Mycological Spectrum (e-ISSN:3107-6203)
https://mycologicalspectrum.org/
Published by Association of Fungal Biologists, India

Review Article

Fungi That Hunt: Diversity, Mechanisms, and Evolutionary Perspectives

Purnendu Paul, and Prakash Pradhan*

West Bengal Biodiversity Board, Prani Sampad Bhawan, 5th Floor, LB-2, Sector-III, Salt Lake, Kolkata, West Bengal, India – 700 106

*Corresponding author: Prakash Pradhan: Email: shresthambj@gmail.com

Abstract

Carnivorous fungi, also known as nematode-trapping fungi, represent a unique group of soil-dwelling organisms that have evolved intricate mechanisms to capture and digest nematodes. These fungi offered promising solutions for sustainable nematode management in agriculture. This review explored their diversity, habitat preferences, seasonal occurrence, substrate specificity and global distribution. These fungi evolved monophyletically, and genomic and transcriptomic studies have provided valuable insights into the evolution of their carnivorous lifestyle and the regulation of pathogenicity-related genes. The review presented a comprehensive analysis of the various trap types employed by nematophagous fungi, including adhesive nets, knobs, branches, and constricting rings, highlighting their structural diversity and evolutionary significance. Emphasis was placed on the genera *Arthrobotrys*, *Dactylella*, and *Monacrosporium,* which were extensively studied for their potential in sustainable agriculture. The influence of environmental factors, including pH, temperature, and nutrient availability, on trap formation and predatory efficiency was also examined. Furthermore, the review evaluated the application of nematophagous fungi in integrated pest management programs, their compatibility with other biocontrol agents, and the challenges associated with their large-scale production and field efficacy.

Keywords: Carnivorous fungi, endoparasitic fungi, nematophagous fungi, nematode-trapping structures, sustainable agriculture.

Citation: Paul P, & Pradhan P. (2026). Fungi That Hunt: Diversity, Mechanisms, and Evolutionary Perspectives. *Mycological Spectrum 02(02):13-59.*https://doi.org/10.64993/MS.2.2.2

Received: 17 December 2025 | Accepted: 24 May 2026 | Published: 30 May 2026.

Handling Editor: Dr. Shilpa Verekar | **Reviewer**: Professor K.R. Sridhar and Dr. S.K. Singh.

Copyright: ©2026 Paul & Pradhan. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution, or reproduction in other forums is permitted, provided the original author(s) or licensor are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution, or reproduction is permitted that does not comply with these terms.

1. Introduction

Fungi, a kingdom that represents a major reservoir of genetic diversity on Earth, play indispensable roles in life-sustaining processes. Exhibiting remarkable species richness, estimated at 2.2-3.8 million (Hawksworth & Lücking, 2017), these ubiquitous organisms colonize nearly all terrestrial and aquatic ecosystems. Due to the absence of chlorophyll, these fungi have consequently evolved diverse strategies to exploit readily available organic substrates. These strategies include saprotrophism, parasitism, symbiotic associations, osmotrophism, and, notably, predation or carnivory (Pathak *et al.,* 2012; Zhang *et al.,* 2014a). Genomic and transcriptomic studies have further revealed the extensive metabolic plasticity of fungi and their ability to regulate nutrient-acquisition pathways in response to environmental cues (Haridas *et al*., 2020; Kiss *et al*., 2019).

While predation as a feeding strategy is predominantly observed in the animal kingdom and in a few plant lineages, its occurrence in fungi represents an adaptive response to nutrient scarcity (Wang *et al*., 2014; Kuo *et al.,* 2020; Zhang *et al*., 2023). Specifically, the transition to a predatory lifestyle in fungi is often triggered by environmental nutrient limitations, particularly the reduced availability of essential nutrients (Yang *et al.,* 2012; Hsueh *et al.,* 2017; Jiang *et al.,* 2017; Lakshmi *et al.,* 2024). Although most predatory fungi possess an inherent saprophytic ability and primarily thrive through the decomposition of organic matters. They can facultatively switch to a predatory mode of nutrition under nutrient deprivation, particularly nitrogen limitation, to ensure survival and resource acquisition (Li *et al*., 2011; Yang *et al*., 2012; Zhu *et al*., 2022). The ecological hypothesis suggests that in nitrogen-poor ecosystems, the direct capture and assimilation of nitrogen by small invertebrates or microorganisms confer a distinct selective advantage on carnivorous fungi compared with those that rely solely on the often unpredictable, spatially heterogeneous process of decomposition.

Carnivory, or predation in fungi exhibits defining characteristics that distinguish it from other heterotrophic nutritional modes. Fungi that colonize the superficial tissues (epidermis, nails, hair, skin, scales, or feathers) of living vertebrates, or those that decompose animal cadavers, are typically classified as dermatophytes or saprobes, respectively, rather than true predatory fungi. Similarly, fungal species that inhabit the orifices and digestive tracts of various animals are not considered carnivorous. The classification of entomopathogenic fungi, which infect and proliferate within insect hosts, is also interesting. While occasionally grouped with carnivorous fungi, a study by Bava *et al*., (2022) indicates that their nutritional strategy aligns more closely with a specialized form of heterotrophic metabolism. Where, the host is exploited through involvement of infection, colonization and proliferation within the insect hosts through a series of specialized germination and colonization steps, rather than active capture and consumption of prey.

The defining trait of carnivorous fungi is their capacity to adopt a predatory lifestyle, depending on specific types of microfauna, predominantly nematodes and other small invertebrates. This is achieved through the development of sophisticated, morphologically diverse trapping structures that arise from modifications of the fungal mycelium. These traps function by actively capturing, rapidly paralyzing, and effectively immobilizing the targeted prey. Once the prey is secured, the carnivorous fungi penetrate the victim's cuticle or cell walls with their specialized hyphal filaments, facilitating the absorption of internal nutrients and the subsequent consumption of the captured organism (Nordbring-Hertz *et al*., 2011).

To date, over 700 species from more than 150 genera of carnivorous fungi have been identified, with the majority exhibiting nematophagous behaviour (Hsueh *et al*., 2017; Jiang *et al*., 2017; Soares *et al*., 2024). These predatory fungi demonstrate a polyphyletic distribution across the fungal kingdom, with representative taxa found within the phylum *Zygomycota* (family *Zoopagaceae*), *Basidiomycota* (genus *Nematoctonus*), *Chytridiomycota* and *Ascomycota* (class *Orbiliomycetes*) (Nordbring-Hertz *et al*., 2011; Hsueh *et al*., 2017). Among the nematophagous fungi, several genera have been particularly well-studied, including *Arthrobotrys*, *Dactylellina, Drechmeria*, *Fusarium*, *Hirsutella*, *Nematophthora*, *Pochonia*, and *Purpureocillium* (Gray, 1983; Jatal, 1986; Siddiqui & Mahmood, 1996; Kuo *et al*., 2020).

Beyond the well-documented nematode-trapping fungi, other lineages of carnivorous fungi have evolved specialized mechanisms for predating amoebae. *Zoophagus insidiosus*, within the order *Zoopagales* (phylum Zygomycota), has evolved intricate trapping structures, primarily adhesive hyphae, to capture free-living amoebae in the trophozoite stage. The predatory sequence involves initial adhesion of the amoeba to the fungal hyphae, followed by hyphal invasion and the subsequent formation of specialized intracellular structures known as haustoria, which penetrate the amoeba's cytoplasm to facilitate nutrient extraction and assimilation. Notably, certain *Zoopagales* have been reported to prey on rotifers, highlighting the diverse evolutionary trajectories and resulting predatory strategies within this fungal group (Scheid, 2018).

This review aims to provide a comprehensive overview of the diversity of carnivorous fungi, elucidate their diverse predatory mechanisms at the morphological and cellular levels, and explore their ecological significance within various ecosystems. It examines the remarkable array of specialized adaptations that have evolved across different taxonomic groups to enable the active capture and consumption of prey. Furthermore, the mechanisms of fungal parasitism will be discussed to clearly delineate predatory fungi from other parasitic and saprophytic fungal species. A key focus will be on the evolutionary pathways that have led to the emergence of carnivory in fungi, examining how specific fungal lineages have undergone divergence and adaptation to acquire this unique mode of nutrition. The genetic, structural, and ecological factors that have influenced this evolutionary transition will be analysed to provide deeper

insights into the origins and subsequent diversification of predatory fungi. Beyond their intrinsic ecological roles, this review will also highlight the potential of carnivorous fungi as biocontrol agents in agricultural systems. Numerous species, particularly nematophagous fungi, play a crucial role in regulating plant-parasitic nematode populations, which cause substantial crop losses worldwide. By naturally suppressing nematode populations, these fungi offer a promising avenue for reducing the reliance on synthetic nematicides, thereby contributing to more sustainable agricultural practices. Their strategic application in integrated pest management programs has the potential to provide an effective and ecologically sound alternative to chemical control, mitigating soil contamination and promoting biodiversity in agroecosystems.

2. Diversity and Ecology

Fungi are among the most diverse groups of organisms on Earth (Wijayawardene *et al*., 2024). However, the diversity of carnivorous fungi constitutes a small fraction, less than 0.5%, of the total fungi known to date (Yang *et al*., 2012). Notably, approximately 90% of these carnivorous fungi belong to the class *Orbiliomycetes* within the *Ascomycota* (Yang *et al*., 2012; *Rahman et al*., 2024). Literature reviews further indicate that most fungi exhibiting carnivorism are nematophagous (Jiang *et al*., 2017; Yang *et al*., 2020).

The phylum *Nematoda* is the second largest in the animal kingdom, encompassing an estimated 500,000 species and a substantial biomass (Bongers & Bongers, 1998; Zhang *et al*., 2020a). There are over 4,100 documented species of plant parasitic nematodes (PPNs) including cyst nematodes (*Heterodera* spp. and *Globodera* spp.), root-knot nematodes (*Meloidogyne* spp.), lesion nematodes (*Pratylenchus* spp.), and dagger nematodes (*Xiphinema* sp.) (Nicol *et al*., 2011). Nematodes are ubiquitous, and over 90% reside in the topsoil zone (the upper 15 cm), including the rhizosphere, the soil region directly influenced by plant roots. Correspondingly, fungi also inhabit this zone, facilitating substantial interactions between these two groups of organisms (Bongers & Bongers, 1998; Yang *et al*., 2020).

The life cycle of nematodes is a complex and well-defined process comprising multiple developmental stages, including an embryonic stage, four to five larval (juvenile) stages, and an adult stage (Rahman *et al*., 2024). In certain species, additional specialized stages may occur, such as the infective or dauer stage, which facilitates survival under adverse environmental conditions and enhances host colonization. Nematodes cause significant damage to crop primarily through parasitic interactions with plant roots, leading to symptoms such as root gall formation, disruption of nutrient and water uptake, and overall reduction in plant vigour. Furthermore, some nematode species act as vectors, transmitting plant pathogens between hosts, thereby exacerbating disease incidence and severity (Bernard *et al*., 2017; Gamalero & Glick, 2020; Wielkopolan *et al*., 2021; Pulavarty *et al*., 2021). Nematode-trapping fungi (NTF)

comprise a taxonomically heterogeneous group distributed across *Ascomycota*, *Basidiomycota*, *Chytridiomycota*, *Oomycota*, and *Zygomycota*. These fungi utilize specialized structures, or traps, to capture free-living nematodes in the soil. Approximately 380 species of NTF have been documented worldwide (Zhang *et al*., 2011; Jiang *et al.,* 2017). The *Orbiliomycetes* represent the largest group of NTF, including about 116 species (Glockling & Dick, 1994; Li *et al.,* 2006; Wu *et al*., 2012a; Li *et al*., 2013; Liu *et al.,* 2014b; Zhang & Hyde 2014; Quijada *et al*., 2020; Zhang *et al*., 2020a; Zhang *et al*., 2020b; Zhang *et al.,* 2022), currently classified into the asexual genera *Arthrobotrys* (67 species), *Dactylellina* (34 species), and *Drechslerella* (15 species) (Scholler *et al*., 1999; Li *et al*., 2005; Yang *et al*., 2007a; Zhang & Hyde, 2014; Zhang *et al*., 2014). NTF exhibit a facultative nutritional mode, capable of living both saprophytically and as active predators in response to environmental cues. Trap formation signifies a shift from saprophytic to predatory behaviours (Cooke, 1962; Jansson, 1982). Most NTF species are generalist predators that capture a wide variety of soil nematodes (Yang *et al*., 2020). Interestingly, recent research (Yesayan *et al.*, 2024) indicates that predatory efficiency is highest when both fungi and nematodes are isolated from the same local environment.

2.1 Habitat Distribution and Substrate Preferences

Nematode trapping fungi are ubiquitous, colonizing a diverse range of ecosystems, including deciduous and coniferous leaf litter, dung, pasture soils, agricultural lands, moss cushions, decaying vegetation, composts, peatlands, and coastal areas (Gray 1983; Shams Ghahfarokhi *et al.*, 2004; Saxena, 2008; Kelly *et al*., 2009; Liu *et al*., 2009; Kumar *et al.,* 2011).

2.1.1 Agricultural soils

Agricultural soils represent the most extensively researched habitat for nematode-trapping fungi (NTF) due to their significant potential as biological control agents against plant-parasitic nematodes (PPNs) (Bontempo *et al*., 2014; Baheti *et al*., 2015; Hussain *et al*., 2018; Kiriga *et al*., 2018; Noura *et al*., 2018; Ghahremani *et al*., 2019; Zhang *et al*., 2021; Yao *et al*., 2023). These environments are characterized by high levels of biological activity and nutrient availability, which support a wide array of fungal taxa (Zhang *et al*., 2020a). In the cropping system, the NTF community is dominated by several key genera known for their diverse trapping and parasitic mechanisms, includes *Arthrobotrys*, *Dactylella* (and its segregated genus *Dactylellina*), and *Drechslerella, Pochonia (*notably *P. chlamydosporia)* and *Purpureocillium (*notably *P. lilacinum)* (Kassam *et al*., 2021). The prevalence of these fungi in crop soils is often directly correlated with the presence of high-density populations of economically damaging PPNs including *Meloidogyne*, *Heterodera, Globodera, Pratylenchus.* The agricultural practices influence the abundance of NTFs. Comparative studies have shown that organically managed agricultural soils support higher abundance and diversity of NTFs than conventionally managed soils (Colagiero *et al*., 2025), although certain species, such as *Arthrobotrys haptotyla* and *A.*

thaumasia, are more common in conventionally managed plots (Jaffee *et al.*, 1998). The NTF are generally more abundant in organic-rich, biologically active soils where nematode populations are also high (Wachira *et al*., 2009; Singh *et al*., 2023; Pinto *et al*., 2024).

2.1.2 Rhizosphere soils

Rhizosphere soils tend to support higher densities and greater species richness of NTF compared to other soils, likely due to elevated nematode activity and root exudates that may serve as trophic signals to attract nematodes, creating a favourable microhabitat (Zhang *et al*., 2020a). In Sweden, nematode-trapping fungi (NTF) densities were 5–20 times higher in the rhizosphere of pea plants than in root-free soils, with *Arthrobotrys oligospora* identified as the dominant species (Persmark & Jansson, 1997). The study by Bordallo *et al.*, (2002) demonstrated that *Pochonia chlamydosporia* (formerly known as *Verticillium chlamydosporium*) and *Arthrobotrys oligospora* are capable of endophytic colonization, enabling them to interact directly with sedentary endoparasitic nematodes within or around the root zone. Such habitats are particularly significant in crops such as tomato, cucumber, banana, and cereals, where nematode pressure is often high.

2.1.3 Forest soils and litter

Forest soils support elevated levels of diversity because of abundant organic matter, stable moisture, dense microfauna, and low disturbance. The abundance also depends upon forest stands, management practices (Yeates, 2007; Richter *et al*., 2023). Coniferous leaf litter tends to support the highest fungal abundance (Gray, 1984), however temperate deciduous forests usually have higher mean species. In deciduous forests, NTF are primarily found within the upper 35 cm of the soil profile, a distribution that correlates with nematode populations (Gray & Bailey, 1985). Trap types also show stratification by soil depth: constricting rings, adhesive branches, and adhesive knobs are more prevalent in the organic-rich upper layers, whereas net-forming predators, such as *Arthrobotrys* species, are more abundant in deeper mineral soils (Jaffee *et al*., 1998). Regional studies from Berlin indicated that mesotrophic beech forests yielded the highest numbers of fungal isolates, while riverbank forests exhibited greater species richness despite lower isolate numbers (Sünder & Lysek, 1988). In India, Kumar *et al.* (2011) documented 17 species of NTF across various substrates, with the highest colonization rates observed in leaf litter.

2.1.4 Pasture systems, Animal dung and faecal habitats

Pastures, animal dung and faecal habitats are important especially for fungi associated with animal-parasitic nematodes. The study by Kelly *et al*., (2009) showed that the permanent sheep pasture harbours a promising array of nematophagous fungi. In China, 8 genera and 28 taxa of

NTF were identified from the samples associated with cattle faecal habitats and barn soil (Cai *et al*., 2016). The study of Gray (1984) also revealed that dung habitats harbour the greatest species diversity. In India the study of cow dung manure also shows the high colonization rate of NTF (Kumar *et al.*, 2011). NTF such as *Duddingtonia flagrans* are important in pasture ecology because they can trap nematode larvae in faeces and surrounding soil (Fernández *et al*., 2023).

2.1.5 Aquatic and semi-aquatic habitats

Aquatic and semi-aquatic ecosystems are also reported to harbour NTF. Hao *et al.* (2005) isolated 35 species, predominantly *Arthrobotrys oligospora*, *A. musiformis*, *A. thaumasia*, and *A. longiphorum*, from shallow freshwater environments. However, fungi were absent in deeper sediments (≥4 meters). In mangrove forests, *Arthrobotrys mangrovispora* was discovered (Swe *et al.,* 2008), and subsequent surveys indicated that terrestrial environments supported greater species richness than mangrove and freshwater habitats (Swe *et al*., 2009).

2.1.6 Disturbed and urban soils

The disturbed soils also contain nematophagous fungi; a positive relationship has been observed between NTF diversity and lead concentrations in polluted soils (Mo *et al*., 2006). The study by Hastuti *et al*., (2023) isolates *Drechslerella brochopaga*, *Arthrobotrys thaumasia* and *Arthrobotrys* sp. from the municipal waste-contaminated soil in Medan City, Indonesia.

