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Communication

Nematophagous *Pleurotus* Species Consume Some Nematode Species but Are Themselves Consumed by Others

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Abstract: *Pleurotus* species are said to be nematophagous because they paralyze and consume some bacterial-feeding nematodes. It has never been clear whether that means all nematodes. Here we tested thirteen bacterial-feeding nematode species: seven of family Rhabditidae, three of Cephalobidae (one with three populations), two of Panagrolaimidae, and one of Diplogastridae. Nematodes interacted on water agar with toxin-producing isolates of *Pleurotus pulmonarius* (Fr.) Quél. and *Pleurotus ostreatus* (Jacq.) P. Kumm. Of the thirteen species, nine were susceptible to *P. pulmonarius* (all individuals were paralyzed) but four (four populations of two cephalobid species, one rhabditid, and one panagrolaimid) survived exposure to *P. pulmonarius*. The resistant four species not only survived but multiplied their numbers by consuming *P. pulmonarius*. A similar trend was observed with nematodes interacting with *P. ostreatus*; however, six species were resistant to *P. ostreatus*. Interestingly, four of these six species were susceptible to *P. pulmonarius*, and interactions overall were differential. *Pleurotus* species are nematophagous toward some nematodes but are also consumed by others in three of the four families assayed. Species-specific interactions point to the need for studies of the host ranges of both “nematophagous” fungi and “fungivorous” nematodes, especially if they are to be used for biological control.

Keywords: host range; soil; Rhabditidae; Cephalobidae; toxin; fungivorous

1. Introduction

Nematodes are roundworms, generally microscopic, that include parasites of animals and plants as well as beneficial species. Killing parasites has become problematic as resistance has developed to many previously useful therapeutic chemicals [1]. Therefore, biocontrol agents of nematodes may provide less toxic and more sustainable control with more varied and complex mechanisms that are harder for nematodes to resist.

Nematophagy implies the consumption of nematodes. The predatory consumer could be another invertebrate, such as a mite [2], or bacteria, such as *Bacillus thuringiensis* employing a toxin [3] or *Chryseobacterium nematophagum* producing enzymes [4], or a fungus. However, how do fungi manage this? Reviews of the subject frequently focus on the trapping and feeding mechanisms employed by nematophagous fungi [5]. Others focus on the diversity [6], and phylogenetic relationships [7] of those 700 or so fungal species discovered thus far to be nematophagous. Traps, adhesive spores, and specialized structures have been reported along with toxins. Nematophagous fungi are also sometimes called carnivores because they consume the "meat" of the trapped or toxin-stunned nematodes [8]. Some are termed predators whereas others are endo-parasitoids. The most recent proposal for mechanism-based classification of nematophagous fungi is for five groups: "nematode-trapping/predators, opportunistic or ovicidal, endoparasites, toxin-producing fungi and producers of special attack devices" [9].

Few studies address the topic of host range in nematophagous fungi; host ranges of toxin-producing fungi appear to be particularly neglected. The host range of a nematophagous fungus should comprise all susceptible species of nematodes attacked and consumed by that fungus. Experimental determination of the host range would require testing of many nematode species, but all too often, only a single or a few species were tested. There are exceptions, where numerous nematode species were used to determine the host range. For example, Tzean & Liou (1993) [10] employed 11 different nematode species across multiple feeding guilds to determine that nematophagous *Hyphoderma* species have specific nematode host ranges; some nematodes were not affected at all by the fungus. However, in the absence of experimental determinations, host range may be assumed to encompass more species of nematodes than is actually the case. In the case of *Pleurotus ostreatus* (Jacq.) P. Kumm., its host range has been assumed to be broad since its toxin, *trans*-2-decenoic acid, derived from linoleic acid, has even been said to affect "not only nematodes, but also insects and other fungi" [9].

