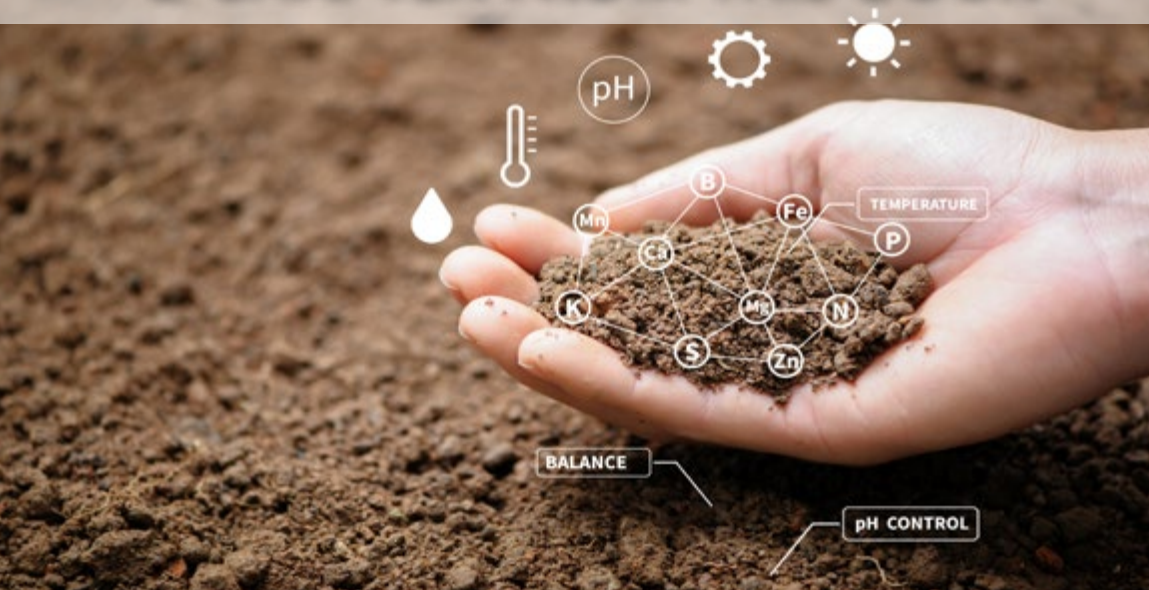# Understanding and utilising soil microbiomes for a more sustainable agriculture

Edited by Professor Kari E. Dunfield, University of Guelph, Canada

E-CHAPTER FROM THIS BOOK

Nematodes and their trophic interactions in the soil microbiome

Liliane Ruess, Humboldt-Universität zu Berlin, Germany

1 Introduction

1.1 Nematodes in the soil microbiome

The soil microbiome is teeming with diverse microorganisms and fauna. These interact with each other, forming complex and dynamic interrelationships. The soil microbiome includes all soil type-dependent microorganisms, including microfaunal grazers, nematodes and protists (Costa et al., 2018). However, microbial metazoa are rarely considered as a key component in the soil microbiome, and most research focuses on prokaryotic taxa (Bik, 2019). This is mainly due to the complex taxonomy of this microfauna as well as the lack of published molecular data for barcoding (di Montanara et al., 2022). For example, in nematodes, most of the available genome data sets are on parasitic taxa and the model species *Caenorhabditis elegans* (Zhang et al., 2017; Qing et al., 2020; Powers et al., 2021). Free-living nematodes, which predominate in the soil microbiome, are understudied: they are in a 'Goldilocks zone of neglect' (Bik, 2019).

To achieve a holistic view of microbiome processes, soil nematodes should be embraced as a key element in microbial ecology. The present chapter

therefore introduces the major functions of free-living as well as plant parasitic nematodes in the soil and rhizosphere environment, with a focus on arable systems. It addresses their role as central components of food webs and as biological indicators for soil and plant health (Section 2). Further, it highlights the importance of root-feeding taxa for plant–microbe interactions in the rhizosphere (Section 3). Finally, nematodes as vectors for human pathogens among microbial hotspots and the potential for foodborne diseases are discussed (Section 4).

1.2 The 'good guys' – free-living nematodes

Nematodes are the most abundant and diverse multicellular soil organisms, with numerous species and millions of individuals, e.g. up to 200 species m^{-2} in one site and trophic groups at all food web levels (Yeates et al., 1993; Yeates, 2010). Globally it has been estimated that there is a total nematode biomass of approximately 0.3 giga tonnes in surface soils (van den Hoogen et al., 2019). Within the soil microbiome, bacterial and fungal grazers regulate community structure and activity, which, in turn, affects nutrient mineralisation by their microbial prey (Whalen et al., 2013; Richter et al., 2019; Mielke, et al., 2022). Although, when compared with microorganisms, nematodes represent only a small amount of biomass in this micro-consortium, they have a key position in energy flow and nutrient cycling (e.g. Nieminen, 2008; Neher, 2010). Moreover, nematode life history traits and feeding relationships provide a framework to understand food web disturbance, structure and diversity as well as processes such as carbon (C) pathways (Bongers, 1990; Ferris et al., 2001; Ruess and Ferris, 2004). This concept of 'nematode fauna analysis' has proven useful as a tool for relating soil and plant health to land use and arable management (Mulder and Maas, 2017).

1.3 The 'bad guys' – plant parasitic nematodes

In contrast to free-living nematodes, the role of plant parasites is well known in agriculture. Nematodes are among the most widespread root feeders: they break down plant cells, disrupt physiological processes and modify immune responses (Gillet et al., 2017; Liu and Park, 2018; Siddique et al., 2022). This damage is of great agricultural and economic importance, and the annual loss is estimated at ~14% of the world's crop production (Nicol et al., 2011). The primary effects of root feeders are on plant resource allocation pattern and tissue nutrient concentrations (Maboreke et al., 2017; Gilarte et al., 2020; Bell et al., 2021). Secondary effects are nematode-induced 'leakage' of plant cell content, increasing C translocation to the rhizosphere, which stimulates the associated microbiome (Yeates et al., 1999; Poll et al., 2007). Through these diverse synergistic and antagonistic effects, nematodes alter microbial

community patterns, C fluxes and root signalling pathways and, in turn, the organisation of the rhizosphere microbiome.

1.4 Nematodes and food-borne diseases

A growing concern in agriculture is outbreaks of food-borne illness linked to consumption of fresh or partially processed products in both industrialised and developing countries. Human pathogens enter arable soil mainly via recycled waste water in surface irrigation or via animal manure used as fertiliser (Roth et al., 2015; Iwu and Okoh, 2019). Bacteria such as *Escherichia coli* and *Salmonella enterica* can then persist in the soil for long periods of time (Tran et al., 2020; Ramos et al., 2021). However, these pathogens have to be transported between microbial hotspots, e.g. from manure patches to the rhizosphere microbiome, in order to contaminate crops. A neglected aspect of this dissemination is soil-inhabiting fauna. As the most predominant metazoan in soil, nematodes have a considerable potential as a vector for pathogenic bacteria (Nykyri et al., 2014; Diaz and Restif, 2014; Kroupitski et al., 2015). This may be particularly important in sustainable agriculture, with greater application of animal manure as an organic soil amendment. However, there is still a lack of knowledge about the role of nematodes (as well as other soil fauna) as vectors for human pathogens.

2   Nematodes as key biota in the soil micro-food web

2.1 Functional diversity and role of nematodes in the micro-food web

Nematodes dominate all soil ecosystems in terms of biomass and abundance due to their multiple adaptations to differing environmental conditions (Andrássy, 2005). Their high trophic diversity encompasses functional groups at each level of the soil food web (Fig. 1). Nematode diets range from bacteria, fungi and algae to microfauna, predominantly other nematodes (Yeates et al., 1993). On the other hand, nematodes often become prey of soil mesofauna such as mites and springtails (Chernova et al., 2007; Walter and Proctor, 2013; Rueda-Ramírez et al., 2023). Through these multiple trophic interactions, nematodes connect microbial and faunal soil food web compartments, i.e. they couple the soil microbiome with higher trophic levels.

Due to this high complexity in trophic relationships, functional groups are formed, including species with a similar trophic level and feeding pattern and a comparable function in the food web (Ferris and Tuomisto, 2015; Heijboer et al., 2017). Nematode functional groups are established in two major soil food chains (Crotty et al., 2014; Lazarova et al., 2021):

- the herbivore ('green') chain; and
- the detritivore ('brown') chain.
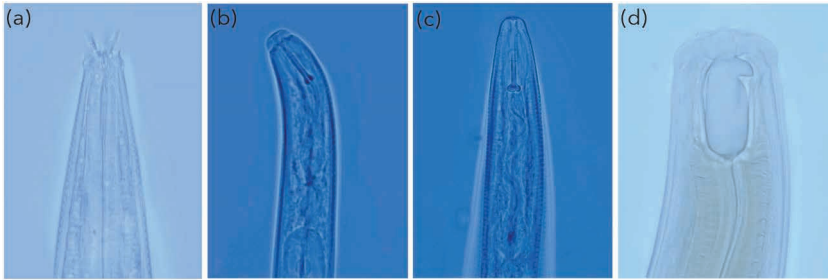
Figure 1 Common nematode trophic groups. (a) *Acrobeles* – bacterial feeder with an unarmed mouth cavity, the lip appendages (probolae) likely serve to sort bacteria; (b) *Aphelenchoides* – fungal feeder with a stylet with delicate knobs to pierce fungal hyphae; (c) *Merlinius* – root feeder with a strong stylet with prominent knobs used to rupture the plant cell wall and suck cell content. (d) *Prionchulus* – predator with a barrel-shaped oral cavity bearing a dorsal tooth and opposite a ridge with rasp teeth.

Living root tissue opens the herbivore C and energy channels by serving as a resource for root feeders, while bacterial and fungal feeders occupy the detrital decomposition pathway. Via cross-feeding, omnivores and predators can trigger energy and nutrient flows between both food chains (Wolkovich, 2016). Nematodes not only have a central role in the carbon and energy flux in the microbiomes of soil (brown chain) and rhizosphere (green chain) but also connect the fluxes between these two fundamental pathways.

Nematodes can both contribute to and detract from agricultural production systems given their diverse functional roles. In the area of plant production, bacterial feeders can act as vectors for both beneficial and harmful bacteria in the rhizosphere microbiome (Nykyri et al., 2014; Martins et al., 2022). Their preference for grazing on plant pathogens can also promote competing beneficial microbiota and vice versa (Bonkowski et al., 2009; Rønn et al., 2013). While root feeders are a severe plant pest, omnivores and predators can function as their control agents. The impact of nematode functional diversity thereby is not restricted to the microbiome itself. It acts at different scales, from the soil and rhizosphere microbiome to single plants and on to cultivated fields (Lazarova et al., 2021).

