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## Passage of spores of the dung moss *Tayloria callophylla* (Splachnaceae) through an avian digestive tract—a novel mode of dispersal?

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### Abstract

The dispersal of reproductive material plays a key role in the ecology of plants. Dung mosses (Splachnaceae), have evolved to utilise insects to disperse spores to habitat sites consisting of dung or dead animals—a marked departure from the wind based spore dispersal seen in other mosses. However, adapting to insect dispersal likely precludes long distance airborne dispersal, and limits dispersal events to the movements of the spore bearing insect. However, there are several disjunct populations of these mosses, incompatible with insect dispersal, raising questions over the manner of their origin. Hypotheses put forward include the dispersal of the mosses to these sites by birds. Here, the possibility that insectivorous birds could internally transport spores is explored by feeding insects bearing spores to captive myna birds. We tested if the spores of the New Zealand dung moss, *Tayloria callophylla*, can survive gut passage. Ultimately 9 of 10 dung samples produced viable moss colonies after a period of 30 days, demonstrating the survival of the spores through an avian digestive tract. Our results provide evidence for a unique model of dispersal in dung mosses, where a spore bearing insect is eaten by a bird that eats insects transports the spores in its gut over a much greater distance than otherwise likely with the insect alone.

**Key words:** Dispersal, Endozoochory, Spore, Dung Moss, Splachnaceae, Bryo-zoophily

### Introduction

Dispersal is a key aspect of the biology of an organism (Vellend 2010) and plays an integral role in genetic heterogeneity and colonisation events (Howe and Smallwood 1982; Vellend 2010; Wenny 2001). While dispersal events within a population often happen in predictable ways, e.g. dispersal events taking place over long distances or across other barriers such as high mountains, large rivers, etc., they can be more stochastic (Nathan 2006). Organisms have a wide range of adaptations to facilitate this dispersal (Howe and Smallwood 1982; Valenta and Nevo 2020; Wenny 2001) but, some strategies seem more successful than others in long distance events (Nathan 2006). Mosses, in particular, seem well suited to wind mediated dispersal over significant barriers, with many species having cosmopolitan ranges and showing little diversification over those ranges (Shaw 2008). Other mosses have hugely disjunct populations that have been slow to speciate, such as mosses within the genus *Polytrichum* Hedwig (1801:88) which have large regional distributions across North America and Europe as well as bipolar distributions as seen in *P. juniperinum* Hedwig (1801:89) (Van Der Velde and Bijlsma 2003). Additionally, some mosses, such as *Scopelophila cataractae* (Mitten 1869:135) Brotherus in Engler and Prantl (1902: 436), are known from extremely isolated locations all over the world (Shaw 1993). While some evidence has been put forward suggesting a vicariance-based model, i.e. continental drift, for broad distributions (Schofield and Crum 1972), strong evidence exists supporting more directed and strategic long distance dispersal of reproductive material in bryophytes (Lewis *et al.* 2014), suggesting the evolution of specific dispersal strategies.

While many moss species are well adapted for dispersal via wind or water (Shaw 2008), there are many taxa for which wind dispersal is not a satisfactory explanation for their distribution—notable among these are entomophilous mosses in the Splachnaceae Greville and Walker-Arnott (1824:442) family or dung mosses. Around half the species

in this unique moss family are adapted to utilize insects as dispersers, to transport the moss between its unusual habitat of animal dung or carcasses. The moss exploits insects that are themselves attracted to decaying carcasses or droppings, known as coprophilous insects (Koponen 1990; Marino et. al 2009). The spores of the entomophilous Splachnaceae mosses are generally characterized as thin walled and oblong in shape and are produced in association with a sticky mucilage (Koponen 1990). These characteristics are thought to aid the moss spore in sticking to insect visitors (Koponen 1990; Marino et. al 2009), but would make wind dispersal difficult.

Transport of Splachnaceae spores via coprophilous insects explains dispersal within a single metapopulation, but dispersal events between populations separated by large geographic distances or other barriers to normal insect movement are harder to explain. Several entomophilous species of Splachnaceae mosses are known to have widely disjunct populations, most notably *Splachnum pensylvanicum* (Bridel 1817:45) Grout ex Crum (1966:206), which is mostly found in North America, with isolated populations occurring in Brazil and Europe (Lüth and Goffinet 2005). In other plant taxa, migratory animals are known or suspected to facilitate dispersal events internally or externally over distances or barriers not otherwise possible (Nathan 2006). Ectozoochory, the external dispersal of propagules (e.g. on fur, etc.), has been demonstrated in general for both moss spores and vegetative propagules (Lewis *et al.* 2014) and endozoochory, the internal dispersal of propagules (e.g. through the digestive tract) has been demonstrated for vegetative fragments (Parsons *et al.* 2007; Wilkinson *et al.* 2017). However, the possibility of endozoochorous movement of moss spores remains unexplored. Dung mosses could be uniquely positioned to take advantage of endozoochorous spore dispersal through predation of their spore-bearing insect dispersers by insectivorous birds. Could this explain the wide and disjunct distributions of several dung moss species?

