1 Roles of Nematodes in Ecosystems: Their Biology and Ecology

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Abstract

The organisms of soil and aquatic food webs perform ecological functions and services that are essential for life on Earth. Nematodes, the most abundant multicellular animals on the planet, are prevalent in terrestrial, marine and freshwater ecosystems. Humans have likely been aware of the indicator characteristics of nematodes since before recorded history, first as human and animal parasites by their presence in faeces, skin lesions and sputum, and progressively, with improvements in microscopy, as free-living soil and aquatic forms. The abundance and diversity of nematodes with different feeding habits and ecological functions in soil systems, for example, indicate resource availability and the favourability of environmental conditions. Because of their diversity and ubiquity, nematodes are convenient indicators of similar functions performed by other organisms in their environment. In this chapter we provide insights into the biological and ecological properties of nematodes that underlie their usefulness as environmental indicators.

1.1 Introduction

Human society and, in fact, life on the planet are entirely dependent on a variety of ecosystem services, many of them provided by soil biodiversity (Wall, 2004; Millennium Ecosystem Assessment, 2005). Nematodes play a major role in most soil-borne ecosystem services. They influence the provisioning of food, fibre, clean water and air, and regulation of pests and diseases. Nematodes participate in the transformation of organic matter into mineral and organic nutrients that provide plant nutrition and crop productivity and are available to other organisms in soil and sediment food webs (Ingham *et al*., 1985; Ferris *et al*., 1998, 2004c). Nematode feeding activities on soil microbes and other organisms contribute to food web stability through a variety of complex metabolic and behavioural interactions. However, their feeding activities may also destabilize food webs, leading to ecosystem transitions. Some nematodes cause plant, animal or human diseases, while others may influence pest damage to plants by regulating insect abundance (Viglierchio, 1991). In natural ecosystems, nematodes contribute to spatial and temporal diversity in plant communities and, therefore, to the diversity of plant-associated communities of microbes and invertebrates, both above- and below-ground (De Deyn and Van der Putten, 2005). Most effects in

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which nematodes are involved may be due to the combined influences of nematodes with many other soil organisms (Kardol *et al.*, 2005; Sánchez-Moreno *et al.*, 2008).

1.1.1 Indicator value

Because nematodes are so omnipresent and abundant in ecosystems, they may serve as relatively easily obtainable and informative indicators of environmental disturbance (Bongers 1990; Ferris *et al.*, 2001; Yeates, 2003; Höss *et al.*, 2004; Schratzberger *et al.*, 2006; Heininger *et al.*, 2007; Ridall and Ingels, 2021; Du Preez *et al.*, 2022). In fact, a recent review of the literature documented 672 instances of the use of nematodes as bioindicators (Du Preez *et al.*, 2022). One nematode species, *Caenorhabditis elegans* (Rhabditina), has become a central model for genomic studies that aim to relate gene expression to the development and functioning of organisms. Indeed, *C. elegans* was the first multicellular organism whose genome was sequenced (CESC, 1998). Studies on *C. elegans* underpin many of the advances in molecular biology. With advances in technology, several other nematode genomes have been sequenced, leading to greater understanding of the effects of environmental cues on nematode development, moulting, ageing, longevity, behaviour and other life-history characteristics.

There are estimates of between 40,000 and 10,000,000 species in the phylum Nematoda (Blaxter, 1998; Yeates and Boag, 2006). Clearly, continued exploration activities are necessary to verify these and other estimates. For example, one provocative speculation is that there might be as many as 100,000,000 nematode species, even before considering the cryptic diversity among morphologically indistinguishable taxa (Lambshead, 1993; Nadler and Perez-Ponce de Leon, 2011). Molecular techniques have improved understanding of the phylogenetic relationships of nematodes with other animal groups. There has been considerable debate about their associations relative to the ecdysozoan theory based on the occurrence of the *Hox* gene in various animal groups (De Rosa *et al.*, 1999; Gutierrez and Sommer, 2004). However, that theory is disputed by studies that included a larger number of genes in the analysis (Blair *et al.*, 2002). Nematodes are now generally classified as the phylum Nematoda in the Acoelomata of the Metazoa (see outline classification in Appendix 1).

1.1.2 Body structure

Nematodes are built on a simple plan, with the digestive tract and body wall being concentric tubes. The typical nematode has a mouth (= oral aperture) leading to a stoma (= buccal cavity), connected to the lumen of a muscular and/or glandular pharynx (= oesophagus) that leads to a tubular intestine, a rectum and posterior anus. The lack of a complete mesodermal lining of the body cavity led to the characterization of nematodes as pseudocoelomate (Hyman, 1951). The body is cylindrical or spindle-shaped and the tail beyond the anus varies enormously in length. Adult females range in length from 0.3 mm to 8 m. A vast range of head structures that facilitate food ingestion parallels the great diversity of nematodes and can be useful indicators of feeding habits (Fig. 1.1). The tubular gonads lie in the cavity between the digestive tract and body wall, and they, together with the associated genital structures, are further sources of species differentiation. The typical life history of nematodes includes an egg and, usually, four juvenile stages (= 'larvae') preceding the adults. The morphology of the juvenile stages converges with that of the adult; there is no metamorphosis.

1.1.3 History

There is a long history to our knowledge of nematodes. They were recorded as human parasites by the Chinese around 2700 BC and as plant parasites by Shakespeare in 1594 (Viglierchio, 1991) and more formally by Needham (1744). Although our attention has been drawn to nematode species that, through parasitism, adversely affect the quality of life of humans, domestic animals and food sources, the vast majority of nematode taxa are 'free-living'; they feed on bacteria, algae, fungi, diatoms, microinvertebrates and the epistrate deposits of aquatic sediments (Yeates *et al.*, 1993; Moens and Vincx, 1997; Traunspurger *et al.*, 1997; Schratzberger *et al.*, 2019; Hodda, 2022). With growing awareness

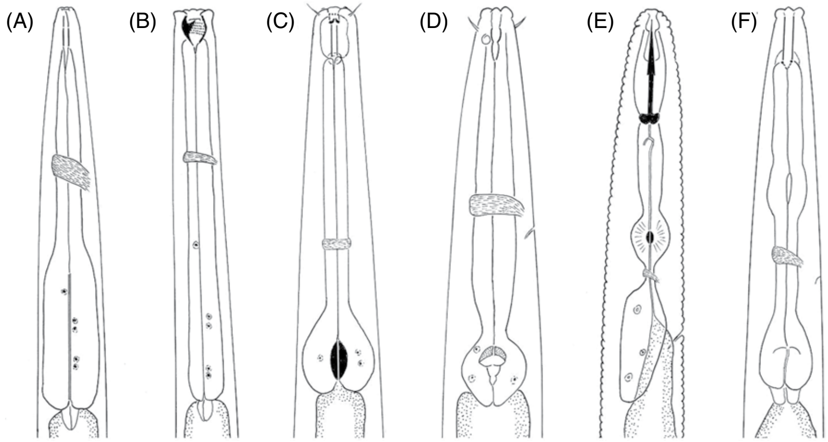

Fig. 1.1. Head and pharyngeal regions of six nematodes found in soil and water environments. (A) Dorylaimida: Dorylaimidae, *Dorylaimus*; (B) Mononchida, Mylonchulidae, *Mylonchulus*; (C) Chromadorida, Ethmolaimidae, *Ethmolaimus*; (D) Plectida, Plectidae, *Plectus*; (E) Tylenchina, Hoplolaimidae, *Rotylenchus*; (F) Rhabditina, Rhabditidae, *Rhabditis*. In most, the location of the circum-pharyngeal nerve ring, pharyngeal gland nuclei and amphid are shown. The diameter of the stylet lumen is ~5 μm in (A) and ~0.1 μm in (E). Diagrammatic and not to scale. (Author's own image compiled from various sources and observations.)

of the potential extinction of yet undescribed species – of both nematodes and other phyla – our ignorance of nematode diversity, habitat range and ecological amplitude continues to be challenged. In the latter part of the 20th century, the roles of nematodes in biological turnover in soil came to be appreciated (Yeates, 1984; Ingham *et al.*, 1985; Ferris *et al.*, 1997, 2004c). Awareness of the impact of nematode activity on populations of other organisms, and thus on ecosystem processes, developed concomitantly with awareness of the importance of biodiversity. Understanding of the possibilities of interpreting the abundance and diversity of nematode assemblages in various habitats has led to the development of information-rich 'indices' that may be used to characterize disturbance and other environmental conditions (Bongers, 1990; Ferris *et al.*, 2001; Yeates, 2003; Du Preez *et al.*, 2022).

1.2 Nematode Biology – Individuals and Populations – An Outline

1.2.1 Feeding by nematodes

Most nematodes utilize the energy fixed by plant photosynthesis. They may feed directly on primary producers, such as higher plants (e.g. *Aphelenchoides* on foliar parts, *Ditylenchus* on stems, *Pratylenchus* and *Meloidogyne* on roots) and unicellular algae (e.g. *Chromadorita*, *Daptonema* and *Pareudiplogaster* on diatoms), or on microbes associated with decomposing plant material (e.g. *Aphelenchus*, *Filenchus* on fungal hyphae; *Rhabditis*, *Plectus*, *Leptolaimus* on bacteria). Soil organic matter, litter, marine detritus, animal faeces and cadavers are important resources for microbes and thus for microbial- and epistrate-feeding nematodes. Higher trophic levels feed as predators of nematodes and other microinvertebrates (e.g. *Mononchus*, *Nygolaimus*, *Enoploides*, *Sphaerolaimus*) or as parasites of invertebrate and vertebrate animals (e.g. *Strongyloides*, *Thelastoma*, *Ascaris*). Therefore, except for herbivores in the second trophic level, most nematodes are third (bacterivores, fungivores) or fourth (carnivores) trophic-level organisms. Omnivores may predate on all trophic levels, depending on the trophic position of the resources that they feed on. A few marine species in low-oxygen environments obtain energy from chemical bonds in their environment or from symbiotic sulfur-oxidizing bacteria (e.g. *Astomomema*) (Polz *et al.*, 2000; Van Gaever *et al.*, 2006; Blaxter and Koutsovoulos, 2015).

1.2.2 Physical environments occupied by nematodes

Nematodes are influenced by the nature of their physical environment (e.g. soil or sediment texture, water chemistry) and by gradients within it (e.g. redox potential, plant root distribution, temperature, moisture). There is a clear distinction between the physical environment occupied by a nematode and the food resource it uses, and each may vary with the nematode life stage. In typical bacterial-feeding, hyphal-feeding and predacious nematodes, all post-hatching stages, while feeding, occupy soils, sediments or decaying vegetation. Plant-feeding nematodes such as *Pratylenchus* and *Radopholus* feed solely on plant cell contents but migrate between plants and soil. The cyst nematodes, *Heterodera* and *Globodera*, and the root-knot nematode *Meloidogyne*, hatch as second-stage juveniles that migrate, without feeding, into roots, where they develop into saccate females feeding on plant resources via highly specialized transfer cells.

In terrestrial habitats, eggs of ascarids (e.g. *Ascaris*) do not hatch outside the invertebrate or vertebrate host and they complete their life histories within the living host; adults inhabit the stomach and intestine of the definitive host and primarily consume food ingested by the host. In contrast, intestinal parasites of vertebrate hosts (e.g. *Ancylostoma*, *Strongylus*, *Trichostrongylus*, *Haemonchus*) feed in the intestinal mucosa, commonly evidenced by blood in host intestines and faecal matter. Their eggs hatch in faeces and grow as bacterial-feeding stages in a non-living substrate before reinfecting a new vertebrate host. Other nematode parasites of humans and other vertebrates (e.g. *Dracunculus*) have complex life cycles with invertebrates as secondary hosts that are consumed by definitive hosts in which the nematodes complete their life cycle. Nematodes that feed on bacteria, fungi, and on other component organisms of decomposition food chains, aggregate where their food sources are plentiful, such as the plant rhizosphere or near the soil surface where decay of leaf litter and other organic debris is occurring. Of course, their abundance in any environment will depend on favourable conditions of temperature, moisture and aeration, and the activity of predators.