Table 1. Ecological Distribution, Taxa, and Key Observations of Nematode-trapping Fungi (NTF)

Habitat Type	Key Characteristics	Dominant/Representative Taxa	Key Ecological Observations	References
Agricultural Soils	High biological activity; nutrient-rich; influenced by management (organic *vs.* conventional).	*Arthrobotrys, Dactylella, Dactylellina, Drechslerella, Pochonia chlamydosporia, Purpureocillium lilacinum*	Abundance correlates with PPN density. Organic soils generally support higher diversity, though specific species (*A. haptotyla*) favour conventional plots.	Bontempo *et al*., (2014); Hussain *et al*., (2018); Zhang *et al*., (2021); Yao *et al*., (2023); Colagiero *et al.*, (2025); Jaffee *et al.,* (1998); Singh *et al.,* (2023).
Rhizosphere Soils	Elevated root exudates and trophic signals; favourablemicrohabitats.	*Arthrobotrys oligospora, Pochonia chlamydosporia.*	Densities are 5–20 times higher than root-free soil. Capable of endophytic colonization in crops like tomato, cucumber, and banana.	Persmark & Jansson, (1997); Bordallo *et al*., (2002); Zhang *et al*., (2020a).
Forest Soils & Litter	Abundant organic matter; stable moisture;	*Arthrobotrys* spp. (mineral layers); various taxa in	Trap types vary by depth: constricting	Gray, (1984); Gray & Bailey,

	low disturbance; depth-based stratification.	coniferous and deciduous litter.	rings/knobs in organic upper layers; net-formers in deeper mineral soils. High colonization in leaf litter.	(1985); Jaffee *et al.*, (1998); Sünder & Lysek, (1988); Kumar *et al*., (2011); Richter *et al.*, (2023)
Pastures & Animal Dung	High organic content; focused on animal-parasitic nematodes.	*Duddingtonia flagrans*	Dung habitats harbour high species diversity. Important for biological control of nematode larvae in faecal matter.	Gray (1984); Kelly *et al.,* (2009); Cai *et al.,* (2016); Kumar *et al.,* (2011); Fernández *et al.*, (2023)
Aquatic & Semi-aquatic	Shallow freshwater and mangrove ecosystems; limited by water depth.	*Arthrobotrys oligospora, A. musiformis, A. thaumasia, A. mangrovispora*	Fungi are generally absent in sediments ≥4 m. Terrestrial environments typically show higher richness than mangrove/ aquatic habitats.	Hao *et al*., (2005); Swe *et al*., (2009).
Disturbed & Urban Soils	Contaminated environments (e.g., municipal waste, heavy metals).	*Drechslerella bronchopaga, Arthrobotrys thaumasia, Arthrobotrys* sp.	Positive correlation observed between NTF diversity and lead (Pb) concentrations in polluted soils.	Mo *et al*., (2006); Hastuti *et al.*, (2023)

2.2 Seasonal and Geographical Distribution

The distribution and abundance of nematode-trapping fungi (NTF) are influenced by seasonal variations, with temperature playing a critical role. Fluctuations in seasonal temperature not only affect the physical and chemical properties of the soil but also directly affect two key ecological factors, viz., organic matter decomposition and soil moisture retention, which are essential for the survival, growth, and trap formation of NTF, as they support microbial activity and provide a conducive environment for fungal development. A study by Singh *et al.*, (2015), conducted in Varanasi, India, observed that nematode-trapping fungi peaked in January, when cooler temperatures and higher moisture levels prevailed, and declined significantly by May, the peak of the Indian summer. This reduction in fungal occurrence during the summer is attributed to decreased soil moisture and accelerated decomposition of organic matter due to elevated temperatures. In apple and grape orchards in China, Zuoqing & Xingzhong (2003) observed peak fungal abundance in late spring and early summer, with *Drechslerella dactyloides*, *Arthrobotrys oligospora*, *A. conoides*, and *Stylopage* sp. as dominant species. Su *et al.*, (2007) found that fungal diversity in plateau cattle faeces was highest during summer and declined with increasing

altitude. Similarly, Saumell & Padilha, (2000) reported NTF presence mainly during dry and early rainy seasons in Brazilian cattle and heifer faeces. In Sweden, nematode-trapping fungal populations peaked during late summer and autumn in the rhizospheres of barley, pea, and white mustard crops (Persmark *et al*., 1996). The study of Kerry & Hammrick,(2002) also found the NTF population peak in similar seasons.

Global distribution studies on NTF reveal active research in various regions, including Canada (Mahoney & Strongman, 1994), China (Liu & Zhang, 1994; Su *et al*., 2011; Zhang *et al*., 2022; Deng *et al*., 2023), Taiwan (Kuo *et al*., 2020), Cuba (Hidalgo-Diaz *et al*., 2000), Brazil (Vilela *et al*., 2012), Ethiopia (Berhanu *et al*., 2022), Kenya (Wachira *et al.,* 2015), Europe (Boag & Lopez-Llorca, 1989), India (Saxena & Mukerji, 1991; Singh *et al*., 2015; Kassam *et al*., 2021), Latin America (Rubner, 1994), and South Africa (Durand *et al*., 2005).

Table 2. Predatory strategies and trap characteristics of nematophagous fungi

Ecological strategy	**Trap type**	**Mode of action**	**Adaptation**	**Habitat preference**	**Efficiency**	**Known Genera/ Species and References**
Active trapping	Constricting rings	Rapid swelling of ring cells	Rapid response to motile prey	Moist-organic-rich soils	Very high	*Arthrobotrys dactyloides* Nordbring-Hertz *et al.,* (2011)
Passive Adhesion	Adhesive Networks	Sticky 3D hyphae entangle nematodes	Effective in diverse soil environments	Loamy soils, leaf litter	High	*Arthrobotrys oligospora* Ahman *et al.,* (2002); Yang *et al*., (2007a)
Localized Adhesion	Adhesive Knobs	Sticky knobs trap nematode cuticle	Economical use of fungal resources	Decaying plant debris	Moderate	*Monacrosporium gephyropagum* Tunlid & Ahman, (2003)
Columnar Adhesion	Adhesive Columns	Tall, stacked cells with sticky tops	Efficient in semi-aquatic conditions	Flood-prone soils	Moderate	*Monacrosporium thaumasium* Barron, (1977); Gray *et al.*, (1999)
Morpho-logical Traps	Endo-parasitic Spores	Spores attach and penetrate directly	Seen in aquatic or high-density areas	Aquatic sediments	Low–High	*Haptoglossa* spp., *Harposporium* spp. Dijksterhuis *et al.,* (1991)
No Physical Trap (Parasitic)	Endo-parasitism	Spores attach and penetrate directly	Seen in aquatic or high-density areas	Aquatic sediments	Low–High	*Haptoglossa* spp., *Harposporium* spp. Dijksterhuis *et al.,* (1991)

3. Evolution of Carnivorism

The evolution of carnivory in fungi represents a compelling example of adaptive innovation driven by nutrient limitation and ecological opportunity. Unlike higher plants, where carnivory is mostly associated with adaptation to nutrient-poor soils, carnivory in fungi primarily evolved as a response to nitrogen limitation in terrestrial ecosystems (Thorn & Barron, 1984, Wang *et al*., 2014; Kuo *et al.,* 2020; Zhang *et al*., 2023). When the carbon-to-nitrogen (C: N) ratio is very high, nematode-trapping fungi tend to adopt a saprophytic lifestyle. However, under nitrogen-limited and carbon-rich conditions, they switch to a parasitic mode of life (Singh *et al*., 2015). Carnivorous fungi have independently evolved multiple times across different fungal lineages, including Ascomycota, Basidiomycota, Chytridiomycota, and even Oomycota, indicating that carnivory is a case of convergent evolution (Yang *et al.*, 2012; Yang *et al.,* 2020).

3.1 Evolutionary Timeline and Divergence

Reconstructing the evolution of carnivory in fungi has been challenging due to the scarcity of fossils. However, the molecular clock methodology has facilitated precise estimation of the divergent time using known fossil records (Berbee & Taylor, 2010).

Molecular phylogenetic studies based on ribosomal and protein-coding genes have consistently shown that carnivorous fungi form monophyletic groups, with the majority of nematode-trapping fungi evolving within the order *Orbiliales* (*Ascomycota*) (Yang *et al*., 2012; Zhang *et al*., 2014a). Yang *et al.,* (2012) conducted a landmark study using phylogenies based on five protein-encoding genes from 16 carnivorous Ascomycota species. Their molecular clock analyses, calibrated using two fossil records, revealed that fungal carnivory in the *Ascomycota* diverged from saprophytism approximately 419 Mya-well after nematodes themselves first appeared around ~550–600 Mya. This temporal gap implies that nematodes were already established prey before fungi evolved the capacity to exploit them. This divergence may have coincided with changing environmental conditions following the Devonian period.

Subsequently, a major split occurred between fungi with active mechanical traps (constricting rings) and fungi with passive adhesive traps (adhesive networks, knobs, branches) around 246 Mya, shortly after the Permian–Triassic extinction event, which drastically altered global ecosystems (Yang *et al.,* 2012; Zhang *et al.*, 2020c). Adhesive traps, such as adhesive networks and knobs, evolved through a series of modifications, including the elongation of adhesive stalks and the proliferation of adhesive structures (Jiang *et al.*, 2017). Interestingly, different trapping mechanisms appear to have evolved independently within various fungal groups. Adhesive traps, such as networks and knobs, are considered ancestral because they are simpler and energetically less costly to produce (Li *et al.,* 2005; Yang *et al.,* 2007a). Constricting rings, which are

mechanically more complex and energetically expensive to form, are regarded as a more derived trait that evolved later to capture faster or more resistant nematodes (Barron, 1977; Nordbring-Hertz *et al*., 2011).

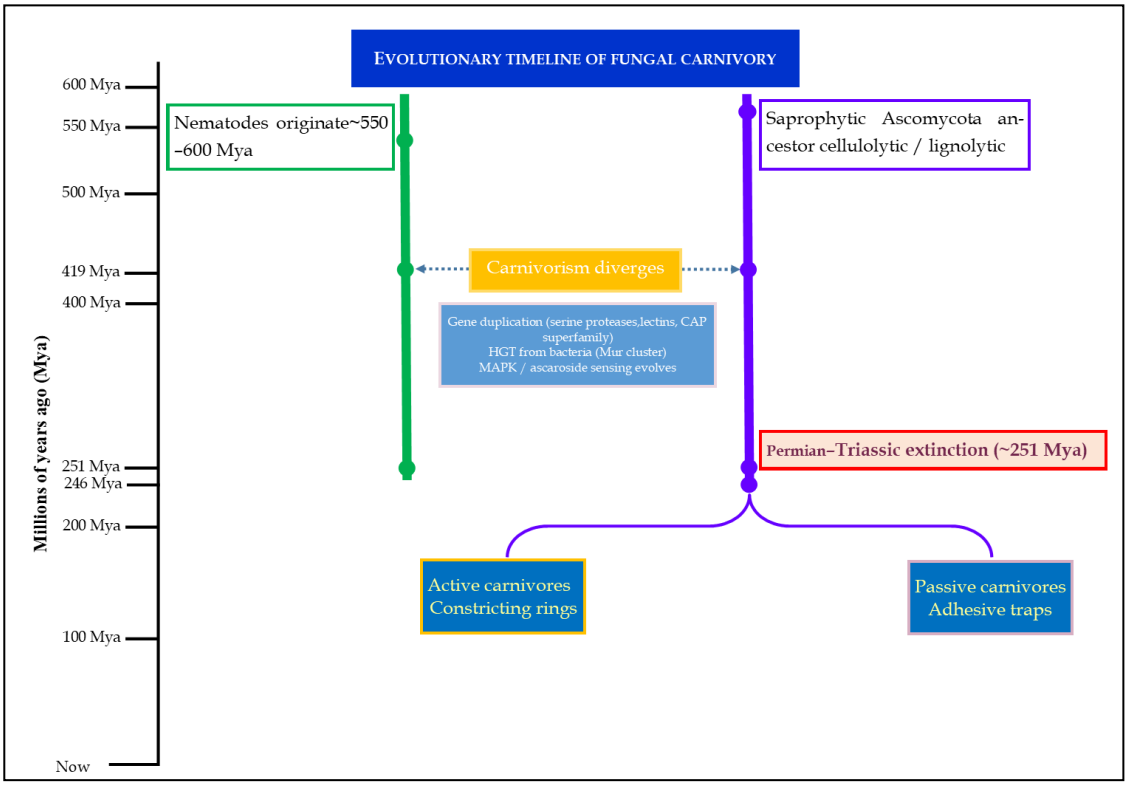

Figure 1. Evolutionary timeline of fungal carnivory

3.2 Molecular mechanisms of the evolution of carnivory

Early studies on the transition from a saprophytic to a predatory lifestyle in carnivorous fungi were highly focused on morphological observation, physiological assays, and classical genetics. A major shift in our understanding occurred with the application of high-throughput sequencing to NTF model organism. The genomic era for nematode-trapping fungi began with the sequencing of *A. oligospora* by Yang *et al.*, in 2011. Since then, the application of genomics, transcriptomics, and proteomics across species with varied trap structures has enabled researchers to compare and uncover the shared and lineage-specific traits driving fungal carnivory.

The molecular evolution of fungal carnivory has been increasingly clarified through comparative omics research. These studies propose two main evolutionary pathways: first, the acquisition of novel genes through duplication; and second, the altered regulation of existing genes, demonstrated by distinct orthologous gene expression profiles between carnivorous fungi and

their saprophytic relatives (Meerupati *et al*., 2013; Andersson *et al*., 2014). NTFs exhibit significant expansions in gene families encoding hydrolytic enzymes like subtilisin-like serine proteases, chitinases, and collagenases, which are critical for nematode digestion (Yang *et al*., 2011; Zhang *et al.*, 2020c). A comparative analysis against 10 other ascomycete genomes (both pathogenic and non-pathogenic) revealed that *A. oligospora* shares significantly more genes with pathogenic than with non-pathogenic fungi and also harboured 398 homologous genes from the pathogen-host interaction (Yang *et al.,* 2011). One of the most striking features of the *A. oligospora* genome is its high proportion of orphan genes-sequences absent from other sequenced fungi (53.64%), consistent with the phylogenetic divergence of *Orbiliomycetes* from other sequenced Ascomycota (Yang *et al*., 2011). These species-specific genes likely reflect the complex, multifaceted lifestyles of *A. oligospora* as a saprophyte, nematode pathogen, mycoparasite, and plant root colonizer (Yang *et al*., 2011; Nordbring-Hertz *et al*., 2011). The proteomics study by Yang *et al*., (2011) also revealed that 90 genes were significantly upregulated during the early stage of trap formation (10 hours after nematode extract treatment), with most involved in translation, amino acid metabolism, carbohydrate metabolism, and cell wall and membrane biogenesis. Notably, surface adhesion genes have expanded in nematode-trapping fungi, enhancing the adhesive properties of traps and improving predatory efficiency (Yang *et al.,* 2020). Additionally, studies have shown that nematophagous fungi can sense small nematode-secreted molecules called ascarosides, triggering trap formation. According to Hsueh *et al.,* (2013), ascarosides are an evolutionarily ancient and highly conserved family of small signaling molecules constitutively secreted by multiple nematode species. These molecules act as nematode-associated molecular patterns (NAMPs), which NTF recognize to initiate trap formation. These molecules function as communication signals within nematode populations (pheromones), and predatory fungi appear to have evolved the capacity to eavesdrop on this inter-nematode chemical communication. Triggered solely by nutrient starvation, this ascaroside-induced morphogenesis is a conserved response across closely related nematophagous fungal species (Hsueh *et al*., 2013). This means that fungi switch to predation only to scarcity of nutrient sources to avoid the metabolic costs of trap construction. The evolutionary analogy with microbe-associated molecular patterns (MAMPs) recognized by plant and animal immune systems suggests convergent evolution of molecular pattern recognition across biological kingdoms.

The prey recognition system highlights the high level of molecular specialization involved in fungal carnivory (Jiang *et al*., 2017). The study by Liu *et al*. (2014a) showcases that *Drechslerella stenobrocha* (a constricting-ring-forming NTF) has eight gene expression clusters associated with trap formation and pathogenesis. Analyses of *Monacrosporium haptotylum*, a knob-forming nematode-trapping fungus, compared with the genome of *A. oligospora* revealed that the expansion of protein domain families and the emergence of large numbers of species-

specific genes are indicative of gene duplication events followed by functional diversification (Andersson *et al*., 2014). Compared to non-pathogenic ascomycetes, A. oligospora possesses an enriched repertoire of duplicated genes encoding adhesive proteins, subtilisin-class serine proteases, cellulases, cellobiohydrolases, and pectinesterases (Yang *et al*., 2011). Carnivorism-associated gene expansions identified in comprehensive multi-genome analyses include those encoding adhesive proteins of the CAP (Cysteine-rich secretory proteins, Antigen 5, and pathogenesis-related proteins) superfamily, eukaryotic aspartyl proteases, and serine-type peptidases (Fan *et al*., 2025). The broad involvement of CAP superfamily proteins in cross-kingdom host-pathogen interactions suggests that NTF evolved their predatory lifestyle by repurposing existing molecular frameworks associated with pathogenesis.

A recently characterized molecular innovation in NTF is the acquisition of bacterial genes via horizontal gene transfer (HGT). Fan *et al*. (2025) identified that NTFs have acquired the Mur gene cluster, a set of enzymes typically involved in the synthesis of peptidoglycan in bacterial cell walls, through HGT. Disruption of MurE, a gene within this cluster, significantly reduces nematode attraction in NTF, highlighting the critical role of bacteria-derived metabolic pathways in prey sensing and luring. Additionally, HGT-acquired Hyl genes, encoding a virulence factor in animal hosts, have been incorporated into the NTF genome, potentially contributing to nematocidal activity. These findings highlight that inter-kingdom gene flow has contributed meaningfully to the molecular toolkit for fungal carnivory. Furthermore, evolutionary studies suggest that strains intrinsically more efficient at sensing nematodes and forming traps demonstrated higher fitness, and genomic studies showed these highly predatory strains formed distinct evolutionary clades (Yang *et al.,* 2020). Despite morphological diversity, all traps share certain structural features, including abundant dense bodies (specialized peroxisome-like organelles involved in adhesion and energy supply) and extensive extracellular polymers that enhance nematode adhesion (Yang *et al.,* 2020).

4. Mechanism of Carnivorism

The majority of nematode-trapping fungi inhabit the soil rhizosphere zone. These fungi often employ a sophisticated, step-by-step mechanism to infect nematodes that attack plant roots, including attraction, adhesion, penetration, and nutrient digestion and storage. As most NTF function as generalist predators, direct host specificity has not been widely observed among nematode-trapping species. However, the endoparasite *Dactylellina coniospora* shows some host preference (Nordbring-Hertz *et al.,* 2011).

By secreting specific chemoattractants, NTF manipulate nematode behaviour, luring the prey directly toward the fungal network. For instance, *Arthrobotrys superba* attracts second-stage juveniles (J2) of *Meloidogyne* species by producing specific secondary metabolites, such as

lectins (Robinson & Jaffee, 1996). In an interaction study involving *A. oligospora* and nematodes, a fungal lectin with specificity for GalNAc (N-acetyl-D-galactosamine) bound to receptors on the nematode surface (Nordbring-Hertz & Mattiasson, 1979). Other studies similarly emphasize the importance of lectins in mediating host-parasite recognition (Rosenzweig & Ackroyd, 1983; Nordbring-Hertz& Chet, 1986).