We first began thinking about the host range of nematophagous fungi when reading two research articles on nematode feeding habits in which mention was made of *Pleurotus ostreatus* as a good host for fungal-feeding *Filenchus* species. [11,12]. Interactions with *P. ostreatus* varied based on nematode species. For example, *Filenchus misellus* was capable of avoiding paralysis and feeding on *P. ostreatus* hyphae, while *Aphelenchus avenae* was always trapped and consumed by the fungus. However, the two media employed in this research did not include water agar, on which nematophagy by *Pleurotus* is normally assayed. Instead, *P. ostreatus* was grown on soil and potato dextrose agar (PDA), even though Barron & Thorn (1987) [13] had found that the *Pleurotus* toxin is not as effective when grown on PDA; the toxin is most potent when the fungus is grown on a nutrient-limited media such as water agar. The soil used in the *Filenchus* assay was amended with soybean, a source of nitrogen, so it is again possible the fungal toxin was not at its maximum potency. Since the nematodes had not likely been exposed to the toxin in its most potent form, definitive inferences could not be drawn. Okada et al. (2005b) [14] discovered that *Tylencholaimus parvus*, a fungivorous nematode species, can survive exposure to both *Pleurotus pulmonarius* (Fr.) Quél. and *Pleurotus ostreatus* when the fungus is grown on water agar. Additionally, the nematode could consume the *Pleurotus* hyphae. Like their prior study [11], *Aphelenchus avenae* (control) was consumed by both *Pleurotus* species on the water agar. This study opened the door to the idea that *Pleurotus* species have specific host ranges of nematodes that they are capable of consuming.

Toxins are deleterious chemical compounds that are produced by, and that enhance the fitness of, living organisms. Typically, toxins are effective against some, but not all, other organisms. Species of white-rot fungi in *Pleurotus* possess a unique mechanism of toxin-assisted nematode trapping, which has been demonstrated on both water agar and wood [13,15]. Multiple studies have confirmed that bacterial-feeding nematodes belonging to various families in the order Rhabditida are susceptible to toxins produced by *Pleurotus* species [13,16–18]. When grown in a nitrogen-poor environment like wood, *P. ostreatus* will produce a toxin on aerial hyphae. Instead of diffusing into the environment, the toxin remains as a droplet on the hyphae. In this manner, the toxin remains undetected by the unfortunate nematode until contact is made; the nematode is promptly paralyzed by the toxin. Hyphae will then colonize the nematode, and eventually digest it [13]. In 1992, this toxin of *P. ostreatus* was characterized and named *trans*-2-decenedioic acid [18].

Other species of *Pleurotus* produce toxins with nematode-stunning activity similar to that of *trans*-2-decenedioic acid. *Pleurotus pulmonarius*, also used in our study of nematophagy, produces

S-coriolic acid, linoleic acid, panisaldehyde, *p*-anisyl alcohol, 1-(4-methoxyphenyl)-1,2-propanediol, and 2-hydroxy-(4′-methoxy)-propiophenone [19]. We used the standard assay on water agar to determine the interactions of 13 species of nematodes with both *P. pulmonarius* and *P. ostreatus*. *P. pulmonarius*-resistant species were then further tested to confirm the fungus-feeding ability by pairing them with *Rhizoctonia solani*.

2. Materials and Methods

2.1. Fungal Culture

Pleurotus pulmonarius was isolated in early spring from a fresh basidiocarp collected on a *Picea abies* (L.) H. Karst. log in the University of Idaho Old Arboretum. *Pleurotus ostreatus* was isolated from mushrooms purchased at a local grocery store; the identity of this species was confirmed morphologically. *Pleurotus ostreatus* and *Pleurotus pulmonarius* are very similar, but *P. pulmonarius* grows on conifer wood in the Pacific Northwest and fruits in the spring [20]. Our *Pleurotus* isolates were transferred to oatmeal agar where cultures were allowed to grow at room temperature (approximately 21 degrees C). For testing, 7-mm plugs were taken from growing cultures and transferred to plates containing 2% water agar (WA). These cultures were kept at room temperature and allowed to grow until the hyphae reached the edge of the plate (7 to 14 days). At that time, toxin production was noticeable.