1.2.3 Nematode response to stimuli

Behavioural responses to stimuli are essential for the success of nematodes in locating food resources, hosts and mates. While thermotaxis, phototaxis and geotropism are responses to basic environmental cues, they are important in host location in taxa as diverse as *Ancylostoma*, *Stephanurus*, *Anguina*, *Mermis* and *Trichostrongylus*. Chemotaxis is commonly involved in food finding and food selection by free-living nematodes. Responses to different kinds of chemicals and/or bacterial food tend to be highly species-specific and potentially contribute to the small-scale patchiness of nematode populations (Venette and Ferris, 1998; Moens *et al.*, 1999; Höckelmann *et al.*, 2004; Wilschut *et al.*, 2017). There is an increasing knowledge base regarding semiochemical signalling between plant roots and both parasitic and beneficial nematodes (Rasmann *et al.*, 2012; Ali and Davidson-Lowe, 2015; Pineda *et al.*, 2015). However, although plant-parasitic nematodes are highly efficient in locating plant roots, only a few plant signals that allow root location have been identified and characterized (Kulkarni *et al.*, 2018). For example, CO_2 attracts many species of plant-parasitic nematodes (McCallum and Dusenbery, 1992; Robinson, 1995), ethylene attracts *Heterodera* juveniles (Wubben *et al.*, 2001), and onion-root exudates attract *Ditylenchus* juveniles (Spiegel *et al.*, 2003). Rühm *et al.* (2003) found that an unknown kairomone in *Sinapsis alba* exudates served as an attractant to *Heterodera schachtii* juveniles and a range of root metabolites that impact the behaviour of soil nematodes has been documented (Sikder and Vestergard, 2020). An interesting example of molecular interactions between host and parasite is that of an ascaroside pheromone released by nematodes that is metabolically edited by plant cells to generate chemical signals that repel infective stages (Manohar *et al.*, 2020). Clearly, to successfully invade their host plants, plant-parasitic nematodes must evolve molecular mechanisms to overcome plant defence responses (Ali *et al.*, 2018).

Some of the responses of nematodes to stimuli seem to be species-specific; root exudates from favourable host plants increase egg hatching of cyst nematodes of the Heteroderidae (Wang *et al.*, 1997; Zasada *et al.*, 2013) and exudates of cotton roots increase egg hatching of *Rotylenchulus* *reniformis* (Sankaralingam and McGawley, 1994). Among the early work on sex attractants was that of Green and Plumb (1970) with *Heterodera* spp. and *Globodera* spp.; other work has included studies on *Panagrolaimus*, *Rhabditis*, *Panagrellus*, *Ditylenchus*, *Belonolaimus* and Trichostrongylidae. The sensitivity of nematode response to chemical stimuli in their environment is demonstrated by the ability of *C. elegans* to detect and distinguish between odour compounds at picomolar (10^{-12}) concentrations (Bargmann and Mori, 1997) and the attraction to plant roots of bacterial-feeding nematodes with adhering rhizobium bacteria (Horiuchi *et al.*, 2005).

1.2.4 Abundance and diversity of nematodes

A square metre of soil, forest litter or aquatic sediment may contain millions of individual nematodes belonging to over 400 species. Nematodes may also be abundant and diverse within living substrates. N.A. Cobb (1915) recorded 40,000 individual nematodes from the stomach of a wallaby. In New Zealand, domestic cattle and sheep can be infected by as many as 27 and 29 nematode species, respectively (McKenna, 1997). As a result, identifying the taxa in each nematode assemblage, and assessing the absolute and relative contribution of each taxon to the nematode assemblage, would be a prodigious task. Unless a study is restricted to a particular group (e.g. comparing pre-planting and post-harvest populations of plant-feeding nematodes or assessing the abundance of infective juveniles of Trichostrongylidae on pasture herbage), it is useful to present results in information-rich indices. Such indices may be either those widely used in ecological studies, such as the Shannon–Weiner index of diversity (H′), Margalef index of richness (D or SR) and Pielou's evenness (J′) (Pielou 1975; Yeates, 1984; Magurran, 1988; see Chapter 4, this volume), or indices specifically developed for nematodes (Bongers, 1990; Ferris *et al.*, 2001; see Chapter 5, this volume).

Nematode grazing on microbes can significantly increase nutrient cycling and plant responses in localized patches (Ingham *et al.*, 1985; Ferris *et al.*, 1998; Zhang *et al.*, 2017). Although there have been various studies, there is a need for understanding the factors governing the distribution of patches, when scaling up from a roughly homogeneous patch (e.g. a uniform agricultural field) to the landscape and regional scales for policy development (Coleman *et al.*, 1992; Müller and Lenz, 2006; Sánchez-Moreno *et al.*, 2008). The organizational structure of ecosystems is mediated by the energy available to develop network designs that maximize the energy fluxes through them that are compatible with the constraints of the environment. The eco-exergy of a system includes not only the free energy of matter, but also the available energy of embodied information utilized for interactions and the performance of ecosystem processes (Jørgensen and Mejer, 1979; Odum, 1988).

1.2.5 Effects of nematodes on their resources

Nematodes may affect the growth rates, health and yield of plants or animals (e.g. infection of soybeans or potatoes with cyst nematodes or of grazing mammals with trichostrongylids). In contrast, grazing and bioturbation by microbial feeding nematodes may stimulate nutrient cycling and plant yield (Ingham *et al.*, 1985; Alkemade *et al.*, 1992; Aller and Aller, 1992; Fu *et al.*, 2005). By its very nature, parasitism involves mutual adjustment between host and parasite to permit coexistence without serious harm to either component of the interaction. Indeed, some studies suggested that low burdens of plant-feeding nematodes may stimulate plant growth under favourable conditions, perhaps by causing or stimulating release of root exudates that result in microbial activity and plant growth promotion that more than offsets the damaging effects of parasitism (Bardgett *et al.*, 1999). On the other hand, there is loss of production, or fitness, when the parasite burden increases (De Rooij-Van der Goes, 1995) or when the host is additionally stressed.

An important effect of nematodes on their resources is what might be considered resource farming. A substantial proportion of the bacteria consumed by bacterial-feeding nematodes survives passage through the nematode digestive tract (Yeates, 1969a,b). Additionally, bacteria adhere to the nematode cuticle. As the nematodes move through the soil in response to semiochemical signals from other resources, they distribute the internal and external burden of bacteria to those resources and new colonies are established (Fu *et al.*, 2005; Horiuchi *et al.*, 2005). Similarly, entomopathogenic nematode species carry *Photorhabdus* and *Xenorhabdus* bacteria into the bodies of insects where they are released and multiply. In well-documented cases, nematodes are the phoretic passengers in distribution to their food sources; for example, the phoretic relationship between nematode of the genus *Bursaphelenchus* and insect vectors. Nematodes of the family Chambersiellidae (e.g. *Diastolaimus*, *Macrolaimus*) are assumed to be transported by insects between lichen colonies on above-ground parts of plants. The nematodes may also benefit from necromeny in that they have access to bacteria involved in decomposition of the insect cadaver after its death (Cid del Prado-Vera *et al.*, 2023).

For both soil-inhabiting and aquatic nematodes, physical conditions can be more important than seasonal changes or management practices in determining the structure of the nematode assemblage (Yeates, 1984; Heip *et al.*, 1985; Griffiths *et al.*, 2003; Bardgett, 2005). Feeding rates of the predacious marine nematode *Enoploides longispiculosus*, which may exert a strong top-down control over nematode and ciliate prey communities, are strongly reduced or even completely impeded by subtle shifts in silt content, mean grain size and water content of intertidal flats (Gallucci *et al.*, 2005). Stressful abiotic factors may interact; for example, a classic experiment by Griffiths *et al.* (2000) demonstrated that, because of their effects on soil biodiversity, ‘stress on stress’ combinations of adverse environmental conditions strongly influenced the stability of ecosystem services. Similarly, damaging effects of plant-feeding nematodes may depend on external conditions, such as drought (Haverkort *et al.*, 1992) or the presence of other pathogens or symbionts, which may lead to synergistic (De Rooij-Van der Goes, 1995) or antagonistic (Brinkman *et al.*, 2005; Hol *et al.*, 2007) interactions.

Nematodes may differentially stress one plant species, thereby indirectly benefiting other plant species. For example, damage to clover roots by cyst nematodes may result in the leakage of nitrogen compounds, which benefit grasses that are not directly affected by the nematodes (Bardgett *et al.*, 1999). Damage to roots by *Meloidogyne incognita* reduces plant vigour and provides a competitive advantage to *Cyperus* weed species, which are damaged less by the nematodes (Thomas *et al.*, 2005).

In many cases, nematologists have identified individual nematode species as primary causes of crop losses. However, ecologists point to the importance of the spatial and temporal patterns in communities of organisms in soils and sediments (Blanchard, 1990; Traunspurger, 2000; Ettema and Wardle, 2002; Ettema and Yeates, 2003; Fisher, 2003; Yeates, 2003; Van Gaever *et al.*, 2004; Bardgett *et al.*, 2005; Michiels and Traunspurger, 2005). Even in agricultural fields, which are considered to have relatively homogeneous soils and to be uniformly managed, there is considerable variability in the spatial and temporal composition and abundance of plant-parasitic nematode species (Quist *et al.*, 2019). A variety of approaches has been used in efforts to understand this heterogeneity (Goodell and Ferris, 1980; Ferris *et al.*, 1990; Prot and Ferris, 1992; Robertson and Freckman, 1995; Quist *et al.*, 2019). Spatial and temporal patterns and variation also are important when considering the roles of nematodes in natural ecosystems, which are far less homogeneous than agricultural soils, and when using nematodes as environmental indicators. In such conditions, it is important to understand the determinants and consequences of nematode diversity within samples (alpha diversity), between samples within fields (beta diversity) and between fields within landscapes (gamma diversity). Further, it is important to consider that, as conditions change and resources become depleted, successional changes will lead to altered species dominance. Such compositional developments are relevant factors to be included in included in diversity assessments.

With respect to effects of the diversity of nematodes on resources, Laakso and Setälä (1999) regarded diversity among functional groups as more important than diversity within them. On the other hand, a diversity of sizes and activities of microbial-feeding nematodes may provide access of predators to a greater range of soil structural channels and to the microbes that are at the bases of these energy channels. When the parasitic nature of nematodes is considered, and when parasitism is host-species- or even variety-specific, such as that of potato cyst nematodes (*Globodera* spp.), resolution at the functional group level is inadequate. In such cases, identification at the species or even pathotype level is necessary, for example when designing nematode control strategies (Folkertsma *et al.*, 2001). Similar examples may also exist in food web interactions. For example, taxonomically very closely related bacterial-feeding nematode species may have differential effects on phytodetritus decomposition and on the activity and community composition of the associated bacteria (Venette and Ferris, 1998; De Mesel *et al.*, 2003, 2004; Fu *et al.*, 2005). Therefore, the necessary levels of identification for functional interpretation depend on the specific nature of the ecosystem functions, the nematodes involved in performing them and the environmental conditions in which they are being performed. Considering the time-consuming processes and uncertainties involved in morphological and morphometric identification of nematodes species and their functions, molecular diagnostic approaches will increasingly play key roles in soil ecology studies in the future (Geisen *et al.*, 2018).

