CSIRO PUBLISHING

RESEARCH PAPER
https://doi.org/10.1071/BT22128

Australian Journal of Botany

Myxomycetes associated with the bark, cones and leaves of Australian cypress pines (*Callitris* spp.)

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Handling Editor:
Garry Cook

Received: 16 November 2022
Accepted: 8 February 2023
Published: 15 March 2023

Cite this:
Stephenson SL *et al.* (2023)
Australian Journal of Botany, **71**(3), 157–165.
doi:10.1071/BT22128

ABSTRACT

Context. The diversity of myxomycetes associated with Australia's most diverse native conifer genus, *Callitris*, has been incompletely studied. **Aims.** In this study, we examine the diversity of myxomycetes associated with outer bark, fallen cones and dead litter (leaves/needles) of four *Callitris* species. **Methods.** Substrate samples were collected from 13 localities in New South Wales, Queensland and the Northern Territory. Samples were used to prepare moist-chamber cultures, and species of associated myxomycetes were identified. **Key results.** Twenty-three species in 15 genera were recorded. Percentage occurrence of myxomycetes varied depending on substrate, being 87% (cones), 83% (bark) and 63% (litter). Bark yielded the most species (17), followed by litter (10) and cones (6). Only two species (*Arcyria cinerea* and *S. fusca*) were recorded from all three substrates. Substrate pH is often an important factor for the occurrence of myxomycetes, but the mean values recorded for cones (5.7), litter (5.8), and bark (5.9) showed little difference. This suggests that other undetermined factors contributed to the differences in species occurrence. In addition to the records generated in the present study, we provide a list of previous records of myxomycetes found in association with *Callitris*. **Conclusions.** This study has highlighted, for the first time, the diversity of myxomycetes associated with members of the genus *Callitris* and has shown the importance of cypress pines as a substrate for myxomycetes. **Implications.** This study leads to a better understanding of the biogeography, distribution and ecology of myxomycetes and their associated organisms.

Keywords: amoebozoans, conifer myxomycete ecology, Cupressaceae, microbial ecology, moist chamber cultures, myxogastrids, plasmodial slime moulds, slime moulds.

Introduction

One of the earliest branches of the eukaryote tree of life consists of an assemblage of amoeboid protists referred to as the supergroup Amoebozoa (Fiore-Donno *et al.* 2010). The most diverse members of the Amoebozoa are the eumycetozoans, commonly referred to as slime molds (Stephenson and Stempen 1994). Of these, the myxomycetes are the best known group, with approximately 1200 morphologically recognisable species (Lado 2005–2022). Myxomycetes are free-living predators of other eukaryote protists and bacteria and have been recorded from every terrestrial habitat investigated (Stephenson 2021). The two trophic stages (amoeboflagellates and plasmodia) in the life cycle are usually cryptic, but the fruiting bodies are often large enough to be observed directly in nature. Fruiting bodies release spores that are dispersed by air or (more rarely) by animal vectors (Stephenson and Stempen 1994). Under favorable conditions, these spores germinate and give rise to amoeboflagellates, from which the plasmodium is ultimately derived (Martin *et al.* 1983).

Myxomycetes are associated with a wide variety of substrates that occur in a wide range of microhabitats. The most important substrates are considered to be coarse woody debris, ground litter, aerial litter and the bark surface of living trees (Stephenson 1988). Specimens for study can be obtained as fruiting bodies that have developed in the field under natural conditions or were cultured in the laboratory. A substantial body of data on the worldwide biodiversity and distribution of myxomycetes has been assembled over the past 200 years. More recently, an appreciable body of data has become available on various aspects of the biology, ecology, phylogeny, and genetics of these organisms (Rojas and Stephenson 2021). However, there are still various aspects of their distribution and ecology that remain understudied. Considerable research has been conducted on the assemblages of myxomycetes associated with conifers and forest communities dominated by conifers around the world (e.g. Novozhilov *et al.* 2010; Takahashi and Hada 2010; Takahashi and Harakon 2012; Adamonytė *et al.* 2016; Stephenson *et al.* 2020*a*). Because most species of conifers occur in the northern hemisphere, studies of conifer–myxomycete associations have typically focused on locations outside of Australia, unless they involved plantations of imported pines. Very limited sampling conducted in western Queensland by the present authors in 2019 suggested that *Callitris* provides a favourable substrate for these organisms (Table 1). The genus *Callitris* (known as cypress pine) is the most diverse group of conifers native to Australia. In all, 13 of the 16 recognised species are endemic to Australia; the remaining three are endemic to New Caledonia (Piggin and Bruhl 2010; Crisp *et al.* 2019). Previous studies of myxomycetes in Australia have incidentally reported a diversity of species to occur on substrates (mostly samples of bark) derived from *Callitris* (Table 1), but the present study is the first to focus on these associations.

