparison to the commonly occurring *D. sapinea* (Burgess et al. 2004a; Bihon et al. 2010).

The *Botryosphaeriales* have been well studied on *Eucalyptus* spp. in many parts of the world, including South Africa (Maleme 2009; Pillay et al. 2013; Slippers et al. 2004; Smith et al. 1996a; Pavlic et al. 2007; Smith et al. 1994), Australia (Burgess et al. 2006; Slippers et al. 2004; Taylor et al. 2009), Chile (Ahumada 2003), China (Chen et al. 2011), Colombia (Rodas et al. 2009), Congo (Roux et al. 2000), New Zealand (Billones-Baaijens et al. 2012), Portugal (Barradas et al. 2016), Spain (Iturritxa et al. 2011), Uganda (Nakabonge 2002), Uruguay (Pérez et al. 2008; Pérez et al. 2009) and Venezuela (Mohali et al. 2007). By 2009, at least 23 species of these fungi had been recorded from *Eucalyptus* in different countries of the world (Slippers et al. 2009). Of these, eight species have been found on *Eucalyptus* spp. in South Africa and many of these have been isolated from diseased plant tissue. For example, *N. australe*, *N. eucalyptorum, N. eucalypticola, N. parvum*, and *N. kwambonambiense* have been identified from die-back and stem cankers in South Africa (Maleme 2009; Slippers et al. 2004; Smith et al. 1996a). Other than *N. australe*, the remaining species are commonly present on *Eucalyptus* in South Africa (Slippers et al. 2009; Pillay et al. 2013).

Several *Botryosphaeriales* species, including *L. theobromae, B. dothidea* and *Diplodia* spp., have been identified from both symptomatic and asymptomatic *A. mearnsii* in South Africa (Roux et al. 1997; Gibson 1975). More recent studies have also revealed the presence of a *Dothiorella* sp. (Synonym: *Spencermartinsia* sp.) (Slippers et al. 2014), *N. australe, N. vitifusiforme* and *Sphaeropsis variabilis* on *A. mearnsii* in South Africa (Van der Linde et al. 2010). Pathogenicity trials have shown that *B. dothidea* and *N. australe* can be important pathogens on *A. mearnsii* (Roux 1998; Van der Linde et al. 2010).

Botryosphaeriales associated with fruit and ornamental trees

Botryosphaeriales are important pathogens of fruit trees. They cause disease symptoms on various plant tissues such as die-back and canker of branches and twigs, leaf necrosis, and post-harvest fruit decay. Namibia does not have a significant fruit industry and consequently there are no studies reported from that country. However, various fruit trees in South Africa are affected (Table 1), including almond, apple, apricot, avocado, citrus, mango, nectarine, peach, pear, plum and prune (Slippers et al. 2007; Damm et al. 2007; Martínez-Minaya et al. 2015; Crous et al. 2000), as well as grapevine that have been well studied in South Africa (Fourie and Halleen 2001; Van Niekerk et al. 2004, 2006, 2010a, b, 2011). Eleven species of *Botryosphaeriales* have been identified from grapevines and 18 species from the other fruit trees in South Africa. Among these species, *N. australe* and *D. seriata* are the most commonly encountered species on stone fruits. All of the identified species have been shown to produce significant lesions in inoculation trials and are considered as potential pathogens, but *Do. viticola* is considered less pathogenic than the other species on fruit trees (Damm et al. 2007).

Botryosphaeriales species are associated with the die-back of ornamental trees such as *Schizolobium parahyba* and *Terminalia catappa* in South Africa (Begoude et al. 2010; Mehl et al. 2014). Three *Botryosphaeriales* species have been identified on these trees, of which *N. parvum* is the most common species. It is important to recognize that the capacity to colonize wood may not always be directly correlated with the ability to cause symptoms such as decline and die-back. This should be more thoroughly explored in future studies.

Host and geographical structure

The numbers of species of *Botryosphaeriales* known from a variety of hosts in South Africa and Namibia has grown significantly in recent years. Here we consider these reports to characterize patterns of host and geographic distribution for this group of fungi in southern Africa.

