

# Global geographic distribution and host range of *Dothistroma* species: a comprehensive review

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#### Summary

Dothistroma needle blight (DNB) is one of the most important diseases of pine. Although its notoriety stems from Southern Hemisphere epidemics in *Pinus radiata* plantations, the disease has increased in prevalence and severity in areas of the Northern Hemisphere, including Europe, during the last two decades. This increase has largely been attributed to expanded planting of susceptible hosts, anthropogenic dispersal of the causative pathogens and changes in climate conducive to disease development. The last comprehensive review of DNB was published in 2004, with updates on geographic distribution and host species in 2009. Importantly, the recognition that two species, *Dothistroma septosporum* and *D. pini*, cause DNB emerged only relatively recently in 2004. These two species are morphologically very similar, and DNA-based techniques are needed to distinguish between them. Consequently, many records of host species affected or geographic location of DNB prior to 2004 are inconclusive or even misleading. The objectives of this review were (i) to provide a new database in which detailed records of DNB from 62 countries are collated; (ii) to chart the current global distribution of *D. septosporum* and *D. pini*; (iii) to list all known host species and to consider their susceptibility globally; (iv) to collate

the published results of provenance trials; and (v) to consider the effects of site factors on disease incidence and severity. The review shows that DNB occurs in 76 countries, with *D. septosporum* confirmed to occur in 44 and *D. pini* in 13. There are now 109 documented Pinaceae host taxa for *Dothistroma* species, spanning six genera (*Abies*, *Cedrus*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga*), with *Pinus* being the dominant host genus, accounting for 95 host taxa. The relative susceptibilities of these hosts to *Dothistroma* species are reported, providing a resource to inform species choice in forest planting. Country records show that most DNB outbreaks in Europe occur on *Pinus nigra* and its subspecies. It is anticipated that the collaborative work described in this review will both underpin a broader global research strategy to manage DNB in the future and provide a model for the study of other forest pathogens.

## 1 | INTRODUCTION

*Dothistroma* needle blight (DNB) is one of the most damaging foliage diseases in natural pine stands and plantations worldwide (Barnes, Crous, Wingfield, & Wingfield, 2004; Bulman, Ganley, & Dick, 2008; Jankovský, Bednářová, & Palovčíková, 2004; Karadžić, 1989a). The disease first emerged as a serious problem in the 1950s and 1960s in plantations of *Pinus radiata* in the Southern Hemisphere and on a number of pine species in North America (Gibson, 1972, 1974). It significantly curtailed large-scale pine planting of *P. radiata* in East Africa (Gibson, 1974) and India (Bakshi & Singh, 1968) and continues to be a major constraint for pine plantation forestry in New Zealand, Chile and other areas of the Southern Hemisphere (Ahumada, 2013; Bulman et al., 2013; Rodas, Wingfield, Granados, & Barnes, 2016). Since the 1990s, DNB has increased in incidence and severity in the Northern Hemisphere, especially in Canada and, more recently, in some European countries (Barnes, Wingfield, Carbone, Kirisits, & Wingfield, 2014; Bradshaw, 2004; Drenkhan, Hantula, Vuorinen, Jankovský, & Müller, 2013; Hanso & Drenkhan, 2008; Markovskaja & Treigienė, 2009; Millberg, Hopkins, Boberg, Davydenko, & Stenlid, 2016; Müller, Hantula, & Vuorinen, 2009; Solheim & Vuorinen, 2011; Welsh, Lewis, & Woods, 2014). The rising incidence and severity of DNB in the Northern Hemisphere has been linked to changing climatic conditions, particularly higher temperatures and changes in precipitation patterns conducive for disease development (Hanso & Drenkhan, 2013; Watt, Kriticos, Alcaraz, Brown, & Leriche, 2009; Welsh et al., 2014; Woods et al., 2016).

The causal agents of DNB are ascomycete fungi that have undergone a number of taxonomic name changes (Barnes et al., 2004, 2016). Up until 2004, DNB was considered to be caused by one pathogen species with occasional variety designations (Sutton, 1980). It was interchangeably referred to in the literature as either *Dothistroma septospora* (*septosporum*), *Dothistroma pini*, *Mycosphaerella pini* or *Scirrhia pini*. Taxonomic clarity was established when Barnes et al. (2004) showed that isolates causing DNB reside in two different phylogenetic lineages representing distinct species. The two species were named

*D. pini* Hulbary, representing the lineage that was found in the USA after the description of Hulbary (Hulbary, 1941), and *D. septosporum* (Dorogin) M. Morelet, representing the lineage that included isolates from many different parts of the world, including Europe. Following the "One fungus, one name" rule of fungal nomenclature, earlier sexual names for *D. septosporum* (*Mycosphaerella pini* and *Scirrhia pini*), are no longer valid (Crous, Hawksworth, & Wingfield, 2015; Hawksworth, 2011). As it currently stands, DNB is caused by either one of two fungal species: *D. pini* Hulbary, designated with an epitype from Michigan, the USA, and *D. septosporum* (Dorogin) M. Morelet, designated with a neotype from St. Petersburg, Russia (Barnes et al., 2016).

*Dothistroma* needle blight occurs in almost every country where susceptible hosts are found, a range that includes climates from tropical to subarctic (Watt et al., 2009). Although *D. septosporum* is reported to have a worldwide distribution, its exact distribution based on reports validated using molecular methods has never been mapped. In contrast, *D. pini* appears to have a more limited geographic distribution based on reports from north-central USA and Europe (Barnes, Kirisits, Wingfield, & Wingfield, 2011; Barnes, Walla, Bergdahl, & Wingfield, 2014; Barnes et al., 2004; Barnes, Kirisits et al., 2008; Ios et al., 2010; Piškur, Hauptman, & Jurc, 2013; Queloz, Wey, & Holdenrieder, 2014; Siziba et al., 2016). Similarly, although more than 82 pine species, as well as a growing number of non-pine species in the Pinaceae, have been recorded as hosts of *Dothistroma* species (Bednářová, Palovčíková, & Jankovský, 2006; Drenkhan, Adamson, Jürimaa, & Hanso, 2014; Watt et al., 2009), the exact number of hosts affected by each of the pathogen species is unknown. There is no single body of literature that synthesizes all the current knowledge regarding the distribution and host range of the two DNB pathogens.

An ongoing problem for researchers dealing with DNB is that it is not possible to know which species was being studied or referred to in some of the literature published prior to 2004, particularly from the Northern Hemisphere, where both species are now known to co-occur in some regions. Furthermore, *D. septosporum* and *D. pini* produce similar symptoms on their hosts (Barnes et al., 2011) and it is almost impossible to discriminate between the two pathogens based on

morphological characteristics (Anonymous, 2008; Barnes et al., 2004). DNA-based identification techniques, including direct sequencing of gene regions such as the Internal Transcribed Spacer (ITS) region (Barnes et al., 2016) therefore remain the only reliable option for the correct determination of species of *Dothistroma* (Barnes et al., 2011, 2016; loos et al., 2010). loos et al. (2010) developed conventional and real-time PCR methods for the rapid detection of *D. septosporum* and *D. pini*, as well as *Lecanosticta acicola* (Thüm.) Syd., the brown spot needle blight pathogen with which the DNB pathogens are often confused. These methods can be used to identify species associated with DNB outbreaks and also to validate species directly from herbarium specimens or collections linked to older literature (Fabre, loos, Piou, & Marçais, 2012).

The incidence and severity of DNB is strongly influenced by both environmental/climatic conditions (Peterson, 1973; Woods, Coates, & Hamann, 2005; Woods et al., 2016) and host susceptibility (Fraser, Woodward, & Brown, 2015; Ivory, 1968; Rodas et al., 2016). Moisture is a key environmental factor, as DNB outbreaks occur in areas or years with high levels of summer rainfall or frequent warm rain events (Woods et al., 2005, 2016). Host species and provenance also affect DNB severity with several reports of both inter- and intraspecific variation in susceptibility to *Dothistroma* species (e.g. Cobb & Miller, 1968; Fraser, Woodward et al., 2015; Ivory, 1968). The relative susceptibility of host species and provenances often varies across sites (Fraser Mullett, Woodward, & Brown, 2016; Watt et al., 2009). This variability demonstrates the importance of the interactions between pathogen, host and environment in defining DNB severity. Collating information on these three factors, particularly host susceptibility, will contribute to the development of management guidelines for foresters.

The speed at which new reports of DNB have appeared over the last two decades, and the suggestion that increased incidence may be related to changes in climate, pathogen virulence and/or anthropogenic movement of infected plant material is of great concern. Developing new tactics to manage and limit the impact of this globally important disease is clearly important. To accomplish this goal, it is essential to consolidate knowledge of the global distribution of both *D. septosporum* and *D. pini*, their host ranges, as well as host susceptibility and environmental factors that affect disease severity. Consequently, an important objective of this review has been to collate so-called grey literature, together with more accessible literature, to provide a summary of the host and geographic distribution of the DNB pathogens. An important secondary goal is to highlight disease trends at both spatial and temporal scales. Although a global framework is presented, the main focus is on highlighting recent trends in Europe, consistent with the goals and objectives of the DIAROD EU COST Action FP1102 (Determining Invasiveness And Risk Of Dothistroma, [http://www.cost.eu/COST\\_Actions/fps/Actions/FP1102?](http://www.cost.eu/COST_Actions/fps/Actions/FP1102?)).

A practical and ongoing outcome of the work described here is a new database with an interactive map including historical and updated monitoring information for DNB, available at <http://arcgis.mendelu.cz/monitoring/>. The map provides detailed information for the locations where DNB has been reported and, where molecular confirmation of the pathogen is available, the species causing the disease is mapped.

## 2 | The geographic range of DNB and its causal agents

Dothistroma needle blight occurs across a wide range of climates (Watt et al., 2009) showing that the disease agents tolerate highly variable climatic conditions (see section 5). The last published synthesis of the distribution of DNB was by Watt et al. (2009) who documented the presence of the disease in 61 countries. Due to the problems associated with identifying the species of *Dothistroma* involved, the specific distributions of the two DNB pathogens were not differentiated. Results of collated publications and reports from 40 countries in collaboration with DIAROD (see Supporting Information) have provided the most comprehensive documented distribution of DNB to date and, more specifically, the global distribution of both pathogens causing this disease. In compiling this review, we found that DNB occurs in 76 different countries (Table 1; Figs 1 and 2). New country reports since Watt et al., (2009) include those from Belarus, Belgium, Estonia, Finland, Latvia, Lithuania, Netherlands, Norway, Russia (including Far East Russia), Sweden, Turkey, Bhutan, Kazakhstan and Bolivia (see Table 1 for references). Although Nicaragua and North Korea were reported to have DNB (Watt et al., 2009), we found no evidence or valid references to support these claims; however *L. acicola* (often confused with *Dothistroma* species) was reported as present in Nicaragua (Evans, 1984). In terms of species distribution, *D. septosporum* has a worldwide distribution, having been confirmed using molecular methods in 44 countries across Europe, Asia, the Americas, Africa and Oceania (Table 1; Fig. 2). In contrast, *D. pini* has a substantially restricted distribution, having only been detected in 13 countries on two continents in the Northern Hemisphere: North America (in the USA) and Europe.

An interactive map generated in this study, and available at <http://arcgis.mendelu.cz/monitoring/>, currently contains the geographic co-ordinates of 3232 sampling or observation records (as well as records for 37 countries and states where geographical co-ordinates are not known) and documents the presence of both species in 76 countries. These data are summarized in Table 1, Figs 1 and 2. Below we highlight key trends in disease distribution for each continent, with a major focus on Europe.

### 2.1 | Europe

Dothistroma needle blight has been recorded in 35 of 50 European countries, with *D. septosporum* and *D. pini* confirmed, using molecular methods, in 29 and 12 of these countries, respectively (Table 1; Fig. 2). The oldest record of DNB from Europe, and in fact in the world, comes from herbarium samples collected in Denmark in 1880 (Munk, 1957). Inspection of herbarium collections from France suggests that DNB has also been present in north-eastern France since 1907 (Fabre et al., 2012). The first description of the pathogen (as *Cytosporina septospora* Dorogin) causing DNB was made from *Pinus montana* (a synonym of *Pinus mugo*) samples collected in north-west Russia in 1910 (Doroguine, 1911), and symptoms of DNB were also present on herbarium samples of *P. sylvestris* collected by L. Kaznowski in 1914 in the Kiev region

**TABLE 1** The geographic distribution of *Dothistroma* needle blight in different countries including the date the disease was first recorded.

Continent/Country/ State	Year DNB was first recorded	References	DS	DP	References
<b>Africa</b>					
Ethiopia	1972	Gibson (1972)			
Kenya	1960	Gibson et al. (1964)	*		Barnes et al. (2004)
Malawi	1961	Bates (1962)			
South Africa	1965	Gibson (1972)	*		Barnes et al. (2004)
Swaziland	1967	Gibson (1972)			
Tanzania	1957	Gibson et al. (1964)			
Uganda	1964	Gibson et al. (1964)			
Zambia	1994	Ivory (1994)			
Zimbabwe	1943	Gibson et al. (1964)			
<b>Asia</b>					
Bhutan	2005	Barnes, Kirisits et al. (2008)	*		Barnes, Kirisits et al. (2008)
Brunei	1972	Peregrine (1972)			
China	1987	Ivory (1987)			
India	1968	Bakshi and Singh (1968)			
Japan	1952	Ito et al. (1975)			
Kazakhstan	1992	Arapova (1992)			
Nepal	1985	Ivory (1990)			
Pakistan	1986	Zakaullah and Abdul (1987)			
Philippines	1987	Ivory (1987)			
Russian Far East	2014	Barnes et al. (2016)	*		Barnes et al. (2016)
South Korea	1983	Kim and Yi (1984)			
Sri Lanka	1987	Ivory (1987)			
Turkey (Asian part)	2013	F. Oskay, unpubl. data	*		F. Oskay, unpubl. data
<b>Europe</b>					
Austria	1960	Petrak (1961)	*		Barnes et al. (2004)
Belarus	2012	V. Zviagintsev, unpubl. data	*		S. Markovskaja and A. Kačergius, unpubl. data
Belgium	2007	EPPO (2008)	*	*	Schmitz, Gischer, and Chandelier (2013)
Bosnia-Herzegovina	1988	Karadžić (1989a)			
Bulgaria	1977	Zlatanov (1977)			
Croatia	1963	Milatović (1976)			
Czech Republic	2000	Jankovský, Šindelková, and Palovčíková (2000)	*	*	Tomšovský et al. (2013); Bergová and Kryštofová (2014); Barnes et al. (2016)
Denmark	1880	Munk (1957); Evans (1984)	*		Barnes et al. (2016)
Estonia	2006	Hanso and Drenkhan (2008)	*		Hanso and Drenkhan (2008)
Finland	2007	Müller et al. (2009)	*		Müller et al. (2009)
France	1907	Morelet (1968); Fabre et al. (2012)	*	*	loos et al. (2010)
Georgia	1965	Shishkina and Tsanova (1966b)			
Germany	1983	Butin and Richter (1983)	*		Barnes et al. (2004)
Greece	1969	Kailidis and Markalas (1981)	*		Tsopelas, Barnes, Soulioti, and Wingfield (2013)
Hungary	1990	Szabó (1997); Koltay (1997)	*	*	Barnes, Kirisits et al. (2008); Barnes et al. (2011)
Italy	1976	Magnani (1977)			
Latvia	2008	Drenkhan and Hanso (2009)	*		Drenkhan and Hanso (2009); Kiesnere (2014)
Lithuania	2002	Jovaišienė and Pavilionis (2005)	*		A. Kačergius and S. Markovskaja, unpubl. data
Macedonia	1980	Papazov (1988)			
Montenegro	1979	Karadžić (1986)	*	*	Lazarević, Davidenko, and Millberg (2015)
Netherlands	2007	EPPO (2007)	*		Quaedvlieg et al. (2012)
Norway	2009	Solheim and Vuorinen (2011)	*		Solheim and Vuorinen (2011)
Poland	1990	Kowalski and Jankowiak (1998)	*		Barnes et al. (2004)
Portugal	1984	Neves, Moniz, De Azevedo, Ferreira, and Ferreira (1986)	*		H. Bragança, unpubl. data
Portugal incl. Azores	1979	Fonseca (1980)	*		H. Bragança, unpubl. data
Romania	1968	Gremmen (1968)	*	*	Barnes, Wingfield et al. (2014); Barnes et al. (2016)

(Continues)

TABLE 1 (continued)