Materials and methods

Samples of the non-living outer bark, fallen female cones, and litter (dead leaves/needles from the ground) were collected from four species of *Callitris* (*C. columellaris* F.Muell., *C. glaucophylla* J.Thomp. & L.A.S.Johnson, *C. intratropica* R.T.Baker & H.G.Smith, and *C. rhomboidei* R.Br. ex Rich. & A.Rich.; Fig. 1). Samples were sourced from *Callitris* populations at 13 localities in New South Wales, Queensland, and the Northern Territory (Table 2). Samples were from areas of high mean annual rainfall for Australia, ranging from the temperate to tropical climate zones to the transitional to arid climate zone. Each sample was placed in a paper bag, air dried, and sent to the Eumycetozoan Laboratory at the University of Arkansas in the United States. These samples were used to prepare three series of moist-chamber cultures (bark, cones, and litter) in the manner described by Stephenson and Stempen (1994). The series prepared with bark consisted of 40 cultures, the series prepared with litter consisted of 38 cultures, and the series prepared with cones consisted of 38 cultures. Each culture consisted of a 90 mm plastic disposable Petri dish, with the bottom lined with filter paper. Enough sample material was placed in each dish to cover most of the filter paper. Once prepared, enough distilled water was added to each culture to cover most of the sample material. After approximately 24 h, the pH of each culture was determined and recorded and then most of the water was poured off. All cultures were set aside out of direct sunlight and then examined with the aid of a dissecting microscope at weekly intervals over a period of 3 months. Any fruiting bodies of myxomycetes appearing in these cultures were collected or recorded. Those collected were placed in small pasteboard boxes for permanent storage in the herbarium of the University of Arkansas (UARK). Standard references for myxomycetes (e.g. Martin and Alexopoulos 1969) were used to identify the collections.

Results

Of the 116 moist-chamber cultures prepared in this study, 90 (78%) yielded evidence (plasmodia or fruiting bodies) of myxomycetes. Twenty-three species in 15 genera were recorded. The percentage of positive cultures was 87% (cones), 83% (bark), and 63% (litter). The differences among the three substrates were more appreciable when numbers of species were considered. Seventeen species were recorded from bark, 10 from litter, and six from cones. Only two species (*Arcyria cinerea* and *S. fusca*) were recorded from all three substrates. As is the case for other studies of myxomycetes, a record is based on the occurrence of at least one specimen of the species in question. However, it is possible for a record to be based on many hundreds of specimens. This is especially true for some of the smaller species.

Acryria cinerea (18 specimens) was the most abundant species, but *Cribraria confusa* (eight specimens), *Diderma effusum* (eight specimens), *C. minutissima* (five specimens), *Perichaena vermicularis* (five specimens), and *Physarum decipiens* (five specimens) were also relatively common. Mean values of pH recorded for the three sets of cultures displayed little variation, with a range of only 5.7–5.9. The values recorded for cultures prepared with bark were the most variable (3.9–6.8), with the highest value a conspicuous outlier.

Annotated list of species

Species of myxomycetes recorded in the present study are listed alphabetically by genus and then species. Nomenclature used follows Lado (2005–2022). The total number of specimens recorded for each species, their distribution with respect to the three substrates, the species of *Callitris* and the specific localities from which the species was recorded,

Table 1. List of myxomycetes reported to occur in association with *Callitris* compiled from our study and a comprehensive review of the literature.

