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Pathogens of the Araucariaceae: How Much Do We Know?

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Abstract

Purpose of Review The Araucariaceae is a family of ancient conifers containing iconic tree species from diverse parts of the world. Thirty-eight extant species are present in three genera. Extensive reduction of natural populations has occurred for many species of Araucariaceae, largely due to anthropogenic disturbances. This has occurred to the extent where most species are classified at some level of extinction risk. In recent decades, several diseases have emerged on trees in the family, which has highlighted a general lack of knowledge regarding the factors impacting the health of Araucariaceae. We addressed this by compiling all available literature regarding pathogens and diseases of the Araucariaceae. Insights are given into how globalization and climate change may have, and will potentially, play a role in the emergence of current and future disease threats. These threats are considered from both an ecological and economic perspective.

Recent Findings A total of 227 disease reports were found for the family (58 for *Agathis*, 161 for *Araucaria* and eight for *Wollemia*), of which 88% related to only eight tree species. Consequently, there was a considerable number of species in the Araucariaceae for which no disease reports were found. The most prevalent pathogens reported were species of *Phytophthora*, root rotting basidiomycetes such as *Phellinus* or *Armillaria*, and pathogens within the Botryosphaeriaceae. However, only 25% of the pathogens found have had their pathogenicity confirmed through tests, and only 22% have had their identity confirmed through DNA sequencing, making evident the limited amount of research carried out on this topic.

Summary There is a general lack of baseline information on diseases for trees in the Araucariaceae. The effects that pathogens have had, and may have in the future, in this iconic family of trees are concerning as most of the species have been declared at some level of risk of preservation. Both globalization and climate change have indicated the potential effects they can have, and how unpredictable they can be. This lack of a solid baseline understanding may become an important constraint on attempts to preserve these species, and thus, it is evident that research efforts on these topics are much needed.

Keywords *Agathis* · Anthropogenic activities · *Araucaria* · Climate change · Emerging pathogens · Forest diseases · Invasive forest pathogens · *Wollemia*

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Introduction

Tree diseases are among the main factors causing forest disturbances globally [1]. Pathogens have been responsible for severe economic losses in plantation forests [2] and have led to catastrophic tree death and damage to natural woody ecosystems [3–5]. This has primarily been driven by globalization and climate change; two factors placing increasing pressure on forests, resulting in an increasingly regular emergence of new diseases and declines [6, 7•].

Recently, an outbreak of a dieback and canker disease on *Araucaria araucana* (Araucariaceae) has emerged in these iconic trees within their native range in Chile and Argentina [8, 9]. During studies carried out to determine the aetiology of this canker disease, we considered the availability and status of literature regarding fungal diseases of *A. araucana* and its relatives. Abundant literature was encountered referring to the negative impact that human activity has had on these trees; these included issues such as intensive logging [10, 11], changes in fire regimes [12, 13] and cattle ranching [14]. However, most literature regarding fungal diseases and pathogens on *A. araucana* was fragmented, outdated and/or difficult to access.

An increasing number of cases of dieback have been reported on species within the Araucariaceae. These include those on *A. cunninghamii* and *A. bidwillii* in Australia [15], *Araucaria heterophylla* in Norfolk Island [16, 17] and *Agathis montana* in New Caledonia [18•, 19]. Importantly, information on fungal diseases and pathogens of these tree species was at best scarce and/or difficult to access. Such a lack of accessible information limits the ability to identify damaging fungi and/or to comprehend symptoms that these trees may exhibit in the case of a disease outbreak. This may also result in resources being unnecessarily expended on duplicated research.

In order to address a distinct lack of knowledge regarding diseases of the Araucariaceae and considering the global importance of these trees, this study sought to access available information on this topic. The overall aim was to provide a comprehensive compilation of the fungal diseases occurring on species of the Araucariaceae, including their status regarding taxonomy, pathogenicity, and relative importance. Perspectives are provided on the threats these diseases pose to Araucariaceae species and how globalization and climate change have had, and could have, an impact on these trees in the future.

The Hosts: Araucariaceae: Description, Phylogeny, Distribution and Socio-economic Importance

Description

The Araucariaceae is a family of mostly robust tree species, of which several reach sizes of up to 50 m tall and 2–3 m in diameter. Species in the family are evergreen, mainly monoecious (with only two dioecious species) [20–22], and contain long living species (documented cases of trees over a thousand years of age) [23–26]. They undergo episodic recruitment, which is highly dependent on gap creation following natural disturbances [27]. The family includes three genera, namely *Agathis* Salisb. (17 species), *Araucaria* Juss. (20 species) and *Wollemia* W.G. Jones (one species), which are easily differentiated from each other by basic morphological features such as shape and organization of the leaves or ornamentation of the seeds.

Phylogeny

The Araucariaceae is a monophyletic clade sister to Podocarpaceae, which collectively make up the Araucariales [28, 29•]. Within the Araucariaceae, *Agathis* species form a monophyletic clade, which along with *Wollemia* (*Wollemia nobilis*) form the "Agathoid clade" sister to the monophyletic *Araucaria* clade (Fig. 1). The genus *Araucaria* is sub-divided into four sections: *Araucaria* (two species), *Bunya* (one species), *Eutacta* (16 species) and *Intermedia* (1 species), defined by their morphology [30, 31] and further supported with molecular data [29•, 32]. The largest of these sections, *Eutacta*, almost exclusively includes species endemic to New Caledonia and forms a unique clade within *Araucaria* sister to a clade that accommodates the other three sections [29•, 33]. Section *Araucaria* accommodates the South American species, *A. araucana* and *A. angustifolia*. Sections *Intermedia* and *Bunya* each include the single species, *A. hunsteinii* and *A. bidwillii*, respectively.

Geographical Distribution

The current geographical distribution of the extant species in the Araucariaceae is almost completely restricted to the southeast Asia–Pacific regions except for two species occurring in South America (Fig. 2). Most of the species grow exclusively in the Southern Hemisphere, except for a few *Agathis* species that occur in peninsular Malaysia, northern Borneo and the Philippines. The current hotspot of Araucariaceae diversity is New Caledonia, with 14 *Araucaria* species and four *Agathis* endemic to this island [32, 34].

Most species of Araucariaceae grow in rainforests, *Agathis* in tropical to sub-tropical environments, while most *Araucaria* species in sub-tropical to temperate environments. Some species of *Araucaria* have adapted to grow in rough environments; this includes, for example, a number of New Caledonian species that grow in the ultramafic

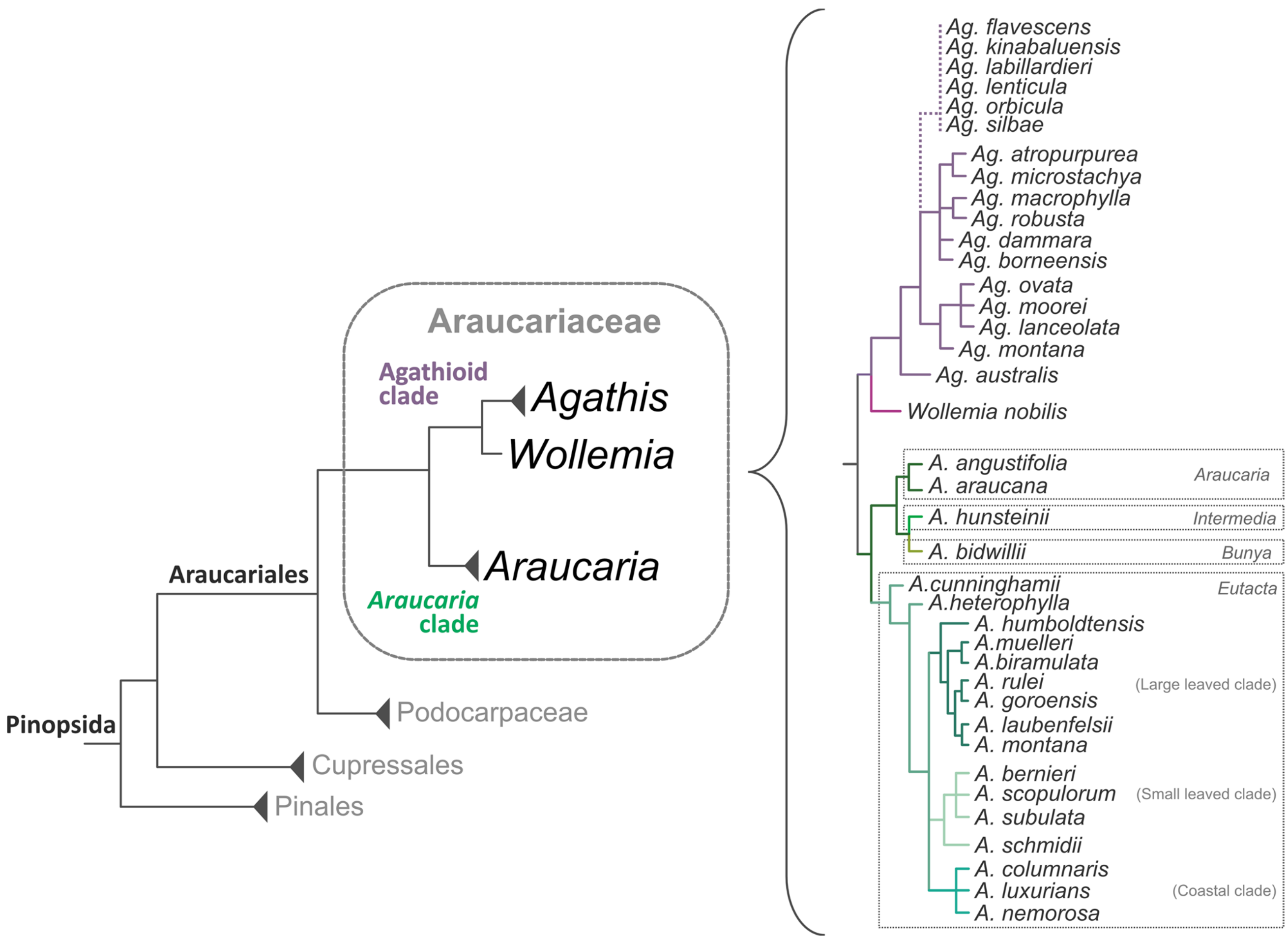


Fig. 1 Theoretical phylogeny for the Araucariaceae constructed based on Farjon (2010), Escapa and Catalano (2013), Ruhsam et al. (2015) and Mill et al. (2017)

maquis, and the South American *A. araucana* that grows in the Andes mountain range on volcanic derived soil and which has adapted to conditions with snow [21, 35]. The monotypic genus *Wollemia* includes only the relatively recently discovered species, *W. nobilis*. This species was discovered in 1994 and has a very restricted distribution in the Blue Mountains of Australia [22, 36].