Host associations

Of the 62 *Botryosphaeriales* species isolated from 66 hosts during the course of the last decade in South Africa and Namibia (Table 1; Fig. 1), 12 have been described as new taxa from non-native hosts and 27 as new from native hosts (Table 1) (Maleme 2009; Pavlic et al. 2004; Denman et al. 2003; Jami et al. 2012, 2014, 2015; Mehl et al. 2014; Osorio et al. 2017). Eleven of the *Botryosphaeriales* species have been isolated from both native and non-native trees in the region, and these represent species with an almost cosmopolitan distribution and very broad host ranges (Fig. 1, Table 1).

The number of hosts from which each *Botryosphaeriales* species has been reported varies significantly. Many species are apparently rare and have been isolated only in low numbers. Their host records might thus be influenced by their rare occurrence, and not necessarily provide a true reflection of their ability to infect other plants. Thirteen *Botryosphaeriales* species have been isolated from only two hosts, and 22 species have been isolated from more than three hosts in South Africa and Namibia. *Neofusicoccum parvum* has been isolated from 30 hosts (14 natives, 16 non-natives) and shows the highest host diversity in South Africa and Namibia. *Neofusicoccum australe* and *B. dothidea* are the next most commonly encountered species, and have been reported from 13 (three natives, nine non-natives) and nine (five natives, four non-natives) different hosts, respectively (Table 1). Interestingly, *N. parvum* and *N. australe* have been found on greater numbers of non-native than native plants in South Africa and Namibia (Table 1).

Of the 66 host plants considered in South Africa and Namibia, 24 were infected with only one species of *Botryosphaeriales* while the remaining tree species were hosts to more than one species (Fig. 4). *Vachellia karroo* as host to 18 *Botryosphaeriales* species had the highest diversity of these fungi in South Africa and Namibia (Slippers et al. 2014; Jami et al. 2015). *Podocarpus henkelii* (Ndove 2015), *Vitis vinifera* (Van Niekerk et al. 2004), *S. cordatum* (Pavlic et al. 2007; Pavlic et al. 2004), *Sclerocarya birrea* subsp. *caffra* (Mehl et al. 2017a) and mangrove trees (Osorio et al. 2017) have also yielded a high diversity of these fungi, ranging from 9 to 14 species each. While these data are interesting, they should be viewed against a background of a greater intensity and breadth of geographical sampling of these hosts compared to others in the region. The data illustrate the extent to which a host plant can be infected by multiple species of *Botryosphaeriales*. For example, Jami et al. (2015) showed that various species of *Botryosphaeria*, *Dothiorella* and *Neofusicoccum* frequently co-occur on *V. karr*oo across South Africa, with ranging from 1 to 8 species per site. If sampled more intensively, the same pattern might be expected for other hosts.

Species distribution

The *Botryosphaeriales* occur throughout southern Africa. While some species occur fairly broadly, others appear to have a limited geographic distribution. It is necessary to be cautious not to over interpret the results of studies conducted thus far because obvious gaps clearly still exist. But the record of occurrence is becoming sufficiently complete to begin to understand some of the emerging patterns of diversity of the *Botryosphaeriales*. Also to consider how these might be related to climate or other factors shaping their distribution (Mehl et al. 2017a).

Botryosphaeria dothidea is one of the most widespread *Botryosphaeriales* species in the world (Marsberg et al. 2017) and it has been found from 17 sites in different parts of South Africa and Namibia (Fig. 2). This species has been found across parts of these countries with climates ranging from Mediterranean, to continental to sub-tropical as well as very dry and desert-like (Http://en.wikipedia.org/wiki/Climate_of_South_Africa 2007; Conradie 2012). This is perhaps not surprising given that recent studies have shown that *B. dothidea* can survive and grow effectively at a broad range of temperatures and its pycnidia appear to be long-lived and produce conidia for at least 6 years (Urbez-Torres et al. 2010; Copes and Hendrix 2004; Michailides and Morgan 1992). As with other species of the *Botryosphaeriales*, rain and wind play an important role in spreading *B. dothidea*, which limits the distance of its distribution. The broad host range, however, would mean that it has a more or less continuous distribution of potential hosts that would make migration between regions possible (Ahimera et al. 2004; van Niekerk et al. 2010b).