Species	*Callitris* sp.	Reference
Arcyria cinerea	*Callitris* sp., *C. columellaris*, *C. glaucophylla*, *C. intratropica*, *C. rhomboidea*	Wellman (2019); this study
Arcyria pomiformis	*Callitris* sp.	Rosing *et al.* (2007), Wellman (2019)
Badhamia sp.	*Callitris glaucophylla*	S. L. Stephenson (unpubl. data)
Badhamiopsis ainoae	*Callitris* sp.	Wellman (2019)
Calomyxa metallica	*Callitris* sp., *C. glaucophylla*	Rosing *et al.* (2007), Wellman (2019), S. L. Stephenson (unpubl. data), this study
Clastoderma confusum	*Callitris columellaris*	Knight and Lado (2020)
Clastoderma debaryanum	*Callitris intratropica*	This study
Comatricha elegans	*Callitris* sp.	Wellman (2019)
Comatricha ellae	*Callitris* sp.	Wellman (2019)
Comatricha laxa	*Callitris glaucophylla, C. intratropica, C. rhomboidea*	S. L. Stephenson (unpubl. data), this study
Comatricha nigra	*Callitris glaucophylla, C. intratrophia*	This study
Cribraria confusa	*Callitris columellaris, C. intratropica*	This study
Cribraria minutissima	*Callitris glaucophylla, C. intratropica*	This study
Cribraria rufa	*Callitris columellaris*	Kylin *et al.* (2013)
Diderma effusum	*Callitris glaucophylla, C. rhomboidea*	This study
Didymium dubium	*Callitris* sp.	Wellman (2019)
Didymium nigripes	*Callitris intratropica*	This study
Echinostelium minutum	*Callitris* sp., *C. glaucophylla*, *C. intratropica*	Rosing *et al.* (2007); this study
Echinostelium vanderpoelii	*Callitris* sp.	McHugh *et al.* (2003)
Enerthenema papillatum	*Callitris* sp.	Wellman (2019)
Licea kleistobolus	*Callitris* sp., *Callitris glaucescens, C. intratropica*	McHugh *et al.* (2003), Wellman (2019); this study
Licea operculata	*Callitris columellaris, C, glaucophylla, C. intratropica*	This study
Licea testudinacea	*Callitris* sp.	Rosing *et al.* (2007)
Macbrideola decapillata	*Callitris glaucophylla, C. intratropica*	This study
Macbrideola oblonga	*Callitris* sp.	Wellman (2019)
Paradiacheopsis cribrata	*Callitris* sp.	Rosing *et al.* (2007)
Paradiacheopsis rigida	*Callitris glaucophylla*	This study
Perichaena corticalis	*Callitris glaucophylla*	This study
Perichaena vermicularis	*Callitris columellaris, C. glaucophylla*	S. L. Stephenson (unpubl. data), this study
Physarum cinereum	*Callitris intratropica*	This study
Physarum crateriforme	*Callitris* sp.	Wellman (2019)
Physarum decipiens	*Callitris* sp., *C. glaucophylla*	Wellman (2019); this study
Physarum leucophaeum	*Callitris* sp., *C. glaucophylla*	Wellman (2019), this study
Physarum notabile	*Callitris glaucophylla*	Stephenson (unpub. data)
Physarum pusillum	*Callitris intratropica*	This study
Physarum viride	*Callitris intratropica*	This study
Stemonitis fusca	*Callitris columellaris, C. intratropica, C. rhomboidea*	This study
Trichia erecta	*Callitris intratropica*	This study

Distribution data for bark, litter, and cones are from the present study. All reports are from within Australia, except the report by Kylin *et al.* (2013) of *Cribraria rufa*, which was from Papua New Guinea. The reference cited as 'Stephenson (unpubl. data)' is the result of a pilot study conducted by the authors (SLS, TFE, KE and KV) on 9 December 2018. These samples were from *Callitris glaucophylla* substrate material collected about 75 km west of St George on the Balonne Highway (Highway 49) at 27°57′45.138″S, 147°50′56.07″E. The methods in this pilot study were not the same as those in our current study, so these data are not included in the text of this paper and are mentioned only in this table.