Here, we propose that endozoochorous avian dispersal is a viable explanation for disjunct distributions of Splachnaceae mosses. In this study we investigate potential of one such moss, *Tayloria callophylla* (Müller 1851:546) Mitten (1882:65), to survive such passage. The implications of such survival could suggest a novel avenue of colonisation of new habitats separated by long distances by Splachnaceae mosses.

## Materials and methods

We conducted this study in a population of wild caught adult common myna birds (*Acridotheres tristis* Linnaeus (1766:167)) which were part of other behavioural studies. The birds were caught using PeeGee traps in private locations in Auckland, New Zealand 8 months prior to this study. The birds were transported to a temperature-controlled (23°C ± 1°C), restricted-access lab in the University of Auckland where they were housed in individual cages measuring 103 x 45 x 60cm. The aviary had a 12h light/dark cycle with the light cycle starting at 06:00. Individuals were fed once a day with softened dog pellets, mealworms (*Tenebrio molitor* Linnaeus (1758:417)), and sliced fruits, and had access to water *ad libitum*. Housing and experiments were conducted under approval by the University of Auckland Animal Ethics Committee (Approval No. AEC2557).

*Tayloria callophylla* capsules containing spores were collected from wild populations of the moss from a site in Swanson, Auckland New Zealand. These capsules were stored in a paper envelope and allowed to dry naturally. Spores were extracted from 10 capsules by chopping the capsules on a glass slide with a razor blade. The resulting mixture was sieved through a fine mesh to separate out larger pieces of capsule wall from the much smaller spores.

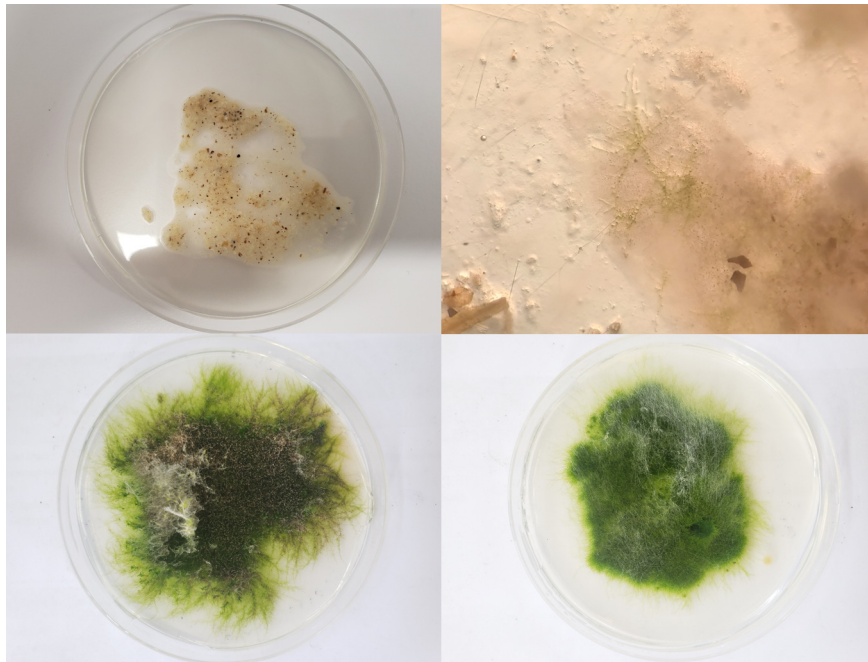
Three mealworms were presented, in petri dishes, to 15 birds. Mealworms dusted with collected spores were placed in the cages of 10 birds while undusted mealworms were placed in the cages of 5 birds as a control. All mealworms offered were taken within minutes. After all mealworms were consumed, we removed the petri dishes, and placed parchment paper over the present bedding material. Droppings were monitored periodically and collected after a period of 5 hours when visible evidence of mealworm parts ceased being apparent in the droppings. Droppings were then scraped off the parchment paper and placed in 10ml plastic tubes. Individual droppings from each bird were homogenised by adding water and agitating the tubes. These were then placed in a centrifuge and spun at 2000rpm for two minutes. The liquid was then poured off the resulting solid pellet. When not being processed samples were refrigerated at 2°C.

To test for spore viability, 10g of pellet produced by the centrifuging of droppings was smeared on agar plates mixed at a rate of 3.5g agar powder, 1g Murashige and Skoog basal medium, 0.25g MES buffer, and 500ml of water. The pH of this mixture was adjusted to 5.7 with a KOH buffering solution and then autoclaved. Work on the growth plates was conducted in a laminar flow hood. These plates were then exposed to a 24-hour cycle of 14 hours light (180 lumens) at 23° C and 10 hours dark at 17° C. Samples were examined under a dissecting scope after an initial

period of 7 days, then daily for a period of 23 days, and periodically thereafter for a following 60 days (90 days total observation). Viability was assessed by the presentation of protonema visible under magnification.