Continent/Country/ State	Year DNB was first recorded	References	DS	DP	References
Russia	1910	Doroguine (1911)	*	*	Barnes, Kirisits et al. (2008); Musolin et al. (2014)
Serbia	1955	Krstić (1958); Karadžić (1986)	*	*	Galovic et al. (2011, 2015); N. Keča, R. Drenkhan, H. Solheim, unpubl. data.
Slovakia	1996	Kunca and Foffová (2000)	*		Barnes et al. (2004)
Slovenia	1971	Maček (1975)	*	*	Piškur et al. (2013)
Spain	1974	Fernández (1975)	*	*	Ortiz de Urbina et al. (2015); Barnes et al. (2016)
Sweden	2007	Millberg et al. (2016)	*		Millberg et al. (2016)
Switzerland	1989	A. Angst, unpubl. data	*	*	Queloz et al. (2014)
Turkey	2013	F. Oskay, unpubl. data	*		F. Oskay, unpubl. data
Ukraine	1914	Barnes et al. (2004); Barnes, Kirisits et al. (2008)	*	*	Groenewald et al. (2007); Davydenko (2014)
United Kingdom					
England	1954	Murray and Batko (1962)	*		Barnes et al. (2016)
Northern Ireland	2014	D. Craig, unpubl. data	*		D. Craig, unpubl. data
Scotland	1985	British Mycological Society <sup>a</sup>	*		Barnes et al. (2016)
Wales	1958	Brown and Webber (2008)	*		M. S. Mullett, unpubl. data
Oceania					
Australia					
New South Wales	1975	Edwards and Walker (1978)	*		Barnes et al. (2004)
Queensland	1980	Eldridge, Dowden, and Lind (1980)			
Tasmania	1984	Podger (1984)	*		Prihatini et al. (2015)
Victoria	1979	Marks (1981)			
New Zealand	1964	Gilmour (1965)	*		Barnes et al. (2004)
Papua New Guinea	1997	EPPO (2015)			
North America					
Canada					
Alberta	1999	Reid, Mathur, Basu, and Penner (1999)			
British Columbia	1941	DAVFP <sup>e</sup> record 2077	*		Barnes et al. (2004); Dale et al. (2011)
Manitoba	1966	Elliott, Laut, and Brandt (1967)			
Newfoundland	2000	Pfister, Halik, and Bergdahl (2000)			
Ontario	1991	Myren (1991)			
Quebec	2000	Pfister et al. (2000)			
Saskatchewan	1966	Elliott et al. (1967)			
Jamaica	1982	Evans (1984)			
Mexico	1979	Gibson (1979)			
United States of America			*		Barnes et al. (2016)
Alaska	1982	Peterson (1982)			
Arizona	1973	Peterson (1973)			
California	1967	Cobb and Miller (1968)			
Colorado	Unknown	Widely prevalent fungi of the United States <sup>b</sup>			
Delaware	Unknown	Widely prevalent fungi of the United States <sup>b</sup>			
Florida	1975	Anonymous (1977)			
Hawaii	1987	Ivory (1987)			
Idaho	1917	Evans (1984)	*		Barnes et al. (2004)
Illinois	1917	Saccardo (1920); Peterson (1982)			
Indiana	1973	Peterson (1982)		*	Barnes, Walla et al. (2014)
Iowa	1934	Hulbary (1941)			
Kansas	1951	Rogerson (1953); Peterson (1982)			
Kentucky	1973	Peterson (1982)			
Maryland	1973	Peterson (1982)			
Michigan	1973	Peterson (1982)		*	Barnes et al. (2004)
Minnesota	1971	Nicholls and Hudler (1971)		*	Barnes et al. (2004)
Missouri	1973	Peterson (1982)			
Montana	1914	Thyr and Shaw (1964)	*		Barnes, Walla et al. (2014)
Nebraska	1950	Peterson (1967b)		*	Barnes et al. (2004)



TABLE 1 (continued)

Continent/Country/ State	Year DNB was first recorded	References	DS	DP	References
New Hampshire	1988	NAPIS <sup>c</sup>			
New Mexico	2006	Fairweather, McMillin, Rogers, Conclin, and Fitzgibbon (2006)			
New York	1992	NAPIS <sup>c</sup>			
North Dakota	2010	Barnes, Walla et al. (2014)		*	Barnes, Walla et al. (2014)
Ohio	1932	Hulbary (1941)			
Oklahoma	1934	Hulbary (1941)			
Oregon	1972	Peterson and Harvey (1976)	*		Barnes et al. (2004)
Pennsylvania	1982	Peterson (1982)			
South Dakota	2011	Barnes, Walla et al. (2014)		*	Barnes, Walla et al. (2014)
Tennessee	1989	NAPIS <sup>c</sup>			
Texas	1991	NAPIS <sup>c</sup>			
Vermont	1994	Pfister et al. (2000)			
Virginia	1972	Skelly (1972)			
Washington	1973	Peterson (1981)			
Wisconsin	1973	Peterson (1981)			
Central America					
Costa Rica	1980	Ford (1982); Evans (1984)			
Guatemala	1983	Evans (1984)	*		Groenewald et al. (2007)
Honduras	1981	Evans (1984)			
South America					
Argentina	1968	Fresa (1968)			
Bolivia	1995	Herb IMI 367865 <sup>d</sup>			
Brazil	1969	Figueiredo and Namekata (1969)	*		Groenewald et al. (2007)
Chile	1965	Dubin and Staley (1966)	*		Barnes et al. (2004)
Colombia	2008	Rodas et al. (2016)	*		Rodas et al. (2016)
Ecuador	1982	Evans and Oleas (1983)	*		Barnes et al. (2004)
Peru	1979	Gibson (1979)			
Uruguay	1967	Peterson (1969)			

\*Indicates if the identity of either pathogen, DS for *Dothistroma septosporum*, and DP for *D. pini*, was identified in the country using molecular methods.

<sup>a</sup>British Mycological Society. The Fungal Records Database of Britain and Ireland. <http://www.fieldmycology.net/FRDBI/FRDBIrecord.asp?intGBNum=7910>.

<sup>b</sup>Widely prevalent fungi of the United States. <http://www.prevalentfungi.org/subject.cfm?id=688>.

<sup>c</sup>NAPIS = National Agricultural Pest Information System, Purdue University. "Survey Status of Dothistroma needle blight - *Dothistroma septosporum* (All years)." Published: 06/02/2015. <http://pest.ceris.purdue.edu/map.php?code=FBAVDDX&year=alltime>. Accessed: 06/02/2015.

<sup>d</sup><http://www.herbimi.info/herbimi/specimen.htm?imi=367865>.

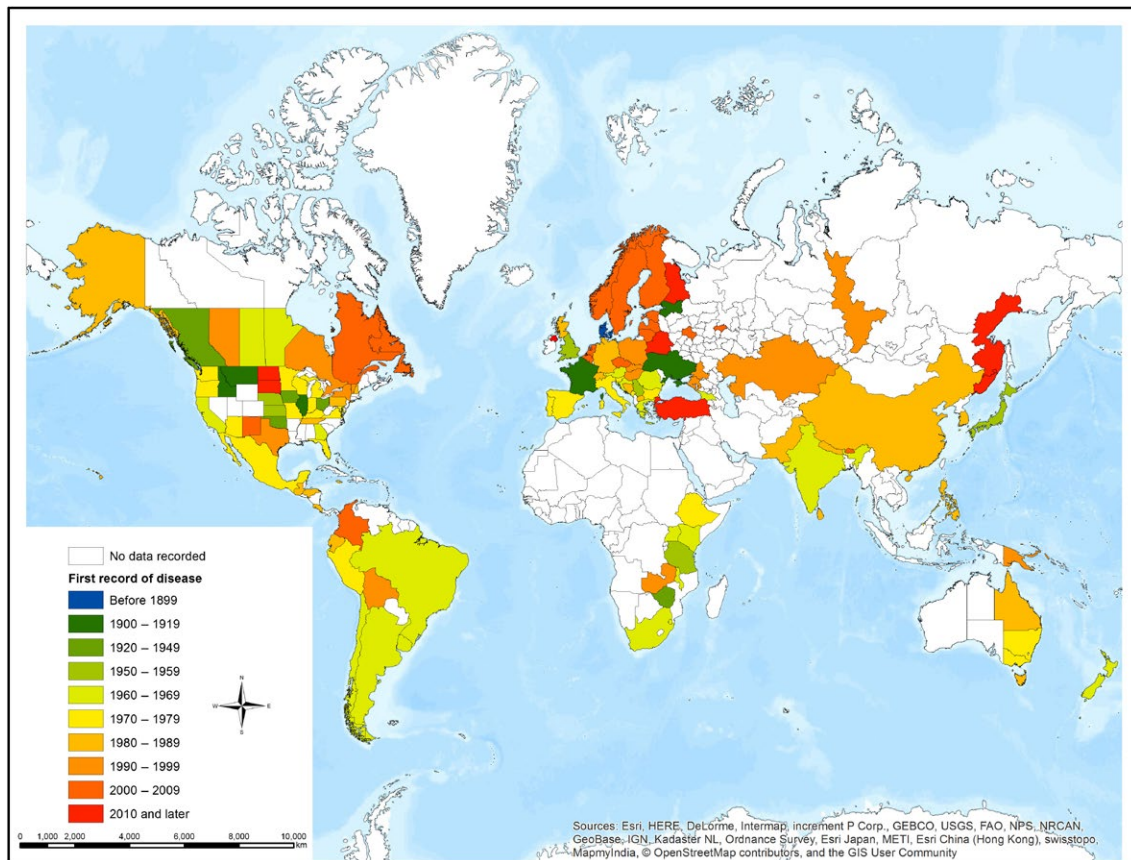
<sup>e</sup>DAVFP (Department of Agriculture, Victoria, Forest Pathology): Fernando, A.; Ring, F.; Lowe, D.; Callan, B., 1999: Information Report BC-X-385 "Index of plant pathogens, plant-associated microorganisms and forest fungi of British Columbia" [http://cfs.nrcan.gc.ca/herbarium/fungus/2071?lang=en\\_CA](http://cfs.nrcan.gc.ca/herbarium/fungus/2071?lang=en_CA).

of Ukraine. Unfortunately, all the original herbarium material from Denmark and Russia has been lost, and molecular confirmation of the species causing the disease on the old herbarium specimens from Ukraine has not been successful. It is therefore still unknown which of the two *Dothistroma* species was responsible for these early records of DNB in Europe.

After the first description of the DNB pathogen in 1911 (Doroguine, 1911), no new observations of DNB were made in Europe until 1954 when the disease was found on *P. nigra* and *Pinus ponderosa* nursery stock in England (Murray & Batko, 1962). In 1955, DNB was found on *P. nigra* in Serbia (Krstić, 1958). Between the 1960s and 1980s, reports of DNB also came from several southern and central European countries (Fig. 1; Table 1), but no serious damage was reported. It was only during the 1990s that the incidence and severity of DNB increased dramatically in several areas of Europe (Villebonne & Maugard, 1999; Brown & Webber, 2008; see also Supporting Information). A new record of DNB in Lithuania in 2002 (Jovaišienė & Pavilionis, 2005) marked the

start of a rapid increase in reports of the disease in the Baltic countries and Fennoscandia between 2006 and 2009 (Hanso & Drenkhan, 2008; Millberg et al., 2016; Müller et al., 2009; Solheim & Vuorinen, 2011). The disease is now widespread and commonly encountered in these countries (Drenkhan & Hanso, 2009; Markovskaja & Treigienė, 2009; Millberg, 2015; Müller et al., 2009). Molecular identification of samples collected from the abovementioned countries in recent years has confirmed the presence of *D. septosporum* (Table 1).

The presence of *D. pini* in Europe spans an area from Spain to Russia (Table 1; Fig. 2). The first record of *D. pini* was based on isolates collected in Ukraine (2004) and Russia (2006) on *P. nigra* subsp. *pallasi* (Barnes, Kirsits et al., 2008). However, the oldest record of *D. pini* was on *P. sylvestris* herbarium material collected in France in 1907 and recently confirmed using real-time PCR methods (Fabre et al., 2012). About half of the reports of DNB from France in recent years are associated with *D. pini*, with the pathogen being mostly present in the southern part of the country (Fabre et al., 2012). *Dothistroma septosporum*



**FIGURE 1** The global distribution of *Dothistroma* needle blight (DNB) according to the date the disease was first recorded (see Table 1). DNB is confirmed based on literature and molecular methods, including 37 states and territories without geographical co-ordinates. The global emergence of the disease in time is shown in an additional interactive link “First record of DNB” on the monitoring map legend: <http://arcgis.mendelu.cz/monitoring/>

occurs in all countries of Europe where *D. pini* has been reported. In the majority of these cases, both pathogens have been found in the same regions (Fig. 2, see interactive map) and can even co-occur on the same needle (Barnes et al., 2011; Piškur et al., 2013).

To date, DNB has not been reported in fifteen European countries. These countries include Albania, Andorra, Armenia, Azerbaijan (partly in Asia), Cyprus, Iceland, Republic of Ireland, Kosovo, Liechtenstein, Luxembourg, Malta, Republic of Moldova, Monaco, San Marino and Vatican City. Many of these countries are small, where the number of susceptible species is low or the forest area is limited (e.g. Iceland has a forest area of only 0.3%). In other countries, however, where the forest area is larger (e.g. 43% in Liechtenstein and 28% in Albania) and where conifer species grow naturally or are cultivated (Karoles & Relve, 2013), *Dothistroma* species are probably present, but have not yet been detected, most likely due to limited forest surveillance for this disease. This is probably also the case for the Republic of Ireland, where *Pinus contorta* is a commonly used forest plantation species, given that DNB was observed in Northern Ireland in 2014 (D. Craig, unpublished data).

## 2.2 | Asia

*Dothistroma* needle blight has been reported in 13 Asian countries (Table 1, Fig. 2); however, little is known regarding the distribution

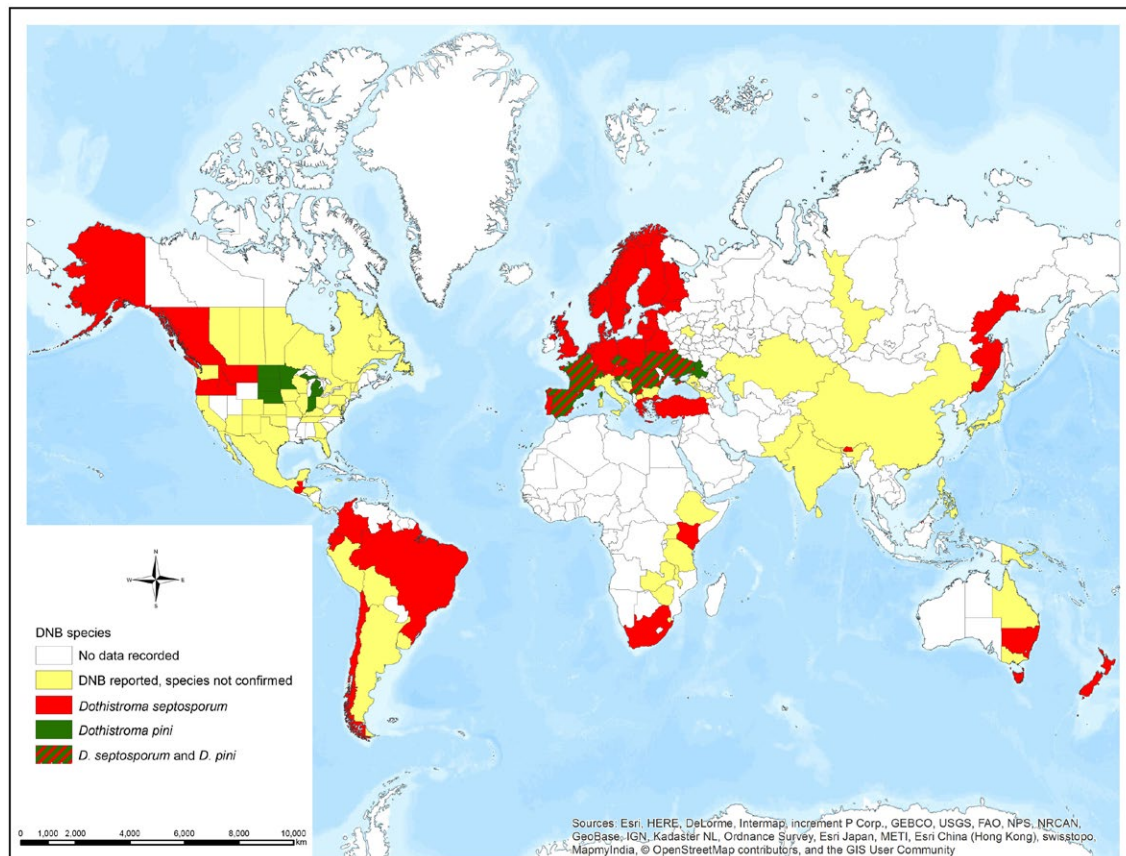
of the *Dothistroma* species on this continent. The presence of *D. septosporum* has been confirmed in Bhutan (Barnes, Kirisits et al., 2008) and Far East Russia (Barnes et al., 2016), but the causal agent of DNB in the other Asian countries is unknown. *Dothistroma pini* has never been reported in the region.

The first observation of DNB in Asia was in 1952 from Japan (Ito, Zinno, & Suto, 1975), where it was mostly found on exotic pine species in Honshu and Hokkaido. Ito et al. (1975) also found DNB on two native species, *P. densiflora* and *P. thunbergii*, although serious damage was not observed. The disease was subsequently reported in India on exotic *P. radiata*, where it led to the abandonment of this species for forestry (Bakshi & Singh, 1968). Later, DNB was reported in Brunei (Peregrine, 1972) and on native *P. wallichiana* in high altitude areas in Nepal (Ivory, 1990) (Fig. 2).

## 2.3 | North America

In North America, DNB has been reported from the USA, Canada, Mexico and Jamaica (Table 1; Fig. 1). DNB was recorded in Mexico in 1979 and in Jamaica in 1982 (Evans, 1984; Gibson, 1979), but the causal agents in these countries have not been determined. In the USA, the disease has been reported in 34 of the 50 states (Table 1; Fig. 2). The earliest reports of DNB in the USA were from *P. ponderosa* needles collected in 1914 from Montana (Thyr





**FIGURE 2** The geographic distribution of *Dothistroma* needle blight (DNB). Molecular methods were used to identify the causal agents of DNB: species are shown by different colours. Where this information was not available, the presence of DNB (identified using morphological methods) is shown (see map: <http://arcgis.mendelu.cz/monitoring/>)

& Shaw, 1964) and from Idaho and Illinois in 1917 on *P. ponderosa* (Evans, 1984; Saccardo, 1920). In the USA, *D. septosporum* has been confirmed only in the north-western states of Idaho, Montana and Oregon (Barnes et al., 2004; Barnes, Walla et al., 2014) and it has not emerged as a serious problem in these areas. In contrast, the first molecular confirmation of *D. pini* in 2004 was based on isolates obtained from Michigan, Nebraska and Minnesota, all affecting *P. nigra* subsp. *nigra* plantations (Barnes et al., 2004). Subsequent to these reports, *D. pini* has now been confirmed as present in six states (Barnes, Walla et al., 2014; Table 1), all of which are located in north-central USA, where *D. septosporum* has never been detected.