1.3 Nematode Feeding and its Ecosystem Consequences

1.3.1 Food resources of nematodes

Many of the ecosystem functions and services provided by nematodes are direct consequences of their feeding activity and of the physiological processes of digestion and metabolism. Across the diversity of the phylum are representatives that ingest a vast array of resources to drive their metabolic processes. We might divide them into general categories of *grazers* or *browsers*, which feed on food resources that continue to live, and *predators* whose feeding results in the death of their prey. Within these two general categories we can separate nematodes according to the nature of the food resource: (i) *herbivores* feeding on living tissues of higher plants; (ii) *carnivores* feeding on animal tissues, vertebrate (as parasites) or invertebrate (as predators or parasites); (iii) *fungivores* feeding on fungi; (iv) *bacterivores* feeding on prokaryotic organisms; and (v) *unicellular eukaryote feeders*, feeding on ciliates, other protozoans or diatoms and unicellular algae (Yeates *et al.*, 1993). Elsewhere in this chapter we have used terms such as *plant feeders* and *microbial feeders*, but it is useful to recognize that more precise terminology can be applied. Some nematodes (e.g. in the families Ascarididae and Thelastomatidae) that inhabit the gastrointestinal tract of vertebrates or invertebrates may actually be grazing on intestinal microbes, or on food ingested by the host, rather than on tissues of the host. In some cases, it is difficult to link a specific food source with the nematode feeding habit. For example, a soil-dwelling member of the family Rhabditidae, siphoning the soil solution to ingest bacteria, may also be obtaining other resource molecules from the solution. Similarly, large-mouthed nematodes in freshwater or marine sediments may be ingesting an assortment of organisms and material besides diatoms; consequently, they are conveniently classified as *epistrate feeders* (Moens and Vincx, 1997; Traunspurger, 2000).

In each case, and as detailed below, there are nematodes that are *specialists* in their feeding habits with stoma structures, behavioural attributes or specific biochemical requirements (e.g. transfer cells of *Heterodera* and *Meloidogyne*) that are adaptations to high-intake feeding on a narrow range of food sources; others are *generalists* and capable of obtaining resources from a wider range of sources. Some of the latter are omnivores, crossing feeding-type boundaries and feeding at more than one trophic level in the food pyramid. For example, some may be carnivorous as well as bacterial-feeding (e.g. *Pristionchus*), or bacterial-feeding as well as feeding on unicellular eukaryotes (e.g. *Daptonema*, *Thalassomonhystera*). Omnivory appears to be quite common in some nematodes, and food sources from different trophic levels may be utilized simultaneously (e.g. many Dorylaimida), in different life stages (e.g. bacterial-feeding juveniles of hookworms whose adults parasitize the gastrointestinal tract of mammals), or follow temporal or environmental fluctuations in the availability of different resources (e.g. the marine nematode *Enoplus brevis* feeding on cyanobacteria, diatoms, oligochaetes, nematodes and rotifers) (Hellwig-Armonies *et al.*, 1991).

Of course, in a group with enormous diversity of habitat, there are exceptions to the simplistic categorizations of feeding types. Some nematodes appear to be able to transport, or allow diffusion, of dissolved organic molecules across the cuticle, as an alternative to, or perhaps in addition to, stomal ingestion. Cuticular microvilli are used in the insect-inhabiting *Bradynema*; *C. elegans* has been cultured on chemically defined media, without other living organisms (Vanfleteren, 1980); dissolved organic matter may be ingested via the stoma (Chia and Warwick, 1969). Several marine nematodes, including some newly discovered species of the anoxic oceanic abyss, lack any orifice for the digestive system and derive their resources either directly or via symbiotic bacteria (e.g. *Astomonema* and several Stilbonematinae) (Hentschel *et al.*, 1999; Dover, 2000).

The characterization of such unusual feeding strategies, and the challenges of modelling the roles and functions of nematodes in a food web context, may benefit from stable isotope approaches, using both natural and experimentally enriched abundances of, mainly, ^{13}C and ^{15}N (Moens *et al.*, 2002, 2005a). Chemosynthetically produced carbon, for instance, is typically very depleted in ^{13}C, while ^{15}N fractionates significantly with trophic level and is thus a useful tracer of trophic position. The technology has been used successfully in tracking the fate of carbon from plant residues into the microbial biomass and into nematodes (Minoshima *et al.*, 2007), and from microalgae and bacteria of intertidal regions into nematodes (Moens *et al.*, 2002; Van Oevelen *et al.*, 2006).

Stoma morphology in the phylum Nematoda ranges from simple apertures of fixed diameter, which apparently limit the size of the ingested material, to permanently cavernous features or structures that can be opened to enormous size for ingestion of large prey. Even simple tubular stomata adapted for ingestion of bacteria (e.g. in the Rhabditidae) or diatoms (e.g. in *Gonionchus*, *Praeacanthonchus*) often have small teeth or denticles, presumably to abrade, crush or filter ingested particles. Additionally, there may be other cuticular structures in the stoma and/or pharynx that serve to abrade or rupture food before it enters the intestine; for example, the grinder in the bulbous posterior region of the pharynx of many rhabditid nematodes.

Intestinal parasites of vertebrates are often equipped with teeth that allow tearing of mucosa to provide access to tissue and blood (e.g. *Ancylostoma*). Many other nematodes are equipped with fixed or moveable teeth (Chromadoridae, Diplogastridae, Enoplidae, Mononchida), or with hollow spears or stylets (Dorylaimida, Tylenchida) for piercing a resource and withdrawing contents. In most Tylenchida, and the plant-feeding Longidoridae, the stylet lumen is very narrow (~0.1 and 0.5 μm in diameter, respectively), significantly limiting type and size of ingested material. Many omnivorous and predatory Dorylaimida have a wide stylet lumen (≥ 6 μm) or just a single mural tooth (e.g. *Nygolaimus*), allowing ingestion of larger food sources. The stoma and its armature are, however, not a definitive indicator of food resource; some nematodes with narrow stylet lumens are effective predators. For example, *Seinura* spp. ingest their food resources from large-bodied prey through a <0.5 μm stylet aperture, while other predators (e.g. *Anatonchus tridentatus*), with a wide stoma, may ingest whole organisms and are frequently observed to have intact nematode prey in their intestine (Small, 1987). Others (e.g. *Tripylina* and other Tripylidae) are able to open an apparently narrow stoma very wide to ingest nematode prey intact (Cid del Prado-Vera *et al.*, 2012).

1.3.2 Microbial feeding in soils and sediments

Nematode activities in soils and sediments include the redistribution of resources so that they are more available to other consumers. Some nematodes, such as bacterivores, may also transport adherent microbes to other locations where they gain access to new resources (Fu *et al.*, 2005). Their ability to locate suitable feeding patches from a distance, for example by sensing cues of decomposition-associated end products such as CO_2 (Klingler, 1965; Pline and Dusenbery, 1987; Riemann and Schrage, 1988) or responding to semiochemical signals (Horiuchi *et al.*, 2005; Ali *et al.*, 2011), contributes to their phoretic efficiency (e.g. Jatala *et al.*, 1974). Generalist bacterivores include those considered ‘enrichment opportunists’ (*sensu* Ettema and Bongers, 1993) which appear to simply imbibe aqueous suspensions of their food, with larger particles restricted only by stomatal diameters of 2 μm or less. These nematodes apparently have little other restriction on the types of bacteria ingested (Venette and Ferris, 1998; Salinas *et al.*, 2007) and it may be the stomatal dimensions of the feeding stage that limits food size for maintenance of populations. Other bacterivore nematodes feed with activities involving simple to elaborate head probolae, muscular contractions to open a closed stoma during ingestion, sweeping motions of the head, or thrashing motions of the whole body. Such behaviours provide access to food by stirring sediments or disrupting adherence of bacteria to surfaces (Moens *et al.*, 2004).

Several important ecosystem functions and services are well documented for bacterial-feeding nematodes in soils and aquatic systems. Nematode grazing on microbes may result in greater metabolic activity in their prey populations, essentially keeping in a growth phase and reproductively active. Besides redistribution of bacteria adherent on the nematode cuticle, around 30% of the bacteria ingested by bacterial-feeding nematodes are not digested and assimilated; in fact, they may still be alive when defecated (Yeates, 1969a,b; Ingham *et al.*, 1985; Bird and Ryder, 1993; Fu *et al.*, 2005; Ghafouri and McGhee, 2007). The proportion of ingested bacteria that survives passage through the nematode intestine may vary with food availability and bacterial density (Moens *et al.*, 2006). In effect, the redistribution of bacteria is a form of ‘resource farming’, to be compared with ants that manage aphids or fungi for their own food provisioning: it results in the increase of resource provisioning for bacterivorous nematodes; however, this predator–prey dynamics may be distorted by overgrazing (Fu *et al.*, 2005). Another example of such nematode-aided bacterial farming is the migration of entomopathogenic nematodes into arthropods where they release toxic bacteria that kill the arthropod. The bacteria multiply in the cadaver and provide food for the nematode (Boemare, 2002).

It has been suggested that nematodes can discriminate among soil microbes. Rodger *et al.* (2004) cultured bacterial-feeding nematodes (*C. elegans*, *Coarctadera cystilarva*; Rhabditidae) on four species of bacteria and measured nematode attraction to those bacteria. On agar, there seemed to be a ‘substrate legacy’ affecting the subsequent ability of these bacterial-feeding nematodes to locate the food on which they had been cultured. Venette and Ferris (1998) observed differences among population growth rates of bacterial-feeding nematode species on different bacterial colonies. This area of food selectivity within nematode feeding types needs further exploration in order to understand its ecological implication.

1.3.3 Excretion by bacterial-feeding soil nematodes

Another important ecosystem service emerges from the nature of the substrate ingested and subsequently assimilated across the intestinal wall. Bacterial-feeding soil nematodes may excrete materials assimilated that are in excess of their needs, in forms that are available to other organisms. A familiar example of the mineralization of digested organic molecules is the participation of most organisms in the carbon cycle. In liberating energy from ingested materials, nematodes have been calculated to release, across the cuticle, about 40% of the ingested carbon in the form of CO_2 (Klekowski *et al.*, 1972; Ferris *et al.*, 1995). CO_2 returns to the atmosphere and is available to plants for photosynthetic fixation of complex molecules. But the ingested molecules from which the respired carbon is derived may contain minerals in excess of the needs of the nematode for maintenance, growth and reproduction. Such excesses are excreted in mineral forms that can be taken up by plants and are a key mechanism explaining how nematodes contribute to primary production.

The best-studied example is the excretion of excess nitrogen in the form of ammonium, which is then available for uptake by plants or for bacterial transformation to nitrates and, subsequently, to atmospheric nitrogen, including the potent greenhouse gas N_2O. The mineralization service resulting from nematode digestion of organic molecules may be enhanced by differences in the molecular ratios of the food and the consumer. The C:N ratio of the biomass of many bacteria is in the range of 4:1 while that of their nematode predators is around 5.9:1 (Ferris *et al.*, 1997). The C:N ratio of some fungi averaged 8.5:1 while that of their nematode grazers was 9.1:1 (Chen and Ferris, 1999). Ratios of C:N in these ranges suggest that for every atom of

C ingested, the bacterial-feeding nematode ingests about 8% more than its body requirement for N. After respiratory mineralization of around 40% of the ingested C, the nematode has, in total, about 18% more N than required for body structure and reproductive output. The excretions of bacterial-feeding nematodes alone may enhance available mineral N in the soil by 20% or more (Ferris *et al.*, 1998). Even though the C:N ratios of fungal-feeding nematodes are apparently similar to those of their food substrate, the N associated with respired C (around 5% of N intake) is excreted as excess, varying with fungal substrate (Chen and Ferris, 1999; Okada and Ferris, 2001). The combined excretions of all consumer organisms in the soil food web may account for 80% of total mineralized N (Sánchez-Moreno *et al.*, 2008). This point is often overlooked in microbial ecology that is classically excluding the role of soil fauna in ecosystem functioning and ecosystem productivity.