2.2 Trophic interactions shaping microbiome communities and processes

The structure and function of the micro-food web play a key role in the composition and activity of microbial assemblages and, in turn, soil nutrient cycling, which is crucial for plant production (De Vries and Wallenstein, 2017; Fierer, 2017; Jiang et al., 2022). Microfaunal grazers contribute to

the microbial loop in the rhizosphere microbiome, a tri-tropic interaction that makes nutrients available to plants (Bonkowski et al., 2009; Zheng et al., 2022). Nematodes and protozoa are 'the' bacterial predators in the soil microbiome, and their predation pressure is a driving force in bacterial evolution. Soil bacteria have developed diverse defence strategies to survive or escape from their predators. The strategies include physical adaptations, e.g. to prevent contact, recognise and attack (e.g. engulfing predators), and chemical defence such as antibiotics (Martins et al., 2022). The impact of microfaunal grazing on microbial community structure as well as mineralisation processes in the soil microbiome is discussed comprehensively elsewhere in this book (see chapter on protists). Some aspects specific to nematodes are summarised later.

The global abundance of bacterial-feeding nematodes has been estimated as high as 1.9×10^{20} Ind. g^{-1} soil dry weight, distributed in 43 families comprising at least 129 species (van den Hoogen et al., 2019). Dunger (2008) investigated an afforested dune soil and found 6.9×10^6 Ind. m^{-2} nematodes residing at a 0–25 cm depth. Approximately 42% of these nematodes were bacterial feeders, consuming approximately 16.6 g of bacterial cells and 5.3 g of protein per year. These trophic interactions directly affect microbial activity and C release from the microbial biomass (Richter et al., 2019). Nematode grazing activity further accounts for an additional release of ammonium, estimated as high as 32–38% of annual nitrogen (N) mineralisation in an arable land (Whalen et al., 2013).

However, bacterial feeders do not just drive microbiome community structure and function. Fungal feeders also impact on fungal and bacterial α-diversity and stimulate C and N cycling (Kane et al., 2023). In a $^{13}CO_2$-labelling field study, Pausch et al. (2016) showed that, despite a fungal C stock being less than half of that of bacteria, the C transfer from fungi via fungal-feeding nematodes into higher trophic levels of the fungal decomposition channel far exceeded that of the bacterial pathway. Recent micro-food web studies suggested that the transformation of exogenous C from bacteria to bacterial feeders accelerates the turnover of the C pool, while the C flux from fungi to fungal feeders, and then to omnivores and predators, contributes to exogenous C sequestration (Zhang et al., 2023). This highlights the role of the functional diversity of nematodes in shaping microbiome community structure and processes.

2.3 Ecological tools to assess soil conditions and plant health

The high abundance and diversity of nematodes, multiple trophic links and impact on microbiome processes make them good indicators of soil and

food web conditions (Ferris, 2010a; Ferris and Tuomisto, 2015; Mulder and Maas, 2017). Morphological traits and functional roles in nematodes show phylogenetic clustering and some genetic conservation at the genus level (Ross et al., 2022), paving the way for a framework of functional indices. These consider nematode population dynamics based on the family structure in relation to:

- soil ecosystem disturbance (Maturity Index; Bongers, 1990);
- nutrient availability (Enrichment Index; Ferris et al., 2001); and
- structure and function of the micro-food web (Structure Index; Ferris et al., 2001).

More details on different nematode indices are presented in Table 1. The indices are widely used as ecological tools to determine soil health and identify sustainable management practices (e.g. Lu et al., 2020; Melakeberhan et al., 2021; Biswal, 2022).

Functional indices as ecological tools are very useful in assessing the impact of environmental changes on soil conditions, but they do not show the magnitude of ecosystem response. To account for this, Ferris (2010b) developed 'metabolic footprints', including nematode biomass (i.e. weight) and metabolic activity (i.e. respiration). This concept combines form and function by taking advantage of the vermiform body-shape and standardised morphometrics in nematodes. This trait-based approach was tested across 200 sites (arable fields, managed grassland and wooded areas) as a functional descriptor of land use (Mulder and Maas, 2017). Using conversion factors for C content, C pools and fluxes in different parts of the microbiome were quantified, ranging from top soil to subsoil micro-food webs (Pausch et al., 2018). An overview of the different footprints and their indicator values are presented in Table 1.

The use of nematodes as biological indicators in soil systems has been successfully applied to relate soil and food web conditions to grassland, arable and forest habitats, as shown in a meta-analysis across 83 sites (Ruess, 2003). More recently, nematode community analysis-based models have been used to identify sustainable soil health management. For example, Melakeberhan et al. (2021) designed models to assess the impact of more sustainable and integrated arable practices. A comprehensive review of nematodes as soil indicators is provided by Biswal (2022), and further case studies are summarised in Table 1. Nematode community analyses have great potential to support the maintenance of environmental quality and sustainable production practices in the future.

Table 1 Nematode functional indices and metabolic footprints as ecological tools according to Bongers (1990), Ferris et al. (2001) and Ferris (2010b). Given are the indicated soil (microbiome) and micro-food web conditions as well as related case studies in agricultural systems

Ecological tool	Soil and/or food web conditions	Case studies in arable land inferring the impact of
Functional index		
Maturity index (MI)	Disturbance	Manure application (Roth et al., 2015; Yang et al., 2016); tillage (Neher et al., 2019; Bongiorno, 2020); pesticides (Neher et al., 2011; Gupta et al., 2019); sewage sludge (Georgieva et al., 2002; Johansen et al., 2023)
Channel index (CI)	Major decomposition pathways	Irrigation (Ferris et al., 2001; Ewald et al., 2022); plant residues (Scharroba et al., 2012; Glavatska et al., 2017; Maina et al., 2021); tillage and crop rotation (Zhang et al., 2015)
Enrichment index (EI)	Nutrient (N) enrichment	Fertilisation (Ferris and Matute, 2003; Pan et al., 2020; Hu et al., 2022); litter amendment (Scharroba et al., 2012); cover crops (Ferris et al., 2001; Djigal et al., 2012)
Structure index (SI)	Food web structure and diversity	N addition (Zhou et al., 2022); intensive cultivation (Karuri, 2023), tillage (Zhang et al., 2015; Zhong et al., 2017)
Metabolic footprint		
Enrichment footprint	Response to resource pulses	Fertilisation (Pan et al., 2020); crop growth (Yang et al., 2020; Ewald et al., 2022)
Structure footprint	Impact on higher trophic levels	Crop growth (Yang et al., 2020; Ewald et al., 2022); continuous cropping (Yang et al., 2022)
Functional footprint	Overall food web response	Tillage (Zhang et al., 2015; Pothula et al., 2022; Schmidt et al., 2022); fertiliser type (Maina et al., 2021), crop rotation (Zhang et al., 2015; Zhang et al., 2016)
Herbivore, bacterial and fungal footprint	C and energy flux in the green and brown food chain	Litter amendment (Ewald et al., 2020); fertilisation (Pan et al., 2020); crop presence (Ewald et al., 2020; Karuri, 2023), pest management (Yang et al., 2022)
Composite footprint	Entire metabolic response of the population	Intercrop (Leiririo et al., 2022); crop growth (Yang et al., 2020)

3   Plant parasites and microbiomes

3.1 Modification of the soil microbiome by plant parasitic nematodes

Microbiomes play a vital role in plant fitness and health, including those in bulk soil and those in the rhizosphere (Fierer, 2017; O´Brien et al., 2021). The

composition and dynamics of microbial communities in these small-scale habitats are controlled by multiple abiotic and biotic factors. In particular the rhizosphere microbiome is characterised by a multitude of chemical signals from plants, bacteria and nematodes that shape environmental conditions and influence which organisms will flourish (Berg et al., 2014; Lakshmanan et al., 2014; Markalanda et al., 2022). Plant–microbiome interactions are therefore an important factor in sustainable agriculture (Gupta et al., 2021; Omotayo and Babalola, 2021).

Root-feeding nematodes have evolved several functional groups differing in parasitic lifestyle (Yeates et al., 1993), including:

- migratory and sedentary ectoparasites; and
- migratory and sedentary endoparasites.

Migratory ectoparasites have the most primitive mode of parasitism. They remain outside the root and use their stylet to feed on epidermal cells or root hairs. Sedentary ectoparasites also remain outside the root, feeding from a single plant cell for a prolonged period of time. Migratory endoparasites enter the root and periodically feed as they migrate, while sedentary endoparasites inhabit galls or cysts, and establish specialised feeding sites at the vascular bundle. All functional groups induce leakage of root cell content, i.e. sugars, amino acids and carbolic acids, into the rhizosphere environment as shown by ^{13}C- or ^{14}C-labelling experiments (Denton et al., 1998; Yeates et al., 1999; Poll et al., 2007; Maboreke et al., 2017). Herbivore nematodes can thus shift microbial diversity and community structure (Maboreke et al., 2017; Malacrinò et al., 2021).

A special position in these interactions is held by root-knot nematodes. The rhizosphere microbiome undergoes major modifications when roots are infected with these parasites. Changes can be caused by the disruption of secondary metabolite synthesis, e.g. flavonoids (Skider et al., 2022) or negative interference with rhizobia mutualism (Wood et al., 2018). Root-knot nematodes also enhance bacteria that contain plant cell wall-degrading enzymes, thereby promoting nematode root colonisation (Lu et al., 2023). The microbiome community on the surface of root-knots is very specific, suggesting adaptions in functional capabilities to inhabit this 'gallobiome' (Haase et al., 2007; Masson et al., 2020). More details on these multitrophic interactions are provided in the case study presented in Section 5.

3.2 Turning the tables: soil microbiome effects on plant parasitic nematodes

Microbiomes in the soil and plant rhizosphere protect crops against multiple stressors including phytopathogens such as root-feeding nematodes. This

impact can be mediated via antagonistic bacteria as well as growth-promoting bacteria (Silva et al., 2018; Dukare et al., 2022) or mutualistic rhizosphere interactions (Markalanda et al., 2022). Plant secondary metabolites and systemic resistance are also important (Thahira et al., 2022). Details on these effects are discussed elsewhere in this book. In a nutshell, the different plant–microbiome interactions are key for plant fitness and resistance against plant parasitic nematodes.

Most is known about root-knot nematodes of the genus *Meloidogyne* (see review by Ciancio et al., 2016). *Meloidogyne*-based disease complexes harbour specific bacterial communities. These pathosystems can devastate important crops such as coffee and tomato (Lamelas et al., 2020). The soil microbiome can decrease root invasion of second-stage juveniles (J2) and progeny in *Meloidogyne hapla*. The former is related to plant-mediated non-direct effects of the microbiome, while the latter is caused by a direct negative impact of microbiome taxa on nematode reproduction (Topalović et al., 2020). Specific microorganisms are known as antagonists, e.g. *Bacillus amyloliquefaciens*, producing acetophenone and killing 99% of *M. incognita* J2 within 24 h (Zhao et al., 2023). Arbuscular mycorrhizal fungi in combination with *Pseudomonas fluorescens* can also reduce root infestation by *M. javanica* (Sharma et al., 2021).