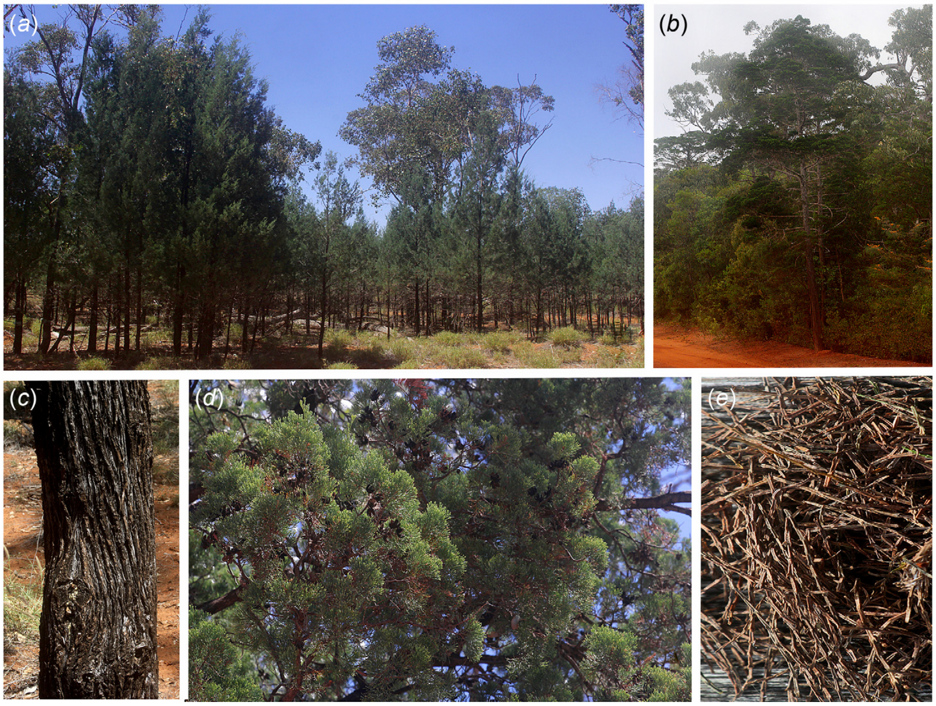

Fig. 1. Examples of Australian cypress pines and the different portions that were sampled for associated myxomycetes. (*a*) *Callitris glaucophylla* woodland, showing a typical habitat representing one of the types of habitat where the three substrates were collected. (*b*) A representative stand of several *C. intratropica* in the tropics of Cape York, Queensland. This species seldom formed the near-monodominant stands of some of the other species. (*c*) The bark of *C. glaucophylla* that was a substrate in this study. Only the outer flakey layers of bark were collected (the cambium of trees was not damaged). (*d*) Cones of *C. glaucophylla* still present in this tree. We selected these cones as a substrate only once they had fallen to the ground. (e) Fallen litter (composed of needles/leaves), such as the ones shown in these images, were collected as our third substrate. All images in Fig. 1 © Todd F. Elliott.

Table 2. Localities where samples of *Callitris* needles, cones and bark were collected in the present study.

Site	Substrate species	Collection date	GPS location	Town and state	Elevation (m)
1	*C. rhomboidea*	9 July 2020	29°25′12″S, 153°21′38″E	Iluka, NSW	6
2	*C. columellaris*	11 July 2020	29°45′37″S, 153°17′35″E	Minnie Water, NSW	1
3	*C. glaucophylla*	6 Aug. 2020	27°39′32.0″S, 150°19′13.0″E	Moonie, Qld	267
4	*C. intratropica*	12 Aug. 2020	16°59′08″S, 145°30′06″E	Mareeba Qld	416
5	*C. intratropica*	28 Aug. 2020	11°42′10″S, 142°41′48″E	Shelburne, Qld	207
6	*C. intratropica*	29 Aug. 2020	11°23′10″S, 142°24′55″E	Shelburne, Qld	68
7	*C. intratropica*	30 Aug. 2020	11°23′02″S, 142°24′49″E	Shelburne, Qld	70
8	*C. intratropica*	30 Aug. 2020	11°39′19″S, 142°37′07″E	Shelburne, Qld	108
9	*C. intratropica*	30 Aug. 2020	11°37′04″S, 142°49′08″E	Shelburne, Qld	21
10	*C. glaucophylla*	6 Sep. 2020	25°22′23″S, 148°38′47″E	Upper Dawson, Qld	497
11	*C. glaucophylla*	7 Sep. 2020	28°24′47″S, 148°49′26″E	Thallon, Qld	221
12	*C. intratropica*	14 May 2021	13°06′02″S, 130°47′09″E	Litchfield Park, NT	119
13	*C. intratropica*	8 May 2021	11°46′38″S, 130°33′41″E	Wurrumiyanga, NT	56

and comments on their abundance and ecology are also provided. The latter is based on Stephenson (2021) and the Atlas of Living Australia (https://ror.org/018n2ja79). Numbers given in parentheses are those of the first author.

