REVIEW



Current status of the Botryosphaeriaceae in Australia

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Abstract

The Botryosphaeriales, and in particular the Botryosphaeriaceae, are a well-studied group of fungi best known for the canker diseases they cause on woody hosts especially in stressed or damaged trees. Australian Plant Pathology herbaria contain many records for this group, but due to considerable taxonomic changes over the past decade, many of the species names have since been reclassified. In this article we used all published records with available sequence data of the Botryosphaeriaceae in Australia to examine the distribution and host range of these taxa. There are 24 genera encompassing 222 species in the Botryosphaeriaceae; 9 genera and 62 species have been recorded in Australia. Some genera such as *Neoscytalidium* are only found in warm, humid climates while *Dothiorella* species are more common in temperate climates. There were species, such as *Lasiodiplodia theobromae*, *Neofusicoccum parvum* and *Botryosphaeria dothidea*, which had a wide host range with many records. However, there were also several species found only in one location on a single host. While systematic data collection is still required, the information presented here provides a baseline of species present in Australia and will underpin future studies into this group of important pathogens.

Keywords Lasiodiplodia · Neofusicoccum · Dothiorella · Mangifera indica · Vitis vinifera · Phylogenetic conservatism

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Fungi within the Botryosphaeriales have global distribution with a wide range of hosts. They are best known for the diseases they cause in cultivated trees, as primary pathogens or latent pathogens residing in the woody tissue of asymptomatic hosts (Slippers and Wingfield 2007). The Botryosphaeriales have been subjected to numerous molecular systematic and taxonomic revisions in recent years resulting in the recognition of many new species and new species complexes. In the most recent review of the Botryosphaeriales, Slippers et al. (2017) listed nine families, 33 genera and 279 species based on DNA sequences. Since then, the number species has increased to over 300. The Botryosphaeriaceae is the largest family within the Botryosphaeriales (Yang et al. 2017).

Most historical records for this family found in pest databases and mycological collections provided names assigned on the basis of morphological identification or host association. Fungal taxonomy has since been revolutionised by the application of DNA sequencing methods. Jacobs and Rehner (1998) first applied DNA sequence analysis for the Botryosphaeriaceae and confirmed that the sexual and asexual morphs of many species were the same organism, and thus reduced many names to synonymy. DNA sequences have also revealed many species to actually represent complexes of phylogenetically distinguishable, but morphologically indistinguishable cryptic species (Pavlic et al. 2009; Sakalidis et al. 2011b). Yang et al. (2017) sequenced over 100 isolates initially identified by morphology and deposited as Botryosphaeria sp. and Dothiorella sp. in the culture collection of the Westerdijk Fungal Biodiversity Centre (CBS). They found the isolates represented 36 species, with several in other genera, namely Diplodia, Lasiodiplodia, Macrophomina and Neofusicoccum. There is an urgent need to validate herbaria records where identifications have been based on morphology (Tan et al. 2018).

While members of the Botryosphaeriales occur on many hosts, some are highly host specific with limited geographical distribution, while others have a broad distribution and host range (Slippers and Wingfield 2007). In general, those taxa recovered in agriculture and forestry tend to be distributed widely, often across continents (Sakalidis et al. 2013). For example, Neofusicoccum parvum and Lasiodiplodia theobromae have been found on over 90 and 50 hosts, respectively, from all continents except Antarctica (Mehl et al. 2017; Sakalidis et al. 2013). Some widespread species have a limited host range, for example, Diplodia sapinea, which is usually found on conifers (Bihon et al. 2012; de Wet et al. 2008). Taxa recovered from natural ecosystems are often known from just a single region and often only a single host. For example Dothiorella casuarinae (De Wet et al. 2009), Dothiorella santali (Taylor et al. 2009) and Dothiorella acacicola (Crous et al. 2016) are named after their hosts, while Dothiorella californica (Lawrence et al. 2017), Dothiorella italica (Dissanayake et al. 2017) and *Dothiorella pretoriensis* (Jami et al. 2015) have, so far, only been found in the region after which they are named.

There is no accurate phylogeographic pattern for the Botryosphaeriales, although it has been suggested that some genera are more common in different climates, for example *Diplodia* in temperate regions (Burgess and Wingfield 2002) and *Lasiodiplodia* in tropical and sub-tropical regions (Burgess et al. 2006; Mohali et al. 2005). However, Jami et al. (2017) found both *Diplodia* and *Lasiodiplodia* occurred in sub-tropical and temperate regions in South Africa. Recent studies on *Botryosphaeria dothidea* (Marsberg et al. 2017), *L. theobromae* (Mehl et al. 2017) and *N. parvum* (Sakalidis et al. 2013) did not find a phylogeographic pattern for these species.