Neofusicoccum parvum is the second most widespread species, being reported from 12 sites across South Africa (Fig. 2). This fungus has the widest global distribution and host range and it is one of the most pathogenic *Botryosphaeriales* on woody plants (Slippers and Wingfield 2007). *Neofusicoccum parvum* has been absent from samples collected in the south-western parts of South Africa. It is unlikely that this is host related, because plants such as *V. karoo* sampled in that part of the country are infected by this fungus in other regions (Jami et al. 2015). It is possible that this distribution is weather related, as this is also the driest part of the country (Conradie 2012). Conversely, it is also one of the least sampled areas of the country, which might also have influenced this observed pattern.

Neofusicoccum australe has been reported from 10 countries and 46 hosts and is particularly common in the southwestern parts of Western Australia (Sakalidis et al. 2011; Burgess et al. 2006; Taylor et al. 2009). This species is also one of the dominant *Botryosphaeriales* in South Africa. It is the most widespread species in the country after *B. dothidea* and *N. parvum*, having been reported from nine areas (Fig. 2). This species has been found in both desert and temperate areas of South Africa. In parts of Western Australia, it is common in areas with a Mediterranean climate, with hot and dry summers and cool wet winters (Burgess et al. 2006; Cunnington et al. 2007; Taylor et al. 2009).

Lasiodiplodia theobromae is an important species in South Africa (Fig. 2). This fungus has a wide host range both as endophyte and pathogen (Slippers and Wingfield 2007). It has a world-wide distribution (Punithalingam 1976) and has been reported on more than 500 hosts (Punithalingam 1980), although many of these host reports might refer to cryptic sister species in *L. theobromae* sensu *lato* (Swart 1986; Phillips et al. 2013). Recent studies in South Africa have shown that *L. theobromae* occurs mostly in the northern and western parts of the country (Fig. 2), and not in central and eastern parts (Mehl et al. 2011; Begoude et al. 2010; Pavlic et al. 2007; Van Niekerk et al. 2004; Jami et al. 2015). These patterns are likely due to climate as *L. theobromae* is known to be confined, or most common, in tropical to sub-tropical climates (Mehl et al. 2017a).

A number of recent studies illustrate a high level of anthropogenic movement of *Botryosphaeriales* species around the world (Pavlic et al. 2009; Slippers 2003; Slippers and Wingfield 2007; Sakalidis et al. 2013; Marsberg et al. 2017). For example, *N. parvum* has been reported from 29 countries on 90 hosts (Sakalidis et al. 2013), *B. dothidea* reported from 24 host genera (representing 17 families) and 18 countries and both species exist across six continents (Marsberg et al. 2017). This result suggests strongly that movement of *N. parvum* has been human-mediated irrespective of whether it has been moved from native to non-native hosts or vice-versa. Similarly, *D. sapinea, L. theobromae* and *N. australe*, which are commonly reported in South Africa, have more or less cosmopolitan distributions, and have most likely been moved by humans. The results of studies in South Africa illustrate how widely such species can spread once introduced into a country, including into remote and fairly undeveloped regions such as the Northern Cape (Fig. 2). Unfortunately, this also illustrates the fact that current quarantine measures are entirely unable to restrain the global movement of latent pathogens such as the *Botryosphaeriales* (Burgess et al. 2016).

Conclusions

During the last two decades, focused studies on the *Botryosphaeriales* have revealed 38 new species and genera from South Africa and Namibia. Increasing numbers are also being described as surveys are expanded to new areas and hosts. These fungi have been isolated from a wide range disease symptom on important native and non-native trees in southern Africa. Many species have also been isolated from healthy plant tissues. Whether isolated from healthy or diseased tissue, all the species that have been tested in inoculation trials have been shown to induce lesions and are thus considered to have some degree of pathogenicity. However, studies have also revealed that the pathogenicity for different species is variable and it varies between hosts. There is a clear need to characterize the interaction between *Botryosphaeriales* species, hosts and disease and studies focused on these questions should be encouraged.