Interestingly, Balogh & Rosén, (2003) demonstrated that deleting the lectin-encoding gene in *A. oligospora* did not eliminate recognition ability, suggesting the presence of compensatory molecular mechanisms. This indicates that both attraction and recognition rely on a complex interplay of multiple molecules, rather than a single mediating factor. The parasitic nature of the fungus also influences the strength of nematode attraction, where more parasitic fungi typically exhibit stronger attraction signals than their saprophytic counterparts (Nordbring-Hertz *et al*., 2011). A study by Wang *et al.,* (2023) highlighted that all the metabolites produced by nematode-trapping fungi (NTFs) to attract nematodes are small organic, fat-soluble molecules (Hsueh *et al.,* 2017; Wang *et al.,* 2018), which can more easily pass through the nematode's cell membrane, triggering an odor-stimulated behavioural response (Simons *et al*., 2004). This study also found that most attractant compounds, such as methyl 3-methyl-2-butenoate, 2-heptanone, 1-pentanol, and 2-cyclohexylethanol, are fat-soluble and facilitate efficient chemosensory communication with nematodes. Interestingly, certain compounds exhibit concentration-dependent effects; for instance, diacetyl and isoamyl alcohol attract nematodes at low concentrations but repel them at higher levels. In contrast, a few molecules, such as benzoate and butyric acid, are hydrophilic yet still effective in influencing nematode behaviour. Some sulphur- and nitrogen-containing compounds, such as 4-chlorobenzyl mercaptan, benzyl mercaptan, and dimethylthiazole, also act as strong attractants.

From an evolutionary perspective, NTF's ability to respond to nematode-secreted, highly conserved chemical signal molecules, such as ascarosides, further suggests coevolution between predator and prey. This attraction response is typically triggered under nutrient-deprived conditions, indicating an adaptive strategy that links environmental stress to predatory behaviour (Hsueh *et al.*, 2013). The molecular basis of predation involving G-protein signaling for ascaroside sensing and/or trap formation in *A. oligospora* likely involves GPCRs (G protein-coupled receptors) as ascaroside receptors (Yang *et al*., 2022; Kuo *et al.,* 2024). The study by Chou *et al.,* (2001) demonstrated that in *A. oligospora*, the MAPK signaling pathway help, to recognize the nematode.

Following the initial attraction, adhesion represents an important step in the infection process, securing the nematode to the fungal structure. In *Arthrobotrys oligospora*, adhesive three-dimensional hyphal nets are surrounded by extracellular fibrils even before contact with nematodes. Upon contact, these fibrils reorient perpendicularly to the nematode surface,

anchoring the prey and facilitating fungal invasion (Nordbring-Hertz *et al*., 2011; Yang *et al.,* 2020). In contrast, the endoparasitic fungus *Drechmeria coniospora* constitutively produces radiating fibrils on its spores, which specifically adhere to the sensory organs at the nematode's anterior end. This adhesion impairs nematode mobility and interferes with its ability to respond to external stimuli or locate other fungal species (Nordbring-Hertz *et al*., 2011). Distinct adhesion strategies are observed across fungal phyla. In Zygomycota, fungi use adhesive hyphae or hyphal protuberances to capture small invertebrates, whereas members of the Basidiomycota deploy specialized adhesive knobs or sticky spores to capture prey (Yang *et al*., 2012). Among the *Orbiliomycetes* (*Ascomycota*), members of *Monacrosporium* and *Drechslerella* construct vertically aligned, glue-coated adhesive columns designed for efficient nematode entrapment (Yang *et al*., 2020).

Upon successful adhesion, nematophagous fungi initiate penetration into the nematode cuticle. Extracellular enzymes play an important role in this process by disrupting the nematode's outer cell layer. This involves the formation of a penetration tube (in the case of *A. oligospora*) or a penetration peg, often combined with mechanical pressure and enzymatic activity (Mostafanezhad *et al*., 2014; Jiang *et al*., 2017; de Freitas *et al*., 2018). Key enzymes involved include subtilisin-like serine proteases and chymotrypsin-like proteases, chitinases, and collagenases, which degrade the protein-rich cuticle (Bonants *et al.*, 1995; Åhman *et al.,* 1996; Wang *et al.,* 2006; Yang *et al*., 2013). Serine proteases are a class of enzymes that catalyze the hydrolysis of peptide bonds via a highly reactive serine residue in their active sites (Schultz 2025; Siezen *et al*., 1997). Alkaline serine proteases are highly effective enzymes that degrade nematode cuticles within a few hours, thereby impairing the mobility of species such as *Panagrellus redivivus* (Yang *et al*., 2005). In contrast, neutral serine proteases produced by *Arthrobotrys oligospora* have been directly associated with its pathogenic activity against various nematodes (Minglian *et al.,* 2004). This fungus has demonstrated strong biocontrol potential in the laboratory against both *Haemonchus contortus* and *Caenorhabditis elegans* (Junwei *et al.,* 2013; Yang *et al*., 2022). *Monacrosporium thaumasium* produces high concentrations of serine proteases that exert destructive effects on the eggs of *Meloidogyne javanica*, contributing to its nematicidal efficacy (de Souza Gouveia *et al*., 2017).

Similarly, specific nematophagous fungi deploy chitinases to target the chitin structurally integral to plant-parasitic nematodes and their eggshells. The nematode-trapping fungus *M. thaumasium* produces chitinases and exhibits nematicidal activity against the nematode *Panagrellus redivivus* (de Freitas Soares *et al.,* 2014). These chitinases facilitate penetration of the eggshell and the initiation of infection. Notably, one of the earliest characterized chitinases, termed Chi43, was isolated from two nematode-parasitizing fungal species, *Planktothrix rubescens* and *Pochonia chlamydosporia* (Tikhonov *et al.,* 2002). In *A. oligospora*, subtilisin

protease PII not only assists in penetration and digestion but also exhibits nematotoxic properties (Åhman *et al.*, 2002). After breaching the cuticle, the fungus proceeds to digest the nematode internally. In *A. oligospora*, the penetration tube swells to form an infection bulb inside the nematode, followed by the growth of trophic hyphae (Nordbring-Hertz *et al.,* 2011). These structures maintain an active metabolism, possess a dense endoplasmic reticulum, and store assimilated nutrients within accumulated lipid droplets. Additionally, during the infection process, *A. oligospora* produces *Arthrobotrys oligospora* lectin (AOL). This protein initially accumulates within the trophic hyphae before being redistributed to fuel growth throughout the rest of the mycelial network (Rosen *et al*., 1997). The AOL lectin binds to glycan structures typical of animal glycoproteins, but absent in fungi, suggesting a role in the recognition and internal colonization of nematode prey. Following penetration, the nematode is digested by the invading fungi, which obtain nutrients for their growth and reproduction (Schmidt *et al.,* 2007*;* Yang *et al.,* 2007b).

4.1 Types of Traps

Nematode-trapping fungi have been classified into four types based on their mechanisms of action against nematode prey. These categories include: 1. Nematode-trapping fungi utilizing morphological hyphal traps (adhesive or mechanical); 2. Endoparasitic fungi employing their spores; 3. Egg-parasitic fungi that attack nematode eggs; and 4. Toxin-generating fungi that immobilize nematodes prior to invasion (see Table 2) (Nordbring-Hertz *et al.,* 2011; Moosavi & Zare, 2012; Zhang & Hyde, 2014; Zhang *et al.*, 2020a; Rahman *et al.,* 2023).The diversity of trapping strategies across these four categories reflects extensive adaptive radiation in the nematophagous lifestyle. Comparative analyses integrating trap morphology, predation mechanisms, and fungal genera reveal that different trapping strategies are associated with distinct levels of efficiency and target specificity (see Figure 2). The Alluvial diagram (Figure 2b) further demonstrates that trap type, predation mechanism, and capture efficiency are interconnected traits distributed across multiple genera in a non-linear fashion, suggesting convergent evolution.

4.1.1 Nematode-Trapping Fungi Using Morphological Hyphal Traps

Among the nematode-trapping fungi, the vegetative hyphae can produce diverse trapping devices. In Ascomycota, these traps are often sophisticated and can be either active or passive. The active mechanical traps include constricting rings, while passive traps encompass five types: sessile adhesive knobs, stalked adhesive knobs, adhesive nets, adhesive columns, and non-constricting rings (Nordbring-Hertz *et al*., 2011; Yang *et al*., 2012; Jiang *et al.,* 2017).

4.1.1.1 Constricting Rings

Constricting rings are composed of three circularly arranged hyphal cells. These three curved hyphal cells form a loop, typically elevated above the substrate by a short stalk. The outer diameter of these rings ranges from 20 to 40 µm, accommodating nematode sizes from 20 to 40 µm (Poinar, 1988; Su *et al*., 2015). Upon contact with a nematode, the constricting ring encircles the nematode with the inner edge of the trap and rapidly closes. The nematode is strangled by the inward swelling resulting from the expansion of an internally located cell wall within the ring cells. This rapid swelling is driven by water influx, leading to an increase in the volume of the cells forming the ring (Heintz & Prame, 1972). As shown in Figure 2a, constricting rings represent the very high efficiency category among all trap types, reflecting the speed and mechanical certainty of this active immobilization mechanism.

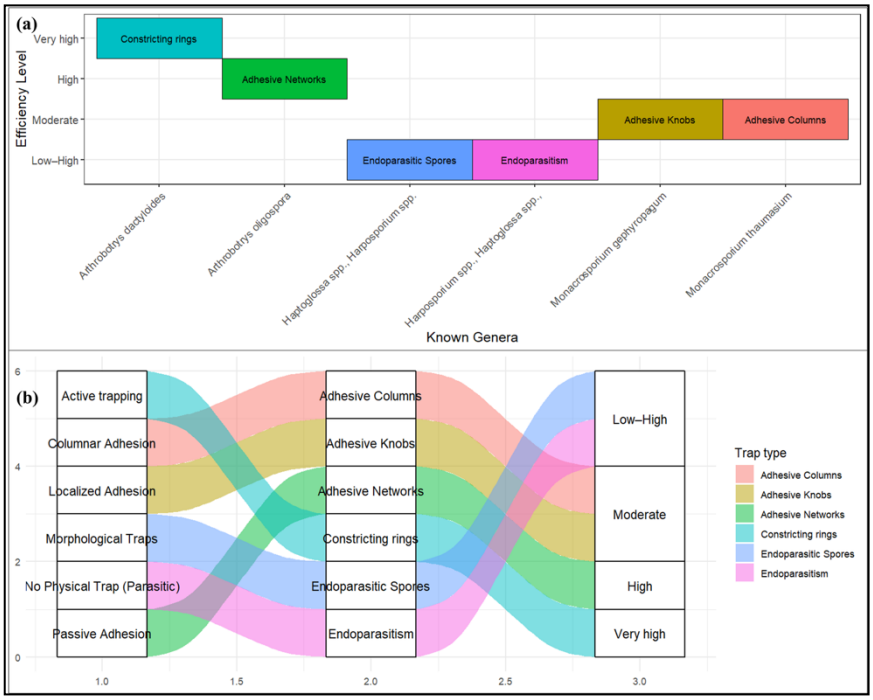

Figure 2. Trap efficiency and predation strategy across nematophagous fungal genera. (a) Bar chart depicting the efficiency levels of different trapping mechanisms across known genera. Constricting rings (*Arthrobotrys dactyloides*) exhibit very high efficiency; Adhesive Networks (*Arthrobotrys oligospora*) rank at high efficiency; Adhesive Knobs (*Monacrosporium gephyropagum*) and Adhesive Columns (*Monacrosporium thaumasium*) display moderate efficiency; while Endoparasitic Spores (*Haptoglossa* spp., *Harposporium* spp.) exhibit low to high efficiency depending on host and conditions. (b) Alluvial (Sankey) diagram showing the relationships between predation mechanism category (left), trap type (centre), and efficiency level (right), illustrating that mechanistically distinct predation strategies can converge on similar efficiency outcomes and that a single genus may employ multiple trap types with different efficiencies.

Environmental factors, particularly humidity, significantly influence the efficiency of ring closure. Higher ambient humidity levels correlate with increased ring closure frequency, indicating the importance of water availability for the trap's functionality (Moore *et al.*, 2011). Interestingly, even after detachment from the parent hypha, constricting rings can retain their trapping capability, suggesting they can absorb moisture directly from the surrounding environment or from the thin water layer enveloping nematodes (Su *et al*., 2015). Moreover, the activation of constricting rings can be chemically induced. Exposure to certain alcohols, such as methanol, ethanol, propanol, or butanol, as well as to chlorobutanol vapor, has been shown to trigger ring closure within 10 to 15 seconds. Conversely, substances like benzene, ether, and chloroform do not elicit this response, indicating specificity in the chemical sensitivity of the trap mechanism (Higgins & Pramer, 1967).

Kriegler *et al.,* (2025) demonstrated in *Arthrobotrys flagrans* that cell-end marker proteins (CEMPs)-specifically TeaA and TeaC-are essential for the curved hyphal growth required to form closed ring structures. Deletion of either teaA or teaC results in linear adhesive sticks rather than closed rings, while deletion of teaR reduces ring diameter but does not prevent closure.

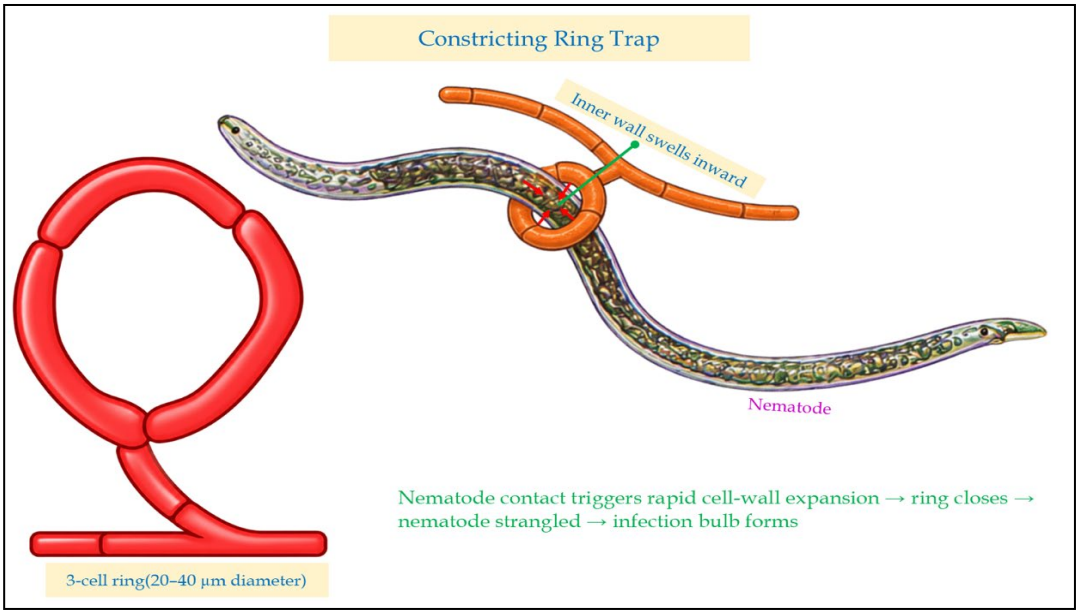

Figure 3. Constricting ring trap of nematode-trapping fungi. The three-celled constricting ring (20–40 µm in diameter) that rapidly closes upon nematode contact due to inward swelling of the inner cell walls. This mechanical response leads to immediate entrapment and strangulation of the nematode, followed by penetration and formation of an infection bulb for subsequent digestion. **Adapted from Pires et al. (2022), Pathogens, 11, 1178, licensed under CC BY 4.0. Modified from the original.**

These findings establish that the unique cellular polarity machinery in NTF has been specifically repurposed to enable the three-dimensional morphogenesis required for ring trap construction. *Drechslerella daliensis* and *D. xiaguanensis* are characterized by the production of constricting rings to capture nematodes (Liou & Tzean, 1997; Pfister, 1997; Åhrén *et al*., 1998; Scholler *et al.* 1999; Li *et al.,* 2005; Zhang & Hyde, 2014).

4.1.1.2 Adhesive Columns

Adhesive branches or columns are morphologically simpler than other types of nematode-trapping structures. These formations consist of one to three cells that fuse via anastomosis, forming adhesive loops or mesh-like networks that appear as flat, crochet-like, or linear patterns. When a nematode contact these branches, it is rapidly attached by a fine layer of adhesive covering the structure. The proximity of the branches often leads to further entanglement of nematodes in surrounding sticky hyphae, making escape more difficult. A notable species in having such adhesive branches is *Dactylella cionopaga* (Poinar, 1988). This trapping mechanism is also characteristic of *Monacrosporium cionopagum* and *M. gephyrophagum* (Saxena, 2018). For example, *M. cionopagum* produces adhesive branches that capture and immobilize the sugar beet cyst nematode *Heterodera schachtii* (Andersson *et al*., 2014).

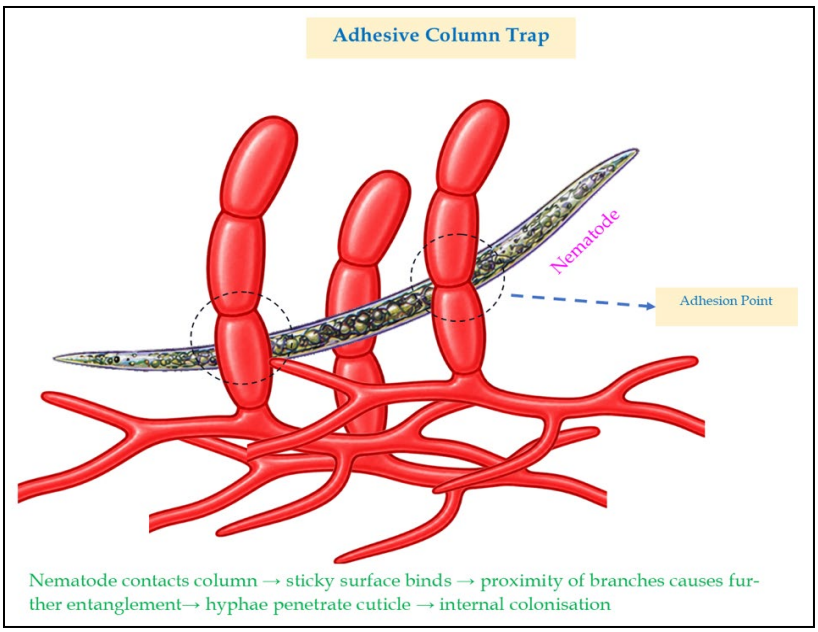

Figure 4. Adhesive column trap of nematode-trapping fungi. The multicellular adhesive columns arising from hyphal networks that capture nematodes through a sticky surface. Upon contact, the nematode adheres to the column, and surrounding hyphal branches enhance entanglement. This is followed by cuticle penetration and internal colonization of the host.

The predatory efficiency of adhesive columns is constrained by the contact surface area available per adhesive structure, which is comparatively limited compared to three-dimensional adhesive networks.

4.1.1.3 Adhesive Hyphal Network

Adhesive networks, commonly found in various fungi, consist of upright lateral branches that originate from vegetative hyphae and extend approximately 20–25 µm from the main hyphal structure (Nordbring-Hertz *et al.,* 1989). These networks exhibit greater longevity than standard hyphae (Veenhuis *et al.,* 1985) and form through the development of complex three-dimensional structures. The fungus *Arthrobotrys oligospora,* which has a worldwide distribution, is the most frequently encountered species associated with this type of trapping mechanism (Niu & Zhang, 2011) and represents the dominant representative of the high-efficiency category for passive adhesive traps (Figure 2a).

Adhesive nets are initiated when a single lateral branch curves and may later reconnect with the parent hypha. They are considered an evolutionary advancement from simpler adhesive branches. As the network develops, additional lateral hyphae emerge from the parent hypha, or loops form that can further branch into new loops, resulting in a dense, multidirectional array of interconnected loops. The surface of these networks is coated with a fine adhesive layer that attracts and captures nematodes upon contact (Martinelli *et al.,* 2010). The trap-enriched proteins (TEPs)-particularly the DUF3129 domain-containing family-are now known to be critically enriched on adhesive network surfaces and are essential for nematode adhesion, as demonstrated by Lin *et al*., (2023) through gene deletion experiments.