Microbiome biota therefore have great potential in ecofriendly nematode pest-management. Specialised pathogens such as the parasitic bacterium *Pasteuria penetrans* or the nematode-trapping fungus *Pochonia chlamydosporia* are commonly used (Ciancio et al., 2016). Other microbial taxa and free-living nematodes are less studied as biocontrol tools. In the case of the ectoparasite *Tylenchorhynchus*, a study from Piśkiewicz et al. (2009) revealed a preference for nematode migration towards roots without microbial predators. Castillo et al. (2017) investigated different farms growing potatoes and found that soil with a high abundance of *Bacillus*, *Arthrobacter* and *Lysobacter*, and a nematode community comprising at least 30% fungal feeders, had the lowest populations of the migratory endoparasite *Pratylenchus neglectus*. In addition to antagonistic interactions in the rhizosphere microbiome, the soil microbiome can affect plant parasitic nematodes while migrating between crop plants. The question of whether and how free-living nematodes influence this parasitic interaction remains a task for future research.

3.3 The nematode gut microbiome – gateway to a new understanding of the host–parasite relationship?

As previously stated, the impact of root-feeding nematodes on plant health is affected by the soil microbiome. However, very little is known about the influence

of the nematode gut microbiome on this host-parasite interaction. Investigations of the model nematode *C. elegans* showed that the worms' gut microbiota were assembled from the surrounding microbial environment (Berg et al., 2016; Clark and Hodgkin, 2016). Thereafter, composition is shaped by the nematode host, predominantly by immune, xenobiotic and metabolic signalling pathways (Zhang et al., 2021). Ecological network analyses revealed strong bacteria-to-bacteria interactions, with distinct community shifts in competitive species (Johnke et al., 2020). Overall, the assembly of the nematode gut microbiome is non-random, and its composition is different from that in the soil (Zheng et al., 2020).

This native gut microbiome influences nematode fitness, which, in turn, can have implications for nematode parasitism with respect to plants. Gut bacteria promote nematode life history traits, e.g. body size as well as energy allocation from lipid storage to reproduction (Lo et al., 2022). Gut microbes enhance nematode fitness under stresses such as high temperature, changes in osmolarity or exposure to chemicals (Dirksen et al., 2016; Lee et al., 2020). It has been shown recently that the composition of the gut microbiome can foster the development of the parasitic bacterium *Pasteuria penetrans* in the root-knot nematode *M. javanica*, offering potential for biocontrol (Lindo-Seminario et al., 2022).

The nematode gut microbiome is also shaped by agricultural management, particularly fertilisation practice. Zheng et al. (2020) reported that fertiliser type (none, inorganic or mixed) had a greater influence than fertilisation duration (5, 8, or 10 years). For example, the use of inorganic fertilisers significantly decreased the diversity of gut microorganisms, while the use of organic fertilisers had no impact on composition (Zheng et al., 2019). This may be important in the dissemination of antibiotic resistance genes that organic fertilisers, in particular, spread. Shared antibiotic resistance genes among soil and nematodes after the application of slurry (pig manure with antibiotics) indicate horizontal gene transfer (Zheng et al., 2019). Nematode gut microbiomes might therefore serve as a refuge or vector for antibiotic resistance genes and enhance dispersal of resistomes in the soil ecosystem. Taken together, with the effects on nematode fitness, parasite gut microbiomes can significantly influence host relationships.

4   Nematodes and food-borne diseases

4.1 The soil microbiome as a source for human pathogens

Soil microbiomes are a cornerstone of the one health concept. This includes beneficial microorganisms, plant and human pathogens, and overall microbial diversity (Banerjee and van der Heijden, 2023). Over the last decade, the soil microbiome in arable systems has developed as a 'battleground' for human pathogens (van Overbeek et al., 2014). A major hazard in fresh produce is shiga-toxin producing strains of *Escherichia coli* and *Salmonella enterica*
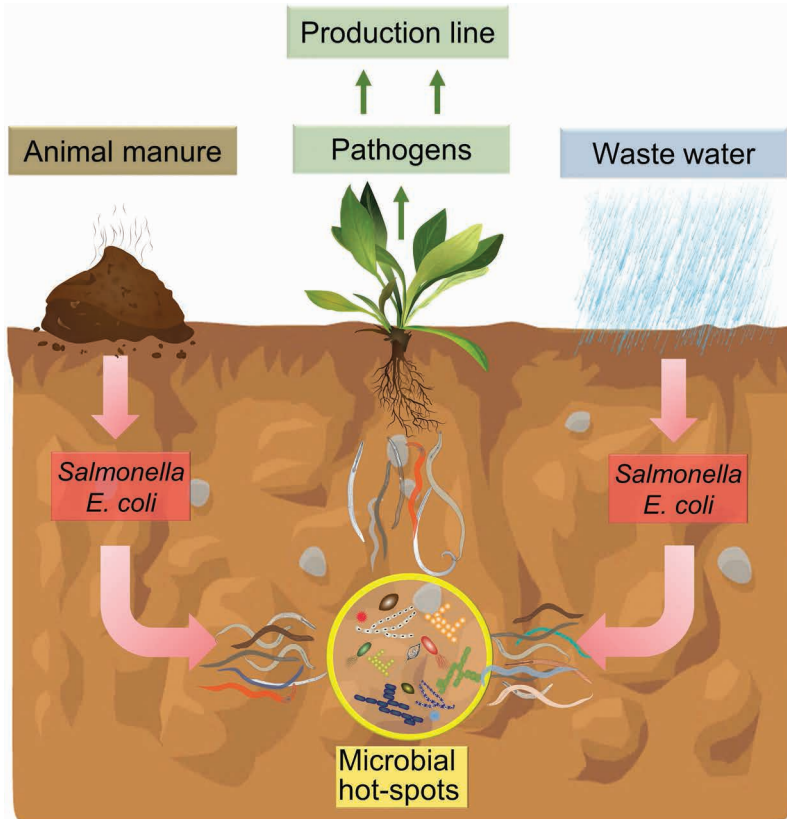
Figure 2 Nematodes as vectors for food-borne diseases. Human pathogens such as the shiga-toxin-producing strains of *Escherichia coli* and *Salmonella enterica* are introduced into the soil by agricultural practice, primarily inadequately treated animal manure and waste water. Nematodes share their environment with bacteria and can harbour, protect and disperse them. By moving between bacterial hotspots, they transport human pathogens into the rhizosphere (bacterial feeders) or even into the plant (root feeders), eventually entering the food production line.

(Fig. 2). As a nutrient-rich microbial hotspot, the plant rhizosphere is a reservoir for opportunistic pathogens such as *Enterobacter* and *Staphylococcus* (Berg et al., 2005; Mendes et al., 2013). A major concern is that these pathogens often acquire antimicrobial resistance, further aggravating risks to human and environmental health (Iwu and Okoh, 2019).

Fruits and vegetables grown on open fields can become contaminated with human pathogenic microorganisms before and during harvest. Major transmission routes are contaminated irrigation water (e.g. recycled wastewater) and raw or improperly composted animal manure as an organic amendment (Nicholson et al., 2005; Franz and van Bruggen, 2008; Roth et al., 2015) (Fig. 2).

Once released into the environment, these human pathogens can persist in the soil for months (Jamieson et al., 2002; Guan and Holley, 2003; Iwu and Okoh, 2019). The most important environmental drivers for their persistence are soil conditions (temperature, moisture, pH and type) and arable management such as type or method of incorporation of manure (van Overbeek et al., 2014; Iwu and Okoh, 2019; Tran et al., 2020).

Complex biotic interactions in the microbiome are critical for the survival of human pathogens in the soil environment. Indigenous microbial communities in soil and rhizosphere provide a strong barrier against allochthonous taxa. However, many human pathogenic bacteria are highly competitive and good colonisers. They accumulate nutrients competitively and produce antimicrobial metabolites, allowing proliferation in the presence of autochthonous taxa (Mendes et al., 2013). The high nutrient content of manure-amended soil, in particular, promotes successful establishment (van Overbeek et al., 2010). Soil bacterial diversity has been shown to be negatively correlated with pathogen survival (van Elsas et al., 2012), highlighting the importance of a diverse soil microbiome for food safety.

4.2 Nematodes as vectors for bacterial pathogens

As dominant soil bacteria predators, bacterial feeders are key to disease management for both plant and human health (Martins et al., 2022; Nykyri et al., 2014). It has long been known that they harbour, protect and disperse bacteria (e.g. Wasilewska and Webster, 1975; Sutherland and Webster, 1993; Anderson et al., 2003). They engulf bacteria via the unarmed stoma (Fig. 1) and defecate 30–60% of ingested cells at viable conditions (Freckman and Caswell, 1985).

Interactions of *E. coli* and *S. enterica* with the model nematode *C. elegans* have been investigated the most (Diaz and Restif, 2014). Key aspects reported were:

- nematode attraction by and migration to bacteria (Caldwell et al., 2003; Kenney et al., 2006);
- bacterial ingestion and protection against sanitisers (Caldwell et al., 2003; Park et al., 2014);
- bacterial persistence in the gut (Kenney et al., 2005); and
- shedding of viable cells (Anderson et al., 2006)

Other taxa with known vector potential for human pathogens are the thermotolerant *Diploscapter*, found in compost, sewage and agricultural soil (Gibbs et al., 2005), and the opportunist *Acrobeloides buetschlii*, which is

widespread across many soils (Kroupitski et al., 2015; Hemmerling et al., 2023). By moving between bacterial hotspots, e.g. soil and rhizosphere microbiome, bacterial feeders have a great vector potential for pathogen transfer from soil to crop roots (Fig. 2).

In contrast, plant parasites carry a mouth stylet and cannot ingest bacteria undamaged (Fig. 1). They are nevertheless vectors and transport bacteria externally on their cuticle (Topolović et al., 2019). This attachment is mediated by surface epitopes or specific carbohydrates on their surface coat (Spiegel and McClure, 1995; Davies and Curtis, 2011). The bacterial community carried can be diverse, with, e.g. 24 bacterial strains isolated from the pine wood nematode *Bursaphelenchus xylophilus* (Zhao et al., 2003). Injuries caused by parasitic nematodes also serve as entry sites for human pathogens (Tyler and Triplett, 2008).

Using plant parasitic nematodes as a vehicle, pathogenic bacteria can access roots (Hallman et al., 1998; Maghodia et al., 2008). Under appropriate conditions, they grow in the plant tissue as in the case for *Salmonella* in lettuce and *E. coli* in maize, resulting in subsequent dissemination to aerial parts of the plant (Bernstein et al., 2007a,b). On the other hand, Fornefeld et al. (2018) did not find that *M. hapla* and *Pratylenchus crenatus* improved internalisation of lettuce by *Salmonella*. Overall, plant parasites can assist pathogen invasion by providing wounds for pathogen entry and by actively transferring bacterial cells on their external surface into the plant (Fig. 2). However, their vector function is not as well documented as that for bacterial feeders, and further studies are needed.