The first record of DNB in Canada was in 1963 from Vancouver Island (Parker & Collis, 1966). Surveys across British Columbia (BC) between 1964 and 1966 showed that the disease was widely distributed on *P. contorta* in the province (Parker & Collis, 1966). Reports in the Canadian Forest Insect and Disease Survey (FIDS) database suggest that DNB was present on *P. contorta* in north-west BC as early as 1941 and possibly as early as 1900 (DAVFP Collections Database). Dendrochronological studies, however, indicate that DNB has been present in the northern temperate forests of British Columbia at least as early as 1831 (Welsh, Lewis, & Woods, 2009; Welsh et al., 2014). The disease has been recorded in seven of the 10 Canadian provinces

(Table 1; Fig. 1) and has caused extensive defoliation and mortality in *P. contorta* var. *latifolia* plantations since the 1990s (Welsh et al., 2009; Woods et al., 2005). The pathogen responsible for these disease epidemics in British Columbia was confirmed to be *D. septosporum* (Barnes et al., 2004; Dale, Lewis, & Murray, 2011).

## 2.4 | Central America

*Dothistroma* needle blight has been documented in three Central American countries (Table 1; Fig. 1). The first record of DNB in Central America was from Costa Rica in 1980 on young plantation trees of *P. caribaea* (Evans, 1984; Ford, 1982). In Honduras, the disease was reported in 1981 on *P. maximinoi* (Evans, 1984) and in Guatemala, in 1983 on several native pine species, including *P. maximinoi*, *P. michoacana*, *P. oocarpa* and *P. tecunumanii* (Evans, 1984). Only *D. septosporum* has been confirmed to occur in Central America, where it was isolated in Guatemala (Barnes et al., 2016; Groenewald et al., 2007).

## 2.5 | South America

In South America, DNB has been recorded in eight of twelve countries, including Argentina, Bolivia, Brazil, Chile, Colombia, Ecuador,

Peru and Uruguay (Table 1; Fig. 1). The first report of DNB was from Chile in 1965 where plantations of susceptible *P. radiata* were infected (Dubin & Staley, 1966). The majority of the reports of DNB in South America occurred in the 1960s, including those from Uruguay (Peterson, 1969), Argentina (Fresa, 1968) and Brazil (Figueiredo & Namekata, 1969; Groenewald et al., 2007). In Colombia, the disease was first observed in 2008 on *P. tecunumanii*, *P. keyisia* and *P. oocarpa* (Rodas et al., 2016). Only *D. septosporum* is known to occur in South America, where it has been confirmed as present in Brazil, Chile, Colombia and Ecuador (Barnes et al., 2004; Groenewald et al., 2007; Rodas et al., 2016; see Table 1).

## 2.6 | Africa

*Dothistroma* needle blight has been present on the African continent since at least the early 1940s, having been observed on *P. radiata* herbarium material collected in Zimbabwe in 1943 (Gibson, Christensen, & Munga, 1964). The disease was subsequently recorded in eight more of the 57 African countries, including Ethiopia, Kenya, Malawi, South Africa, Swaziland, Tanzania, Uganda and Zambia (Table 1; Fig. 1). The DNB epidemic in East Africa led to the abandonment of *P. radiata* plantation forestry (Gibson, 1972). Among the above reports, the pathogen causing the disease has been confirmed in only two countries: *D. septosporum* is present in Kenya and South Africa (Barnes et al., 2004). In all other cases, the species responsible for the disease has not been confirmed, but the distribution and association with non-native *P. radiata* suggests that only *D. septosporum* is causing DNB in Africa.

## 2.7 | Oceania

In Oceania, DNB has been found in New Zealand, Australia and Papua New Guinea (Table 1; Fig. 1). In New Zealand, DNB was recorded for the first time in 1964 (Gilmour, 1965) on planted *P. radiata* and is now widespread throughout the country. In Australia, DNB was first observed in 1975, also affecting *P. radiata* plantations (Edwards & Walker, 1978). The disease in Australia seems to be limited to the Australian Capital Territory, New South Wales, Queensland, Tasmania and Victoria (Podger, 1984; Reddy, Puri, Singh, & Pandey, 1976). In both these countries, only *D. septosporum* has been identified (Barnes et al., 2004; Prihatini, Glen, Wardlaw, & Mohammed, 2015). Nothing is known regarding the DNB agent in Papua New Guinea.

## 3 | Origin, sexual reproduction and population structure of *Dothistroma* species

Host specific pathogens are more likely to be native to areas in which their hosts are native (Gilbert, 2002). Before it was known that two species cause DNB, *Dothistroma* was hypothesized to have originated within either the cloud forests of Central America (Evans, 1984) or in the Himalayas (Ivory, 1994). In Central America, Evans (1984) found both the asexual and sexual state of *Dothistroma* and

suggested that *Dothistroma* co-evolved with indigenous pine species, such as *P. caribaea*, *P. devoniana*, *P. maximinoi* and *P. tecunumanii* in that region. In the Himalayas, Ivory (1994) discovered the pathogen in remote native *P. wallichiana* stands, hundreds of miles from known outbreak areas and, therefore, postulated that *Dothistroma* must be native to this area. Gibson (1974) and Evans (1984) suggested that *Dothistroma* was also native on pines in parts of Europe and North America. Consideration of the early literature and herbarium material shows that *Dothistroma* has been present on both these continents for over 100 years (see section 2.1 and 2.3 above).

An understanding of the origin as well as the occurrence and extent of sexual reproduction within the *Dothistroma* species can aid in management of DNB. At the centre of origin, the host and pathogen may have co-evolved, resulting in less susceptible hosts and, overall, low levels of disease. Thus, this area may serve as a source of less susceptible provenances or genotypes for future breeding programmes. In areas where *Dothistroma* species are introduced, their reproductive strategy governs how adaptive they can be. *Dothistroma* species are heterothallic, where individuals carry a gene of either mating type (*MAT1-1-1* or *MAT1-2* idiomorphs), and individuals of both mating types are required for sexual reproduction to occur (Groenewald et al., 2007). Sexual reproduction, and the associated genetic recombination, can give rise to haplotypes with novel gene combinations, some of which may increase virulence, overcome resistance mechanisms or be better suited to new environments (McDonald & Linde, 2002; McDonald, Mundt, & Zhan, 1999). In contrast, purely clonal reproduction allows less opportunity for such adaptation.

The possible origin of *D. septosporum* and *D. pini* can be inferred by studying their global population structures and sexual reproduction modes. Frequent sexual recombination events increase haplotypic diversity. It would thus be reasonable to assume that both haplotypic and genetic diversity of the respective populations would be greatest at their centres of origin and that haplotypic diversity would be high due to frequent sexual recombination events (Allendorf & Lundquist, 2003; Goodwin, Dunkle, & Zismann, 2001; McDonald et al., 1999). Alternatively, multiple introductions of a number of different haplotypes of a pathogen into an area could also increase the genetic diversity of the pathogen population to be similar to the diversity that would be expected in native populations (Barnes, Wingfield et al., 2014; Burgess, Wingfield, & Wingfield, 2001).

Recent population genetics research suggests that *D. septosporum* could be native in British Columbia (Canada) and in some areas of Europe (Barnes, Wingfield et al., 2014; Dale et al., 2011; Drenkhan et al., 2013). The sexual state of the fungus (as *Scirrhia pini*) was first formally described by Funk and Parker (1966) from material in British Columbia. In Europe, the sexual state has been recorded in 11 countries (Table 2). Tests for random mating on *D. septosporum* populations support these observations and illustrate the impact of sexual recombination on the population structure of the pathogen in a number of areas (Dale et al., 2011; Drenkhan et al., 2013; Mullett, Brown, & Barnes, 2015; Tomšovský et al., 2013). *Dothistroma septosporum* populations in Canada showed high gene and haplotypic diversity (Dale et al., 2011). Population studies on isolates from Austria, Czech Republic, France, Hungary, Poland, Romania and Slovakia

**TABLE 2** Geographic distribution of *Dothistroma septosporum* and *D. pini* mating types and sexual state in Northern and Southern Hemispheres.

Location	<i>Dothistroma</i> sp.	MAT1-1-1	MAT1-2	References
Australia				
Canaberra	<i>D. septosporum</i>		*	Groenewald et al. (2007); Barnes, Wingfield et al. (2014)
Tumut	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Austria				
Gstatterboden, Gesäuse (Styria)	<i>D. septosporum</i>	*	*	Barnes, Wingfield et al. (2014)
Hollenstein/Ybbs (Lower Austria)	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013); Barnes, Wingfield et al. (2014)
Forest experimental garden "Knödelhütte" (Vienna)	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Raumberg (Styria)	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Thenneberg (Lower Austria)	<i>D. septosporum</i>	*	*	Groenewald et al. (2007); Barnes, Wingfield et al. (2014)
Wr. Neustadt (Lower Austria)	<i>D. septosporum</i>	*		Barnes, Wingfield et al. (2014)
Belarus				
Vitebsk	<i>D. septosporum</i>	*		A. Kačergius and S. Markovskaja, unpubl. data
Bhutan				
Lamey Goemba (Bumthang dzongkhag)	<i>D. septosporum</i>	*	*	Barnes, Wingfield et al. (2014)
Tangsibi (Bumthang dzongkhag)	<i>D. septosporum</i>	*	*	Barnes, Wingfield et al. (2014)
Ura (Bumthang dzongkhag)	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Yusipang (Thimphu dzongkhag)	<i>D. septosporum</i>	*	*	Barnes, Wingfield et al. (2014)
Brazil				
São Paulo	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Canada <sup>a</sup>				Funk and Parker (1966)
Bell Irving River, British Columbia (BC)	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Brown Bear Road, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Bulkley Canyon, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Evelyn Pasture, BC	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Goldstream River, BC	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Jonas Creek, BC	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Kinskutch Road, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Kisgegas Canyon, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Kuldo Creek, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Mitten Road, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Mosque River, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Motaze Lake and Squingula River, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Nangeese Road, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Nash Y, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
North Kuldo Road, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Orendo, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Sanyam River, BC	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Squingula River Mine, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Sunday Lake, BC	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
Chile				
Canteras, Bio Bio, VIII Region	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Dollinco, Valdivia, X Region	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Naguilan, Valdivia, X Region	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Costa Rica <sup>a</sup>				Evans (1984)
Croatia <sup>a</sup>				Milatović (1976)
Czech Republic <sup>a</sup>				L. Jankovský and V. Tomešová-Haataja, unpubl. data
Chodská Lhota	<i>D. pini</i>	*		Bergová and Kryštofová (2014)
Borkovická Blata	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Bynina	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Havlíčkův Brod	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Jakule	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Jandovka	<i>D. septosporum</i>	*		Tomšovský et al. (2013)
Jarcová	<i>D. septosporum</i>		*	Tomšovský et al. (2013)

(Continues)

TABLE 2 (continued)

Location	<i>Dothistroma</i> sp.	MAT1-1-1	MAT1-2	References
Jasenice	<i>D. septosporum</i>	*		Tomšovský et al. (2013)
Karolínka	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Koryčany	<i>D. septosporum</i>	*		Tomšovský et al. (2013)
Křtiny	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Lanžhot	<i>D. septosporum</i>	*	*	Barnes, Wingfield et al. (2014)
Lidmilův mlýn	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Luhačovice	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Mezina u Bruntálu	<i>D. septosporum</i>	*		Tomšovský et al. (2013)
Mštenovice	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Nová Pec	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Nové Hradky – Sušidla	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Pernek	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Rožnov pod Radhoštěm	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Řícmanice	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Sádek u Poličky	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Soběslavská Blata	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Strhaře	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Sušidla	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Šance	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Tišnov	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Valašské Klobouky	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Vídeň u Velkého Meziříčí	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Zašová	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Zubří	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013)
Denmark <sup>a</sup>				Munk (1957)
Fredensborg	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data.
Hørsholm	<i>D. septosporum</i>		*	I. Barnes, unpubl. data
Ecuador				
Cotopaxi	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Estonia				
Kautsi	<i>D. septosporum</i>	*	*	R. Drenkhan, unpubl. data
Konguta	<i>D. septosporum</i>	*	*	R. Drenkhan, unpubl. data
Finland				
Pyhtää	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Suonenjoki	<i>D. septosporum</i>	*	*	Tomšovský et al. (2013); R. Drenkhan, unpubl. data
Ähtäri	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
France <sup>a</sup>				Morelet (1967)
Bois du Meinguen, Bretagne	<i>D. septosporum</i>	*	*	Mullett et al. (2015)
Forêt Domaniale du Cranou, Bretagne	<i>D. septosporum</i>	*	*	Mullett et al. (2015)
Forêt Domaniale du Huelgoat, Bretagne	<i>D. septosporum</i>	*	*	Mullett et al. (2015)
Forêt Domaniale du Mesnil, Bretagne	<i>D. septosporum</i>	*	*	Mullett et al. (2015)
La Ferté-Imbault	<i>D. pini</i>	*	*	Siziba et al. (2016); I. Barnes, unpubl. data
La Feuillée	<i>D. septosporum</i>	*	*	Mullett et al. (2015)
Meurthe-et-Moselle	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Neung-sur-Beuvron	<i>D. pini</i>	*		I. Barnes, unpubl. data
Sainte-Brigitte	<i>D. septosporum</i>	*	*	Mullett et al. (2015)
Selles-Saint-Denis	<i>D. pini</i>	*	*	I. Barnes, unpubl. data
Souesmes	<i>D. pini</i>	*	*	Siziba et al. (2016); I. Barnes, unpubl. data
Villefranche-sur-Cher	<i>D. pini</i>	*	*	I. Barnes, unpubl. data
Georgia <sup>a</sup>				Shishkina and Tsanova (1966b)
Germany <sup>a</sup>				Butin and Richter (1983)
Bavarian Alps	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Greece				
Lagada	<i>D. septosporum</i>	*	*	Tsopelas et al. (2013)
Guatemala <sup>a</sup>				Evans (1984)
Sierra de Chuacús	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Honduras <sup>a</sup>				Evans (1984)

TABLE 2 (continued)

Location	<i>Dothistroma</i> sp.	MAT1-1-1	MAT1-2	References
Hungary				
Csabrendek	<i>D. septosporum</i>	*	*	Barnes et al. (2011)
Csabrendek	<i>D. pini</i>		*	Barnes et al. (2011)
Diszel	<i>D. septosporum</i>	*	*	Barnes, Wingfield et al. (2014)
Diszel	<i>D. pini</i>		*	Barnes et al. (2011)
Sopron	<i>D. septosporum</i>	*	*	Barnes, Wingfield et al. (2014)
Jamaica <sup>a</sup>				Evans (1984)
Kenya <sup>a</sup>				
Napkoi	<i>D. septosporum</i>	*	*	Ivory (1972) Barnes, Wingfield et al. (2014)
Latvia				
Kegums	<i>D. septosporum</i>	*	*	Kiesnere (2014)
Skujas	<i>D. septosporum</i>	*	*	R. Drenkhan, unpubl. data
Lithuania				
Marijampolė, Ažuolų Būda	<i>D. septosporum</i>	*		A. Kačergius and S. Markovskaja, unpubl. data
Prienai	<i>D. septosporum</i>	*	*	A. Kačergius and S. Markovskaja, unpubl. data
Šalčininkai, Rūdinkai, Jašiūnai, Baltoji Volė	<i>D. septosporum</i>	*		A. Kačergius and S. Markovskaja, unpubl. data
Trakai, Aukštadvaris	<i>D. septosporum</i>	*	*	A. Kačergius and S. Markovskaja, unpubl. data
Varėna, Čepkeliai	<i>D. septosporum</i>		*	A. Kačergius and S. Markovskaja, unpubl. data
Vilnius, Kairėnai, Lake Gulbinas	<i>D. septosporum</i>	*	*	A. Kačergius and S. Markovskaja, unpubl. data
New Zealand				
Bay of Plenty	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Golden Downs	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Hokonui Forest	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Kaharoa Nursery, Rotorua	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Kaingaroa Forest	<i>D. septosporum</i>		*	Groenewald et al. (2007); Barnes, Wingfield et al. (2014)
Karioi	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Kinleith	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Lake Okareka, Rotorua	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Mt. Maunganui	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Tongariro	<i>D. septosporum</i>		*	Groenewald et al. (2007)
West Coast South Island	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Norway				
Rundhaug	<i>D. septosporum</i>		*	Tomšovský et al. (2013)
Hedmark, Engerdal, Semmings	<i>D. septosporum</i>	*	*	H. Solheim and R. Drenkhan, unpubl. data
Poland <sup>a</sup>				
Brynek (Świerklaniec Forest District)	<i>D. septosporum</i>	*	*	Kowalski and Jankowiak (1998)
Bzowo (Dąbrowa Forest District)	<i>D. septosporum</i>	*	*	Boroń, Lenart-Boroń, and Mullett (2016)
Czernichów	<i>D. septosporum</i>		*	Boroń et al. (2016)
Dębowiec (Prudnik Forest District)	<i>D. septosporum</i>		*	Boroń et al. (2016)
Domiaraki (Miechow Forest District)	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Kamyk (Krzeszowice Forest District)	<i>D. septosporum</i>		*	Groenewald et al. (2007); Barnes, Wingfield et al. (2014); Boroń et al. (2016)
Leśnice (Lębork Forest District)	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Łysa Polana	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Pększyn (Oborniki Śląskie Forest District)	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Połomia (Świerklanice Forest District)	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Prusice (Oborniki Śląskie Forest District)	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Strzeszewo (Lębork Forest district)	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Strzybnica (Świerklanice Forest District)	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Tarnowskie Góry	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Trybsz	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Wista	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Wróblew	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Wrocław	<i>D. septosporum</i>	*	*	Boroń et al. (2016)
Zawiercie (Siewierz Forest District)	<i>D. septosporum</i>	*		Boroń et al. (2016)
Portugal <sup>a</sup>				Fonseca (1998)
Romania <sup>a</sup>				
Valea Putnei	<i>D. septosporum</i>	*		Gremmen (1968) Barnes, Wingfield et al. (2014)