In this overview, we have gathered data for all records of the Botryosphaeriaceae in Australia that have been verified by DNA sequence analysis. We have compiled a database which includes host, location and climate and have addressed the following questions: (1) Are there common and rare species?; (2) Is there evidence for species with broad or narrow host ranges?; (3) Is there evidence for species with broad or narrow geographic ranges?; and (4) Is the distribution of genera influenced by climate?

Data sources and analyses

All records in databases without associated sequence data were disregarded. The database of Botryosphaeriaceae used in this study was compiled from published literature with additional data obtained as an outcome of a symposium (Botryosphaeriaceae Menace: Taxonomy, Disease Impact, Ecology & Management held on 25 Sep. 2017 in association with Science Protecting Plant Health 2017), and from the Queensland Plant Pathology Herbarium (BRIP) and the Victorian Plant Pathology Herbarium (VPRI), where identifications are routinely made based on sequence identity. Accessions were also included from the Murdoch University Culture Collection (MUCC). Sequence data were obtained for a representative isolate of each species present in Australia and an alignment of the concatenated internal transcribed spacer (ITS) region and the translation elongation factor 1-alpha (tef1 α) gene was generated in Geneious R10 (Biomatters Ltd). Pseudofusicoccum species known from Australia were included as outgroup taxa. Phylogenetic analyses of sequence data were performed within Geneious software using MrBayes plugin for Bayesian analysis. The identity of all Dothiorella, Lasiodiplodia and Neofusicoccum species was confirmed by phylogenetic analyses. Genbank accession numbers for new BRIP and VPRI accessions are given in Appendix S1. Where available the host and location of each isolate is also provided. Isolates were also assigned to a climatic zone based on temperature and humidity as found at the Australian Bureau of Meteorology (Fig. 1 http://www.bom.gov.au/jsp/ncc/ climate_averages/climate-classifications/index.jsp).

To examine phylogenetic conservatism in the distribution of species in the Botryosphaeriaceae (in other words, the degree to which related species are on the average more or less likely to occupy similar climate/geographic zones relative to random species pairs) we performed the following steps. First, Principal Components Analysis (PCA) was used to convert the species × climate zone presence-absence matrix (Fig. 2, boxes) into two uncorrelated, quantitative metrics corresponding to the first two principal component axes (PC1 and PC2). PC1 accounted for 41% of the variance in distribution within zones among species and PC2 for an additional 20%. We then calculated local Moran's I values for pairwise phylogenetic distances between species as well as global metrics of phylogenetic signal in our data, and produced auto-correlation diagrams using phylogenetic distance as the "spatial" component, with 95% CI's derived using non-parametric bootstrapping. Finally, we overlayed local Moran's I values for each species to visualize regions or clades on the tree where trait correlations were more strongly positive or negative than expected by chance. All of these approaches treat climate zone distribution as a trait which is not strictly the case (although underlying traits like thermal tolerance and temperature-dependent growth rate contribute strongly). As such, we prefer evolutionary model-free metrics like C_{mean} and Moran's I in our interpretations. All analyses were performed using the phylosignal package in R (Keck et al. 2016; R Core Team 2017).

Species in Australia

A database containing 551 accessions was compiled; 504 in the Botryosphaeriaceae and the additional 47 accessions are for



Fig. 1 Climatic zones in Australia based on temperature and humidity adapted from Australian Bureau of Meteorology (BOM)



Fig. 2 Phylogram of concatenated ITS and tefl α sequence data for Botryosphaeriaceae known from Australia. *Pseudofusicoccum* species were also included as outgroup taxa. The climatic zones where each species has been reported is given on the right. Colours for climatic zones are given in Fig. 1

Pseudofusioccum, Saccharata and Aplosporella (Appendix S1). Molecular taxonomic studies have identified 24 genera in the Botryosphaeriaceae, of which 9 are represented in Australia (Table 1). To date, the following genera are not known in Australia, Alanphillipsia, Bahusutrabeeja, Barriopsis, Botryobambusa, Cophinforma, Kellermania, Marasasiomyces, Mucoharknessia, Neodeightonia, Oblongocollomyces, Phaeobotryon, Sakireeta, Sardiniella and Umthunziomyces. Although Sphaeropsis has previously been recorded in Australia, S. sapinea has since been renamed Diplodia sapinea. Of the 222 species found globally, 62 are found in Australia. Most of the species found in Australia are from the large common genera, namely Botryosphaeria, Diplodia, Dothiorella, Lasiodiplodia, Neofusicoccum, and Neoscytalidium.