2.2. Nematode Culture

Nematode feeding habits are only partially known. For example, "bacterial-feeding" nematodes can also graze on hyphae of at least some fungi. For our study, we selected 13 species of bacterial-feeding nematodes from four families, including Rhabditidae, known to include species susceptible to species of *Pleurotus*. All species of nematodes were grown and maintained on nematode growth media (NGM) agar with *Escherichia coli* OP50 as their food [21]. The following nematodes were then used in our *Pleurotus*-nematode interaction assay (described further below):

- Family Rhabditidae
  Oscheius dolichura (Schneider) Sudhaus [LKC50], *Oscheius myriophilus* (Poinar) Sudhaus [DF5020], *Oscheius tipulae* (Lam and Webster) Sudhaus [LKC57], *Caenorhabditis elegans* (Maupas) Dougherty [N2], *Mesorhabditis inarimensis* (Meyl) Dougherty [LKC51], *Poikilolaimus oxycercus* (de Man) Sudhaus and Koch [LKC64], and *Metarhabditis rainai* (Carta and Osbrink) Sudhaus [LKC20]
- Family Cephalobidae
  Zeldia punctata (Thorne) Thorne [PS1192], *Acrobeloides varius* Kim, Kim and Park [LKC52], *Acrobeloides varius* [PS1959], *Acrobeloides varius* [LKC27], and *Acrobeloides* sp. cf *amurensis* Truskova [PS1146]
- Family Panagrolaimidae
  Panagrolaimus artyukhovskii Blinova & Mishina [LKC44] and *Panagrellus redivivus* (Linnaeus) Thorne [PS1163]
- Family Diplogastridae
  Pristionchus aerivorus (Cobb in Merrill & Ford) Chitwood [LKC54]
  To avoid redundancy, only one population of *A. varius* (LKC52) was used for the *P. ostreatus* assay. All three populations were tested with *P. pulmonarius*.

2.3. Pleurotus–Nematode Interaction Assay

Twenty active individuals, varying in age, of each nematode species were transferred to respective WA plates containing live mycelium of either *P. pulmonarius* or *P. ostreatus*. For the *P. pulmonarius* assay, we checked for paralysis due to toxin immediately after transfer and then every hour for the next six hours. The cultures were also checked one and two weeks after the nematode transfer for survival and reproduction of nematodes. Since we were only interested in the long-term survival of the nematode population, we checked *P. ostreatus* plates only after one week following the nematode transfer. For the purpose of this study, we defined resistance as survival of some individuals after contact with *Pleurotus* on water agar, and their subsequent ability to reproduce. Susceptible nematode species were defined as ones in which all 20 individuals perished during the first few hours on the water agar plate containing the *Pleurotus* mycelium.

2.4. Phylogenetic Analysis

DNA from nematode species was processed for the 18S rDNA marker [22] or taken from GenBank (Table 1). Taxa in Table 1 are phylogenetically disjunct in the tree containing only these taxa (Figure 1) so corresponding clades from a comprehensive large tree of 18S sequences [23,24] is referenced and shown. Sequences were aligned with Clustal W [25] and a Bayesian likelihood tree was constructed with a general time reversible (GTR) model and 10^6 chain length in the MRBAYES plugin [26] in Geneious ver. 11.1.5 (Biomatters, Auckland, New Zealand) in Figure 1.

Table 1. Nematode cultures tested and represented in phylogenetic tree of Figure 1.