(Continues)



TABLE 2 (continued)

Location	<i>Dothistroma</i> sp.	MAT1-1-1	MAT1-2	References
Russia				
Kamenskiy district (Rostov Region)	<i>D. pini</i>		*	Barnes et al. (2011)
Krasnosulinskiy district (Rostov Region)	<i>D. pini</i>		*	Barnes et al. (2011)
Karelia, Ruskeala (north-west Russia)	<i>D. septosporum</i>	*	*	R. Drenkhan, unpubl. data
St. Petersburg	<i>D. septosporum</i>	*	*	I. Barnes and R. Drenkhan, unpubl. data
Tarasovskiy district (Rostov Region)	<i>D. pini</i>		*	Barnes et al. (2011)
Serbia <sup>a</sup>				Karadžić (1986)
Pasuljanske livade	<i>D. septosporum</i>	*	*	N. Keča and R. Drenkhan, unpubl. data
Slovakia				
Strážovské vrchy	<i>D. septosporum</i>	*	*	Barnes, Wingfield et al. (2014)
Slovenia				
Dutovlje	<i>D. pini</i>		*	I. Barnes, unpubl. data
Hruševica	<i>D. pini</i>		*	I. Barnes, unpubl. data
Ljubljana	<i>D. septosporum</i>		*	Piškur et al. (2013)
Panovec	<i>D. pini</i>		*	Piškur et al. (2013)
Pivka	<i>D. septosporum</i>	*	*	Piškur et al. (2013)
Pivka	<i>D. pini</i>		*	Piškur et al. (2013)
Podčetrtek	<i>D. septosporum</i>	*	*	Piškur et al. (2013)
Podčetrtek	<i>D. pini</i>		*	Piškur et al. (2013)
Pokljuka	<i>D. septosporum</i>		*	B. Piškur, unpubl. data
Radenci	<i>D. septosporum</i>	*	*	Piškur et al. (2013)
Radenci	<i>D. pini</i>		*	Piškur et al. (2013)
Ribčev Laz	<i>D. septosporum</i>		*	Piškur et al. (2013)
Rimš	<i>D. septosporum</i>	*	*	Piškur et al. (2013)
Stara Fužina	<i>D. septosporum</i>	*	*	Piškur et al. (2013)
Škocjan	<i>D. septosporum</i>	*		B. Piškur, unpubl. data
Škocjan	<i>D. pini</i>	*	*	Siziba et al. (2016); B. Piškur, unpubl. data
Trenta	<i>D. septosporum</i>		*	B. Piškur, unpubl. data
Volčji Potok	<i>D. septosporum</i>	*		Piškur et al. (2013)
South Africa				
Haenertsburg (Tzaneen)	<i>D. septosporum</i>	*	*	Groenewald et al. (2007); Barnes, Wingfield et al. (2014)
Hogsback	<i>D. septosporum</i>	*	*	Groenewald et al. (2007); Barnes, Wingfield et al. (2014)
Switzerland <sup>a</sup>				R. Engesser, unpubl. data
Egg <sup>a</sup>	<i>D. septosporum</i>	*	*	R. Engesser and V. Queloz, unpubl. data
Walensee	<i>D. pini</i>	*	*	Queloz et al. (2014)
Tanzania <sup>a</sup>				Gibson (1972)
Turkey				
Western Burdur province	<i>D. septosporum</i>	*	*	M. S. Mullett and F. Oskay, unpubl. data
Ukraine				
Hola Prystan	<i>D. pini</i>	*	*	Siziba et al. (2016); I. Barnes and R. Drenkhan, unpubl. data
Mykolaiv Kinburn Peninsula	<i>D. pini</i>	*	*	Siziba et al. (2016); I. Barnes and R. Drenkhan, unpubl. data
Nova Zburivka	<i>D. pini</i>	*	*	I. Barnes and R. Drenkhan, unpubl. data
Tsjurupinsk	<i>D. pini</i>	*	*	Groenewald et al. (2007); Barnes et al. (2011)
Kharkiv	<i>D. septosporum</i>	*	*	R. Drenkhan, unpubl. data
United Kingdom				
England - Forest Districts				
Central England	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
East England	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Forest of Dean	<i>D. septosporum</i>	*		Groenewald et al. (2007)
New Forest	<i>D. septosporum</i>	*	*	Groenewald et al. (2007)
North England	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
South East England	<i>D. septosporum</i>		*	Groenewald et al. (2007)
South England	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
West England	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
West Midlands	<i>D. septosporum</i>		*	Groenewald et al. (2007)
Yorkshire	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data

TABLE 2 (continued)

Location	<i>Dothistroma</i> sp.	MAT1-1-1	MAT1-2	References
Scotland - Forest Districts				
Cowal & Trossachs	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Dumfries & Borders	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Galloway	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Inverness, Ross & Skye	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Lochaber	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Moray & Aberdeenshire	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
North Highland	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Scottish Lowlands	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Tay	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
West Argyll	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
Wales	<i>D. septosporum</i>	*	*	M. S. Mullett, unpubl. data
United States of America <sup>a</sup>				Peterson and Harvey (1976)
Alaska <sup>a</sup>	<i>D. septosporum</i>			Peterson (1982); Barnes et al. (2016)
California <sup>a</sup>				Cobb and Miller (1968)
Idaho, Lochsa Historical Ranger Station	<i>D. septosporum</i>		*	Barnes, Wingfield et al. (2014)
Indiana, Shelby County	<i>D. pini</i>		*	Barnes, Walla et al. (2014)
Michigan, Massaukee County, Riverside Township	<i>D. pini</i>	*	*	Groenewald et al. (2007); I. Barnes, unpubl. data
Michigan, Montcalm County, Crystal Township	<i>D. pini</i>	*	*	Groenewald et al. (2007)
Michigan, Montcalm County, Evergreen Township	<i>D. pini</i>	*	*	Groenewald et al. (2007); I. Barnes, unpubl. data
Minnesota (Central)	<i>D. pini</i>	*		Groenewald et al. (2007)
Montana, Missoula Lola National Forest	<i>D. septosporum</i>	*		Barnes, Wingfield et al. (2014)
Nebraska, Lincoln	<i>D. pini</i>	*	*	Groenewald et al. (2007)
North Dakota, Cass County	<i>D. pini</i>	*		Barnes, Walla et al. (2014)
North Dakota, Pembina County	<i>D. pini</i>	*		Barnes, Walla et al. (2014)
Oregon, Bandon <sup>a</sup>	<i>D. septosporum</i>		*	Peterson and Harvey (1976); Groenewald et al. (2007)
South Dakota, Brookings County	<i>D. pini</i>	*		Barnes, Walla et al. (2014)
Zimbabwe <sup>a</sup>				Gibson (1972)

\*Indicates the identity of *Dothistroma septosporum* and *D. pini* mating types.

<sup>a</sup>Areas where the sexual state has been reported.

also showed high levels of genetic diversity as well as gene flow, indicative of native populations (Barnes, Wingfield et al., 2014; Mullett et al., 2015; Tomšovský et al., 2013). In addition, population studies on *D. septosporum* from Estonia and Finland showed that these pathogen populations are genetically diverse and thus most likely native and not originating from recent introductions from central Europe (Drenkhan et al., 2013).

In the Southern Hemisphere, *D. septosporum* is known to be an invasive and alien species, as the native ranges of its hosts are almost entirely in the Northern Hemisphere. The sexual state has been reported from only three African countries (Table 2). Population genetic studies in South Africa and Kenya have shown that both mating types of *D. septosporum* are present in these countries, consistent with the observation of the sexual state in Kenya and the moderate levels of genetic diversity in these populations (Barnes, Wingfield et al., 2014). The results are consistent with the long history of pine cultivation in these areas, where multiple introductions of the pathogen could have occurred due to trade of plant material and the establishment of non-native pine plantations for commercial purposes (Gibson, 1972).

In contrast to Africa, only MAT1-2 strains have been found in Oceania and South America and the homogeneity of *D. septosporum* populations is likely the consequence of more recent human-mediated introductions of the pathogen into these areas (Barnes, Wingfield

et al., 2014; Goodwin, Cohen, & Fry, 1994; Taylor, Jacobson, & Fisher, 1999). For example, the New Zealand population has been clonal for more than 60 years (Barnes, Wingfield et al., 2014; Groenewald et al., 2007; Hirst, Richardson, Carson, & Bradshaw, 1999). These highly clonal populations of *D. septosporum* present possible strategies for control by avoiding the introduction of the opposite mating type or new, more virulent haplotypes (Barnes, Wingfield et al., 2014).

In Asia, only one small population of *D. septosporum* from Bhutan has been analysed (Barnes, Wingfield et al., 2014). Preliminary investigations using microsatellite markers (Barnes, Cortinas, Wingfield, & Wingfield, 2008) showed that this population in Bhutan was genetically diverse and distinct from other populations studied outside Asia, suggesting that the pathogen could be indigenous to this area (Barnes, Wingfield et al., 2014). Although the sexual state of the fungus has been reported from six countries in North and Central America (Table 2), population studies in these areas have not been conducted and remain an important gap in our knowledge regarding the population genetics of the DNB pathogens on a global scale.

The sexual state of *D. pini* has never been described, despite the presence of both mating types reported in the USA and Europe (France, Slovenia, Switzerland and Ukraine) and in the same sampling area (Table 2). It is, however, important to note that some of

the early observations of the sexual state of *D. septosporum* were within the geographic range of *D. pini* (e.g. in France; Morelet, 1967) and these findings could have been the sexual state of this species. There is evidence to suggest that recent introductions of the pathogen might have occurred in certain geographic areas, as only the MAT1-2 idiomorph, for example, has been identified in a population from Hungary (Table 2).

Microsatellite markers have recently been developed for *D. pini* (Siziba et al., 2016) making it possible to study the population diversity of this pathogen in all areas reported. Preliminary studies show that *D. pini* is clonal in Pivka, Slovenia and genetically diverse in La Ferté-Imbault, France (Siziba et al., 2016). No other population genetic studies have been conducted on *D. pini* and it is currently not possible to consider the origin of this pathogen. A global population study of both pathogens, especially from areas of their hypothesized native origins, would provide more information regarding the possible origin of *Dothistroma* species. There is currently an on-going project related to one of the objectives of the DIAROD Working Group 1 (dealing with the DNB pathogens) that will address these knowledge gaps.

## 4 | HOST RANGES OF THE DOTHISTROMA PATHOGENS

All reported hosts of *Dothistroma* species belong to the Pinaceae, and the vast majority of these are in the genus *Pinus* (Table 3). *Pinus* species are often dominant members of native forest vegetation across the Northern Hemisphere (Richardson et al., 2007). They are also commonly grown commercially throughout both the Northern and Southern Hemispheres to produce timber, pulp and other wood products, as well as seed and resin (Richardson et al., 2007). In a previous review of the hosts of *Dothistroma* species, Watt et al. (2009) listed 89 host taxa (species, subspecies, varieties and hybrids). These included 82 *Pinus* taxa, as well as *Larix decidua*, five *Picea* species and *Pseudotsuga menziesii*. Watt et al. (2009) did not differentiate the host ranges of the two *Dothistroma* species. In this review, we have attempted to accomplish this task, but it was not always possible and in several cases we can refer only to *Dothistroma* species in general.

Surveys forming part of the DIAROD project have shown that there are now 109 known host taxa for *Dothistroma* species, 95 of which are within the genus *Pinus* (Table 3). The known host range of *D. septosporum* includes 52 taxa in six genera (*Abies*, *Cedrus*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga*), 42 of which are in the genus *Pinus*. In contrast, the known host range of *D. pini* consists of only 12 *Pinus* taxa, 11 of which are also hosts of *D. septosporum*. For the remaining 56 host taxa the *Dothistroma* species observed has not been confirmed with molecular methods. The one host species for which only *D. pini* has been confirmed is *Pinus albicaulis* (Barnes, Walla et al., 2014). It is likely that *P. albicaulis* is also a host of *D. septosporum*, because DNB has been reported on this host in

Montana (Taylor & Walla, 1999), where molecular methods have confirmed only the presence of *D. septosporum* to date (Barnes, Wingfield et al., 2014).

### 4.1 | Newly recorded hosts

Information regarding the 20 newly reported hosts of *Dothistroma* species is presented in Table 4. There are two factors that could explain the recent growth in the number of recorded hosts from 89 to 109. One possibility is that the pathogens are undergoing an expansion of their host ranges. A more likely situation, however, is an increased awareness of the disease in Europe and other areas, partly resulting from the DIAROD COST Action, leading to a deeper study of literature in both English and local languages. There has also been a recent increase in surveys and monitoring for the pathogens in forests, plantations, botanical gardens, arboreta and parks. Three observations support this view. Firstly, six of the 20 “newly reported” hosts were recorded before 2008, but were either overlooked by Watt et al., (2009) or were published in less-accessible local language journals. Of these hosts, three experienced severe DNB damage (Table 4; Cobb & Libby, 1968; Peterson, 1984; Shishkina & Tsanova, 1966a,b), demonstrating the importance of re-visiting older literature when considering pathogen host ranges. Secondly, the low DNB severity reported on many of the 14 host taxa recorded after 2008 suggests that *Dothistroma* species on these hosts may have been overlooked in the past. Finally, several of the newly reported hosts are subspecies, or varieties of three species already ranked as highly susceptible to infection by *Dothistroma* species (*Pinus brutia*, *P. contorta* and *P. nigra*). It is thus possible that *Dothistroma* species have been observed on these taxa before, but that the host subspecies/variety was not reported.

Since 2008, *Dothistroma* species have been observed on fourteen new hosts (Table 4). *Dothistroma septosporum* was confirmed on 13 of these host species using molecular methods and it likely also occurs on *Pinus parviflora* in Latvia and Lithuania, given the locations of these reports (Kiesnere, 2014; S. Markovskaja & A. Kačergius, unpublished data). Only one of the newly recorded hosts, *P. nigra* subsp. *pallasiana*, is a confirmed host of *D. pini* (Barnes, Kirisits et al., 2008). Rather than *D. septosporum* truly having a broader host range than *D. pini*, the reason for the predominance of new *D. septosporum* host reports could be that most of these records come from areas, such as the UK and the Baltic countries, where only *D. septosporum* is known to occur. All of these new host reports come from Europe, probably partly due to increased interest in *Dothistroma* species emerging from the DIAROD COST Action and the extensive network of arboreta found in this region. However, the climatic suitability of northern Europe is also known to be increasing for *Dothistroma* species (Woods et al., 2016), which may have contributed to the observed increase in DNB incidence and severity and a possible true host expansion. Severe DNB symptoms have been observed on only two of these newly recorded hosts. The extensive damage caused by *D. pini* in *P. nigra* subsp. *pallasiana* plantations in the Ukraine and southwest Russia (Barnes, Kirisits et al., 2008) shows that even newly recorded hosts of *Dothistroma* species can be badly affected by