Jia *et al.*, (2024) further demonstrated that temperature has a significant influence on the efficiency of adhesive network formation. In *Arthrobotrys cladodes*, *A. conoides*, and *A. robusta*, trap formation area and nematocidal efficiency both increased and then decreased with rising temperature, and serine protease genes involved in autophagy were identified as key molecular mediators linking temperature to trap morphology and predatory efficacy.

4.1.1.4 Adhesive Knobs

Adhesive knobs are specialized fungal cells coated with a thin adhesive layer. When a nematode contacts these spherical knobs, the limited surface area of adhesion gives it a chance to resist and potentially escape. However, if the nematode touches a broader, flatter adhesive pad, the fungus gains an advantage by increasing contact area, resulting in a stronger grip and more effective entrapment. This enhanced attachment facilitates fungal penetration through a combination of enzymatic activity and mechanical force. For instance, the fungus produces collagenase, an enzyme that helps break down the nematode's cuticle, while the firm, adhesive pad provides

structural support, enabling the invading hyphae to pierce the nematode's body (Poinar 1988). Following successful penetration, a spherical infection bulb forms, from which assimilative hyphae emerge to consume the nematode's internal contents (Barron, 1977; Gray, 1988). Species such as *Dactylellina arcuata*, *D. asthenopaga*, *D. leptosphora*, *D. copepodii*, and *D. ellipsospora* utilize adhesive knobs to capture and infect nematodes (Li *et al*., 2005; Xie *et al*., 2010; Wu *et al.*, 2012b).

4.1.1.5 Non-Constricting Rings

Non-constricting rings are specialized three-celled structures that develop on short supporting stalks arising from prostrate, septate hyphae. During predation, nematodes exhibit passive behavioural responses upon entering these rings. The junction between the ring and its supporting stalk is relatively weak. As a result, when a nematode attempts to escape, the ring often detaches and remains tightly encircling the nematode's body. This phenomenon suggests that the fungus may facilitate the nematode's movement while still attached to the ring, potentially enhancing the fungus's dispersal throughout the soil environment (Soares *et al.*, 2015). For instance, fungi such as *Dactylaria candida* and *D. lysipaga*, known to produce non-constricting rings, also form adhesive knobs and capture nematodes using these ring structures (Drechsler, 1937; Li *et al.*, 2005; Wu *et al*., 2012b). A similar trapping mechanism has been reported in *Dactylellina daliensis*, which also employs non-constricting rings for nematode capture (Su *et al*., 2008).

The non-constricting ring represents an evolutionary intermediate between adhesive traps and the mechanically active constricting ring. Unlike constricting rings, non-constricting rings do not expand upon prey contact; instead, they rely on the structural trap formed by the ring geometry itself in combination with adhesive properties of the inner ring surfaces. This architectural simplicity may confer lower energetic costs compared to constricting rings, while providing a degree of size-selective filtration of prey not easily achieved by adhesive knob or network traps.

4.2 Egg- and Female-Parasitic Fungi

These fungi employ a variety of infection structures, including appressoria (in *Purpureocillium* spp. and *Pochonia* spp.), zoospores (*Nematophthora gynophila*), lateral mycelial branches, and penetration pegs, to infect eggs, females, and other developmental stages of plant-parasitic nematodes (Lopez-Llorca *et al*., 2008). *In vitro* studies evaluating the parasitic activity of 10 *Pochonia chlamydosporia* isolates against *Globodera pallida* eggs reported pathogenicity levels ranging from 34% to 49%. Notably, *P. chlamydosporia* was more effective at parasitizing immature eggs than those containing second-stage juveniles, often triggering spontaneous hatching (Vieira Dos Santos *et al*., 2019). Furthermore, both the wild-type *Beauveria bassiana* strain 08F04 and its transformant G10 significantly reduced the population of cereal cyst

nematode females in plant roots (Zhang *et al.* 2020d). In a separate greenhouse study, inoculation with the arbuscular mycorrhizal fungus (*Glomus etunicatum*) led to a 28.21% reduction in *Heterodera glycines* (soybean cyst nematode) females in root systems compared to untreated controls. This suggests that *G. etunicatum* may enhance host plant resistance or tolerance to soybean cyst nematode infestation (Benedetti *et al.* 2021).

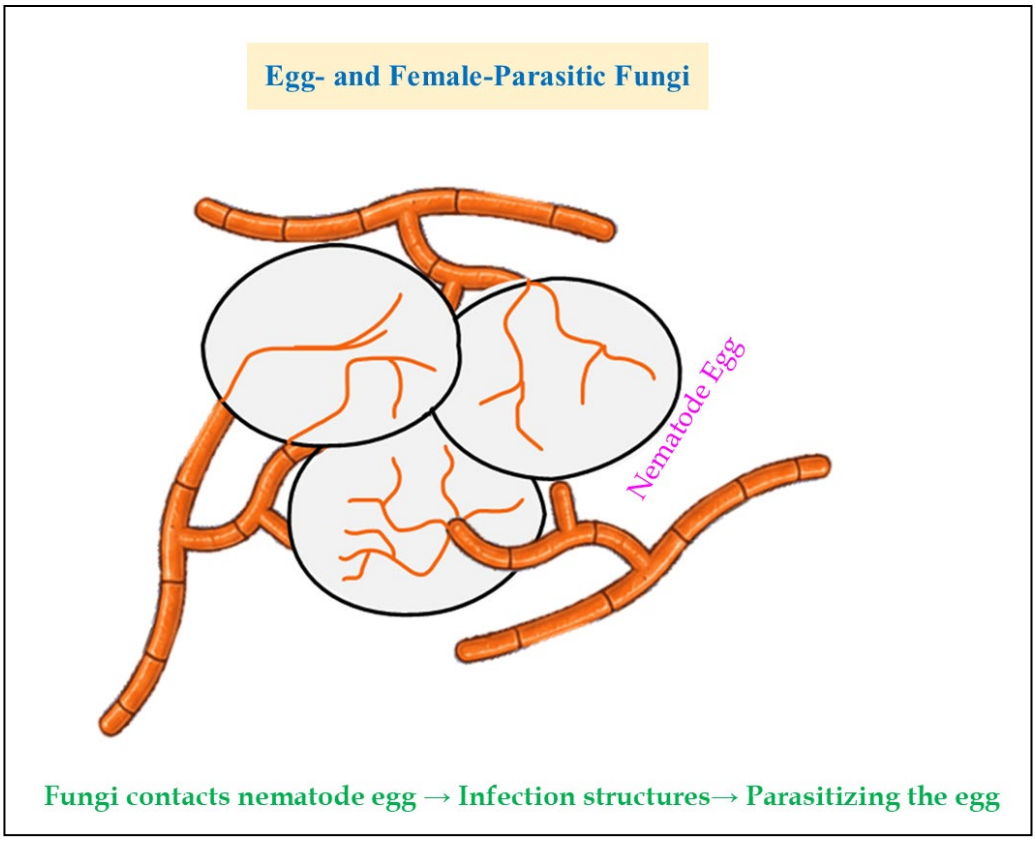

Figure 5. Egg and female-parasitic fungi infecting nematodes. Fungal hyphae in contact with nematode eggs, forming specialized infection structures that penetrate the eggshell. **Adapted from Pires et al. (2022), Pathogens, 11, 1178, licensed under CC BY 4.0. Modified from the original.**

4.3 Endoparasitic Fungi

Endoparasitic nematophagous fungi represent a group that infects nematodes through spore production. These spores initiate infection either by being ingested by the nematodes or by adhering to their epidermis (Dijksterhuis *et al.*, 1991; Tunlid *et al.,* 1992; Liu *et al*., 2009). These fungi show considerable diversity in their infection strategies, particularly in the number of conidia produced per infected nematode. For instance, *Drechmeria coniospora* can generate up

to 10,000 conidia from a single hyphal structure, whereas *Harposporium rhossoliensis* produces a relatively lower number, ranging between 100 and 1,000 conidia per nematode. Once the conidia germinate, assimilative hyphae penetrate the host cuticle and consume the nematode's internal contents, facilitating complete colonization. Among these fungi, *D. coniospora* is recognized as a highly aggressive endoparasite with strong nematode-infecting capacity. The *D. coniospora* YMF1.01759 strain, in particular, demonstrated effective nematode suppression by inhibiting egg hatching, infecting the nematodes with spores, and producing bioactive metabolites that ultimately led to nematode mortality (Nordbring-Hertz *et al.,* 2011; Wan *et al.,* 2021).

4.4 Toxin Production

Some nematophagous fungi produce toxins that not only kill nematodes but also influence plant defence and resistance responses against parasitic nematodes (Sarker *et al.,* 2020; Comans-Pérez *et al*., 2021; Girardi *et al.,* 2022). These toxin-producing fungi belong to diverse taxonomic groups across multiple orders and families. Rather than relying solely on direct physical interaction, these fungi often immobilize nematodes by secreting inhibitory metabolites (Lopez-Llorca *et al.*, 2008). Once immobilized, the fungal hyphae then penetrate the nematode cuticle.

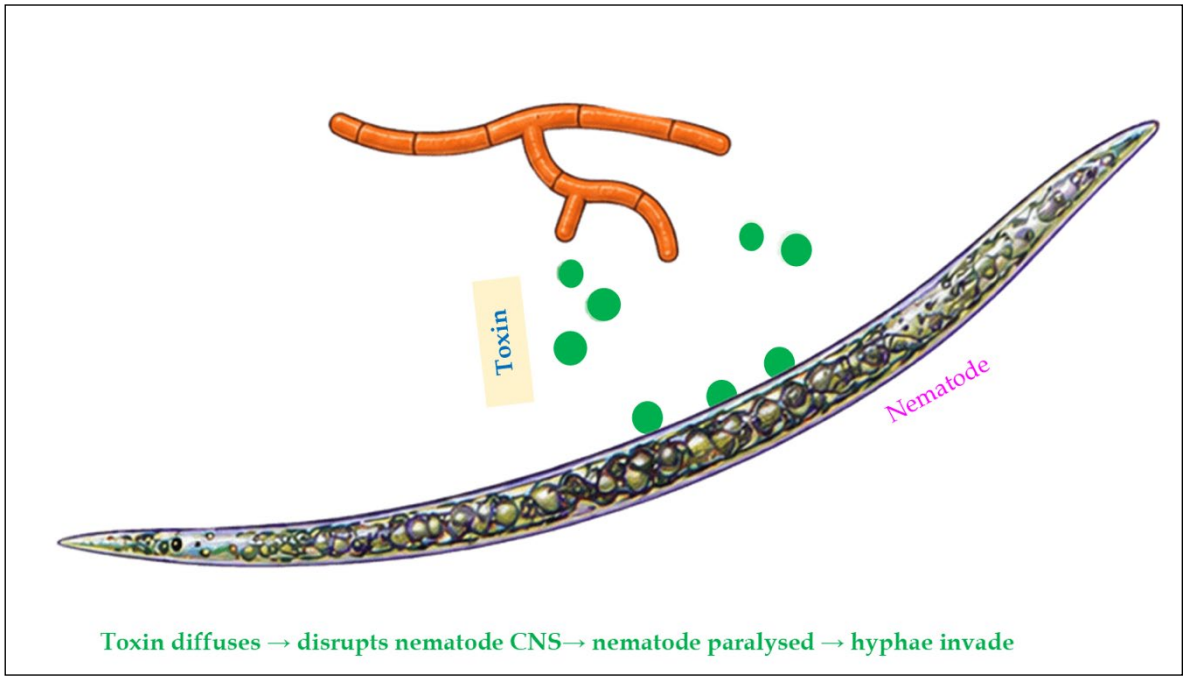

Figure 6. Toxin-mediated immobilization of nematodes by nematophagous fungi. The fungal hyphae release diffusible toxins that affect the nematode. **Adapted from Pires et al. (2022), Pathogens, 11, 1178, licensed under CC BY 4.0. Modified from the original**.

Culture filtrates of such fungi have been shown to contain potent proteolytic and chitinolytic enzymes, as well as low-molecular-weight metabolites and specific non-volatile oil-based compounds. These biochemical agents can either induce larval mortality or prevent egg hatching by disrupting embryonic development and altering egg morphology (Westphal & Becker, 2001). In addition to enzymes, certain fungi secrete toxic compounds that paralyze nematodes before they are digested and absorbed by fungal structures (Satou *et al*., 2008).

Basidiomycetes are among the most prominent fungal groups known for their toxin production. Studies on *Coprinus comatus* and *Stropharia rugosoannulata* have demonstrated that the modes of action of their nematotoxic compounds are complex and varied (Luo *et al*., 2006). Among the Basidiomycetes, several species of *Pleurotus* are particularly well-known for producing nematotoxic substances. For example, *Pleurotus ostreatus* synthesizes trans-2-decenoic acid, a linoleic acid derivative that exhibits toxic effects not only on nematodes but also on insects and other fungi (Satou *et al.,* 2008).

5. Use of the Carnivorous Fungi

Over 4000 species of plant-parasitic nematodes have been identified as significant threats to agricultural and horticultural crops, capable of causing severe yield reductions. These plant parasites cause an estimated USD 120-125 billion in losses annually in agriculture and related crops (Rahman *et al.,* 2023; Yesayan *et al*., 2024).

The chemical and toxic substances employed against these pathogens pose a serious threat to human health and the environment (Degenkolb & Vilcinskas, 2016). The detrimental effects of nematicidal chemicals have led to bans by the US Environmental Protection Agency (EPA) and/or the European Commission (Chitwood, 2003; Degenkolb & Vilcinskas, 2016). Products such as the systemic organothiophosphate fosthiazate (Nemathorin 10 G®) and the dithiocarbamate dazomet (Basamid®), used as nematicides, have demonstrated toxic effects on birds and aquatic organisms. In humans, dazomet is a lachrymator and a topical and respiratory irritant, potentially causing respiratory edema (Degenkolb & Vilcinskas, 2016).

Therefore, biological control agents hold significant promise for managing nematode infections due to their environmentally friendly and economically sustainable nature (Braga *et al.*, 2013; Singh *et al.,* 2012). NTF, which attract and actively feed on plant-pathogenic nematodes, can potentially reduce nematode populations and minimize the impact of these pathogens on crops. NTF have a history of use as biocontrol agents against these nematodes (Cooke, 1962; Duponnois *et al.,* 2001; Degenkolb & Vilcinskas*,* 2016; Vidal-Diez de Ulzurrun & Hsueh, 2018; Zhang *et al.*, 2020a). Biological control of nematodes using nematophagous fungi can generally be implemented through two main strategies: introducing large quantities of fungal inoculum

into the soil or enhancing the activity of native fungal populations via soil amendments. Initial research focused on nematode-trapping fungi, such as *Arthrobotrys* and *Monacrosporium* species. Over time, the focus expanded to include other functional groups, including endoparasitic fungi such as *Harposporium rhossoliensis* and *Drechmeria coniospora*, as well as egg-parasitic fungi such as *Pochonia chlamydosporia*. However, the effectiveness of these biocontrol agents has been inconsistent, and to date, commercially viable products have not been widely developed or adopted (Nordbring-Hertz *et al.,* 2011; Rahman *et al.,* 2023). Increased knowledge in the last decade regarding nematodes, nematode-trapping fungi, and the rhizosphere has led to increased and improved applications of NTF. For example, genetically modified mutants of the nematode-trapping fungus, *A. oligospora* overexpressing a protease gene (*PII*) produced more infection structures and captured and killed nematodes more quickly (Åhman *et al.,* 2002). A study by Fa *et al.,* (2024) highlighted that the addition of low concentrations of urea significantly accelerated the formation of trapping structures and enhanced their yield in nematode-trapping fungi (NTF). This finding suggests that even modest amendments of nitrogen-rich compounds can positively influence the parasitic capabilities of these fungi. Importantly, the study emphasizes that effective nematode capture is not limited to genetically modified NTF strains; conventional organic or inorganic fertilizers, such as urea, can also stimulate trap production and enhance nematode suppression.

5.1 Agricultural Applications

Nematophagous fungi have been evaluated against all major plant-parasitic nematodes (PPNs) and have demonstrated significant reductions in nematode populations. *Arthrobotrys oligospora* and *A. dactyloides*, delivered in alginate granule formulations, have shown significant reductions in root-knot nematode populations (Rahman *et al*., 2024). A study by Nordbring-Hertz *et al*., (2011) also demonstrated that *A. dactyloides* can reduce root-knot nematode infection in tomatoes, establishing this species as a candidate for horticultural biocontrol applications. *Pochonia chlamydosporia* has been identified as a biological control agent for root-knot nematodes, particularly *Meloidogyne* spp. (Bourne *et al.*,1996). *Arthrobotrys* spp. are also known to prey on free-living nematodes such as *Panagrellus* spp. under in vitro conditions, confirming their broad nematophagous capacity (Gomes *et al*., 2001). *Dactylellina haptotyla*, a trapping species employing adhesive knobs and non-constricting loops, has been documented to capture *M. incognita* second-stage juveniles (J2s) under laboratory conditions (Lei *et al*., 2023). More recently, *Dactylellina phymatopaga* has been evaluated specifically against *Meloidogyne graminicola* on rice (*Oryza sativa,* L.), demonstrating significant biological control efficacy and establishing the potential utility of NTF in flooded agroecosystems where chemical nematicide application is particularly problematic (Kumar, 2024).

Bourne *et al.*, (1996) established the foundational evidence base for *Pochonia chlamydosporia* as a biological control agent for root-knot nematodes, particularly *Meloidogyne* spp., in early laboratory and glasshouse trials. Subsequent research by Ayaz *et al.,* (2024) confirmed egg and female parasitism efficacy of 34-49% against *Globodera pallida* in vitro and significantly reduced *M. incognita* infection rates and female reproductive output in tomato by 32-43% in greenhouse studies, implicating both the secretion of serine proteases and the chitinolytic disruption of eggshell integrity as mechanisms of parasitism. *Purpureocillium lilacinum* (formerly *Paecilomyces lilacinus*) is a cosmopolitan soil fungus with demonstrated efficacy against multiple developmental stages of *M. javanica*, *M. incognita*, *M. arenaria*, and *M. hapla*, as well as against immature cysts of *Heterodera avenae* and *Radopholus similis* (Khan *et al.,* 2006; Khan & Tanaka*,* 2023; Sharma *et al*., 2020). It is a member of the family *Ophiocordycipitaceae* (*Ascomycota*: *Hypocreales*) and functions primarily as an egg parasite, penetrating eggshells via enzymatic and mechanical means. It is particularly effective against *M. incognita* in both soil and root substrates, and its efficacy is enhanced when combined with plant growth-promoting bacteria such as *Pseudomonas fluorescens* or *Serratia marcescens* in consortium applications (Khan & Tanaka, 2023). Commercial formulations of *P. lilacinum* are registered for use in several countries under trade names including BioAct® and MeloCon® WG. Manzanilla-Lopez *et al*., (2013) documented that *P. chlamydosporia* acts as a semi-endoparasite capable of effectively controlling nematodes from the genera *Globodera*, *Heterodera*, *Meloidogyne*, *Nacobbus*, and *Rotylenchulus*-a remarkably broad spectrum of sedentary PPN genera that underscores its versatility as a biocontrol agent. *Trichoderma harzianum*, primarily recognized as an antagonist of soil-borne fungal pathogens, has also demonstrated potential against *M. javanica* by reducing egg mass production and gall formation in infected root systems, with the biocontrol mechanism involving both direct mycoparasitism of nematode eggs and indirect induction of systemic resistance in the host plant (Sharon *et al*., 2001; Heidari & Olia, 2006; Sahebani & Hadavi, 2008).

