



# Relationship Between Nematodes and Fungi for Biological Control: Review

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## Abstract

Among the most common species in soil ecosystems are nematodes and fungi. In addition to providing vital ecological functions, these two extremely abundant groups of creatures interact in various ways to support nutrient cycling and the stability of food webs. This review offers a detailed overview of the relationship between nematodes and fungi, focusing specifically on their effects on crops and ecosystems. The variety and evolutionary relationships of fungi that have close interactions with nematodes are covered in the paper, such as those that feed on them or act as a food source. Extensive research has been done on the diversity, evolution, and molecular interaction mechanisms between nematophagous fungi and nematodes, concentrating on those that create specialized nematode-trapping devices. A few nematodes and fungi are important pests and pathogens that harm crop plants. The article provides an overview of the ecological and molecular mechanisms that have been found thus far and that affect the interactions between crop plants, phytopathogenic nematodes, and phytopathogenic fungi, either directly or indirectly. There is also discussion of the possible uses of biological control in managing these interactions additionally soil-borne fungal diseases and phytophagous nematodes in agricultural fields. The importance of integrating biological control into sustainable farming practices is highlighted by looking at how biological control techniques might enhance productivity in agriculture and ecological stability. By understanding these relationships, researchers can develop innovative biological management strategies to reduce the detrimental effects of pests and harmful pathogens on crops.

**Keywords:** Fungi; Nematode; Phytopathogenic Nematodes; Nematophagous Fungi; Fungivorous Nematodes

## Abbreviations

PPNs: Plant-Parasitic Nematodes; AM: Arbuscular Mycorrhizal; DEGs: Differentially Expressed Genes; NTF: Nematode-Trapping Fungi; ROS: Reactive Oxygen Species; AMF: Arbuscular Mycorrhizal Fungus; ISR: Induced Systemic Resistance.

## Introduction

There are many different kinds of animals in ecosystems, including minute animals like nematodes and many microscopic life forms including bacteria, fungi, protozoa, and archaea. These creatures collaborate with macroscopic biota to perform vital ecosystem activities, such as plants

and large animals [1]. There are several ways in which interactions between the wide range of creatures that make up ecosystems might take place. These interactions between two or more partner species can be direct or indirect, and they can take the form of different ecological mechanisms such as mutualism, parasitism, competition, or predation [1]. The stability and balance of ecosystem functioning depend on these intricate interspecific interactions between the constituent organisms [1]. The complex network of biotic interactions preserves the precarious equilibrium needed for ecosystems to continue offering vital functions and harboring a variety of living forms. Two of the most common species in terrestrial habitats are nematodes and fungi. With an estimated 500,000 documented species, the second largest phylum in the animal kingdom is called Nematoda, commonly known as roundworms [2].

Through nitrogen mineralization, 90% of terrestrial nematodes are vital to the nitrogen cycle and reside in the top 15 cm of the soil [3]. Nematodes are parasitic or free-living organisms that feed on other living things rather than directly decomposing organic materials [3]. But because they are the primary decomposers of decaying organic matter, fungi are essential to the nutrient cycle in ecosystems. From an evolutionary standpoint, fungi are more closely linked to animals than to plants, despite their seeming plant-like appearance. All animals, including fungi and nematodes, are categorized as heterotrophic creatures [4,5]. Nematodes and fungi frequently coexist in a wide range of naturally occurring and artificially created environments, especially in the rhizosphere that envelops the roots of plants, including agricultural ones. The domains of forestry and agriculture are significantly impacted by this co-occurrence [4,5]. The phyla Nematoda and Fungi first appeared between 550 and 600 million years ago and 1050 million years ago, respectively. These two species might have coexisted and interacted in various soil conditions before plants started to form terrestrial colonies and ecosystems some 450 million years ago [4,5]. Understanding the mutualistic or antagonistic, direct or indirect, coexistence and interactions between nematodes and fungi is essential to comprehending their influence on ecosystems and potential applications in farming. Finding new ways to combat soil-borne fungal infections and phytophagous (plant-feeding) Since nematodes increase the quantity and quality of agricultural output, they are An essential long-term objective for managing agricultural pests and diseases. The knowledge that is currently available about the interactions between nematodes and fungi is summarized in this review. In particular, the relationships between these two groups of organisms that, either directly or indirectly, display mutualistic and antagonistic relationships are the main subject of interest (Figure 1) [6]. It's critical to remember that the different nematode and fungal species may interact

in radically different ways. Additionally, the nature and intensity of the interactions between the two species can be influenced by external circumstances, indicating that they are dynamic [6].