**TABLE 3** The hosts of Dothistroma needle blight pathogens and their susceptibility to the disease.

Susceptibility/Host species <sup>a, b, c, d</sup>	Common English names	References for host susceptibility data <sup>e</sup>	DS <sup>f</sup>	Dp <sup>f</sup>	References for molecular identification
<b>Highly susceptible</b>					
<i>Pinus attenuata</i> Lemmon	Knobcone pine, narrowcone pine	Gilmour (1967b); Gibson (1979)	*		I. Barnes and M. S. Mullett, unpubl. data
<i>Pinus × attenuatadiata</i> Stockw. et Righter	Knobcone pine x Monterey pine	Gilmour (1967b); Gibson (1979)			
<i>Pinus brutia</i> Ten.	Calabrian pine, Turkish pine, East Mediterranean pine, Brutia pine	Ivory (1968); Gibson (1979)	*		Tsopelas et al. (2013)
<i>Pinus brutia</i> Ten. var. <i>pityusa</i> (Steven) Nahal\$	Pitsundian pine	Shishkina and Tsanova (1966a,b)			
<i>Pinus canariensis</i> C. Sm.‡	Canary pine, Canary Islands pine	Gilmour (1967b); Ivory (1968)	*		I. Barnes, unpubl. data
<i>Pinus caribaea</i> Morelet var. <i>bahamensis</i> (Griseb.) W.H. Barrett et Golfari	Bahamas pine, Caicos pine, Caribbean pine	Watt et al. (2009)			
<i>Pinus caribaea</i> Morelet var. <i>caribaea</i>	Caribbean pine, Nicaragua pine, pitch pine	Watt et al. (2009)			
<i>Pinus caribaea</i> Morelet var. <i>hondurensis</i> (Sénécl.) W.H. Barrett et Golfari	Honduras pine, Caribbean pine	Ford (1982)			
<i>Pinus cembroides</i> Zucc.	Mexican nut pine, pinyon pine	Ivory (1968); Gibson (1979)			
<i>Pinus contorta</i> Douglas ex Loudon‡	Lodgepole pine, Tamarack pine, shore pine	Gibson (1979)	*		Barnes et al. (2004)
<i>Pinus contorta</i> Douglas ex Loudon var. <i>latifolia</i> (Engelm.) Critchf.	Lodgepole pine	Woods et al. (2005)	*		Barnes et al. (2004)
<i>Pinus engelmannii</i> Carrière	Apache pine	Ivory (1968); Gibson (1979)			
<i>Pinus halepensis</i> Mill.‡	Aleppo pine	Ivory (1968); Gibson (1979)	*		M. S. Mullett, unpubl. data
<i>Pinus jeffreyi</i> Balf.‡	Jeffrey pine, Jeffrey's pine	Gilmour (1967b); Bulman et al. (2004)	*		M. S. Mullett, unpubl. data
<i>Pinus kesiya</i> Royle. ex Gordon	Khasia pine, Khasi pine, Benguet pine	Rodas et al. (2016)	*		Rodas et al. (2016)
<i>Pinus mugo</i> Turra‡	Mountain pine, dwarf mountain pine	Drenkhan et al. (2013); P. Boroń, unpubl. data	*	*	Barnes et al. (2004, 2011)
<i>Pinus muricata</i> D. Don.‡	Bishop pine	Gilmour and Noorderhaven (1969); Gibson (1979); Fraser, Woodward et al. (2015)	*		Barnes et al. (2004)
<i>Pinus nigra</i> J.F. Arnold	Black pine	Gibson (1979); Jankovský, Bednářová et al., (2004)	*	*	Barnes et al. (2004)
<i>Pinus nigra</i> J.F. Arnold subsp. <i>nigra</i> ‡	Austrian pine	Geo-database ( <a href="http://arccgis.mendelu.cz/monitoring/">http://arccgis.mendelu.cz/monitoring/</a> )	*	*	Barnes et al. (2004); Fabre et al. (2012)
<i>Pinus nigra</i> J.F. Arnold subsp. <i>laricio</i> (Poir.) Maire	Corsican pine	Gilmour (1967b)	*	*	Fabre et al. (2012)
<i>Pinus nigra</i> J.F. Arnold subsp. <i>pallasiana</i> (Lamb.) Holmboe\$	Crimean pine	Barnes, Kirisits et al. (2008)	*	*	Barnes, Kirisits et al. (2008); M. S. Mullett, unpubl. data
<i>Pinus oocarpa</i> Schiede ex Schltdl.‡	Egg-cone pine	Rodas et al. (2016)	*	*	Rodas et al. (2016)
<i>Pinus pinaster</i> Aiton‡	Maritime pine	Gilmour and Noorderhaven (1969)	*	*	M. S. Mullett, unpubl. data; Département de la Santé des Forêts database <sup>h</sup>
<i>Pinus pinea</i> L.‡	Umbrella pine, stone pine	Ivory (1968); Gibson (1979)			
<i>Pinus ponderosa</i> Douglas ex C. Lawson‡	Western yellow pine, ponderosa pine	Gilmour and Noorderhaven (1969); Fraser, Woodward et al. (2015)	*	*	Barnes et al. (2004); Barnes, Walla et al. (2014)
<i>Pinus ponderosa</i> Douglas ex C. Lawson var. <i>ponderosa</i> \$	Pacific ponderosa pine, ponderosa pine, western yellow pine, bull pine	Peterson (1984)			
<i>Pinus radiata</i> D. Don	Monterey pine, radiata pine	Ivory (1968); Gilmour and Noorderhaven (1969); Gibson (1979)	*	*	Barnes et al. (2004); Piou and Ioo\$ (2014)

(Continues)

TABLE 3 (continued)

Susceptibility/Host species <sup>a, b, c, d</sup>	Common English names	References for host susceptibility data <sup>e</sup>	DS <sup>f</sup>	DP <sup>f</sup>	References for molecular identification
<i>Pinus radiata</i> D. Don var. <i>binata</i> (Engelm.) Lemmon	Guadalupe Island pine, Cedros Island pine	Cobb and Libby (1968)			
<i>Pinus radiata</i> D. Don <i>radiata</i> \$	Monterey pine, Cambria pine, radiata pine	Cobb and Libby (1968)	*		M. S. Mullett, unpubl. data
<i>Pinus sabiniana</i> Douglas ex D. Don† (syn. <i>Pinus sabiniana</i> )	Ghost pine, grey pine, California foothill pine, digger pine, bull pine	Ivory (1968)			
<i>Pinus sylvestris</i> L.†	Scots pine	Gibson (1979)	*	*	Barnes et al. (2004); Fabre et al. (2012)
<i>Pinus thunbergii</i> Parl.	Japanese black pine	Gibson (1979)			Rodas et al. (2016)
<i>Pinus tecunumanii</i> Low Elevation Eguiluz & J. P. Perry	Schwerdtfeger's pine	Rodas et al. (2016)	*		
<b>Moderately susceptible</b>					
<i>Pinus bungeana</i> Zucc. ex Endl.	Lacebark pine	Gibson (1979)			
<i>Pinus canariensis</i> C. Sm.†	Canary pine, Canary Islands pine	Gadgil (1984); Bulman et al. (2004)	*		I. Barnes, unpubl. data
<i>Pinus caribaea</i> Morelet	Caribbean pine	Gibson (1979)			
<i>Pinus clausa</i> (Chapm. ex Engelm.) Sarg.	Sand pine, Florida spruce pine	Ivory (1968); Karadžić (2004)			
<i>Pinus coulteri</i> D. Don†	Coulter pine, big-cone pine	Gibson (1979)	*		Barnes et al. (2004)
<i>Pinus cubensis</i> Griseb.	Cuban pine	Ivory (1968); Gibson (1979)			
<i>Pinus densiflora</i> Siebold & Zucc.	Japanese red pine	Gibson (1979)			
<i>Pinus echinata</i> Mill.	Shortleaf pine	Ivory (1968); Gibson (1979)	*		M. S. Mullett, unpubl. data
<i>Pinus elliotii</i> Engelm.†	Slash pine	Gilmour and Noorderhaven (1969); Gibson (1979)			
<i>Pinus elliotii</i> Engelm. var. <i>elliottii</i> \$	Slash pine	Ivory (1968)	*		
<i>Pinus elliotii</i> Engelm. var. <i>densa</i> Little & Dorman	South Florida slash pine	Ivory (1968)	*		M. S. Mullett, unpubl. data
<i>Pinus flexilis</i> E. James	Limber pine, Rocky Mountain white pine	Gibson (1979); Taylor and Walla (1999)	*	*	Barnes, Walla et al. (2014); Barnes, Wingfield et al. (2014)
<i>Pinus jeffreyi</i> Balf.†	Jeffrey pine, Jeffrey's pine	Gibson (1979)	*		M. S. Mullett, unpubl. data
<i>Pinus kesiya</i> Royle. ex Gordon <i>kesiya</i>	Khasia pine, Khasi pine, Benguet pine	Ivory (1968)	*		Rodas et al. (2016)
<i>Pinus lambertiana</i> Douglas	Sugar pine	Gadgil (1984)			
<i>Pinus massoniana</i> Lamb.	Masson's pine, Chinese red pine	Ivory (1968); Gibson (1979)			
<i>Pinus monticola</i> Douglas ex D. Don†	Western white pine	Gibson (1979)	*		Barnes et al. (2004, 2011)
<i>Pinus mugo</i> Turra†	Mountain pine, dwarf mountain pine	Gibson (1979)	*	*	
<i>Pinus muricata</i> D. Don†	Swiss mountain pine	Gibson (1979)	*		Barnes et al. (2004)
<i>Pinus nigra</i> J.F. Arnold subsp. <i>nigra</i> †	Bishop pine	Ivory (1968); Bulman et al. (2004)	*	*	Barnes et al. (2004); Fabre et al. (2012)
	Austrian pine	Fabre et al. (2012); Fraser, Woodward et al. (2015)	*		
<i>Pinus occidentalis</i> Sw.	Hispaniolan pine	Ivory (1968); Gibson (1979)			
<i>Pinus palustris</i> Mill.	Longleaf pine, Florida pine	Ivory (1968); Gibson (1979)	*		M. S. Mullett, unpubl. data; Département de la Santé des Forêts database <sup>h</sup>
<i>Pinus pinaster</i> Aiton†	Maritime pine	Ivory (1968); Gibson (1979)	*	*	
<i>Pinus ponderosa</i> Douglas ex C. Lawson†	Ponderosa pine	Ivory (1968)			
<i>Pinus ponderosa</i> Douglas ex C. Lawson subsp. <i>scopulorum</i> (Engelm.) E. Murray	Rocky Mountain yellow pine	Peterson (1984)			
<i>Pinus pungens</i> Lamb.	Table Mountain pine, prickly pine, hickory pine	Gibson (1979)			
<i>Pinus resinosa</i> Aiton	Red pine, Norway pine	Gibson (1979)			



TABLE 3 (continued)

Susceptibility/Host species <sup>a, b, c, d</sup>	Common English names	References for host susceptibility data <sup>e</sup>	DS <sup>f</sup>	DP <sup>f</sup>	References for molecular identification
<i>Pinus roxburghii</i> Sarg.	Long-leaved Indian pine, chir pine	Ivory (1968); Gibson (1979)			
<i>Pinus strobiformis</i> Engelm.	Southwestern white pine, southern limber pine	Gibson (1979)			
<i>Pinus strobus</i> L.†	Eastern white pine, Weymouth pine	Gilmour and Noorderhaven (1969); Gibson (1979)	*		Département de la Santé des Forêts database <sup>g</sup>
<i>Pinus taeda</i> L.‡	Loblolly pine	Ivory (1968); Gibson (1979)			
<b>Slightly susceptible</b>					
<i>Abies alba</i> Mill.\$	European silver fir, silver fir	Drenkhan et al. (2014)	*		Drenkhan et al. (2014)
<i>Abies concolor</i> (Gord. et Glend.) Lindl.\$	White fir	Drenkhan et al. (2014)	*		Drenkhan et al. (2014)
<i>Cedrus atlantica</i> (Endl.) Manetti ex Carrière var. <i>glauca</i> \$	Blue Atlas cedar	Mullett and Fraser (2015)	*		Mullett and Fraser (2015)
<i>Cedrus deodara</i> (Lamb.) G. Don.\$ <sup>g</sup>	Deodar cedar, Himalayan cedar	Mullett and Fraser (2015)	*		Mullett and Fraser (2015)
<i>Cedrus libani</i> A.Rich. subsp. <i>libani</i> . \$ <sup>g</sup>	Lebanon cedar, cedar of Lebanon	Mullett and Fraser (2015)	*		Mullett and Fraser (2015)
<i>Larix decidua</i> Mill.	European larch	Bassett (1969); Bulman et al. (2004); Kirisits, Halmischlager, Hintsteiner, Barnes, and Cech (2013)	*		I. Barnes, M. Hintsteiner, T. L. Cech and T. Kirisits, unpubl. data
<i>Picea abies</i> (L.) H. Karst.	Norway spruce	Lang and Karadžić (1987); Bednářová et al. (2006)	*		Tomšovský et al. (2013)
<i>Picea omorika</i> (Pancić) Purk.	Serbian spruce	Karadžić (1994); Bulman et al. (2004)			
<i>Picea pungens</i> Engelm.	Blue spruce, Colorado spruce	Jankovský, Palovčíková et al. (2004)			
<i>Picea shrenkiana</i> Fisch. & C.A. Mey.	Schrenk spruce	Bednářová et al. (2006)			
<i>Picea sitchensis</i> (Bong.) Carrière	Sitka spruce	Bulman et al. (2004)	*		M. S. Mullett, unpubl. data
<i>Pinus aristata</i> Engelm.	Colorado bristlecone pine, hickory pine	Jankovský, Bednářová et al. (2004)	*		I. Barnes, unpubl. data
<i>Pinus ayacahuite</i> Ehrenb. ex Schltdl.	Mexican white pine	Gilmour and Noorderhaven (1969)			
<i>Pinus cembra</i> L.	Arolla pine, Swiss stone pine	Kirisits and Cech (2006, 2007)	*	*	Barnes, Walla et al. (2014); Barnes, Wingfield et al. (2014)
<i>Pinus contorta</i> Douglas ex Loudon†	Lodgepole pine, Tamarack pine, shore pine	Bulman et al. (2004); Fraser, Woodward et al. (2015)	*		Barnes et al. (2004)
<i>Pinus coulteri</i> D. Don†	Coulter pine, big-cone pine	Bulman et al. (2004)	*		Barnes et al. (2004)
<i>Pinus devoniana</i> Lindl.	Michoacan pine	Gilmour and Noorderhaven (1969); Gibson (1979); Bulman et al. (2004)	*		Barnes et al. (2004)
<i>Pinus elliottii</i> Engelm.‡	Slash pine	Bulman et al. (2004)	*		M. S. Mullett, unpubl. data
<i>Pinus halepensis</i> Mill.‡	Aleppo pine	Fabre et al. (2012)	*		M. S. Mullett, unpubl. data
<i>Pinus hartwegii</i> Lindl.	Hartweg's pine	Gilmour and Noorderhaven (1969); Gibson (1979)			
<i>Pinus heldreichii</i> H. Christ	Heldreich's pine, Bosnian pine	Bednářová et al. (2006)			
<i>Pinus koraiensis</i> Siebold & Zucc.	Korean pine	Lang and Karadžić (1987)			
<i>Pinus maximinoi</i> H.E. Moore	Thin-leaf pine	Rodas et al. (2016)	*		Rodas et al. (2016)
<i>Pinus merkusii</i> Jungh. & de Vriese	Merkur's pine	Gibson (1979)			
<i>Pinus montezumae</i> Lamb.	Montezuma pine, rough-branched Mexican pine	Gilmour and Noorderhaven (1969); Ivory (1968)			
<i>Pinus monticola</i> Douglas ex D. Don†	Western white pine	Bulman et al. (2004)			
<i>Pinus mugo</i> Turra subsp. <i>uncinata</i> (Ramond ex D. C.) Domin.	Mountain pine	Fabre et al. (2012)	*		Tomšovský et al. (2013)

(Continues)

TABLE 3 (continued)

Susceptibility/Host species <sup>a, b, c, d</sup>	Common English names	References for host susceptibility data <sup>e</sup>	DS <sup>f</sup>	DP <sup>f</sup>	References for molecular identification
<i>Pinus nigra</i> J.F. Arnold subsp. <i>nigra</i> ‡	Austrian pine	Gadgil (1984); Bulman et al. (2004)	*	*	Barnes et al. (2004); Fabre et al. (2012)
<i>Pinus oocarpa</i> Schiede ex Schltdl.‡	Egg-cone pine	Ivory (1968)	*		Rodas et al. (2016)
<i>Pinus patula</i> Schiede ex Schltdl. & Cham.	Jejecote pine, Mexican weeping pine	Gilmour (1967b)	*		I. Barnes, unpubl. data
<i>Pinus peuce</i> Griseb.	Balkan pine, Macedonian pine	T. Kirisits, S. Markovskaja, R. Drenkhan, unpubl. data	*		Barnes et al. (2004)
<i>Pinus pinaster</i> Aiton‡	Maritime pine	Fabre et al. (2012)	*	*	M. S. Mullett, unpubl. data, Département de la Santé des Forêts database <sup>h</sup>
<i>Pinus pinea</i> L.‡	Umbrella pine, stone pine	Département de la Santé des Forêts database <sup>h</sup>			
<i>Pinus pseudostrobus</i> Lindl.	False Weymouth pine	Gilmour and Noorderhaven (1969); Ivory (1968)			
<i>Pinus rigida</i> Mill.	Pitch pine, hard pine	Bednářová et al. (2006)			
<i>Pinus sabiniana</i> Douglas ex D. Don‡ (syn. <i>Pinus sabiniana</i> )	Ghost pine, grey pine, California foothill pine, digger pine, bull pine	Bulman et al. (2004)	*		M. S. Mullett, unpubl. data
<i>Pinus serotina</i> Michx.	Pond pine, marsh pine	Bulman et al. (2004)			
<i>Pinus sibirica</i> Du Tour	Siberian stone pine, Siberian pine	Jankovský, Bednářová et al., 2004			
<i>Pinus strobus</i> L.‡	Eastern white pine, Weymouth pine	Bulman et al. (2004); Département de la Santé des Forêts database <sup>h</sup>	*		Département de la Santé des Forêts database <sup>h</sup>
<i>Pinus strobus</i> L. var. <i>chiapensis</i> (Martínez) Andresen	Chiapas white pine	Ivory (1968)			
<i>Pinus sylvestris</i> L.‡	Scots pine	Lang and Karadžić (1987); Bulman et al. (2004); Fabre et al. (2012); Fraser, Woodward et al. (2015)	*	*	Barnes et al. (2004); Fabre et al. (2012)
<i>Pinus tabulaeformis</i> Carrière	Chinese red pine	Lang and Karadžić (1987)			
<i>Pinus taeda</i> L.‡	Loblolly pine	Bulman et al. (2004); Département de la Santé des Forêts database <sup>h</sup>			
<i>Pinus torreyana</i> Parry ex Carrière	Torrey pine, Soledad pine, Del Mar pine	Ivory (1968)	*		M. S. Mullett, unpubl. data
<i>Pinus wallichiana</i> A.B. Jacks.	Himalayan white pine	Ivory (1990); Watt et al. (2009)	*		Barnes, Cortinas et al. (2008)
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	Douglas fir	Dubin and Walper (1967); Bulman et al. (2004)	*		Tomšovský et al. (2013)
<b>Unknown susceptibility</b>					
<i>Cedrus atlantica</i> (Endl.) Manetti ex Carrière\$	Atlas cedar	Petrescu (1976)			
<i>Abies balsamea</i> (L.) Mill.\$	Balsam fir	Kiesner (2014)	*	*	Kiesner (2014)
<i>Pinus albicaulis</i> Engelm.	Whitebark pine	Taylor and Walla (1999)	*		Barnes, Walla et al. (2014)
<i>Pinus arizonica</i> Engelm. var. <i>cooperi</i> (C. E. Blanco) Farjon	Cooper's pine	Browne (1968)	*		M. S. Mullett, unpubl. data
<i>Pinus banksiana</i> Lamb.	Jack pine, black pine	Jankovský, Bednářová et al. (2004)			
<i>Pinus brutia</i> Ten. var. <i>eldarica</i> (Medw.) Silba\$	Iranian pine	Soylu, Kurt, and Soylu (2001)			
<i>Pinus contorta</i> Douglas ex Loudon x <i>Pinus banksiana</i> Lamb. <sup>e</sup>	Lodgepole pine x jack pine	Parker and Collis (1966); Funk and Parker (1966)			