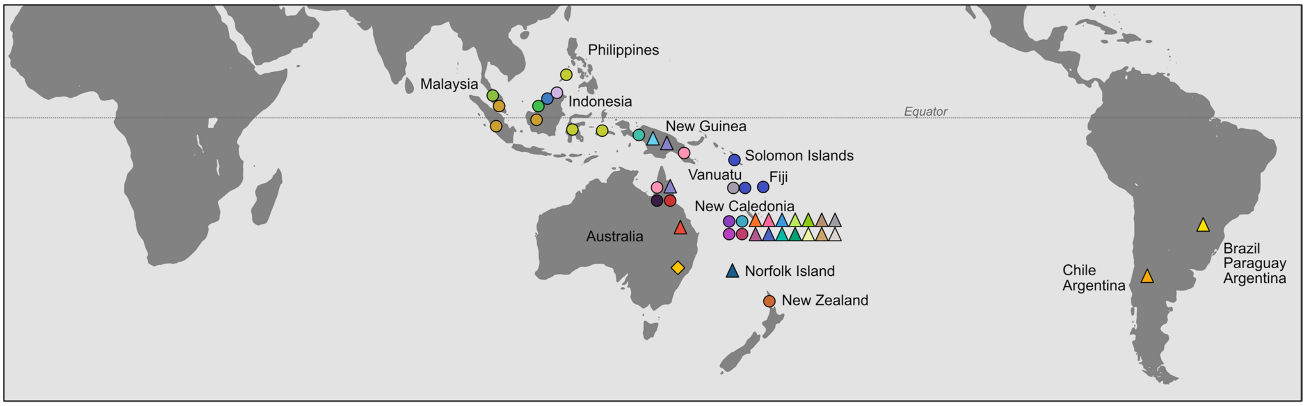
The Araucariaceae has a rich fossil record [35, 37] from which several species have been described from countries in both the Northern and the Southern Hemispheres [38–45]. This has led to the conclusion that the current distribution of the family is relictual of a broad expansion that occurred during the late-Mesozoic and early-Cenozoic eras [35].

Socio-economic Importance

Most species in the Araucariaceae are not well known, with their occurrence restricted to their natural ranges. However, a number of species are recognized for their cultural importance and/or economic value. For example, *Araucaria araucana*, the type species of the family and genus, derives its name from Arauco, the homeland of the Mapuche Pewenche people who consider this tree sacred [46]. Similarly, *Agathis australis*, commonly referred to as kauri, is of symbolic importance for the Maori people of New Zealand [47], as is *A. bidwillii*, the Bunya pine, to the indigenous people of southern Queensland and northern New South Wales in Australia [48, 49]. Species including *Ag. australis* [50], *A. cunninghamii* [51], *A. angustifolia* [52, 53] and *A. hunsteinii* [54] have been planted for silvicultural purposes, while *A. heterophylla* (Norfolk Island pine) [55] and *A. columnaris* [56] are commercialized as ornamentals in many parts of the world.

Diseases of the Araucariaceae

Generally, species in the Araucariaceae have been described as not very susceptible to diseases [57], and greater attention has been given to their insect pests. Only a small number of species in the family have been the subject of studies on



Species	Altitude range	Species	Altitude range	Species	Altitude range
Agathis		*Ag. orbicula*	450 - 1050	*A. humboldtensis*	750 - 1600
Ag. atropurpurea	900 - 1500	*Ag. ovata*	150 - 1150	*A. hunsteinii*	600 - 2000
Ag. australis	0 - 630	*Ag. robusta*	5 - 1900	*A. laubenfelsii*	400 - 1400
Ag. borneensis	1 - 2400	*Ag. silbae*	450 - 760	*A. luxurians*	0 - 1000
Ag. dammara	0 - 2200	***Araucaria***		*A. montana*	500 - 1400
Ag. flavescens	1200 - 1350	*A. angustifolia*	500 - 2300	*A. muelleri*	550 - 1000
Ag. kinabaluensis	1500 - 2400	*A. araucana*	600 - 1800	*A. nemorosa*	20 - 185
Ag. labillardieri	50 - 2000	*A. bernieri*	100 - 500	*A. rulei*	400 - 800
Ag. lanceolata	200 - 1100	*A. bidwillii*	150 - 1200	*A. schmidii*	1400 - 1630
Ag. lenticula	1050 - 1700	*A. biramulata*	190 - 1150	*A. scopulorum*	5 - 600
Ag. macrophylla	75 - 900	*A. columnaris*	1 - 100	*A. subulata*	150 - 1070
Ag. microstachya	400 - 1100	*A. cunninghamii*	15 - 3355	***Wollemia***	
Ag. montana	1000 - 1629	*A. goroensis*	150 - 550	*W. nobilis*	670 - 780
Ag. moorei	250 - 1000	*A. heterophylla*	5 - 316		

Fig. 2 Natural distribution of current extant Araucariacea species. Constructed based on IUCN (2021), Palmer et al. (2006) and Silba (1983)

diseases and for which the contributing pathogens have been well described.

Published Literature on Araucariaceae Diseases

Multiple searches using the Google scholar browser (https://scholar.google.es/) with a diverse combination of terms was used to compile all reports of diseases occurring on the Araucariaceae. These included (i) the host taxon names for the family, genera and each species and (ii) keywords such as "disease", "pathogen", "decline", "dieback", "damage" or a specific genus or species of pathogen. The disease reports found using these searches were grouped by pathogen-host-environment combinations, and for each of these, the methods used for assessing the identity of the causal agent and pathogenicity, and the abundance of literature available about it were recorded and ranked into categories.

A total of 227 disease reports were found for the Araucariaceae (Fig. 3). Of these, 58 were for *Agathis* (Table 1), 161 were for *Araucaria* (Table 2) and 8 for *Wollemia* (Table 3). Eighty-eight per cent of the reports found for the family related to only eight species (*Ag. australis*, *Ag. macrophylla*, *A. angustifolia*, *A. araucana*, *A. bidwillii*, *A. cunninghamii*, *A. heterophylla* and *W. nobilis*), all of which have been used for commercial purposes. It was consequently clear that there remains a large number of species for which information is extremely limited. These include 12 *Araucaria* spp. and nine *Agathis* spp. for which no reports of diseases were found.

The environment from which the reports originated were linked to the main use of the host species (Fig. 4). For example, diseases reported on *Ag. australis* and *A. angustifolia*, two tree species exploited and planted for timber in their countries of origin, were mostly from natural forests, plantations and nurseries in their countries of origin. This was also the case for *A. araucana*, a tree of ethnobotanical, conservation and ornamental interest, for which most of the disease reports were from natural forests in Chile and Argentina. *Araucaria cunninghamii*, which has been used extensively within, and outside its natural range for timber plantations and ornamental plantings, had a larger geographical range in the origins of disease reports. These reports included those from its countries of origin (Australia and Papua New Guinea) and countries where it has been established as an exotic. In contrast, *A. heterophylla*, used widely as an ornamental in several countries of the world, had 26 reports of diseases but only one of which was from its country of origin (Norfolk Island).

Most Common Pathogens of the Araucariaceae

A total of 205 host–pathogen combinations were found for species in the Araucariaceae, irrespective of the environment in which the trees occurred. These included a total of 111

Fig. 3 Diseases on species in the Araucariaceae. **A** Dieback of ornamental *Araucaria columnaris* caused by fungi in the Botryosphaeriaceae in South Africa. **B** Rust disease of *Araucaria araucana* caused by *Mikronegeria fagi* in Chile. **C**–**D** Dieback of *Araucaria araucana* associated to cankers caused by *Pewenomyces kutranfy* in Chile. **E** Potted plant of *Wollemia nobilis* wilting after inoculation with *Phytophthora cinnamomi* in Australia. **F** Dieback of *Agathis australis* associated to *Phytophthora agathidicida* in New Zealand (photo credits: A: Trudy Paap; B, D: Felipe Balocchi; C: Rodrigo Ahumada; E: Edward Liew; F: Peter Scott)

fungal and oomycete pathogens species. However, this number could be misleading, as species identity was confirmed using molecular tools for only 22% of these host–pathogen combinations. In addition, for 17% of the host–pathogen combinations, the associated organisms had only been identified to the genus level (Table 4).

Importantly, confirmation of the host–pathogen–symptom interactions following Koch's postulates was only fulfilled for 51 of the 205 (25%) reported cases. However, while lacking pathogenicity studies, several pathogens had consistent in-field observations (mostly root rotting basidiomycetes) or were obligate biotrophs (e.g., rusts diseases), providing some support to the presumption of pathogenicity. Overall, despite the uncertainties surrounding the available disease reports and the reliability for the identification of the causal organisms, the most prevalent pathogens for tree species in the Araucariaceae are those residing in the Oomycete genus *Phytophthora*, root rotting basidiomycetes such as *Phellinus* and *Armillaria*, and fungi residing in the Botryosphaeriaceae (Tables 1, 2 and 3).

Table 1 Diseases on *Agathis* spp.