Species	Culture Isolate	GenBank Accession/Isolate	Clade in van Megen et al., 2009 [23]
Oscheius dolichura	LKC50	KP756940 JU72	9A Rhabditomorpha
Oscheius myriophilus	DF5020	U81588	9A
Oscheius tipulae	LKC57	CEW1 KP756939	9A
Caenorhabditis elegans	N2	NR000054	9A
Mesorhabditis inarimensis	LKC51	90A3 * MK636575	9A
Poikilolaimus oxycercus	LKC64	101A3* MK636576	9A
Metarhabditis rainai	LKC20	AF083008 PS1191	9A
Pristionchus aerivorus	LKC54	90C1 * MK636577	9A Diplogasteromorpha
Panagrolaimus artyukhovskii	LKC44	90E9 * MK636578	10A Panagrolaimomorpha
Panagrellus redivivus	PS1163	AF083007	10A
Zeldia punctata	PS1192	U61760	11 Cephalobomorpha
Acrobeloides amurensis	PS1146	AF034391	11
Acrobeloides varius **	LKC27	94A6 * MK636581	11
Acrobeloides varius	LKC52	100H3 * MK636579	11
Acrobeloides varius **	PS1959	104M16 * MK636580	11
Plectus rhizophilus	PlecRhi1	AY593928	6 (Outgroup)

* new sequence in this study. ** only tested with *Pleurotus pulmonarius.*

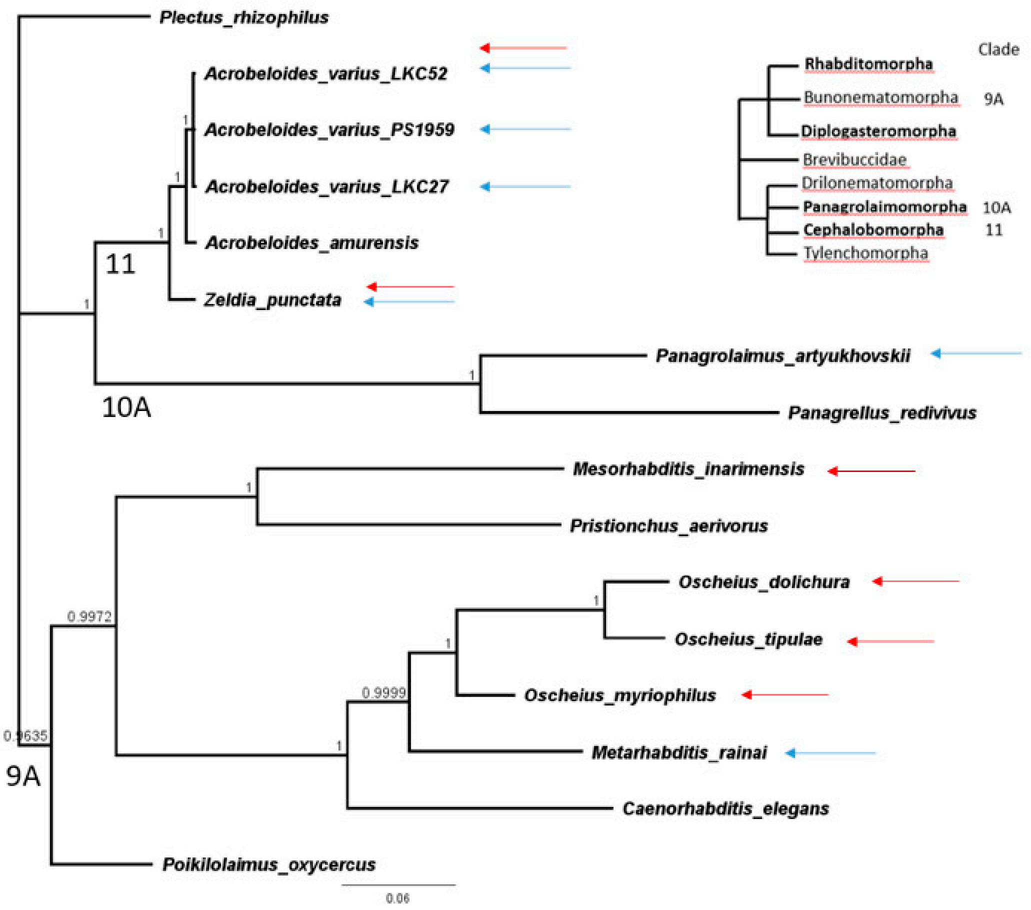

Figure 1. MRBAYES Bayesian likelihood phylogenetic tree based on a Clustal W alignment of 18S rDNA sequences as implemented in Geneious ver. 11.1.5. Upper right schematic tree of van Megen et al., 2009 [23] provides phylogenetic context. Blue and red arrows indicate taxa resistant to *P. pulmonarius* and *P. ostreatus*, respectively.