TABLE 3 (continued)

Susceptibility/Host species <sup>a, b, c, d</sup>	Common English names	References for host susceptibility data <sup>e</sup>	DS <sup>f</sup>	DP <sup>f</sup>	References for molecular identification
<i>Pinus contorta</i> Douglas ex Loudon var. <i>contorta</i>	Shore pine, beach pine	Peterson and Harvey (1976)	*		Barnes, Wingfield et al. (2014); Fraser, Woodward et al. (2015)
<i>Pinus contorta</i> Douglas ex Loudon var. <i>murrayana</i> (Balf.) Engelm. \$	Tamarack pine, Sierra lodgepole pine	M. S. Mullett, unpubl. data	*		M. S. Mullett, unpubl. data
<i>Pinus echinata</i> Mill. × <i>Pinus taeda</i> L.	Shortleaf pine × loblolly pine	Parker and Collis (1966); Funk and Parker (1966)			
<i>Pinus gerardiana</i> Wall. ex D. Don \$	Chilgoza pine	M. S. Mullett, unpubl. data	*		M. S. Mullett, unpubl. data
<i>Pinus monophylla</i> Torr. & Frém \$	Single leaf pinyon pine, one-leaved nut pine	V. Queloz, unpubl. data	*		V. Queloz, unpubl. data
<i>Pinus mugo</i> subsp. <i>rotundata</i> (Link) Janchen & Neumayer	Bog pine	Bednářová et al. (2006)			
<i>Pinus nigra</i> J.F. Arnold subsp. <i>dalmatica</i> (Vis.) Franco \$	Dalmatian black pine	J. Lazarevic, unpubl. data	*		J. Lazarevic, unpubl. data
<i>Pinus nigra</i> J.F. Arnold subsp. <i>salzmannii</i> (Dunal) Franco \$	Pyrenean pine, Atlas Mountains black pine	M. S. Mullett, unpubl. data	*		M. S. Mullett, unpubl. data
<i>Pinus parviflora</i> Siebold & Zucc. \$	Japanese white pine	Kiesner (2014); S. Markovskaja and A. Kačergius, unpubl. data			
<i>Pinus pumila</i> (Pall.) Regel \$	Siberian dwarf pine, dwarf Siberian pine, dwarf stone pine, Japanese stone pine, creeping pine	Kiesner (2014); S. Markovskaja and A. Kačergius, unpubl. data	*		Kiesner (2014)
<i>Pinus sylvestris</i> L. var. <i>mongolica</i> Litv.	Mongolian Scots pine, Mongolian pine, Hailar pine	Li et al. (1998)			

<sup>a</sup>Host taxonomy is based on Farjon (2001).<sup>b</sup>Host species that have been rated differently by various authors and are therefore in more than one category are marked with a “+.”<sup>c</sup>“New” host species not recorded by Watt et al. (2009) are marked with a “\$.”<sup>d</sup>Two unconfirmed possible new host records from the Pacific Forestry Centre's Forest Pathology Herbarium (Canada) were excluded from Table 3. The report on already included the same as *P. contorta* × *banksiana* *Pinus contorta* var. *murrayana* × *P. banksiana* (syn. *P. murrayana* × *banksiana*) (DAVFP 16702) is likely in the Table. The report on *Abies lasiocarpa* (Hooker) Nuttall (DAVFP 21525) was never confirmed (B. Callan, pers. Comm.).<sup>e</sup>For species with unknown susceptibility the reference for the host report is given.<sup>f</sup>Where molecular methods have been used to identify the *Dothistroma* species causing DNB, this information is also included and indicated with a “\*\*” (DS, *D. septosporum*; DP, *D. pinii*).<sup>g</sup>DNB has only been observed on artificially inoculated *Cedrus libani* subsp. *libani* and *Cedrus deodara*.<sup>h</sup>Département de la Santé des Forêts database: <http://agriculture.gouv.fr/departement-de-la-sante-des-forets>.

**TABLE 4** Newly reported hosts of *Dothistroma* species.

Host	<i>Dothistroma</i> species	Susceptibility	Notes/source	Reference
<b>Recorded before 2008</b>				
<i>Cedrus atlantica</i>	Unknown	Unknown	Recorded in Romania.	Petrescu (1976)
<i>Pinus brutia</i> var. <i>eldarica</i>	Unknown	Unknown	DNB only found in plantations of this variety that had been severely damaged by other pathogens in Turkey.	Soylu et al. (2001)
<i>Pinus brutia</i> var. <i>pityusa</i>	Unknown	Unknown	DNB caused severe damage and even mortality in young stands in wet and warm regions of western Georgia.	Shishkina and Tsanova (1966a,b)
<i>Pinus elliotii</i> var. <i>elliottii</i>	<i>D. septosporum</i> <sup>a</sup>	Moderate	Slightly attacked under moderate and high disease hazard in Kenyan arboreta.	Ivory (1968)
<i>P. elliotii</i> var. <i>elliottii</i>	Unknown	Unknown	Recorded in Japan.	Ito et al. (1975)
<i>Pinus ponderosa</i> var. <i>ponderosa</i>	<i>D. pini</i> <sup>a</sup>	High	Greater susceptibility than the inland form <i>P. ponderosa</i> var. <i>scopulorum</i> in central USA.	Peterson (1984)
<i>Pinus radiata</i> var. <i>radiata</i>	<i>D. septosporum</i> <sup>a</sup>	High	Greater susceptibility than <i>P. radiata</i> var. <i>binata</i> in California.	Cobb and Libby (1968)
<b>Recorded after 2008</b>				
<i>Abies alba</i>	<i>D. septosporum</i>	Slight	<i>Dothistroma septosporum</i> confirmed molecularly from mature trees growing with infected exotic pines and <i>Pseudotsuga menziesii</i> in northern Latvia. Severity was slight, with symptoms confined to the lower canopy.	Drenkhan et al. (2014)
<i>Abies balsamea</i>	<i>D. septosporum</i>	Unknown	<i>Dothistroma septosporum</i> was found on trees growing close to an infected <i>Pinus cembra</i> stand in the National Botanic Garden in Latvia. Severity was slight, with symptoms confined to the lower branches	Kiesnere (2014)
<i>Abies concolor</i>	<i>D. septosporum</i>	Slight	<i>Dothistroma septosporum</i> isolated from mature trees growing in an arboretum near an infected <i>Pinus sylvestris</i> stand in south east Estonia. Incidence and severity was low. Needles with symptoms were confined to the lower canopy.	Drenkhan et al. (2014)
<i>Cedrus atlantica</i> var. <i>glauca</i>	<i>D. septosporum</i>	Slight	<i>Dothistroma septosporum</i> isolated from a mature tree growing near a heavily infected <i>Pinus jefferyi</i> in an arboretum in Scotland. Symptom severity was only slight.	Mullett and Fraser (2015)
<i>Cedrus deodara</i>	<i>D. septosporum</i>	Slight	Conidiomata developed after artificial inoculation with a <i>D. septosporum</i> isolate from <i>C. atlantica</i> var. <i>glauca</i> .	Mullett and Fraser (2015)
<i>Cedrus libani</i> subsp. <i>libani</i>	<i>D. septosporum</i>	Slight	Conidiomata developed after artificial inoculation with a <i>D. septosporum</i> isolate from <i>C. atlantica</i> var. <i>glauca</i> .	Mullett and Fraser (2015)
<i>Pinus contorta</i> subsp. <i>murrayana</i>	<i>D. septosporum</i>	Unknown	<i>Dothistroma septosporum</i> isolated and confirmed using molecular methods. The tree was growing in the southeast of England.	M. S. Mullett, unpubl. data
<i>Pinus gerardiana</i>	<i>D. septosporum</i>	Unknown	<i>Dothistroma septosporum</i> isolated and confirmed using molecular methods. The tree was growing in the national pinetum (an arboretum specializing in <i>Pinus</i> sp.) in the southeast of England. Previously classified as "immune" in Kenya by Ivory (1968).	M. S. Mullett, unpubl. data
<i>Pinus monophylla</i>	<i>D. septosporum</i>	Unknown	Two trees growing in different locations were severely affected in Switzerland. Only one-needed pine species. Second pinyon pine (subsection <i>Cembroides</i> ) species to be recorded as a host of <i>Dothistroma</i> species after <i>P. cembroides</i> .	V. Queloz, unpubl. data

TABLE 4 (continued)

Host	<i>Dothistroma</i> species	Susceptibility	Notes/source	Reference
<i>Pinus nigra</i> subsp. <i>dalmatica</i>	<i>D. septosporum</i>	Unknown	Seed stand in Montenegro.	J. Lazarevic, unpubl. data
<i>Pinus nigra</i> subsp. <i>pallasiana</i>	<i>D. pini</i>	High	Severe epidemics reported in plantations in Ukraine and in regions of southwest Russia.	Barnes, Kirisits et al. (2008)
<i>P. nigra</i> subsp. <i>pallasiana</i>	<i>D. septosporum</i>	Unknown	<i>Dothistroma septosporum</i> isolated and confirmed using molecular methods. The trees were growing in the southeast of England and were moderately affected by DNB.	M. S. Mullett, unpubl. data
<i>Pinus nigra</i> subsp. <i>salzmannii</i>	<i>D. septosporum</i>	Unknown	<i>Dothistroma septosporum</i> isolated and confirmed using molecular methods. The tree was growing in the southeast of England.	M. S. Mullett, unpubl. data
<i>Pinus parviflora</i>	<i>D. septosporum</i> <sup>a</sup>	Unknown	Disease severity was slight on trees growing in arboreta, botanic gardens and parks in Latvia and Lithuania.	Kiesnere (2014); S. Markovskaja and A. Kačergius, unpubl. data
<i>Pinus pumila</i>	<i>D. septosporum</i>	Unknown	<i>Dothistroma septosporum</i> found on this species growing c. 100 m from infected <i>P. sylvestris</i> in the National Botanic Garden in Latvia. Severity was moderate. Symptoms mostly found in the lower canopy, but also observed at greater heights.	Kiesnere (2014)

<sup>a</sup>*Dothistroma* species not confirmed using molecular techniques, but DNB was probably caused by the noted *Dothistroma* species, given the location of the report.

DNB. Severe damage caused by *D. septosporum* was also observed on two *P. monophylla* trees growing in different locations in Switzerland (V. Queloz, unpublished data). *Pinus monophylla*, the sole one-needle pine species, is only the second pinyon pine (subsection *Cembroides*) species to be recorded as a host of *Dothistroma* after *P. cembroides*, a species ranked as being highly susceptible by Ivory (1968).

## 4.2 | Susceptibility rankings of hosts of *Dothistroma* species

Susceptibility rankings of hosts are listed in Table 3. Because confusion remains over which *Dothistroma* species is being referred to in work either carried out prior to 2004 or in areas where both pathogens occur, we have not attempted to separate host susceptibility based on *Dothistroma* species. Watt et al. (2009) listed 16 hosts as highly susceptible, 22 as moderately susceptible and 26 as slightly susceptible to attack by *Dothistroma* species. Thirteen species had unknown susceptibility, and the remaining 12 were classified differently by various authors. We have rated 20 of the host species as highly susceptible, 20 as moderately susceptible and 33 as slightly susceptible to *Dothistroma* species. Eighteen species have unknown susceptibility and 18 were classified differently by various authors (Table 3). These susceptibility rankings were based on results from both field observations and experimental trials reported in both peer-reviewed and “grey” literature. The majority of these rankings were based on surveys of naturally infected trees in arboreta, field trials and mixed or single species stands (Cobb & Miller, 1968; Gibson et al., 1964; Ivory, 1968; Muir & Cobb, 2005; Peterson, 1967a), but others emerged from experimental trials with limited numbers of species (Cobb & Libby, 1968; Fraser, Woodward et al., 2015; Gibson et al., 1964; Rodas et al., 2016). The susceptibility rankings of some species, for example *P. torreyana* (Ivory, 1968), are based on small numbers of individuals growing in arboreta and should thus be considered as “preliminary” and requiring further confirmation.

### 4.2.1 | Modifications to susceptibility rankings of hosts of *Dothistroma* species

Recent research has elucidated the susceptibility of several hosts for which this information was previously unknown. These species include *P. maximinoi* and *P. tecunumanii*, the relative susceptibilities of which were investigated by Rodas et al. (2016) after the emergence of a serious *D. septosporum* epidemic in Colombia. These authors found that *P. maximinoi* was only slightly susceptible to *D. septosporum*, while *P. tecunumanii* showed intraspecific variation in susceptibility; the low elevation provenance was highly susceptible, whereas the high elevation provenance remained symptom free. Following surveys in Europe, *P. peuce* is now considered as slightly susceptible, as it is only known as a host of *D. septosporum* in four European countries (Austria, Estonia, Lithuania and Montenegro) and appears to be less susceptible than some other exotics in Estonia (see Country notes, Supporting Information).



*Pinus mugo* subsp. *uncinata* has also been placed in the slightly susceptible category based on data from French forest disease surveys (Fabre et al., 2012). Similarly, *P. cembra* is now classified as slightly susceptible, due to the frequent observation of symptoms of DNB on this species in some parts of its natural range in the Austrian Alps (Kirisits & Cech, 2007; see also Supporting Information).

The susceptibility ranking for several other hosts has also been updated. Cobb and Libby (1968) reported that *P. radiata* var. *binata* was less susceptible than *P. radiata* var. *radiata*, and Watt et al. (2009) therefore placed the former variety in the moderately susceptible category. However, Cobb and Libby (1968) also reported that *P. radiata* var. *binata* was more susceptible than *P. muricata*, a moderately to highly susceptible host and accordingly, this variety of *P. radiata* has now been moved to the highly susceptible category. Rodas et al. (2016) found that *P. kesiya* and *P. oocarpa* were highly susceptible to *D. septosporum* in Colombia. This report was in contrast to earlier reports of moderate susceptibility for *P. kesiya* var. *kesiya* and slight susceptibility for *P. oocarpa* to *D. septosporum* in Kenya (Ivory, 1968). *Pinus mugo*, ranked as moderately susceptible by Gibson (1979), is now also ranked as highly susceptible to *Dothistroma* species (see section 4.2.2). *Pinus nigra* subsp. *nigra* was previously described as slightly susceptible to what was probably *D. septosporum* in New Zealand (Bulman, Gadgil, Kershaw, & Ray, 2004; Gadgil, 1984), but is now also ranked as moderately susceptible to this pathogen (Fraser, Woodward et al., 2015) and highly susceptible following analysis of the geo-database data (see section 4.2.2). Both *P. halepensis* and *P. pinea*, which were both previously described as highly susceptible to *D. septosporum* when growing in East Africa (Ivory, 1968), have also been placed in the slightly susceptible category following analysis of forest disease survey data

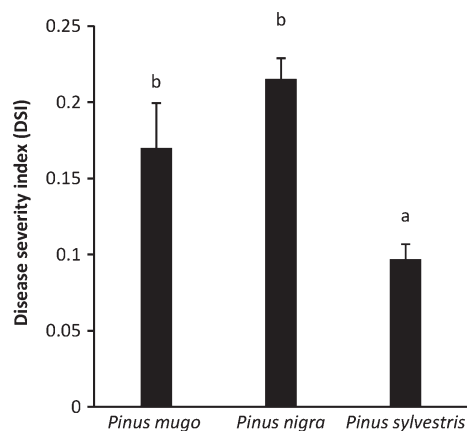
from France, where both *Dothistroma* species occur (Fabre et al., 2012; Département de la Santé des Forêts database). Further support for the repositioning of the susceptibility ranking of *P. pinea* comes from south-western Turkey where a small *P. pinea* plantation had no DNB symptoms, despite being surrounded by *P. brutia* stands heavily infected by *D. septosporum* (F. Oskay, unpublished data). *Pinus pinaster*, previously ranked as moderately susceptible to *D. septosporum* by Ivory (1968), is now placed in all susceptibility categories. This host was found to have similar levels of susceptibility to *D. septosporum* as several highly susceptible *Pinus* species in New Zealand (Gilmour & Noorderhaven, 1969). In France, however, where more than a million hectares of *P. pinaster* are present, this host has been reported to be only slightly susceptible to *Dothistroma* species (Fabre et al., 2012).

