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Eat or be eaten: fungus and nematode switch off as predator and prey



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ABSTRACT

Use of the parasitic nematode *Deladenus siricidicola* to control invasive pine-killing *Sirex noctilio* woodwasps in the Southern Hemisphere is one of the most successful examples of classical biological control. Both nematode and woodwasp rely on the white rot fungus, *Amylostereum areolatum*, for continued survival, and the nematode is commercially mass produced in its mycophagous phase on this fungus. We tested the hypothesis that a role reversal can occur wherein fungal hyphae invade and kill nematode eggs. *Deladenus siricidicola* eggs were exposed to *A. areolatum* to quantify the number of eggs lost to fungal invasion. Additionally, *A. areolatum* and *A. chailletii* were observed via cryogenic scanning electron microscopy and fluorescence microscopy to document their ability to parasitize eggs and adults of *D. siricidicola*, *D. proximus*, and an undescribed *Deladenus* species. This study reports evidence of a basidiomycete destroying nematode eggs, as well as a novel trapping mechanism used to capture and parasitize three species of adult female *Deladenus* nematodes.

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Introduction

Many species of fungi, spanning Basidiomycota, Ascomycota, Zygomycota, and Chytridiomycota, have been found to have antagonistic relationships toward nematodes and their eggs, often using them for nutrition (Chen and Dickson, 2004). Barron (1977, 1992) and Lopez-Llorca et al. (2007) suggested that wood rot fungi in particular, which are often in a nitrogen-limited environment, might be expected to use nematodes as a nitrogen supplement. Additionally, Barron (1977) suggested that because many fungi are parasitized by stylet-bearing fungal-feeding nematodes, these fungi might have evolved an antagonistic relationship towards such nematodes as a protective strategy.

The basidiomycete *Amylostereum areolatum* (Russulales: Amylostereaceae) is a wood rot fungus integral to an intriguing ecological system. The fungus is necessary for the development of the invasive pine-killing woodwasp, *Sirex noctilio* (Thompson et al., 2014), as well as being the fungal food source for the mycophagous phase of the most successful biological control agent used to target *S. noctilio*, the parasitic nematode *Deladenus siricidicola* (Tylenchida: Neotylenchidae) (Bedding, 2009). Due to the invasive pest status of *S. noctilio* (Borchert et al., 2007), the role that *A. areolatum* plays for both the woodwasp and the nematode necessitates an understanding of the many individual interactions occurring between woodwasp, fungus, and nematode.

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In adult female *S. noctilio*, fragments of *A. areolatum* called ‘oidia’ or ‘arthrospores’ are carried within paired internal organs at the base of the ovipositor called ‘mycangia’ (Coutts and Dolezal, 1969). Oidia are injected into the pine tree during *S. noctilio* oviposition. The fungus is critical to *S. noctilio* in two main ways. First, phytotoxic venom is simultaneously injected into the tree along with the fungus, and in concert, the fungus and venom cause lethal pine wilt of the tree (Coutts, 1969; Bordeaux and Dean, 2012; Bordeaux et al., 2012). This allows *S. noctilio* larvae to develop in the xylem unhindered by tree defenses. The second critical role played by *A. areolatum* relative to *S. noctilio* is that early instar larvae require the fungus to develop to adults (Madden and Coutts, 1979) and are unable to survive to adulthood in the absence of the fungus (Ryan and Hurley, 2012). The symbiotic fungus liberates organic compounds from the wood, which are, remarkably, externally digested by the larvae (Thompson et al., 2014).

The nematode *D. siricidicola* has a dual life strategy, in which fungal feeding (mycophagous) nematodes in the tree feed exclusively on the growing hyphal tips of *A. areolatum*. In the presence of woodwasp larvae, however, the nematode switches its life strategy and develops into a parasitic form. Females of the parasitic form of *D. siricidicola* invade woodwasp larvae, eventually leading to sterilization of parasitized *S. noctilio* hosts, although parasitization of a woodwasp by a *Deladenus* nematode does not always lead to sterilization (Kroll et al., 2013; Yu et al., 2009; Zondag, 1975). A single generation of the parasitic nematodes is followed by numerous mycophagous generations (Bedding, 2009; Bedding and Iede, 2005). Mycophagous generations can continue indefinitely, a trait which is exploited for the mass production of this nematode for biological control.