Fig. 2. Examples of four species of myxomycetes that we found in association with *Callitris* in this study. (*a*) *Arcyria cinerea*. (*b*) *Comatricha laxa*. (*c*) *Cribraria minutissima*. (*d*) *Licea operculata*. Image *b* © Joe Takano. Images *a*, *c* and *d* © Yuri Novozhilov.

Arcyria cinerea (Bull.) Pers. (Fig. 2*a*)

Specimens: 18 specimens in total, with three from bark, 11 (including 34 522 and 34 613) from litter, and four (including 34 463) from cones [pH 4.1–6.3]. *A. cinerea* was recorded from eight localities (1, 2, 3, 4, 6, 8, 9 and 10) and all four species of *Callitris*.

Comments: A. cinerea was considered to be cosmopolitan by Martin and Alexopoulos (1969) and is very common in Australia. Wellman (2019) previously reported the species from the bark of *Callitris* (Table 1).

Calomyxa metallica (Berk.) Nieuwl.

Specimens: three specimens (including 34 500) on bark [pH 5.6–5.7]. *C. metallica* was recorded from two localities (3 and 11) on *Callitris glaucophylla*.

Comments: Martin and Alexopoulos (1969) reported *C. metallica* as widely distributed in Europe and temperate North America, with additional records from scattered localities throughout the rest the world. The species has been reported from a number of localities in Australia, but does not appear to be common. Wellman (2019) previously reported the species from the bark of *Callitris*.

Clastoderma debaryanum A.Blytt

Specimen: one specimen (34 505) on cones [pH 5.4]. *C. debaryanum* was recorded from one locality (4) on *Callitris intratropica*.

Comments: Martin and Alexopoulos (1969) reported *C. debaryanum* as abundant in the tropics, but also known from scattered non-tropical localities. The species has been recorded from scattered localities in Australia, but is not especially common.

Comatricha laxa Rostaf. (Fig. 2*b*)

Specimens: four specimens, with three (including 34 501) on bark and one (34 540) on litter [4.5–5.7]. *C. laxa* was recorded from three localities (1, 3 and 12) on *C. glaucophylla*, *C. intratropica*, and *C. rhomboidea*.

Comments: Martin and Alexopoulos (1969) listed *C. laxa* from only Europe, Asia, temperate North America, and Tahiti. However, Ing (1999) considered the species as probably cosmopolitan. It is known from scattered localities in Australia, but is not particularly common.

Comatricha nigra (Pers. Ex J.F.Gmel.) J.Schröt.

Specimens: three specimens (including 34 503), all on bark [pH 3.9–6.3]. *C. nigra* was recorded from two localities (8 and 10) on *C. glaucophylla* and *C. intratropica*.

Comments: Martin and Alexopoulos (1969) considered *C. nigra* to be cosmopolitan. It is known from scattered localities throughout Australia, but small forms of this species commonly appear in moist-chamber cultures.

Cribraria confusa Nann.-Bremek. & Y. Yamam.

Specimens: eight (including 34 508), all on bark [pH 4.1–4.7]. *C. confusa* was recorded from three localities (2, 4 and 5) on *Callitris columellaris* and *C. intratropica*.

Comments: C. confusa was not recognised as distinct from *C. minutissima* at the time when the monograph by Martin and Alexopoulos (1969) was published. On the basis of Australian records, the species is relatively common.

Cribraria minutissima Schwein. (Fig. 2*c*)

Specimens: five specimens (including 34 507), all on bark [pH 4.1–5.0]. *C. minutissima* was recorded from three localities (5, 8 and 10) on *C. glaucophylla* and *C. intratropica*.