The greatest species diversity for the *Botryosphaeriales* has been observed in the Western Cape Province of South Africa with 17 different species occurring there (Fig. 2). The lowest diversity is currently known from the Northern Cape Province (Fig. 2). This might be related to the number of studies in these areas, where most have focused on the Western Cape or the eastern to north-eastern coast of South Africa, and fewer have been done in central or north-western areas. It could also be associated with the greater plant diversity and density in the Western Cape, compared to, for example, the Northern Cape, as well as the harsher (drier) weather conditions in the latter region. However, recent studies on *V. karroo* in South Africa (Jami et al. 2015) showed that the species diversity was higher in the Tshwane Metropolitan Area than elsewhere in South Africa, even after correcting for sampling intensity. It is not clear what drives this increased diversity, but one possibility is that the higher plant diversity in the urban areas that arised via introductions for horticulture. This, together with the higher frequency of trade (with Pretoria as one of the main urban centres in the country), and compared to other sampled sites could influence the surrounding diversity in *Botryosphaeriales*. Other factors, such as the intensive human activities, pollution and physical damage to name just a few possibilities could also influence this pattern of diversity.

The application of molecular tools and particularly DNA sequence based analyses has revolutionized the identification of species in the *Botryosphaeriales* (also see a summary in Slippers et al. 2017). The emerging data has led to a complete revision of the taxonomy of the group including a clear need to re-evaluate previous reports of species, distributions, host associations and other factors relevant to understanding the processes influencing biodiversity patterns. The new technologies have also led to the discovery of a large diversity of species, and new insights into its distribution and host associations. This is especially true in South Africa and Namibia where these fungi have been sampled at least as much, or even more intensively, than in many other parts of the world. No hybrid species have been reported in the region yet, but as Cruywagen et al. (2017) and Rodríguez-Gálvez et al. (2017) have recently shown that this needs to be considered for the Botryosphaeriales and in particular for *Lasiodiplodia* spp.

All the records considered in this review are based on isolations of fungi in culture. It is well known today that many of endophytic fungi either do not grow well in culture, or are easily overlooked because they grow more slowly than other common endophytes. Making isolations is also time consuming and often not practiced with sufficient rigor. An emerging solution to this problem is to use the high-throughput, culture independent and barcoding based approaches of next generation sequencing (Kemler et al. 2013). Such studies will likely be used in the future to map the distribution of *Botryosphaeriales* across regions and different hosts more accurately.

The *Botryosphaeriales* result in asymptomatic infections in their hosts and those species that cause disease usually do so after the onset of stress (Slippers and Wingfield 2007). These fungi clearly form an important natural component of the microbiome, particularly of woody plants. This is sometimes referred to as part of the ‘second genome” (Zenni et al. 2016). The consequence is that these fungi can easily be accidentally moved to new evironments through trade in plants and plant products, including for example fruit (Crous et al. 2016; Burgess and Wingfield 2017). Once they have been introduced into new environments and particularly given the wide host ranges of many species, they are able to infect new hosts via host shifts or range expansions (Slippers et al. 2005; Crous et al. 2012).

It is consequently reasonable to expect that they will be increasingly important as pathogens of woodly plants in the future, both in Southern Africa but also globally.

Acknowledgements

We thank members of the Tree Protection Cooperative Programme (TPCP), the DST/NRF Centre of Excellence in Tree Health Biotechnology (CTHB) and the University of Pretoria, South Africa for financial support.

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Supplementary material

Table2. *Botryosphaeriales* presence/absence in Namibia and South Africa.