Disease / Pathogen	Host	Location	Environment [a]	Path. [b]	Tax. [c]	Lit. [d]	Symptoms	Observations	Ref.
Root rots									
Armillaria limonea	*Ag. australis*	New Zealand	Nf Pl	As	Md iS	2+	root rot on young trees		[47, 58-60]
A. novae-zelandiae	*Ag. australis*	New Zealand	Nf Pl	As Is	Md dS	2+	root rot on young trees		[47, 59-61]
Corticium kauri	*Ag. australis*	New Zealand	Nf	As Is	Md	1s	brown rot of stumps		[62, 63]
Erythricium salmonicolor	*Ag. macrophylla*	Pacific Islands	Nf	As	Md	1s	root rot	"Pink disease" (=*Corticum salmonicolor*).	[64, 65]
	Ag. dammara	Indonesia	Pl	As	Md	2+	dieback, death of trees		[23]
Ganoderma spp.	*Ag. dammara*	Indonesia	Pl	As Is	Md	2+	root rot and death of trees, rizomorphs under bark	Five potential species have been found, one suggested as *G. applanatum* based on the fruiting bodies morphology.	[66, 67]
Phellinus noxius	*Ag. macrophylla*	Pacific Islands	Nf Pl	As	Md	DR	root rot, death of trees		[65, 68]
Phytophthora agathidicida	*Ag. australis*	New Zealand	Nf	As Is Pt	Md dS	2+	root and collar rot, girdles the trunks, dieback and death of trees	(= *Phytophthora* taxon Agathis; PTA) Originally reported as *P. heveae*.	[69-71]
P. cinnamomi	*Ag. australis*	New Zealand	Nf	As Pt	Md dS	2+	root rot associated to tree death in poor drained stands	Pathogenicity tests show low aggressivity.	[70, 72, 73]
P. cryptogea	*Ag. australis*	New Zealand	Nf	As Is Pt	Md dS	1s	root rot associated to diseased seedlings and soil	Pathogenicity tests show low aggressivity.	[70, 74]
P. kernoviae	*Ag. australis*	New Zealand	Nf	As Pt	Md iS	1s	from soil, not associated with symptoms	Detected in the soil in natural environments, a unique report from soil under a dead adult tree, inoculations indicate low aggressivity.	[75, 76]
P. multivora	*Ag. australis*	New Zealand	Nf	As Is Pt	Md dS	2+	weak pathogen detected from soil		[70, 72]
P. nicotianae	*Ag. australis*	New Zealand	Nf	Is	Md	1s	bleeding cankers on trunk	A unique report from a bleeding lesion on a young tree.	[75, 77]
Pyrrhoderma lamaënse	*Ag. moorei*	New Caledonia	Nf	As	Md	DR	basidiocarps on diseased trees	Epithet with several variations: *lamaoense, lamaense* or *lamaensis*.	[78, 79]
	Ag. ovata	New Caledonia	Nf	As	Md	DR	basidiocarps on diseased trees	(=*Phellinus lamaoense, Phellinidium lamaoense*)	[78, 79]
Wood rots and stains									
Fomes hemitephrus	*Ag. australis*	New Zealand	Nf	As Is	Md iS	2+	white heart rot	(=*Fomitopsis hemitephra*)(=*Pilatoporus hemitephrus*)	[47]
Fuscoporia contigua	*Ag. australis*	New Zealand	Nf	As Is	Md	1s	white rot	(=*Phellinus contiguus*)	[62]
Ganoderma applanatum	*Ag. australis*	New Zealand	Nf Pl	As	Md iS	DR	white heart rot extending to the sapwood	(=*Elfvingia applanata*)	[47, 80]
Heterobasidion araucariae	*Ag. australis*	New Zealand	Nf	As Is	Md dS	2+	minor sapwood and heartwood decay	Originally recorded as *Heterobasidion annosum* (=*Fomes annosum*).	[47, 62, 81, 82]
	Ag. macrophylla	Fiji	Nf	As Is	Md iS	1s	basidiocarps on stumps or dead standing and fallen wood		[64, 81, 83]
Phaeolus schweinitzii	*Ag. australis*	New Zealand	Nf	As Is	Md	2+	red-brown cubical butt rot on adult trees	Taxonomic revision of New Zealand's material is required.	[62, 84]
Phellinus gilvus	*Ag. australis*	New Zealand	Nf	As	Md	DR	white rot	Authors indicate it occurs mostly on fallen wood.	[62]
Canker diseases									
Acremonium charticola	*Ag. macrophylla*	Malaysia	Pl	As Is	Md	1s	associated with stem cankers	Ahmad (1986) cites Ivory (1975) incorrectly mentioning this pathogen on *Ag. dammara.*	[85, 86]
Fusarium sp.	*Ag. macrophylla*	Malaysia	Pl	As Is	Md	1s	associated with stem cankers	Ahmad (1986) cites (Ivory 1975) incorrectly mentioning this pathogen on *Ag. dammara.*	[85, 86]
Lasiodiplodia theobromae	*Ag. macrophylla*	Malaysia	Pl	As Is	Md	1s	associated with stem cankers	Ahmad (1986) cites Ivory (1975) incorrectly mentioning this pathogen on *Ag. dammara.*	[85, 86]
Neofusicoccum mangiferae	*Ag. robusta*	Australia	Nf	As Is	Md	2+	infecting leaves and causing twig dieback	(=*Hendersonula agathi*)	[87, 88]
Rusts and Smuts									
Araucariomyces balansae	*Agathis* sp.	New Caledonia	Nf	As Is	Md	1s	hypertrophies to shoot blight	(=*Aecidium balansae*) Believed to be endemic to New Caledonia.	[89]
	Ag. moorei	New Caledonia	Nf	As Is	Md	1s	hypertrophies to shoot blight		[89, 90]
	Ag. ovata	New Caledonia	Nf	As Is	Md	1s	hypertrophies to shoot blight		[89, 90]
A. fragiforme	*Agathis* sp.	Malaysia	Nf	As Is	Md	2+	hypertrophies to shoot blight	(=*Aecidium fragiforme*)	[86, 89, 90]
	Agathis spp.	Pacific Islands	?	As Is	Md	2+	hypertrophies to shoot blight		[91]
Araucariomyces fragiforme	*Ag. borneensis*	Malaysia	Nf	As Is	Md	2+	hypertrophies to shoot blight	(=*Ag. alba*, =*Ag. dammara*)	[86, 89, 90]
	Ag. labillardieri	New Guinea	Nf	As Is	Md	2+	hypertrophies to shoot blight		[89]
	Ag. macrophylla	Fiji	Nf	As Is	Md	2+	hypertrophies to shoot blight	(=*Ag. vitiensis*)	[89, 91]
	Ag. robusta	Australia	Nf	As Is	Md dS	2+	hypertrophies to shoot blight	(=*Ag. palmerstonii*)	[89, 92]
Leaf spots and blights									
Calonectria pteridis	*Ag. macrophylla*	Pacific Islands	Nf	Is	Md	DR	foliage blight	(=*Cylindrocladium macrosporum*)	[65]
Colletotrichum sp.	*Ag. australis*	New Zealand	Nu	Is	Md	DR	isolated from dead and dying seedlings	Only *C. aotearoa* has been identified from *Ag. australis* [93].	[62]
	Ag. moorei	New Caledonia	?	Is	Md	DR	not specified		[78]
	Ag. ovata	New Caledonia	?	Is	Md	DR	anthracnose	Mentions *C. gloeosporioides.*	[78]
C. gloeosporioides	*Agathis* spp.	Pacific Islands	Nu	As Is	Md	1s	leaf cast, can ultimately kill plants		[91]
Diaporthe sp.	*Ag. australis*	New Zealand	?	As Is	Md	DR	leaf spots		[62]
Lophodermium agathidis	*Ag. australis*	New Zealand	Nf	Is	Md dS	1s	fruiting bodies have been found only in dead leaves		[94-96]
L. mahuianum	*Ag. australis*	New Zealand	Nf	Is	Md	DR	fruiting bodies have been found only in dead leaves		[97]
Phyllosticta sp.	*Ag. australis*	New Zealand	?	As Is	Md	DR	isolated from living leaves	Also reported *Guignardia* sp.	[62]
	Ag. macrophylla	Vanuatu	?	As Is	Md	1s	leaf spots	(=*Guignardia pini)*	[64]
Setameliola agathidis	*Ag. robusta*	Australia	?	As Is	Md	1s	leaf spots	(=*Meliola agathidis*) (=*Ag. palmerstonii)*	[98]
Trichothallus niger	*Ag. australis*	New Zealand	Nf	As Is	Md	1s	sooty mould	(=*Trichopeltheca asiatica*)	[62]
Vizella tunicata	*Ag. australis*	New Zealand	?	As Is	Md	1s	leaf spots		[62]
Damping off and nursery diseases									
Botrytis cinerea	*Ag. australis*	New Zealand	Nu	Is	Md	DR	grey mould, on living leaves and leaf litter.		[62]

Table 1 (continued)

Disease / Pathogen	Host	Location	Environment [a]	Path. [b]	Tax. [c]	Lit. [d]	Symptoms	Observations	Ref.
Clonostachys candelabrum	*Ag. australis*	New Zealand	Nu	Is Pt	Md	DR	not specified, inoculations showed pathogenicity	(=*Sesquicillium candelabrum*)	[62]
Fusarium sp.	*Ag. australis*	New Zealand	Nu	As Is Pt	Md	1s	isolated from dead and dying seedlings		[62]
Pestalotiopsis sp.	*Ag. australis*	New Zealand	Nf Nu	As Is Pt	Md	DR	death of recently emerged seedlings	Authors indicate is a secondary pathogen.	[47, 62]
P. funerea	*Ag. australis*	New Zealand	Nf Nu	As Is	Md	DR	death of recently emerged seedlings	Authors indicate is a secondary pathogen.	[47, 62]
Pyrenochaeta sp.	*Ag. australis*	New Zealand	Nu	As Is	Md	DR	isolated from dead and dying seedlings		[62]
Pythium irregulare	*Ag. australis*	New Zealand	Nu	As Is	Md	DR	damping-off		[99]
P. ultimum	*Ag. australis*	New Zealand	Nu	As Is	Md	DR	damping-off		[62,100]
Thanatephorus cucumeris	*Ag. australis*	New Zealand	Nu	As Is	Md	DR	damping-off		[62]
Verticillium sp.	*Ag. australis*	New Zealand	Nu	As Is	Md	DR	isolated from dead and dying seedlings		[62]

[a] Environment: **Nf**: natural forests, **Pl:** plantations, **Nu:** nurseries, **Or:** ornamental, **Sb:** seed batches, **?**: not specified.
[b] Path: Pathogenicity **As:** associated to diseased trees, **Is:** isolated from diseased tissues, **Pt:** pathogenicity confirmed through inoculations.
[c] Tax: Taxonomic position: **Md:** identified through morphology, **iS:** indirectly sequenced (e.g., isolates from same or close environments but different hosts or obsolete techniques), **dS:** directly sequenced.
[d] Lit: Literature abundance: **DR:** disease records, brief or no description of symptoms and methods, **1s:** a unique report, with descriptions of methods, **2+:** two or more reports.

Phytophthora species cause the most extensive and damaging diseases recorded for the Araucariaceae. Multiple species of *Phytophthora* have been associated with severe symptoms in hosts residing in all three genera in the family, including important diseases within natural forests. Iconic cases include *Phytophthora agathidicida* (=*Phytophthora* taxon *Agathis*, PTA) causing kauri dieback (*Ag. australis*) in its natural range in New Zealand [69, 75] (Fig. 3F), and *P. cinnamomi* causing serious severe root rot and dieback of *Wollemia nobilis* within its limited natural range in Australia [204, 205] (Fig. 3E) and on *A. angustifolia* in Brazil in areas reforested with the species [118]. There are also numerous reports of *Phytophthora* species causing disease on *Araucaria* species in nurseries within and outside their countries of origin [119, 121, 125–127].

Root rotting basidiomycetes have commonly been associated with trees displaying disease symptoms in natural stands and plantations. Among these, *Phellinus noxius* is one of the most serious root rot pathogens of *Agathis* and *Araucaria* [68, 114], among which *A. cunninghamii* trees, especially those in plantations in Australia and Papua New Guinea, have been the most seriously affected [112]. *Armillaria* species have also been associated with severe root rots and resination on species of *Agathis* and *Araucaria*, both in plantations and natural stands [47, 101, 103, 107]. *Agathis* species in the southeast Asia–Pacific region are known to be susceptible to root rots caused by other pathogenic basidiomycetes such as *Ganoderma* spp. [66], the crust fungus *Corticium kauri* [62] and *Erythricium salmonicolor*, the causal agent of "pink disease" [23, 64].

Several fungal species residing in different genera in the Botryosphaeriaceae, a family accommodating well-studied endophytic latent pathogens [208], have been associated with dieback, canker diseases, leaf blights and damping-off on tree species of all genera of the Araucariaceae [85, 87, 152, 155, 162, 163, 166, 205]. Among the pathogens of Araucariaceae, the Botryosphaeriaceae have the widest global distribution, with reports from trees planted as ornamentals or in botanical gardens in many parts of the world [125, 151, 157, 159–161] (Fig. 3A).

