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https://doi.org/10.1079/9781845933852.0001

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NEMATODES AS ENVIRONMENTAL INDICATORS

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A catalogue record for this book is available from the British Library, London, UK.

Library of Congress Cataloging-in-Publication Data

Nematodes as environmental indicators / edited by Michael J.
Wilson, Thomais Kakouli-Duarte.
p. cm.
Includes bibliographical references and index.
ISBN 978-1-84593-385-2 (alk. paper)
1. Nematodes–Ecology. 2. Indicators (Biology) I. Wilson,
Michael J. (Michael John), 1964- II. Kakouli-Duarte, Thomais. III. Title.

QL391.N4N382 2009
592'.5717--dc22
2008049111

ISBN-13: 978 1 84593 385 2

Typeset by SPi, Pondicherry, India.
Printed and bound in the UK by the MPG Books Group.

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The Role of Nematodes in Ecosystems

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Introduction

Human society is entirely dependent on a variety of ecosystem services (Wall, 2004; Millennium Ecosystem Assessment, 2005). Nematodes play a major role in component processes of most ecosystem services, such as the provision of food, fibre, clean water and air, pest and disease regulation. As nematodes are heterotrophic, differences in, for example, C:N:P ratios between them and their food lead inevitably to their excreting minerals. In soil food webs, nematodes are involved in the transformation of organic matter into mineral and organic nutrients which can be taken up by plants, as well as in influencing plant growth and crop productivity (Ingham *et al.*, 1985; Ferris *et al.*, 1998, 2004a). Nematode feeding activity contributes to soil food web stability. When soils are degraded there may be adverse effects on ground- and surface water quality. Nematodes cause animal and human diseases, and nematodes can 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 both above- and below-ground (De Deyn and Van der Putten, 2005). However, plant community development is not necessarily indicative of below-ground nematode assemblage development (Kardol *et al.*, 2005; Sánchez-Moreno *et al.*, 2008), so that restoration and conservation of nematode assemblages in the soil cannot be inferred from plant community composition. On the other hand, because nematodes are so abundant and omnipresent in ecosystems, they serve as elegant indicators of environmental disturbance (Bongers 1990; Ferris *et al.*, 2001; Yeates, 2003; Höss *et al.*, 2004; Schratzberger *et al.*, 2006; Heininger *et al.*, 2007). Finally, one nematode, *Caenorhabditis elegans* (Rhabditina), has become a central model for genomic studies that aim to relate gene expression to the

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development and functioning of organisms. Indeed *C. elegans* was the first multicelleular organism whose genome was sequenced (CESC, 1998). Many of the advances in molecular biology are underpinned by studies on *C. elegans*. The apparent determinate development and cell constancy (eutely) of nematode species were among the reasons that *C. elegans* was selected for study and the phylum continues to be a focus of studies in basic biology, with cell differentiation, moulting, and ageing being of particular interest.

There are estimates of between 40,000 and 10,000,000 species in the phylum Nematoda (Blaxter, 1998; Yeates and Boag, 2006). One provocative estimate speculates that there might be as many as 100,000,000 species, even before considering the cryptic diversity among morphologically indistinguishable taxa (Lambshead, 1993; Hodda *et al.*, Chapter 2, this volume). The key roles of nematodes in agricultural and natural ecosystems, as well as their usefulness for indicator and molecular studies, make them an important focus for taxonomic, ecological, physiological and molecular research.

Nematodes are built on a simple plan, with the gut 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 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.

The great diversity of nematodes is paralleled by a vast range of head structures which facilitate food ingestion 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 typically four juvenile stages (= 'larvae') preceding the adults. The morphology of the juvenile stages converges with that of the adult; there is no metamorphosis.

Throughout the 20th century, the nature of the nematode body cavity was debated, the supposed lack of complete mesodermal lining suggesting the terminology 'pseudocoelom' (Hyman, 1951). Cilia were not detected in nematodes until the advent of the electron microscope (Roggen *et al.*, 1966). While cilia are now known to occur widely and there have been studies of their sensory role in the behaviour of taxa as diverse as *Caenorhabditis* spp., *Haemonchus contortus* (Rhabditina) and *Onchocerca volvulus* (Spirurina), ciliated epithelia remain unknown in the phylum.

Molecular techniques have improved understanding of the phylogenetic relationships of nematodes with other animal groups. However, there is still vigorous debate about their most likely position and the significance of the ecdysozoan theory based on the occurrence of the *Hox* gene in various animal groups (de Rosa *et al.*, 1999; Gutierrez and Sommer, 2004) although this 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).

Nematodes were recorded as human parasites by the Chinese around 2700 BC and as plant parasites by Shakespeare in 1594 (Viglierchio, 1991) and

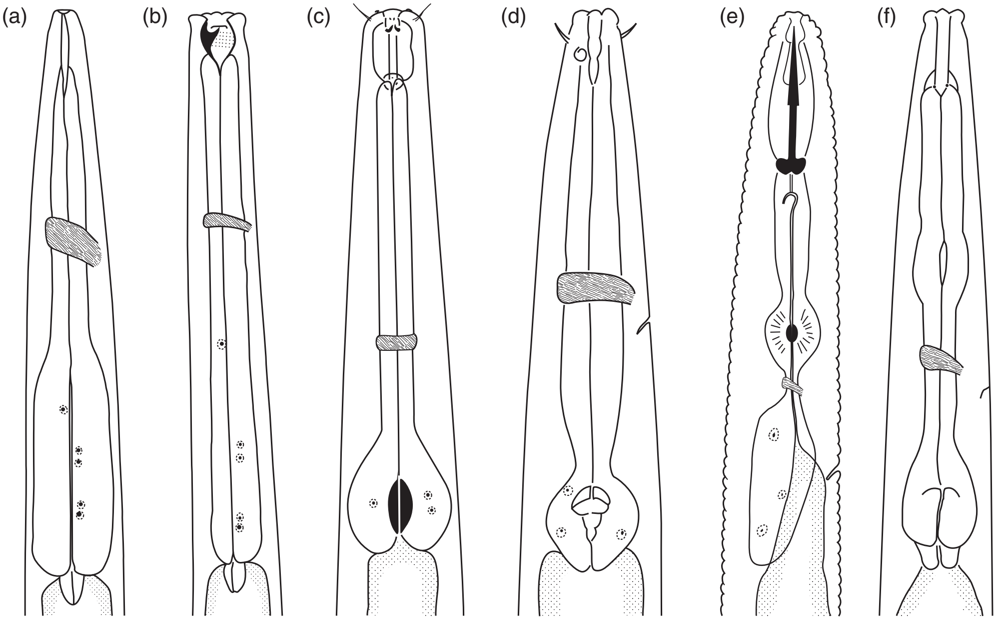

Fig. 1.1. Head and pharyngeal regions of six nematodes found in soil and water environments. (a) Dorylaimida: Dorylaimidae, *Dorylaimus*, (b) Mononchida, Mylonchulidae, *Mylonchulus*, (c) Chromadorida, Ethmolaimidae, *Ethmolaimus*, (d) Plectida, Plectidae, *Plectus*, (e) Tylenchina, Hoplolaimidae, *Rotylenchus*, (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. (Compiled from various sources and observations.)

more formally by Needham (1744). At a time when there is concern about potential extinction of as yet undescribed species – of both nematodes and other phyla – our ignorance of nematode diversity, habitat range and ecological amplitude continues to be challenged. While European workers have contemplated the extinction in the wild of the vinegar eelworm, *Turbatrix aceti* – the first 'free-living' nematode reported (1656) – it has recently been recorded from spoiled vinegar in Brazil (De Moura *et al.*, 2006). On the other hand, there is a strong desire to eliminate *Onchocerca volvulus*, microfilarial juveniles of which cause river blindness in humans.