Comments: Martin and Alexopoulos (1969) listed this species as widely distributed in the United States and as infrequently recorded elsewhere. Like for the morphologically similar *C. confusa*, there are enough records of *C. minutissima* from Australia to consider it as relatively common.

Diderma effusum (Schwein.) Morgan

Specimens: eight specimens (including 34 557 and 34 539), all on bark [pH 5.6–6.7]. *D. effusum* was recorded from three localities (1, 3 and 11) on *C. glaucophylla* and *C. rhomboidea*.

Comments: this species was considered as cosmopolitan by Martin and Alexopoulos (1969). It is widespread in Australia and often not uncommon on dead leaves and other similar types of plant debris.

***Didymium nigripes* (Link) Fr.**

Specimens: two specimens, with one (34 553) on cones [pH 3.9] and one (34 618) on litter [pH 5.7]. *D. nigripes* was recorded from two localities (5 and 6) on *C. intratropica*.

Comments: Martin and Alexopoulos (1969) considered this species to be cosmopolitan. However, there are relatively few records of *D. nigripes* from Australia, but it appears to be more common than the morphologically similar *D. iridis* (Ditmar) Fr., with which it is sometimes confused (Stephenson 2021).

***Echinostelium minutum* de Bary**

Specimens: four specimens, with two (including 34 520) on cones and two (including 34 554) on bark [pH 4.4–5.9]. *E. minutum* was recorded from four localities (3, 4, 10 and 13) on *C. glaucophylla* and *C. intratropica*.

Comments: E. minutum was considered as cosmopolitan by Martin and Alexopoulos (1969), and it has been recorded in virtually every survey for myxomycetes ever undertaken. This situation applies to Australia (Stephenson 2021)

***Licea kleistobolus* G.W.Martin**

Specimen: one observed but not collected, on bark [pH 3.9]. *L. kleistobolus* was recorded from one locality (8) on *C. intratropica*.

Comments: Martin and Alexopoulos (1969) listed on a few localities for this species, but Ing (1999) considered it as probably cosmopolitan. Like for the vast majority of species in the genus *Licea*, the fruiting bodies are small and easily overlooked. However, *L. kleistobolus* is distinct enough so that it is unlikely to be confused with any other species, and there are enough records from Australia to consider it as relatively common. Wellman (2019) previously reported the species from the bark of *Callitris*.

***Licea operculata* (Wingate) G.W.Martin (Fig. 2*d*)**

Specimens: four, with two (including 34 510) on bark and two (including 34 499) on cones [pH 4.9–5.7]. *L. operculata* was recorded from three localities (2, 3 and 4) on *C. columellaris*, *C. glaucophylla*, and *C. intratropica*.

Comments: Martin and Alexopoulos (1969) listed *L. operculata* from scattered localities in the northern hemisphere, with most of these from North America. Since then, the species has been reported from the southern hemisphere, although it does not appear to be common. There are relatively few records from Australia.

***Macbrideola decapillata* H.C.Gilbert**

Specimens: four, with two (including 34 559) on litter and two (including 34 525) on bark [pH 3.9–6.2]. *M. decapillata* was recorded from three localities (3, 8 and 11) on *C. glaucophylla* and *C. intratropica*.

Comments: Martin and Alexopoulos (1969) reported this species from a few localities in the United States and there was one record from Costa Rica. It is now known from scattered localities throughout the world, but is never very common. *M. decapillata* is known from just a few records in Australia.

***Paradiacheopsis rigida* (Brândza) Nann.-Bremek.**

Specimen: one specimen (34 573) on bark [pH 5.7]. *P. rigida* was recorded from one locality (3) on *C. glaucophylla*.

Comments: the concept of *Paradiacheoplus ridida* was not firmly established at the time when the Martin and Alexopolous monograph (1969) was published. This appears to be an uncommon species worldwide (Ing 1999), and there are very few records from Australia. It should be noted that the material of *P. ridida* obtained in the present study consisted of a single sporocarp and it is only provisionally referred to this species. However, it was clearly different from any other species recorded from *Callitris*.

***Perichaena corticalis* (Batsch) Rostaf.**

Specimen: one specimen (34 558) on litter [pH 6.2]. *P. corticalis* was recorded from one locality (11) on *Callitris glauophylla*.