Hirsutella rhossiliensis, an endoparasitic fungus in the family *Ophiocordycipitaceae*, has demonstrated efficacy against the soybean cyst nematode *Heterodera glycines*, a major constraint on soybean (*Glycine max*) production across North America, China, and Brazil, by attaching conidia to the nematode cuticle and invading the body, ultimately causing mortality (Chen & Liu, 2005). *Nematophthora gynophila*, a member of the Lagenidiaceous group (*Oomycota*), has demonstrated potential to reduce populations of cereal cyst nematodes, including *Heterodera avenae* on wheat and *Heterodera schachtii* on sugar beet, acting as a zoosporic pathogen of females during the exposed portion of their life cycle (Kerry & Crump, 1980). Similarly, Lagenidiaceous fungi more broadly are known to attack cyst nematode females, particularly *Heterodera* spp., representing an Oomycete complement to the predominantly Ascomycete NF biocontrol toolkit (Kerry & Crump, 1980).

In Armenian agricultural soils, native isolates of *Orbilia oligospora* (syn. *A. oligospora*) and *Orbilia brochopaga* demonstrated superior nematocidal enzyme activity against *Globodera rostochiensis* (potato cyst nematode) compared to commercially available trade biopesticide preparations- a result the authors attributed to the strain-specific adaptation of endemic isolates to locally prevalent nematode populations and soil conditions (Yesayan *et al.,* 2024). This finding has important implications for biocontrol programme design, suggesting that region-specific strain selection based on local isolate screening may outperform the application of generic commercial strains, particularly in areas with distinct edaphic or climatic characteristics.

Members of the genus *Esteya* specifically target the pinewood nematode (*Bursaphelenchus xylophilus*), a major cause of pine wilt disease (Pires *et al.* 2022). Members of the *Pleurotus* genus are known to control a wide range of nematodes, including *Poikilolaimus oxycercus*, *Caenorhabditis elegans*, *Pristionchus aerivorus*, *P. redivivus*, and *Acrobeloides amurensis* (Marlin *et al.*, 2019). *Verticillium lecanii* culture filtrates have demonstrated toxicity against various developmental stages of *H. glycines* (Shinya *et al*., 2008).

5.2 Veterinary Applications

Animal-parasitic nematodes cause significant health issues and weight loss in livestock, and traditional anthelmintic treatments are increasingly ineffective due to resistance. A promising alternative involves feeding animals fungal spores (e.g., *Duddingtonia flagrans*), due to its ability to produce large numbers of heat-resistant chlamydospores that survive gastrointestinal transit without losing predatory activity, germinate within faeces, and form adhesive trapping networks that capture L3 larvae like *Haemonchus contortus*, *Ostertagia ostertagi*, *Cooperia* spp., and *Trichostrongylus* spp., reducing field contamination (Mendoza-de-Gives *et al.*, 2022; Hao *et al.*, 2024). Also, genetic studies show that *D. flagrans* is largely clonal, with a low recombination rate, making it a safe biological control agent. Additionally, nematophagous fungi are being explored for their potential to produce new nematicidal compounds (Åhrén *et al.,* 2004).

The commercial product BioWorma® (containing *D. flagrans NCIMB 30336*) has demonstrated efficacy in reducing pasture larval contamination in multiple livestock species across several countries, representing the most advanced commercial implementation of carnivorous fungal biocontrol to date (Mendoza-de-Gives *et al*., 2022). Bioverm® (containing *D. flagrans* isolate *AC001* at 10^5 chlamydospores per gram) is registered in Brazil for use in goats, sheep, and cattle (Hao *et al*., 2024). Similarly, a lyophilised *D. flagrans* preparation evaluated in Tibetan sheep in China demonstrated an 89.8% larval reduction rate when administered alone, rising to near 100% larval reduction when combined with ivermectin or albendazole within 72 hours of administration (Hao *et al.,* 2024).

6. Challenges in the Applications

Despite the numerous applications of nematode-trapping fungi (NTF), several practical challenges limit their effectiveness. The performance of these biological control agents often varies under field conditions, as they require specific environmental factors for optimal functioning. Additionally, many species exhibit a limited host range and a high degree of specialization toward particular nematode species. These constraints significantly restrict the large-scale commercial applicability of NTF as biocontrol agents (Zhang *et al*., 2014a; Singh *et al.*, 2015; Rahman *et al*., 2023).

6.1. Laboratory-to-Field Efficacy

Most biocontrol studies are conducted under controlled laboratory or greenhouse conditions, in which nematode-trapping fungi (NTF) routinely achieve larval reduction rates of 70–99% at relatively low spore densities. However, their efficacy under field conditions is typically lower, more variable, and highly context-dependent (Rahman *et al.,* 2024). This discrepancy primarily arises from the complexity of natural soil or faecal environments, which introduce factors such as competitive microbiota, fluctuating moisture gradients, physicochemical stressors, and spatial heterogeneity—conditions that are largely absent or minimized in artificial laboratory systems.

6.2 Temperature and Seasonal Variability

Temperature is one of the most critical environmental regulators of predatory activity in nematode-trapping fungi (NTF). The optimal range for peak activity generally lies between 20 and 27 °C; deviations from this range can significantly reduce their efficiency. *Arthrobotrys* species exhibit a temperature-dependent response, as demonstrated by Jia *et al.*, (2024), who reported that both trap formation area and nematocidal efficiency increased up to an optimum and subsequently declined with further temperature fluctuations. Similarly, the predatory activity of *Duddingtonia flagrans* against cattle nematodes varies markedly across seasons, with peak performance observed under warm, moist conditions and minimal activity during colder winter months. This seasonal variability presents a significant challenge for programmes aiming to maintain consistent larval suppression on pasture throughout the grazing period (Mendoza-de-Gives *et al.,* 2022).

6.3 Mass Production and Scale-Up

Large-scale production of NTF chlamydospores remains a major bottleneck. Optimised solid-state media (e.g., enriched Sabouraud agar) can significantly enhance spore yield while maintaining biological activity (Southwell *et al.,* 2025). Although submerged fermentation allows scalable production, it often yields lower chlamydospore densities, and prolonged

cultivation reduces spore viability (Wang *et al.,* 2024). Formulation parameters, including excipient ratios, are also critical for ensuring product stability and integrity (Hao *et al*., 2024).

Another challenge in scaling up spore production is developing effective carrier and delivery systems. Various delivery strategies have been explored for nematode-trapping fungi (NTF). Sodium alginate pellets are widely used, as they provide protection during gastrointestinal transit and form the basis of commercial products such as Bioverm®. Freeze-dried formulations enable precise dosing and facilitate integration with anthelmintics, thereby improving efficacy. Alternative carriers, such as rice bran and soy protein matrices, support spore survival and enable controlled release. Emerging approaches, such as nanoparticle-based formulations, show promise but require further validation for large-scale application (Mendoza-de-Gives *et al.,* 2022; Fonseca *et al.,* 2025).

Table 3. Summary of formulation types for carnivorous fungal biocontrol products.

Formulation type	Key species	Advantages	Limitations	Reference
Sodium alginate pellets	*D. flagrans*	GI transit survival; well-validated; commercially available	Requires cold storage; short field shelf life	Hao *et al.,* (2024)
Lyophilised tablet/capsule	*D. flagrans*	Precise dosing; combinable with anthelmintics; stable storage	Production cost; tablet integrity challenges	Hao *et al.,* (2024)
Rice bran pellets	*D. flagrans*	Nutritive substrate; simple production; low cost	Variable spore release; limited to swine/cattle	Mendoza-de-Gives *et al.* (2022)
Alginate granules (soil)	*A. oligospora, A. dactyloides*	Soil delivery; mycrocosm efficacy demonstrated	Poor field-level efficacy in pots; not yet field-validated	Rahman *et al.,* (2024)
Nanoparticle biosynthesis	*D. flagrans (AgNPs)*	Ovicidal activity; novel MOA; nanotechnology integration	Scale-up viability uncertain; regulatory pathway unclears	Fonseca *et al*., (2025)

7. Conclusion and Way Forward

This review synthesizes evidence that fungal carnivory is a convergent, ecologically adaptive trait that has evolved independently in *Ascomycota*, *Basidiomycota*, *Chytridiomycota*, *Oomycota*, and *Zygomycota* for efficient nutrient acquisition. Molecular clock analyses place the divergence

of nematode-trapping *Orbiliomycetes* from saprophytism at approximately 419 Mya, with the subsequent split between active mechanical traps and passive adhesive structures occurring around 246 Mya. This has led to a wide range of specialized predation strategies targeting microfaunal organisms, particularly nematodes and amoebae, which form a crucial link in soil food webs. By regulating nematode populations, especially in the rhizosphere, nematophagous fungi can influence nutrient cycling and indirectly affect plant health through complex belowground interactions. Phylogenetic and genomic studies have revealed key points of divergence in the evolution of various trapping mechanisms, suggesting adaptive diversification shaped by environmental pressures. The predatory transition has been substantiated by gene family expansions in hydrolytic enzymes, neofunctionalization of CAP-superfamily adhesins, and inter-kingdom horizontal acquisition of bacterial Mur and Hyl gene clusters that mediate prey attraction and nematocidal activity. Ascaroside-triggered trap induction—operative specifically under nutrient deprivation and mediated via GPCR-linked signaling—mirrors pattern-recognition immunity in metazoans, establishing NTF as a compelling model for studying convergent molecular evolution across biological kingdoms. Despite this mechanistic richness, several critical knowledge gaps remain unresolved. The functional roles of the majority of NTF-specific orphan genes (representing over 53% of the *A. oligospora* genome) are unknown, and comparative multi-omic data for endoparasitic and egg-parasitic lineages—which constitute the bulk of NTF functional diversity—remain sparse relative to the nematode-trapping Orbiliomycetes. The molecular basis of host sensing and trap induction outside the *Orbiliomycetes* is essentially uncharacterized. These gaps constrain both mechanistic understanding and the rational design of improved biocontrol strains.

The growing demand for sustainable agricultural solutions, especially in light of significant crop losses caused by plant-parasitic nematodes and the negative impacts of chemical nematicides on ecosystems and human health, has brought carnivorous fungi into focus as promising biocontrol agents. The *Arthrobotrys oligospora*, *Pochonia chlamydosporia*, *Purpureocillium lilacinum*, and *Duddingtonia flagrans* have collectively demonstrated suppression of *Meloidogyne*, *Heterodera*, *Globodera*, and key gastrointestinal nematode genera under controlled conditions, and commercial products BioWorma® and Bioverm® confirm that field deployment and regulatory approval are achievable. Although fungal species have shown strong nematicidal activity in laboratory and controlled environments, their consistent success in real-world field conditions remains limited. This is due to challenges, including fluctuating environmental conditions, limited host range, and difficulties in producing, formulating, and delivering fungal inoculum at large scale.

Future studies must take an integrated and multidisciplinary approach to overcome these challenges, which include: (a) improving cultivation and formulation methods to increase fungal

viability, persistence, and activity in the field (b) investigating the molecular processes involved in host detection, trap development, penetration, and digestion, using transcriptomics and proteomics to identify important genetic traits for strain selection or improvement (c) studying the ecological interactions between introduced fungi and native soil organisms, including possible cooperation or competition with other beneficial microbes and assessing any unintended effects (d) isolating and characterizing bioactive compounds produced by these fungi, with a view to developing them into direct-use products or as models for safer, bio-based nematicides and (e) exploring the biology and biocontrol potential of less-studied groups such as endoparasitic and egg-parasitic fungi, which may offer more targeted approaches to disrupting nematode life cycles. A deeper understanding of the ecological roles and molecular mechanisms underlying fungal carnivory is essential for developing reliable, environmentally friendly nematode management strategies in agriculture.

References

Ahman, J., Ek, B., Rask, L., & Tunlid, A. (1996). Sequence analysis and regulation of a gene encoding a cuticle-degrading serine protease from the nematophagous fungus *Arthrobotrys oligospora*. *Microbiology* 142(7), 1605–1616. https://doi.org/10.1099/13500872-142-7-1605

Ahman, J., Johansson, T., Olsson, M., Punt, P. J., van den Hondel, C. A., & Tunlid, A. (2002). Improving the pathogenicity of a nematode-trapping fungus by genetic engineering of a subtilisin with nematotoxic activity. *Applied and Environmental Microbiology*, *68*(7), 3408-3415. https://doi.org/10.1128/AEM.68.7.3408-3415.2002

Åhrén, D., Faedo, M., Rajashekar, B., & Tunlid, A. (2004). Low genetic diversity among isolates of the nematode-trapping fungus *Duddingtonia flagrans*: Evidence for recent worldwide dispersion from a single common ancestor. *Mycological Research*, *108*(10), 1205-1214. https://doi.org/10.1017/s0953756204000942

Åhrén, D., Ursing, B. M., & Tunlid, A. (1998). Phylogeny of nematode-trapping fungi based on 18S rDNA sequences. *FEMS Microbiology Letters*, *158*(2), 179-184. https://doi.org/10.1111/j.1574-6968.1998.tb12817.x

Andersson, K.M., Kumar, D., Bentzer, J., Friman, E., Ahrén, D., & Tunlid, A. (2014). Interspecific and host-related gene expression patterns in nematode-trapping fungi. *BMC Genomics*, *15*(1), 968. https://doi.org/10.1186/1471-2164-15-968

Ayaz, M., Zhao, J. T., Zhao, W., Chi, Y. K., Ali, Q., Ali, F., Khan, A. R., Yu, Q., Yu, J. W., Wu, W. C., Qi, R. D., & Huang, W. K. (2024). Biocontrol of plant parasitic nematodes by bacteria and fungi: A multi-omics approach for the exploration of novel nematicides in sustainable agriculture. *Frontiers in Microbiology*, 15, 1433716. https://doi.org/10.3389/fmicb.2024.1433716

Baheti, B. L., Dodwadiya, M., Rathore, B. S., and Bhati, S. S. (2015). Bioagents: An effective and ecofriendly option for the management of maize cyst nematode, Heterodera zeae on sweet corn (*Zea mays* L. *saccharata*). *Journal of Biopesticide*, 8, 141–146. https://doi.org/10.57182/jbiopestic.8.2.141-146

Balbino, H. M., de Souza Gouveia, A., Monteiro, T. S. A., Morgan, T., & de Freitas, L. G. (2022). Overview of the nematophagous fungus *Duddingtonia flagrans*. *Biocontrol Science and Technology*, *32*(8), 911-929. https://doi.org/10.1080/09583157.2022.2094891

Balogh, J., Tunlid, A., & Rosén, S. (2003). Deletion of a lectin gene does not affect the phenotype of the nematode-trapping fungus *Arthrobotrys oligospora*. *Fungal Genetics and Biology*, *39*(2), 128-135. https://doi.org/10.1016 /S1087-1845(03)00023-9

Barron, G. L. (1977). *The nematode-destroying fungi* Canadian Biological Publications.

Bava, R., Castagna, F., Piras, C., Musolino, V., Lupia, C., Palma, E., Britti D, & Musella, V. (2022). Entomopathogenic fungi for pests and predators control in beekeeping. *Veterinary Sciences*, *9*(2), 95. https://doi.org/10.3390/vetsci9020095

Benedetti, T., Antoniolli, Z. I., Sordi, E., Carvalho, I. R., & Bortoluzzi, E. C. (2021). Use of the *Glomus etunicatum* as biocontrol agent of the soybean cyst nematode. *Research, Society and Development*, *10*(6), e7310615132. https://doi.org/10.33448/rsd-v10i6.15132

Berbee, M.L., & Taylor, J.W. (2010). Dating the molecular clock in fungi – how close are we? *Fungal Biology Reviews*, 24, 1-16. https://doi.org/10.1016/j.fbr.2010.03.001

Berhanu, M., Waktole, H., Mamo, G., & Terefe, G. (2022). Isolation of nematophagous fungi from soil samples collected from three different agro-ecologies of Ethiopia. *BMC Microbiology*, *22*(1), 159. https://doi.org/10.1186/s12866-022-02572-4

Bernard, G. C., Egnin, M., & Bonsi, C. (2017). The impact of plant-parasitic nematodes on agriculture and methods of control. In Shah, M. M. & Mahamood, M. (Eds.), Nematology: Concepts, characteristics and control (p. 121). InTech. https://doi.org/10.5772/intechopen.68958

Boag, B., & Lopez-Llorca, L.V. (1989). Nematodes and nematophagous fungi associated with cereal fields and permanent pasture in Eastern Scotland. *Crop Research* (Edinburgh), *29*, 1–10 https://doi.org/10.1111/j.1744-7348.1990.tb04226.x

Bonants, P. J., Fitters, P. F., Thijs, H., Belder, E. D., Waalwijk, C., & Henfling, J. W. D. (1995). A basic serine protease from *Paecilomyces lilacinus* with biological activity against *Meloidogyne hapla* eggs. *Microbiology*, *141*(4), 775-784. https://doi.org/10.1099/13500872-141-4-775

Bongers, T., & Bongers, M. (1998). Functional diversity of nematodes. *Applied Soil Ecology*, *10*(3), 239-251. https://doi.org/10.1016/S0929-1393(98)00123-1

Bontempo, A. F., Fernandes, R. H., Lopes, J., Freitas, L. G., and Lopes, E. A. (2014). *Pochonia chlamydosporia* controls Meloidogyne incognita on carrot. *Australas. Plant Pathol*. 43, 421–424. https://doi.org/10.1007/s13313-014-0283-x

Bordallo, J. J., Lopez-Llorca, L. V., Jansson, H. B., Salinas, J., Persmark, L., & Asensio, L. (2002). Colonization of plant roots by egg-parasitic and nematode-trapping fungi. *The New phytologist, 154(2)*, 491–499. https://doi.org/10.1046/j.1469-8137.2002.00399.x

Bourne, J. M., Kerry, B. R., & De Leij, F. A. A. M. (1996). The importance of the host plant on the interaction between root-knot nematodes Meloidogyne spp. and the nematophagous fungus, *Verticillium chlamydosporium* Goddard. *Biocontrol Science and Technology*, *6*(4), 539-548. https://doi.org/10.1080/09583159631172

Braga, F. R., Araújo, J. V., Soares, F. E. F., Araujo, J. M., Tavela, A. D. O., de Carvalho, L. M., ... & Queiroz, J. H. (2013). Interaction of the nematophagous fungus *Duddingtonia flagrans* on *Amblyomma cajannense* engorged females and enzymatic characterisation of its chitinase. *Biocontrol Science and Technology*, *23*(5), 584-594. https://doi.org/10.1080/09583157.2013.789481

Cai, K. Z., Liu, J. L., Liu, W., Wang, B. B., Xu, Q., Sun, L. J., Chen, M. Y., Zhao, M. W., Wu, J. Y., Li, X. S., Yang, J., Wei, S., Chen, C. R., Ma, Z. R., Xu, C. L., Wang, F., Hu, Q. L., Fang, W. X., Zheng, T. H., Wang, Y. Y., … Liu, Y. Q. (2016). Screening of different sample types associated with sheep and cattle for the presence of nematophagous fungi in China. *Journal of basic microbiology*, 56(3), 214–228. https://doi.org/10.1002/jobm.201500281

Chen, S., & Liu, X. (2005). Control of the soybean cyst nematode by the fungi *Hirsutella rhossiliensis* and *Hirsutella minnesotensis* in greenhouse studies. *Biological Control*, *32*(2), 208-219. https://doi.org/10.1016/j.biocontrol.2004.09.013

Chitwood, D. J. (2003). Nematicides. In: J. R. Plimmer (Eds.), *Encyclopedia of agrochemicals* (*Vol. 3*, pp. 1104–1115). John Wiley & Sons.