2.5. Fungal-Feeding Ability

In order to confirm fungal-feeding ability of the *P. pulmonarius*-resistant nematodes, all of which were known as bacterial feeders prior to this study, approximately 10 mixed-stage juvenile nematodes were rinsed in sterile water from the bacterial plate and transferred using a pipette to PDA plates containing 7- to 10-day-old mycelial cultures of *Rhizoctonia solani*. They were then observed for consumption of the fungus and production of nematode eggs.

3. Results

3.1. *Pleurotus pulmonarius*–Nematode Interaction Assay

All 20 individuals of each of nine susceptible species were stunned or paralyzed by toxin in the first few hours after their introduction to *Pleurotus* plates. They were then consumed by *Pleurotus* hyphae. In the case of each of the six resistant populations of four species, a few individual nematodes appeared stunned during the first few hours. However, other individuals were not, and they went on to reproduce and feed on *Pleurotus* hyphae. Of the fifteen populations of thirteen species, nine were susceptible. Six of seven rhabditid species were susceptible: *Oscheius dolichura* (LKC50), *Oscheius myriophilus* (DF5020), *Oscheius tipulae* (LKC57), *Caenorhabditis elegans* (N2), *Mesorhabditis inarimensis* (LKC51), and *Poikilolaimus oxycercus* (LKC64). Only one of five populations of three cephalobid species was susceptible: *Acrobeloides* sp. cf *amurensis* (PS1146). One of two panagrolaimid species was susceptible: *Panagrolaimus artyukhovskii* (LKC44). Finally, the only species of diplogastrid assayed was susceptible to *P. pulmonarius*: *Pristionchus aerivorus* (LKC54).

Six populations representing four species of nematode were resistant to *P. pulmonarius*: four of five cephalobid populations comprising two species, one of seven rhabditids, and one of two panagrolaimid species.

3.2. *Pleurotus ostreatus*–Nematode Interaction Assay

Susceptible and resistant nematode interactions with *P. ostreatus* were also observed (Figure 2). Of the thirteen nematode species tested with *P. ostreatus*, seven species were susceptible. Three of the seven rhabditids were susceptible: *Caenorhabditis elegans* (N2), *Poikilolaimus oxycercus* (LKC64), and *Metarhabditis rainai* (PS1191). The only species of diplogastrid assayed, *Pristionchus aerivorus* (LKC54), was susceptible. Both panagrolaimid species were susceptible: *Panagrolaimus artyukhovskii* (LKC44) and *Panagrellus redivivus* (PS1163). Finally, similar to *P. pulmonarius*, only one of the three cephalobid species was susceptible: Acrobeloides amurensis (PS1146). Six species were resistant to *P. ostreatus*: four rhabditid species and two cephalobid species (Figure 1). All four rhabditid species resistant to *P. ostreatus* were susceptible to *P. pulmonarius*.