Comments: P. corticalis was considered to be cosmopolitan by Martin and Alexopoulos (1969). The typical form is relatively common in Australia (Stephenson 2021), but the small form with little or no capillitium present is apparently known from only a single record (McHugh *et al.* 2009). The latter is recognised as a distinct species (*Perichaena liceoides* Rosstaf.) in some treatments of the myxomycetes.

***Perichaena vermicularis* (Schwein.) Rostaf.**

Specimens: five specimens, with three (including 34 651) on litter and two (including 34 504) on bark [pH 5.5–6.0]. *P. vermicularis* was recorded from two localities (1 and 3) on *Callatris columellaris* and *C. glaucophylla*.

Comments: P. vermicularis was considered as cosmopolitan by Martin and Alexopoulos (1969). This species is relatively common in Australia and appears to be somewhat more abundant than the somewhat similar *P. corticalis*.

***Physarum cinereum* (Batsch) Pers.**

Specimen: one specimen (recorded but not collected) on litter [pH 6.2]. *P. cinereum* was recorded from one locality (6) on *C. intratropica*.

Comments: Martin and Alexopoulos (1969) considered *P. cinereum* as cosmopolitan. It is common and sometimes abundant throughout Australia.

***Physarum decipiens* M.A.Curtis**

Specimens: five specimens, with all (including 34 657) on bark [pH 6.3–6.7]. *P. decipiens* was recorded from three localities (3, 10 and 11) on *C. glaucophylla*.

Comments: Martin and Alexopoulos (1969) listed *P. decipiens* from widely scattered localities throughout the world, but also commented that it is sometimes confused with *P. auriscalpium* Cooke and *P. serpula* Morgan, two morphologically similar species. *P. decipiens* is not common in Australia (2021), but was reported previously from *Callitris* bark by Wellman (2019).

Physarum leucophaeum Fr. & Palmquist

Specimens: three specimens (including 34 523) on bark [pH 6.7]. *P. leucophaeum* was recorded from one locality (11) on *C. glaucophylla*.

Comments: Martin and Alexopoulos (1969) listed *P. leucophaeum* as not common, but Ing (1999) considered it as probably common. In Australia, this species is widely distributed but not particularly common. Wellman (2019) previously reported the species from the bark of *Callitris*.

Physarum pusillum (Berk. & M.A.Curtis) G.Lister

Specimen: one specimen (34 617) on litter [pH 5.8]. *P. pusillum* was recorded from one locality (4) on *C. intratropica*.

Comments: P. pusillum was considered to be cosmopolitan by Martin and Alexopoulos (1969). The species is relatively common in Australia (Stephenson 2021).

Physarum viride (Bull.) Pers.

Specimen: one specimen (34 615) on bark [pH 4.4]. *P. viride* was recorded from one locality (13) on *C. intratropica*.

Comments: this distinctive species was considered to be cosmopolitan by Martin and Alexopoulos (1969). *P. viride* is one of the more common species of *Physarum* found throughout Australia. Interestingly, the specimen from bark recorded in the present study consisted of only a single sporocarp.

Stemonitis fusca Roth

Specimens: four specimens, with one (34 570) on bark, one (34 647) on litter, and two (including 3464) on cones [pH 4.9–5.1]. *S. fusca* was recorded from three localities (1, 2 and 9) on *C. columellaris*, *C. intratropica*, and *C. rhomboidea*.

Comments: S. fusca was considered to be cosmopolitan by Martin and Alexopoulos (1969). It is one of the most common members of the genus *Stemonitis* found in Australia. Because of their small size and the fact that they appeared in moist-chamber cultures, the specimens recorded in the present study would be referred to *S. fusca* var. *nigrescens* (Rex) Torrend. The latter is sometimes recognised as a distinct species (*Stemonitis nigrescens* Rex).

Trichia erecta Rex

Specimens: two specimens (including 34 555) on litter [pH 5.2–5.3]. *T. erecta* was recorded from one locality (6) on *C. intratropica*.

Comments: most of the records of *T. erecta* listed by Martin and Alexopoulos (1969) were from North America, and this species appears to be relatively uncommon throughout the rest of the world. There are relatively few records from Australia (Stephenson 2021).