Colagiero, M., Pocasangre, L., Ciancio, A., Pentimone, I., & Rosso, L.C. (2025). Farming System and Nematodes Affect the Rhizosphere Microbiome of Tropical Banana Plants. *Environmental microbiology reports*, *17*(4), e70155. https://doi.org/10.1111/1758-2229.70155

Comans-Pérez, R. J., Sánchez, J. E., Al-Ani, L. K. T., González-Cortázar, M., Castañeda-Ramírez, G. S., Mendoza-de Gives, P., Sánchez-García, A.D., Millán-Orozco, J., & Aguilar-Marcelino, L. (2021). Biological control of sheep nematode *Haemonchus contortus* using edible mushrooms. *Biological Control*, *152*, 104420.https://doi.org/10.1016/j.biocontrol.2020.104420

Cooke, R. C. (1962). The ecology of nematode-trapping fungi in the soil. *Annals of Applied Biology*, *50*(3), 507-513.https://doi.org/10.1111/j.1744-7348.1962.tb06045.x

de Almeida, G. L., Santurio, J. M., Filho, J. O. J., Zanette, R. A., Camillo, G., Flores, A. G., da Silva, J.H.S., & de la Rue, M. L. (2012). Predatory activity of the fungus *Duddingtonia flagrans* in equine strongyle infective larvae on natural pasture in the Southern Region of Brazil. *Parasitology Research*, *110*(2), 657-662. https://doi.org/10.1007/s00436-011-2537-7

de Freitas Soares, F. E., de Queiróz, J. H., Braga, F. R., de Oliveira Tavela, A., Araújo, J. M., da Fonseca, L. A., de Souza Gouveia A, & de Araújo, J. V. (2014). Action of the nematophagous fungus *Pochonia chlamydosporia* on *Dioctophyma renale* eggs. *Biocontrol Science and Technology*, *24*(4), 399-406. https://doi.org/10.1080/09583157.2013.863828

de Freitas Soares, F. E., Sufiate, B. L., & de Queiroz, J. H. (2018). Nematophagous fungi: Far beyond the endoparasite, predator and ovicidal groups. *Agriculture and Natural Resources*, *52*(1), 1-8. https://doi.org/10.1016/j.anres.2018.05.010

de Souza Gouveia, A., de Freitas Soares, F. E., Morgan, T., Sufiate, B. L., Tavares, G. P., Braga, F. R., Monteiro, T.S.A., Geniêr, H.L.A., de Freitas, L.,G., & de Queiroz, J.H. (2017). Enhanced production of *Monacrosporium thaumasium* protease and destruction action on

root-knot nematode *Meloidogyne javanica* eggs. *Rhizosphere*, *3,* 13-15. https://doi.org/10.1016/j.rhisph.2016.12.001

Degenkolb, T., & Vilcinskas, A. (2016). Metabolites from nematophagous fungi and nematicidal natural products from fungi as an alternative for biological control. Part I: metabolites from nematophagous ascomycetes. *Applied Microbiology and Biotechnology*, *100*(9), 3799-3812. https://doi.org/10.1007/s00253-015-7233-6

Deng, W., Zhang, F., Li, Y. P., Zhang, X., Fornacca, D., Yang, X. Y., & Xiao, W. (2023). Uncovering the biogeographic pattern of the widespread nematode-trapping fungi *Arthrobotrys oligospora*: watershed is the key. *Frontiers in Microbiology*, *14*, 1152751. https://doi.org/10.3389/fmicb.2023.1152751.

Dijksterhuis, J., Harder, W., Wyss, U., & Veenhuis, M. (1991). Colonization and digestion of nematodes by the endoparasitic nematophagous fungus *Drechmeria coniospora*. *Mycological Research*, *95*(7), 873-878. https://doi.org/10.1016/S0953-7562(09)80052-X

Drechsler, C. (1937) Some hyphomycetes that prey on free-living terricolous nematodes. *Mycologia, 29*,447–552. https://doi.org/10.1080/00275514.1937.12017222

Duponnois, R., Chotte, J., Sall, S., & Cadet, P. (2001). The effects of organic amendments on the interactions between a nematophagous fungus *Arthrobotrys oligospora* and the root-knot nematode *Meloidogyne mayaguensis* parasitizing tomato plants. *Biology and Fertility of Soils*, *34*(1), 1-6. https://doi.org/10.1007/s003740100344

Durand, D.T., Boshoff, H.M., Michael, L.M., & Krecek, R. C. (2005). Survey of nematophagous fungi in South Africa: research communication. *Onderstepoort Journal of Veterinary Research*, *72*(2), 185-187. https://doi.org/10.4102/ojvr.v72i2.217

Fa, Z., Shuaiyi, H., Boonmee, S., Wen, X., & Xiaoyan, Y. (2024). Urea regulates soil nematode population by enhancing the nematode-trapping ability of nematode-trapping fungi. *Scientific Reports*, *14*(1), 14296.https://doi.org/10.1038/s41598-024-65167-1

Falbo, M.K., Soccol, V. T., Sandini, I. E., Vicente, V. A., Robl, D., & Soccol, C. R. (2013). Isolation and characterization of the nematophagous fungus *Arthrobotrys conoides*. *Parasitology Research*, *112*(1), 177-185. https://doi.org/10.1007/s00436-012-3123-3

Fan, Y., Du, M., Zhang, W., Deng, W., Yang, E., Wang, S., Yan, L., Zhang, L., Kang, S., Steenwyk, J. L., An, Z., Liu, X., & Xiang, M. (2025). The genomes of nematode-trapping fungi provide insights into the origin and diversification of fungal carnivorism. *Molecular Phylogenetics and Evolution*, *212*, 108423. https://doi.org/10.1016/j.ympev.2025.108423

Fernández, S., Zegbi, S., Sagües, F., Iglesias, L., Guerrero, I., & Saumell, C. (2023). Trapping Behaviour of *Duddingtonia flagrans* against Gastrointestinal Nematodes of Cattle under Year-Round Grazing Conditions. *Pathogens (Basel, Switzerland),* 12(3), 401. https://doi.org/10.3390/pathogens12030401

Fonseca, J. d. S., Barbosa, B. B., Silva, A. P., Vázquez, M. S. A., Cazapal Monteiro, C. F., Santos, H. A., & de Araújo, J. V. (2025). Using Biocontrol Fungi to Control Helminthosis in Wild Animals: An Innovative Proposal for the Health and Conservation of Species. *Pathogens*, *14*(8), 775. https://doi.org/10.3390/pathogens14080775

Gamalero, E., & Glick, B. R. (2020). The Use of Plant Growth-Promoting Bacteria to Prevent Nematode Damage to Plants. *Biology,* 9(11), 381. https://doi.org/10.3390/biology9110381

Ghahremani, Z., Escudero, N., Saus, E., Gabaldón, T., and Sorribas, F. J. (2019). *Pochonia chlamydosporia* induces plant-dependent systemic resistance to *Meloidogyne incognita*. *Front. Plant Sci.* 10:457876. https://doi.org/10.3389/fpls.2019.00945

Girardi, N.S., Sosa, A. L., Etcheverry, M. G., & Passone, M. A. (2022). In vitro characterization bioassays of the nematophagous fungus *Purpureocillium lilacinum*: Evaluation on growth, extracellular enzymes, mycotoxins and survival in the surrounding agroecosystem of tomato. *Fungal Biology*, *126*(4), 300-307. https://doi.org/10.1016/j.funbio.2022.02.001

Glockling, S. L., & Dick, M. W. (1994). *Dactylella megalobrocha*, a new species of nematophagous fungus with constricting rings. *Mycological Research*, *98*(8), 845-853. https://doi.org/10.1016/S0953-7562(09)80252-9

Gomes, A. P. S., Vasconcellos, R. S., Ramos, M. L., Guimarães, M. P., Yatsuda, A. P., & Vieira-Bressan, M. C. R. (2001). In vitro interaction of Brazilian strains of the nematode-trapping fungi *Arthrobotrys* spp. on *Panagrellus sp*. and *Cooperia punctata*. *Memórias do Instituto Oswaldo Cruz*, *96*, 861-864. https://doi.org/10.1590/s0074-02762001000600021

Gray, N. (1984). Ecology of nematophagous fungi: Methods of collection, isolation and maintenance of predatory and endoparasitic fungi. *Mycopathologia 86*, 143–153. https://doi.org/10.1007/BF00441123

Gray, N. F. (1988). Fungi attacking vermiform nematodes. In G. O. Poinar & H. B. Jansson (Eds.), *Diseases of nematodes* (Vol. 1, 1st ed., pp. 3–38). CRC Press. https://doi.org/10.1201/9781351071468

Gray, N. F. (1983). Ecology of nematophagous fungi: distribution and habitat. *Annals of Applied Biology*, *102*(3), 501-509.https://doi.org/10.1111/j.1744-7348.1983.tb02721.x

Gray, N. F., & Bailey, F. (1985). Ecology of nematophagous fungi: vertical distribution in a deciduous woodland. *Plant and Soil*, *86*(2), 217-223. https://doi.org/10.1007/BF02182896

Hao, L., Guo, Y., Wang, X., Gao, M., Liu, T., Ma, Y., Zhang, Y., Li, Q., Wang, R., & You, X. (2024). Preparation and application of biocontrol formulation of nematode-trapping fungus-*Duddingtonia flagrans*. *Veterinary parasitology*, *327*, 110119. https://doi.org/10.1016/j.vetpar.2024.110119

Hao, Y.E., Mo, M., Su, H., & Zhang, K. (2005). Ecology of aquatic nematode-trapping hyphomycetes in southwestern China. *Aquatic Microbial Ecology*, *40*(2), 175-181. https://doi.org/10.3354/ame040175

Haridas, S., Albert, R., Binder, M., Bloem, J., LaButti, K., Salamov, A., Andreopoulos, B., Baker, S. E., Barry, K., Bills, G., Bluhm, B. H., Cannon, C., Castanera, R., Culley, D. E., Daum, C., Ezra, D., González, J. B., Henrissat, B., Kuo, A., Liang, C., … Grigoriev, I. V. (2020). 101 Dothideomycetes genomes: A test case for predicting lifestyles and emergence of pathogens. *Studies in Mycology*, 96, 141–153. https://doi.org/10.1016/j.simyco.2020.01.003

Hastuti, L. D. S., Sari, R. W., Fauzi, F., Naibaho, D. C., Purba, R. T., & Putri, Q. A. (2023). Nematophagous fungi isolated from municipal waste-contaminated soil in Medan City, North Sumatera: Morphological identification, phylogeny analysis and assessment as root-knot nematodes biocontrol. *Yuzuncu Yil University Journal of Agricultural Sciences*, 33(4), 522–533. https://doi.org/10.29133/yyutbd.1230261

Hawksworth, D. L., & Lücking, R. (2017). Fungal diversity revisited: 2.2 to 3.8 million species. *Microbiology Spectrum*, *5*(4), 79–95. https://doi.org/10.1128/microbiolspec.funk-0052-2016

Heidari, F., & Olia, M. (2016). Biological control of root-knot nematode, *Meloidogyne javanica*, using vermicompost and fungus *Trichoderma harzianum* on tomato. *Iranian Journal of Plant Pathology*, *52*(1), 109-124.

Heintz, C.E., & Pramer, D. (1972). Ultrastructure of nematode-trapping fungi. *Journal of Bacteriology*, *110*(3), 1163-1170. https://doi.org/10.1128/jb.110.3.1163-1170.1972

Hidalgo-Diaz, L., Bourne, J. M., Kerry, B. R., & Rodriguez, M. G. (2000). Nematophagous *Verticillium* spp. in soils infested with *Meloidogyne* spp. in Cuba: isolation and screening. *International Journal of Pest Management*, *46*(4), 277-284. https://doi.org/10.1080/09670870050206046

Higgins, M. L., & Pramer, D. (1967). Fungal morphogenesis: ring formation and closure by *Arthrobotrys dactyloides*. *Science*, *155*(3760), 345-346. https://doi.org/10.1126/science.155.3760.345

Hsueh, Y. P., Gronquist, M. R., Schwarz, E. M., Nath, R. D., Lee, C. H., Gharib, S., Schroeder, F.C., & Sternberg, P. W. (2017). Nematophagous fungus *Arthrobotrys oligospora* mimics olfactory cues of sex and food to lure its nematode prey. *Elife*, *6*, e20023. https://doi.org/10.7554/eLife.20023

Hsueh, Y. P., Mahanti, P., Schroeder, F. C., & Sternberg, P. W. (2013). Nematode-trapping fungi eavesdrop on nematode pheromones. *Current Biology*, *23*(1), 83-86. https://doi.org/10.1016/j.cub.2012.11.035

Hussain, M., Zouhar, M., & Ryšánek, P. (2018). Suppression of Meloidogyne incognita by the entomopathogenic fungus *Lecanicillium muscarium*. *Plant Disease*, *102*(5), 977-982. https://doi.org/10.1094/PDIS-09-17-1392-RE

Jaffee, B. A., Ferris, H., & Scow, K.M. (1998). Nematode-trapping fungi in organic and conventional cropping systems. *Phytopathology*, *88*(4), 344-350. https://doi.org/10.1094/PHYTO.1998.88.4.344

Jansson, H. B. (1982). Predacity by nematophagous fungi and its relation to the attraction of nematodes. *Microbial Ecology*, *8*(3), 233-240. https://doi.org/10.1007/BF02011427

Jatala, P. (1986) Biological control of plant-parasitic nematodes. *Annual Review of Phytopathology* 24:453–489. https://doi.org/10.1146/annurev.py.24.090186.002321

Jia, H., Xia, R., Zhang, R., Liang, G., Zhuang, Y., Zhou, Y., Li, D., & Wang, F. (2024). Transcriptome analysis highlights the influence of temperature on hydrolase and traps in nematode-trapping fungi. *Frontiers in Microbiology*, 15, 1384459. https://doi.org/10.3389/fmicb.2024.1384459

Jiang, X., Xiang, M., & Liu X (2017). Nematode-Trapping Fungi. *Microbiology Spectrum. 5(1):FUNK-0022-2016.* https://doi.org/10.1128/microbiolspec.funk-0022-2016

Junwei, W., Qingling, M., Jun, Q., Weisheng, W., Shuangqing, C., Jianxun, L., Chunguang Z, & Chuangfu, C. (2013). The recombinant serine protease XAoz1 of *Arthrobotrys oligospora* exhibits potent nematicidal activity against *Caenorhabditis elegans* and *Haemonchus contortus*. *FEMS Microbiology Letters*, *344*(1), 53-59. https://doi.org/10.1111/1574-6968.12154

Kassam, R., Yadav, J., Chawla, G., Kundu, A., Hada, A., Jaiswal, N., Bollinedi, H., Kamil, D., Devi, P. & Rao, U. (2021). Identification, characterization, and evaluation of nematophagous fungal species of *Arthrobotrys* and *Tolypocladium* for the management of *Meloidogyne incognita*. *Frontiers in Microbiology*, *12*, 790223. https://doi.org/10.3389/fmicb.2021.790223.

Kelly, P., Good, B., Hanrahan, J. P., Fitzpatrick, R., & de Waal, T. (2009). Screening for the presence of nematophagous fungi collected from Irish sheep pastures. *Veterinary Parasitology*, *165*(3-4), 345-349. https://doi.org/10.1016/j.vetpar.2009.07.026

Kerry, B. R., & Crump, D. H. (1980). Two fungi parasitic on females of cystnematodes (*Heterodera* spp.). *Transactions of the British Mycological Society*, *74*(1), 119-125. https://doi.org/10.1016/S0007-1536(80)80017-9

Kerry, B. R., & Hominick, W. B. (2002). Biological control. In Lee, D. L. (Ed.), *The biology of nematodes* (pp. 483–510). Taylor & Francis. https://doi.org/10.1201/b12614

Khan, A., Williams, K. L., & Nevalainen, H. K. (2006). Infection of plant-parasitic nematodes by *Paecilomyces lilacinus* and *Monacrosporium lysipagum*. *BioControl*, *51*(5), 659-678.