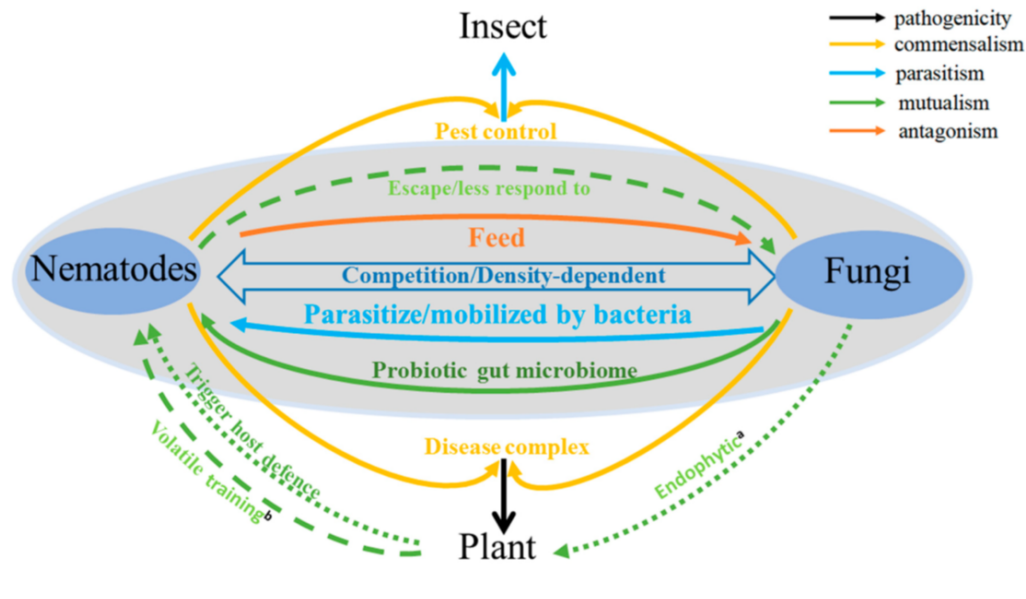
### Hostile Exchanges

There are many different types of antagonistic interactions between nematodes and fungi. Numerous nematode species can feed on a variety of fungal taxa, including three species: *Paraphelenchus acontioides*, *Aphelenchoides spp.*, and *Aphelenchus avenae*. The term "fungivorous nematodes" is frequently used to describe these nematodes [7]. However, several fungal species, including *Arthrobotrys oligospora*, can consume nematodes and their eggs. We refer to these fungi as nematophagous fungi [8]. These antagonistic interactions, where some nematodes feed on fungi while certain fungi consume nematodes, represent a significant aspect of the multifaceted relationships between these two groups of organisms within ecosystems.

### Nematodes Eating Fungi and Upsetting Them

Many nematode species commonly feed on fungi; in fact, certain worm species only consume specific kinds of fungi [9]. The diversity, abundance, and overall structure of fungal communities can all be significantly influenced by nematodes, they are a vital part of the soil food chain. This covers the effects on crop growth and soil pollution tolerance. Fungivorous nematodes often occupy soils that support a wide variety of fungal species.

However, several fungal species, including *Arthrobotrys oligospora*, can consume nematodes and their eggs [10]. These fungivorous nematodes are thought to be multiparous because they frequently eat a wide variety of soil fungi, such as mycorrhizal, saprophytic, and plant-pathogenic fungi [11]. These nematodes can greatly affect the dynamics and makeup of fungal communities in the soil environment using their feeding activities. When provided with appropriate fungal food supplies, despite having lower soil densities than phytoparasitic (plant-feeding) and bacterivorous nematodes, fungivorous nematodes can nonetheless have rapidly expanding populations [10]. The whole soil ecology and crop productivity may be significantly impacted by nematodes feeding on soil fungus, contingent upon the makeup of the soil microbiome. An essential dynamic in the intricate soil food web is the capacity of fungivorous worm populations to multiply quickly in the presence of suitable fungus prey. This emphasizes how nematode-fungal interactions can significantly impact environmental processes and agricultural systems. For example, fungivorous nematodes may decrease the number of plant-pathogenic fungi in the soil if they feed exclusively on these varieties of fungus.



**Figure 1:** a) Certain endophytic fungi that colonize plant tissues can elicit defensive responses in the host plant, potentially mitigating the impacts of plant-parasitic nematodes (PPNs). b) Plants may employ the release of volatile organic compounds as a means to “guide” or “train” nematodes to avoid fungal threats in the soil environment. The relationships between soil fungi and nematodes are complex and not yet fully understood. Further research is needed to elucidate the distinct mechanisms by which endophytic fungi modulate plant defenses, and how nematodes perceive and respond to these fungal cues and plant-derived volatiles. A deeper understanding of these fungi-nematode interactions could provide insights relevant to sustainable agricultural practices and soil ecosystem management. The phrasing aims to present the information in a measured, scientific tone appropriate for a research context.

Conversely, if the nematodes fed on mycopathogenic fungi (such as those in the genera *Gliocladium* and *Trichoderma*) can result in plant diseases, reducing the positive effects of these antagonistic fungi on plants.