Discussion

Numerous previous studies have investigated the occurrence of myxomycetes in different types of habitats (e.g. tropical forests, temperate forests, grasslands, and deserts) or on different substrates (e.g. the bark of living trees, coarse woody debris, ground litter, and dung; Härkönen 1977; Blackwell and Gilbertson 1984; Stephenson 1988, 1989; Novozhilov *et al.* 2000; Schnittler and Stephenson 2000; Wrigley de Basanta 2000; Lado *et al.* 2003; Snell *et al.* 2003; Takahashi 2004; Estrada-Torres *et al.* 2009; Ndiritu *et al.* 2009; Adamonyte *et al.* 2011; Dagamac *et al.* 2012; Wellman 2019; Stephenson *et al.* 2020*b*, 2022; White *et al.* 2020). Many species of myxomycetes appear to be widely distributed worldwide and are found in virtually all habitats and microhabitats investigated. However, studies have indicated that it is often possible to define the ecological niche of a particular species, a concept first described for myxomycetes by Stephenson (1988). For example, on a large scale, there are some species that appear to be largely or completely restricted to tropical or temperate regions of the world. On a small scale, there are some species that appear to be specialists that primarily associate with coarse woody debris, whereas others almost exclusively associate with the bark of living trees. The ecological niche has been demonstrated to be relatively broad for some species and narrow for others. Among the species recorded in the present study, *A. cinerea* has a broad niche, because it can be found in virtually any habitat or microhabitat. In contrast, species such as *C. confusa* appear to have a narrow niche; virtually all available records suggest that it is largely or completely confined to tree bark (Keller *et al.* 1988). Just what factors determine the niche breadth of different species of myxomycetes is still incompletely known, but substrate pH is considered to be an important factor determining the natural distribution of myxomycetes. However, the mean values of pH recorded for cones (5.7), litter (5.8), and bark (5.9) in the present study were not significantly different.

Any consideration of the ecological or geographical distribution of myxomycetes must take into account the fact that a particular morphospecies (i.e. a species recognised solely on the basis of clearly evident morphological features) can sometimes consist of a complex of biotypes or biospecies (i.e. distinct taxonomic entities defined on the basis of genetic sequences). These biospecies have been demonstrated to display evidence of possible ecological differentiation with respect to substrate and habitat in a number of studies (e.g. Feng and Schnittler 2015; Dagamac *et al.* 2017). Such is the case for *A. cinerea*, the most abundant species recorded in the present study. Molecular approaches have only recently begun to be used to study myxomycete taxonomy and ecology; it is therefore plausible that many morphologically valid species that we report could be species complexes.

We are not aware of any previous studies that have examined the assemblages of myxomycetes associated with different portions of the same type of plant, and our data suggest that species of myxomycetes may 'distinguish' among the *Callitris*-derived substrates. Further studies with more replicates are needed to conduct a statistical analysis of these differences. The fact that the highest number of species was recorded from bark is not surprising, because it has long been known that bark is an especially favourable substrate for myxomycetes. The lower totals recorded for cones and ground litter suggest that these two substrates are less favourable; however, why this is the case is not possible to determine in the context of this study. As noted earlier, the fact that only two species (*A. cinerea* and *S. fusca*) were recorded from all three substrates was an unexpected result and provides evidence that there is still a lot to be learned about niche relationships in myxomycetes.

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Data availability. Any additional data are available upon reasonable request from the authors.

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. TFE received funding for fieldwork for this project from two University of New England Robine Enid Wilson Grants and two Holsworth Wildlife Research Endowment Grants from the Ecological Society of Australia. The School of Environmental and Rural Science at the University of New England provided TFE with an International Postgraduate Research Fellowship and a 4WD to travel from Armidale, NSW, to Cape York, Queensland.

Acknowledgements. We express our gratitude to the Traditional Owners of the sites where the samples processed in the present study were collected. We want to thank the Northern Kuuku Ya'u Kanthanampu Aboriginal Corporation RNTBC Land Trust and the Tiwi Islands Land Council for granting us access permits. We are grateful for the logistical assistance and local knowledge provided by Tiwi Island Land Rangers Colin Kerinaiua and W. Rioli. Brooke Kennedy was vital in helping us navigate the permit requirements to access Bathurst Island. We thank Yuri Novozhilov and Joe Takano for contributing images to Fig. 2.

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