Some other pathogens of the Araucariaceae that have received attention are those host-specific and unique to the family. These include, for example, the rust pathogens, *Araucariomyces balansae* (=*Aecidium balansae*) and *A. fragiforme* (=*Aecidium fragiforme*) that cause leaf deformation on *Agathis* species, mostly in their native range [89], and *Mikronegeria fagi* that produces its haplont phase on *Araucaria araucana*, causing severe leaf symptoms in Chile and Argentina [168] (Fig. 3B). Similarly, the smut fungus *Uleiella* includes two species that cause diseases on *Araucaria* spp. These include *U. chilensis* that infects the female cones of *A. araucana* and *U. paradoxa* that rots the male cones of *A. angustifolia* [169, 170].

Most recently, the ascomycete *Pewenomyces kutranfy*, residing in the Coryneliaceae, has been described causing girdling cankers on branches of *A. araucana* in its natural range [8] (Fig. 3D). To date, this fungal species is known only from that host and location. Additionally, a group of pathogenic fungi has been described from unique hosts in the Araucariaceae, causing in most cases only mild leaf diseases. These fungi include species such as *Araucasphaeria foliorum*, *Mycosphaerella wollemiae*, *Kalmusia araucariae*, *Phyllosticta acicola*, *Setameliola agathidis* and *S. araucariae* [98, 173, 185, 191, 207].

Species of Araucariaceae cultivated in nurseries have also been reported as susceptible to diseases typical of these environments. Among these are several reports of diseases caused by pathogens residing in typically wide host range genera such as *Fusarium* [62, 85, 102, 179, 205], *Calonectria*, *Botrytis* [62, 196], *Pythium* [99, 100, 102], *Rhizoctonia* [102, 111, 198], *Colletotrichum* [179] and in the Botryosphaeriaceae [111, 151, 162, 163, 205]. These disease reports arise from diverse locations and species in the family. All these pathogens are known to cause similar symptoms on a wide range of other hosts, suggesting that their association with Araucariaceae is likely driven by the exposure of these tree species to nursery environments.

Table 2 Diseases on *Araucaria* spp

Disease / Pathogen	Host	Location	Environment [a]	Path. [b]	Tax. [c]	Lit. [d]	Symptoms	Observations	Ref.
Root rots									
Armillaria sp.	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	root rot on trees of all ages	Originally as *A. mellea*.	[101, 102]
A. fuscipes	*A. cunninghamii*	Zimbabwe	Pl	Is	Md dS	1s	not specified	In some reports as *A. heimii*.	[103, 104]
A. mellea	*A. araucana*	Chile	Nf	As	Md	DR	root rot	Taxonomy needs revision.	[105]
	A. heterophylla	Spain	Or	Is	Md iS	1s	not specified	Detected on screening isolations from soil, identified by RFLP.	[106]
A. novae-zelandiae	*A. cunninghamii*	Australia	Pl	As Is	Md	1s	root rot, commonly found on stumps	Identification supported by interfertility tests.	[107]
Calonectria brassicae	*A. angustifolia*	Brazil	Nf Pl Nu	As Is Pt	Md iS	2+	root rot, resination, leaf blight	(=*Cylindrocladium clavatum*)	[102, 108, 109]
Cylindrocladiella sp.	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	decline and death of trees		[101]
Desarmillaria tabescens	*A. araucana*	Mexico	Or	As Is	Md dS	1s	root rot and tree death	(=*Armillaria tabescens*). On a single tree.	[110]
Hendersonula sp.	*A. angustifolia*	Brazil	Pl Nu	As Is	Md	1s	collar and root rot of seedlings, rotting of male cones	Original record inaccessible.	[101, 102]
Helicobasidium longisporum	*A. cunninghamii*	Australia	Nu	As Is	Md	1s	root rot and tree death	(=*Helicobasidium compactum*) Similarity with *H. purpureum* has led to incorrect records. Original record inaccessible.	[111]
Mortierella alpina	*A. araucana*	Argentina	Nf	Is Pt	Md dS	1s	isolated from necrotic tissues in stems and collars	A unique pathogenic isolate has been reported.	[9]
Mortierella aff. *basiparvispora*	*A. araucana*	Argentina	Nf	Is Pt	Md dS	1s	isolated from necrotic tissues in stems and collars	A unique pathogenic isolate has been reported.	[9]
Phellinus sp.	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	root and collar rot, death of trees		[101]
P. noxius	*A. cunninghamii*	Australia	Pl	As Is Pt	Md	2+	root rot and butt rot that leads to the death of trees	(=*Fomes*, =*Phellinidium*), =*Pyrrhoderma*? [79]	[112, 113]
		Taiwan	Or	As Is	Md dS	1s	brown rot on declining trees		[114-116]
	A. heterophylla	Taiwan	?	As Is	Md	1s	brown rot on declining trees		[114]
Pyrrhoderma lamaënse	*A. columnaris*	New Caledonia	Nf	As	Md	DR	basidiocarps on diseased trees	Epithet with several variations: *lamaoense, lamaense* or *lamaensis* (=*Phellinus lamaoense, Phellinidium lamaoense*).	[78, 79]
Phytophthora castanae	*Araucaria* sp.	Papua New Guinea	?	As	Md iS	DR	no description of symptoms	(=*Phytophthora katsurae*)	[117]
P. cinnamomi	*A. angustifolia*	Brazil	Nf Pl	Is Pt	Md dS	1s	root rot, severe crown symptoms and death of trees		[118]
		Spain	Or	As	Md dS	1s	obtained from soil, no association to symptoms		[106]
		South Africa	Nu	As	Md iS	DR	associated to diseased plants in nurseries, root rot		[119]
	A. araucana	Chile	Nu	As	Md	DR	root and collar rot		[120]
		New Zealand	Nu	Pt	Md	1s	inoculated seedlings show reduction in growth	Inoculations were done with a mixture of isolates obtained from other hosts.	[121]
	A. bidwillii	Spain	Or	As	Md dS	1s	obtained from soil, no association to symptoms		[106]
	A. cunninghamii	Papua New Guinea	Pl	As	Md iS	1s	associated to chlorotic trees	Species identity confirmed by sequencing isolates obtained from other hosts.	[122, 123]
	A. heterophylla	Hawaii	?	As	Md	DR	seedling root rot and tree decline	Original record inaccessible.	[124]
		New Zealand	Nu	Pt	Md	1s	inoculated seedlings stunted and with needle chlorosis	Seedlings inoculated with a mixture of *P. cinnamomi* isolates.	[121]
P. citrophthora	*A. angustifolia*	Argentina	Nu	As	Md	DR	root rot		[125]
	A. araucana	Chile	Nu	As Is Pt	Md dS	1s	seedlings with decay, chlorosis, dieback, root rot.		[126]
P. cryptogea	*A. araucana*	United Kingdom	Nu	As	Md dS	1s	no description of symptoms		[127]
P. multivora	*A. araucana*	Chile	Nu	As Is Pt	Md dS	1s	seedlings with decay, chlorosis, dieback, root rot		[126]
P. nicotianae	*A. araucana*	Iran	Nu	As Is	Md	DR			[128]
	A. heterophylla	Perú	Or	As	Md	DR	stem cankers and branch dieback	(=*Phytophthora parasitica*) on (=*Araucaria excelsa*)	[125]
Rosellinia bunodes	*A. angustifolia*	Brazil	Nf Pl	As Pt	Md iS	2+	black root rot, death of trees	Inoculations and sequencing done with isolates obtained from poplar plantations.	[102, 129]
Wood rots and stains									
Aureobasidium pullulans	*A. angustifolia*	Brazil	Nf Pl	As Is	Md	DR	root and collar rot		[101]
Fomitopsis nivosa	*A. cunninghamii*	Australia	Nf	As Is	Md	1s	brown wood rot	(=*Trametes hispidans*)	[130, 131]
Fusarium angustifolium	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	staining of wood	No other record of this fungal species could be found in any database.	[102]
Ganoderma sp.	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	staining of wood	(=*Elfwingia*)	[102]
G. australe	*A. angustifolia*	Argentina	?	As	Md	DR	white heart rot		[132, 133]
G. applanatum	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	wood rot on field		[102]
G. mexicanum	*A. angustifolia*	Brazil	Nf	As	Md	1s	not specified		[134]
Heterobasidion araucariae	*A. bidwillii*	Australia	Nf	As Is	Md iS	1s	fruiting bodies on a log		[83, 135]
	A. cunninghamii	Australia	Nf	As Is	Md dS	2+	on stumps or dead standing and fallen wood		[81, 83, 135, 136]
		Papua New Guinea	Nf Pl	As Is	Md dS	2+	basidiocarps isolated from trunk of dead trees	Originally recorded as *Heterobasidion annosum* (=*Fomes annosum*).	[84, 137, 138]
Huntiella moniliformis	*A. araucana*	Chile	Nf	As Is	Md iS	1s	blue stain in sapwood and in the edge of logged trunks	(=*Ceratocystis moniliforme*)	[105, 139]
Lentinus villosus	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	staining of wood	.	[102]
Mycoenterolobium platysporum	*A. heterophylla*	United States (Hawaii)	?	As Is	Md	DR	described from decaying wood	Genus and species described from a specimen on wood.	[124, 140]
Ophiostoma araucariae	*A. araucana*	Chile	Nf	As Is Pt	Md dS	1s	blue stain in sapwood and in the edge of logged trunks	Staining ability was confirmed by inoculating fresh sterile wood.	[141-143]

Table 2 (continued)