These fungi can coexist in the same ecological niches, despite their varying connections with nematodes and each other. Moreover, the capacity of fungi to draw fungivorous nematodes varies among those that provide food for worms. The current state of the environment can affect its attraction. Furthermore, nematodes and fungi are both somewhat mobile, albeit via distinct processes, which enables them to spread throughout many ecological niches [2,9]. These sophisticated dynamics that can occur within soil ecosystems and have consequences for agricultural management are highlighted by the complex, context-dependent interactions among plant-pathogenic fungi, fungivorous nematodes, and beneficial mycopathogenic fungi. Mycorrhizal fungi are one type of fungi that worms are known to consume.

Nematode grazing has spurred a significant amount of research because fungivorous nematodes are interested in interactions that could affect how mycorrhizal connections

affect nutrient intake and host plant growth between fungus and fungivorous worms. Survey data indicates that ectomycorrhizal fungi often produce fungal fruiting bodies, or mushrooms, which serve as worm homes. By releasing nutrients previously held in fungal biomass, worms fed by fungi can nourish bacteria [12]. In addition to ectomycorrhizal fungi, endomycorrhizal fungi, like arbuscular mycorrhizal (AM) fungi, interact with nematodes. For instance, co-inoculation with AM fungus can promote the development of *Aphelenchoides sp.* worms, which is low- Given that soils encourage plant growth and increase tolerance to arsenic (As) contamination [13]. Changes in the infectivity and composition of field assemblages of AM fungus could result from this in important ways. On the other hand, endomycorrhizal fungi of the species *Glomus* and pine roots can't coexist harmoniously if nematodes of the genus *Aphelenchus* are present. In these situations, fumigant nematicides may be required to properly disinfect the soil before planting pine seedlings. In addition to facilitating the pine plants' ability to use the dead nematodes as a beneficial source of nutrients, soil fumigation also promotes the endomycorrhizal infection of pine roots [6]. These examples highlight the complex and context-dependent interactions

between fungivorous nematodes and mycorrhizal fungi, with implications for plant health and ecosystem processes. Within ecosystems, fungivorous nematodes can fulfill a variety of purposes. It has been demonstrated, for instance, that the non-parasitic fungivorous worm *Aphelenchus avenae* controls plant-pathogenic fungus [7]. It has been noted that *Aphelenchoides* spp. and *A. avenae* each other impede *Rhizoctonia solani* and reduce the disease incidence in seedling cauliflower [14].

Moreover, *A. avenae* can stop *Ditylenchus destructor*, a plant-parasitic nematode, from spreading, suggesting that it could be employed as a biocontrol factor against specific nematodes that parasitize plants and fungi that cause plant disease [15]. Genetic studies of these enzymes support the potential of *A. avenae*'s cell wall-degrading enzymes to feed on a plant-parasitic nematode a plant-pathogenic fungus [16].

Notably, the pinewood worm *Bursaphelenchus xylophilus* was discovered to have a cellulase that resembles those found in fungi [17]. The most likely way that this cellulase obtained its gene during the evolution of its plant-parasitic lifestyle was by horizontal gene transfer. These results emphasize the potential of fungivorous nematodes to control plant diseases and to be the subjects of intricate evolutionary adaptations about their host relationships and feeding preferences. When nematode predators are present in the predator-prey connection, fungal prey, similar to other kinds of interactions between prey and predators, can adapt resistance mechanisms to fend off nematode predation.

The production and release of harmful secondary metabolites and proteins is one kind of defense mechanism used by fungal prey [18]. Nematodes, for instance, can be destroyed if they come into contact with the poisonous substance produced by the model mushroom *Coprinopsis cinerea* [19]. *C. cinerea* produced a bacterial toxin resembling cytolysin in response to nematode predation, displaying a broad range of differentially expressed genes (DEGs). Certain DEGs found in *C. cinerea* belong to a novel family of fungal effector proteins that are antagonistic towards nematodes [20]. These results display that to defend themselves against nematode predation, fungi, acting as the prey in this predator-prey interaction, have evolved an assortment of defense mechanisms, including the evolution of poisonous chemicals. A crucial component of the intricate ecological interactions between nematode predators and their fungal prey is the ongoing evolutionary arms race.

### Fungi that Resist Nematodes

While nematodes are shown resisting fungus and feeding on it in the preceding stated cases, the opposite is also possible

and occurs frequently in nature. The link between nematodes and nematophagous fungi has been crucial in understanding the more general dynamics of fungal-nematode interactions. Nematophagous fungi, also known as predaceous, nematode-trapping, or nematode-destroying fungi, are remarkably adept at ensnaring worms and lowering the number of plant-parasitic nematodes in their population. These skills are highly applicable in the agricultural sector [21,22]. Studies of nematophagous fungus and their interactions with nematodes have shown an abundance of mechanisms of their interactions at the molecular, cellular, organismal, and ecological levels. These studies have improved these relationships as model systems for studying coevolution in the kingdoms of prey and predator additionally for creating biocontrol applications [23-29].

Another important aspect of the intricate and varied connections between these two groups of animals within ecosystems is the antagonistic relationship in which some fungi prey on nematodes.

