An Introduction to Roundworms

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The Earth's Most Abundant Animal Group and its Impacts on Humankind

By

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To God,

for allowing me to explain to people a tiny bit of His creation

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Preface

It was June 2020; as usual, I was power walking while listening to the great radio program Science Friday. It was the Best Summer Science Books Day, and the host recommended enjoyable vacation reading on the science behind topics as variable as bees, sequoias, asteroids, and coffee brewing.

Suddenly, it struck me how little scientists dedicated to nematodes[1] address the *general public* about their field of study. I emphasize the general public—such as high school students and their teachers, or science enthusiasts with backgrounds as diverse as law, mechanics, or accounting—for whom the vast technical and scientific literature on nematodes is not easy to grasp.

That the general public needs science education is indisputable. Also indisputable, albeit little known, is the tremendous impact of nematodes on humankind. But how best to educate people on the role played by nematodes in all sorts of ecosystems; in human health; in agriculture; and in biology, biomedicine, paleontology, and astronautics, among other science fields? Could I, a scientist trained to write in precise detail, produce an enjoyable and readable book? For over a year, I pushed this challenge away because I thought I was not capable of tackling it. And another year went by following the passing of our daughter Lara in early 2022, because this challenge and indeed all others felt pointless.

But in the end, I gave in! The result is in your hands. It is a text focused on the multipronged impact of nematodes on humankind, with language and a level of detail for the general public. With this focus and audience in mind, I avoided excessive information on nematodes' morphology, biology, ecology, and behavior, which are often emphasized in technical and scientific texts. The complex topic of nematode morphology and evolution

[1] Nematode is a more technical term for roundworms.

is presented in an 8-minute video posted on YouTube, with a URL link and QR code in the book. This video is narrated by Prof. James G. Baldwin, Emeritus Professor of Nematology at the University of California, Riverside (USA). I cannot thank him enough for his willingness to contribute to this book.

But science is not only about data; people are involved. To engage the reader's heart and mind with nematodes, I invited a constellation of scientists from different fields to talk about their personal trajectory, challenges, and ideas on their research on nematodes. I thank each and every one for their contribution to this book. I should also thank Susan Casement, who revised all the chapters for grammatical correctness, and Alison Duffy and her team at Cambridge Scholars Publishing.

I hope that I have managed to combine the text, video, and interviews to produce an enjoyable reading experience for the general public, including, why not, the relatives of nematologists who often don't quite understand what we do and ask with a hint of disdain, "What are they called? Oh yeah, worms…".

CHAPTER 1

INTRODUCTION

As a nematologist, it strikes me how little lay people know about nematodes[1]. By the end of high school, students may have been taught about two or three nematodes that parasitize humans. In high schools that include a teaching lab, they may have glanced at fixed specimens in a jar. Unless a college degree in biology or related field is pursued, most people will not hear again about nematodes. An exception may be on TV news channels, which occasionally report biomedical discoveries made possible by the use of, how odd, "a worm"! On the other hand, many biologists, ecologists, and agronomists have only superficial knowledge about nematodes, even when their professional subject, e.g., a forest, the sea, or a soybean field, is markedly affected by nematodes. As we'll see in the chapters ahead, nematodes may be *the* most important players in such environments, although most of them are not visible to the naked eye.

Perhaps you just had an understandably skeptical reaction: Are you saying that one of the least taught, googled or instagrammed groups of invertebrates is a major player in Nature? Well, yes. It has been estimated that 4 out of 5 individual animals on Earth are nematodes. This means that nematodes outnumber the most abundant group of animals that you may think of, say, insects, fish, or earthworms. To give you a specific figure, a recent study[2] estimated that about 4.4×10^{20} nematodes live in the upper layer of soils worldwide. Nematologists also estimate that a staggering number of nematodes live in the oceans, lakes, and rivers and, when they

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[1] Nematode is a more technical term for roundworms. Nematodes are quite distinct from other invertebrates popularly known as earthworms, flatworms and horsehair worms.

[2] van den Hoogen, J. et al. 2019. Soil nematode abundance and functional group composition at a global scale. Nature, 572:194–198. https://doi.org/10.1038/s41586-019-1418-6

are parasites, in their plant, invertebrate or vertebrate host. We'll deal with the global environmental impact of nematodes in Chapter 2, but for now it may suffice to say that, through their breathing, soil nematodes expel at least 1.32 gigatons of carbon into the atmosphere per year. This corresponds to 15% of the world's carbon emissions from fossil fuels. Nope! As we'll see later, nematodes should not be eliminated for the sake of mitigating climate change!