Disease / Pathogen	Host	Location	Environment [a]	Path. [b]	Tax. [c]	Lit. [d]	Symptoms	Observations	Ref.
O. triangulosporum	*A. angustifolia*	Brazil	Nf Pl	As Is	Md dS	1s	blue stain in sapwood and in the edge of logged trunks		[144, 145]
Phellinus swieteniae	*A. angustifolia*	Argentina	?	As	Md	DR	white heart rot on a dead standing tree	Authors indicate doubtful identification.	[133]
Phomopsis sp.	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	staining of wood		[102]
Picnoporus cinnabarinus	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	staining of wood		[102]
Pleurotus ostreatus	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	wood rot on field		[102]
Rigidoporus microporus	*A. angustifolia*	Brazil	Nf Pl	As	Md iS	DR	staining of wood	(=*Fomes lignosus*)	[102]
R. ulmarius	*A. angustifolia*	Brazil	Nf	As	Md	1s	collected from bark of living trees		[146]
R. vinctus	*A. cunninghamii*	Australia	Pl	As Is	Md	1s	root and butt rot, tree death	(=*Junghuhnia vincta*; =*Chaetoporus radulus*)	[147-149]
		Kenya	Pl	As Is	Md	1s	root and butt rot	(=*Poria vincta*)	[150]
Trametes versicolor	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	wood rot on field	(=*Coriolus versicolor*)	[102]
	A. araucana	Chile	Nf	As	Md iS	DR	rotting stumps and logs		[105]
Canker diseases									
Botryosphaeria dothidea	*A. cunninghamii*	Taiwan	Or	As Is	Md dS	1s	associated to declining trees		[151]
	A. rulei	New Caledonia	Nf	As	Md	DR	fruiting bodies on female cones (anthracnose)		[125]
Diplodia africana	*A. araucana*	Chile	Nf	As Is Pt	Md dS	1s	associated to twig death	Isolated from a single tree.	[152]
D. mutila	*A. araucana*	Chile	Or	As Is Pt	Md dS	1s	associated to bleeding cankers		[153]
D. sapinea	*A. angustifolia*	Brazil	Nf Pl Nu	As Is Pt	Md	2+	dieback, damping-off	(=*Sphaeropsis sapinea*) (=*Diplodia pinea*)	[102, 154]
	A. cunninghamii	Australia	Pl Nu	As Is Pt	Md iS	2+	dieback, death of trees staining of wood, damping-off	(=*Diplodia pinea*)	[111, 125]
D. seriata	*A. araucana*	Chile	Nf	As Is Pt	Md dS	1s	gummy cankers on branches		[155]
	A. heterophylla	Australia	?	As Is	Md dS	DR	not specified		[156]
Dothiorella sp.	*A. heterophylla*	Hawaii	?	As	Md	DR	associated to bleeding cankers	Original record inaccessible.	[124]
Fusicoccum araucariae	*A. araucana*	Italy	Nu	As Is	Md	2+	collar rot and stem cankers	(=*Cryptosporella araucariae*; perfect state)	[157, 158]
Lasiodiplodia theobromae	*A. cunninghamii*	Australia	Nu	As	Md	DR	rotting the base of stems and damping-off		[111]
		Malaysia	Pl Nu	As Is Pt	Md	1s	dieback of weakened trees, damping-off	Original record innaccessible	[85]
		Taiwan	Or	As Is	Md dS	1s	dieback		[151]
	A. heterophylla	Taiwan	Or	As Is	Md dS	1s	dieback		[151]
		Hawaii	Or	As Is Pt	Md	1s	associated to bleeding cankers		[159]
		Ethiopia	Or	Is Pt	Md	1s	stem cankers and needle blight		[160]
Neofusicoccum hongkongense	*A. cunninghamii*	China	Or	As Is	Md dS	1s	not described		[161]
Neofusicoccum mangiferae	*A. heterophylla*	Taiwan	Or	As Is	Md dS	1s	associataed to tree decline		[151]
N. nonquaesitum	*A. araucana*	Chile	Nu	As Is Pt	Md dS	1s	dieback and death of trees		[162]
N. occulatum	*A. cunninghamii*	Australia	Nu	Is	Md dS	1s	not specified		[163, 164]
N. parvum	*A. heterophylla*	New Zealand	Nu	As Is	Md dS	1s	associated to dieback		[163, 165]
	A. heterophylla	Australia	Or	As Is Pt	Md dS	1s	dieback associated to drought		[166, 167]
N. ribis	*A. araucana*	Mauritius	Or	As	Md	DR	dieback		[125]
	A. cunninghamii	Mauritius	Or	As	Md	DR	dieback		[125]
		Australia	Nu	As	Md	DR	stem cankers		[111]
Pewenomyces kutranfy	*A. araucana*	Chile	Nf	As Is Pt	Md dS	1s	girdling cankers on branches and stems		[8]
Rusts and Smuts									
Mikronegeria fagi	*A. araucana*	Chile	Nf	As Pt	Md iS	2+	leaf damage, death of weak seedlings	(=*Caeoma sanctae-crucis*)	[90, 105, 168]
		Argentina	Nf	As	Md	DR	leaf damage, death of weak seedlings		[90, 105, 168]
Uleiella chilensis	*A. araucana*	Chile	Nf	As Is	Md dS	2+	smut fungus that rots female cones and seeds	In some reports identified as *U. paradoxa*, considered synonym.	[105, 169]
U. paradoxa	*A. angustifolia*	Brazil	Nf	As Is	Md	2+	smut fungus that rots male cones and seeds	Some authors wrongly mention this pathogen on *A. imbricata* (=*A. araucana*).	[170, 171]
Leaf diseases									
Appendiculella araucariae	*A. angustifolia*	Brazil	Nf	As Is	Md	1s	parasitic on leaves	Species described and reported uniquely from this host.	[172]
Araucasphaeria foliorum	*A. araucana*	Chile	Nf	As Is	Md dS	1s	leaf spots		[173]
Atotospora araucariae	*A. araucana*	Chile	Nf	As Is	Md	1s	associated to spots diseased leaves	Referred as a weak pathogen.	[105, 174]
Caliciopsis brevipes	*A. araucana*	Chile	Nf	As Is	Md	1s	Leaf galls	Similar symptoms have also been attributed to mite damage [175].	[105, 176]
Calonectria spathulata	*A. angustifolia*	Brazil	?	As Is	Md dS	1s	no description	Description based on leaf spots on *Eucalyptus* spp.	[108, 177]
		Colombia	?	As Is	Md dS	1s	no description	Description based on leaf spots on *Eucalyptus* spp.	[108, 177]
Cirsosiopsis violacescens	*A. angustifolia*	Brazil	Nf	As Is	Md	1s	necrotic spots and discoloration in the base of the leaves	Monotypic genus described from *A. angustifolia*.	[172, 178]
Coccomyces araucariae	*A. angustifolia*	Brazil	Nf	As Is	Md	1s	associated to spots on diseased leaves	Referred as a weak pathogen.	[172]
Colletotrichum sp.	*A. hunsteinii*	Papua New Guinea	Nu	As	Md	DR	leaf spots, bud blight on seedlings		[179]
Cycloschizon araucariae	*A. angustifolia*	Brazil	Nf	As Is	Md	1s	leaf spots		[172]
Didymella araucariae	*A. araucana*	Italy	Or	As Is	Md	2+	needle blight	(=*Araucaria imbricata*)	[157, 180]
Episphaerella araucariae	*A. angustifolia*	Brazil	Nf	As Is	Md	1s	leaf spots	Species description from this host is the only report.	[172]
E. serialis	*A. angustifolia*	Brazil	Nf	As Is	Md	1s	leaf spots	Species description from this host is the only report.	[172]
Gloeosporium araucariae	*A. rulei*	New Caledonia	Nf	As Is	Md	DR	emerging from female cones and leaves	Two separate species descriptions with the same name.	[181-184]
	Araucaria sp.	USA (Hawaii)	?	As	Md	DR	not specified		[123]
Kalmusia araucariae	*A. bidwillii*	USA	Or	As Is	Md dS	DR	associated to leaf blight		[185]
Neocucurbitaria cava	*A. araucana*	USA	Or	As	Md	DR	needle blight	(=*Phyllosticta araucariae*)	[186, 187]
	A. bidwillii	Italy	Or	As Is	Md	DR	sporulating on leaves	(=*Phyllosticta araucariae*, =*araucariecola*)	[187, 188]

Table 2 (continued)

Disease / Pathogen	Host	Location	Environment	Path.	Tax.	Lit.	Symptoms	Observations	Ref.
Pestalotia sp.	*A. angustifolia*	Brazil	Nf Pl	As	Md	DR	rotting of female cones		[101]
Phaeocryptopus araucariae	*A. araucana*	Chile	Nf	As Is	Md	1s	weak or secondary leaf blight		[105, 189]
Phyllosticta acicola	*A. angustifolia*	Brazil	Nu	As	Md	DR	severe leaf spots	(=*Phyllosticta brasiliensis*)	[125]
	A. heterophylla	Japan	Or	As Is	Md	1s	brown needle blight	(=*Phyllosticta drummondii*)	[190]
		USA (Hawaii)	Or	As Is	Md	1s	lesions on cones		[191]
	Araucaria sp.	Canada	Or	As Is	Md	1s	needle blight, dieback and lesions on cones		[191]
Phyllosticta concentrica	*A. heterophylla*	Norfolk Island	?	As Is	Md	DR	lesions on cone scales		[191]
		New Zealand	?	As Is	Md	DR	lesions on cone scales		[191]
Pseudomeliola brasiliensis	*A. angustifolia*	Brazil	Nf	As Is	Md	1s	circular, light brown and raised leaf spots	Species description from this host is the only report.	[172]
Rhizothyrium parasiticum	*A. araucana*	Chile	Nf	As Is	Md	1s	leaf spots	Species description from this host is the only report.	[192]
Seiridium sp.	*A. angustifolia*	Brazil	Nu	As Is	Md	DR	kills old leaves of seedlings	(=*Pestalozzia* sp.)	[102]
Setameliola araucariae	*A. cunninghamii*	Australia	?	As Is	Md	1s	leaf spots, may cause the death of leaves and branchlets	(=*Meliola araucariae*)	[98]
Xenomeris acicola	*A. angustifolia*	Brazil	Nf	As Is	Md	1s	necrotic discolouration and spots on leaf surface	Species described and reported only once, only from this host.	[172]
Damping-off									
Athelia rolfsii	*A. bidwillii*	Brazil	Nu	As Is Pt	Md dS	1s	collar rot and damping off		[193]
	A. cunninghamii	Australia	Nu	As	Md	DR	collar rot	(=*Sclerotium rolfsii*)	[111]
		Papua New Guinea	Nu	As	Md	DR	collar rot	(=*Sclerotium rolfsii*)	[194]
	Araucaria sp.	Brazil	Nu	As	Md	DR	collar rot	(=*Sclerotium rolfsii*)	[195]
Botrytis cinerea	*A. araucana*	New Zealand	?	As	Md	DR	not specified		[196]
Calonectria cylindrospora	*A. angustifolia*	Brazi	Nu	As Is	Md	DR	damping-off and stem cankers	(=*Cylindrocladium scoparium*)	[102]
C. pacifica	*A. heterophylla*	Hawaii	Nu	As	Md dS	DR	collar rot	(=*Cylindrocladium kyotensis; =Cylindrocladium floridanum*)	[124, 197]
Fusarium sp.	*A. angustifolia*	Brazil	Nu	As Is	Md	2+	damping-off		[101, 102]
		Egypt	Sb	Is Pt	Md	1s	damping-off		[198]
	A. cunninghamii	Malaysia	Nu	As Is	Md	1s	root rot		[85]
		Egypt	Sb	Is Pt	Md	1s	damping-off		[198]
	A. araucana	Chile	Nu	As	Md	DR	root a collar rot		[120]
	A. hunsteinii	Papua New Guinea	Nu	As	Md	DR	wilting and death of seedlings		[179]
	A. heterophylla	Egypt	Sb	Is Pt	Md	1s	damping-off		[198]
F. lateritium	*A. angustifolia*	Brazil	Nu	As	Md	DR	stem cankers with resin exudation		[102]
Fusarium robustum	*A. angustifolia*	Argentina	Nu	As Is Pt	Md dS	2+	collar rot on seedlings		[199-201]
Fusarium oxysporum	*A. angustifolia*	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198]
	A. bidwillii	Egypt	Sb	Is	Md	1s	damping-off and seed rot		[198]
	A. cunninghamii	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198]
	A. heterophylla	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198, 202]
Glomerella cingulata	*A. cunninghamii*	Malaysia	Nu	As	Md	DR	root rot on six-month-old seedlings		[85]
Macrophomina phaseolina	*A. araucana*	Chile	Nu	As	Md	DR	root a collar rot		[120]
Neocosmospora solani	*A. angustifolia*	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot	(=*Fusarium solani*)	[198]
	A. bidwillii	Egypt	Sb	Is	Md	1s	damping-off and seed rot		[198]
	A. cunninghamii	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198]
	A. heterophylla	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198, 202]
Phytophthora spp.	*A. angustifolia*	Brazil	Nu	As	Md	DR	damping-off		[102]
Pythium sp.	*A. angustifolia*	Brazil	Nu	As	Md	DR	damping-off		[102]
		Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198]
	A. cunninghamii	Australia	Nu	Is	Md	1s	damping-off and seed rot		[111]
		Egypt	Sb	Is	Md	1s	damping-off and seed rot		[198]
	A. heterophylla	Egypt	Sb	Is Pt	Md	1s	seed rot		[198, 202]
		USA	Nu	Is	Md	DR	not specified		[203]
P. irregulare	*A. heterophylla*	New Zealand	Nu	As Is	Md	DR	damping-off		[99]
P. ultimum	*A. columnaris*	New Zealand	Nu	As Is	Md	DR	damping-off		[62,100]
Rhizoctonia sp.	*A. cunninghamii*	Australia	Nu	Is	Md	1s	damping-off		[111]
	A. angustifolia	Brazil	Nu	As	Md	DR	damping-off		[101]
Rhizoctonia solani	*A. angustifolia*	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198]
	A. bidwillii	Egypt	Sb	Is	Md	1s	damping-off and seed rot		[198]
	A. cunninghamii	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198]
	A. heterophylla	Egypt	Sb	Is Pt	Md	1s	damping-off and seed rot		[198, 202]