### Variability and Development of Fungi-Based Predation Systems

Historically, nematophagous fungi have been divided into four primary groups according to how they prey on nematodes:

- Fungi that trap nematodes: These fungi produce knobs, constricting rings, and extensive hyphal networks that act as traps to capture and stop living nematodes.
- Endoparasitic fungi are mandatory parasites that attach themselves to the surfaces of nematodes or ingest them whole. They exist in the environment as conidia. From that point on, the infection grows, begins to sprout, and ultimately kills the nematode host.
- Fungi that parasitize nematodes' eggs and cysts are facultative parasites that develop on and feed on their stationary stages.
- Fungi that produce toxins: These plants create poisonous substances that hurt nematodes. Most of the nematodes, except the egg stage, are mobile, which poses a problem for the comparatively slow-growing and stationary fungal parasites.

Nonetheless, several nematophagous fungi have developed complex predation structures to parasitize nematodes in their mobile phases. These structures include:

- encasing worms in structures to render them immobile
- Conidia that are sticky to adhere to and colonize the pseudocolor of the worm
- Stephanocysts, spiny balls, and acanthocytes eat and destroy the nematode cuticle.
- "Gun cells" that shoot tube-shaped structures straight at nematodes as their target

These many methods show how nematophagous fungi have evolved to combat the mobility of their worm prey [8,30-32]. In response to nematodes, nematophagous fungi undergo morphogenesis and virulence gene expression, signifying a change in stage from saprobic to phagocytic. Fungus that consumes nematodes has emerged extensively spread across numerous phylogenetically different taxonomic families, suggesting that the capacity to feed on nematodes has undergone multiple independent evolutionary cycles [23,33].

Nematode-trapping fungi contain a variety of trapping structures that are derived from the vegetative hyphae.

These include adhesive nets and adhesive columns, and both stalked and sessile sticky knobs are available [34]. They also include five different kinds of adhesive traps and non-constricting rings. Nematophagous fungi have developed special trapping structures to successfully seize and demolish their worm prey, which is in motion. The fungus-nematode predator-prey interaction is important for ecology, as evidenced by the convergent evolution of these predatory skills across several fungal lineages. The Orbiliaceae family of fungi contains five different types of trapping structures. These findings are consistent with the multiple independent evolutionary origins of nematode-catching abilities. Conidial traps are produced by *Arthrobotrys dactyloides*, *Arthrobotrys superba*, *Arthrobotrys oligospora*, and *Monacrosporium gephyropagum*, among other Orbiliaceae fungi, which are traps made entirely of the asexual spores, or conidia, of the fungi. In environments where food is scarce, microorganisms may engage in violent competition for resources. In this instance, the fungal spores' capacity to immediately develop into structures trap may confer a considerable ecological advantage to the nematophagous fungus [35,36].

The Orbiliaceae family of fungi exhibits a variety of trapping methods, including the direct conversion of spores into traps, which emphasizes the evolutionary adaptations of these fungi to effectively capture and devour mobile nematode prey in situations with low nutrients. Two species of fungi from different fungal phyla have been found to generate similar trapping structures, supporting the theory of convergent evolution. Particularly, to catch nematode prey, Sticky knobs can be grown by Zoophagus species (phylum Zygomycota) and Nematoconus species (phylum Basidiomycota) [37]. This specific trapping technique has independently evolved across four taxonomically diverse fungal families, indicating convergent adaptations for nematode predation. This convergent evolution of specialized trapping structures implies that the capacity to catch mobile nematode prey confers important ecological benefits, which are responsible for the predatory capabilities' recurring appearance across several fungal lineages. This study demonstrates how,

despite their evolutionary distances, several morphological and functional characteristics of nematophagous fungi have evolved convergently due to the intricate connection between nematodes and their prey. Although adhesive hyphae-based traps are only found in the Zygomycete phylum's fungal genera Stylopage and Cystopage [38], Adhesive spore traps include the well-known nematode-parasitizing fungus *Hirsutella rhossiliensis* and *Hirsutella minnesotensis* [30].

Certain endoparasitic fungal species have evolved morphologically modified conidia that lodge in the host's esophagus or buccal cavity when swallowed by worms. The genus Harposporium is the only one that contains these unique conidial traps [39]. Only the basidiomycete genus Hypoderma contains stephanocysts, among other unique nematode-trapping features [40]. Within the phylum Basidiomycota, only two Agaricales fungi, *Coprinus comatus*, and *Stropharia rugosoannulata*, are known to have spiny balls and acanthocytes, respectively [41,42].

Lastly, the endoparasitic oomycete fungus in the genus *Haptoglossa* develops a highly specialized assault mechanism known as the "gun cell" [43]. Diverse fungal taxonomic groups exhibit a wide range of trapping and predation structures, indicating the remarkable evolutionary adaptations that have developed to aid the capture and devouring of nematode prey. Among the several kinds of nematophagous fungi, the one that uses specific morphological changes to capture nematodes is of special interest. These NTFs can change from saprophytes to carnivores in response to specific environmental stimuli. This remarkable shift has made NTFs into valuable model systems for researching communication across kingdoms, specifically the mechanisms behind fungal disease and adaptation across kingdoms [23,27,44]. Conversely, our understanding of host-microbe interactions has greatly increased in recent years thanks to the application of -omics technologies, even when the microbes are difficult to culture in a lab setting [45]. Our understanding of the evolutionarily diverse tactics employed by fungi for pathogenicity against nematodes has significantly increased the genome sequencing of several important species in the context of fungi-nematode interactions.