1.3.4 Phoresy or vectoring by and of plant-feeding nematodes

Feeding activities of nematodes, in addition to facilitating nitrogen mineralization, contribute to other ecosystem services. Stylet-bearing nematodes may provide avenues of ingress into host or prey tissues; for example, access of bacteria and fungi through the migration and feeding activities of endoparasitic herbivores in roots and plant storage organs. This may be associated with weakened physical barriers and defence mechanisms allowing fungal and bacterial infections of plant tissue (e.g. *Fusarium*, *Phytophthora parasitica* and *Pseudomonas solanacearum* in tobacco) (Powell, 1971). Also, stylet-bearing nematodes may provide phoretic transport of bacteria or viruses into hosts (Hewitt *et al.*, 1958; Brown *et al.*, 1993). The reported instances seem to provide no obvious advantage to the nematode; in fact it may be to the detriment of the nematode, as it appears to enable exploitation of nematode behaviour and biology by other organisms. For example, the transport of *Clavibacter* bacteria by *Anguina* spp. to their developing seed galls in Gramineae, where the nematode may be outcompeted for the resource by the bacteria (Bird and Stynes, 1977).

Plant viruses vectored by *Longidorus* spp. and *Xiphinema* spp. may weaken the host and render it a poorer resource for the nematode (Brown *et al.*, 1993, 1995). While there might be reciprocal, but hitherto uncovered benefits for both organisms, a clearer example of mutually beneficial phoresy is the transport of *Bursaphelenchus xylophilus* by long-horned beetles (Coleoptera: Cerambycidae: *Monochamus*) to healthy pine trees where they enter through feeding wounds on young twigs. Invasion of the nematodes into the pine tree, and the damage they cause in resin canals, renders the tree less vigorous and more favourable for oviposition by the beetles, followed by larval development and pupation. The emerging adults become contaminated by nematodes nictating in the pupal chamber and transfer them to healthy trees (Togashi and Shigesada, 2006).

1.4 Effects of Nematodes as Regulators of Populations and on Ecosystem Production and Succession

Nematode feeding has the potential to control the magnitude of available resources and consequently impact ecosystem structure and function. Some general examples are shown in Fig. 1.2 and more specific observations are provided in the following sections.

1.4.1 Effects of nematode feeding on plant community composition

In addition to the much-studied effects of plant-feeding nematodes on plant performance and crop yield, the reduction in the growth rate and fitness of higher plants potentially decreases the exclusionary competitiveness of those plants and confers relatively greater fitness on their competitors. Consequently, ecosystem succession progresses, and plant diversity is increased (Van der Putten, 2003). The result in natural systems is that the susceptible and less competitive plants are reduced or even eliminated from the plant community (Wilschut and Geisen, 2021). More constrained examples are provided in agricultural systems where aggressive strains

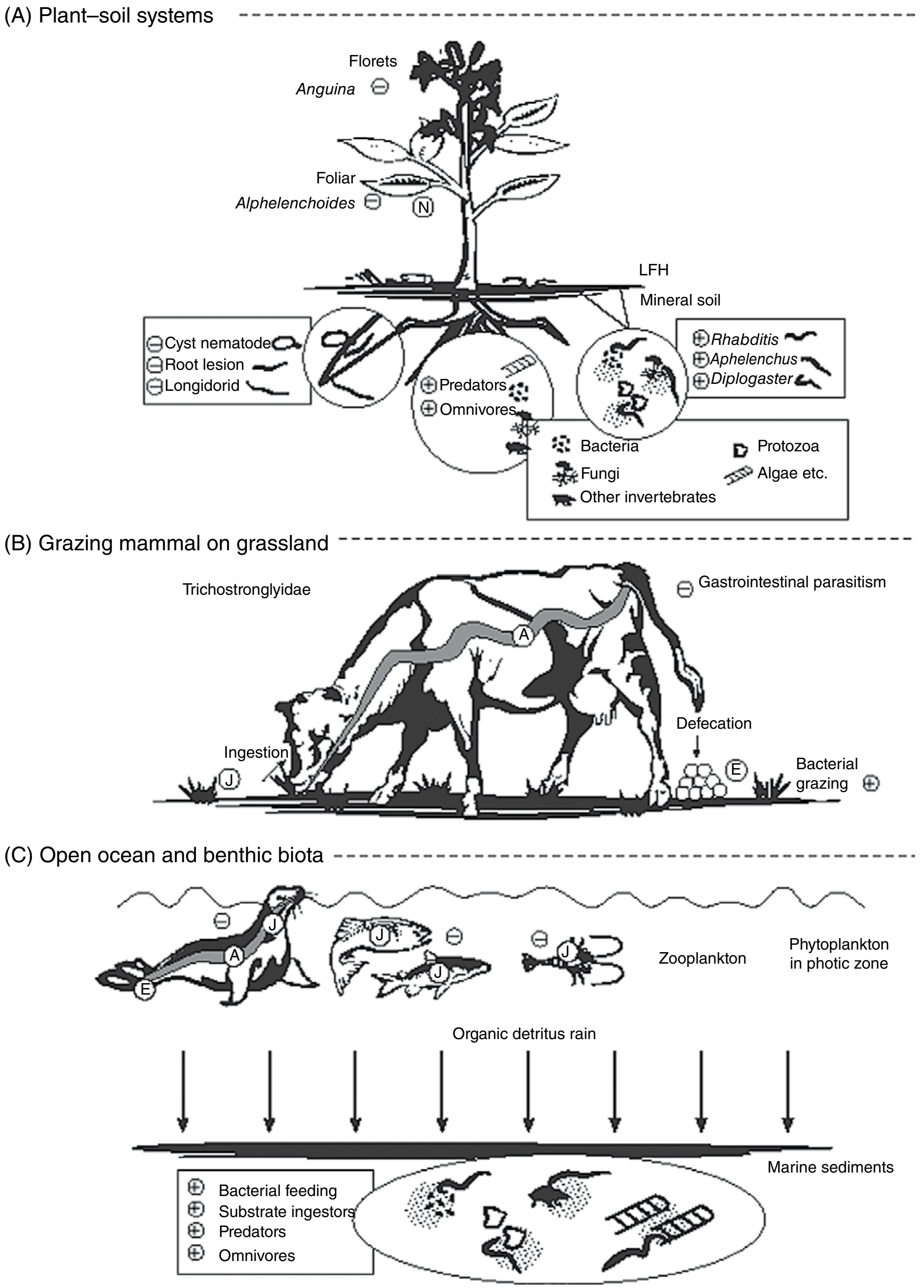

Fig. 1.2. Potential consequences of nematode feeding on food resources (+, positive effects of grazing on microbes and nutrient availability; –, potential loss of plant or animal production) in (A) plant–soil systems, (B) grassland with grazing mammals and (C) open ocean pelagic and benthic biota; LFH indicates the organic soil horizons: L (litter), F (partially decomposed), H (humus). Nematode metabolic activities and excretion are not specifically shown. For simplicity only selected nematode groups are included. Sites of nematode activity are labelled E, J, A or N to represent occurrence of egg, juveniles, adults or the species as a whole; in soils and sediments developmental stages are not separated. (Inspiration from Wardle *et al.*, 2004.)

of plant-feeding nematodes have often been introduced with their susceptible, but agronomically desirable, hosts (Ferris *et al.*, 2003). A seeding rate designed for maximizing production will provide a less vigorous stand of the crop in the presence of nematode herbivores, opening up the canopy and reducing competitiveness with weeds, resulting into yield losses (Alston *et al.*, 1991; Schroeder *et al.*, 2005). Interestingly, applied ecologists have seldom exploited the effects of nematode herbivory on plant competition by designing cropping systems to enhance herbivore nematode species that render the weeds less competitive. For example, seed- and bud-feeding nematodes of the family Anguinidae may reduce the fitness of certain weeds, which clearly affects the plant community. The effects of *Mesoanguina amsinckiae* on the growth of coast fiddleneck (*Amsinckia intermedia*: Boraginaceae) in wheat was modelled by Pantone *et al.* (1989a,b), and in a field trial in Texas *Ditylenchus phyllobius* reduced the density of the target silverleaf nightshade (*Solanum elaeagnifolium*) plants by 66% (Northam and Orr, 1982). Thus far, exploiting root-feeding nematodes to reduce competitiveness of weed species has been relatively unsuccessful (Thomas *et al.*, 2005).

1.4.2 Nematode parasites of vertebrates

Similar examples of reduced competitiveness certainly occur among vertebrates, including humans, when parasitized by nematodes. Individuals with genetic characteristics or behaviour patterns that render them more susceptible to nematode infections may be selected against, resulting in greater average fitness or tolerance in the population. Multigenerational selection by farmers of the sheep in a flock that perform better under uniform parasite challenge can lead to sheep more tolerant of nematode infection (Bisset and Morris, 1996; Morris *et al.*, 2000).

The shift from mixed cropping and mixed grazing to more intensive livestock farming has often led to significant problems with nematode parasites of grazing animals for which anthelmintic drenches provided relief. However, apart from perceived non-target effects, these drenches have resulted in genetic selection for anthelmintic-resistant nematodes. Alternatively, the use of the nematode-trapping fungus *Duddingtonia flagrans* has reduced nematode parasitism of sheep with acceptable economic return (Waller *et al.*, 2004).

The functional impact of nematode parasitism in human populations is to stimulate societal responses of sanitation and other public health measures and the search for appropriate parasite management tools. River blindness in humans, caused by *Onchocerca volvulus*, can be controlled by annual treatment with the orally administered microfilaricidal drug, Mectizan® (ivermectin) (Cupp and Cupp, 2005). Elephantiasis or lymphatic filariasis, caused by *Wuchereria bancrofti*, can be locally eliminated using two drugs: ivermectin (Mectizan®) and albendazole in sub-Saharan Africa, or diethylcarbamazine and albendazole elsewhere (Richard-Lenoble *et al.*, 2003). However, for dracunculiasis, caused by Guinea worm (*Dracunculus medinensis*), no vaccine or medication is available, and public health programmes are designed to reduce exposure to infective juveniles. Nature-based solutions for nematode control might provide more sustainable control measures, but more work is needed in order to test the feasibility and applicability of this principle.

1.4.3 Nematode regulation of populations of other invertebrates

Several families of nematodes include associates of arthropods. Among those most studied, because of their potential as biocontrol agents, are the families Allantonematidae, Heterorhabditidae, Mermithidae, Phaenopsitylenchidae, Sphaerulariidae, Steinernematidae and Tetradonematidae (Kaya and Stock, 1997; Lacey *et al.*, 2001). The potential regulation of arthropods by nematodes has been most clearly demonstrated by the exploitation of heterorhabditid and steinernematid nematodes that carry toxic bacteria, *Photorhabdus* and *Xenorhabdus*, respectively, into their hosts. Mass production of these nematodes on artificial diets has fostered an industry dedicated to biological approaches in management of those insects that have a life stage in the soil (Ehlers and Shapiro-Ilan, 2005). There have also been attempts to capitalize on the direct parasitism and feeding of *Romanomermis culicivorax* on mosquito larvae (Petersen, 1985) and *Deladenus* *siricidicola* has been used successfully in biocontrol of the wood wasp *Sirex* in New Zealand and Australia (Bedding, 1993).