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). Until that time, so-called free-living nematodes were little more than scientific curiosities. Awareness of the impact of nematode activity on other populations, and thus on ecosystem processes, developed concomitant with awareness of 'biodiversity', a term which first appeared in print in 1988 (Wilson, 1988), and a range of ways in which the abundant, diverse nematode assemblages found in various habitats could be summarized in, and interpreted through, information-rich 'indices', were proposed (Bongers, 1990; Ferris *et al.*, 2001; Yeates, 2003).

Nematode Biology – Individuals and Populations – an Outline

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*, *Pareudiplogaster* and *Daptonema* on diatoms), or on microbes associated with decomposing plant material (e.g. *Aphelenchus*, *Filenchus* on fungal hyphae; *Rhabditis*, *Plectus*, *Leptolaimus* and many Monhysteridae on bacteria). Both animal faeces and cadavers are important resources for microbes and thus for microbial-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. *Thelastoma*, *Ascaris*) themselves dependent on plants. Nematodes feeding at more than one trophic level are termed omnivores. There is increasing awareness of atypical nematodes found in anoxic environments that utilize the energy bound in chemicals as their resource, either directly or via symbiotic bacteria (Polz *et al.*, 2000; Van Gaever *et al.*, 2006).

Substrates 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). As far as we know there have not been any formal, quantitative indices proposed to measure nematode response to such differences in environmental conditions.

There is a clear distinction between the substrate 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 feed and typically live entirely in non-living substrates such as soils, sediments and decaying vegetation while feeding. Plant-feeding nematodes such as *Pratylenchus* and *Radopholus* feed solely on plant tissue but migrate between living plant and non-living soil substrates; they typically hatch as second-stage juveniles. *Heterodera* and *Meloidogyne* also emerge as second-stage juveniles, and 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 the complete life history occurs within the living host; adults inhabit the stomach and intestine of the definitive host and consume food ingested by the host. In contrast, while adult hookworms (e.g. *Ancylostoma*), strongylids (e.g. *Strongylus*) and trichostrongyles (e.g. *Trichostrongylus*, *Haemonchus*) also feed and develop within their vertebrate hosts, commonly evidenced by blood in host intestines, their eggs hatch in faeces and grow as bacterial-feeding stages, in non-living substrate, before reinfecting the living substrate of new vertebrate hosts.

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*, Mermithidae and Trichostrongylidae. 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). Some of the attractants that nematodes use as chemical guides in locating roots have been identified and characterized. 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 *H. schachtii* juveniles. Some of these interactions seem to be species-specific; tobacco root exudates increase egg hatching of tobacco cyst nematodes (Wang *et al.*, 1997) and exudates of cotton roots increase egg hatching in *Rotylenchulus reniformis* (Sankaralingam and McGawley, 1994). However, although plant-parasitic nematodes are highly efficient in locating plant roots, not very many substances have been positively identified as nematode attractants. Amongst the early work on sex attractants was that of Green and Plumb (1970) with *Heterodera* spp. and *Globodera* spp., with other work including 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 *Caenorhabditis elegans* to detect and distinguish between olfactory and taste odour compounds at picomolar (10^{-12}) concentrations (Bargmann and Mori, 1997).

Abundance and diversity of nematodes

In ecological terms ‘communities’ are made up of interacting species. In the various habitats they occupy, nematodes interact with the species providing their food (e.g. bacteria, fungi, plants etc.), other organisms using the same food resource (e.g. bacterial-feeding protozoa, rotifers), and there are predator:prey interactions (e.g. protozoa, fungi and mites as well as nematodes prey on soil nematodes), and the myriad of other organisms inhabiting their environment. The nematode species occurring in a sample do not themselves comprise an ecological community and we prefer to term the collection of populations as an assemblage. We reserve the term 'fauna' for the list of taxa present in a sample, field or landscape.

Each 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 recorded 40,000 individual nematodes from the stomach of a wallaby, and radiation within the Macropodinae (kangaroos and wallabies) has led to a swarm of 112 species of *Cloacina* (Strongyloidea) (Cobb, 1915; Beveridge *et al.*, 2002). In New Zealand, domestic cattle and sheep are infected by 27 and 29 nematode species respectively (McKenna, 1997).

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-plant and post-harvest populations of plant-feeding nematodes; assessing infective juveniles of Trichostrongylidae on pasture herbage) it is common to present results in information-rich indices. Such indices may be either those widely used in ecological studies such as the Shannon–Wiener Index of diversity (H'), Margalef Index of richness (D or SR) and Pielou's evenness (J') (Pielou 1975; Yeates, 1984; Magurran, 1988; Neher and Darby, Chapter 4, this volume) or indices specifically developed for nematodes (Ferris and Bongers, Chapter 5, this volume). The former have been widely applied across organisms and ecosystems and can be regarded as robust, while the latter need to be carefully examined for circularity. The validity of all interpretations need to be tested against current understanding of population dynamics and ecological processes and interactions (Wardle, 2002; Bardgett, 2005; Schratzberger *et al.*, 2007). Nematode grazing on microbes can significantly increase nutrient cycling and plant response in localized patches (Ingham *et al.*, 1985). Although there have been various studies, there is a need for understanding of the factors governing the distribution of patches, when scaling up from a roughly homogeneous patch (e.g. a pedon or uniform agricultural field) to the landscape scale (Coleman *et al.*, 1992; Müller and Lenz, 2006; Sánchez-Moreno *et al.*, 2008). This is also important if one tries integrating across levels by applying frameworks such as the holistic Eco-Energy concept of Jørgensen and Mejer (1979).

Effects of nematodes on their resources

Populations of nematodes may affect the growth rates, health, and yield of plants or animals (e.g. infection of soybeans or potatoes with cyst nematodes or 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). Such effects are dependent on the ecological setting and are usually greater when the system is subject to other stresses. Conversely, adequate levels of nutrition can mask the consequences of infections.

By its very nature, parasitism involves mutual adjustment between host and parasite to permit coexistence without serious harm to either component of the interaction. Typically, there is loss of production, or thriftiness, when the parasite burden increases, or the host is additionally stressed. Indeed, low burdens of plant-feeding nematodes have been found to stimulate plant growth under favourable conditions. Examples of the range of interactions were found in a study of *Heterodera glycines*-resistant and susceptible soybean (*Glycines max*) cultivars across ten states in the United States. Yield loss due to *H. glycines* was greatly confounded by other stress factors, including temperature and moisture extremes (Donald *et al.*, 2006). In terms of beneficial effects of nematode activity, when plant nutrients are non-limiting in the soil nutrient mineralization by bacterial-feeding nematodes will not be reflected in plant yield (Ferris *et al.*, 2004a). Interpretation of such relationships involves a functional, rather than taxonomic, analysis of the populations.