Among them include *Pochonia chlamydosporae*, a parasite of nematodes and their eggs [46]. The fungus that traps nematodes *Drechslerella stenobrocha* [47], *Monacrosporium haptotylum* [25], and *Arthrobotrys oligospora* [44], as well as the endoparasite facultative nematode *Hirsutella minnesotensis* [48]. The nematode-trapping fungi, with their ability to transition between lifestyles and diverse predatory mechanisms, have emerged as important model systems for elucidating the complex interactions between fungi and nematodes at the genomic and molecular levels. Using nematode-trapping fungi (NTF) within the phylum

Ascomycota as model systems, phylogenetic analyses based on both nuclear and mitochondrial genes and genomes confirm that the nematode-trapping mechanisms within the order Orbiliales have evolved along two main lineages. In one lineage, constricting rings act as trapping characteristics of fungal species. Adhesive traps, such as three-dimensional hyphal networks, adhesive hyphal branches, and adhesive knobs, are developed by the species in the second lineage [23,33,49]. Additionally, based on two fossil records, The connections between NTF and nematodes most likely date back more than 419 million years in co-evolution, according to a five-gene phylogeny and molecular clock calibration combination. After the Permian-Triassic mass extinction catastrophe, which occurred around 251.4 million years ago both passive and aggressive predators (fungi with sticky traps and constricting rings). are thought to have split off from one another about 246 million years ago [23]. However, there hasn't been any significant divergence in fungus carnivorism linked to the extinction event of the Cretaceous-Tertiary period. fungal predatory powers evolved in reaction to these enormous extinction episodes, more research is required to understand this.

These results demonstrate the complex evolutionary history and divergence of specialized nematode-trapping systems of ascomycete fungi. While nematode-trapping structures can have a variety of appearances, they are distinguished from the fungus's vegetative hyphae by two fundamental structural features. One feature all trap cells have in common is the abundance of organelles in the cytoplasm, sometimes referred to as dense bodies.

Only nematode-trapping fungi possess these peroxisomal dense structures; Nematophagous endoparasitic fungus that disseminate their infection they are absent from adhesive or non-adhesive spores. The thick bodies of the invasive fungus appear to supply structural elements to the hyphae. Moreover, they seem involved in the attachment process of nematode life [50,51]. According to a recent study, *Arthrotrrys oligospora*' s deletion of the *Aoime 2* gene reduced the number of bodies in trap cells that are rich in electrons and the construction of traps, which in turn led to a significant decrease in the number of nematodes that the mutant fungi were able to catch [52]. Adhesive traps with columns, networks, and knobs have a second characteristic in common: they have thick layers of extracellular polymers. These extracellular polymers are thought necessary for the traps to stick to the nematode surface [53]. Comparative genomic and structural studies have shown that stickier fungal trap surfaces are linked to the evolution of adhesion-related genes in nematode-trapping fungus genomes. These changes probably played a significant part in the fungal evolution's ability to capture, pierce, and break down nematode prey [27]. These structural similarities

demonstrate how specialized mechanisms have evolved convergently to improve the capacity of nematode-trapping fungi to unsnap and parasitize their mobile worm hosts (Figure 2) [27].

### Identification, Adhesion, Specificity, and Infection Process of the Host

All nematophagous fungal species can identify their nematode hosts and adhere to their cuticles or eggshells, which are the initial stages of the infection process. Nematodes' strong exoskeleton, or cuticle, is made mostly of proteins and serves as a defense against invasive pathogens and environmental stressors [54]. The exact mechanisms of fungus that capture nematodes (NTF) pierce the nematode exoskeleton are still unclear. However, recent studies indicate that NTF-secreted enzymes are essential to the nematode invasion method. Proteases, collagenases, and chitinases are examples of extracellular hydrolytic enzymes that are required. for the nematode cuticle to penetrate, according to genetic, ultrastructural, and histochemical investigations [55].

Phylogenetic analysis has revealed that from a shared ancestral lineage, Entomopathogenic and nematophagous fungi's pathogenicity-related serine proteases developed [56-79]. Fresh fungal biomass is produced both inside and outside the nematode host by the fungi as they break down the contents of the worm once they have entered it.

The passage (Table 1) lists the four main stages of the nematophagous fungal infection process for the four main groups, along with a fifth group that makes specialized attack tools to mechanically rip apart the nematode cuticle [21,30]. An effective illustration of the fundamental strategies employed by several nematophagous fungi to successfully parasitize their worm hosts may be found in this complex infection process.