Other examples of regulation of invertebrates are the parasitism of slugs and snails by nematodes in the families Agfidae, Alloionematidae, Angiostomatidae and Rhabditidae. Of these, species of *Phasmarhabditis* have been developed as biological control agents for slugs (Wilson and Grewal, 2005).

1.4.4 Nematode influence on aquatic bacterial community diversity

Perhaps less spectacular, but with potentially important consequences for instance in decomposition processes, are observations that mucus secretions by aquatic nematodes may selectively favour settlement of specific strains of bacteria (Moens *et al.*, 2005b). Even low grazing rates by nematodes may significantly affect bacterial community composition, while high grazing rates may depress bacterial community diversity (De Mesel *et al.*, 2004).

1.4.5 Nematode suppression of mycelial growth

The feeding of aphelenchid nematodes (Riffle, 1967; Sutherland and Fortin, 1968; Ruess and Dighton, 1996) (Table 1.1) may reduce the rate of spread of saprophytic and mycorrhizal fungi in Petri dishes. Under standard conditions, feeding on fungi affects both the populations and morphometrics of particular Aphelenchidae, Tylenchidae and Tylencholaimidae (Faulkner and Darling, 1961; Townshend and Blackith, 1975; Ruess and Dighton, 1996; Okada and Kadota, 2003). Nematode populations may reduce, as well as be reduced by, fungi. For example, *Pleurotus ostreatus* (Basidiomycetes) supported population increase of *Filenchus misellus* and *Tylencholaimus parvus*, whereas *Aphelenchus avenae* populations were reduced as a result of predation by *P. ostreatus* (Okada and Kadota, 2003; Okada *et al.*, 2005). Feeding by Tylenchidae and Tylencholaimidae on decomposer fungi in mineral and organic soil horizons may enhance mineralization of nitrogen in those horizons (Okada and Ferris, 2001).

Nematode grazing on fungal mycelia may play other roles in complex interactions in soils. Laboratory studies suggest that feeding by *Aphelenchoides* sp. on the biocontrol fungus *Trichoderma harzianum* may constrain its efficacy as a biocontrol agent (Bae and Knudsen, 2001) and nematode feeding on mycorrhizal fungi could reduce exploration of the soil matrix by their mycelia (Table 1.1). *Aphelenchoides* spp. suppress colonization of *Pinus ponderosa* seedlings by the ectomycorrhiza *Suillus granulatus* (Riffle, 1975). In a pot study, Hussey and Roncadori (1981) demonstrated that grazing by *A. avenae* on the vesicular-arbuscular endomycorrhizae *Glomus margarita* and *Glomus etunicatus* could retard shoot and root growth of cotton. However, they concluded that the large population levels of *A. avenae* required probably precluded any significant interactions under field conditions.

There are many studies of fungi as biological control agents of nematodes (e.g. Timper, 2014). Often, the interactions are complex. Moreover,

Table 1.1. Colony size of two ectotrophic mycorrhizal fungi grown for 3 weeks at 25°C after addition of five initial densities of *Aphelenchus avenae* (Aphelenchidae). (After Sutherland and Fortin, 1968.)

	Amanita rubescens		*Suillus granulatus*	
Initial nematode population	Colony diameter (mm)	Final nematode population	Colony diameter (mm)	Final nematode population
0	49^{a}	0^{a}	40^{a}	0^{a}
5	47^{a}	18,166^{b}	34^{b}	5,322^{b}
10	43^{a}	57,055^{c}	26^{c}	18,011^{b,c}
25	34^{b}	57,555^{c}	21^{d}	34,811^{c,d}
50	25^{c}	81,360^{d}	16^{e}	37,011^{d}

$^{a–e}$In each column, values not followed by the same superscript letter differ significantly at $P < 0.01$.

while *Pochonia chlamydosporia* is being assessed as a potential biocontrol agent for economically important plant-feeding nematodes, such as *Globodera* spp., *Heterodera* spp. and *Meloidogyne* spp., its intraspecific variants differ in their host preference. Further, its persistence in soil requires saprophytic activity (Mauchline *et al.*, 2004), raising questions about its functional activities in the soil food web. Therefore, while being spectacular to observe, fungal biocontrol of nematodes needs more work in order to result in predictable applications.

1.4.6 Nematode predation and omnivory

Undisturbed soils often have abundant specialist predators of nematodes, for example Diplogastrida and Mononchida, as well as an abundance of generalist predators, mainly Dorylaimida. Observational evidence of such systems supports the hypothesis that the predators, in combination with organisms of other taxa that benefit from similar environmental conditions, have regulatory, or even suppressive, effects on the abundance and temporal stability of nematodes occupying lower trophic levels in the food web, including herbivores, fungivores and bacterivores (e.g. Wardle *et al.*, 1995; Jackson *et al.*, 2019). Specialist and generalist predators are, however, quite sensitive to soil disturbance and chemical amendments (Korthals *et al.*, 1996; Berkelmans *et al.*, 2003; Tenuta and Ferris, 2004). For those reasons, they are at relatively low abundance in agricultural soils, where their potential prey exhibit unregulated population increase when provided with suitable resources and environmental conditions. Interestingly, conversion of such disturbed systems to reduced tillage and organic production does not immediately result in a more structured soil food web with greater connectance to higher trophic levels. This is probably because predators may be slow colonizers, have longer life cycles and lower productivity. Colonization and regulatory balance in the soil food web may require considerable time, often being decades rather than years, including recovery of soil structure (Korthals *et al.*, 1996; Yeates *et al.*, 1999a; Sánchez-Moreno *et al.*, 2006; Morriën *et al.*, 2017).

In some marine sediments, predacious nematodes may reach high abundances and dominate biomass and densities of other nematodes in the assemblage. Both laboratory and field evidence indicate that nematodes of the genus *Enoploides* exert substantial top-down control over prey density and community composition (Moens *et al.*, 2000; Hamels *et al.*, 2001; Gallucci *et al.*, 2005). Many other aquatic nematodes are presumed (based on stoma morphology) to be predators, but the lack of empirical evidence on their actual food sources and feeding rates hampers proper assessment of the importance of top-down regulation within the meiobenthic component of aquatic food webs. However, a recent compilation of nematode feeding habits based on observations of diets and on stomatal and pharyngeal morphology of the entire phylum Nematoda (Hodda, 2022) provides a useful basis for ecological analyses where direct observations are lacking.

1.5 Nematodes in a Community and Ecosystem Context

1.5.1 Economic crop loss due to plant-feeding nematodes

Galled wheat florets ('cockles') (Needham, 1744), galls on cucumber roots (Berkeley, 1855) and patches of stunted plants in sugarbeet fields (beet tiredness) (Schacht, 1859) were among the first-documented signs of nematode damage to plants. Over the past 150 years, there have been many investigations of the management of the pathogenic effects of plant-feeding nematodes. There are examples in books edited by Perry and Moens (2006), Subbotin and Chitambar (2018) and Sikora *et al.* (2021).

1.5.2 Management of microbial-feeding nematode function in an agricultural context

Nematode management activities in agricultural fields are usually aimed at reductions in abundance of plant-parasitic nematodes, often without consideration of the concomitant effects on microbial-feeding or predator nematodes. In the development of more sustainable agricultural systems, focus on the nurture of other components of the soil food web may be important. As an example, in the Mediterranean climate of the central valley of Northern California, annual crops are grown during the spring and summer months with the aid of irrigation. Following harvest in August or September, fields are left fallow, irrigation ceases and the soil becomes very dry prior to the start of winter rainfall in November. During the September to November fallow period, soil temperatures would be conducive to biological activity if water was available. Cover crops, when used, are usually planted with the first rain in late November. In a study of the transition from conventional to organic farming practices, crops planted in the spring following incorporation of a winter-grown legume cover crop but without application of mineral fertilizers exhibited symptoms of nitrogen deficiency. Microbial biomass was at high levels following cover crop incorporation, but population levels of bacterial-feeding nematodes were very low (Fig. 1.3). About six weeks after planting the summer crop, bacterial-feeding and fungal-feeding nematodes had increased on the newly available resources and the nitrogen-deficiency symptoms in the crop disappeared, with crop yield and mineral N concentrations being strongly correlated (Fig. 1.4).

In microcosm experiments, soil mineral N levels could be increased by 20% or more when bacteria were grazed upon by bacterial-feeding nematodes (Ferris *et al.*, 1998) and fungal-feeding nematodes may also contribute to nitrogen mineralization (Chen and Ferris, 1999; Zhang *et al.*, 2017). The abundance of bacterial-feeding nematodes was considered an indicator of concomitant abundance of other bacterial grazers,

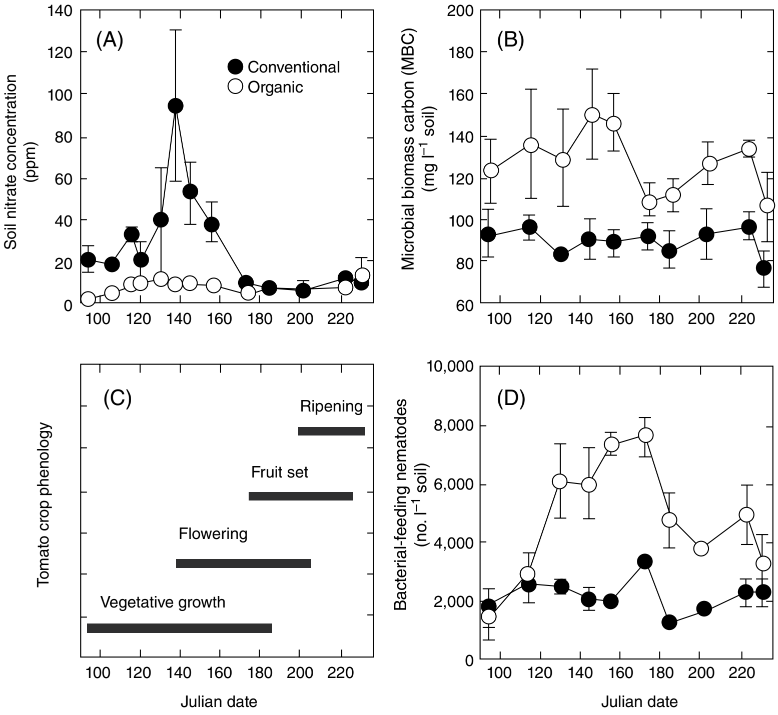

Fig. 1.3. Relationship of soil nitrate availability, microbial biomass and bacterial-feeding nematode abundance in soils under organic and conventional farming systems to tomato crop phenology. Data are means and standard errors across four replicates; Julian days run from 1 January. (A) Extractable soil nitrate concentration (from Temple, 1993). (B) Microbial biomass expressed as microbial biomass carbon (data from Gunapala and Scow, 1998). (C) Tomato crop phenology (data from Flint, 1985). (D) Abundance of bacterial-feeding nematodes (redrawn from Ferris *et al.*, 1996).