Nematode activities cannot be considered in isolation from abiotic environmental conditions. Physical conditions are important and, for both soil-inhabiting and aquatic nematodes, several studies have shown that soil type is more important than time of year or management practices in determining the overall makeup of the nematode assemblage (Yeates, 1984; Heip *et al.*, 1985; Griffiths *et al.*, 2003). A classic experiment by Griffiths *et al.* (2000) demonstrated that, because of their effects on soil biodiversity, combinations of stressful conditions may heavily impact 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, clover cyst nematodes may selectively influence clover roots resulting in the leakage of nitrogen compounds, which benefit grasses that are not affected by the nematodes (Bardgett *et al.*, 1999). 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).

Traditionally, agricultural nematologists have considered single nematode species as causes of crop losses. More recently, however, ecologists have become concerned with 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; 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, there is considerable variability in the spatial and temporal plant parasitic nematode species composition and abundance; a variety of approaches has been used in efforts to understand this heterogeneity (Goodell and Ferris, 1980; Ferris *et al.*, 1990; Robertson and Freckman, 1995). These spatial and temporal patterns also are important when studying the role of nematodes in natural ecosystems, which are far less homogeneous than agricultural soils, and when using nematodes as environmental indicators. In these conditions, it is crucial to understand the drivers and consequences of nematode diversity within samples (α-diversity), between samples within fields (β-diversity) and between fields within landscapes (γ-diversity).

The contribution of nematodes to foodweb interactions and ecosystem processes, such as the cycling of nitrogen and carbon, may not require species level identification, if the complementary activities of species with similar ecological adaptations and feeding at the same trophic level are considered (i.e. uses the functional guild approach). In terms of ecosystem structure and function, Laakso and Setälä (1999) regarded diversity among functional groups as more important than diversity within them. However, when the parasitic nature of nematodes is considered, and when parasitism is host or even race species-specific, such as that of potato cyst nematodes (*Globodera* spp.), the functional approach requires identifications down to the species, or even pathotype level (Folkertsma *et al.*, 2001). Even 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 (De Mesel *et al.*, 2003, 2004). Therefore, functional interpretations depend on the specific nature of the functions and the nematodes involved in performing them.

Nematode Feeding and its Ecosystem Consequences

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 producing, and *predators* whose feeding results in the death of their prey. Nematodes that appear to be feeding on dead organic matter such as detritus and cadavers are typically grazing or preying on organisms associated with that dead matter.

Within these two general categories we may 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. Some nematodes (e.g. ascarids, thelastomatids) that inhabit the gastrointestinal tract of vertebrates or invertebrates, graze on microbes rather than being carnivores.

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 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. For example, some may be carnivorous as well as bacterial feeding (e.g. Mononchida), or bacterial feeding as well as feeding on unicellular eukaryotes (e.g. *Thalassomonhystera, Daptonema*). 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 occur in 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)).

As might be expected in a group with enormous diversity of habitat, there are exceptions to these 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 recently 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, as well as some of the difficulties in 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), or from tidal flat microalgae and bacteria into nematodes (Moens *et al.*, 2002; van Oevelen *et al.*, 2006). The relative ^{15}N enrichment of *Graphidium strigosum* and *Passalurus ambiguus* in rabbits, compared with depletion in cestodes, has been used to suggest differing trophic relationships (Boag *et al.*, 1998).

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

Praeacanthonchus, *Gonionchus*) often have small teeth or denticles, presumably to abrade, crush or filter ingested particles as was demonstrated by Bird and Ryder (1993) in *Acrobeloides nanus* (Cephalobidae). 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. 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 nematodes are equipped with fixed or moveable teeth (Mononchida, Diplogastridae, Chromadoridae, Enoplidae) or with hollow spears or stylets (Dorylaimida, Tylenchida) for piercing a resource and withdrawing contents. In most Tylenchida and the plant-feeding Longidoridae, the spear lumen is very narrow (~0.1 and 0.5 μm in diameter respectively), significantly limiting what is ingested. Many omnivorous and predatory Dorylaimida have a wide stylet lumen (≥ 6 μm) or even just a single mural tooth (e.g. *Nygolaimus*). The stoma is, however, not a simple indicator of food resource, with some *Seinura* spp. (Aphelenchidae) being predacious and ingesting their requirements through a <0.5 μm aperture, while other predators (e.g. *Anatonchus tridentatus* (Anatonchidae)) are frequently observed to have intact nematode prey in their intestine (Small, 1987).

Microbial feeding in soils and sediments

The ecosystem functions associated with location and ingestion of food by nematodes include the redistribution of resources so that they are more available to other consumers, and the transport of prey organisms to other locations where they gain access to new resources and stimulation of grazed populations (Fu *et al.*, 2005). Their ability to locate suitable feeding patches from a distance, e.g. by sensing cues of decomposition-associated end-products such as CO_2 (Klingler, 1965; Pline and Dusenbery, 1987; Riemann and Schrage, 1988), renders nematodes efficient vectors in transferring microorganisms between suitable resource patches (e.g. Jatala *et al.*, 1974). Generalist obligate bacterial feeders include those ‘enrichment opportunists’ (*sensu* Ettema and Bongers, 1993) which appear to simply draw in aqueous suspensions of their food, with larger particles restricted only by oral diameters of 2 μm or less, but with apparently little other restriction on the types of bacteria ingested (Venette and Ferris, 1998; Salinas *et al.*, 2007). Rather than the dimensions of the adult mouth or stoma, it is the oral dimensions of the first post-hatching (i.e. feeding) stage that limits food size for species population maintenance. Other bacterial feeders are more specialist, feeding actively with, for example, simple to elaborate head probolae, muscular contractions to open a closed (or ‘collapsed’) stoma during ingestion and sweeping motions of the head which allow them access to food by stirring sediments or disrupting adherence of the bacteria to surfaces (Paul de Ley in Moens *et al.*, 2004).

Several important ecosystem functions and services are well-documented for bacterial-feeding nematodes in soils and aquatic systems. Nematodes grazing on microbes may result in greater metabolic activity in their prey populations – essentially nematode grazing on a bacterial population may keep it young and reproductively active. In addition, around 30% of the bacteria ingested by bacterial-feeding nematodes are not digested and assimilated; in fact, they may still be alive when defaecated (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 survive passage through the nematode intestine may vary with food availability and bacterial density (Moens *et al.*, 2006). Some bacteria adhere to the cuticle of bacterial-feeding nematodes. As nematodes move away from the bacterial colony into other areas of the substrate, bacteria are transferred to new areas and to new substrate both as surface 'passengers' and through nematode defaecation. Such 'resource farming' results in the bacterial food resource for the nematodes increasing until predator:prey dynamics are such that overgrazing occurs (Fu *et al.*, 2005). Another example of such nematode-aided bacterial farming is the migration of entomopathogenic nematodes into arthropods where they release bacteria toxic to the arthropod which multiply in the arthropod cadaver and provide food for perhaps two generations of the nematode (Boemare, 2002).

It has also 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. They then measured migration towards, that is their attraction to, those bacteria. On agar plates there seemed to be a 'substrate legacy' affecting the subsequent ability of these bacterial-feeding nematodes to locate the same food. They also carried out experiments in sand and, as verified by Fu *et al.* (2005), commented that the migration that did occur presumably had a role in dispersing bacteria through the soil.