These strategies include host recognition, adhesion, enzymatic breakdown, and content digesting. Generally speaking, nematode-trapping fungi (NTF) are not host-specific and can obtain a broad range of soil-dwelling nematode species [80]. Endoparasitic fungi, on the other hand, show a higher level of host specificity.

Obligate parasites and endoparasitic fungi are mostly found in the environment as conidia. As the endoparasitic fungus *Drechmeria coniospora* has shown, certain identification signals are necessary for effective infection even when these conidial spores adhere to a specific nematode species [71,81]. Many common soil saprophytes that parasitize nematodes primarily target the sedentary nematode's female and egg stages, or sedentary nematode species, including *Meloidogyne*, *Globodera*, and *Heterodera* [30]. fungus

poisonous to nematodes can produce toxic chemicals that can immobilize and kill nematode hosts. The creation of these nematode-toxic chemicals is sometimes associated with the effectiveness and efficacy of nematode attacks by fungi that use specialized attack devices, such as sharp “sword-like” structures, acanthocytes (spiny balls), and stephanocysts [41]. These specialized tools mechanically damage the nematode’s cuticle, allowing the fungal hyphae to fully colonize the host organism and facilitate the evacuation of the nematode’s internal contents. The diversity of adaptations that have emerged among the vast nematophagous fungi to hold onto their hosts, nematodes is seen in the variances in host specificity and infection strategies.

### Fungi that Trap Nematodes and Nematodes in Rivalry

Armies of evolution between viruses and their hosts are frequently seen. There’s proof that nematode and nematode-trapping fungi (NTF) are engaged in such arms races. Fungal predators constantly develop new predatory techniques in these never-ending arms races to take control of nematodes and secure a food source.

As a result, the nematode prey has developed defense mechanisms against their fungal predators, including stronger inherent immunity and advanced neurological systems. Many factors can affect the dynamics of these evolutionary arms races. For example, in addition to acting as predators and prey, NTF populations and the nematodes they feed on interact with nearby fungi and nematodes in soil habitats.

In addition, abiotic variables like nutrition levels and biotic factors like different bacteria and plants might affect how NTF and nematodes interact. thorough investigation of the interactions between bitrophic creatures (NTF and nematode) and multitrophic organisms (plants, soil microbes, nematodes, and NTF) in their natural habitats

is necessary to gain a comprehensive grasp of the variables affecting the environment and development of these intricate predator-prey dynamics. The book’s second section provides recent findings about potential mechanisms underpinning the evolutionary arms race between nematode-trapping fungi and the nematodes they prey on.

### Nematode Innate Immune Defenses Responses

Nematodes are protected from fungal infections by physical barriers like their collagen-rich cuticle and epidermis.

Nematodes may also recognize fungal infections and counter them using a variety of defense mechanisms, including the innate immune system-regulated synthesis of antimicrobial peptides. The model nematode *Caenorhabditis elegans*’s

innate immune response consists of a surge in reactive oxygen species (ROS) production to combat bacterial and fungal infections that may target the nematode’s gut or cuticle [82]. Their genomes also contain a substantial number of genes that encode antimicrobial peptides (AMPs), which are vital to nematode innate immunity. One of the AMPs, NLP-31, had potent antifungal activity against many fungi, such as *Aspergillus fumigatus*, *Neurospora crassa*, and *Drechmeria coniospora*, when *C. elegans* was infected in one study [83]. In addition to evidence of their in vivo function and positive selection signatures on the nlp29 gene cluster, the recent genome sequencing discovery of the AMP-encoding nlp gene family suggests that these genes are critical for *C. elegans* survival when interacting with the spores of the endoparasitic fungus *D. coniospora* [84]. These results demonstrate the complex defense mechanisms that worms have developed to defend themselves, such as physical barriers and inducible antimicrobial peptides.

For worms to survive fungal infection and injury, the conserved insulin/IGF-1 signaling (IIS) pathway requires the FOXO transcription factor DAF-16, which is necessary [85]. Additional RNA sequencing (RNA-seq) investigation has revealed signaling channels controlled by DAF-16/FOXO transcriptionally, both common and distinct. These investigations have demonstrated the significance of the innate immune systems and intestine DAF-16 regulatory elements operations in preventing nematode fungus disease [86-88]. As a component of the IIS pathway, the transcription factor DAF-16 for FOXO appears essential for coordinating the nematode’s defense mechanisms against fungi. The employment of RNA sequencing (RNA-seq) data has enabled a thorough comprehension of the intricate signaling networks and regulatory processes that oversee nematode innate immune responses and their ability to fend off fungal infections. These results highlight the crucial function of the DAF-16/FOXO transcription factor in coordinating the nematode’s immunological and physiological defenses against fungal pathogen invasions.