Morris et al. (2014) described how reproduction of two species of *Deladenus* nematodes, *D. siricidicola* and *D. proximus*, varied significantly when feeding on different species and strains of *Amylostereum* fungus; in some cases, nematodes failed to lay many eggs when feeding on a given fungus, but in other cases, nematodes laid many eggs, but the eggs were subsequently grown over by the fungus and failed to hatch. Additionally, an earlier study showed that *D. siricidicola* numbers increased most successfully when feeding on the slowest growing *A. areolatum* strains (Morris et al., 2012). Given nematophagy in Basidiomycota may be more widespread

than previously thought (Lopez-Llorca et al., 2007), the *Deladenus*–*Amylostereum* relationship warranted closer scrutiny.

Studies were carried out to investigate the interactions between four associated pairs of *Amylostereum*–*Deladenus* species and strains. The pairings were chosen either based on natural associations found in the field or, in the case of *D. siricidicola* strain Kamona, because the associated fungal strain (*A. areolatum* BDF) is used to mass produce the nematode for biological control. Given that most *D. siricidicola* eggs are laid at the growing edge of a fungal colony and hatch between 3 and 5 d later (E.E. Morris, unpublished data), it was hypothesized that if the fungus was provided with more nutrients, hyphae would overgrow the stationary nematode eggs before the eggs could hatch, ultimately producing fewer hatched juveniles. Cultures of two strains of *A. areolatum* were inoculated with eggs of two strains of *D. siricidicola*. The ability of these fungal strains to grow over and kill *Deladenus* eggs, with and without rich growing medium, was quantified, in order to estimate how much impact a given fungal strain can have on nematode population growth. The ability of these fungal species and strains to invade and kill their associated nematodes’ eggs, juveniles and adults was further studied via fluorescence microscopy. Cryogenic scanning electron microscopy was used to examine a strain of *A. areolatum* invading *D. siricidicola*.

Materials and methods

Fungal cultures

To establish a fungal culture, a 3 mm diameter plug from the edge of a growing culture was transferred to the center of a 90-mm diameter Petri plate containing half-strength potato dextrose agar (Difco, Sparks, MD) with a total of 25 g l⁻¹ agar to make this medium harder (1/2PDaH) (R.A. Bedding, personal communication). The fungal cultures were incubated for 5 d at 23 °C in darkness prior to use in experiments.

Nematode strains

Four combinations of nematode and fungus were included in this study (Table 1). The Kamona strain of *D. siricidicola* was obtained in 2006 from Ecogrow Environment (Queanbeyan,

Table 1 – Nematodes and fungi included in this study

Nematode species	Nematode strain	Fungal species and IGS ^a strains tested	Insect fungal host	Fungus collection location
<i>Deladenus siricidicola</i>	Kamona	<i>A. areolatum</i> BDF	<i>Sirex juvencus</i> ^b	Sopron, Hungary ^b
<i>Deladenus proximus</i>	Non-sterilizing	<i>A. areolatum</i> BD	<i>Sirex noctilio</i>	Fulton Co., NY
<i>Deladenus</i> sp. (undescribed)		<i>A. areolatum</i> BE	<i>Sirex nigricornis</i>	Warrensburg, NY
		<i>A. chailletii</i> G	<i>Sirex californicus</i>	Seattle, WA

a Strains identified by intergenic spacer regions (IGS), as described in Nielsen et al. (2009) and Hajek et al. (2013).

b This fungal strain is used to mass produce *D. siricidicola* Kamona. While detailed records have been kept on the isolation of this nematode, originally isolated from *S. juvencus* in Sopron, Hungary and later reisolated from *S. noctilio* in the Kamona forest of Tasmania, there is no official record for where this fungal strain was initially isolated, the information is given for *D. siricidicola* Kamona, instead.

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