[a] Environment: **Nf**: natural forests, **Pl:** plantations, **Nu:** nurseries, **Or:** ornamental, **Sb:** seed batches, **?**: not specified.
[b] Path: Pathogenicity **As:** associated to diseased trees, **Is:** isolated from diseased tissues, **Pt:** pathogenicity confirmed through inoculations.
[c] Tax: Taxonomic position: **Md:** identified through morphology, **iS:** indirectly sequenced (e.g., isolates from same or close environments but different hosts or obsolete techniques), **dS:** directly sequenced.
[d] Lit: Literature abundance: **DR:** disease records, brief or no description of symptoms and methods, **1s:** a unique report, with descriptions of methods, **2+:** two or more reports.

Disease Threats

Tree pathogens represent a serious threat to the species in the Araucariaceae. The impact of tree pathogens is often quantified in terms of economic losses for plantation species. Although this could be applied for some species of Araucariaceae, it is not as concerning as the potential impact pathogens may have from an ecological perspective. This is in light of most of the species having a reduced natural distribution, to the extent where many have been declared at some level of risk by the

Table 3 Diseases on *Wollemia nobilis*

Disease / Pathogen	Host	Location	Environment [a]	Path. [b]	Tax. [c]	Lit. [d]	Symptoms	Observations	Ref.
Root rots									
Phytophthora cinnamomi	*W. nobilis*	Australia	Nf	As Pt	Md dS	2+	root rot associated to tree decline and death		[204-206]
P. multivora	*W. nobilis*	Australia	Nf	As Is Pt	Md dS	1s	root rot associated to tree decline		[206]
Canker diseases									
Botryosphaeria sp.	*W. nobilis*	Australia	Nu	Is Pt	Md	1s	not specified	Pathogenicity tests showed high aggressivity.	[205]
Fusarium oxysporum	*W. nobilis*	Australia	Nu	Is Pt	Md	1s	root rot	Two out of nine inoculated plants showed symptoms.	[205]
Neofusicoccum australe	*W. nobilis*	Australia	Nu	As Is	Md dS	1s	dieback		[163]
N. occulatum	*W. nobilis*	Australia	Nu	As Is Pt	Md dS	1s	dieback		[163, 164]
N. parvum	*W. nobilis*	Taiwan	Or	As Is	Md dS	2+	dieback	Isolates caused symptoms to *A. cunninghamii* and *A. heterophylla* when inoculated.	[151]
Leaf spots and blights									
Mycosphaerella wollemiae	*W. nobilis*	Australia	Nf	As Is	Md	DR	leaf spots		[207]

[a] Environment: **Nf**: natural forests, **Pl**: plantations, **Nu**: nurseries, **Or**: ornamental, **Sb**: seed batches, **?**: not specified.
[b] Path: Pathogenicity **As**: associated to diseased trees, **Is**: isolated from diseased tissues, **Pt**: pathogenicity confirmed through inoculations.
[c] Tax: Taxonomic position: **Md**: identified through morphology, **iS**: indirectly sequenced (e.g., isolates from same or close environments but different hosts or obsolete techniques), **dS**: directly sequenced.
[d] Lit: Literature abundance: **DR**: disease records, brief or no description of symptoms and methods, **1s**: a unique report, with descriptions of methods, **2+**: two or more reports.

IUCN [209]. Along with threats posed by fragmentation, climate change, altered fire regimes and anthropogenic activities such as cattle grazing, logging and seed collection, diseases can have devastating effects on the preservation of species.

Ecological Threats

The threat of *Phytophthora* species is among the most concerning of the disease risks to Araucariaceae. For example, in Australia, *P. cinnamomi* and *P. multivora* have been detected within the extremely limited native range of *W. nobilis* [204, 206]. This tree species is known to be highly susceptible to both pathogens [206], which is even more concerning for a tree species that represents a single population with low genetic diversity [210] and a limited number of trees at a reproductively mature age [211]. Similarly, *P. agathidicida*, the causal agent of kauri dieback (*Ag. australis*) in New Zealand, is an aggressive primary pathogen that can spread rapidly and can girdle trunks and kill trees of all ages [212••]. This disease has had a significant impact on the kauri population by decreasing the number of individuals, which will also translate into a negative effect on the reproduction rate of the species.

Less aggressive diseases caused by *Phytophthora* species can also represent relevant threats to Araucariaceae forests. For example, *P. cinnamomi*, *P. multivora* and *P. cryptogea* have frequently been detected within the natural range of kauri [72] and pathogenicity to kauri has been demonstrated [70]. Although these *Phytophthora* species are not considered to cause severe disease symptoms, there is evidence to suggest that *P. cinnamomi* may have an important negative impact in the regeneration of the species by causing pre- and post-emergence damping-off to seedlings [75]. Differences in susceptibility to these *Phytophthora* species among the accompanying species, as observed with *P. agathidicida* [212••], are presumed to reduce the regeneration of kauri forests species, favouring their replacement and thus altering a unique indigenous ecosystem [24].

Another threat that diseases pose on natural forests is the disturbance of sexual reproduction. There are pathogens known to directly disturb this process on some Araucariaceae growing under natural conditions. These include, for example, *Uleiella* spp. that rot male and female cones of the South American species *A. angustifolia* and *A. araucana* respectively [105, 169, 170]. Other pathogens may disturb this process indirectly, for example, by reducing the abundance of cones by infecting and killing branches of sexually mature trees. This could be the case for canker pathogens such as *P. kutranfy* on *A. araucana* [8] and Botryosphaeriaceae pathogens that occur on diverse Araucariaceae species [87, 88, 152, 154, 155]. The slow nature of the reproduction cycle observed on the long-lived species in the Araucariaceae [213], including long time frames for trees to reach sexual maturity [214–217], relatively long time frames for cones to mature [94, 215, 218] and high mortality rates of natural regeneration [214, 217–219], make these trees especially sensitive to these disturbances. The impact of pathogens on the reproduction of Araucariaceae has not been quantified; however, it is likely underestimated and should be taken seriously.

Pathogens can limit opportunities to preserve species using approaches such as restoration or commercialization. Diseases caused by pathogenic fungi are a common problem during tree production activities, and Araucariaceae are not an exception. As mentioned previously, a diverse range of fungal and oomycete pathogens have been reported from Araucariaceae in nurseries [62, 102, 111, 126, 163, 205]. Although most of these pathogens are common in nursery environments, in some cases, *Araucaria* species have shown higher levels of susceptibility than has been reported for other hosts. Examples include *Athelia rolfsii* on *A. bidwillii* in Brazil [193], *Fusarium robustum* on *A. angustifolia* in

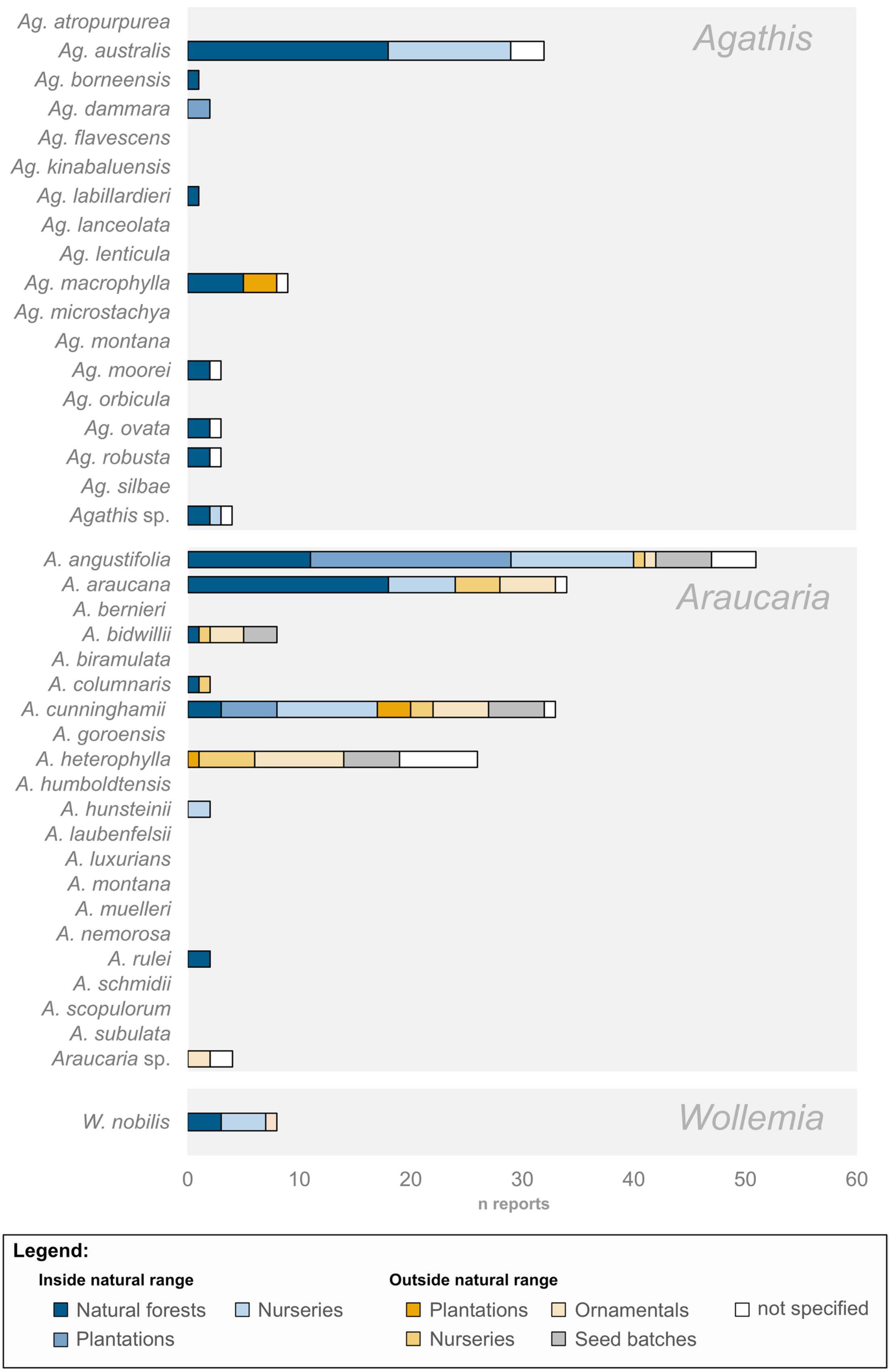


Fig. 4 Number of pathogen reports found in literature for species within Araucariaceae. Reports are categorized as inside of the host's natural range (tones of blue), outside (tones of yellow), seed batches (grey) and not specified (white)