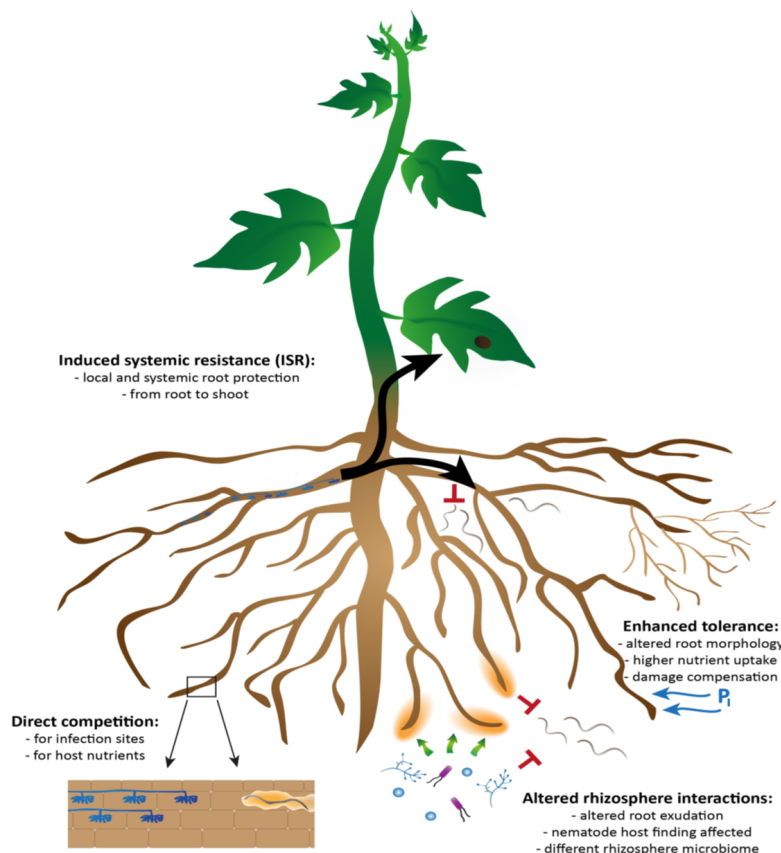
### Competition Between Nematodes and Several Fungus Species

Nematodes and nematophagous fungi (NTF) have to traverse a variety of competing forces and stresses in the soil environment to survive and proliferate. Competition can occur between different kinds of nematodes, between NTF and nematodes, and between different fungal predators. Surveys show that many NTF species share an ecological niche, indicating that competition for shared prey supplies likely exists in these species’ natural habitats. For example, sympatrically distributed generalist nematodes more than 63% of the natural sites that have been studied contain predators like *A. thaumasia* and *A. musiformis*. Significant

variation may be seen in the predatory effectiveness, prey-detecting skills, and competitive relationships amongst wild isolates of *Arthrobotrys oligospora*. Research has shown that a range of NTF species can simultaneously catch or colonize nematodes and that these predators engage in competitive interactions. For instance, *A. oligospora* hyphae frequently degenerate or die when near the live mycelia of the endoparasitic fungus *Dactylella coniospora*, indicating hostile behavior under certain circumstances. According to research by El-Borai, et al. [89], Certain nematodes are drawn to Myzocytiium and catenary, two genera of activated endoparasitic fungi, but repulsed by activated *Arthrobotrys* species. In soil conditions, antagonistic interactions have been found between nematophagous fungi (NTF) and nematodes. An increase in nematophagous fungal (NTF) density is correlated with a decrease in nematode prey density, according to evidence of density-dependent parasitism. Due to a complicated interplay within the environment, the nematode population increases as a result of the fall in nematode density. Nematodes are also subject to

a negative frequency-dependent selection that controls the densities of both animal species populations. This particular model has been successful in explaining differences in the nematophagous fungus *Hirsutella rhossiliensis*'s *Heterodera schachtii* parasitism about host density; The disease dynamics in soil microcosms show both a host threshold density and a temporal density-dependent parasitism.

Nematophagous fungi (NTFs) like *Monacrosporium cionopagum* and *Hirsutella rhossiliensis* reduce the root-knot nematode *Meloidogyne javanica*. This suppression is positively connected with the density of the nematode host, *Steinenema glaseri*. Different NTF species exhibit different suppression dynamics. The nematophagous fungus *H. rhossiliensis* has been sampled spatially, and the results show that the amount of parasitism and the abundance of hosts (like *Criconentella xenoplax*) are correlated. This demonstrates that in certain areas of agricultural fields, the two interacting partners undergo identical density-dependent behavior.