#### 4.2.2 | Analysis of geo-database data and country notes

Analysis of the geo-database data and inspection of the country notes (see Supporting Information) enabled analysis of the relative susceptibility of the three most common European pine species, *P. mugo*, *P. nigra* and *P. sylvestris*. In addition to being important components of native forests, *P. nigra* and *P. sylvestris* are important species in plantation forestry, while *P. mugo* is widely used as an ornamental tree. The country notes indicated that most DNB outbreaks in Europe (involving either *D. pini* or *D. septosporum*) are on *P. nigra* (and its subspecies) and that this host appears to be more susceptible than *P. sylvestris* to *Dothistroma* species. This was true for many countries, including Austria, Britain (Fig. 3), Bulgaria, Czech Republic, Estonia, Hungary, Lithuania, Poland, Serbia,



**FIGURE 3** *Pinus nigra* subsp. *laricio* showing severe *Dothistroma* needle blight (DNB) symptoms (centre and right of picture) growing adjacent to green *Pinus sylvestris* trees showing little or no apparent DNB symptoms (left of picture) in the south of England (Photo Credit: M.S. Mullett)



**FIGURE 4** Dothistroma needle blight (DNB) severity on the three most common host species in Europe (*Pinus mugo*, *P. nigra* and *P. sylvestris*). The data obtained from geo-database see the Supporting Information. The disease severity index was calculated by multiplying the mean percentage of crown damaged and percentage of trees affected in the stand. Different letters above bars indicate significantly different means (Generalized Welch procedure 0.2 trimmed means,  $p = 0.05$ , procedures of statistical analyses are presented in the Supporting Information). Note: pine species with less than 30 records were excluded from the analysis

Slovakia and Ukraine. The greater susceptibility of *P. nigra* compared to *P. sylvestris* is also clear from the analysis of the disease severity index derived from the geo-database data (Fig. 4). Previous reports also suggested greater susceptibility of *P. nigra* compared to *P. sylvestris*, with the latter species showing little or no DNB symptoms, even when planted adjacent to or mixed with severely affected *P. nigra* (Lang & Karadžić, 1987; Peterson, 1967a).

Data obtained from the geo-database indicate that DNB severity levels on *P. mugo* are significantly greater than those on *P. sylvestris* and not different to those on *P. nigra* (Fig. 4). Both *D. pini* and *D. septosporum* have been found on *P. mugo*, and this pine species was frequently recorded as a host in the country notes. In Switzerland, where it is widely planted in parks and gardens, *P. mugo* is the most common host. In the Czech Republic and Slovakia, *P. mugo* was the second most common host after *P. nigra*. Ornamental *P. mugo* has also been recorded as a common host in several countries, including Austria, Estonia, Finland, Hungary and Lithuania, with severe damage caused by *D. septosporum* in both Estonia and Lithuania. In both Poland and Slovakia, damage caused by *D. septosporum* was observed on ornamental *P. mugo*, but not on *P. mugo* growing in natural/native stands. In Switzerland and France, *Dothistroma* species have been observed in native stands of *P. mugo* subsp. *uncinata*. Country notes (see Supporting Information) from Romania, Slovenia and Ukraine also list *P. mugo* as a host of *Dothistroma* species.

Analysis of the geo-database data allowed for an investigation of the relative susceptibility of two *P. nigra* subspecies, *P. nigra* subsp. *nigra* and *P. nigra* subsp. *pallasiana*. Combined data for DNB caused by both *Dothistroma* species suggested that there were no significant differences in disease severity between these two subspecies across different countries ( $F_{We} = 0.22$ ,  $p = 0.62$ ). For this reason, *P. nigra* subsp. *nigra* was included in the highly susceptible category, as well as in the slightly

and moderately susceptible categories. The placement of *P. nigra* subsp. *nigra* in these other susceptibility categories is based on comparisons of this subspecies with *P. nigra* subsp. *laricio* and other species, which have produced contrasting results. Surveys in New Zealand and in France, where *P. nigra* subsp. *laricio* and *P. nigra* subsp. *nigra* are widely planted, suggest that *P. nigra* subsp. *nigra* is less susceptible to *Dothistroma* species (B. Marçais & L. Bulman, unpublished data). Fraser, Woodward et al. (2015) found *P. nigra* subsp. *nigra* to have moderate susceptibility to *D. septosporum* in experiments in Britain. The susceptibility of two other *P. nigra* subspecies, *P. nigra* subsp. *dalmatica* and *P. nigra* subsp. *salzmannii* to either *Dothistroma* species is unknown.

#### 4.2.3 | Species with variable susceptibility rankings

The susceptibility ranking of 18 hosts varied between reports. The susceptibility for most of these species did not vary considerably, spanning either slight to moderate (e.g. *Pinus coulteri*) or moderate to high susceptibility (e.g. *P. mugo*). However, six species (*P. contorta*, *P. halepensis*, *P. oocarpa*, *P. pinea*, *P. sabineana* and *P. sylvestris*) have been categorized as both slightly and highly susceptible to *Dothistroma* species. For example, Ivory (1968) reported that *Pinus oocarpa* growing in arboreta in Kenya was slightly susceptible, but this host has recently been seriously affected by *D. septosporum* in Colombia (Rodas et al., 2016). For *P. sylvestris*, the majority of authors have reported lower disease incidence and severity compared to other pines and have suggested that it is only slightly susceptible to these pathogens (Fraser, Woodward et al., 2015; Gilmour, 1967a,b; Karadžić, 1989b; Lang & Karadžić, 1987; Peterson, 1967a). In contrast, Millberg et al. (2016) found that *P. sylvestris* seedlings were more susceptible to *D. septosporum* than *P. contorta* seedlings in Sweden. Consistent with the fact that Gibson (1979) ranked *P. sylvestris* as highly susceptible, DNB-induced mortality on this host was observed in a Christmas tree plantation in Virginia, the USA (Skelly, 1972) and on natural regeneration in Norway (H. Solheim, unpublished data). *Pinus contorta* has been rated as slightly susceptible to *D. septosporum* by some authors (Bulman et al., 2004; Fraser, Woodward et al., 2015), but as highly susceptible (Gibson, 1979) and prone to mortality due to *D. septosporum* infection in several areas by others (Graham & Heutte, 2014; Parker & Collis, 1966; Woods et al., 2005).

There are several possible explanations for the inconsistency in host susceptibility rankings between reports, which centre on different aspects of the disease triangle. These include between-provenance variation in susceptibility (Table 5), an interaction between environmental conditions and relative host susceptibility, variation in the relative virulence of *Dothistroma* species, haplotypes or populations on different host species (although this is yet to be demonstrated), variation in the relative susceptibility of a species at different ages, differences in the interpretation of susceptibility categories by different assessors and the comparison of different sets of host species by different authors. Of these possible explanations, between-provenance variation in susceptibility to *Dothistroma* species has received the most attention and will subsequently be discussed here.

**TABLE 5** Between-provenance variation in host susceptibility to *Dothistroma* species.

Host <sup>a</sup>	<i>Dothistroma</i> species	Location	Notes	Reference
<i>Pinus caribaea</i>	<i>D. septosporum</i> <sup>b</sup>	East Africa	No clear trend with provenance altitude.	Ivory (1968)
<i>Pinus contorta</i>	<i>D. septosporum</i> <sup>b</sup>	New Zealand	Provenance trial. Lower altitude provenances less susceptible. Some coastal provenances very resistant.	Gilmour and Noorderhaven (1969)
	<i>D. septosporum</i>	UK	Disease surveys of plantations. Coastal origins are less susceptible than interior origins. Alaskan origins seem to be the least susceptible.	A. Brown (unpubl. data)
<i>Pinus elliotii</i>	<i>D. septosporum</i> <sup>b</sup>	East Africa	No details given.	Gibson (1972)
<i>Pinus monticola</i>	<i>D. septosporum</i> <sup>b</sup>	British Columbia, Canada	Provenance trials. Interior provenances were more susceptible than coastal BC provenances.	Hunt, Roke, Cleary, Carlson, and Berger (2011)
<i>Pinus muricata</i>	<i>D. septosporum</i> <sup>b</sup>	California	Mixed planting. Northern provenance less susceptible.	Muir and Cobb (2005)
	<i>D. septosporum</i> <sup>b</sup>	Australia	Provenance trials. Northern provenances less susceptible.	Ades, Simpson, Eldridge, and Eldridge (1992)
<i>Pinus nigra</i>	<i>D. pinl</i> <sup>b</sup>	Nebraska	Provenance trials. Seed from the Tara Plateau, Montenegro, had low susceptibility. Seed sourced from eastern Austria had moderate susceptibility. Other provenances had high or variable susceptibility.	Peterson and Read (1971)
<i>Pinus ponderosa</i>	<i>D. septosporum</i> <sup>b</sup>	Australia	Provenance trial. Arizona less susceptible than maritime provenances.	Eldridge et al. (1980)
	<i>D. pinl</i> <sup>b</sup>	Great Plains, USA	Provenance trials. Southern Rockies, New Mexico, Arizona and one Nebraskan provenances less susceptible than others.	Peterson (1984)
<i>Pinus radiata</i>	<i>D. septosporum</i> <sup>b</sup>	California	Natural infection experiments. Island provenances less susceptible than Monterey provenances.	Cobb and Libby (1968)
	<i>D. septosporum</i> <sup>b</sup>	California	Natural infection experiments. Guadalupe Island less susceptible than Monterey, Año Nuevo and New Zealand provenances.	Power and Dodd (1984)
	<i>D. septosporum</i> <sup>b</sup>	New Zealand	Provenance trials. Monterey, Año Nuevo and New Zealand less susceptible than island and Cambria provenances.	Burdon and Bannister (1973)
	<i>D. septosporum</i> <sup>b</sup>	Australia	Provenance trials. Monterey and Año Nuevo less susceptible than Cambria provenances.	Ades and Simpson (1991)
<i>Pinus sylvestris</i>	<i>D. septosporum</i>	UK	Artificial inoculation and natural infection experiments. Scottish populations varied in susceptibility. Relative susceptibility varied between years and sites.	Fraser, Brown et al. (2015); Fraser et al. (2016)
	<i>D. septosporum</i>	UK	Natural infection experiments. Some Scottish provenances more susceptible than some continental European provenances.	Fraser, Woodward et al. (2015)
	<i>D. septosporum</i>	Estonia	Provenance trial. Needle disease severity (including DNB) greater on northern Finland than southern Finland and Estonia provenances.	R. Drenkhan, unpubl. data
<i>Pinus tecunumanii</i>	<i>D. septosporum</i>	Colombia	Provenance trial. Susceptibility was greater on low elevation (c. 100% incidence and c. 40% severity) than on high elevation (0% incidence) provenances.	Rodas et al. (2016)

<sup>a</sup>Except for *P. tecunumanii*, all these hosts have been placed in more than one susceptibility category (when subspecies and varieties are included).<sup>b</sup>*Dothistroma* species not confirmed using molecular techniques, but DNB was probably caused by the noted *Dothistroma* species; given the location of the report.

There is some support for the role of between-provenance variation in susceptibility, as it has been reported for ten *Pinus* species (Table 5), including half of the 18 species that are placed in more than one susceptibility category (when subspecies and varieties are included). Two widespread species, *P. contorta* and *P. sylvestris*, which have been classified as both highly and slightly susceptible, provide prime examples of the possible effect of between-provenance variation. *Pinus contorta* comprises three varieties, all of which are known hosts of *D. septosporum*. The most widespread variety, *P. contorta* var. *latifolia*, has been classified as highly susceptible to *D. septosporum* following a widespread and highly damaging epidemic on this variety in British Columbia (Woods et al., 2005). The two other varieties, *P. contorta* var. *contorta* and *P. contorta* var. *murrayana*, have unknown susceptibility to *D. septosporum*. Results from early work in New Zealand suggested that *P. contorta* provenances varied significantly in DNB symptom expression (Gilmour & Noorderhaven, 1969) and, similarly, surveys in the UK indicated that provenances varied significantly in susceptibility to *D. septosporum*. However, recent artificial inoculation and natural infection experiments in the UK, including provenances of both *P. contorta* var. *contorta* and *P. contorta* var. *latifolia*, revealed no evidence for variations in susceptibility (Fraser, Woodward et al., 2015). Moreover, DNB-induced mortality on *P. contorta* var. *contorta* was observed recently in Alaska (Graham & Heutte, 2014), further suggesting that variation in susceptibility ranking may be caused by other factors besides varietal differences and that susceptibility may be strongly dependent on the area where trees are planted.

Recent research has also shown intraspecific variation in susceptibility to *D. septosporum* within *P. sylvestris*. Artificial inoculation experiments suggested that native Scottish populations of *P. sylvestris* varied in susceptibility to *D. septosporum* (Fraser, Brown, & Woodward, 2015). Subsequent natural infection experiments with the same populations also showed between-population variation in susceptibility, but relative susceptibility varied between years and sites, suggesting local adaptation in either the *P. sylvestris* or *D. septosporum* populations (Fraser et al., 2016). Surveys in a *P. sylvestris* trial in Estonia, which included provenances from Estonia and Finland, demonstrated that needle disease severity (including DNB caused by *D. septosporum*) was greatest on northern Finland provenances (R. Drenkhan, unpublished data). Field experiments in Scotland with *P. sylvestris* provenances from across Europe indicated that some Scottish provenances might be more susceptible to *D. septosporum* than some continental provenances, although these differences were not always significant (Fraser, Woodward et al., 2015). Although this work showed that *P. sylvestris* provenances from across Europe vary in susceptibility to *D. septosporum*, it also demonstrated that all *P. sylvestris* provenances were less susceptible than the highly susceptible *P. muricata* and *P. ponderosa*. This finding suggests that the placement of *P. sylvestris* in the highly susceptible category may be erroneous or caused by factors other than provenance differences, although examination of the susceptibility of a wider range of *P. sylvestris* provenances is needed before this can be conclusively proven.

Collectively, these findings show that, although important, between-provenance variation in susceptibility to *Dothistroma* species may not fully explain the different susceptibility rankings reported by various authors. Furthermore, although it may be due to lack of research in this area, between-provenance variation has not been reported for the four other host species (*P. halepensis*, *P. oocarpa*, *P. pinea* and *P. sabineana*) that were ranked as both highly and slightly susceptible, or for *P. pinaster* which has been placed in all susceptibility categories. Little is currently known about the effect of environment or pathogen variation on the relative susceptibility of *Dothistroma* species hosts, which remain alternative explanations for the observed variation.

## 5 | IMPACT OF THE ENVIRONMENT, OTHER FUNGAL SPECIES AND ANTHROPOGENIC FACTORS ON DNB

### 5.1 | Environmental impacts on the distribution of DNB agents and DNB severity in different habitats

Understanding the impact of abiotic factors can facilitate an understanding of the recent increase in incidence and severity of DNB. Abiotic factors such as temperature (Peterson, 1973), precipitation (Cobb & Miller, 1968; Gibson, Christensen, & Dedan, 1967; Murray & Batko, 1962; Woods et al., 2016), light (Gibson et al., 1964), topography and tree density (Marks & Hepworth, 1986), can all influence disease development and are covered in other reviews in this issue (Bulman et al., 2016; Woods et al., 2016). Of these abiotic factors, moisture is the most important. Severe outbreaks have been observed in years and locations with high rainfall and humidity (Bulman et al., 2013; Fabre et al., 2012; Murray & Batko, 1962; Peterson, 1973; Rodas et al., 2016; Rogerson, 1953; Woods et al., 2005). Conversely, DNB outbreaks do not occur in drier years or dry regions, as observed in many countries in Europe (Murray & Batko, 1962; Fraser et al., 2016; Supporting Information).

The influence of climate on disease development can serve to mask the presence of *Dothistroma* species in regions that are marginal or unsuitable for disease development (Hanso & Drenkhan, 2013). This observation could explain the apparent incongruity in northern Europe, where *D. septosporum* has been known for over 100 years in Denmark and Russia, but has only recently been recorded in Baltic and Fennoscandia countries. The warmer and wetter weather experienced during the last two decades in northern Europe may have contributed to increased disease severity and, combined with greater effort spent looking for DNB over that time, may have resulted in the recent discovery of the disease in this part of Europe (Hanso & Drenkhan, 2008; Müller et al., 2009; Solheim & Vuorinen, 2011). This is despite the likelihood that *Dothistroma* was already present in these areas for a long period of time.

There are several regions in the world where the climate is predicted to be suitable for the development of the disease and where susceptible hosts occur, but where DNB has not yet been recorded

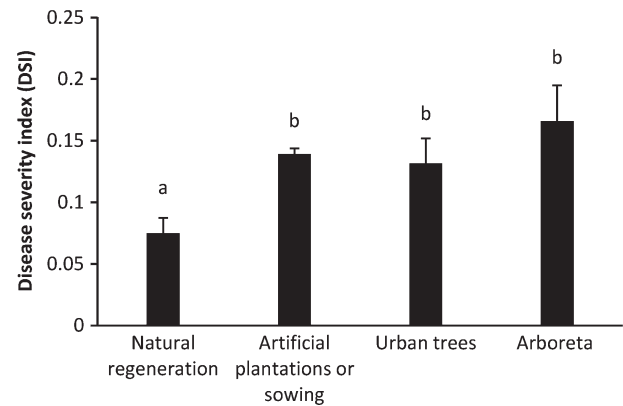


(Watt et al., 2009). Such regions are found in all continents, especially Asia (Figs 1 and 2). It is not known whether *Dothistroma* species occur in these areas and remain undetected or whether these areas are truly free of *Dothistroma* species (see section 2.2). The former is more likely given the recent observation of *D. septosporum* in areas, such as Turkey and the Far East Russia, that were predicted to be suitable by Watt et al. (2009), but were not previously recorded as having DNB. Preliminary population genetic analyses show that a population of *D. septosporum* from Turkey includes both mating types and has a high haplotypic diversity (M. S. Mullett & F. Oskay, unpublished data). This suggests that the pathogen has been in Turkey, unnoticed, for some time. This may also be the case for the Far East Russia (Fig. 2) where *D. septosporum* was first recorded in 2014 (Barnes et al., 2016).