5   Case study: root parasites shape the microbiome and rhizosphere processes of their host plant

The nature and outcome of the multitrophic interactions in the rhizosphere are vital for plant fitness and health. Plant parasitic nematodes have severe negative impacts on crops. Only two nematode genera, *Meloidogyne* and *Heterodera*, are responsible for ~10% reduction of the global food production (Nicol et al., 2011), which calls for effective and sustainable pest management. The primary concern is direct damage to specific plant hosts, i.e. the nematode's removal of carbon and energy, resulting in lower crop yield. Common solutions include crop rotation and the use of tolerant or resistant plants. Other more recent approaches include molecular breeding to improve plant defence (Liu and Park, 2018) or rhizosphere engineering to promote plant growth (Hakim et al., 2021) to develop a more eco-friendly, sustainable agriculture. However, a big gap in knowledge exists on the interplay between plant parasitic nematodes, microbiome community dynamics and host-plant responses.

As mentioned previously (see Section 3.1), feeding by nematodes leads to the release of plant metabolites in the rhizosphere, which promotes microbial communities. However, this goes beyond just increasing microbial substrates (e.g. sugars) in the rhizosphere. An illustration of this is a greenhouse experiment on barley (*Hordeum vulgare*) infected with the root-knot nematode *M. incognita*, and root hair morphology and rhizodeposition were investigated (Haase et al., 2007) as well as the rhizosphere microbiome, plant C allocation and biomass (Poll et al., 2007). The experiment studied a whole parasitic cycle, from the entry of second-stage juveniles at the root tip to feeding site establishment at the vascular cylinder and to the formation of root-knots by the host plant. Infestation rates of barley were kept below severe damage to allow the assessment of direct and indirect effects. The entire cycle of interactions between nematodes, microorganisms and plants is presented in Fig. 3.
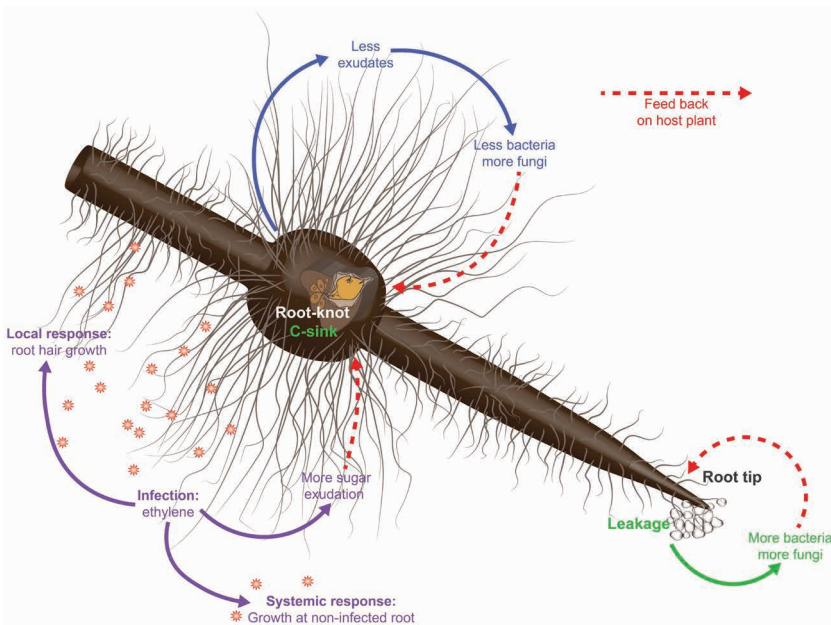
Figure 3 Root-knot nematodes and their multitrophic interactions in the rhizosphere. The second-stage juveniles penetrate near the root tip, resulting in the *leakage* of plant metabolites that promote microorganisms. *Root-knots* with mature females represent an active metabolic sink for plant carbon, reducing its availability for microorganisms. The *altered exudation pattern* on the surface of root-knots fosters fungi over bacteria. Phytohormones as host response to nematode infestation cause *local and systemic changes in root hair morphology*, i.e. an increase in length. These microscale modifications increase sugar exudation into the rhizosphere. Both the metabolic and morphological changes have feedback mechanisms (red arrows) on microbiome processes and thus nutrient dynamics and plant production.

Pulse-labelling barley with $^{13}CO_2$ showed that infestation with *M. incognita* enhanced plant C translocation to the rhizosphere, which altered microbial community dynamics (Poll et al., 2007). Barley root biomass and C content in shoots increased. However, with increasing densities of *M. incognita*, less plant C was sequestered by microorganisms and bacterial and fungal biomass decreased, indicating the shift from a mutualistic relationship to a parasitic interaction at higher infection rates. This highlights the positive impact of nematode-induced leakage on the rhizosphere microbiome at low levels of root herbivory (Fig. 3), as reported in other studies (Denton et al., 1998; Yeates et al., 1999; Maboreke et al., 2017).

This general pattern was modulated by the nematode life cycle. Positive responses of bacterial and fungal biomass occurred at the point when nematodes entered the root. Moreover, the composition of the soil microbiome changes with time and shifted in favour of fungi after root-knot development. The root exudation pattern also mirrored the life cycle of *M. incognita*. Enhanced release of total sugars and amino acids as well as the carboxylic acid fumarate from roots occurred only during nematode invasion, i.e. with mechanical penetration that causes leakage (Haase et al., 2007). After establishment inside roots, nematodes acted as a strong C sink (Fig. 3). ^{13}C labelling revealed that recent photo-assimilates were transferred to parasites and that availability of plant C for rhizosphere microorganisms was reduced (Poll et al., 2007).

Finally, the presence of *M. incognita* also had a striking impact on root hair morphology. Root infestation reduced root hair numbers but stimulated root hair length (Haase et al., 2007) (Fig. 3). Such changes are often related to phytohormone signalling, e.g. via ethylene, which is triggered by local wounding. However, as elongation of root hairs was apparent in both infected and uninfected roots of the same barley plant, nematodes had a systemic impact. The enlarged root surface further resulted in a higher sugar release across the entire root system. These microscale morphological modifications were connected to the nematode's life cycle and diminished after feeding site establishment.

Root-knots formed a specific microhabitat within barley roots. Compared with uninfected and infected root zones, the release rates of total amino acids were significantly reduced, and carboxylates malate and fumarate were absent even at root-knots (Fig. 3). This altered exudation pattern increased the biomass of saprotrophic fungi, while bacteria declined, particularly gram-positive taxa. Overall, this suggests competitive consumption of plant metabolites by the nematode in the root-knot, as reported by Gommers and Dropkin (1977), resulting in an adapted microbiome, the so-called 'gallobiome' (Masson et al., 2020).

In summary, the infection of crops by root-feeding nematodes leads to changes in root morphology, exudation pattern and the microbiome, which can all have feedback mechanisms affecting plant fitness and health (Fig. 3). The results from this study offer a basis for more sustainable crop management. The anatomical traits reported have the potential for the inhibition of similar events in plant molecular breeding, while the biochemical traits triggering microbiome interactions can be used to foster beneficial bacteria in rhizosphere engineering. Given the considerable economic impact of root parasitic nematodes, the response pattern of the plant and microbiome should be pooled to develop management measures for sustainable crop production.

6 Conclusion

Maintaining agricultural production on a sustainable basis requires conservation of soil biodiversity and ecosystem services. Nematodes play a central role in soil food webs and have important effects on processes such as the mineralisation of nutrients or the flow of C and energy from microorganisms to the meso- and macrofauna. These multiple functions make nematodes well-suited indicators to assess the impact of agricultural management, e.g. the shift from conventional to organic farming. Nematode indices can track microbiome disturbance, nutrient enrichment, decomposition channels and food web conditions. Nematodes thus provide a holistic measure of soil conditions, supporting research into approaches for improved and sustainable crop production.

On the other hand, root-feeding nematodes are serious plant pests with major effects on plant health and yield. Managing these impacts on crop production in a sustainable manner is a challenge for agriculture. However, indirect effects on the rhizosphere microbiome as well as the synergistic effects on plant hormone balance offer the potential for biotic control. Microbiome-based agronomic approaches, viewing the plant and its rhizosphere microbiome as a holobiont, co-evolving with root parasites, may promote more sustainable management of plant diseases.

Finally, specific agricultural practices can foster food-borne diseases. This applies particularly to organic farming with the application of manure and the use of recycled or waste water for irrigation in arid areas. The latter is likely to increase with climate change. The role of nematodes as vectors for human pathogens has received little attention, although they influence pathogen presence in the rhizosphere of crops and also in the crops themselves. Integration of these biotic interactions into a 'One Health' framework would lead to more efficient pathogen regulation strategies and, in turn, healthy fresh produce in sustainable agriculture.

7 Future trends

The framework for micro-food web diagnostics offered by nematode faunal analysis is a valuable tool to understand the structure and function of the soil microbiome. It links species, morphological traits and measured or inferred functional roles, therewith reflecting the multifunctionality of soil food webs (Potapov, 2022). However, the potential of nematodes as bioindicators is complicated by the enormous diversity of the phylum. A future trend is to match genetic inter-relatedness and functional trait expression, so that soil conditions and health can be assigned without the need for exact taxonomic identification. Initial attempts to link functional traits to novel sequences of nematodes have been made by Ross et al. (2022).

Over the last decade, improving the soil microbiome for sustaining ecosystem services has become a popular area of research (Chernov and Semenov, 2021). Biofertiliser and bio-pesticide products are used in organic and low-input farming to augment the soil microbial community (Rengalakshmi et al., 2018; Cornell et al., 2021). These bio-inputs play an integral role in maintaining soil quality. A future option is to exploit interactions with soil fauna. For instance, the fungal-feeding nematode *Aphelenchus avenae* has been shown to promote soil microbial activity, thereby alleviating damping-off disease caused by *Pythium ultimum* in tomato (Zhang et al., 2023). Climate change also affects belowground food chains. Thakur et al. (2021) showed that warming altered the dynamics in the rhizosphere microbiome differently, i.e. extreme heat events were detrimental for microorganisms, while their microfaunal grazers exhibited thermal acclimation. Future effective microbiome management therefore should include soil fauna to achieve healthy and sustainable farming systems.

Recently, conservation of soil mite predators using free-living nematodes as prey has been suggested as a way to improve agricultural ecosystem performance and sustainability (Azevedo et al., 2019; Rueda-Ramírez et al., 2023). Many predatory mites are generalists and feed on a diverse diet, making them excellent candidates for biological control programmes. Free-living nematodes serve as prey for many soil predatory mites (Heidemann et al., 2014a,b). For some mite species, they are an essential food in order to lay eggs (Walter et al., 1987) or undergo complete development into adults (Rueda-Ramírez et al., 2019), while other species show increased fecundity with a nematode diet (Moreira et al., 2015). Free-living nematodes can thus harness the soil food web for biological control of root-knot nematodes or other soil-borne pests.