Host association

Most host records (>98%) are for woody crop plants and forestry plantations including *Mangifera indica*, various *Eucalyptus* and *Pinus* species, *Persea americana* and *Vitis vinifera* (Appendix S1). There have been very few studies in natural ecosystems, restricted predominantly to Western Australia (Sakalidis et al. 2011a; Taylor et al. 2009). It is possible to make some host observations, for example, *N. australe* is widely distributed within natural ecosystems, while *N. parvum* has only been recovered from woody crops and exotic urban trees.

Common species including *B. dothidea*, *N. parvum*, *L*. *pseudotheobromae* and *L. theobromae* that are widely

Family	Genus	Year	Species	Australia
Botryosphaeriaceae	Alanphillipsia	2013	7	0
Botryosphaeriaceae	Bahusutrabeeja	1977	1	0
Botryosphaeriaceae	Barriopsis	2008	5	0
Botryosphaeriaceae	Botryobambusa	2012	1	0
Botryosphaeriaceae	Botryosphaeria	1863	7	3
Botryosphaeriaceae	Cophinforma	2012	3	0
Botryosphaeriaceae	Diplodia	1834	23	5
Botryosphaeriaceae	Dothiorella	1880	38	14
Botryosphaeriaceae	Eutiarosporella	2015	7	3
Botryosphaeriaceae	Kellermania	1885	19	0
Botryosphaeriaceae	Lasiodiplodia	1896	38	15
Botryosphaeriaceae	Macrophomina	1923	2	1
Botryosphaeriaceae	Marasasiomyces	2015	1	0
Botryosphaeriaceae	Mucoharknessia	2015	2	0
Botryosphaeriaceae	Neodeightonia	1970	7	0
Botryosphaeriaceae	Neofusicoccum ^a	2006	37	17
Botryosphaeriaceae	Neoscytalidium	2006	4	2
Botryosphaeriaceae	Oblongocollomyces	2016	1	0
Botryosphaeriaceae	Phaeobotryon	1915	4	0
Botryosphaeriaceae	Sakireeta	1957	1	0
Botryosphaeriaceae	Sardiniella	2016	2	0
Botryosphaeriaceae	Sphaeropsis	1880	9	0
Botryosphaeriaceae	Tiarosporella	1919	2	2
Botryosphaeriaceae	Umthunziomyces	2016	1	0
Aplosporellaceae	Alanomyces	2017	1	0
Aplosporellaceae	Aplosporella	1880	16	1
Aplosporellaceae	Bagnisiella	1880	1	0
Endomelanconiopsisaceae	Endomelanconiopsis	2008	2	0
Melanopsaceae	Melanops	1870	1	0
Pseudofusicoccumaceae	Pseudofusicoccum	2006	7	3
Saccharataceae	Saccharata	2004	20	8
Septorioideaceae	Septorioides	2013	2	0
Phylostictaceae	Phyllosticta	1818	39	nd

^a includes *Dichomera versiformis* which resides in the Neofusicoccum clade

Table 1Genera in theBotryosphaeriales known fromDNA sequence, the year of firstdescription, the total number ofspecies and the number of speciesreported for Australia

associated as pathogens of woody crops globally, are also widely distributed on these crops in Australia (Appendix S1). However, there are also many species, especially those isolates from natural ecosystems, which appear to have a limited host range. There is also evidence for the local acquisition of Botryosphaeriaceae from adjacent native vegetation. In order to make such observations, sampling must be conducted both in the orchards and in the adjacent native vegetation. This has been done for *Mangifera indica*, in the isolated Kimberley region of northern Western Australia (the Kimberleys) (Table 2). Thirty two species of Botryosphaeraceae (plus *Pseudofusicoccum*) have been reported globally from *M. indica* (Table 2, Appendix S2). Of those reported from outside Australia, only *L. theobromae* was found in both the Kimberleys and in Queensland. Two common global species, *B. dothidea* and *N. parvum*, were found in Queensland orchards, but were not found in the Kimberleys. Most species recovered from *M. indica* in the Kimberleys (90%) were also recovered from adjacent native vegetation and many of these species are known to be endemic to the region (Table 2).