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, but in excess of their needs, in forms that are available to other organisms. A familiar example of the mineralization of digested (i.e. simplified) 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). The CO_2 returns to the atmosphere and is available to plants to be once again fixed into complex molecules through the process of photosynthesis. But, the ingested molecules from which the respired carbon is derived may also contain other elements in excess of the needs of the nematode for maintenance, growth and reproduction. Such excess minerals are presumably excreted in mineral form, rather than defaecated.

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 either nitrates or to atmospheric nitrogen. 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). Although some of these C:N ratios may be revised after further work, they suggest that for every molecule 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).

Differences in elemental ratios among organisms and their differential excretion can lead to uncoupling of conventional C:N:P ratios and element cycling – an emerging area which merges with the stoichiometry of biogeochemical cycling (Sterner and Elser, 2002).

Phoresy or vectoring by and of nematodes

Feeding activities of stylet-bearing nematodes, in addition to facilitating nitrogen mineralization, contribute to other ecosystem services. First, they may provide avenues of ingress into host or prey tissues, for example, access to 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)). Second, they 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 and represent 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). In vectoring of plant viruses, *Longidorus* spp. and *Xiphinema* spp, may weaken the host and render it a poorer resource for the nematode (Brown *et al.*, 1995). A mutually beneficial example of such phoresy is provided by 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 favorable 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).

Nematodes as Regulators of Populations, Succession and Production

The feeding of nematodes on their food sources, besides providing the required energy and nutrient resources, has the potential to regulate or even suppress the magnitude of those resources and consequently impact on ecosystem structure and function. Such effects are in addition to excretion arising from the metabolic costs of nematodes building and maintaining somatic tissue and reproduction. Some general examples are shown in Fig. 1.2 and the following sections give more specific findings.

Plant-feeding nematodes may affect plant community composition

In addition to the much-studied effects of plant-feeding nematodes on plant performance and crop yield, there are many examples in which the reduction in the rate of growth and fitness of higher plants potentially decreases the exclusionary competitiveness of those plants and confers relatively greater fitness on their competitors. Consequently, ecosystem succession increases and plant diversity is increased (Van der Putten, 2003). The result in natural systems is that the susceptible and less fit are reduced or even eliminated from the plant community. More constrained examples are provided in agricultural systems, where aggressive strains of plant-feeding nematodes have often been introduced with their susceptible, but agronomically desirable, hosts. A seeding rate designed for maximizing production in the absence of nematodes will provide a less vigorous stand of the crop in the presence of nematode herbivores. This opens up the canopy and reduces competitiveness with weeds which may out-compete the crop so that the resultant losses of yield can be enormously magnified (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 that enhance herbivores that render the weeds less competitive. Some examples suggest that seed and bud-feeding nematodes may render certain weeds less effective and this clearly affects the plant community. For example, the effects of *Anguina amsinckiae* (Anguinidae) 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 phyllobia* (Anguinidae) reduced the density of the target silverleaf nightshade (*Solanum elaeagnifolium*: Solanaceae) plants by 66% (Northam and Orr, 1982).

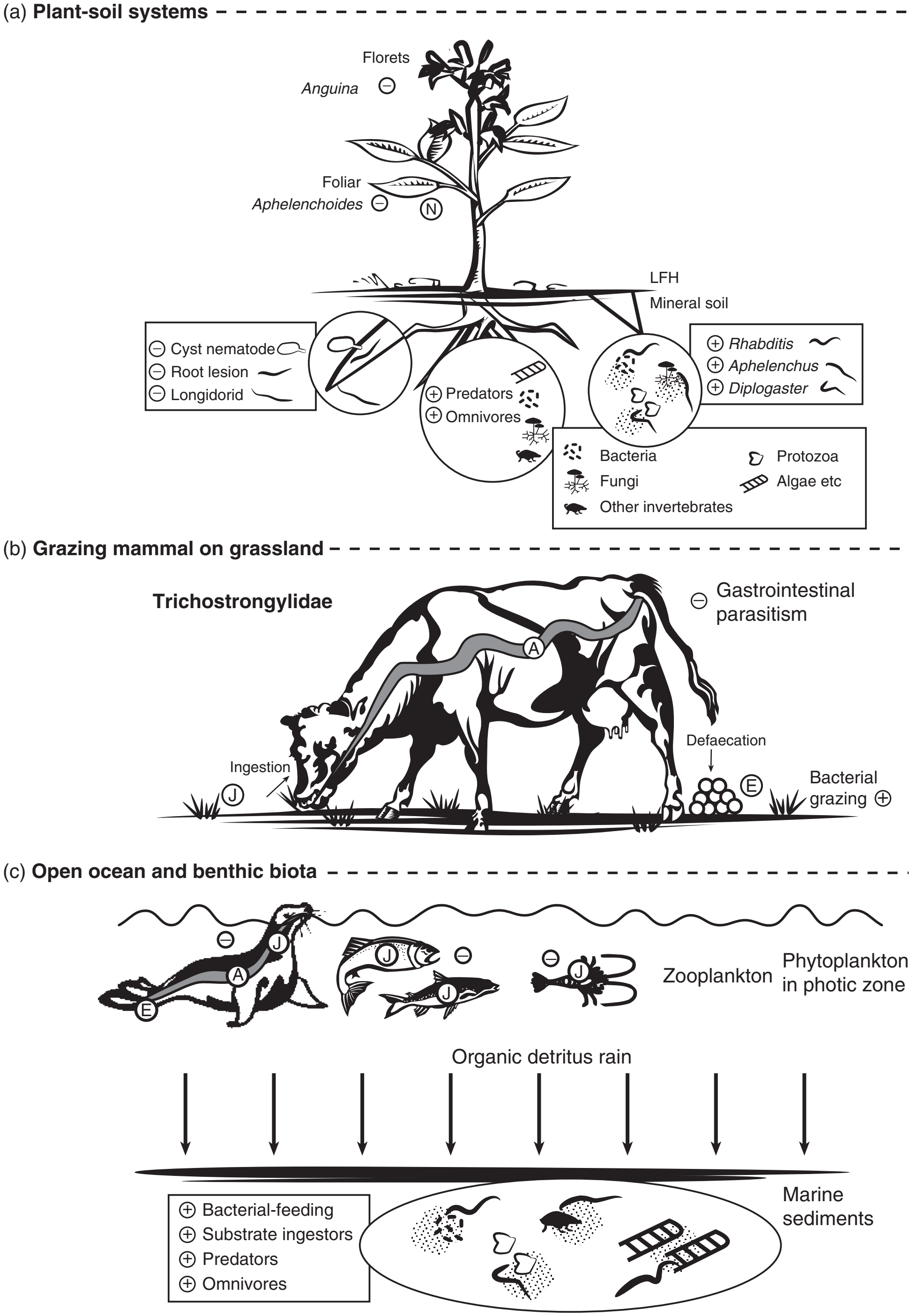

Fig. 1.2. Potential consequences of nematode feeding on food resources [code + being positive effects of grazing on microbes and nutrient availability; – being potential loss of plant or animal production] in (a) plant/soil systems, (b) grassland with grazing mammals, and (c) open ocean pelagic and benthic biota. 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).

Nematodes in vertebrates

Similar examples of reduced competitiveness certainly occur among vertebrates, including humans. 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. Multigenerational selection by farmers of those sheep in a flock performing better under uniform parasite challenge can lead to selection of sheep less susceptible to nematode infection (Bisset and Morris, 1996; Morris *et al.*, 2000). In this work, nematode faecal egg counts are useful as an indicator.