**Figure 2:** A review of the scientific literature on the potential methods by which plant-parasitic nematodes (PPNs) can be controlled by arbuscular mycorrhizal fungus (AMF) AMF's Direct Effects on Pathogens - AMF and PPNS competing for nutrients and space (bottom left) Plant-Mediated Indirect Effects - Plant tolerance to nematode infection and damage compensation (top right)- Plant defense responses (Induced Systemic Resistance, or ISR) are triggered by AMF (upper left). - Plant defenses against PPNS and their interactions with AMF (bottom right)



More recent greenhouse experiments have shown a substantial relationship between the nematode density of soybean cysts and *H. rhossiliensis* parasitism. These results elucidate the intricate interactions and dynamics established inside agricultural ecosystems involving nematophagous fungi, nematodes, and their respective host organisms. On a larger geographical scale, an examination of Florida's flatwood and central ridge ecoregions home to 53 citrus groves demonstrated that differences in the entomopathogenic nematode species' spatial patterns of nematode species such as *Catenaria sp.*, *A. musiformis*, and *Arthrobotrys dactyloides* were affected by their vulnerability to fungal species that feed on nematodes. *Gamsylella gephyropaga*, *A. oligospora*, and *Paecilomyces lilacinus* in various environments in a recent study that observed Three microbial nematode enemies—*Catenaria spp.*, *H. rhossiliensis*, and *Pasteuria penetrans* were found to have significant and diverse top-down management impacts on the coastal dunes' nematode community. These enemies also showed a positive or negative correlation with

the number of plant parasitic nematodes in the population. These results point to the possibility of species-specific impacts in agricultural and natural environments for the nematode and fungus partners.

Apart from customized recently, the relationships have been examined using metagenomic techniques. that are in place between nematodes and fungi (and bacteria) in natural environments; the results show a variety of spatial relationships similar to those between nematophagous fungi and plant parasitic nematodes.

It is essential to recognize that the various proposed mechanisms are not mutually exclusive; instead, a combination of direct and indirect effects is likely to occur, contributing to the efficacy of biocontrol strategies.

Further research is necessary to fully understand the underlying mechanisms of the complex interactions that occur between nematodes, plants, and AMF.

Collective	Typical Species	Appreciation of the Host	Stickiness	Infiltration	breakdown
Traps for fungi nematodes	<i>A. oligospora</i>	Lectin- Coordinated interactions between fungal surface proteins and sugar molecules A pheromone peculiar to nematodes, called ascaroside [24], nematode cuticle (GalNAc [57], AOL [58], AofleA [59], and AoMad1 [60]), or olfactory mimicry that draws in nematode prey [29].	A cell-to-cell During the trap creation and adhesion process, a set of volatile chemical molecules called furanone, pyrone, and maltol [62], nitrate [63], and autophagy [64], as well as physical interaction between the nematodes and the trap cells, are necessary for the transition from the saprophytic to the pathogenic stage.	Using the development of a penetrating tube, fungi use a mix of extracellular hydrolytic enzymes and mechanical pressure to pierce the cuticle. such as collagenase, chitinase [55], serine proteases (PII [65], Aoz1 [55], Ac1 [66], Ds1 [67], Dv1 [68], Mlx [69], and Mc1 [70]).	Lipid droplets are created from the nematode material by the fungi. use as food for growth and reproduction.
Fungal endoparasitoids	<i>Coniospora drechmeria</i>	The term "obligate parasites" refers to parasites that attach themselves to the host's cuticle or eat conidia [71].	When sticky conidia adhere to the cuticle, the cuticle will form an appressorium that presses firmly against the nematode's cuticle. The injection tube is created when motile zoospores encyst on the surface of worms and germinate in order to infect them with a sporidium. [37].	an aggressive development of the trophic hyphae, in conjunction with enzymatic action and mechanical force, to infiltrate nematodes [72-74].	Within the cadaver, At the tips of trophic hyphae, bulbs give rise to new conidiophores. Tightly packed to the inside surface of the cuticle, these bulbs stop host nutrients from leaking out, disrupt nematode metabolism, and ultimately kill nematodes [75].

Fungi that parasitize eggs and cysts	<i>Pochonia chlamydosporia</i>	Strong toxicity and host recognition were demonstrated by Aurovertin D [76].	Appressoria and glycoproteins are in charge of conidia's adhesion and the eggshell's hyphae [77].	Proteases and chitinases, such as Ver112 from <i>Lecanicillium pallidum</i> and PrC from <i>Clonostachys rosea</i> [78].	uses the carbohydrates in the egg as a carbon source and colonizes the host tissues to get nutrients [46].
Fungi that produce toxins.	<i>Pleurotus ostreatus</i>	causes paralysis by nematode sensory neuron cilia [79].	<i>P. ostreatus</i> can affect <i>C. elegans</i> at any stage of development. When nematodes come into touch with <i>P. ostreatus</i> hyphae, they become paralyzed.	Over-influx of calcium and nematode contraction of the pharyngeal and head muscles.	Toxins induce many tissues throughout the organism to quickly and systemically necrotize.
Manufacturers of special fungus that target nematodes	<i>Coprinus comatus</i> ; <i>Stropharia rugosoannulata</i>	The nematode's cuticle is mechanically damaged by the sharp projections of the specific assault devices [41,42].	Through the use of mechanical forces and enzymatic processes, the nematode cuticle can be punctured by the penetration peg that is made.	Hyphae extend themselves from the infected nematode and colonies its interior.	Need poisons to help them perform their nematocidal role (spiny balls).

**Table 1:** The nematophagous fungal infection process.

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## Conflict of Interests

The authors declare that they have no conflict of interest.

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