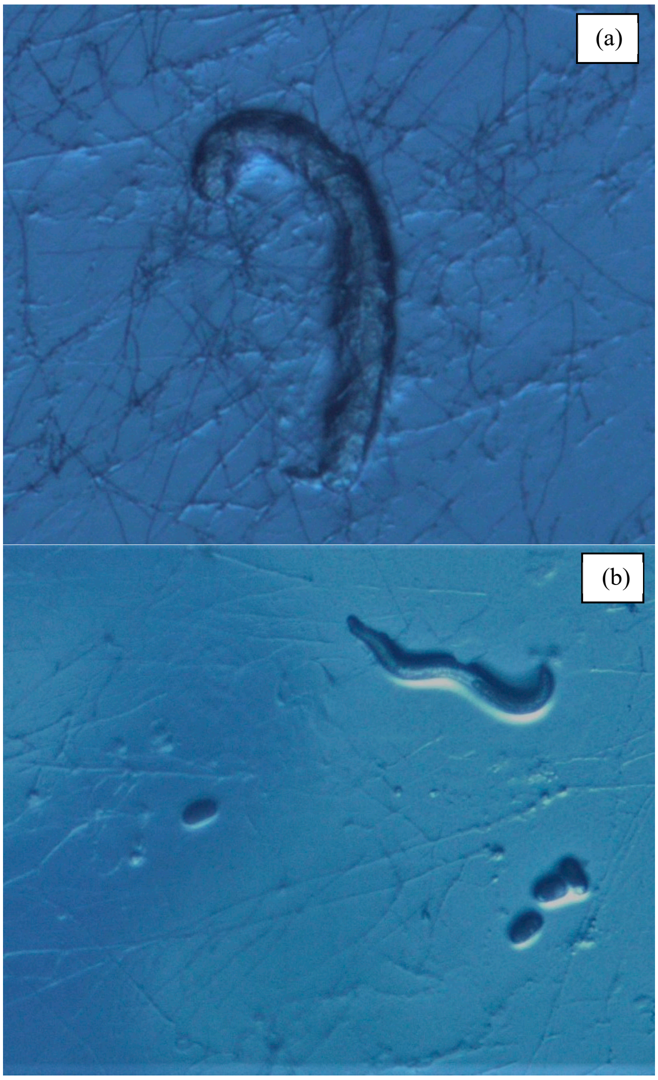

Figure 2. (**a**) Susceptible rhabditid species (*Poikilolaimus oxycercus*) being consumed by *Pleurotus ostreatus* hyphae. (**b**) Resistant cephalobid species, *Zeldia punctata*, interacting with *Pleurotus ostreatus* hyphae. Reproductive capability evidenced by the presence of eggs.

It is evident from Figure 1 that *Pleurotus* resistance may have multiple origins among at least three families, including even the Rhabditidae, a family traditionally associated with *Pleurotus* susceptibility and which, here, was mostly susceptible to *P. pulmonarius* but surprisingly resistant to *P. ostreatus*. Resistance was especially common among species of Cephalobidae, including multiple isolates of one species, *Acrobeloides varius*, when confronted with *P. pulmonarius*.

3.3. Phylogenetic Analyses

The relative phylogenetic distance of the species and genera of nematodes is shown in trees of Figure 1. GenBank sequence accession numbers for some of the taxa generated for this work are listed in Table 1.

3.4. Feeding Ability

The ability of the *P. pulmonarius*-resistant, bacterial-feeding populations to multiply on another fungus, *Rhizoctonia solani*, was confirmed. This was not completely clear after two weeks. However, after three weeks of culturing on *R. solani*, all six of the *Pleurotus*-resistant nematode populations had produced eggs and multiplied their numbers.

4. Discussion

Our findings support earlier work [14] and provide evidence that *Pleurotus* species are more specialized within Nematoda than previously believed. In other words, nematophagous species of fungi have host ranges, a term applied by Barron (1978) [27], analogous to the host ranges of parasitic fungi [28], or the tree hosts of mycorrhizal fungi [29] or the range of mycorrhizal fungi parasitized by mycoheterotrophic plants [30]. The term applies not only to nematophagous fungi but also to fungivorous nematodes that might consume *P. pulmonarius* and *R. solani*, as here, but would likely be unable to consume others.