The functional role of nematode parasitism in human populations stimulates the societal response of sanitation and other public health measures and the search for appropriate parasite management tools. River blindness in humans, caused by *Onchocerca volvulus* (Filarioidea), can be controlled by annual treatment with the orally administered microfilaricidal drug, ivermectin (Mectizan®) (Cupp and Cupp, 2005). Elephantiasis or lymphatic filariasis, caused by *Wuchereria bancrofti* (Filarioidea), 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*: Dracunculoidea), no vaccine or medication is available, and public health programmes are used to reduce exposure to infective juveniles.

Regulation of arthropod populations

Several families of nematodes include associates of arthropods. Among those most studied because of their potential as biocontrol agents have been families Mermithidae, Tetradonematidae, Allantonematidae, Phaenopsitylenchidae, Sphaerulariidae, Steinernematidae, and Heterorhabditidae (Kaya and Stock, 1997; Lacey *et al.*, 2001). The regulatory potential of nematodes for arthropods has been most evidently 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. 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 woodwasp *Sirex* in New Zealand and Australia (Bedding, 1993).

Influence on aquatic bacterial community diversity

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), and that 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).

Suppression of mycelial growth

The rate of spread of saprophytic and mycorrhizal fungi in Petri dishes may be reduced by the feeding of aphelenchid nematodes (Riffle, 1967; Sutherland and Fortin, 1968; Ruess and Dighton, 1996) (Table 1.1). Under standard conditions, different fungi have been found to differ in their effects on both the populations and morphometrics of particular Aphelenchidae, Tylencholaimidae and Tylenchidae feeding on them (Faulkner and Darling, 1961; Townshend and Blackith, 1975; Ruess and Dighton, 1996; Okada and Kadota, 2003). It should be noted that Okada and Kadota (2003), Okada *et al.* (2005) found that while *Pleurotus ostreatus* (Basidiomycetes) supported population increase of *Filenchus misellus* and *Tylencholaimus parvus*, in contrast, *Aphelenchus avenae* populations were reduced as a result of predation by *P. ostreatus*. Recent success in maintaining certain Tylenchidae and Tylencholaimidae on fungi provides the opportunity for more specific studies on interactions between mycelial-feeding nematodes and their food supply, including the complexities of decomposer fungi in mineral and organic soil horizons and mineralization of nutrients as a result of nematodes grazing in those horizons as initially explored by Okada and Ferris (2001).

Nematode grazing on mycelia may play other roles in complex interactions in soils. Laboratory studies suggest that feeding by *Aphelenchoides* spp. on the biocontrol fungus *Trichodema harzianum* may constrain its efficacy as a biocontrol agent (Bae and Knudsen, 2001) and Table 1.1 suggests that nematode feeding on mycorrhizal fungi could also reduce exploration of the soil body by their mycelia. *Aphelenchoides* spp. have been found to suppress colonization of *Pinus ponderosa* seedlings by the ectomycorrhiza *Suillus granulatus*

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	49a[a]	0a	40a	0a
5	47a	18 166b	34b	5 322b
10	43a	57 055c	26c	18 011bc
25	34b	57 555c	21d	34 811cd
50	25c	81 360d	16e	37 011d

[a] In each column numbers not followed by the same letter differ significantly at $P < 0.01$.

(Riffle, 1975). In a pot study, Hussey and Roncadori (1981) demonstrated that grazing by *A. avenae* on the vesicular-arbuscular endomycorrhizae *Glomus margarita* and *G. etunicatus* could retard shoot and root growth of cotton. However, they concluded that the large populations of *A. avenae* required probably precluded any significant interactions under field conditions. *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. However, its intraspecific variants differ in their host preference and its persistence in soil requires saprophytic activity (Mauchline *et al.*, 2004), raising further questions about its relationships to the soil biota.

Predacious and omnivorous nematodes

The nematode faunal structure of undisturbed soils often has an abundance of specialist predators of nematodes, for example Mononchida and Diplogastrida, as well as an abundance of generalist predators, mainly Dorylaimida. Observational evidence of such systems, at least partially, supports the hypothesis that the predators have some regulatory, or even suppressive, effect on the relatively low 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). 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). They are at relatively low abundance in agricultural systems, where their potential prey increase to high levels of abundance and biomass and 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. The 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 (Korthals *et al.*, 1996; Yeates *et al.*, 1999a; Sánchez-Moreno *et al.*, 2006).

In some marine sediments, predacious nematodes may reach high abundances and dominate biomass and even densities of nematode assemblages. The genus *Enoploides*, abundant in many fine to medium sandy sediments along coasts and estuaries in NW Europe, is a voracious and selective predator, including oligochaetes, nematodes and ciliates among its prey. Both laboratory and field evidence indicate that it exerts 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 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 compartment of aquatic food webs.

Nematodes in a Community / Ecosystem Context

Economic crop loss due to plant-feeding nematodes

Galled wheat florets ('cockles') and patches of stunted crop plants in sugarbeet and potato fields were among the first noted signs of plant nematode activity. Over the past 150 years there have been many investigations of such plant-feeding nematodes and how their potential pathogenic effects can be managed. Diverse examples can be found in books such as Lee (2002), Luc *et al.* (2005) and Perry and Moens (2006).

Management of microbial-feeding nematode function in an agricultural context

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 nitrogen 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 N mineralization (Chen and Ferris, 1999). The abundance of bacterial-feeding nematodes was considered an indicator of concomitant abundance of other bacterial grazers, 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 since 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 higher 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