		*Sites in South Africa																											
	Namibia	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	9	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**
Aplosporella africana	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. javeedii	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. prunicola	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
A. papillata	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Botryosphaeria dothidea	+	+	+	-	+	+	+	+	+	-	-	+	-	-	+	+	-	+	+	+	-	-	-	-	-	-	+	-	-
B. atrovirens	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
B. avasmontanum	-	+	+	-	+	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
B. fabiceriana	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diplodia allocellula	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
D. estuarina	-	-	-	-	+	-	-	-	-	-	-	+	+	+	-	+	+	-	-	-	-	-	-	-	+	-	-	-	-
D. mutila	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. pseudpseriata	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+	+	+	-	-	-
D. seriata	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. sapinea	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
D. scrobiculata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

		*Sites in South Africa																											
	Namibia	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Dothiorella brevicollis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Do. oblonga	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	-	-	-
Do. capriamissii	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Do. dulcispinea	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Do. pretoriensis	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Do. rosulata	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Do. viticola	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eutiarosporella africana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E graminis	-	+	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E. tritici	-	+	+	-	+	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	+
E. urbis-rosarum	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lasiodiplodida avicenniae	+	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. bruguierae	-	+	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	+	-	-	-	+	-	+	-	+	-	-
L. crassispora	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
L euphorbiicola	-	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. gilanensis	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. gonubiensis	-	+	+	-	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. iraniensis	-	+	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-

		*Sites in South Africa																											
	Namibia	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	9	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**
L. mahajangana	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. pseudotheobromae	+	+	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
L. plurivora	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	-	-
L. pyriformis	+	-	-	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+
L. theobromae	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
***Neofusicoccum* sp.1**	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
***Neofusicoccum* sp.2**	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
N. australe	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. cordaticola	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. crypto-australe	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. eucalyptorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. eucalypti	-	-	-	-	-	+	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	+
N. kwambonambiense	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. luteum	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. mangiferum	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. mediterraneum	-	+	-	-	+	+	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. mangroviorum	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. parvum	-	+	-	-	-	+	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	+

		*Sites in South Africa																											
	Namibia	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	9	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**
N. ptrotearum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. umdonicola	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. ursorum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. vitifusiforme	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. viticlavatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oblongocollomyces variabili	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pseudofusicoccum violaceum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ps. olivaceum	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Saccharata proteae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Spaeropsis Porosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-

* South African sites in the map: **1**= Limpopo, Mokopane, Tzaneen (Limpopo Province); **2**= Sabie, Pretoriuskop (Mpumalanga Province), Phalaborwa (Limpopo Province); **3**= Bracken Hill (Swaziland); 4= Mpumalanga, Piet Retief (Mpumalanga Province); **5**= Pretoria (Gauteng Province), Tweefontein (Mpumalanga Province), Modimolle (Limpopo Province); **6**= Delareyville (North West Province); **7**= Bloemhof (North West Province); **8**= Bloemfontein (Free State Provincce); **9**= Aliwal North (Eastern Cape Province); **10**= Wasbank (KwaZulu-Natal Province); **11**= KwaZulu-Natal Province; **12**= Richards Bay, Mkuze, Kwambonambi, Kosi Bay, Sodwana Bay (KwaZulu-Natal Province); **13**= Haga Haga, East London (Eastern Cape Province); **14**= Queenstown (Eastern Cape Province); **15**= Eastern Cape Province; **16**= Humansdorp (Eastern Cape Province); **17**= Jansenville (Eastern Cape Province); **18**= Graaff-Reinet (Eastern Cape Province); **19**= Beaufort West (Western Cape Province); **20**= Calitzdorp, Buffelskloof (Western Cape Province); **21**= George (Western Cape Province); **22**= Hermanus, Elgine, Jonkershoek (Western Cape Province); **23**= Cape Town (Western Cape Province); **24**= Western Cape Province; **25**= Ceres, Swellendam, Robertson (Western Cape Province); **26**= Hondeklip Bay (Northern Cape Province); **27**= Prieska (Northern Cape Province); **28**= Kuruman, Augrabies, Upington (Northern Cape Province).