8   Acknowledgements

9   Where to look for further information

A standard introduction to nematodes in soil ecosystems is D.W. Freckman, *Nematodes in Soil Ecosystems* (1982, University of Texas Press). Good single sources on nematode management in sustainable agriculture are:

- Meghvansi, M. K. and Chaudhary, K. K. (2022). *Sustainable Management of Nematodes in Agriculture, Vol.1: Organic Management*. Springer, Germany; 425 pp.
- Subbotin, S. A. and Chitambar, J. J. (2019). *Plant Parasitic Nematodes in Sustainable Agriculture of North America, Vol.2: Northeastern, Midwestern and Southern USA*. Springer, Germany; 457 pp.
- Grewal, P. S., Ehlers, R. U. and Shapiro-Ilan, D. I. (2005). *Nematodes as Biocontrol Agents*. CABI, Wallingford, UK; 489 pp.

The international nematological societies inform about recent advances in nematology in both fundamental and economic aspects. They support networking among scientists and promote and extend knowledge in all areas of nematology:

- Society of Nematologists (SON): https://www.nematologists.org/.
- European Society of Nematologists (ESN): https://www.esn-online.org/.
- Organisation of Nematologists of Tropical America (ONTA): https://ontaweb.org/.

There are a number of current online sources with useful information on nematodes:

- Nemaplex is a virtual encyclopaedia on nematodes (mainly soil and plant taxa) developed and maintained by Howard Ferris. The website contains information on biology, ecology, indices and various resources, e.g. collections, methods, teaching (http://nemaplex.ucdavis.edu).
- WormBook is a collection of original, peer-reviewed chapters covering topics related to the biology of *C. elegans* and other nematodes. It also

contains a collection of protocols on methods (http://www.wormbook .org/).

- WormBase provides the research community with current and accessible information concerning the genetics, genomics and biology of *C. elegans* and related nematodes. This international consortium of biologists and computer scientists was founded in 2000 (https://wormbase.org).

10 References

Anderson, G. L., Caldwell, K. N., Beuchat, L. R. and Williams, P. L. (2003). Interaction of a free-living soil nematode, *Caenorhabditis elegans*, with surrogates of foodborne pathogenic bacteria. *J. Food Prot.* 66(9), 1543–1549.

Anderson, G. L., Kenny, S. J., Millner, P. D., Beuchat, L. R. and Williams, P. L. (2006). Shedding of foodborne pathogens by *Caenorhabditis elegans* in compost-amended and unamended soil. *Food Microbiol.* 23(2), 146–153.

Andrássy, I. (2005). Free-living nematodes of Hungary (Nematoda errantia). In: Csuzdi, C. and Mahunka, S. (Eds). *Pedozoologica Hungarica 3*, Hungarian Natural History Museum, Budapest, Hungary, 518 pp.

Azevedo, L. H., Leite, L. G., Chacon-Orozco, J. G., Moreira, M. F. P., Ferreira, M. P., Cano, L. M., Borges, V., Rueda-Ramírez, D., de Moraes, G. J. and Palevsky, E. (2019). Free living nematodes as alternative prey for soil predatory mites: an interdisciplinary case study of conservation biological control. *Biol. Control* 132, 128–134.

Bell, C. A., Magjourilou, E., Urwin, P. E. and Field, K. J. (2021). The influence of competing root symbionts on below-ground plant resource allocation. *Ecol. Evol.* 11(7), 2997–3003.

Berg, G., Eberl, L. and Hartmann, A. (2005). The rhizosphere as a reservoir for opportunistic human pathogenic bacteria. *Environ. Microbiol.* 7(11), 1673–1685.

Berg, G., Grube, M., Schloter, M. and Smalla, K. (2014). Unravelling the plant microbiome: looking back and future perspectives. *Front. Microbiol.* 5, 148.

Berg, M., Stenuit, B., Ho, J., Parke, C., Knight, M., Alvarez-Cohen, L. and Shapira, M. (2016). Assembly of the *Caenorhabditis elegans* gut microbiome from diverse soil microbial environments. *ISME J.* 10, 1998–2009.

Bernstein, S., Sela, S. and Neder-Lavon, S. (2007a). Effect of irrigation regimes on persistence of *Salmonella enterica* serovar Newport in small experimental pots designed for plant cultivation. *Irrig. Sci.* 70, 471–475.

Bernstein, N., Sela, S., Pinto, R. and Loffe, M. (2007b). Evidence for internalization of *Escherichia coli* into the aerial parts of maize via the root system. *J. Food Prot.* 70(2), 471–475.

Bik, H. M. (2019). Microbial metazoan are microbes too. *mSystems* 4(3), e00109-19.

Biswal, D. (2022). Nematodes as ghosts of land use past: elucidating the roles of soil nematode community studies as indicators of soil health and land management practices. *Appl. Biochem. Biotechnol.* 194(5), 2357–2417.

Bnaerjee, S. and van der Heijden, M. G. A. (2023). Soil microbiomes and one health. *Nat. Rev. Microbiol.* 21(1), 6–20.

Bongers, T. (1990). The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83(1), 14–19.

Bongiorno, G. (2020). Novel soil quality indicators for the evaluation of agricultural management practices: a biological perspective. *Front. Agric. Sci. Eng.* 7(3), 257–274.

Bonkowski, M., Villenave, C. and Griffiths, B. (2009). Rhizosphere fauna: the functional and structural diversity of intimate interactions of soil fauna with plant roots. *Plant Soil* 321(1–2), 213–233.

Caldwell, K. N., Adler, B. B., Anderson, G. L., Williams, P. L. and Beuchat, L. R. (2003). Ingestion of *Salmonella enterica* serotype Poona by a free-living nematode, *Caenorhabditis elegans*, and protection against inactivation by produce sanitizers. *Appl. Environ. Microbiol.* 69(7), 4103–4110.

Castillo, J. D., Vivanco, J. M. and Manter, D. K. (2017). Bacterial microbiome and nematode occurrence in different potato agricultural soils. *Microb. Ecol.* 74(4), 888–900.

Chernov, T. I. and Semenov, M. V. (2021). Management of soil microbial communities: opportunities and prospects (a review). *Eurasian Soil Sc.* 54(12), 1888–1902.

Chernova, N. M., Bokova, A. I., Varshav, E. V., Goloshchapova, N. P. and Savenkova, Y. Y. (2007). Zoophagy in Collembola. *Entomol. Rev.* 87(7), 799–811.

Ciancio, A., Colagiero, M., Pentimone, I. and Rosso, L. (2016). Soil microbial communities and their potential for root-knot nematode management. *Environ. Eng. Manag. J.* 15(8), 1833–1839.

Clark, L. C. and Hodgkin, J. (2016). *Caenorhabditis* microbiota: worm guts get populated. *BMC Biol.* 14, 37.

Cornell, C., Kokkoris, V., Richards, A., Horst, C., Rosa, D., Bennet, J. A. and Hart, M. M. (2021). Do bioinoculants affect resident microbial communities? A metanalysis. *Front. Agronom.* 3, 753474.

Costa, J., Oliveira, R. S., Tiago, I., Ma, Y., Galhano, C., Freitas, H. and Castro, P. (2018). Soil microorganisms. In: Sáchnez-Moreiras, A. M. and Reigosa, M. J. (Eds). *Advances in Plant Ecophysiology Techniques*, Springer Nature, Germany, pp. 457–482.

Crotty, F. V., Blackshaw, R. P., Adl, S. M., Inger, R. and Murray, P. J. (2014). Divergence of feeding channels within the soil food web determined by ecosystem type. *Ecol. Evol.* 4(1), 1–13.

Davies, K. G. and Curtis, R. H. (2011). Cuticle surface coat of plant-parasitic nematodes. *Annu. Rev. Phytopathol.* 49, 135–156.

Denton, C. S., Mercer, C. F., Yeates, G. W. and Saggar, S. (1998). Impact of clover cyst nematode (*Heterodera trifolii*) infection on soil microbial activity in the rhizosphere of white clover (*Trifolium repens*) - a pulse-labelling experiment. *Nematologica* 44(1), 81–90.

De Vries, F. T. and Wallenstein, M. D. (2017). Below-ground connections underlying above-ground food production: a framework for optimising ecological connections in the rhizosphere. *J. Ecol.* 105(4), 913–920.

Di Montanara, A. C., Baldrighi, E., Franzo, A., Catani, L., Grassi, E., Sandulli, R. and Semprucci, F. (2022). Free-living nematode research: state of the art, prospects, and future directions. A bibliometric analysis approach. *Ecol. Inform.* 72, 101891.

Diaz, S. A. and Restif, O. (2014). Spread and transmission of bacterial pathogens in experimental populations of the nematode *Caenorhabditis elegans*. *Appl. Environ. Microbiol.* 80(17), 5411–5418.

Dirksen, P., Marsh, S. A., Braker, I., Heitland, N., Wagner, S., Nakad, R., Mader, S., Petersen, C., Kowallik, V., Rosenstiel, P., Félix, M. A. and Schulenburg, H. (2016). The native

microbiome of the nematode *Caenorhabditis elegans*: gateway to a new host-microbiome model. *BMC Biol.* 14, 38.

Djigal, D., Chabrier, C., Duyck, P.-F., Achard, R., Quénéhervé, P. and Tixier, P. (2012). Cover crops alter the soil nematode food web in banana agroecosystems. *Soil Biol. Biochem.* 48, 142–150.

Dukare, A., Mhatre, P., Maheshwari, H. S., Bagul, S., Manjuantha, B. S., Khade, Y. and Kamble, U. (2022). Delineation of mechanistic approaches of rhizosphere microorganisms facilitated plant health and resistance under challenging conditions. *Biotech* 12, 57.

Dunger, W. (2008). *Tiere im Boden* (4th edn.), Westarp-Wissenschaftsverlag, Germany.

Ewald, M., Glavatska, O. and Ruess, L. (2020). Effects of resource manipulation on nematode community structure and metabolic footprints in an arable soil across time and depth. *Nematology* 22(9), 1025–1043.

Ewald, M., Rusch, D., Rißmann, C., Trost, B., Theuerl, S. and Ruess, L. (2022). Effects of irrigation and fertilization practice on soil nematode communities in arable land. *Appl. Soil Ecol.* 177, 104546.

Ferris, H. (2010a). Contribution of nematodes to the structure and function of the soil food web. *J. Nematol.* 42(1), 63–67.

Ferris, H. (2010b). Form and function: metabolic footprints of nematodes in the soil food web. *Eur. J. Soil Biol.* 46(2), 97–104.

Ferris, H., Bongers, T. and Goede, de, R. G. M. (2001). A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Appl. Soil Ecol.* 18(1), 13–29.

Ferris, H. and Matute, M. M. (2003). Structural and functional succession in the nematode fauna of a soil food web. *Appl. Soil Ecol.* 23(2), 93–110.

Ferris, H. and Tuomisto, H. (2015). Unearthing the role of biological diversity in soil health. *Soil Biol. Biochem.* 85, 101–109.

Fierer, N. (2017). Embracing the unknown: disentangling the complexities of the soil microbiome. *Nat. Rev. Microbiol.* 15(10), 579–590.