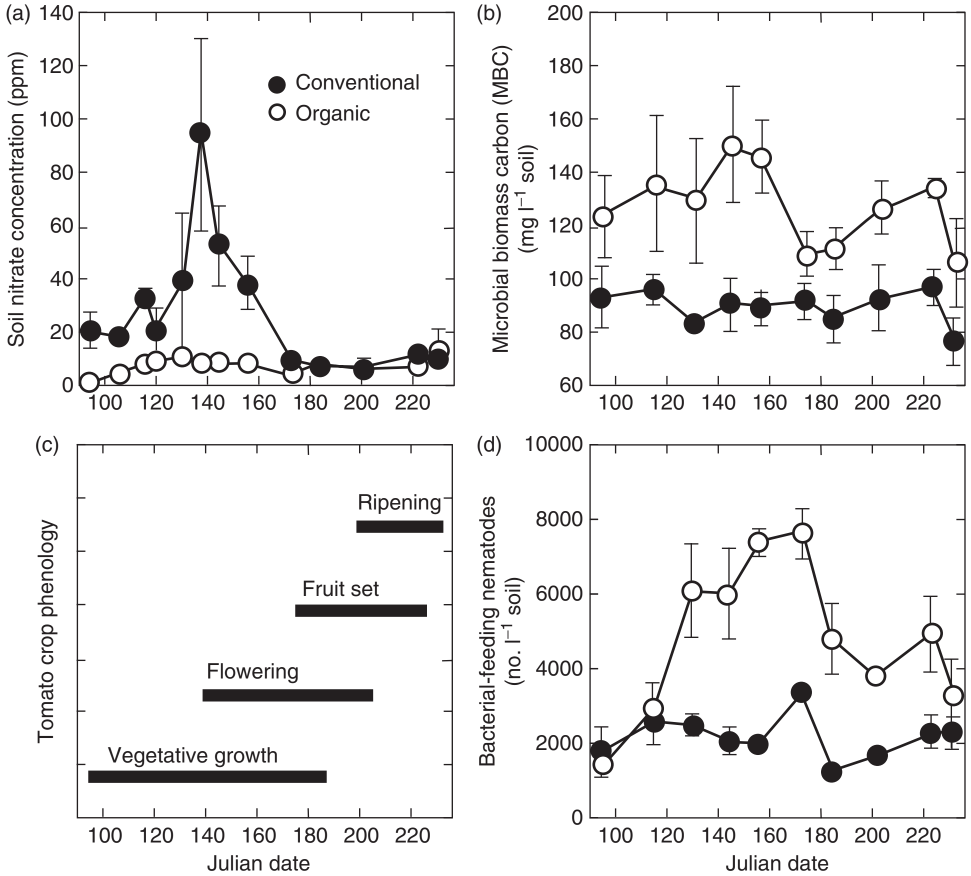

Fig. 1.3. Relationship of soil nitrate availability, microbial biomass and bacterial-feeding nematode abundance in soils under organic and conventional farming systems to tomato crop phenology. Data are means and standard errors across four replicates; Julian days run from 1 January. (a) Extractable 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).

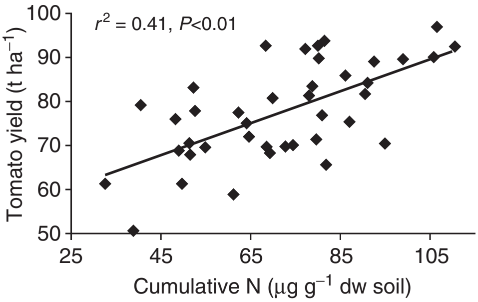

Fig. 1.4. Tomato crop yield in August 1996 in relation to cumulative soil N measurements over five sampling dates in April and May, prior to planting (redrawn from Ferris *et al.*, 1996).

plots. 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.*, 2004a).

Nematode control of game bird population cycles

Cyclic fluctuations in vertebrate numbers have puzzled observers for generations. In Britain red grouse (*Lagopus lagopus scoticus*) is a game bird on which a sizeable industry is built, but it suffers irregular population crashes. The large caeca of red grouse are infected with *Trichostrongylus tenuis* (Rhabditina, Trichostrongylidae) and eggs are passed in the faeces, their development giving rise to infective third-stage juveniles on heather and in the soil; this development is affected by temperature and desiccation (Shaw *et al.*, 1989). Grouse are most likely infected when they feed on heather, their main food plant. The growth rate of the grouse population is negatively related to nematode infection ($r = -0.676$) while grouse brood mortality is positively related to such infection ($r = +0.641$) (Figure 1.5. a, b). Treating adult birds with levamisole hydrochloride (a standard anthelmintic) before breeding increased the number of game birds shot later that year, and reduced the cyclic fluctuation in grouse population compared with untreated populations (Fig. 1.5. c, d). Treatment with anthelmintic in two years gave the most stable game bird populations (Fig. 1.5 e) (Hudson *et al.*, 1998).

Coastal sand dune nematodes are controlled by a multitude of factors

Vegetation succession in coastal foredunes is 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). In other continents, however, the pioneer species marram grass (*Ammophila arenaria*) has been introduced without the specialized nematodes which correlated with plant invasiveness in Europe (Van der Putten *et al.*, 2005). However, all nematodes appeared to be controlled in a species-specific way by 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 (Fig. 1.6). Therefore, the current view is that in the root zone of marram grass, plant-feeding nematodes, albeit some that are potentially harmful to marram grass, are controlled in a multi-factorial manner. This interesting phenomenon may stimulate new thinking about sustainable nematode control in agriculture based on principles derived from natural systems (Van der Putten *et al.*, 2006).

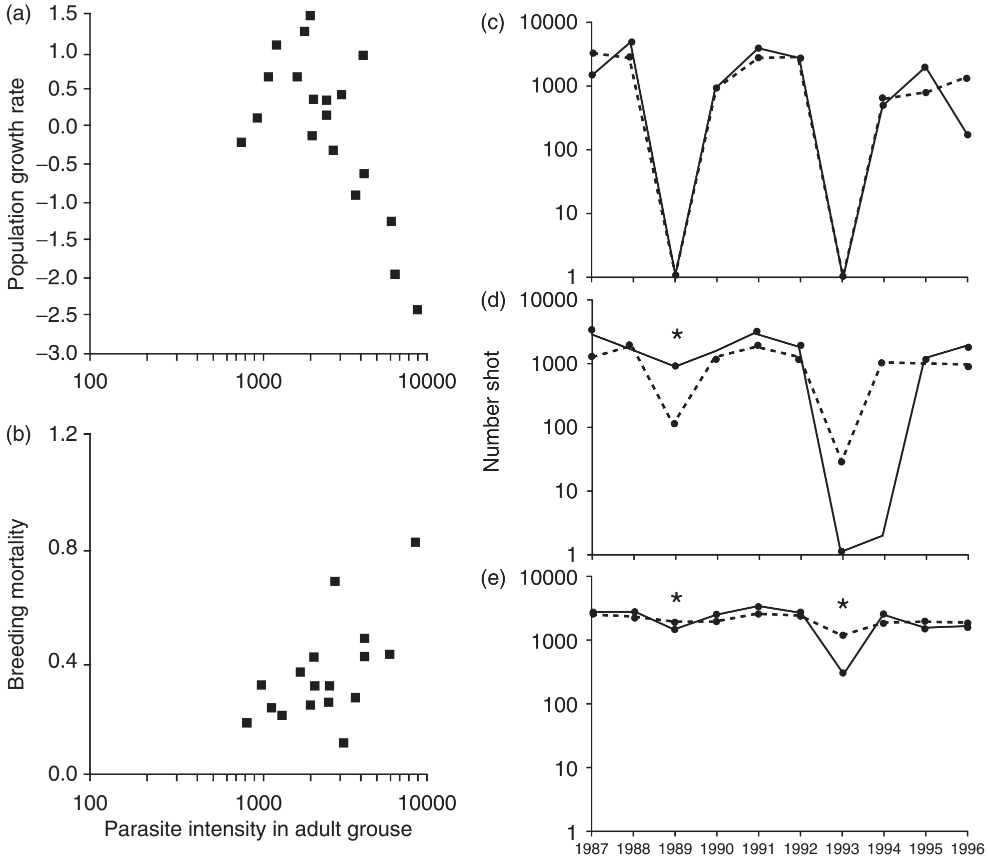

Fig. 1.5. Relationship between populations of red grouse (*Lagopus lagopus scoticus*) in northern England and their infection with the nematode *Trichostrongylus tenuis*. (a) Annual population growth rate [rt = (ln Nt+1 – ln Nt)] against mean log worm intensity in breeding adult grouse. (b) Breeding mortality [log maximum clutch size (12) – log mean brood size at 6 weeks] against mean log worm intensity in breeding adult grouse. Population changes of red grouse as represented by bag records at (c) two control sites, (d) two populations receiving a treatment with levamisole in 1989, and (e) two populations each receiving treatment with levamisole in 1989 and 1993. * indicate the years when treatment reduced nematode burdens in adult grouse (after Hudson *et al.*, 1998).