Khan, M., & Tanaka, K. (2023). *Purpureocillium lilacinum* for plant growth promotion and biocontrol against root-knot nematodes infecting eggplant. *PLoS One*, *18*(3), e0283550. https://doi.org/10.1371/journal.pone.0283550

Kiriga, A. W., Haukeland, S., Kariuki, G. M., Coyne, D. L., & Beek, N. V. (2018). Effect of *Trichoderma spp.* and *Purpureocillium lilacinum* on *Meloidogyne javanica* in commercial pineapple production in Kenya. *Biological Control* 119, 27–32. https://doi.org/10.1016/j.biocontrol.2018.01.005

Kiss, E., Hegedüs, B., Virágh, M., Varga, T., Merényi, Z., Kószó, T., Bálint, B., Prasanna, A. N., Krizsán, K., Kocsubé, S., Riquelme, M., Takeshita, N., & Nagy, L. G. (2019). Comparative genomics reveals the origin of fungal hyphae and multicellularity. *Nature communications, 10(1)*, 4080. https://doi.org/10.1038/s41467-019-12085-w

Kriegler, M., Wernet, V., Hetzer, B., Herrero, S., Wei, A., Wäckerle, J., Dewein, I., & Fischer, R. (2025). Cell-end marker proteins are required for hyphal ring formation and size determination of traps in *Arthrobotrys flagrans*. *Journal of Cell Science*, 138(8), jcs263744. https://doi.org/10.1242/jcs.263744

Kumar, D. (2024). Evaluation of nematophagous and biocontrol efficacy of *Dactylellina phymatopaga* against *Meloidogyne graminicola* on rice (*Oryza sativa* L.). *Biological Control*, *188*, 105425. https://doi.org/10.1016/j.biocontrol.2023.105425

Kumar, N., Singh, R. K., & Singh, K. P. (2011). Occurrence and colonization of nematophagous fungi in different substrates, agricultural soils and root galls. *Archives of Phytopathology and Plant Protection*, *44*(12), 1182-1195. https://doi.org/10.1080/03235408.2010.484945

Kuo, C. Y., Tay, R. J., Lin, H. C., Juan, S. C., Vidal-Diez de Ulzurrun, G., Chang, Y. C., Hoki, J., Schroeder, F.C., & Hsueh, Y. P. (2024). The nematode-trapping fungus *Arthrobotrys*

oligospora detects prey pheromones via G protein-coupled receptors. *Nature Microbiology*, *9*(7), 1738-1751. https://doi.org/10.1038/s41564-024-01679-w

Kuo, T. H., Yang, C. T., Chang, H. Y., Hsueh, Y. P., & Hsu, C. C. (2020). Nematode-trapping fungi produce diverse metabolites during predator–prey interaction. *Metabolites*, *10*(3), 117. https://doi.org/10.3390/metabo10030117

Lakshmi, S. R., Sundar, S., & Kunjiappan, M. (2024). Role of lifestyle pattern and soil microbiome interaction of *Arthrobotrys* species for the biostimulant production. In M. S. Akhtar (Ed.), *Opportunistic fungi, nematode and plant interactions* (pp. 245–268). Springer. https://doi.org/10.1007/978-981-97-2045-3_11

Lei, H. M., Wang, J. T., Hu, Q. Y., Li, C. Q., Mo, M. H., Zhang, K. Q., Li, G.H., & Zhao, P. J. (2023). 2-Furoic acid associated with the infection of nematodes by *Dactylellina haptotyla* and its biocontrol potential on plant root-knot nematodes. *Microbiology Spectrum*, *11*(5), e01896-23. https://doi.org/10.1128/spectrum.01896-23

Li, J. Y., Qian, W. Y., Qiao, M., Bai, Y. L., & Yu, Z. F. (2013). A new *Drechslerella* species from Hainan, China. *Mycotaxon*, *125*(1), 183-188. https://doi.org/10.5248/125.183

Li, L., Ma, M., Liu, Y., Zhou, J., Qu, Q., Lu, K., Fu, D., & Zhang, K. (2011). Induction of trap formation in nematode-trapping fungi by a bacterium. *FEMS Microbiology Letters*, *322*(2), 157-165. https://doi.org/10.1111/j.1574-6968.2011.02351.x

Li, Y., Hyde, K. D., Jeewon, R., Cai, L., Vijaykrishna, D., & Zhang, K. (2005). Phylogenetics and evolution of nematode-trapping fungi (*Orbiliales*) estimated from nuclear and protein coding genes. *Mycologia*, *97*(5), 1034-1046. https://doi.org/10.3852/mycologia.97.5.1034

Li, Y., Jeewon, R., Hyde, K. D., Mo, M. H., & Zhang, K. Q. (2006). Two new species of nematode-trapping fungi: relationships inferred from morphology, rDNA and protein gene sequence analyses. *Mycological Research*, *110*(7), 790-800. https://doi.org/10.1016/j.mycres.2006.04.011

Lin, H. C., de Ulzurrun, G. V., Chen, S. A., Yang, C. T., Tay, R. J., Iizuka, T., Huang, T. Y., Kuo, C. Y., Gonçalves, A. P., Lin, S. Y., Chang, Y. C., Stajich, J. E., Schwarz, E. M., & Hsueh, Y. P. (2023). Key processes required for the different stages of fungal carnivory by a nematode-trapping fungus. *PLoS biology*, 21(11), e3002400. https://doi.org/10.1371/journal.pbio.3002400

Liou, G. Y., & Tzean, S. S. (1997). Phylogeny of the genus *Arthrobotrys* and allied nematode-trapping fungi based on rDNA sequences. *Mycologia*, *89*(6), 876-884. https://doi.org/10.1080/00275514.1997.12026858

Liu, K., Zhang, W., Lai, Y., Xiang, M., Wang, X., Zhang, X., & Liu, X. (2014a). *Drechslerella stenobrocha* genome illustrates the mechanism of constricting rings and the origin of nematode predation in fungi. *BMC Genomics*, *15,* 114. https://doi.org/10.1186/1471-2164-15-114

Liu, S., Su, H., Su, X., Zhang, F., Liao, G., & Yang, X. (2014b). *Arthrobotrys xiangyunensis*, a novel nematode-trapping taxon from a hot-spring in Yunnan Province, China. *Phytotaxa*, *174*(2), 89-96. https://doi.org/10.11646/phytotaxa.174.2.3

Liu, X. Z., & Zhang, K. Q. (1994). Nematode-trapping species of *Monacrosporium* with special reference to two new species. *Mycological Research*, *98*(8):862–868 https://doi.org/10.1016/S0953-7562(09)80255-4

Liu, X., & Zhang, K. (2003). *Dactylella shizishanna* sp. nov., from Shizi Mountain, China. *Fungal Diversity*, *14*(1), 103-107.

Liu, X., Xiang, M., & Che, Y. (2009). The living strategy of nematophagous fungi. *Mycoscience*, *50*(1), 20-25. https://doi.org/10.1007/S10267-008-0451-3

Lopez-Llorca, L. V., Maciá-Vicente, J. G., & Jansson, H. B. (2008). Mode of action and interactions of nematophagous fungi. In A. Ciancio & K. G. Mukerji (Eds.), *Integrated management and biocontrol of vegetable and grain crops nematodes* (*Integrated Management of Plant Pests and Diseases*, Vol. 2, pp. 51–76). Springer. https://doi.org/10.1007/978-1-4020-6063-2_3

Luo, H., Li, X., Li, G., Pan, Y., & Zhang, K. (2006). Acanthocytes of *Stropharia rugosoannulata* function as a nematode-attacking device. *Applied and Environmental Microbiology*, *72*(4), 2982-2987. https://doi.org/10.1128/AEM.72.4.2982-2987

Mahoney, C. J., & Strongman, D. B. (1994). Nematophagous fungi from cattle manure in four states of decomposition at three sites in Nova Scotia, Canada. *Mycologia*, *86*(3), 371-375. https://doi.org/10.1080/00275514.1994.12026422

Manzanilla-Lopez, R. H., Esteves, I., Finetti-Sialer, M. M., Hirsch, P. R., Ward, E., Devonshire, J., & Hidalgo-Díaz, L. (2013). *Pochonia chlamydosporia*: Advances and challenges to improve its performance as a biological control agent of sedentary endo-parasitic nematodes. *Journal of Nematology*, *45*(1), 1-7.

Marlin, M., Wolf, A., Alomran, M., Carta, L., & Newcombe, G. (2019). Nematophagous *Pleurotus* species consume some nematode species but are themselves consumed by others. *Forests*, *10*(5), 404. https://doi.org/10.3390/f10050404

Martinelli, P. R. P., & dos Santos, J. M. (2010). Scanning electron microscopy of nematophagous fungi associated with *Tylenchulus semipenetrans* and *Pratylenchus jaehni*. *Bioscience Journal*, *26*(5), 809–816.

Meerupati, T., Andersson, K. M., Friman, E., Kumar, D., Tunlid, A., & Ahren, D. (2013). Genomic mechanisms accounting for the adaptation to parasitism in nematode-trapping fungi. *PLoS Genetics*, *9*(11), e1003909. https://doi.org/10.1371/journal.pgen.1003909

Mendoza-de Gives, P., Braga, F. R., & Araújo, J. V. de. (2022). Nematophagous fungi, an extraordinary tool for controlling ruminant parasitic nematodes and other biotechnological applications. *Biocontrol Science and Technology*, *32*(7), 777–793. https://doi.org/10.1080/09583157.2022.2028725

Minglian, Z., Minghe, M., & Keqin, Z. (2004). Characterization of a neutral serine protease and its full-length cDNA from the nematode-trapping fungus *Arthrobotrys oligospora*. *Mycologia*, *96*(1), 16-22. https://doi.org/10.1080/15572536.2005.11832991

Mo, M. H., Chen, W. M., Su, H. Y., Zhang, K. Q., Duan, C. Q., & He, D. M. (2006). Heavy metal tolerance of nematode-trapping fungi in lead-polluted soils. *Applied Soil Ecology*, *31*(1-2), 11-19. https://doi.org/10.1016/j.apsoil.2005.04.008

Mo, M. H., Chen, W. M., Yang, H. R., & Zhang, K. Q. (2008). Diversity and metal tolerance of nematode-trapping fungi in Pb-polluted soils. *The Journal of Microbiology*, *46*(1), 16-22. https://doi.org/10.1007/s12275-007-0174-8

Moore, D., Robson, G. D., & Trinci, A. P. J. (2020). *21st Century Guidebook to Fungi*. (2nd Ed). Cambridge University Press. https://doi.org/10.1017/9781108776387

Moosavi, M. R., & Zare, R. (2020). Fungi as biological control agents of plant-parasitic nematodes. In Mérillon,, J. M. & Ramawat, K. G. (Eds.), *Plant defence: Biological control* (pp. 333–384). Springer. https://doi.org/10.1007/978-94-007-1933-0_4

Mostafanezhad, H., Sahebani, N., & Nourinejhad Zarghani, S. (2014). Induction of resistance in tomato against root-knot nematode *Meloidogyne javanica* with salicylic acid. *Journal of Crop Protection*, *3*(4), 499-508.

Nicol, J. M., Turner, S. J., Coyne, D. L., Nijs, L., Hockland, S., & Maafi, Z. T. (2011). Current nematode threats to world agriculture. In Jones, J., Gheysen, G., & Fenoll, C. (Eds.), *Genomics and molecular genetics of plant-nematode interactions* (pp. 21–43). Springer. https://doi.org/10.1007/978-94-007-0434-3_2

Niu, X.M., & Zhang, K.Q. (2011). *Arthrobotrys oligospora*: a model organism for understanding the interaction between fungi and nematodes. *Mycology*, *2*(2), 59-78. https://doi.org/10.1080/21501203.2011.562559

Nordbring-Hertz, B., Jansson, H. B., & Tunlid, A. (2011). Nematophagous fungi. In *Encyclopedia of life sciences*. John Wiley & Sons. https://doi.org/10.1002/9780470015902.a0000374.pub3

Nordbring-Hertz, B., & Chet, I. (1986). Fungal lectins and agglutinins. In D. Mirelman (Ed.), *Microbial lectins and agglutinins: Properties and biological activity* (pp. 393–408). Wiley.

Nordbring-Hertz, B., & Mattiasson, B. (1979). Action of a nematode-trapping fungus shows lectin-mediated host–microorganism interaction. *Nature*, *281*(5731), 477-479. https://doi.org/10.1038/281477a0

Nordbring-Hertz, B., Friman, E., & Veenhuis, M. (1989). Hyphal fusion during initial stages of trap formation in *Arthrobotrys oligospora*. *Antonie van Leeuwenhoek*, *55*(3), 237-244. https://doi.org/10.1007/BF00393852

Noura, C. H., Hajer, R., Asma, L., Lobna, H. H., and Najet, H.-R. (2018). Antagonistic potential of *Verticillium leptobactrum* against *Pratylenchus vulnus* associated with apple rootstock. *Journal of Entomology and Zoology Studies, 6*, 172–176.

Pathak, E., El-Borai, F. E., Campos-Herrera, R., Johnson, E. G., Stuart, R. J., Graham, J. H., & Duncan, L. W. (2012). Use of real-time PCR to discriminate parasitic and saprophagous behaviour by nematophagous fungi. *Fungal Biology*, *116*(5), 563-573. https://doi.org/10.1016/j.funbio.2012.02.005

Persmark, L., & Jansson, H. B. (1997). Nematophagous fungi in the rhizosphere of agricultural crops. *FEMS Microbiology Ecology*, *22*(4), 303-312. https://doi.org/10.1111/j.1574-6941.1997.tb00382.x

Persmark, L., Banck, A., & Jansson, H. B. (1996). Population dynamics of nematophagous fungi and nematodes in an arable soil: vertical and seasonal fluctuations. *Soil Biology and Biochemistry*, *28*(8), 1005-1014. https://doi.org/10.1016/0038-0717(96)00060-0

Pfister, D. H. (1997). Castor, Pollux and life histories of fungi. *Mycologia*, *89*(1), 1-23. https://doi.org/10.1080/00275514.1997.12026750

Pinto, A. G., Kos, T., Puškarić, J., Vrandečić, K., Benković-Lačić, T., & Brmež, M. (2024). Soil Ecosystem Functioning through Interactions of Nematodes and Fungi *Trichoderma* sp. *Sustainability*, 16(7), 2885. https://doi.org/10.3390/su16072885

Pires, D., Vicente, C. S., Inácio, M. L., & Mota, M. (2022). The Potential of *Esteya* spp. for the Biocontrol of the Pinewood Nematode, *Bursaphelenchus xylophilus*. *Microorganisms*, *10*(1), 168. https://doi.org/10.3390/microorganisms10010168

Pires, D., Vicente, C.S.L., Menéndez, E., Faria, J.M.S., Rusinque, L., Camacho, M.J., & Inácio, M.L. (2022). The Fight against Plant-Parasitic Nematodes: Current Status of Bacterial and Fungal Biocontrol Agents. *Pathogens, 11*(10), 1178. https://doi.org/10.3390/pathogens11101178

Poinar, G.O. (1988). Diseases of Nematodes: Volume I (1st ed.). CRC Press. https://doi.org/10.1201/978135071468

Pulavarty, A., Egan, A., Karpinska, A., Horgan, K., & Kakouli-Duarte, T. (2021). Plant Parasitic Nematodes: A Review on Their Behaviour, Host Interaction, Management Approaches and Their Occurrence in Two Sites in the Republic of Ireland. Plants (Basel, Switzerland), 10(11), 2352. https://doi.org/10.3390/plants10112352

Quijada, L., Baral, H. O., Beltrán-Tejera, E., & Pfister, D. H. (2020). *Orbilia jesu-laurae* (*Ascomycota*, *Orbiliomycetes*), a new species of neotropical nematode-trapping fungus from Puerto Rico, supported by morphology and molecular phylogenetics. *Willdenowia*, *50*(2), 241-251. https://doi.org/10.3372/wi.50.50210

Rahman, M. U., Chen, P., Zhang, X., & Fan, B. (2023). Predacious strategies of nematophagous fungi as bio-control agents. *Agronomy*, *13*(11), 2685. https://doi.org/10.3390/agronomy13112685

Rahman, M.U., Zhong, X., Uzair, M. et al. (2024). Application of fungi as biological control strategies for nematode management in horticultural crops. *Phytopathology Research* 6, 38. https://doi.org/10.1186/s42483-024-00257-6

Richter, A. R., Ewald, M., Hemmerling, C., Schöning, I., Bauhus, J., Schall, P., & Ruess, L. (2023). Effects of management intensity, soil properties and region on the nematode communities in temperate forests in Germany. *Forest Ecology and Management*, *529*, 120675. https://doi.org/10.1016/j.foreco.2022.120675

Robinson, A. F., & Jaffee, B. A. (1996). Repulsion of *Meloidogyne incognita* by alginate pellets containing hyphae of *Monacrosporium cionopagum*, *M. ellipsosporum*, or *Hirsutella rhossiliensis*. *Journal of Nematology*, *28*(2), 133-147.

Rosén, S., Sjollema, K., Veenhuis, M., & Tunlid, A. (1997). A cytoplasmic lectin produced by the fungus *Arthrobotrys oligospora* functions as a storage protein during saprophytic and parasitic growth. *Microbiology*, *143*(8), 2593-2604. https://doi.org/10.1099/00221287-143-8-2593

Rosenzweig, W. D., & Ackroyd, D. (1983). Binding characteristics of lectins involved in the trapping of nematodes by fungi. *Applied and Environmental Microbiology*, *46*(5), 1093-1096. https://doi.org/10.1128/aem.46.5.1093-1096.1983

Rubner, A. (1994) Predaceous fungi from Ecuador. *Mycotaxon 51*:143–151

Sahebani, N., & Hadavi, N. (2008). Biological control of the root-knot nematode Meloidogyne javanica by *Trichoderma harzianum*. *Soil Biology and Biochemistry*, *40*(8), 2016-2020. https://doi.org/10.1016/j.soilbio.2008.03.011

Sarker, M. S., Mohiuddin, K. M., Al-Ani, L. K. T., Hassan, M. N., Akter, R., Hossain, M. S., & Khand, M. N. M. (2020). Effect of bio-nematicide and bau-biofungicide against root-knot (*Meloidogyne* spp.) of soybean. *Malaysian Journal of Sustainable Agriculture*, *4*(2), 44-48. https://doi.org/10.26480/mjsa.02.2020.44.48

Satou, T., Kaneko, K., Li, W., & Koike, K. (2008). The toxin produced by Pleurotus ostreatus reduces the head size of nematodes. *Biological and Pharmaceutical Bulletin*, *31*(4), 574-576. https://doi.org/10.1248/bpb.31.574

Saumell, C. A., & Padilha, T. (2000). Influence of weather and time of deposition on sheep faeces colonization by nematophagous fungi in the Mata region of Minas Gerais State, Brazil. *Applied Soil Ecology*, *14*(1), 63-70. https://doi.org/10.1016/S0929-1393(99)00045-1

Saxena, G. (2008). Observations on the occurrence of nematophagous fungi in Scotland. *Applied Soil Ecology*, *39*(3), 352-357. https://doi.org/10.1016/j.apsoil.2008.02.003

Saxena, G. (2018). Biological control of root-knot and cyst nematodes using nematophagous fungi. In B. Giri, R. Prasad, & A. Varma (Eds.), *Root biology* (*Soil Biology*, Vol. 52, pp. 221–237). Springer. https://doi.org/10.1007/978-3-319-75910-4_8

Saxena, G., & Mukerji, K. G. (1991). Distribution of nematophagous fungi in Varanasi, India. *Nova Hedwigia, 52(3/4)*, 487-495

Scheid, P. L. (2018). Amoebophagous fungi as predators and parasites of potentially pathogenic free-living amoebae. *The Open Parasitology Journal*, *6*(1).75–86 https://doi.org/10.2174/1874421401806010075

Schmidt, A. R., Dörfelt, H., & Perrichot, V. (2007). Carnivorous fungi from Cretaceous amber. *Science*, *318*(5857), 1743-1743. https://doi.org/10.1126/science.1149947

Scholler, M., Hagedorn, G., & Rubner, A. (1999). A reevaluation of predatory *orbiliaceous* fungi. II. A new generic concept. *Sydowia 51(1)*:89–113

Schultz, R. M. (2025). Structure-function relationship in protein families. In Devlin, T. M. (ed) *Textbook of Biochemistry with Clinical Correlations*, Wiley-Liss: New York, NY, USA. pp. 1–116.

Shams Ghahfarokhi, M., Razzaghi Abyaneh, M., Ranjbar Bahadori, S., Eslami, A., Zare, R., & Ebrahimi, M. (2004). Screening of soil and sheep faecal samples for predacious fungi: isolation and characterization of the nematode-trapping fungus *Arthrobotrys oligospora*. *Iranian Biomedical Journal*, *8*(3), 135-142.