Grape, *Vitis vinifera*, is host to a large number of Botryosphaeriaceae, many of which are associated with symptoms such as cankers and dieback of the vine and fruit rots. In 2011, at least 21 species of Botryosphaeriaceae had been identified from *V. vinifera* worldwide (Úrbez-Torres 2011). The number continues to grow, with currently 65

Species	Northern WA Native	Northern WA Mango	Queensland Mango	World Mango ^a
Barriopsis iraniana				+
Botryosphaeria dothidea			+	+
Botryosphaeria ramosa	+			
Botryosphaeria sinensis			+	
Botryosphaeria fabicercianum				+
Botryosphaeria scharifii				
Cophinforma mamane				+
Dothiorella longicollis	+			
Lasiodiplodia crassispora	+	+		+
Lasiodiplodia exigua	+			
Lasiodiplodia egyptiacae				+
Lasiodiplodia horomozganensis	+			+
Lasiodiplodia iraniensis	+	+		+
Lasiodiplodia mahajangana	+	+		
Lasiodiplodia margaritaceae	+			
Lasiodiplodia parva	+	+		
Lasiodiplodia pseudotheobromae		+		+
Lasiodiplodia theobromae	+	+	+	+
Neofusicoccum austral				+
Neofusicoccum brasiliense				+
Neofusicoccum luteum			+	
Neofusicoccum mangiferae			+	
Neofusicoccum mangroviorum			+	
Neofusicoccum mediterraneum				+
Neofusicoccum parvum			+	+
Neoscytalidium dimidiatum	+	+		+
Neoscytalidium novaehollandiae	+	+		
Pseudofusicoccum adansoniae	+	+		
Pseudofusicoccum ardesiacum	+	+		
Pseudofusicoccum kimberleyense	+	+	+	
Pseudofusicoccum olivaceum				+
Pseudofusicoccum stromaticum				+

^a Literature used for world data found in Appendix S2

 Table 2
 The horticultural host

 Mangifera indica has different
 endophytic and pathogenic

 species in the Botrysphaeriaceae
 and Pseudofusicoccumaceae

 depending on location and
 climate

species reported from Vitis species worldwide (Farr and Rossman 2018). In 2015, Pitt et al (2015) reported that 10 species had been identified from V. vinifera growing in Australia, but they cautioned the taxonomy of this group of fungi is rapidly changing and identities frequently became uncertain or questionable in light of new knowledge. Our database presented here identifies 18 species from the genera Botryosphaeria, Diplodia, Dothiorella, Lasiodiplodia and Neofusicoccum from V. vinifera were verified as present in Australia (Table 3). Six species (Do. neclivorem, Do. omnivora, Do. plurivora, Do. vidmadera, Do. vinea-gemmae and Do. westralis) have not been reported outside Australia to date. Diplodia mutila, D. seriata, L. citricola and N. australe were found in three or more States, but the other 14 species were found only in one or two States. B. dothidea, Do. neclivorem, Do. vinea-gemmae and N. parvum were restricted to NSW; L. viticola was restricted to Queensland and is the only species confirmed from V. vinifera in that region; Do. iberica, Do. omnivora, Do. plurivora and Do. vidmadera were unique to South Australia; N. luteum was unique to Victoria, and Do. westralis, L. plurivora and L. pseudotheobromae were unique to Western Australia. Nine of the 18 species (from Dothiorella and Lasiodiplodia) were only recorded from V. vinifera, while the other species are known from other woody hosts (Table 3).

Phylogeographic distribution

N. parvum, N. australe and *B. dothidea* are the most commonly reported species in Australia, representing 16, 13 and 5% of records respectively (Appendix S1). These are recovered from numerous hosts, especially woody field crops. The next most common species are *Ne. novaehollandiae, D. seriata, N. occulatum, L. pseudotheobromae, Ne. dimidiatum, L. theobromae, D. sapinea* and *D. mutila.*

A few common species have a very wide distribution across many climatic zones both in the tropics and in temperate regions, most notably *B. dothidea* and *N. parvum* (Fig. 2). Other species found across tropical and temperate regions are *L. iranensis*, *L. pseudotheobromae*, *N. luteum* and *N. occulatum* (Fig. 2). However, the majority of species are confined to either tropical regions with high humidity or temperate regions with cold winters (Fig. 2). *Neoscytalidium*, *Pseudofusicoccum* and most *Lasiodiplodia* species are more commonly found in tropical regions while *Diplodia*, *Dothiorella*, *Eutiarosporella*, and most *Neofusicoccum* species are more common in temperate regions (Figs. 2, 3).