Intertidal nematode populations governed by environmental modulation of top-down control

Nematodes inhabiting intertidal habitats often display vertical migrations in relation to the tidal cycle. The genus *Enoploides*, abundant in many fine to medium sandy sediments along coasts and estuaries in NW 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

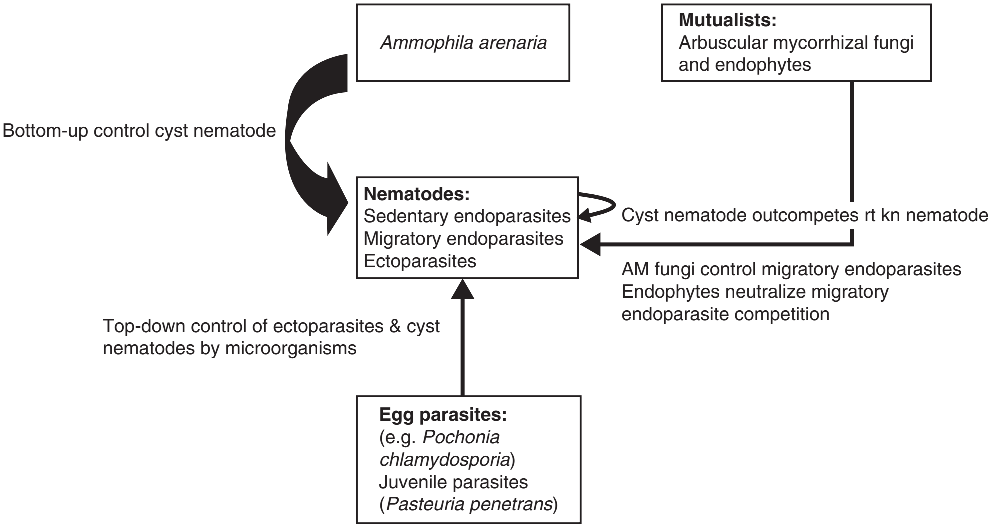

Fig. 1.6. Schematic of multiple controls on root-feeding nematodes on marram grass (*Ammophila arenaria*) in coastal sand dunes in north-western Europe (modified after Van der Putten, 2003).

communities (Moens *et al.*, 2000; Hamels *et al.*, 2001). *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 (SW Netherlands), peak at a depth of 4–5 cm, which is unusual for any type of marine sediment (Steyaert, personal communication). 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 8–18 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 (Gallucci *et al.*, 2005; Steyaert *et al.*, unpublished data).

Pollution experiments suggest 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 (MPB) biomass and nematode abundance and in meiofaunal grazing rates on MPB. Total meiobenthic (copepods + nematodes) grazing was lower in diesel-contaminated than in unaffected plots, suggesting: (i) that MPB biomass is top-down controlled by meiobenthic (here mainly harpacticoid) grazing; and (ii) that harpacticoid copepods and nematodes compete for this limiting resource (Carman *et al.*, 1997; Fleeger *et al.*, 2006). The system is, however, yet more complex 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 MPB abundance, 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.

Nematodes of lakes and seas

In intertidal and shallow sediments, local primary production by microphytobenthos often appears to be the predominant carbon source fuelling nematode assemblages (Riera *et al.*, 1996; Moens *et al.*, 2002, 2005a). In the absence of such local primary production, nematodes in deeper (or light limited) environments are primarily dependent on the rain of organic debris from the productive photic zone above as well as input from rivers and streams. Both in shallow and deep environments, the relative importance of direct grazing on primary production or on associated bacteria and/or heterotrophic remains (especially those of protozoa) is still largely 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).

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 ($r^2 = 0.982$) and nitrogen ($r^2 = 0.971$). 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 to be related to the increase in primary productivity with latitude in this area (Lambshead *et al.*, 2000), a correlation which was also confirmed in the central equatorial 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 particular 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 sulphide-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: the adaptation of *Stilbonema* and *Laxus* (Desmodoridae: Stilbonematinae) to sulphide-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). The unrelated mouthless nematode *Astomonema* (Siphonolaimidae) 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 do appear closely related to the bacterial ectosymbionts on stilbonematinid nematodes and in gutless oligochaetes (Musat *et al.*, 2007). The marine nematode *Oncholaimus campylocercoides* (Oncholaimidae) is adapted to sulphidic 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 (Jones *et al.*, 2006), it will be some time before a comparable data set is available to utilize nematodes in a similar way.

Diversity within vertebrate hosts

There has been radiation/speciation of nematodes in the stomach of kangaroos and wallabies with 55 species of host containing 112 species of the genus *Cloacina* alone. Up to nine nematode species commonly occurred in a host (*Macropus dorsalis*), while particular nematodes occurred in up to 11 hosts (Beveridge *et al.*, 2002). 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).

Nematodes as Environmental Modifiers

Sediment agitation by nematodes

We have already described how microbial grazing can enhance nutrient cycling. In addition, several aquatic studies have demonstrated bioturbation by nematodes, that is physical disturbance of the mineral and organic particles comprising the substrate, to be of major importance through 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 by an 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 a little 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 was later modified into the 'enzyme sharing' concept: nematodes may produce exo-enzymes 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 nutritious dissolved organic matter 'soup' 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 current as well as predation (Nehring *et al.*, 1990; Nehring, 1993).

Nematodes influence ecological succession in grasslands

Effects of nematodes on ecological succession have been studied mainly in terrestrial grassland systems. 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 explained before, plant-feeding nematodes in the root zone of the foredune marram grass (*Ammophila arenaria*) all appear to be controlled. However, in secondary grassland succession following removal of intensive farming practices, nematodes have been shown to influence plant performance (Verschoor *et al.*, 2001) and plant succession

(De Deyn *et al.*, 2003). Usually, abundance of plant-feeding nematode species is relatively low, but their high abundance in local hot spots may allow substantial effects on plant productivity (Verschoor, 2002). Selectivity of the nematodes, or their focusing on 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). Plant species can influence the composition of nematode assemblages in soil; however, the actual species present are more important than the diversity of the plant community per se (De Deyn *et al.*, 2004; Viketoft *et al.*, 2005). Some plant species that enhance specific root-feeding nematodes may indirectly enhance biotic resistance of grassland communities against nematode-sensitive plant species when invading the existing grassland communities (van Ruijven *et al.*, 2005). Most studies mentioned above have involved inoculation experiments. Studies in prairie ecosystems in the 1970s concluded that nematodes use substantial amounts of the net primary productivity (Stanton, 1988). However, these conclusions were mostly based on selective biocides and the results have not been verifiable by inoculation studies, which casts doubt on the assertion that grassland nematodes account for losses up to one quarter of the net primary production.

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 their likely regulation of important ecosystem processes such as organic matter mineralization. Microcosm studies using an estuarine example of the duality of enrichment opportunists (e.g. *Rhabditis 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 which provide them with optimal feeding conditions (T. Moens, Ghent, 1997, personal communication; Santos *et al.*, 2008).