The impact of climatic conditions on DNB incidence and severity underpins the importance of understanding the effect of climate change on the suitability of different areas for infection by *Dothistroma* species. Under climate change projections, the suitable area for *Dothistroma* species is set to decrease by 11–22% over the next 70 years (Watt, Ganley, Kriticos, & Manning, 2011). However, the predicted decrease in the suitable area for *Dothistroma* species was mainly seen in areas of the Southern Hemisphere without pine plantations (Watt et al., 2011). The severity of DNB is predicted to increase in the Northern Hemisphere in areas with substantial natural woodlands and plantation forests, including Fennoscandia, eastern Russia and western Canada (Watt et al., 2011). As this review has shown, this trend is already being witnessed. Although demonstrating causal relationships between climate change and biological phenomena is difficult, Woods et al. (2005) did find a clear mechanistic relationship between a climate trend (increased summer precipitation) and DNB severity in western Canada, one of the areas where Watt et al. (2009) predicted DNB severity to increase with climate change. However, it must also be stressed that several other biotic, abiotic and anthropogenic factors, such as an increase in host use (Woods 2003) or the introduction of more virulent pathogen haplotypes, may also be important drivers of DNB epidemics.

## 5.2 | DNB severity in different habitats and other fungi associated with *Dothistroma* species

The introduction of highly susceptible hosts in plantation forestry or monocultures can alter fungal behaviour and increase disease severity (Evans, 1984). With data obtained from entries in the geo-database and information based on country notes, analysis of the impact of stand type on DNB severity and the association of DNB with other diseases were measured. Significant differences in the damage caused by DNB were confirmed in different habitats ( $N = 372$ ,  $F_{We} = 51.4$ ,  $p < 0.001$ ). Specifically, forests originating from natural regeneration showed lower levels of damage than artificial plantations or sowings, urban trees and arboreta (Fig. 5). Many country also notes reported that trees were infected by *Dothistroma* species in plantations, gardens and arboreta, but less frequently in naturally regenerated woodlands. However, there was no difference in damage caused by DNB between pure and mixed stands ( $N = 875$ ,  $F_{We} = 0.56$ ,  $p = 0.46$ ).



**FIGURE 5** Severity of *Dothistroma* needle blight in different habitats. The data obtained from geo-database see Supporting Information. The disease severity index was calculated by multiplying the mean percentage of crown damaged and percentage of trees affected in the stand. Different letters above bars indicate significantly different means (Generalized Welch procedure 0.2 trimmed means,  $p = 0.05$ , procedures of statistical analyses are presented in the Supporting Information). Note: types of habitats with less than 30 records were excluded from the analysis

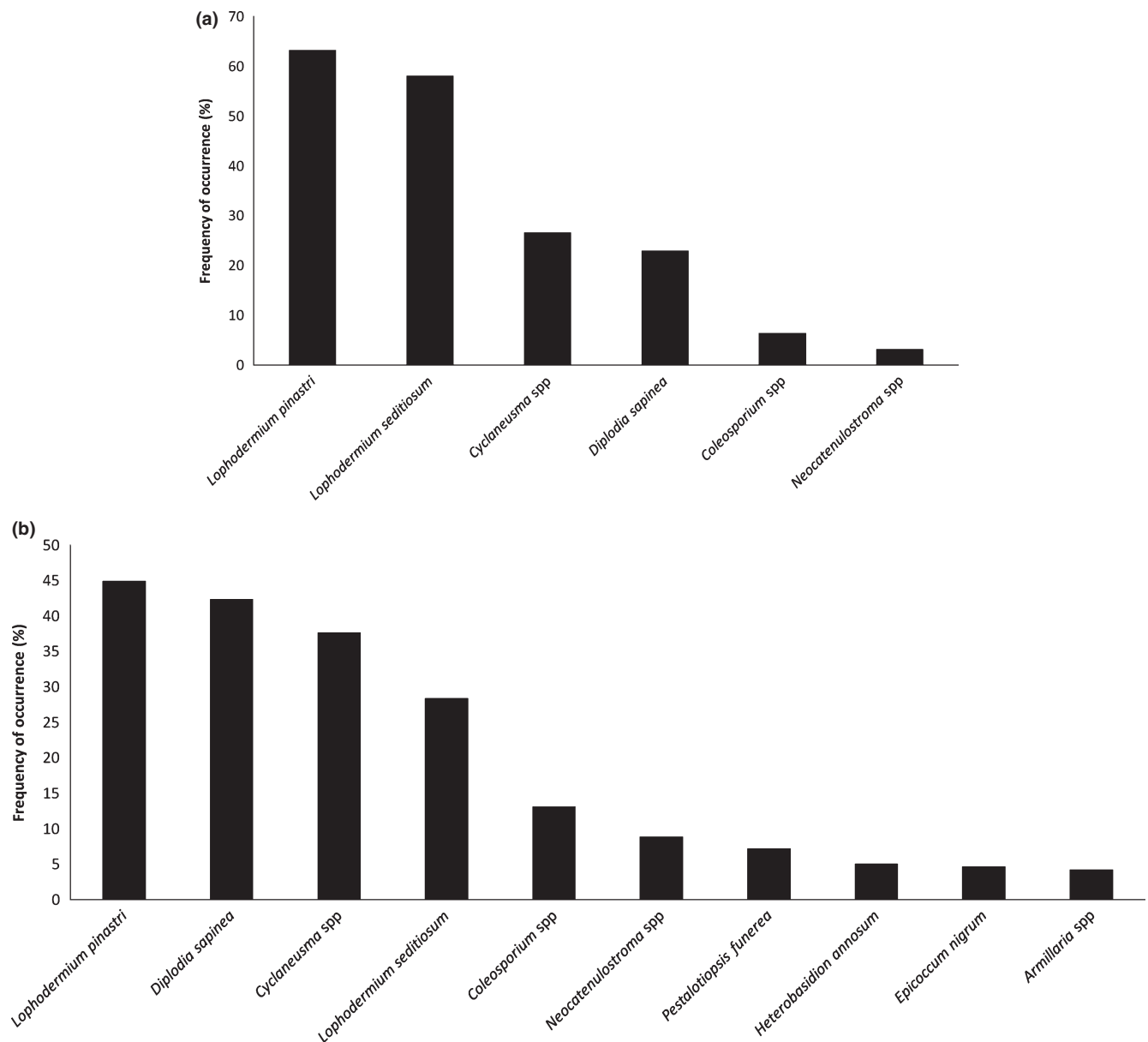
Other needle inhabiting fungi are often overlooked or go unreported during DNB surveys, and little is therefore known regarding the impact of other fungi on *Dothistroma* species and affected trees. Data collected in the geo-database, however, revealed differences in the frequency of other fungal species associated with DNB, at both tree and stand level. In particular, at the tree level the foliar fungi mainly associated with DNB were *Lophodermium pinastri*, *Lophodermium seditiosum*, *Cyclaneusma* spp., *Diplodia sapinea*, *Coleosporium* spp. and *Neocatenulostroma* spp. (Fig. 6a). A similar pattern was found at the stand level, where *L. pinastri* was the most frequent fungus reported, followed by *D. sapinea*, *Cyclaneusma* spp., *L. seditiosum*, *Coleosporium* spp., *Neocatenulostroma* spp., *Pestalotiopsis funerea*, *Heterobasidion annosum* and *Epicoccum nigrum* (Fig. 6b). These fungi were, in most cases, identified based on visual symptoms and morphology (mainly fruiting bodies) and not necessarily confirmed using molecular diagnostics.

Other needle fungi frequently occur together with *Dothistroma* species, on the same host and often on the same needle (Jurc, 2007; Jurc & Jurc, 2010). These fungi often overgrow each other, making it difficult to distinguish between species. In some cases, DNB damage is exacerbated by other pathogens, for example losses caused by *Dothistroma* species increased when *Armillaria* spp. and *Diplodia sapinea* were also causing disease on the same host (Karadžić, 1989b; Shaw & Toes, 1977). As a result, damage to forest stands is often the result of a complex of pathogens, rather than being due to a single particular pathogen.

## 5.3 | Impact of anthropogenic factors on DNB

One of the main factors contributing to the increase in biological invasions by plant pathogens is an expansion in international travel and trade (Liebhold, Macdonald, Bergdahl, & Mastro, 1995).





**FIGURE 6** Frequency of other fungi associated with Dothistroma needle blight (DNB) at the tree level (a) and the stand level (b). The data obtained from geo-database see Supporting Information

Globalization has increased the rate of anthropogenic introductions of plant pathogens to new regions mainly through the trade of infected plant material (Santini et al., 2013). Further trade and movement of plant material within regions can contribute to the local spread of these damaging agents. The most likely pathway for *Dothistroma* species is the movement of infected plants, especially as infected plants can appear symptomless for months before symptom development occurs (Ganley, Hargreaves, & Donaldson, 2015; Millberg et al., 2016). The increase in the trade of live plants is, therefore, a likely contributing factor to the observed increase in the incidence and impact of DNB. Supporting this view, Evans and Oleas (1983) suggested that the isolated occurrence of the *Dothistroma* pathogen in nurseries, and in widely dispersed and recently established smallholdings in Ecuador, indicated that

infected nursery stock constituted the initial inoculum source for DNB outbreaks. Furthermore, identical haplotypes and a lack of genetic diversity of *D. septosporum* in Chile and Ecuador supports the hypothesis that *D. septosporum* may have been introduced into Ecuador from Chile on live plants (Barnes, Wingfield et al., 2014). Similarly, in the Czech Republic, DNB was first reported in 1999 on nursery stock of *Pinus nigra* and *P. mugo* imported from Hungary, and was subsequently found in forest stands (Jankovský, Palovčíková et al., 2004; Jankovský, Bednářová et al., 2004). In Australia and New Zealand, spread of *D. septosporum* has also been attributed to the movement of infected plants (Brown & Wylie, 1991; Bulman et al., 2013).

Another important trend affecting the range expansion or movement of invasive pathogens is the increased planting of susceptible

host plants in suitable climates for the pathogen (Watt et al., 2009). The expansion of DNB in the Southern Hemisphere reflects the anthropogenic history of the introduction and establishment of *P. radiata* plantation forestry (Barnes, Wingfield et al., 2014). In western Canada, recent increases in DNB incidence and severity were linked to the increase in the planting of susceptible *P. contorta* var. *latifolia* (Woods, 2003). While in the UK, the recent DNB outbreak followed an increase in the planting of highly susceptible *P. nigra* subsp. *laricio* over *P. sylvestris*. Likewise, in the rest of Europe, new disease reports of DNB in several countries involved *P. nigra* or its subspecies (see Supporting Information), the most common introduced two-needle pine species in central Europe (Novotný, Modlinger, Pešková, & Čáp, 2012). The high DNB severity index of this host (Fig. 4), and the high susceptibility of this pine species observed in different countries (Table 3), suggests that the introduction of *P. nigra* and its subspecies has likely contributed to the increase in incidence and severity of DNB in Europe. It is not known to what extent, if any, the known cases of non-pine hosts (various species in the genera *Abies*, *Cedrus*, *Larix*, *Picea*, *Pseudotsuga*; see Table 3) contribute to movement of the *Dothistroma* species.

The 2011 IUFRO meeting addressed the important topic of anthropogenic transfers of forest pathogens and published the Montesclaros Declaration (<http://www.iufro.org/science/divisions/division-7/70000/publications/montesclaros-declaration>). This document highlighted the increased risks of international trade of plant material to forest health worldwide and, while recognizing that it is impossible to completely stop trade of biological materials (including, e.g. wooden packaging material and wood chips), declared that pathways with a high phytosanitary risk, and low overall economic importance, should be closed to avoid the spread of pathogens, such as *Dothistroma* species, to new areas. Although this review demonstrates that *Dothistroma* species are already widespread, introduced control mechanisms on the trade of live plants should still be considered to stop the introduction of different *Dothistroma* species or haplotypes that may lead to greater DNB incidence and severity in the future.

## 6 | CONCLUSIONS AND FUTURE PROSPECTS

Collation of information from a wide range of sources has provided the most comprehensive documentation of the global range of DNB made to date. An unprecedented level of information about DNB was compiled using mainstream, “grey” and local language literature, along with re-assessment of herbarium specimens, individual country reports and results from new disease surveys initiated as part of the DIAROD COST Action. DNB is now reported in 76 countries of the world of which 35 are in Europe. The geo-database (<http://arcgis.mendelu.cz/monitoring/>) established to house these data, along with the country reports available in the Supporting Information, record a depth of local knowledge about DNB, such as hosts and pathogens involved, and disease trends and impacts over time. It is envisioned that this database will remain active and that any new information regarding DNB and its associated pathogens will

regularly be added and updated as this information becomes available. In particular, it is hoped that the inclusion of more sample information from poorly studied regions, such as Asia, will provide better knowledge of the distribution of DNB worldwide.

An enhanced understanding of the distribution of the two causal species, *D. septosporum* and *D. pini*, is beginning to emerge due to the more widespread use of molecular identification tools required to distinguish between them. DIAROD training courses in molecular diagnostics enabled many European forest pathologists to determine which of the two *Dothistroma* species are present in their country. *Dothistroma septosporum* was already known to have a worldwide distribution and to be responsible for some recent epidemics in Europe and Canada. What became apparent from the work outlined in this review is that *D. pini* is more prevalent in Europe than previously thought, with 12 country reports for this species. In the USA, the geographic ranges of *D. pini* and *D. septosporum* appear distinct from one another according to current records. These results suggest that we are only just starting to understand the distribution of *D. pini*. It is realistic to anticipate that even broader adoption of the molecular diagnostic tools will show a clearer picture of the ranges of the two species of *Dothistroma*.

The origins or centres of diversity of *D. septosporum* and *D. pini* are still unknown and require further investigation. There is clearly a great need to actively expand efforts to collect cultures of these fungi, particularly from poorly studied areas. In addition, broader use of molecular tools such as microsatellite markers on local and global DNB populations, especially from regions such as the Americas and Asia is needed and will help to test hypotheses about origins and to develop models of migration of the two pathogens. This information will also be important to implement targeted efforts to limit the spread of *Dothistroma* species and to prevent the introduction of new strains of either species into countries that currently have limited genetic diversity of these pathogens.

There are now 109 documented host taxa for both *Dothistroma* pathogens. Of these, 95 are *Pinus* species while the remainder are from five other genera in the Pinaceae. The host ranges of the *Dothistroma* pathogens appear to be increasing, as there have been 14 newly reported hosts (species or subspecies) since 2008, as well as the six that had only been reported in “grey” or local language literature before this date. Of special note are two newly reported hosts on which severe levels of DNB have been observed; *P. nigra* subsp. *pallasiana* in the Ukraine and southwest Russia (Barnes, Kirisits et al., 2008), and *P. monophylla* in Switzerland (V. Queloz, unpublished data). Increased awareness of DNB, along with more widespread disease surveys, clearly accounted for some of these new host records. However, expansion of host ranges by the pathogens, anthropogenic transfer of *Dothistroma* species, or effects of changing climate on host susceptibility may also play a role.

In this review, the rankings of host susceptibility were updated and various factors that influence susceptibility were identified. Based on results from both field observations and experimental trials reported in both peer-reviewed and “grey” literature, relative susceptibility rankings of DNB hosts were comprehensively assessed and updated from

previous summaries. Most DNB outbreaks in Europe have occurred on *P. nigra* and its subspecies, and in general, this host appears to be more susceptible than the widely distributed *P. sylvestris*. The host range and host susceptibility information presented in this review is anticipated to be of immense practical importance to foresters and landscape managers when planning which species to plant in DNB-prone regions. Inconsistent rankings, attributed to 18 of the hosts by different authors, may be accounted for by a range of biotic factors such as host provenance and genetics, host age and pathogen haplotype or abiotic factors (planting site, climate). These inconsistencies highlight that further research is needed to determine the influence of biotic and abiotic factors before accurate predictions can be made about how a specific host will perform at a particular location.

The host–pathogen interactions are an unexplored area of study in *Dothistroma* research. Information about the true host range of each of the *Dothistroma* species is far from complete. This is partly due to the lack of knowledge of pathogen species identity for many of the hosts. It is also partly due to the limited knowledge we have of the global distribution of *D. pini*, despite the new reports of this species in Europe, cited above. Other unanswered questions include how much variation there is in virulence and environmental preferences between *D. pini* and *D. septosporum*, and also between isolates of each of these species. Finally, the influence of both inter- and intraspecific variation of the pathogen on susceptibility of different host species needs to be a focus of future work, so that this important biotic factor can be taken into account when planning forest planting.

The collaborative work described here presents a model that answers the recent call of the president of the International Union of Forest Research Organizations (IUFRO) for a global, rather than single-country, strategy to manage forest pests and diseases (Wingfield, Brouckhoff, Wingfield, & Slippers, 2015). This type of global collaborative research is “vitally important and urgently needed” (Wingfield et al., 2015) and the work of the DIAROD COST Action described in this review provides a platform on which these further studies can be built.

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## SUPPORTING INFORMATION

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