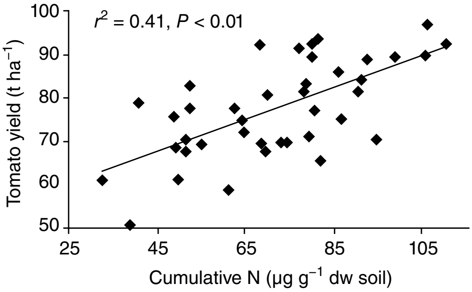

Fig. 1.4. Tomato crop yield in August 1996 in relation to cumulative soil N measurements over five sampling dates in April and May, prior to planting. dw soil = dry weight of soil. (Redrawn from Ferris *et al.*, 1996.)

especially protozoa. The window of opportunity for increasing the abundance of bacterial- and fungal-feeding nematodes and other organisms in field soil in the spring, at the time of cover crop incorporation, was during the warm soil temperature period of September to November. After that period, winter soil temperatures were too cool for nematode reproduction and biological activity.

In field plots where the soil was irrigated during the September to November period, there were greater abundances of bacterial-feeding nematodes in the spring and greater nitrogen availability at the time of establishment of the new crop. Nitrogen-deficiency symptoms were not seen in those plots.

Such field and laboratory studies support the conclusion that designed and holistic management of the soil food web, and indeed the entire soil ecosystem, is a major component of sustainable agricultural production systems. As a caveat, it should be noted that there is a downside to the late summer irrigation. The costs of water and pumping are additional financial overheads in the operation and weeds that would otherwise be dormant at that time may grow actively and require management (Ferris *et al.*, 2004c).

1.5.3 Coastal sand dune nematodes controlled by many factors

Vegetation succession in coastal foredunes is, in part, driven by plant species-specific negative feedbacks with the soil community (Van der Putten *et al.*, 1993). Initially, it was assumed that nematodes play a major role in the soil pathogen complexes, because of the specific occurrence of specialized root feeders in association with the different dominant plant species (Van der Putten and Van der Stoel, 1998). On other continents, the pioneer species marram grass (*Ammophila arenaria*) has been introduced in the absence of the nematode species and became invasive (Van der Putten *et al.*, 2005). This would all point at root-feeding nematodes controlling plant abundance, and specialized nematodes driving succession. However, in the native range nematodes turned out to be controlled by species-specific factors: competition (Brinkman *et al.*, 2005), arbuscular mycorrhizal fungi (De la Peña *et al.*, 2006), endophytes (Hol *et al.*, 2007), soil microorganisms (Piśkiewicz *et al.*, 2007) or by the plants themselves, such that they did not have the opportunity to control plant abundance (Fig. 1.5). Therefore, the current opinion is that, in the root zone of marram grass, damaging levels of plant-feeding nematodes are regulated by multifactorial pressures to levels that are too low to control plant performance. In European dunes, where *A. arenaria* naturally occurs, plant control therefore appears to be the result of the whole assemblage of soil biota. How such assemblages may be plant-species-specific (Van der Putten *et al.*, 1993) is still a question to be resolved. In spite of the uncertainties, these phenomena, such as plants controlling cyst nematodes to sublethal densities, may stimulate new approaches to sustainable nematode management in agricultural systems (Van der Putten *et al.*, 2006).

1.5.4 Intertidal nematode populations governed by environmental modulation of top-down regulation

Nematodes inhabiting intertidal habitats often migrate vertically in relation to the tidal cycle. The genus *Enoploides*, abundant in many fine to medium sandy sediments along coasts and estuaries in north-western Europe, is a voracious and selective predator of, for example, oligochaete, nematode and ciliate prey, and potentially exerts significant top-down control over its prey communities (Moens *et al.*, 2000; Hamels *et al.*, 2001).

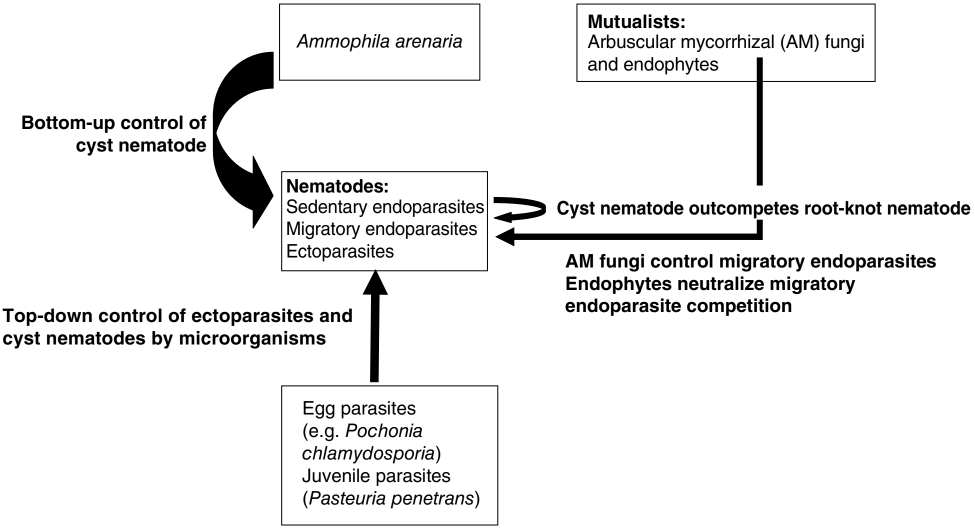

Fig. 1.5. Schematic of multiple controls on root-feeding nematodes on marram grass (*Ammophila arenaria*) in coastal sand dunes in north-western Europe. (After Van der Putten, 2003. Reproduced with permission from John Wiley and Sons.)

Enoploides is generally restricted to the upper 3 cm of the sediment, with clear density peaks in the upper 2 cm. Total abundance of all other nematode species in a fine to medium sandy sediment on the Molenplaat, Schelde Estuary (south-western Netherlands), peaks at a depth of 4–5 cm. These sediments are porous, and groundwater rapidly drains at low tide, leaving the upper sediment relatively dry after a few hours of exposure.

Laboratory experiments have demonstrated that the predation efficiency of *Enoploides* on nematode prey is strongly impaired by even mild sediment desiccation (Gallucci *et al.*, 2005). Since this and similar intertidal sites are exposed for 8 to 18 hours per day, optimal foraging by *Enoploides* must be restricted to relatively short periods during, and shortly after, inundation. Probably as an avoidance of sediment drying, *Enoploides* migrate a short distance into the sediment during low tide. Remarkably, some of its most abundant prey species at the Molenplaat exhibit the opposite vertical migration behaviour, peaking at or near the sediment surface only upon low tide exposure (Steyaert *et al.*, 2001). Many of these prey species rely on diatoms as their principal food. Since diatom production on intertidal flats is largely restricted to the very surface of the sediment (i.e. the photic zone), the upward migration of prey nematodes during low tide at the Molenplaat is likely a strategy to optimize feeding. In contrast, their downward migration upon inundation may be interpreted as an avoidance of predation by *Enoploides*. *Enoploides* distribution, in turn, appears to be largely controlled by sediment effects on the activity of the predator (Steyaert *et al.*, 2001; Gallucci *et al.*, 2005).

1.5.5 Multifactorial control over nematode abundances in a salt marsh benthic food web

Experimentally imposed diesel contamination of a *Spartina alterniflora* salt marsh caused high mortality of meiobenthic harpacticoid copepods and concomitant (transient) increases in both microphytobenthos biomass (MPB) and nematode abundance, and in meiofaunal grazing rates on the MPB. Total meiobenthic (copepods + nematodes) grazing was lower in diesel-contaminated than in unaffected plots, suggesting: (i) that MPB is top-down controlled by meiobenthic (here mainly copepod) grazing; and (ii) that harpacticoid copepods and nematodes compete for this limiting resource (Carman *et al.*, 1997; Fleeger *et al.*, 2006). The system is yet more complex, however, in that inclusion of the naked goby, *Gobiosoma bosc*, a burrowing fish predacious on meiofauna, affects both MPB and meiofauna in a multifactorial manner. Specifically, presence of the naked goby reversed the diesel-induced increase in nematode and abundance of MPB, while at the same time enhancing abundance of cyanobacteria (Fleeger *et al.*, 2006). Bioturbation of the sediment by *G. bosc* physically disrupts the sediment surface and MPB patches, while at the same time limiting light availability to the benthos through an increased turbidity. Hence, the diesel-induced release of the MPB from grazing control by harpacticoid copepods is counteracted by a fish-induced light limitation (which in turn improves the competitive ability of cyanobacteria over diatoms), and nematodes are again bottom-up controlled by a limited availability of MPB.

1.5.6 Nematodes of lakes and oceans

In intertidal and shallow sediments, local primary production by MPB is often the predominant carbon source fuelling nematode assemblages (Riera *et al.*, 1996; Moens *et al.*, 2002, 2005a). Nematodes in deeper (or light-limited) environments are primarily dependent on the rain of organic debris from the photic zone above, as well as input from rivers and streams. In both shallow and deep environments, the relative importance of direct grazing on primary production and associated bacteria and on heterotrophic debris of protozoa and other organisms is somewhat unclear. *Rhabditis marina* is almost uniquely associated with seaweed wrack on beaches (Sudhaus, 1976) and decomposition of dead fish (Gerlach, 1977) or marine mammals (Debenham *et al.*, 2004) has quantifiable impacts on nematode assemblages. Littoral macrophytes, and their associated periphyton, provide limited *in situ* resources for nematodes (Peters and Traunspurger, 2005). However, in sediment-settling studies, nematodes from an intertidal salt marsh settled at four to ten times the densities on to the macrophyte *Fucus* than on other substrates. In addition, nematodes from the deep ocean settled at greater densities on a sulfide medium than on other substrates. The experiments suggest that nematodes and other meiofaunal organisms can settle selectively when suspended in water. That may affect their dispersal in relation to resources (Mevenkamp *et al.*, 2016).

As in soils, meiobenthic nematodes contribute to ecological processes (Alkemade *et al.*, 1992; Aller and Aller, 1992; Montagna 1995; Traunspurger *et al.*, 1997). Energy availability is generally negatively correlated with the depth through which phytodetrital food sinks (Suess, 1980). Tietjen *et al.* (1989) found strong correlations between deep-sea meiofaunal abundance (dominated by nematodes) and fluxes of both organic carbon (r^2 = 0.98) and nitrogen (r^2 = 0.97). Nematode species richness in the deep sea of the North Atlantic Ocean increases with latitude, in contrast to patterns of molluscan and isopod diversity. This is likely related to the increase in primary productivity with latitude in that area (Lambshead *et al.*, 2000), a correlation which was also confirmed at the equator in the Pacific Ocean (Lambshead *et al.*, 2002).

In the deep-sea hydrothermal vents and seeps, as well as in some anoxic coastal sediments (such as subsurface sediments in mangroves) with an abundance of sulfur-reducing bacteria, chemoautotrophic production may replace sedimentation of particulate food from the euphotic zone as the primary carbon and energy source for some nematode genera or assemblages (Dover, 2000). Chemoautotrophic bacteria may be directly grazed upon, as in the case of *Halomonhystera disjuncta* feeding in mats of the sulfide-oxidizing *Beggiatoa* at a 1280 m deep Arctic mud volcano (Van Gaever *et al.*, 2006). However, more specialized relationships between chemoautotrophic bacteria and nematodes have evolved. For example, the adaptation of *Stilbonema* and *Laxus* to sulfide-rich sediments involves bacterial ectosymbionts capable of respiratory reduction of nitrate to nitrite (Hentschel *et al.*, 1999); the nematodes act as vectors for the bacteria, but probably also graze upon them (Polz *et al.*, 2000; Murfin *et al.*, 2012). The unrelated mouthless nematode *Astomonema* lacks a functional stoma and probably derives at least part of its nutrition from bacterial endosymbionts (Giere *et al.*, 1995). These endosymbionts are Gammaproteobacteria which appear closely related to the bacterial ectosymbionts on stilbonematinid nematodes and in gutless oligochaetes (Musat *et al.*, 2007). The marine nematode *Oncholaimus campylocercoides* is adapted to sulfidic sediments by the development of polysulfur chains and S-8 rings in the epidermis; these disappear on return to normal oxygen levels (Thiermann *et al.*, 2000). While populations of deep-sea mussels have been used as bioindicators of habitat condition (Jones *et al.*, 2006), it may be some time before there is sufficient data so that nematodes can be used similarly.