Table 4 Statistics for the disease reports by host genera within Araucariaceae, including number of host–pathogen combinations, confirmation of pathogenicity and level of identification of the causal agent

Host genus	Disease reports[a]			Pathogenicity		Causal agent identification[b]		
	N	Hosts	Countries	Host–pathogen combinations	Pathogenicity confirmed	Species–sequenced	Species–Morphology	Genus–morphology
Agathis	58	8/17	9	58	8 (14%)	8 (14%)	38 (66%)	12 (21%)
Araucaria	161	8/20	28	139	38 (27%)	33 (24%)	85 (61%)	21 (15%)
Wollemia	8	1/1	2	8	5 (63%)	5 (63%)	2 (25%)	1 (13%)
Total	227	17/38	33 [c]	205	51 (25%)	46 (35 [c])	125 (85 [c])	34 (20 [c])

[a]Pathogen-host-location combination

[b]Percentages calculated from the total of host–pathogen combinations

[c]sum of values, excludes repetition among host genera or species

Argentina [199], and *Phytophthora multivora* and *P. citrophthora* on *A. araucana* in Chile [126]. Additionally, where Araucariaceae have been planted in the field for restoration or commercial purposes, they have frequently encountered disease problems. For example, where *A. angustifolia* has been planted in its natural range, in Brazil, it has been damaged by several pathogens including *P. cinnamomi* [118], *Diplodia sapinea* [154], *Calonectria brassicae* (= *Cylindrocladium clavatum*), *Armillaria* sp., *Rosellinia* sp. [102] and *Phellinus* sp. [101]. Given that information for most Araucariaceae is limited, non-recorded (or novel) diseases will likely continue to emerge should they start being propagated in higher quantities, impacting the success of such efforts.

Economic Threats

Diseases represent a significant threat to the potential economic contribution of the Araucariaceae. For example, kauri dieback (caused by *Phytophthora agathidicida*) has had an impact on New Zealand's tourism [212••, 220] and has been considered a potential threat if this species was to be planted for commercial purposes [221]. There was a concern of a similar situation in Chile, when *Araucaria araucana*, a species important to the economy of indigenous people and local tourism [222] began to show dieback symptoms in 2015 [8].

Pathogens can result in significant losses in the production and plantation of species in the Araucariaceae. Examples of pathogens that have been associated with losses in plantations of silvicultural purposes include *E. salmonicolor* (Pink disease) on *Ag. dammara* in Indonesia [23], *P. noxius* on *A. cunninghamii* in Australia [112] and the previously mentioned diverse range of pathogens on *A. angustifolia* in Brazil, including an additional diversity of wood-staining fungi known to occur on this tree [102]. The production of these trees in countries outside their natural range for commercialization as ornamentals, among which the most common are *A. heterophylla*, *A. cunninghamii*, *A. bidwillii* and *A. araucana*, has also been negatively affected by diseases. This is especially by pathogens in the Botryosphaeriaceae, *Phytophthora*, *Pythium* and *Fusarium* [85, 99, 100, 119, 125, 163, 203].

The economic relevance of the Araucariaceae deserves careful consideration. Economic interests are one of the main drivers known to promote monitoring and research on trees in general and, especially tree health. Yet at the same time, economic interests carry with them common triggers for the emergence of diseases. These include movement of plant material, tourism activities or as a direct consequence of planting higher densities of trees [212••, 223••, 224, 225]. These potential risks and benefits must be carefully considered and balanced for any Araucariaceae species before any economic use of these trees should be encouraged or implemented.

Globalization and Climate Change Effects on Araucariaceae Diseases

Among the effects that human activity has had on natural forests, the most damaging and concerning are those related to globalization and climate change [6, 7•]. Among the major drivers for the emergence of forest diseases are the movement of plant material around the world, resulting in accidental introductions of pest and pathogens [226, 227] and the accelerated change in climatic conditions, favouring the biology of pathogens and/or predisposing trees in different manners [7•, 228, 229]. Concerning the Araucariaceae, there are cases of emerging diseases where evidence suggests these are the result of globalization and climate change [8, 19, 108]. However, more research is required to understand the often-complex suite of abiotic and biotic factors driving disease emergence.

Globalization and Anthropogenic Activities as Drivers of Disease

Biological invasions and the movement of pathogens are emerging as a substantial threat to the Araucariaceae. This is well illustrated by the accidental introduction of *Phytophthora* spp. into the native range of *W. nobilis*, now considered among the greatest threats to the preservation of this species [206, 218]. Even though the risk of introduction was recognised [205], nothing could be done to prevent it.

Invasions by introduced mammals have been linked to the dispersal of Araucariaceae pathogens. For example, feral pigs in New Zealand have been shown to be capable of moving *Phytophthora agathidicida* propagules [230]. The introduction of mammals have also caused higher levels of seed predation and seedling browsing and trampling in Chile and Argentina, resulting in reduced reproductive success of *A. araucana* [231, 232].

The planting of foreign tree species in areas where there are native Araucariaceae has been linked to the appearance of unrecorded diseases. In Brazil, *Cylindrocladium clavatum* (= *Calonectria brassicae*) was described causing severe root rot of planted 12 to 15-year-old *A. angustifolia*, and was subsequently found causing even more severe symptoms on neighbouring *Pinus* spp. plantations [109]. Given that *A. angustifolia* is the only native host in Brazil, and that the pathogen has been described on other hosts and locations around the world [108], it is reasonable to assume the disease emerged as a result of an anthropogenic introduction. Similarly, there is abundant evidence of Araucariaceae species being susceptible to pathogens of commercially planted species of *Pinus* and *Eucalyptus* [58, 107, 108, 111, 118, 129, 151, 154, 233]. These non-native species are being planted in several countries where Araucariaceae have native representatives and may carry pathogens that the Araucariaceae have not coevolved with. This, together with the use of Araucariaceae as ornamentals around the world (including countries where other Araucariaceae species are native), leaves a considerable opportunity for the occurrence of future pathogen introductions and host-jumps.

At a local scale, human activities within or near the native range of Araucariaceae can indirectly impact the spread and severity of damage by pathogens. For example, changes in the use of soil (replacing kauri forests with plantations) enhance the sporulation of *P. agathidicida*, creating potential inoculum reservoirs [234]. Activities such as tourism and livestock production are known to move contaminated material and disturb soils on kauri stands [72, 220, 235]. Additionally, cattle ranching and overgrazing within the natural range of some Araucariaceae have negatively impacted the general health of forests and regeneration. Cases include *A. araucana* in Chile and Argentina, including zones within protected areas [14, 236], and *A. heterophylla* in Norfolk Island [16]. Attention needs to be given to how local communities (society) interact with these forests in their native range [237], as their activities may pose risks of direct exposure to novel pathogens, or may result in a reduction in tree vigour leading to a loss of resilience capacity.

Effects of Climate Change on Araucariaceae Diseases

Climate change has been associated with emergent diseases of Araucariaceae. Most reports of emerging dieback diseases on species in the family cite changes in climatic conditions as being among, or the main driver. For example, dieback of *Ag. montana* in its natural range in New Caledonia has been positively correlated with drier years and a trend in rising temperatures [19], although, no biological agent has been consistently found in association with the symptoms. A similar situation was observed in Chile, with *A. araucana* dieback. Climatic conditions were observed to be outside the normal range around the time when symptoms emerged in 2015 [238, 239] and cankers caused by *P. kutranfy* were discovered [8]. In Australia, the emergence of dieback symptoms on ornamental *A. heterophylla* trees associated with infections by fungi in the Botryosphaeriaceae has occurred in two time-independent events, both coinciding with drought/heat periods acting as predisposing factors [166, 167].

There are various means by which climate change can influence diseases in Araucariaceae forests. The most common scenarios are linked to drought stress and increases in temperature, either directly due to the tree's physiological limits being exceeded, or as non-lethal levels of stress predisposing trees to infection by secondary pathogens [240–242]. The previously mentioned cases on *Ag. montana* and *A. heterophylla* serve as examples, as do most cases that involve pathogens within the Botryosphaeriaceae [208]. Studies have shown that the Araucariaceae have ancestral mechanisms for coping with water stress, which places them among the conifers with the least tolerance to water deficits [243, 244•]. Furthermore, climatic predictions indicate that some of the areas naturally suitable for the growth of the Araucariaceae are being reduced [245•, 246, 247], indicating that stress scenarios will become more common with time.

Current trends in increasing temperatures may benefit pathogens of the Araucariaceae in different manners. For example, environments where Araucariaceae occur, such as in high altitude regions, may become more susceptible to biological invasions, including forest pathogens [248, 249]. *Phytophthora cinnamomi*, a common pathogen on several Araucariaceae, has low tolerance to colder temperatures, but based on current climatic projections, it will have the ability to expand its geographical range [4]. The range and impact of native pathogens may also be extended based on the same principle. For example, Swiss needle cast disease of *Pseudotsuga menziesii* in North America, caused by the fungus *Phaeocryptopus gaeumanii*, has led to a substantial increase in disease severity and spread through the years strongly correlated to a sustained rise in winter temperatures and spring precipitation [250]. A similar scenario is hypothesized for the emergence of *P. kutranfy* canker disease on *A. araucana* in Chile [8].

Even mild changes in climatic conditions may impact several factors influencing the extent of diseases. These include, for example, the life cycle of pathogens (including survival and production of inoculum) and the fitness and phenology of the hosts and pathogens when the interaction occurs. Additionally, native disease systems may be influenced indirectly through alterations in their surrounding environment where factors such as abundance or behaviour of insects or other organisms that may act as vectors, sources of mechanical damage or inoculum reservoirs may have been modified [228, 240, 241, 251••, 252].

It is difficult to predict how globalization and climate change interact, and how this will impact forest diseases of the Araucariaceae in the future. As previously stated, both factors may interact in diverse ways with pathogens and/or hosts, but they are not exclusive to each other. Management strategies, both broad and specific, have been proposed to diminish the risks of these uncertain scenarios [237, 240, 241], and some have already been applied for iconic species within Araucariaceae [212••, 253]. However, the applicability of such strategies usually requires a baseline of information or knowledge, which represents an important constraint for most species in the Araucariaceae.