Fornefeld, E., Baklawa, M., Hallmann, J., Schikora, A. and Smalla, K. (2018). Sewage sludge amendment and inoculation with plant-parasitic nematodes do not facilitate the internalization of *Salmonella* Typhimurium LT2 in lettuce plants. *Food Microbiol.* 71, 111–119.

Franz, E. and van Bruggen, A. H. (2008). Ecology of *E. coli* O157:H7 and *Salmonella enterica* in the primary vegetable production chain. *Crit. Rev. Microbiol.* 34(3–4), 143–161.

Freckman, D. W. and Caswell, E. P. (1985). The ecology of nematodes in agroecosystems. *Annu. Rev. Phytopathol.* 23(1), 275–296.

Georgieva, S. S., McGrath, S. P., Hooper, D. J. and Chambers, B. S. (2002). Nematode communities under stress: the long-term effects of heavy metals in soil treated with sewage sludge. *Appl. Soil Ecol.* 20(1), 27–42.

Gibbs, D. S., Anderson, G. L., Beuchat, L. R., Carta, L. K. and Williams, P. L. (2005). Potential role of *Diploscapter* sp. strain LKC25, a bacterivorous nematode from soil, as a vector of food-borne pathogenic bacteria to preharvest fruits and vegetables. *Appl. Environ. Microbiol.* 71(5), 2433–2437.

Gilarte, P., Plett, J., Pendall, E., Carrillo, Y. and Nielsen, U. N. (2020). Direct and indirect trophic interactions of soil nematodes impact chickpea and oat nutrition. *Plant Soil* 457(1–2), 255–268.

Gillet, F., Bournaud, C., de Souza Júnior, J. D. A. and Fatima Grossi-de-Sa, M. (2017). Plant-parasitic nematodes: towards understanding molecular players in stress responses. *Ann. Bot.* 199, 775–789.

Glavatska, O., Müller, K., Butenschoen, O., Schmalwasser, A., Kandeler, E., Scheu, S., Totsche, K. U. and Ruess, L. (2017). Disentangling the root- and detritus-based food chain in the micro food web of an arable soil by plant removal. *PLoS ONE* 12(7), e0180264.

Gommers, F. J. and Dropkin, V. H. (1977). Quantitative histochemistry of nematode induced transfer cells. *Phytopathol.* 67, 869–873.

Guan, T. Y. and Holley, R. A. (2003). Pathogen survival in swine manure environments and transmission of human enteric illness - a review. *J. Environ. Qual.* 32(2), 383–392.

Gupta, D., Bhandari, S. and Bhusal, D. R. (2019). Variation of nematode indices under contrasting pest management practices in a tomato growing agro-ecosystem. *Heliyon* 5(10), e02621.

Gupta, R., Anand, G., Gaur, R. and Yadav, D. (2021). Plant-microbiome interactions for sustainable agriculture: a review. *Physiol. Mol. Biol. Plants* 27(1), 165–179.

Haase, S., Ruess, L., Neumann, G., Marhan, S. and Kandeler, E. (2007). Low-level herbivory by root-knot nematodes (*Meloidogyne incognita*) modifies root hair morphology and rhizodeposition in host plants (*Hordeum vulgare*). *Plant Soil* 301(1–2), 151–164.

Hakim, S., Naqqash, T., Nawaz, M. S., Laraib, I., Siddique, M. J., Zia, R., Mirza, M. S. and Imran, A. (2021). Rhizosphere engineering with plant growth-promoting microorganisms for agriculture and ecological sustainability. *Front. Sustain. Food Syst.* 5, 617157.

Hallman, J., Quadt-Hallman, A., Rodríguez-Kábana, R. and Kloepper, J. W. (1998). Interaction between *Meloidogyne incognita* and endophytic bacteria in cotton and cucumber. *Soil Biol. Biochem.* 30(7), 925–937.

Heidemann, K., Hennies, A., Schakowske, J., Blumenberg, L., Ruess, L., Scheu, S. and Maraun, M. (2014a). Free-living nematodes as prey for higher trophic levels of forest soil food webs. *Oikos* 123(10), 1199–1211.

Heidemann, K., Ruess, L., Scheu, S. and Maraun, M. (2014b). Nematode consumption by mite communities varies in different forest microhabitats as indicated by molecular gut content analysis. *Exp. Appl. Acarol.* 64(1), 49–60.

Heijboer, A., Ruess, L., Traugott, M., Jousset, A. and de Ruiter, P. C. (2017). Empirical methods of identifying and quantifying trophic interactions for constructing soil food web models. In: de Ruiter, P. C., McCann, K. S. and Wolters, V. (Eds), *Adaptive Food Webs - Stability and Transitions of Real and Model Ecosystems*, Jackson College, Moore, Cambridge University Press, UK, pp. 257–285.

Hemmerling, C., Ackermann, M. and Ruess, L. (2023). Food choice between the human pathogen *Salmonella enterica* and common soil bacteria is related to nematode life traits. *Appl. Soil Ecol.* 192.

Hu, H., Yao, Z., Gao, S. and Zhu, B. (2022). Nematode response to long-term fertilization in purple soil. *Biodivers. Sci.* 30(12), 2022189.

Iwu, C. D. and Okoh, A. I. (2019). Preharvest transmission routes of fresh produce associated bacterial pathogens with outbreak potentials: a review. *Int. J. Environ. Res. Public Health* 16(22), 4407.

Jamieson, R. C., Gordon, R. J., Sharples, K. E., Stratton, G. W. and Madani, A. (2002). Movement and persistence of faecal bacteria in agricultural soils and subsurface drainage water: a review. *Can. Biosys. Eng.* 44, 1–9.

Jiang, Y., Wang, Z., Liu, Y., Wang, Y., Wang, Q. and Liu, T. (2022). Nematodes and their bacterial prey improve phosphorous acquisition by wheat. *New Phytol.* 237, 974–986.

Johansen, J. L., Dam, M., Kudjordjie, E. N., Santos, S. S., Palmqvist, A., Magid, J. and Vestergård, M. (2023). Effects of long-term fertilization with contemporary Danish human urine, composted household waste and sewage sludge on soil nematode abundance and community structure. *Sci. Total Environ.* 860, 160485.

Johnke, J., Dirksen, P. and Schulenburg, H. (2020). Community assembly of the native *C. elegans* microbiome is influenced by time, substrate and individual bacterial taxa. *Environ. Microbiol.* 22(4), 1265–1279.

Kane, J. L., Kotcon, J. B., Freedman, Z. B. and Morrissey, E. M. (2023). Fungivorous nematodes drive microbial diversity and carbon cycling in soil. *Ecology* 104(1), e3844.

Karuri, H. (2023). Nematode community response to intensive tomato production in the tropics. *Rhizosphere* 25, 100681.

Kenney, S. J., Anderson, G. L., Williams, P. L., Millner, P. D. and Beuchat, L. R. (2005). Persistence of *Escherichia coli* O157:H7, *Salmonella* Newport, and *Salmonella* Poona in the gut of a free-living nematode, *Caenorhabditis elegans*, and transmission to progeny and uninfected nematodes. *Int. J. Food Microbiol.* 101(2), 227–236.

Kenney, S. J., Anderson, G. L., Williams, P. L., Millner, P. D. and Beuchat, L. R. (2006). Migration of *Caenorhabditis elegans* to manure and manure compost and potential for transport of *Salmonella* Newport to fruits and vegetables. *Int. J. Food Microbiol.* 106(1), 61–68.

Kroupitski, Y., Pinto, R., Bucki, P., Belausov, E., Ruess, L., Spiegel, Y. and Sela, S. (2015). *Acrobeloides buetschlii* as a potential vector for enteric pathogens. *Nematology* 17(4), 447–457.

Lakshmanan, V., Selvaraj, G. and Bais, H. P. (2014). Functional soil microbiome: belowground solutions to an aboveground problem. *Plant Physiol.* 166(2), 689–700.

Lamelas, A., Desgarennes, D., López-Lima, D., Villain, L., Alomos-Sánchez, A., Artacho, A., Latorre, A., Moya, A. and Carrión, G. (2020). The bacterial microbiome of *Meloidogyne*-based disease complex in coffee and tomato. *Front. Plant Sci.* 11, 136.

Lazarova, S., Coyne, D., Rodríguez, G., Peteira, B. and Ciancio, A. (2021). Functional diversity of soil nematodes in relation to the impact of agriculture - a review. *Diversity* 13(2), 64.

Lee, S., Kin, Y. and Choi, J. (2020). Effect of soil microbial feeding on the gut microbiome and cadmium toxicity in *Caenorhabditis elegans*. *Ecotox. Env. Saf.* 187, 109777.

Leiririo, J. L., Karuri, H. and Nyaga, J. M. (2022). Nematode-based soil food web condition in mung bean under semi-arid conditions. *J. Agric. Food Res.* 10, 100465.

Lindo-Seminario, D., Mendez-Farroñan, S., Canta-Ventura, J., Córdova-Campos, J., Condemarin-Montealegre, C., Gutiérrez-Calle, S., Morales-Pizarro, A. and Mialhe-Matonnier, E. (2022). Endosymbiont microbiota of *Meloidogyne javanica* adult females infected by *Pasteuria penetrans*. *Trop. Subtrop. Agroecosys* 25, 132.

Liu, W. and Park, S.-W. (2018). Underground mystery: interactions between plant roots and parasitic nematodes. *Curr. Plant Biol.* 15, 25–29.

Lo, W. S., Han, Z., Witte, H., Rösler, W. and Sommer, R. J. (2022). Synergistic interaction of gut microbiota enhances the growth of nematode through neuroendocrine signaling. *Curr. Biol.* 32(9), 2037–2050.e4.

Lu, P., Shi, H., Tao, J., Jin, J., Wang, S., Zheng, Q., Liu, P., Xiang, B., Chen, Q., Xu, Y., Li, Z., Tan, J. and Cao, P. (2023). Metagenomic insights into the changes in the rhizosphere microbial community caused by the root-knot nematode *Meloidogyne incognita* in tabaco. *Environ. Res.* 216(4), 114848.

Lu, Q., Liu, T., Wang, N., Dou, Z., Wang, K. and Zuo, Y. (2020). A review of soil nematodes as biological indicators for the assessment of soil health. *Front. Agr. Sci. Eng.* 7(3), 275–281.

Maboreke, H. R., Graf, M., Grams, T. E. E., Herrmann, S., Scheu, S. and Ruess, L. (2017). Multitrophic interactions in the rhizosphere of a temperate forest tree affect plant carbon flow into the belowground food web. *Soil Biol. Biochem.* 115, 526–536.

Maghodia, A. B., Spiegel, Y. and Sela, S. (2008). Interaction between *Escherichia coli* and the plant-parasitic nematode *Meloidogyne javanica*. *J. Appl. Microbiol.* 105(6), 1810–1816.

Maina, S., Karuri, H. and Ng´endo, R. N. (2021). Free-living nematode assemblages associated with maize residues and their ecological significance. *J. Nematol.* 53, e2021-038.