1.5.7 Species diversity within vertebrate hosts

Intra-host speciation of nematodes in the fore stomach of the Macropodinae (kangaroos and wallabies) has led to a flock of 36 genera and 256 species of the subfamily Cloacininae (Chabertiidae) (Cobb, 1915; Beveridge *et al.*, 2002; Chilton *et al.*, 2017). Current molecular evidence supports the hypothesis that early radiation of the strongyloid genera in marsupials may have occurred in the marsupial wombats (Marsupialia: Vombatidae) (Sukee *et al.*, 2022). A cladistic analysis of nematode species suggested that the aggregations within a given host are polyphyletic and probably evolved by host switching or colonization rather than by co-speciation. This radiation differs from that in ruminants where overlapping distribution of hosts and human management has confounded host distributions. There are, however, species flocks of strongylid nematodes in equids (Bucknell *et al.*, 1996).

1.6 Nematodes as Environmental Modifiers

1.6.1 Sediment agitation by nematodes

Bioturbation is physical disturbance of the mineral and organic particles comprising the substrate. Bioturbation by nematodes is of major importance in the direct physical enhancement of fluxes of oxygen and nutrients, and indirectly through the stimulatory effect of such enhanced fluxes on microbial activity (Alkemade *et al.*, 1992; Aller and Aller, 1992). Alkemade *et al.* (1992) demonstrated that a 30% enhancement of saltmarsh grass (*Spartina anglica*) decomposition in sediments with an abundant *Diplolaimella dievengatensis* population was almost entirely due to bacterial stimulation through increased oxygen availability as a result of bioturbation by nematodes. Riemann and Schrage (1978) observed that aquatic nematodes rapidly aggregate both sediment and organic matter particles when dispersed in water. They hypothesized an underlying trophic relationship, where mucus secreted by the nematodes stimulates growth of bacteria, which could in turn be grazed upon.

This hypothesis of trophic relationship was later modified into the ‘enzyme sharing’ concept: nematodes may produce exoenzymes that start the decomposition of complex molecules and promote establishment and growth of bacteria, which then take over the organic matter decomposition. Both nematodes and bacteria then feed on the ‘soup’ of dissolved organic matter released from this shared use of enzymes (Riemann and Helmke, 2002). Several chromadorid nematodes from intertidal mudflats (e.g. the widespread and often abundant *Ptycholaimellus ponticus*) build tubes by agglutinating sediment and small organic particles through mucus produced by the ventral gland. This affects sediment stability, enlarges the surface available to decomposers (the total inner surface area of the tube may be up to five times greater than the sediment surface), and probably offers the nematodes shelter against the effects of water currents as well as predation (Nehring *et al.*, 1990; Nehring, 1993).

1.6.2 Nematodes influence ecological succession in grasslands

Effects of nematodes on ecological succession have been studied mainly in terrestrial grassland systems (e.g. Van der Putten *et al.*, 2006). Very few studies have related the occurrence of plant-parasitic nematodes to the performance of aquatic macrophytes (plants) (Fritz *et al.*, 2004) and some studies have investigated the role of nematodes in the decline of wild nitrogen-fixing shrubs (Oremus and Otten, 1981; Maas *et al.*, 1983; Zoon *et al.*, 1993). As already detailed, plant-feeding nematode populations in the root zone of the foredune marram grass (*A. arenaria*) all appear to be regulated by a range of factors. However, in secondary grassland succession following removal of intensive farming practices, nematodes may influence plant performance (Verschoor *et al.*, 2001) and plant succession (De Deyn *et al.*, 2003), although cessation of agricultural production reduces the numbers of root-feeding nematodes to levels that may be too low to reduce growth of the plants (Wubs *et al.*, 2019). Nevertheless, while usually abundance of plant-feeding nematode species is relatively low, local aggregates of high abundance might still result in substantial effects on plant productivity (Verschoor, 2002). Moreover, host preference of some nematodes for dominant, fast-growing plant species may explain their contribution to plant community composition (Van Ruijven *et al.*, 2005) or succession (De Deyn *et al.*, 2003).

Biodiversity–ecosystem functioning studies have greatly fuelled thinking about species diversity versus the presence of individual species. For example, while plant species can influence the composition of nematode assemblages in soil, the actual plant species present can be more important for nematode diversity than the diversity of the plant community per se (De Deyn *et al.*, 2004; Viketoft *et al.*, 2005). The presence of certain plant-feeding nematodes may also enhance biotic resistance of soils against introduced exotic plant species (Van Ruijven *et al.*, 2005). Most studies mentioned above have involved inoculation experiments. Studies in prairie ecosystems in the 1970s concluded that nematodes use up to one-quarter of the net primary productivity (Stanton, 1988). However, that conclusion was based experiments with selective biocides and the results have not been verified by inoculation studies with known nematode abundances.

1.6.3 Nematodes may influence succession of aquatic microbial communities

The transport of, and grazing on, bacteria by nematodes may affect settlement (Moens *et al.*, 2005b), community composition (De Mesel *et al.*, 2004), densities and activity (Traunspurger *et al.*, 1997) of bacteria, and hence likely their contribution to important ecosystem processes such as organic matter mineralization. Microcosm studies using an estuarine sample of enrichment opportunists (e.g. *R. marina*, *Panagrolaimus paetzoldi*) and general opportunists (e.g. several species of Monhysteridae) indicate that the succession often observed from the former group to the latter does not passively follow the organic matter and bacterial dynamics. Instead, overgrazing of bacteria by rhabditid nematodes may facilitate monhysterids by suppressing bacterial densities to levels at which their feeding behaviour provides them with a competitive advantage (Moens *et al.*, 2000; dos Santos *et al.*, 2008).

1.6.4 Nematodes may predispose hosts to other organisms

A classic case of nematode effects on plant physiology that increase susceptibility to another pathogen is that of *Mesocriconema xenoplax*, an ectoparasite, on *Prunus* spp. Feeding by the nematode on the roots increases infection of the above-ground parts of the tree to *Pseudomonas syringae* (Lownsbery *et al.*, 1973; Ferris *et al.*, 2004a). Nematodes may predispose hosts to other nematodes, leading to competitive or facilitative effects. In general, the more complex the relationship between root-feeding nematodes and their host plants, the more competitive they are within and among species (Eisenback, 1993; Umesh *et al.*, 1994). On the other hand, nematodes may avoid direct competition by feeding on different cell layers in the root cortex (Bongers and Bongers, 1998; Siddiqi, 2000). Another issue of competition or facilitation, which has attracted far less attention, is that between root-feeding nematodes and other soil invertebrates. These interactions may lead to contrasting patterns, such as the induction of antagonistic effects by earthworms against cyst nematodes (Blouin *et al.*, 2005), to the facilitative effects of wire worms (Elateridae) on root-knot nematodes by indirect promotion of *Meloidogyne* abundance in mixed plant communities (De Deyn *et al.*, 2007).

Interactions may also be inhibitory; such interactions demonstrated between congeneric species of *Diplolaimelloides* do not appear to be due to direct competition for food or space (De Mesel *et al.*, 2006; dos Santos *et al.*, 2008, 2009). Similarly, inhibition among soil bacterial-feeding nematode species (Bongers *et al.*, 2001; Postma-Blaauw *et al.*, 2005) may not be completely due to competitive interactions but could conceivably be mediated through bacterial defence signals (Venette and Ferris, 1998; Phillips *et al.*, 2003). Probably, when explored more intensively, such indirect effects among nematodes and between nematodes and other organisms will be recognized as important determinants of community interactions.

1.7 Synoptic Integration to System, Landscape and Biosphere Levels

While literature dealing with nematode faunae as soil (health) indicators in different farming and natural systems is abundant (Du Preez *et al.*, 2022), only a few studies have dealt with the complexities of regional/landscape/ocean-floor zone/global distribution patterns of nematode faunae (e.g. Proctor, 1984, 1990; Song *et al.*, 2017; Van den Hoogen *et al.*, 2019). To be comprehensive, such analyses generally require the aggregation of data sets from a wide range of researchers and then development of a strategy for assembly and reporting the conclusions. It can be a formidable undertaking, for example as has been carried out by Van den Hoogen *et al.* (2019). While there are some similar studies for aquatic environments, for example Schratzberger *et al.* (2007) and Van den Hoogen *et al.* (2019), there is an underlying problem that causes of high local diversity in deep-sea sediments and is very poorly understood. Thus, the use of nematode diversity per se as an indicator in deep-sea sediments is not yet well established. However, for freshwater rivers and lakes, systems have been developed as indicators of pollution that are centred on the abundance of nematode 'species at risk' which can be used in combination with DNA metabarcoding (Höss *et al.*, 2011, 2016; Schenk *et al.*, 2020).

In marine systems, there has been a strong emphasis on comparisons of nematode assemblages at beta and gamma scales, but there is a lack of process-oriented or mechanistic understanding of drivers of the patterns. Most studies on nematode assemblages in soil are based on field plots or single-crop farm fields (e.g. Wardle *et al.*, 1995; Berkelmans *et al.*, 2003; Ferris and Matute, 2003). However, feedback loops among above-ground and below-ground biota are important ecological drivers in terrestrial ecosystems (Sánchez-Moreno *et al.*, 2008). The spatial patterns of soil biota have important above-ground consequences on both plant community structure and on individual plants, and vice versa (Ettema and Wardle, 2002). Studies indicate that nematodes can enhance the control of above-ground pests through both bottom-up and top-down control activities (Bezemer *et al.*, 2005). This linking of above- and below-ground subsystems is a new and promising development indicating that proper soil management is an essential foundation for sustainable crop protection against even above-ground pests.

A simple example of the problems of scale and resolution in considering nematode roles and services is in their function as herbivores and entry points for carbon and energy into the soil food web (e.g. Yeates *et al.*, 1999b). Individual nematodes and their activities represent the minimum patch, and the population of a species represents the more general local aggregate of patches. In agriculture, such patches of plant-feeding nematodes may cause local loss of yield, with field-scale loss being determined by the field-scale nematode population level and distribution, which reflects the age of the infestation, edaphic conditions, crop history and management practices. Similarly, strong aggregations of nematodes and other organisms in the root zones of uprooted orchard trees can result in death or poor growth of trees in a subsequent orchard planting (e.g. Ferris *et al.*, 2003, 2004a). As with most bioindicator systems, the aggregation of organisms into patches generates problems in measuring abundance and diversity at local and larger scales. The problem is compounded when the patches are not visible and the assessment of environmental condition is based on a sample, or multiple samples, of soil or water without knowledge of patch distribution (Ferris *et al.*, 1990; Ettema and Wardle, 2002; Ettema and Yeates, 2003). A more extensive spatial sampling study has revealed that various nematode species show individually different abundance relationships with space (Quist *et al.*, 2019).

In another example of functional linkages between above-ground and below-ground biota, an abundance of bacterial-feeding nematodes provides important services in well-managed organic farms, whereas in conventional production systems, where nutrients are supplied from external sources, a similar abundance of nematodes may contribute little benefit to crop growth (Ettema and Bongers, 1993; Ferris *et al.*, 1998). While these effects occur at the ped/microsite level, scaling up by using Geographic Information Systems and multilayer mapping techniques will allow a more comprehensive understanding of the functions and services of nematodes at the landscape level.