## Results

The first protonemal growth was observed after a period of 16 days and after 30 days, protonemal growth was observed in 9 of 10 samples from birds fed spore-inoculated mealworms (Fig. 1.). No moss growth was noted in one sample (of 10 total) from birds fed spore-inoculated mealworms over the total period of observation. No moss growth was noted on control plates (i.e. from birds fed uninoculated mealworms) over the total period of observation. Buds became visible on protonemal growth after a period of about 60 days.



**FIGURE 1.** *Tayloria callophylla* protonemal growth over a period of 60 days. Clockwise from top left: Fresh myna dropping on agar plate (day 0), incipient protonemal growth (day 16), growth after 30 days, growth after 60 days—buds begin to appear.

## Discussion

The results of this experiment demonstrate that the spores of Splachnaceae mosses can remain viable after passing through passerine guts. Additionally, we demonstrated that the droppings of birds fed an omnivorous diet provide suitable habitat for this species of dung moss to progress through its protonemal stage and on to producing buds which is the next stage in the progression towards fully mature gametophytes. This, combined with the plausibility of insectivorous birds consuming spore laden insects, could provide evidence for the dispersal of spores via endozoochory and explain dispersal events over medium distances such as between pockets of habitat within a region (Koponen 1990; Marino et al 2009) and long, intercontinental distances such as those seen in *S. pensylvanicum* (Lüth and Goffinet 2005).

Indeed, several species of Splachnaceae mosses show distribution patterns which likely require such dispersal events. One of the most striking examples is *Splachnum pensylvanicum* which is primarily distributed in northern North America but has a disjunct population in Brazil (Lüth and Goffinet 2005). Perhaps it is not a coincidence that many migratory birds which nest in North America spend boreal winters in South America. There is also the case of *Tayloria octoblepharum* (Hooker 1819:167) Mitten (1882:65) being present throughout the Australasian region despite separation by vast areas of open ocean between many islands from which it is known (Fife 2015; Suleiman and Mustapeng 2019). Finally, there is an interesting case of *Tayloria tasmanica* (Hampe 1876:302) Brotherus in Engel and Prantl (1903: 512), which is normally distributed in Tasmania, turning up on Stewart Island, New Zealand, a distance of approximately 1700km (Fife 2015). The ability of Splachnaceae spores to survive gut passage through insectivorous

birds raises a tantalising possibility of an unexplored means of the dispersal of these mosses.

While this experiment unequivocally demonstrates that *Tayloria callophylla* spores can survive avian gut passage, challenges to this phenomenon as a potential dispersal mechanism remain. The gut retention time for many bird species is far shorter than the time necessary for those birds to travel long distances (Figuerola *et al.* 2010; Murphy *et al.* 1993). Despite this, there is evidence of other reproductive propagules remaining within the digestive tract for much longer than would be expected, for example, smaller seeds remaining in waterfowl digestive tracts for longer periods of time than larger seeds (Figuerola *et al.* 2010). Spore survival over longer periods of time within an avian gut also remains untested. Additionally, spore bearing insects in natural situations would likely carry far fewer spores than were present on the mealworms presented in this study. Low numbers of spores, the unlikelihood of encountering an insect carrying spores, and the necessity of spores remaining in the digestive tract for extended periods of time all make the likelihood of a dispersal event in this manner very low. However, rare events do happen, and these events need not occur frequently in order to maintain metapopulation genetics or seed new populations (Nathan 2006).

While this study focuses on the survival capacity of Splachnaceae spores and the potential for their dispersal by insectivorous birds, the broader potential for endozoochorous and ectozoochorous dispersal of mosses across difficult barriers remains unexplored. Many moss species have enormous ranges and are present throughout much of the globe, such as the rare, but broadly distributed ‘copper moss’, *Scopelophila cataractae*, which is found in North America, Europe, and Asia (Shaw 1993). Moreover, some species of moss are known from isolated populations associated with seabird colonies (Fife 2014; Beever 2014; Fife and Lange 2009). Wind dispersal is often the reason cited despite the lack of direct evidence of such dispersal events occurring *in situ* (Barbé *et al.* 2016; Frahm 2008). Could endozoochorous and ectozoochorous transport of spores play a more prominent role in moss dispersal than is currently known? Perhaps adapted endozoochory could explain anomalous features of some mosses such as the large, colourful capsules with spores released only by decay or disintegration such as those seen in *Acaulon* Müller (1847:99) and *Pleuridium* Rabenhorst (1848:79) species (Shaw 2008) and berry-like volatile compounds produced in unopened capsules of *Tetraplodon mnioides* (Hedwig 1801: 51) Bruch and Schimper (1844: 23–24) (Lüth 2010). Additionally, mosses are known to make up a small, but perhaps important part of the diet of arctic ruminants such as caribou (Joly and Cameron 2018; Boertje 1984). The ingestion of spores and vegetative propagules, intentional or otherwise almost certainly occurs during such feeding behaviour. Could these large migratory mammals be spreading spores all along their seasonal routes? Birds migrating between the northern and southern hemisphere or between remote islands could bear propagules in their plumage or in their guts. This study brings to light that the ecology of moss dispersal across great distances could be much more complex than is presently thought.

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