Sharma, A., Gupta, A., Dalela, M., Sharma, S., Sayyed, R. Z., Enshasy, H. A. E., & Elsayed, E. A. (2020). Linking organic metabolites as produced by *Purpureocillium lilacinum* 6029 cultured on Karanja deoiled cake medium for the sustainable management of root-knot nematodes. *Sustainability*, *12*(19), 8276. https://doi.org/10.3390/su12198276

Sharon, E., Bar-Eyal, M., Chet, I., Herrera-Estrella, A., Kleifeld, O., & Spiegel, Y. (2001). Biological control of the root-knot nematode *Meloidogyne javanica* by *Trichoderma harzianum*. *Phytopathology*, *91*(7), 687-693. https://doi.org/10.1094/PHYTO.2001.91.7.687

Shinya, R., Aiuchi, D., Kushida, A., Tani, M., Kuramochi, K., & Koike, M. (2008). Effects of fungal culture filtrates of *Verticillium lecanii* (*Lecanicillium* spp.) hybrid strains on

Heterodera glycines eggs and juveniles. *Journal of Invertebrate Pathology*, *97*(3), 291-297. https://doi.org/10.1016/j.jip.2007.11.005

Siddiqui, Z. A., & Mahmood, I. (1996). Biological control of plant parasitic nematodes by fungi: a review. *Bioresource Technology*, *58*(3), 229-239. http://doi.org/10.1016/S09608524(96)00122-8

Siezen, R. J., & Leunissen, J. A. (1997). Subtilases: The superfamily of subtilisin-like serine proteases. *Protein science*, *6*(3), 501-523. https://doi.org/10.1002/pro.5560060301

Simons, K., & Vaz, W. L. (2004). Model systems, lipid rafts, and cell membranes. *Annual Review of Biophysics and Biomolecular Structure*, *33*(1), 269-295. https://doi.org/10.1146/annurev.biophys.32.110601.141803

Singh, R. K., Pandey, S. K., & Chattopadhyay, A. (2014). Biodiversity and periodical/seasonal distribution of nematode trapping fungi from different habitats. *Journal of Pure and Applied Microbiology*, *9*(1), 767-776.

Singh, U. B., Sahu, A., Sahu, N., Singh, R. K., Prabha, R., Singh, D. P., Sarma, B. K, & Manna, M. C. (2012). Co-inoculation of *Dactylaria brochopaga* and *Monacrosporium eudermatum* affects disease dynamics and biochemical responses in tomato (*Lycopersicon esculentum* Mill.) to enhance bio-protection against *Meloidogyne incognita*. *Crop Protection*, *35*, 102-109. https://doi.org/10.1016/j.cropro.2012.01.002

Singh, U., Malviya, D., & Vishwakarma, S. (2023). Nematophagous fungi: Biology, ecology and potential application. In U. B. Singh, R. Kumar, & H. B. Singh (Eds.), *Detection, diagnosis and management of soil-borne phytopathogens* (pp. 231–254). Springer. https://doi.org/10.1007/978-981-19-8307-8_12

Soares, P. L. M., de Carvalho R. B., Martinelli, P.R.P., dos S. Paes, V., da Silveira, A. J., dos Santos J. M., Barbosa B. F. F., & Ferreira Junior, R. (2015). Nematophagous fungi: virulence mechanisms. In Askary, T. H., & Martinelli, P. R. P. (Eds.) *Biocontrol agents of phytonematodes*. CABI. https://doi.org/10.1079/9781780643755.0163

Soares, F. E. F., Aguilar-Marcelino, L., & Braga, F. R. (2024). Editorial: Nematophagous fungi as nematode control agents. *Frontiers in Fungal Biology*, 4, 1353132. https://doi.org/10.3389/ffunb.2023.1353132

Southwell, M., Junco, M., Fernández, S., Bernat, G., Zegbi, S., Guerrero, I., & Sagües, F. (2025). Development of an optimized culture medium using meso-inositol and mannitol to maximize chlamydospore production of *Duddingtonia flagrans*. *Veterinary parasitology*, *340*, 110613. https://doi.org/10.1016/j.vetpar.2025.110613

Su, H., Hao, Y. E., Mo, M., & Zhang, K. (2007). The ecology of nematode-trapping hyphomycetes in cattle dung from three plateau pastures. *Veterinary parásitology*, *144*(3-4), 293-298. https://doi.org/10.1016/j.vetpar.2006.10.012

Su, H. Y., Hao, Y. E., Yang, X. Y., Yu, Z. F., Deng, J. S., & Mo, M. (2008). A new species of *Dactylellina* producing adhesive knobs and non-constricting rings to capture nematodes. *Mycotaxon*, *105*, 313-316. https://doi.org/10.5962/p.414262

Su, H., Liu, S., Li, Y., Cao, Y., Chen, M., & Yang, X. (2011). *Arthrobotrys latispora*, a new nematode-trapping fungus from southwest China. *Mycotaxon*, *117*(1), 29-36. https://doi.org/10.5248/117.29

Su, H., Zhao, Y., Zhou, J., Feng, H., Jiang, D., Zhang, K. Q., & Yang, J. (2017). Trapping devices of nematode-trapping fungi: Formation, evolution, and genomic perspectives. *Biological Reviews*, *92*(1), 357-368. https://doi.org/10.1111/brv.12233

Sünder, A., & Lysek, G. (1988). Quantitative investigations on nematode-trapping hyphomycetes from woodland soils. *FEMS Microbiology Ecology*, *4*(5), 285-290. https://doi.org/10.1111/j.1574-6968.1988.tb02674.x-i1

Swe, A. (2009). Biodiversity, systematics and ecology of nematode-trapping fungi from Hong Kong. PhD Thesis. University of Hong Kong, Hong Kong. https://doi.org/10.5353/th_b4163421

Tikhonov, V. E., Lopez-Llorca, L. V., Salinas, J., & Jansson, H. B. (2002). Purification and characterization of chitinases from the nematophagous fungi *Verticillium chlamydosporium* and *V. suchlasporium*. *Fungal Genetics and Biology*, *35*(1), 67-78. https://doi.org/10.1006/fgbi.2001.1312

Tunlid, A., Jansson, H. B., & Nordbring-Hertz, B. (1992). Fungal attachment to nematodes. *Mycological Research*, *96*(6), 401-412. https://doi.org/10.1016/S0953-7562(09)81082-4

Veenhuis, M., Nordbring-Hertz, B., & Harder, W. (1985). An electron-microscopical analysis of capture and initial stages of penetration of nematodes by *Arthrobotrys oligospora*. *Antonie van Leeuwenhoek*, *51*(4), 385-398. https://doi.org/10.1007/BF02275043

Vidal-Diez de Ulzurrun, G., & Hsueh, Y. P. (2018). Predator-prey interactions of nematode-trapping fungi and nematodes: both sides of the coin. *Applied Microbiology and Biotechnology*, *102*(9), 3939-3949. https://doi.org/10.1007/s00253-018-8897-5

Vieira Dos Santos, M. C., Horta, J., Moura, L., Pires, D., Conceicao, I., Abrantes, I., & Costa, S. R. (2019). An integrative approach to selecting *Pochonia chlamydosporia* isolates for biocontrol of potato cyst and root-knot nematodes. *Phytopathologia Mediterranea 58*(1), 187-199. https://doi.org/10.14601/Phytopathol_Mediterr-23780

Vilela, V. L. R., Feitosa, T. F., Braga, F. R., de Araújo, J. V., de Lucena, S. C., Dantas, E. S., Athayde, A.C.R., & Silva, W. W. (2013). Efficacy of *Monacrosporium thaumasium* in the control of goat gastrointestinal helminthiasis in a semi-arid region of Brazil. *Parasitology Research*, *112*(2), 871-877. https://doi.org/10.1007/s00436-012-3078-4

Vilela, V.L.R., Feitosa, T. F., Braga, F. R., de Araújo, J. V., de Oliveira Souto, D. V., da Silva Santos, H. E., da Silva, G.L., & Athayde, A. C. R. (2012). Biological control of goat *gastrointestinal helminthiasis* by *Duddingtonia flagrans* in a semi-arid region of the northeastern Brazil. *Veterinary Parasitology*, *188*(1-2), 127-133. https://doi.org/10.1016/j.vetpar.2012.02.018

Wachira, P. M., Muindi, J. N., & Okoth, S. A. (2015). Survey of nematode destroying fungi from selected vegetable growing areas in Kenya. *Agriculture, Forestry and Fisheries*, 4(4):159-164 https://doi.org/10.11648/j.aff.20150404.12.

Wachira, P., Kimenju, J.W., Okoth, S. A., & Mibey, R. K. (2009). Stimulation of Nematode-Destroying Fungi by Organic Amendments Applied in Management of Plant Parasitic Nematode. *Asian Journal of Plant Sciences 8*(2), 153-159. 10.3923/ajps.2009.153.159.

Wan, J., Dai, Z., Zhang, K., Li, G., & Zhao, P. (2021). Pathogenicity and metabolites of endoparasitic nematophagous fungus *Drechmeria coniospora* YMF1. 01759 against nematodes. *Microorganisms*, *9*(8), 1735. https://doi.org/10.3390/microorganisms9081735

Wang, B. B., Li, Y. L., Tian, S. Y., Wang, H. Z., Li, X., Wang, F. H., & Cai, K. Z. (2024). Chlamydospore dormancy and predatory activity of nematophagous fungus *Duddingtonia flagrans*. *Journal of Basic Microbiology*, *64*(3), e2300365. https://doi.org/10.1002/jobm.202300365

Wang, B. L., Chen, Y. H., He, J. N., Xue, H. X., Yan, N., Zeng, Z. J.,Bennett, J.W., Zhang, K.Q., & Niu, X. M. (2018). Integrated metabolomics and morphogenesis reveal volatile signalling of the nematode-trapping fungus *Arthrobotrys oligospora*. *Applied and Environmental Microbiology*, *84*(9), e02749-17.https://doi.org/10.1128/AEM.02749-17.

Wang, D., Ma, N., Rao, W., & Zhang, Y. (2023). Recent advances in life history transition with nematode-trapping fungus *Arthrobotrys oligospora* and its application in sustainable agriculture. *Pathogens*, *12*(3), 367. https://doi.org/10.3390/pathogens12030367.

Wang, R. B., Yang, J. K., Lin, C., Zhang, Y., & Zhang, K. Q. (2006). Purification and characterization of an extracellular serine protease from the nematode-trapping fungus *Dactylella shizishanna*. *Letters in Applied Microbiology*, *42*(6), 589-594. https://doi.org/10.1111/j.1472-765X.2006.01908.x

Wang, X., Li, G.H., Zou, C.G. et al. (2014). Bacteria can mobilize nematode-trapping fungi to kill nematodes. *Nat Commun*, 5 (5776). https://doi.org/10.1038/ncomms6776

Westphal, A., & Becker, J. O. (2001). Components of soil suppressiveness against *Heterodera schachtii*. *Soil Biology and Biochemistry*, *33*(1), 9-16. https://doi.org/10.1016/S0038-0717(00)00108-5

Wielkopolan B, Jakubowska M and Obrępalska-Stęplowska A (2021) Beetles as Plant Pathogen Vectors. *Front. Plant Sci. 12*:748093. https://doi.org/10.3389/fpls.2021.748093

Wijayawardene, N.N., Hyde, K.D., Mikhailov, K.V. et al. (2024). Classes and phyla of the kingdom Fungi. *Fungal Diversity,* 128, 1–165. https://doi.org/10.1007/s13225-024-00540-z

Wu, H. Y., Kim, D. G., & Zhou, X. B. (2012a). First report of an unrecorded nematode-trapping fungus species *Dactylellina candidum* in Korea. *African Journal of Microbiology Research*, *6*(1), 203-205.https://doi.org/10.5897/AJMR11.356

Wu, H.Y., Kim, D.G., Ryu, Y. H., & Zhou, X.B. (2012b). *Arthrobotrys koreensis*, a new nematode-trapping species from Korea. *Sydowia,* 64(1):129–136.

Xie, H., Aminuzzaman, F. M., Xu, L., Lai, Y., Li, F., & Liu, X. (2010). Trap induction and trapping in eight nematode-trapping fungi (*Orbiliaceae*) as affected by juvenile stage of *Caenorhabditis elegans*. *Mycopathologia*, *169*(6), 467-473. https://doi.org/10.1007/s11046-010-9279-4

Yang, C. T., Vidal-Diez de Ulzurrun, G., Gonçalves, A. P., Lin, H. C., Chang, C. W., Huang, T. Y., Chen, S.A., Lai, C.K., Tsai, I.J., Schroeder, F.C., Stajich, J.E., & Hsueh, Y. P. (2020). Natural diversity in the predatory behavior facilitates the establishment of a robust model strain for nematode-trapping fungi. *Proceedings of the National Academy of Sciences USA*, *117*(12), 6762-6770.https://doi.org/10.1073/pnas.1919726117

Yang, E., Xu, L., Yang, Y., Zhang, X., Xiang, M., Wang, C., An, Z., & Liu, X. (2012). Origin and evolution of carnivorism in the Ascomycota (fungi). *Proceedings of the National Academy of sciences USA*, *109*(27), 10960-10965. https://doi.org/10.1073/pnas.1120915109

Yang, J., Huang, X., Tian, B., Sun, H., Duan, J., Wu, W., & Zhang, K. (2005). Characterization of an extracellular serine protease gene from the nematophagous fungus *Lecanicillium psalliotae*. *Biotechnology Letters*, *27*(17), 1329-1334. https://doi.org/10.1007/s10529-005-0482-1

Yang, J., Liang, L., Li, J., & Zhang, K. Q. (2013). Nematicidal enzymes from microorganisms and their applications. *Applied Microbiology and Biotechnology*, *97*(16), 7081-7095.https://doi.org/10.1007/s00253-013-5045-0

Yang, J., Tian, B., Liang, L., & Zhang, K. Q. (2007b). Extracellular enzymes and the pathogenesis of nematophagous fungi. *Applied Microbiology and Biotechnology*, *75*(1), 21-31. https://doi.org/10.1007/s00253-007-0881-4

Yang, J., Wang, L., Ji, X., Feng, Y., Li, X., Zou, C., Xu, J., Ren, Y., Mi, Q., Wu, J., Liu, S., Liu, Y., Huang, X., Wang, H., Niu, X., Li, J., Liang, L., Luo, Y., Ji, K., Zhou, W., … Zhang, K. Q. (2011). Genomic and proteomic analyses of the fungus *Arthrobotrys oligospora* provide insights into nematode-trap formation. PLoS pathogens, 7(9), e1002179. https://doi.org/10.1371/journal.ppat.1002179

Yang, L., Li, X., Bai, N., Yang, X., Zhang, K. Q., & Yang, J. (2022). Transcriptomic analysis reveals that Rho GTPases regulate trap development and lifestyle transition of the nematode-trapping fungus *Arthrobotrys oligospora*. *Microbiology Spectrum*, *10*(1), e01759-21. https://doi.org/10.1128/spectrum.01759-21

Yang, Y., Yang, E., An, Z., & Liu, X. (2007a). Evolution of nematode-trapping cells of predatory fungi of the *Orbiliaceae* based on evidence from rRNA-encoding DNA and multiprotein sequences. *Proceedings of the National Academy of Sciences*, *104*(20), 8379-8384. https://doi.org/10.1073/pnas.0702770104

Yao, Y., Huo, J., Ben, H., Gao, W., Hao, Y., Wang, W., et al. (2023). Biocontrol efficacy of endophytic fungus, *Acremonium sclerotigenum*, against *Meloidogyne incognita* under *in vitro* and *in vivo* conditions. *Biologia* 78, 3305–3313. http://doi.org/10.1007/s11756-023-01505-4

Yeates, G.W. (2007). Abundance, diversity, and resilience of nematode assemblages in forest soils. *Canadian Journal of Forest Research*, 37(2): 216-225. https://doi.org/10.1139/x06-172

Yesayan, A., Yesayan, T., Babayan, B., Esoyan, S., Hayrapetyan, A., Sevoyan, G., Chakhmakhchyan, A., Nanagulyan, S., & Melkumyan, M. (2024). Carnivorous fungi application for pesticide-free vegetable cultivation. *Functional Food Science, 4*(9), 325-336. https://doi.org/10.31989/ffs.v4i9.1432

Zhang, F. A., Zhou, X. J., Monkai, J., Li, F. T., Liu, S. R., Yang, X. Y., Wen X, & Hyde, K. D. (2020c). Two new species of nematode-trapping fungi (*Dactylellina*, *Orbiliaceae*) from burned forest in Yunnan, China. *Phytotaxa*, *452*(1), 65-74. https://doi.org/10.11646/phytotaxa.452.1.6

Zhang, F., Boonmee, S., Bhat, J. D., Xiao, W., & Yang, X.Y. (2022). New *Arthrobotrys* nematode-trapping species (*Orbiliaceae*) from terrestrial soils and freshwater sediments in China. *Journal of Fungi*, *8*(7), 671. https://doi.org/10.3390/jof8070671

Zhang, F., Boonmee, S., Yang, Y.-Q., Zhou, F.-P., Xiao, W., & Yang, X.-Y. (2023). *Arthrobotrys blastospora* sp. nov. (Orbiliomycetes): a living fossil displaying morphological traits of mesozoic carnivorous fungi. *Journal of Fungi*, 9(4), 451. https://doi.org/10.3390/jof9040451

Zhang, J., Fu, B., Lin, Q., Riley, I. T., Ding, S., Chen, L., Cui, J., Yang, L., & Li, H. (2020d). Colonization of *Beauveria bassiana* 08F04 in root-zone soil and its biocontrol of cereal cyst nematode (*Heterodera filipjevi*). *PLoS One*, *15*(5), e0232770. https://doi.org/10.1371/journal.pone.0232770

Zhang, K. Q., & Hyde, K. D. (Eds.). (2014). *Nematode-trapping fungi* (Vol. 23). Springer Science & Business. https://doi.org/10.1007/978-94-017-8730-7

Zhang, X., Zhang, H., Jiang, Z., Bai, Q., Wu, S., Wang, Y., et al. (2021). A new strain of *Volutella citrinella* with nematode predation and nematicidal activity, isolated from the cysts of potato cyst nematodes in China. *BMC Microbiology*, 21, 323–312. http://doi.org/10.1186/s12866-021-02385-x

Zhang, Y., Li, G. H., & Zhang, K. Q. (2011). A review on the research of nematophagous fungal species. *Mycosystema*, *30*(6), 836-845.

Zhang, Y., Li, S., Li, H., Wang, R., Zhang, K. Q., & Xu, J. (2020a). Fungi–nematode interactions: Diversity, ecology, and biocontrol prospects in agriculture. *Journal of Fungi*, *6*(4), 206. https://doi.org/10.3390/jof6040206

Zhang, Y., Qiao, M., Baral, H. O., Xu, J., Zhang, K. Q., & Yu, Z. F. (2020b). Morphological and molecular characterization of *Orbilia pseudopolybrocha* and *O. tonghaiensis*, two new species of *Orbiliaceae* from China. *International Journal of Systematic and Evolutionary Microbiology*, *70*(4), 2664-2676. https://doi.org/10.1099/ijsem.0.004088

Zhang, Y., Yu, Z. F., Xu, J., & Zhang, K. Q. (2011). Divergence and dispersal of the nematode-trapping fungus *Arthrobotrys oligospora* from China. *Environmental Microbiology Reports*, *3*(6), 763-773. https://doi.org/10.1111/j.1758-2229.2011.00297.x

Zhang, Y., Zhang, K.Q., Hyde, K.D. (2014a) The ecology of nematophagous fungi in natural environments. In Zhang, K.Q., Hyde, K.D. (ed) *Nematode-Trapping Fungi*. Springer, Dordrecht, The Netherlands. pp 211–230 http://doi.org/10.1007/978-94-017-8730-7_4

Zhu, M.C., Li, X. M., Zhao, N., Yang, L., Zhang, K. Q., & Yang, J. K. (2022). Regulatory Mechanism of Trap Formation in the Nematode-Trapping Fungi. *Journal of Fungi (Basel, Switzerland)*, 8(4), 406. https://doi.org/10.3390/jof8040406

Zuoqing, M., & Xingzhong, L. (2003). Notes on the seasonal fluctuation of the nematode-trapping fungi population in orchards at the vicinity of Beijing. *Mycosystema*, *22*(1), 77-81.