1.8 Humans, Nematodes and Ecosystem Management

Nematodes are intrinsic components of natural ecosystems. The early focus of helminthology and nematology on nematodes as pests and parasites of humans, plants and animals has developed into a realization that parasitism plays a role in natural ecosystems in regulating species abundance and maintaining species diversity. Moreover, the awareness of the role of nematodes in decomposition processes as well as their potential role in controlling outbreaks of insect pests and their use as environmental indicators has led to a paradigm shift from consideration of nematodes only as undesirable pests to a broader recognition of their contributions in ecosystem services (e.g. Bongers, 1990; Ferris *et al.*, 2004b; Wilschut and Geisen, 2021). There is increasing awareness that nematode populations may be optimized by managing nature rather than utilizing broad-spectrum control measures with unknown ecological consequences.

Plant-feeding nematodes may contribute to coexistence and succession in natural plant communities (De Deyn *et al.*, 2003) and the same principles drive the need for crop rotation in agriculture (e.g. Ferris *et al.*, 1996; Van der Putten *et al.* 2006). In the past, when wide crop rotations were applied, nematodes were less of a problem. However, the globalization of world food and commodity markets and the development of expensive specialized machinery have led to the need for specialization among growers. Rotations have become so narrow that it is difficult to exploit natural population dynamics to reduce parasite population levels. The side effects of chemical nematicides on soil life and neighbouring aquatic ecosystems, and on groundwater quality, have resulted in awareness that these chemicals threaten the sustainability of crop production and have highlighted the need for biological control and more eco-friendly pesticides (Tenuta and Ferris, 2004). However, biological control, because it represents a series of interlocking biological populations, and their respective environments, is much more variable and less predictable, limiting the generalization of findings in one crop at specific site conditions (Timper, 2014; Van der Putten *et al.*, 2006). This leaves considerable challenges for nematologists, agronomists, entomologists and ecologists to develop farming systems that maximize nematode control while fulfilling the high demands of global trade and economy on cropping systems.

When humans modify natural selection, competition and species replacement, through crop breeding for high yield, disease resistance, weed control and other features, the need for understanding impacts throughout the food chain is paramount. When pests are not subjected to natural regulatory pressures of competition, predation and genetic barriers, massive outbreaks may result, similar to those seen after the application of broad-spectrum pesticides. Biological and organic agriculture each aim for conditions that more or less restore biodiversity and habitat complexity, avoiding chemical crop protection and mineral fertilizers (Tenuta and Ferris, 2004). The question of whether maximal yields are achievable with natural equilibria of plant pests and their antagonists, non-chemical fertilizers and sustainable soil tillage is still open, and nematode management is one of the key issues to be solved in order to reach that state (Temple, 1993). Sustainable crop production will probably require a blending of cropping practices applied in the past and development of new farming systems. Almost certainly, it will include the use of cultivars that have not been selected for maximum yield under the umbrella of synthetic pesticides and mineral fertilizers.

1.9 Suitability of Nematodes as Environmental Indicators

The development of nematodes as bioindicators in soil and aquatic systems has required determination of appropriate ways to assess and quantify their contribution to ecological processes, and the validation of their ability as indicators of environmental condition. Several unique characteristics of nematodes facilitated those developments. In summary, nematodes occur in all soil and aquatic systems: in acidified forest soils, in heavily polluted soil and water, in heavy clay soil, in deep-sea sediments, in rotting plant material, in composts, and in any habitat in which organic material is decomposed. Different nematode taxa exhibit specificities of food sources and changes in the food web are mirrored in shifts among feeding groups. Species in many families within the Tylenchina feed exclusively on the roots of higher plants but never on bacteria. Species in the Cephalobidae and Plectidae feed on bacteria but not on higher plants or fungi. Species in the Mononchidae and Anatonchidae are specialist predators of other nematodes and do not feed on higher plants or fungi. The transparent nature of the nematode body allows easy observation of mouth and pharyngeal structures, which allows inference of feeding habit (e.g. Hodda, 2022). Robust techniques for extracting nematodes from soil and other substrates have been developed and can be applied to all taxonomic and functional groups. Most importantly, nematode species vary in their responses to stress factors and resource enrichment; some species are extremely sensitive to pollutants and others are extremely tolerant (Korthals *et al.*, 1996; Ferris *et al.*, 2004b; Tenuta and Ferris, 2004). They vary in lifespan: some species with a generation time of days, others of months or even a year. The matrix of feeding habit, generation time and sensitivity to environmental disturbance allows the designation of functional guilds of different nematode taxa with similar response characteristics (Bongers and Bongers, 1998; Ferris and Bongers, 2006).

In this chapter, we have hinted at the opportunities of using nematodes as biological indicators of the condition of their environment. This issue is still a wide-open research question, also now the European Union has adopted the law on soil monitoring, which requires insights into the indicator value of soil organisms, as not every individual species may be monitored. However, we have also mentioned the challenges involved in assessing the diversity and abundance of nematode assemblages, let alone of assemblages of all soil biota. Other important considerations are the issues of succession within assemblages of organisms and the timing of population assessments in relation to an environmental perturbation or seasonal event. In an agricultural system, for example, a faunal analysis conducted six weeks after a disturbance or introduction of resources may look quite different than would have been the case two weeks after the disruption. Resources will have changed in abundance and nature as they are utilized and the species with different feeding habits and life-history strategies will have changed accordingly; succession and/or recovery will have occurred in the nematode fauna. In many cases, a single assessment of the nematode assemblage may be inadequate for determination of the short-, medium- and long-term impacts of an environmental event, the video equivalent of a series of samples at appropriate time intervals will be more revealing than the snapshot of a single assessment (Berkelmans *et al.*, 2003; Ferris and Matute, 2003, Ferris *et al.*, 2004b).

Finally, we need to remain cognizant that our planet is always in a state of flux and that the amplitude and frequency of the fluxes are not constant. They are impacted by climate change, geopolitical disturbances, marketing opportunities and pressures, availability of fossil fuels and natural resources, and myriad other forces. While we focus on the bioindicator potential of nematodes with regard to ecosystem services, we need to reflect that the very nature of environmental conditions changes, currently faster than in almost any moment in time. Climate change, biodiversity, land-use intensity and contamination are altering at an alarming rate; for example, the accumulation of microplastics in the ocean and contamination from the effluent of aquaculture systems and human habitation. Therefore, using nematodes as bioindicators appears an open challenge, with targets that are often moving faster than research progresses.

1.10 Concluding Points

1. The nematode body plan and life history, although apparently limiting, are sufficiently adaptable to allow species of the phylum Nematoda to occupy a wide range of physical environments, utilize a wide range of resources, become extremely diverse and achieve large populations. Nematodes are the most abundant multicellular animals on the planet.

2. Nematodes have key impacts on populations of many microbes, plants and animals, and on ecosystem processes. They play key roles in many ecosystem processes and services.

3. The abundance and diversity of nematode species vary with ecosystem, physical environment and management.

4. Nematodes are valuable environmental bioindicators, whether in relation to diverse ecosystem services, plant diseases, management of parasites in grazing mammals, human health or insect control, etc. Some such indicators have been used for decades. The challenge is to use nematodes also as indicators for ecosystem health.

5. There are opportunities for further studies on the use of nematodes as indicators for other ecosystem functions, such as the state of restoration in semi-natural ecosystems and the capacity of soils to sustain diverse plant communities. However, indicators must be tailored for each question and environment, with the response variable(s) and indicator being context-specific.

6. Anthelminthic drenches developed for nematodes of livestock relieve suffering when applied to humans. Nematode-trapping fungi, extensively studied in relation to plant-feeding nematodes, have also been successfully deployed to manage gastrointestinal nematodes of livestock. These cases clearly demonstrate the transferability of knowledge of the relationships between nematodes and their total environment. Their usefulness in soils still needs to be further studied.

7. Root-feeding nematodes influence diversity and succession in natural vegetation, although they may operate in assemblages of many soil-inhabiting species. While their absence correlates with plant invasiveness, especially when plants are introduced into new habitats without their original root feeders, the role in plant abundance control needs further studies. Similarly, changes in environmental and climatic conditions, and availability of resources, influence succession in nematode assemblages, but consequences for ecosystem flows and fluxes need to be further established.

8. In agricultural and natural systems, nematodes and other soil biota influence plant–pest interactions above ground; healthy vegetation and above-ground biodiversity, therefore, depend on the composition of the soil community, and probably also on a healthy soil.

Further information on nematode families, genera and species referred to as examples in this chapter is available in Nemaplex (https://nemaplex.ucdavis.edu, accessed July 2024).

Author Note

The original lead author of Chapter 1 in the first edition of this book, the world-renowned soil biologist, nematologist, ecologist and systematist, Dr Gregor Yeates, died on 6 August 2012. As his co-authors, in revising and updating the material in the chapter, we recognize that each of us made substantial contributions in the first edition to the biology, ecology and insights detailed herein. But it is clear to us that the central thread and organization of the material, and the breadth and depth of the supporting citations, reflect Gregor's energy, drive, passion and synoptic view of nematodes in soil and aquatic ecosystems.

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Appendix 1: Outline Classification of the Phylum Nematoda

Molecular approaches have permitted an integrated view of the phylum. While results are generally congruent with traditional relationships, on one hand they so far have not resolved uncertainty among marine groups while on the other hand the order Rhabditida is a monophyletic group equivalent with all of 'Secernentea' (= Phasmidia) in many previous classifications (Blaxter *et al.*, 1998; De Ley and Blaxter, 2002). The classification below, taken from De Ley and Blaxter (2004), indicates the position of many families of interest to readers of this volume.

CLASS ENOPLEA

Subclass Enoplia

Order Enoplida: Ironidae, Alaimidae
Order Triplonchida: Diphtherophoridae, Trichodoridae, Tobrilidae, Prismatolaimidae, Tripylidae

Subclass Dorylaimia

Order Dorylaimida: Dorylaimidae, Aporcelaimidae, Longidoridae, Belondiridae, Leptonchidae, Tylencholaimidae, Nygolaimidae
Order Mononchida: Bathyodontidae, Anatonchidae, Mononchidae, Mylonchulidae
Order Isolaimida: Isolaimiidea
Order Mermithida: Mermithidae, Tetradonematidae
Order Trichinellida: Capillariidae, Trichinellidae, Trichuridae

CLASS CHROMADOREA

Subclass Chromadoria

Order Desmoscolecida: Desmoscolecidae
Order Chromadorida: Chromadoridae, Ethmolaimidae, Cyatholaimdae
Order Desmodorida: Desmodoridae, Microlaimidae
Order Monhysterida: Monhysteridae, Sphaerolaimidae
Order Araeolaimida: Axonolaimidae, Diplopeltidae
Order Plectida: Leptolaimidae, Bastianiidae, Rhabdolaimidae, Plectidae, Chronogasteridae, Metateratocephalidae, Haliplectidae, Aulolaimidae
Order Rhabditida:
  Suborder Spirurina: Thelastomatidae, Oxyuridae, Rhigonematidae, Hethidae, Camallanidae, Hedruridae, Tetrameridae, Filariidae, Ascarididae, Heterakidae
  Suborder Tylenchina: Panagrolaimidae, Steinernematidae, Cephalobidae, Aphelenchidae, Criconematidae, Anguinidae, Hoplolaimidae, Meloidogynidae, Tylenchidae, Pratylenchidae, Drilonematidae
  Suborder Rhabditina: Bunonematidae, Diplogastridae, Mesorhabditidae, Peloderidae, Rhabditidae, Heterorhabditidae, Trichostrongylidae, Metastrongylidae