Our study adds a new layer to this complexity; differential interactions with the two *Pleurotus* species were observed. Previously [14], differential reactions had not been observed (Table 2). In other words, nematodes were either susceptible to both *Pleurotus* species or resistant to both *Pleurotus* species. However, in our study, this was not the case. As displayed in Table 3, some nematode species were resistant to *P. ostreatus* but susceptible to *P. pulmonarius*, and vice versa. All four sets (RS, SR, RR, and SS) of binary reaction (resistance or susceptibility) were seen. If six species of *Pleurotus* were tested, one might expect 2^6, or 64, unique sets of binary reaction.

Table 2. Nematode interactions with two species of *Pleurotus* grown on water agar from Okada et al. (2005b) [14]. One nematode species was susceptible to both *Pleurotus* species, while the other nematode species was resistant to both *Pleurotus* species. However, differential interactions (i.e., resistance to one *Pleurotus* species but susceptibility to the other), were not observed. S = susceptible, R = resistant.

Nematode Species	*Pleurotus pulmonarius*	*Pleurotus ostreatus*
Tylencholaimus parvus	S	S
Aphelenchus avenae	R	R

Table 3. Our results of bacterial-feeding nematode interactions with two species of *Pleurotus* grown on water agar. Nematode species revealed that the two species of *Pleurotus* were differential interactors with all four sets of interactions across the row: SR, SS, RS, and RR. S = susceptible, R = resistant.

Species	Culture Isolate	*Pleurotus pulmonarius*	*Pleurotus ostreatus*
Oscheius dolichura	LKC50	S	R
Oscheius myriophilus	DF5020	S	R
Oscheius tipulae	LKC57	S	R
Caenorhabditis elegans	N2	S	S
Mesorhabditis inarimensis	LKC51	S	R
Poikilolaimus oxycercus	LKC64	S	S
Metarhabditis rainai	LKC20	R	S
Pristionchus aerivorus	LKC54	S	S
Panagrolaimus artyukhovskii	LKC44	R	S
Panagrellus redivivus	PS1163	S	S
Zeldia punctata	PS1192	R	R
Acrobeloides amurensis	PS1146	S	S
Acrobeloides varius **	LKC27	R	NA
Acrobeloides varius	LKC52	R	R
Acrobeloides varius **	PS1959	R	NA

It seems likely that other toxin-producing nematophagous fungi, including other species in Pleurotaceae, might be similarly specialized if tested in the manner of this study. It is entirely possible that there are other nematophagous fungi that can attack the *Pleurotus*-resistant species of this study. Conversely, it seems possible that the *Pleurotus*-susceptible nematodes of this study would feed on fungi other than *Pleurotus* species. Each of *Pleurotus pulmonarius* and *P. ostreatus* was either the consumer or the consumed. It will be interesting to conduct further research to see whether this zero-sum game might be more widely operational among interacting fungi and nematodes.

In this study, only free-living bacterial-feeding nematodes were assayed because they had previously been used to show that *Pleurotus* species were nematophagous. Evidently, many bacterial-feeding nematodes can survive on fungus as the sole food source. An earlier study in which that was demonstrated involved a bacterial-feeding *Chiloplacus* species that was maintained on a fungal culture (i.e., *Phoma* [31]). Overall, research has focused little on bacterial-feeding nematodes' ability to consume fungi, indicating a gap in knowledge regarding feeding behavior and the potential host range of nematodes. Therefore, there may be a significantly higher number of nematodes that could be considered fungivorous. Future research on resistance or susceptibility to nematophagous *Pleurotus* might involve nematode-trophic groups or feeding guilds other than the bacterial-feeding group tested here. In particular, nematodes that are parasites of vertebrates and plants can be targeted by nematophagous fungi in biological control efforts [32].