Overall there was evidence for moderate phylogenetic signal in the distribution of the Botryosphaeriaceae, particularly in some genera. Strong clustering can be seen for *Dothiorella* species as well as a part of *Lasiodiplodia* (Fig. 4a). Other clades (e.g., the *Neofusicoccum*) are more broadly disturbed across climate zones and do not cluster in PCA space. Overall

Species	WA	VIC	SA	NSW	QLD	WORLD ^b
Botryosphaeria dothidea				+		+
Diplodia mutila	+		+	+		+
Diplodia seriata	+	+	+	+		+
Dothiorella iberica ^a			+			+
Dothiorella neclivorem				+		
Dothiorella omnivore			+			
Dothiorella plurivora ^a			+			
Dothiorella vidmadera ^a			+			
Dothiorella vinea-gemmae ^a				+		
Dothiorella viticola ^a			+	+		+
Dothiorella westralis ^a	+					
Lasiodiplodia citricola ^a		+	+	+		+
Lasiodiplodia plurivora ^a	+					+
Lasiodiplodia pseudotheobromae	+					+
Lasiodiplodia viticola ^a					+	+
Neofusicoccum australe	+	+	+	+		+
Neofusicoccum luteum		+				+
Neofusicoccum parvum				+		+

^a Only reported on Vitis vinifera in Australia

^b many other species reported globally from *Vitis* (Farr and Rossman 2018)

Table 3 There are currently 18verified species from five generain the Botrysphaeriaceae infectingthe host Vitis vinifera in Australia,some of which are known onlyfrom Vitis and/or Australia

Fig. 3 The relative proportion of each genus within the Botryosphaeriaceae (and *Pseudofusicoccum*) in each climatic zone. The number of genera reported for each zone is given at the top of the bar. Colours for climatic zones are given in Fig. 1





Fig. 4 Phylogenetic clustering of climatic distribution in the Botryosphaeriaceae (**a**) Principal Component Analysis (PCA) plot showing species (circled, colored by genus/clade); (**b**) phylogenetic correlogram showing mean local Moran's I (correlation) estimates for

climate indices 1 and 2 as a function of phylogenetic distance calculated from the tree in Fig. 2; and (c) table showing estimates of global phylogenetic signal (Abouheif's C_{mean} , Moran's I, and Pagel's λ)

we detected significant phylogentic autocorrelation up to a tree distance of 0.077 (Fig. 4b), roughly corresponding to the subgeneric level. For reference, Do. moneti and Do. casuarina or N. cordaticola and N. pennatisporum are separated by approximately this distance. Phylogenetic signal was detected globally across the tree for both climate distribution index 1 and 2 (PC1 and PC2; Fig. 4c) and was approximately twice as strong for the former, irrespective of metric. Finally, both positive and negative correlations were detected in local Moran's I estimates (Fig. S1). For some groups (e.g., Lasiodiplodia) these tended to be negative (for climate index 1), and as such very closely related species within this genus are less likely to overlap strongly in distribution than expected by chance. Alternatively, some sub-clades within Neofusicoccum and Dothiorella tended to show positive correlations (more overlap). Climate index 2 also showed some local Moran's I values, including some strong negative correlations within the Botryosphaeria and Neofusicoccum.

Conclusion

A systematic survey of the Botryosphaeriaceae in Australia remains to be completed. The data we have assembled has some inbalances; for example, New South Wales, Tasmania and South Australia were under represented. Additionally, a disproportionate number of records were from woody crops, especially grapes and mangoes. The fungal communities in natural ecosystems are understudied in Australia. Based on a series of studies in natural ecosystems in Western Australia, it is expected that further novel and rare species with narrow distributions and host specificity will be found. However, based on the data available, the following conclusions can be drawn. In Australia, there are common and rare species of Botryosphaeriaceae. The common species tend to have broad host ranges and wide distribution, the rare species tend to have limited number of known hosts and a restricted distribution. The distribution of genera is influenced by climate, in particular there are species with tropical or temperate preferences.

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