Nematodes may predispose hosts to other organisms

There is widespread belief that root-feeding nematodes predispose their host plants to pathogenic soil fungi (Castillo *et al.*, 2003; Back *et al.*, 2006). Although these effects may occur, other studies have argued the interaction effects to be additive, rather than synergistic. In a critique, Sikora and Carter (1987) argued that most studies that showed synergistic interactions were based on similar model systems and experimental procedures. It is often advocated that nematodes create entry points in the roots for pathogenic soil fungi to colonize but the mechanism of predisposition has not always been identified. However, Van Gundy *et al.* (1977), in an elegant experiment, demonstrated that metabolic leakage from roots infested with root-knot nematodes (*Meloidogyne incognita*) stimulated the transformation of *Rhizoctonia solani* from saprophytic to parasitic growth on uninjured roots.

Nematodes may also predispose hosts to other nematodes, which may lead to competitive or facilitative effects. In general, the more complex the relationship between root-feeding nematodes and their host plants is, the more competitive they are within and among species (Eisenback, 1993). 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 facilitative effects of wireworms (Elateridae) on root knot nematodes by indirect promotion of *Meloidogyne* abundance in mixed plant communities (De Deyn *et al.*, 2007). Whereas we have already mentioned facilitative effects among aquatic bacterial-feeding nematodes, inhibitory interactions between congeneric species of *Diplolaimelloides* have been demonstrated and would appear not to be primarily due to direct competition for food or space (De Mesel *et al.*, 2006; Santos *et al.*, 2008).

Similarly, inhibition between 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 (Phillips *et al.*, 2003). Probably, when explored more intensively, such indirect effects among nematodes and between nematodes and other organisms will be found to be important determinants of community interactions.

Synoptic Integration to System, Landscape and Biosphere Levels

Nematodes are among the most diverse soil and benthic organisms and are usually the most abundant of the soil or sediment Metazoa. They are the most important secondary consumers within the soil mesofauna (Mulder *et al.*, 2005). There has been less research in aquatic systems but studies suggest at least a small contribution of nematodes to carbon turnover in aquatic sediments (Soetaert *et al.*, 1997; Coull, 1999). Nematodes have been extensively used as indicators of soil diversity and functioning (Neher, 2001; Mulder *et al.*, 2005). While there are some similar studies for aquatic environments there is an underlying problem that the causes for very high local diversity in, for example, deep-sea sediments, are very poorly understood. Thus the use of nematode diversity per se as an indicator in aquatic sediments is not well established. While literature dealing with nematode faunae as soil health indicators in different farming and natural systems is abundant, few studies deal with regional/landscape/ocean floor zone/distribution patterns of nematode faunae. 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 aboveground and belowground biota are important ecological drivers in terrestrial ecosystems (Sánchez-Moreno *et al.*, 2008). The spatial patterns of soil biota have important aboveground consequences on both plant community structure and on individual plants (Ettema and Wardle, 2002). The reciprocal is also true.

In general, there is a lack of detailed information on the effects of landscape heterogeneity and soil management practices on nematode spatial patterns. In marine systems, on the other hand, there has been a strong emphasis on comparisons of nematode assemblages at β and γ scales, but there is a lack of process-oriented or mechanistic understanding of drivers of the patterns.

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 species population the more general, local patch. 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, 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 zone sites of uprooted orchard trees can result in death of trees in a subsequent orchard planting.

In another example of functional linkages between aboveground and belowground 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. While these effects occur at the ped/microsite level, scaling up by using GIS and multi-layer mapping techniques will allow a more comprehensive understanding of the functions and services of nematodes at the landscape level. Recent studies indicate that nematodes can enhance the control of aboveground pests through increasing both bottom-up and top-down control activities (Bezemer *et al.*, 2005). This linking of above- and belowground subsystems is a new and promising development indicating that sustainable crop protection, even against aboveground pests, may start with proper soil management.

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 gave relief. However, apart from perceived non-target effects, these drenches have resulted in genetic selection for anthelmintic-resistant nematodes. The use of the nematode-trapping fungus *Duddingtonia flagrans* has reduced parasitism with acceptable economic return (Waller *et al.*, 2004). In contrast, two anthelmintic drenches (ivermectin and albendazole) have proved useful for effective, control of river blindness and elephantiasis, caused by filarioid nematodes.

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 controlling 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. 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. 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 expensive specialized machinery have led to the need for specialization among growers. Rotations have become so narrow that natural population dynamics cannot be used to reduce parasite population levels. The side effects of chemical nematicides on soil life and neighboring aquatic ecosystems have resulted in awareness that these chemicals threaten the sustainability of crop production and have highlighted the need for biological control. However, biological control, because it represents a series of interlocking biological populations, is much more variable and less predictable, limiting the generalization of findings in one crop at specific site conditions (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.

Field studies suggest that when humans modify natural selection, competition and species replacement, through crop breeding for high yield, 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. 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. The major question of whether or not to return to cropping practices that were applied in the past or to develop new farming systems has not yet been answered. Almost certainly, the use of cultivars that have not been selected for maximum yield under conditions utilizing pesticides and mineral fertilizers will be necessary. Some studies have shown that nematodes can enhance the control of aboveground pests through enhanced bottom-up and top-down control activities (Bezemer *et al.*, 2005). This linking of above- and belowground subsystems is a new and promising development suggesting that sustainable crop protection, even against aboveground pests, may start with proper soil management.

Suitability of Nematodes as Environmental Indicators

The development of nematodes as bioindicators in soil and aquatic systems required determination of appropriate ways to assess and quantify their contributions to ecological processes, and the validation of their utility 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, on heavy clay, in deep sea sediments, in rotting plant material, in compost 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. Many families within the Tylenchina feed exclusively on the roots of higher plants but never on bacteria. Cephalobidae and Plectidae feed on bacteria but not on higher plants or fungi. Mononchidae and Anatonchidae are specialist predators of other nematodes and do not feed on higher plants or fungi. The transparent nature of nematodes allows easy observation of mouth and pharyngeal structures, which allows inference of feeding habit. 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, nematodes have variable responses to stress factors; some species are extremely sensitive to pollutants and others 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 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).

Concluding Points

- 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 habitats, utilize a wide range of resources, become extremely diverse and achieve large populations. They are the most abundant multicellular animals on earth.

- Nematodes have impacts on populations of many organisms and on ecosystem processes. They play key roles in many ecosystem services and processes.
- The abundance and diversity of nematode species vary with ecosystem, substrate and management.
- Nematodes have been successfully used as 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.
- 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.
- Anthelmintic 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.
- In ecosystem terms, root-feeding nematodes influence diversity and succession in natural vegetation; their absence may result in plant invasiveness, especially when plants are introduced in new habitats without their original root feeders. Further, in cropping terms, nematodes and other soil biota influence plant–enemy interactions above ground; a healthy crop, therefore, depends on a healthy soil.

Acknowledgements

Preparation of this chapter has been aided by funding from the Foundation for Research Science and Technology (New Zealand) and by N.S.F. (US) grant DEB-0120169. T.M. is a postdoctoral fellow with the Flemish Fund for Scientific Research F.W.O.

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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 have so far 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: Monhysteridea, 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, Anguinindea, Hoplolaimidae, Meloidogynidae, Tylenchidae, Pratylenchidae, Drilonematidae
Suborder Rhabditina: Bunonematidae, Diplogastridae, Mesorhabditidae, Peloderidae, Rhabditidae, Heterorhabditidae, Trichostrongylidae, Metastrongylidae