Resistance to toxins, presumably the reported S-coriolic acid, linoleic acid, panisaldehyde, *p*-anisyl alcohol, 1-(4-methoxyphenyl)-1,2-propanediol,2-hydroxy-(4′-methoxy)-propiophenone, and *trans*-2-decenedioic acid allowed six populations of four nematode species to graze on *P. pulmonarius* and six nematode species to graze on *P. ostreatus*. We do note that some of the original individual nematodes in each of the resistant species died, and the reasons for their deaths were not determined. It could be that resistant nematode species are variable and some individuals are susceptible to *Pleurotus* toxins. On the other hand, a few individual deaths per resistant species could have nothing to do with *Pleurotus* toxins. Age-related resistance could factor into this observation; we used individuals of varying life stages in our assay. The mechanism for resistance to these toxins is also yet to be determined, but we can propose the following. First, the toxins may simply be lacking recognition or binding sites in resistant nematodes. This concept has been demonstrated in endoparastic nematophagous fungi, where differential trapping is noted. For example, Jansson et al. (1985) [33] showed that conidia of endoparasitic, nematophagous *Meria coniospora* can only attach and infect some species of nematodes. Their study agrees with prior work that suggests sialic acid on the nematode cuticle proves to be an important recognition and attachment factor for the fungus; reduction of sialic acid by the presence of sialic-acid specific lectin reduced conidial attachment [34].

A second hypothesis is that resistant nematodes may have evolved a mechanism to detoxify toxins before paralysis. Third, members of the microbiome of resistant nematodes could hypothetically offer protection from *Pleurotus* toxins. With respect to the third hypothesis, Dirksen et al. (2016) [35] found that three *Pseudomonas* species in the microbiome of *C. elegans* did exhibit antifungal activity towards pathogenic fungi. Thorough understanding of resistance will also have to integrate the fact that *Pleurotus* species also kill some species of bacteria [15].

The soil bacterium *Burkholderia cepacia* also produces a diffusible paralytic toxin that contributes to killing *Caenorhabditis elegans* [36]. Several strains were tested among a similar phylogenetic spectrum of bacterial-feeding nematodes as in this study. *Zeldia punctata* and *Pristionchus pacificus* were especially resistant among the tested nematodes to the toxic effects of *B. cepacia* [37], in line with their resistance to *Pleurotus* toxins in this work. Another cephalobid nematode, *Acrobeloides maximus*, was attracted to and fed on more bacterial genera than *C. elegans*. This was interpreted as an adaptation to a less enriched ecosystem [38] since cephalobid nematodes are early stage colonizers [39]. Perhaps similar resistance mechanisms are working in nematodes that have resistance to those bacterial toxins and to these fungal toxins.

More extensive testing of host ranges of both nematophagous fungi and fungivorous nematodes, as well as mechanisms for nematode resistance [40], should shed light on the physiology and ecology of interactions needed for targeted, integrated biocontrol. In fact, classical biocontrol agents have to be tested for host range prior to their introduction to an invaded range, to reduce the chance of non-target effects. This is relevant to *Pleurotus* since three nematophagous species (*P. pulmonarius*, *P. ostreatus*, and *P. eryngii*) have been considered as options for biocontrol of the pinewood nematode *Bursaphelnchus xylophilus* in its invaded range in east Asia [41]. Our results suggest that host range studies are needed to avoid undesirable, non-target effects. For example, soil-dwelling nematodes that vector mammalian pathogenic fungi [42] might be positively or negatively impacted by applications of nematophagous *Pleurotus* to pine forests affected by the pinewood nematode. More generally, the consequences of introductions of nematophagous fungi with undetermined host ranges could be both serious and unpredictable given the abundance of nematodes (i.e., famously four of every five animals on Earth) and their functional diversity in food webs [43].

5. Conclusions

Two species of nematophagous *Pleurotus* did not kill and consume all species of nematodes they encountered. We found that some species of nematodes were resistant to both species of *Pleurotus*, but others were resistant to one but susceptible to the other. Yet other species of nematode were susceptible to both species of *Pleurotus.* In each species–specific interaction, either all nematode individuals were killed or most lived and reproduced. Another inference from this study is that many bacterial-feeding nematodes could be fungivorus. Interactions among nematophagous fungi and nematodes could easily serve as a model for studying differential ecological interactions.

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