Malacrinò, A., Wang, M., Caul, S., Karley, A. J. and Bennett, A. E. (2021). Herbivory shapes the rhizosphere bacterial microbiota in potato plants. *Environ. Microbiol. Rep.* 13(6), 805–811.

Markalanda, S. H., McFadden, C. J., Cassidy, S. T. and Wood, C. W. (2022). The soil microbiome increases plant survival and modifies interactions with root endosymbionts in the field. *Ecol. Evol.* 12(1), e8283.

Martins, S. J., Taerum, S. J., Triplett, L., Emerson, J. B., Zasada, I., Toledo, de, B. F., Kovac, J., Martin, K. and Bull, C. T. (2022). Predators of soil bacteria in plant and human health. *Phytobiomes J.* 6(3), 184–200.

Masson, A.-S., Bich, H. H., Simonin, M., Thi Nguyen, H., Czernic, P., Moulin, L. and Bellafiore, S. (2020). Deep modifications of the microbiome of rice roots infected by the parasitic nematode *Meloidogyne graminicola* in highly infested fields in Vietnam. *FEMS Microbiol. Ecol.* 26, fiaa099.

Melakeberhan, H., Bonito, G. and Kravchenko, A. N. (2021). Application of nematode community analyses-based models towards identifying sustainable soil health management outcomes: a review of the concepts. *Soil Syst.* 5(2), 32.

Mendes, R., Garbeva, P. and Raaijmakers, J. M. (2013). The rhizosphere microbiome: significance of plant beneficial, plant pathogenic and human pathogenic microorganisms. *FEMS Microbiol. Rev.* 37(5), 634–663.

Mielke, L., Taubert, M., Cesarz, S., Ruess, L., Küsel, K., Gleixner, G. and Lange, M. (2022). Nematode grazing increases the allocation of plant-derived carbon to soil bacteria and saprophytic fungi, and activates bacterial species of the rhizosphere. *Pedobiologia* 90, 150787.

Moreira, G. F., de Morais, M. R., Busoli, A. C. and de Moraes, G. J. (2015). Life cycle of *Cosmolaelaps jaboticabalensis* (Acari: Mesostigmata: Laelapidae) on *Frankliniella occidentalis* (Thysanoptera: Thripidae) and two factitious food sources. *Exp. Appl. Acarol.* 65(2), 219–226.

Mulder, C. and Maas, R. (2017). Unifying the functional diversity in natural and cultivated soil using the overall body-mass distribution of nematodes. *BMC Ecol.* 17(1), 36.

Neher, D. A. (2010). Ecology of plant and free-living nematodes in natural and agricultural soil. *Annu. Rev. Phytopathol.* 48, 371–394.

Neher, D., Bao, Y. and Chen, S. (2011). Effect of soil disturbance and biocides on nematode communities and extracellular enzyme activity in soybean cyst nematode suppressive soil. *Nematology* 13(6), 687–699.

Neher, D. A., Nishanthan, T., Grabau, Z. J. and Chen, S. Y. (2019). Crop rotation and tillage affect nematode communities more than biocides in monoculture soybean. *Appl. Soil Ecol.* 140, 89–97.

Nicholson, F. A., Groves, S. J. and Chambers, B. J. (2005). Pathogen survival during livestock manure storage and following land application. *Bioresour. Technol.* 96(2), 135–143.

Nicol, J. M. and Turner, S. J., Coyne, L. D., den Nijs, L., Hockland, S., Maafi, Z. T. (2011). Current nematode threats to world agriculture. In: Jones, J., Gheysen, G., and Fenoll, C. (Eds.), *Genomics and Molecular Genetics of Plant-Nematode Interaction*, Springer, Germany, 2011, pp. 21–43.

Nieminen, J. K. (2008). Soil animals and ecosystem processes: how much does nutrient cycling explain? *Pedobiologia* 51(5–6), 367–373.

Nykyri, J., Fang, X., Dorati, F., Bakr, R., Pasanen, M., Niemi, O., Palva, E. T., Jackson, R. W. and Pirhonen, M. (2014). Evidence that nematodes may vector the soft rot-causing enterobacterial phytopahogens. *Plant Pathol.* 63(4), 747–757.

O´Brien, A. M., Ginnan, N. A., Rebolleda-Gómez, M. and Wagner, M. R. (2021). Microbial effects on plant phenology and fitness. *Am. J. Bot.* 108(10), 1824–1837.

Omotayo, O. P. and Babalola, O. O. (2021). Resident rhizosphere microbiome's ecological dynamics and conservation: towards achieving the envisioned sustainable development goals, a review. *Int. Soil Water Cons. Res* 9, 127–142.

Pan, F., Han, X., Li, N., Yan, J. and Xu, Y. (2020). Effect of organic amendment amount on soil nematode community structure and metabolic footprints in soybean phase of a soybean-maize rotation on mollisols. *Pedosphere* 30(4), 544–554.

Park, M. R., Oh, S., Yun, H. S., Kim, S. H., Ko, Y. H., Ryu, J. H., Rhee, M. S., Shin, O. S. and Kim, Y. (2014). Enhanced protection of pathogenic *Escherichia coli* ingested by a soil nematode *Caenorhabditis elegans* against sanitizer treatments. *Biosci. Biotechnol. Biochem.* 78(11), 1917–1922.

Pausch, J., Kramer, S., Scharroba, A., Scheunemann, N., Butenschoen, O., Kandeler, E., Marhan, S., Riederer, M., Scheu, S., Kuzyakov, Y. and Ruess, L. (2016). Small but active – pool size does not matter for carbon incorporation in belowground food webs. *Funct. Ecol.* 30(3), 479–489.

Pausch, J., Hüninghaus, M., Kramer, S., Scharroba, A., Scheunemann, N., Butenschoen,O., Marhan, S., Bonkowski, M., Kandeler, E., Scheu, S., Kuzyakov, Y. and Ruess, L. (2018). Carbon budgets of top- and subsoil food webs in an arable system. *Pedobiologia* 69, 29–33.

Piśkiewicz, A. M., Millano, de, M. J. K., Duyts, H. and van der Putten, W. H. (2009). Plant ectoparasitic nematodes prefer roots without their microbial enemies. *Plant Soil* 316(1–2), 277–284.

Poll, J., Marhan, S., Haase, S., Hallmann, J., Kandeler, E. and Ruess, L. (2007). Low amounts of herbivory by root-knot nematodes affect microbial community dynamics and carbon allocation in the rhizosphere. *FEMS Microbiol. Ecol.* 62(3), 268–279.

Potapov, A. M. (2022). Multifunctionality of belowground food webs: resource, size and spatial energy channels. *Biol. Rev. Camb. Philos. Soc.* 97(4), 1691–1711.

Pothula, S. K., Gray, P. and Bernard, E. C. (2022). Increasing levels of physical disturbance affect soil nematode community composition in a previously undisturbed ecosystem. *J. Nematol.* 54, 10.2478.

Powers, T. O., Harris, T. S., Higgins, R. S., Mullin, P. G. and Powers, K. S. (2021). Nematode biodiversity assessments need vouchered databases: a bold reference library for plant-parasitic nematodes in the superfamily Criconematoidea. *Genome* 64(3), 232–241.

Qing, X., Wang, M., Karssen, G., Bucki, P., Bert, W. and Braun-Miyara, S. (2020). PPNID: a reference database and molecular identification pipeline for plant-parasitic nematodes. *Bioinformatics* 36(4), 1052–1056.

Ramos, T. D. M., Jay-Russel, M. T., Millner, P. D., Baron, J. N., Stover, J., Pagliari, P., Hutchinson, M., Lilley, J., Rowley, N., Haghani, V., Aminabadi, P., Kenney, A., Hashem, F., Martínez-López, B., Bihn, E. A., Clements, D. P., Shade, J. B., Sciligo, A. R. and Pires, A. F. A. (2021). Survival and persistence of foodborne pathogens in manure-amended soils and prevalence on fresh produce in certified organic farms: a multi-regional baseline analysis. *Front. Sustain. Food Syst.* 5, 67476.

Rengalakshmi, R. M. M., Prabavathy, V. R., Prabavathy, V. R., Jegan, S. and Selvamukilan, B. (2018). Building bioeconomy in agriculture: harnessing soil microbes for sustaining ecosystem services. In: *Towards a Sustainable Bioeconomy: Principles, Challenges and Perspectives*, Springer, Germany, pp. 261–277.

Richter, A., Kern, T., Wolf, S., Struck, U. and Ruess, L. (2019). Trophic and non-trophic interactions in binary links affect carbon flow in the soil micro-food web. *Soil Biol. Biochem.* 135, 239–247.

Rønn, R., Vestergård, M. and Ekelund, F. (2013). Interactions between bacteria, protozoa and nematodes in soil. *Acta Protozool.* 51, 223–235.

Ross, G. M., Berg, M. P., Salomon, S. and Nielsen, U. N. (2022). Phylogenies of traits and functions in soil invertebrate assemblages. *Austral. Ecol.* 47(3), 465–481.

Roth, E., Samara, N., Ackermann, M., Seiml-Buchinger, R., Saleh, A. and Ruess, L. (2015). Fertilization and irrigation practice as source of microorganisms and the impact on nematodes as their potential vectors. *Appl. Soil Ecol.* 90, 68–77.

Rueda-Ramírez, D., Rios-Malaver, D., Varela-Ramírez, A. and Moraes, de, G. J. (2019). Biology and predation capacity of *Parasitus bituberosus* (Acari: Mesostigmata: Parasitidae) on *Frankliniella occidentalis* (Thysanoptera: Thripidae) and free-living nematodes as complementary diet. *Pest Manag. Sci.* 75(7), 1819–1830.

Rueda-Ramírez, D., Palevsky, E. and Ruess, L. (2023). Soil Nematodes as a means of conservation of soil predatory mites for biocontrol. *Agronomy* 13(1), 32.

Ruess, L. (2003). Nematode soil faunal analysis of decomposition pathways in different ecosystems. *Nematology* 5(2), 179–181.

Ruess, L. and Ferris, H. (2004). Decomposition pathways and successional changes. *Nematol. Monogr. Perspect.* 2, 547–556.

Scharroba, A., Dibbern, D., Hünninghaus, M., Kramer, S., Moll, S., Butenschoen, O., Bonkowski, M., Buscot, F., Kandeler, E., Koller, R., Krüger, D., Lueders, T., Scheu, S. and Ruess, L. (2012). Effects of resource availability and quality on the structure of the micro-food web of an arable soil across depth. *Soil Biol. Biochem.* 50, 111–119.

Schmidt, J. H., Theisgen, L. V., Finckh, M. R. and Šišić, A. (2022). Increased resilience of peas toward root rot pathogens can be predicted by the nematode metabolic footprint. *Front. Sustain. Food Syst.* 6, 881520.