Limitations to Current Knowledge

Knowledge regarding diseases of the Araucariaceae is relatively scarce and the topic remains largely unexplored. In summary, there are currently 21 species in Araucariaceae for which there are no disease reports. Moreover, for many of the species for which diseases have been reported, these are commonly only for a single or less than five diseases (Fig. 4, Table 4). This illustrates either a lack of research on these species, including a lack of tree health monitoring and/or information is inaccessible (e.g. grey literature). The recent emergence of dieback diseases in some Araucariaceae has highlighted a lack of knowledge regarding pathogens associated with these trees and a more general lack of knowledge of the microbes associated with these trees regarding their identity and role in causing disease.

Most disease reports for the Araucariaceae are several decades old and where pathogen descriptions were based solely on morphology. The implication is that several of these were recognised based on records of pathogens of planted tree species, especially *Pinus* species. There have thus been assumptions that the associated fungi are pathogens of the Araucariaceae without pathogenicity ever being tested. For example, *Heterobasidion araucariae*, a wood rotting basidiomycete was, for a long time, confused with *H. annosum*, a severe root rot pathogen of plantation-grown *Pinus* spp. [81]. Concern was raised regarding the detection of this supposed *H. annosum* on stumps of *Ag. australis* (New Zealand), *Ag. macrophylla* (Fiji), *A. bidwillii* (Australia) and *A. cunninghamii* (Australia and Papua New Guinea) [81], all in natural forests. However, when the fungus found on these native trees was properly studied, it turned out that this was a different and considerably less aggressive species, described as *H. araucariae* [81]. Similar cases have arisen for *Armillaria* species (as *A. mellea*) [59, 102, 105], *Ganoderma* spp. (as *G. applanatum*) [66, 67], *Pyrrhoderma* spp. (as *Phellinus* species) [78, 79] and *Rigidoporus* spp. (=*Junghuhnia vincta*) [147, 148], where identification was based on pathogens of other hosts not in the Araucariaceae. In several instances, the identification of the pathogen has not yet been confirmed, and their role as pathogens has simply been assumed.

There are some pathogens described as being unique to the Araucariaceae that remain obscure, present only in the early literature. Access to these reports is difficult given that they are not found in accessible databases, and some are in less commonly encountered languages. These reports of presumed pathogens mostly represent rare fungal species studied primarily from a mycological rather than plant pathology perspective, and where their role as pathogens has only been assumed. They for example include *Lophodermium agathidis* on *Agathis australis* [95]; *Appendiculella araucariae*, *Cirsosiopsis violacescens*, *Coccomyces araucariae*, *Cycloschizon araucariae*, *Episphaerella araucariae*, *E. serialis*, *Pseudomeliola brasiliensis* and *Xenomeris acicola*, all on *A. angustifolia* [172]; and *Atotospora araucariae* [174]; *Phaeocryptopus araucariae* [189] and *Rhizothyrium parasiticum* [192], on *A. araucana* (Fig. 5). These fungi may be easily overlooked, as they appear in single articles, and lack the DNA sequence data to allow for their accurate identification. Negative consequences of this situation include potentially duplicated species descriptions and a lack of tools for opportune detection. Most of the fungi mentioned above are associated with mild leaf symptoms in natural forests. Nevertheless, as so little is known about them, caution should be applied to prevent or minimise their accidental movement to new environments where congener species of Araucariaceae could be susceptible. This would be similar to the situation with, for example, many pathogens of *Eucalyptus* spp. that have caused more severe disease in areas where they have been introduced [223••].

Most of the known diseases (host–pathogen combinations) for Araucariaceae lack complete or recent studies. As mentioned above, of the 205 host–pathogen combinations found in accessible literature, only 51 (25%) have been subjected to pathogenicity tests, and only 46 (22%) have had the identity of the causal pathogen confirmed using DNA sequence data. There are only a limited number of diseases of the Araucariaceae where both DNA sequencing for the causal agent and

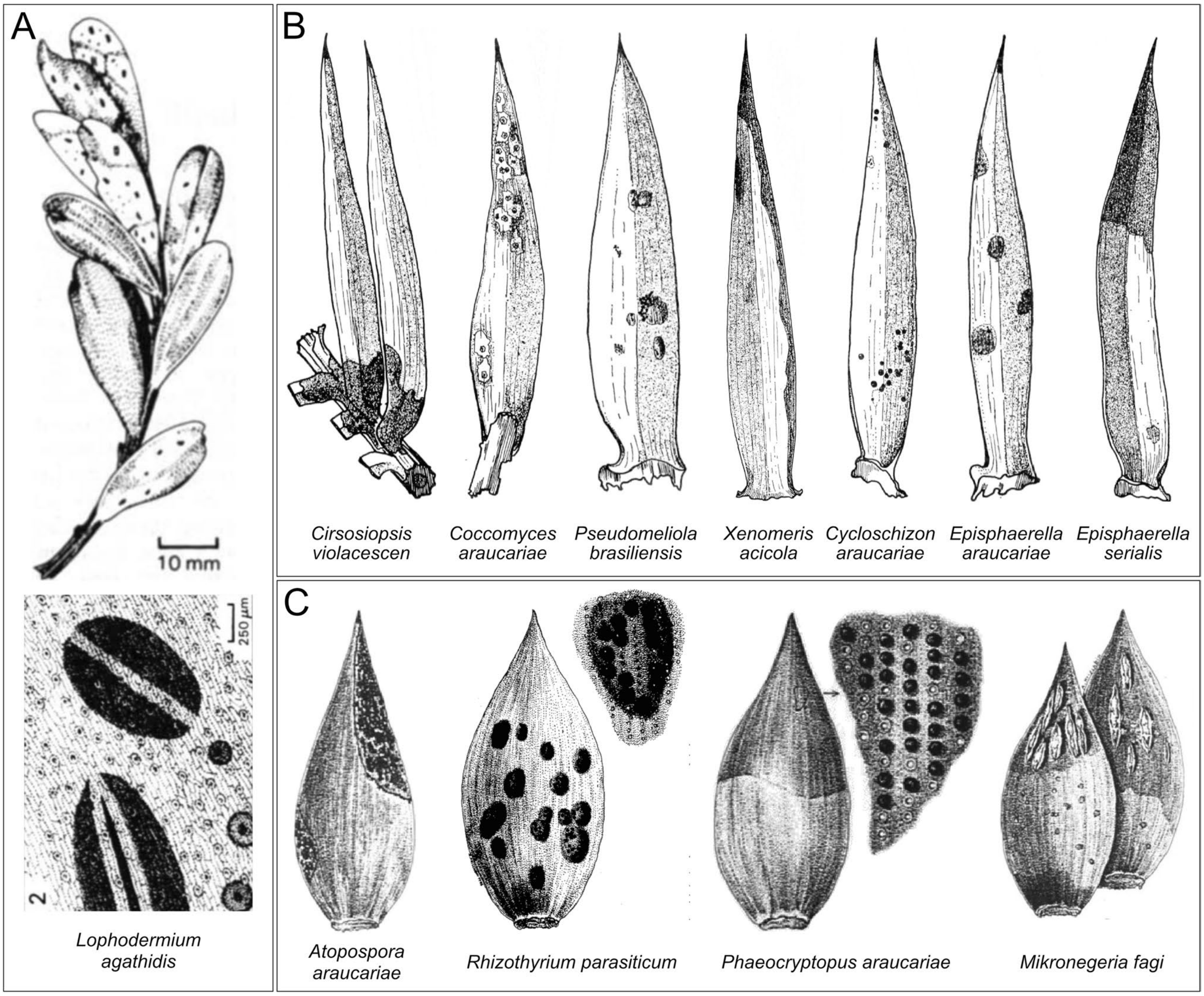


Fig. 5 Diagrams of leaf pathogens described from some species inside Araucariaceae. **A** *Lophodermium agathidis* described from *Agathis australis* in New Zealand (Minter and Hetiige 1983). **B** Leaf pathogens described on *Araucaria angustifolia* from Brazil (Butin and Speer 1978). **C** Leaf pathogens described on *Araucaria araucana* from Chile (Butin 1986; Butin and Peredo 1986)

inoculation experiments have been conducted. These include four for *Agathis* [70, 72, 75], 16 for *Araucaria* [8, 9, 118, 126, 141, 142, 152, 153, 155, 162, 193, 200, 201] and three for *Wollemia* [163, 164, 205, 206]. These low numbers are particularly concerning, as confirmation of both pathogenicity and identity of the causal agent represents the most basic knowledge regarding any disease.

Recent research on emerging or persistent diseases of Araucariaceae has highlighted the problems resulting from the lack of baseline, or in fact any information [8, 16, 17, 19, 254]. This has also demonstrated the challenges in determining the origin of cryptogenic species [255], and the difficulty in answering more advanced questions regarding abiotic and biotic drivers involved in these complex diseases. In this regard, lack of information on pathogens and diseases of the Araucariaceae should not be considered "knowledge gaps" as commonly referred to in science, but rather "knowledge islands", where nothing is known in most cases.

General Conclusions

Knowledge regarding diseases of Araucariaceae is an uneven and gap-filled territory. Except for a few species, for which some diseases have been relatively well studied, most species in the family lack any information regarding this important topic. This void, which is clearly influenced by the socioeconomic importance of each tree species, may result from a lack of monitoring and/or information accessibility. Additionally, disease outbreaks and forest declines, including Araucariaceae, are increasing, and these appear to be driven by globalization and climate change. There are numerous ways in which these factors can interact and impact on Araucariaceae species and the occurrence of diseases. The outcomes of these events are highly unpredictable, and in most cases, may be unmanageable due to the lack of baseline information. This presents a concerning scenario, given the current poor conservation status of most species of the Araucariaceae.

There is an obvious and substantial need to conduct research on the Araucariaceae, and the future of these iconic trees rests firmly on this requirement. New technologies provide many robust opportunities to strengthen the currently weak base knowledge and fulfil existing gaps. This would for example include the sequencing of old herbarium specimens and/or collection of fresh material for correct identification, or epitypification of poorly studied pathogens [256]. Also, multidisciplinary perspectives should be applied to the study of diseases affecting Araucariaceae. This can be done by applying recently proposed frameworks and strategies, such as assessing their impact on the ecological functionality of the host species [257•], and furthermore, to adequately assess the effect of climate on the diseases of these trees [7•] and including invasion biology perspectives to assess forest pathogens [258, 259]. Alternative monitoring strategies such as sentinel plantings and/or including trees in botanical gardens, arboreta and urban areas for early detection should also be considered [260, 261].

Robust research can lead to more efficient monitoring, more adequate regulations, and a greater capacity to respond in the event of a disease emergence. Efforts must also be made to ensure that well-intended actions do not result in harmful situations, e.g., the introduction of pathogens from nurseries to natural environments through restoration programmes [262]. Given the current poor status of knowledge, efforts should focus on protecting these species in their native ranges, through more active monitoring and giving special consideration to limiting the movement of material that could result in the accidental introduction of pathogens or other events that would help spread them.

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Declarations

Human and Animal Rights This article does not contain any studies with human or animal subjects performed by any of the authors.

Conflict of Interest Felipe Balocchi, Michael J. Wingfield, Trudy Paap, Rodrigo Ahumada and Irene Barnes declare that they have no conflict of interest.

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