Sharma, M., Saini, I., Kaushik, P., Aldawsari, M. M., Balawi, T. A. and Alam, P. (2021). Mycorrhiza fungi and *Pseudomonas fluorescens* application reduces root-knot nematode (*Meloidogyne javanica*) infestation in eggplant. *Saudi J. Biol. Sci.* 28(7), 3685–3691.

Siddique, S., Coomer, A., Baum, T. and Williamson, V. M. (2022). Recognition and response in plant-nematode interactions. *Annu. Rev. Phytopathol.* 60, 143–162.

Silva, J. C. P. D., Mederios, F. H. V. D. and Campos, V. P. (2018). Building soil suppressiveness against plant-parasitic nematodes. *Biocont. Sci. Techn.* 28, 423–445.

Skider, M. M., Vestergård, M., Kyndt, T., Topalović, O., Kudjordjie, E. N. and Nicolaisen, M. (2022.). Genetic disruption of *Arabidopsis* secondary metabolite synthesis leads to microbiome-mediated modulation of nematode invasion. *ISME J.* 16(9), 2230–2241.

Spiegel, Y. and McClure, M. A. (1995). The surface coat of plant parasitic nematodes: chemical composition, origin and biological role - a review. *J. Nematol.* 27(2), 127–134.

Sutherland, J. R. and Webster, J. M. (1993). Nematode pests of forest trees. In: Evans, K., Trudgill, D. L. and Webster, J. M. (Eds). *Plant Parasitic Nematodes in Temperate Agriculture*, CAB International, Wallingford UK, pp. 351–380.

Thahira, T., Qadeer, K., Sosso, J. and Zakeel, M. C. M. (2022). Role of plant microbiome in crop protection. In: Soni, R., Suyal, D. C. and Goel, R. (Eds). *Plant Protection: From Chemicals to Biologicals*, De Gruyter, Germany, pp. 573–600.

Thakur, M. P., van der Putten, W. H., Apon, F., Angelini, E., Vreš, B. and Geisen, S. (2021). Resilience of rhizosphere microbial predators and their prey communities after extreme heat events. *Funct. Ecol.* 35(1), 216–225.

Topolavić, O., Elhady, A., Hallmann, J., Richert-Pöggeler, K. R. and Heuer, H. (2019). Bacteria isolated from the cuticule of plant-parasitic nematodes attached to and antagonized the root-knot nematode *Meloidogyne hapla*. *Sci. Rep.* 9(1), 11477.

Topalović, O., Heuer, H., Reineke, A., Zinkernagel, J. and Hallmann, J. (2020). Antagonistic role of the microbiome from a *Meloidogyne hapla* - suppressive soil against species of plant-parasitic nematodes of different life strategies. *Nematology* 22(1), 75–86.

Tran, D. T. Q., Bradbury, M. I., van Ogtrop, F. F. V., Bozkurt, H., Jones, B. J. and McConchie, R. (2020). Environmental drivers for persistence of *Escherichia coli* and *Salmonella* in manure-amended soil: a meta-analysis. *J. Food Prot.* 83(7), 1268–1277.

Tyler, H. L. and Triplett, E. W. (2008). Plants as a habitat for beneficial and/or human pathogenic bacteria. *Annu. Rev. Phytopathol.* 46(1), 53–73.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., de Goede, R. G. M., Adams, B. J., Ahmad, W., Andriuzzi, W. S., Bardgett, R. D., Bonkowski, M., Campos-Herrera, R., Cares, J. E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S. R., Creamer, R., Mauro da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B. S., Gutiérrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A. A., Li, Q., Liang, W., Magilton, M., Marais, M., Martín, J. A. R., Matveeva, E., Mayad, E. H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T. A. D., Nielsen, U. N., Okada, H., Rius, J. E. P., Pan, K., Peneva, V., Pellissier, L., Carlos Pereira da Silva, J., Pitteloud, C., Powers, T. O., Powers, K., Quist, C. W., Rasmann, S., Moreno, S. S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A. V., Trap, J., van der Putten, W., Vestergård, M., Villenave, C., Waeyenberge, L., Wall, D. H., Wilschut, R., Wright, D. G., Yang, J. I. and Crowther, T. W. (2019). Soil nematode abundance and functional group composition at a global scale. *Nature* 572(7768), 194–198.

van Elsas, J. D., Chiurazzi, M., Mallon, C. A., Elhottova, D., Kristufek, V. and Salles, J. F. (2012). Microbial diversity determines the invasion of soil by a bacterial pathogen. *Proc. Natl. Acad. Sci. U. S. A.* 109(4), 1159–1164.

van Overbeek, L. S., Franz, E., Semenov, A. V., De Vos, O. J. and van Bruggen, A. H. C. (2010). The effect of the native bacterial community structure on the predictability

of *E. coli* O157:H7 survival in manure-amended soil. *Lett. Appl. Microbiol.* 50(4), 425–430.

van Overbeek, L. S., van Doorn, J., Wichers, J. H., van Amerongen, A., van Roermund, H. J. W. and Willemsen, P. T. J. (2014). The arable ecosystem as battleground for emergence of new human pathogens. *Front. Microbiol.* 5, 104.

Walter, D. E. and Proctor, H. C. (2013). *Mites: Ecology, Evolution & Behaviour* (2nd edn.), Springer, The Netherlands. 494 pp.

Walter, D. E., Hunt, H. W. and Elliott, E. T. (1987). The influence of prey type on the development and reproduction of some predatory soil mites. *Pedobiologia* 30, 419–424.

Wasilewska, L. and Webster, J. M. (1975). Free-living nematodes as disease factors of man and his crops. *Int. J. Environ. Stud.* 7(3), 201–204.

Whalen, J. K., Kernecker, M. L., Thomas, B. W., Sachdeva, V. and Ngosong, C. (2013). Soil food web controls on nitrogen mineralization are influences by agricultural practices in humid temperate climates. *CAB Rev.* 8, 1–18.

Wolkovich, E. M. (2016). Reticulated channels in soil food webs. *Soil Biol. Biochem.* 102, 18–21.

Wood, C. W., Pilkington, B. L., Vaidya, P., Biel, C. and Stinchcombe, J. R. (2018). Genetic conflict with a parasitic nematode disrupts the legume-rhizobia mutualism. *Evol. Lett.* 2(3), 233–245.

Yang, B., Chen, Q., Liu, X., Chen, F., Liang, Y., Qiang, W., He, L. and Ge, F. (2020). Effects of pest management practices on soil nematode abundance, diversity, metabolic footprint and community composition under paddy rice fields. *Front. Plant Sci.* 11, 88.

Yang, L., Zhang, F., Luo, Y. and Tang, P. (2022). Continuous cotton cropping affects soil micro-food web. *Appl. Soil Ecol.* 171, 104304.

Yang, Y. R., Li, X. G., Zhou, Z. G., Zhang, T. L. and Wang, X. X. (2016). Differential responses of soil nematode community to pig manure application levels in ferric acrisols. *Sci. Rep.* 6, 35334.

Yeates, G. W. (2010). Nematodes in ecological webs. In: *Encyclopedia of Life Sciences*, John Wiley & Sons, Hoboken, pp. 1–11.

Yeates, G. W., Bongers, T., Goede, de, R. G. M., Freckman, D. W. and Georgieva, S. S. (1993). Feeding habits in soil nematode families and genera - an outline for soil ecologists. *J. Nematol.* 25(3), 315–331.

Yeates, G. W., Saggar, S., Hedley, C. B. and Mercer, C. F. (1999). Increase in ^{14}C-carbon translocation to the soil microbial biomass when five species of plant-parasitic nematodes infect root of white clover. *Nematology* 1(3), 295–300.

Zhang, F., Berg, M., Dierking, K., Félix, M. A., Shapira, M., Samuel, B. S. and Schulenburg, H. (2017). *Caenorhabditis elegans* as model for microbiome research. *Front. Microbiol.* 8, 485.

Zhang, F., Weckhorst, J. L., Assié, A., Hosea, C., Ayoub, C. A., Khodakova, A. S., Loeza Cabrera, M. L., Vidal Vilchis, D., Félix, M. A. and Samuel, B. S. (2021). Natural genetic variation drives microbiome selection in the *Caenorhabditis elegans* gut. *Curr. Biol.* 31(12), 2603–2618.e9.

Zhang, P., Zhang, W. and Hu, S. (2023). Fungivorous nematode *Aphelenchus avenae* and Collembola *Hypogastrura perplexa* alleviate damping-off disease caused by *Pythium ultimum* in tomato. *Plant Soil* 482(1–2), 175–189.

Zhang, S., Zeng, H.-C. and Jin, Z.-Q. (2016). Response of soil nematode community composition and diversity to different crop rotations and tillage in the tropics. *Appl. Soil Ecol.* 107, 134–143.

Zhang, Z., Zhang, X., Jhao, J., Zhang, X. and Liang, W. (2015). Tillage and rotation effects on community composition and metabolic footprints of soil nematodes in a black soil. *Eur. J. Soil Biol.* 66, 40–48.

Zhang, Z., Li, B., Wang, H., Zhang, X., Cui, S., An, T., Fu, S., Mahamood, M., Zhang, D. and Wang, J. (2023). The fungal feeding channel of the soil micro-food web contributes to the transformation of exogenous C into soil C – a ^{13}C labelling experiment. *Land Degrad. Dev.* 34(2), 466-477.

Zhao, B. G., Wang, H. L., Han, S. F. and Han, Z. M. (2003). Distribution and pathogenicity of bacteria species carried by *Bursaphelenchus xylophilus* in China. *Nematology* 5(6), 899–906.

Zhao, X., Lin, C., Tan, J., Yang, P., Wang, R. and Qi, G. (2023). Changes in rhizosphere microbiome and metabolites in *Meloidogyne incognita* infested soil. *Plant Soil* 483(1–2), 331–353.

Zheng, F., Zhu, D., Giles, M., Daniell, T., Neilson, R., Zhu, Y. G. and Yang, X. R. (2019). Mineral and organic fertilization alters the microbiome of a soil nematode *Dorylaimus stagnalis* and its resistome. *Sci. Total Environ.* 680, 70-78.

Zheng, F., Zhu, D., Chen, Q. L., Bi, Q. F., Yang, X. R., O′Connor, P. and Zhu, Y. G. (2020). The driving factors of nematode gut microbiota under long term fertilization. *FEMS Microbiol. Ecol.* 96(4), fiaa037.

Zheng, J., Dini-Andreote, F., Luan, L., Geisen, S., Xue, J., Li, H., Sun, B. and Jiang, Y. (2022). Nematode predation and competitive interactions affect microbe-mediated phosphorus dynamics. *mBio* 13(3), e0329321.

Zhong, S., Zeng, H.-C. and Jin, Z.-Q. (2017). Influences of different tillage and residue management systems on soil nematode community composition and diversity in the tropics. *Soil Biol. Biochem.* 107, 234–243.

Zhou, J., Lu, M., Sheng, X. and Wu, J. (2022). Effects of nitrogen addition and warming on nematode ecological indices: a meta-analysis. *Eurp J. Soil Biol.* 110, 103407.