That much carbon expelled by nematodes reminds me that they are masters of adaptation. Most nematodes breath oxygen, which enters metabolic pathways not too different from ours. But unlike us, nematodes will survive hours or days without harm if the environment becomes anoxic. Some nematodes go further: their youngsters breathe oxygen, while the adults live in an anoxic environment! This and many other tricks explain why nematodes are capable of living in such contrasting environments, from fresh water to sea water; from desert-dry soils to soils flooded with brackish water in mangroves; and from the oxygen-rich soil of your garden to the anoxic human intestine. The ubiquity of nematodes has led Nathan Cobb, one of the founders of nematology, to state that "if all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes, and oceans represented by a film of nematodes". Recently, this pervasive presence of nematodes has been dubbed the nematosphere[3].

As invertebrates, nematodes have a relatively simple morphology (Fig. 1-1). But their ubiquity suggests that they must have undergone morphological adaptations to thrive in so many ecosystems. Take humans as an environment. In our large intestine, the nematode *Ascaris lumbricoides* may reach nearly half a meter in length. With a diameter of up

[3] Zawierucha, K. Porazinska, D.L. Ficetola, G.F. Ambrosini, R. Baccolo, G. Buda, J. Ceballos, J.L. Devetter, M. Dial, R. Franzetti, A. Fuglewicz, U. Gielly, Lokas, E. Janko, K. Jaromerska, T.N. Koscinski, A. Kozlowska, A. Ono, M. Parnikoza, I. Pittino, F. Poniecka, E. Sommers, P. Schmidt, S.K. Shain, D. Sikorska, S. Uetake, and J. Takeuchi, N. 2020. A hole in the nematosphere: tardigrades and rotifers dominate the cryoconite hole environment, whereas nematodes are missing. Journal of Zoology, 313:18–36. https://doi.org/10.1111/jzo.12832

to 6 mm, *A. lumbricoides* has the typical thread-like shape of nematodes. *Wuchereria bancrofti* lives in the human lymphatic system, causing lymphatic filariasis. Reaching up to 10 cm long, the females lay youngsters that are exceedingly small (280 µm long[4]) to be picked up by biting mosquitoes for transmission among people. By comparison, that would correspond to a woman 1.7 m tall having babies about 5 millimeters long. Nematodes have also adapted their mouth parts depending on how they parasitize humans. They may have cutting blades to lacerate tissues to feed on blood or they may have an unarmed mouth to feed on intestinal contents, as in *A. lumbricoides*. In chapter 3 we'll see more about human-parasitic nematodes. As for their importance to human health, just keep in mind that five nematodes are members of a group called "the grisly seven", which cause the world's most important and neglected tropical diseases[5].

Fig. 1-1: An egg-laying female of *Caenorhabditis elegans*, probably the second most studied animal on Earth. Scale bar= 100 µm.

While nematodes are generally not beneficial to human health, their effect on plants tell an entirely different story. Here we should bear in mind that different nematodes have distinct food preferences, such as bacterial-feeders and fungal-feeders. In the soil, bacteria and fungi decompose all sorts of organic matter, releasing nutrients that are absorbed by the plants to sustain their growth. Studies have shown that this nutrient recycling is increased when bacterial- and fungal-feeder nematodes are abundant in the

[4] One micrometer (µm) equals 0.001 mm, which is the same to say that 1,000 µm equals 1 mm.
[5] Hotez, P.J. 2010. A plant to defeat neglected tropical diseases. Scientific American, January 2010.
http://www.bio.umass.edu/micro/klingbeil/590s/Reading/Hotez2010.pdf

soil. The nematodes' avid feeding increases the net efficiency of bacteria and fungi, Nature's primary decomposers.

While bacterial- and fungal-feeder nematodes contribute indirectly to increasing the plants' primary production, a third group—that of plant-parasitic nematodes—does exactly the opposite. In their mouth, these nematodes have a stylet with which they puncture the root, leaves or other plant parts. By withdrawing nutrients and altering or damaging plant tissues, plant-parasitic nematodes are a menace to the production of food, fiber, and other products. Major yield (production) losses occur worldwide in crops such as rice, soybean, potato, citrus, and coffee, among many others. In the rural setting there are also nematodes that parasitize horses, sheep, cows, and other livestock. Domestic animals such as dogs and cats need "deworming" soon after birth so that parasitic nematodes don't compromise their development or accidentally infect their owners. We'll give you an account of the importance of nematodes to agriculture in Chapter 4.

As practical beings, humans have learned to benefit from many phenomena in Nature, e.g., energy and physical laws; and many micro- and macro-organisms such as viruses, yeasts, honeybees, and horses. How about nematodes? Nematologists have turned some species[6]—or entire nematode communities—into tools for the benefit of humankind. The most famous case is this: in the 1950s and 60s the South African biologist Sydney Brenner was deeply involved in the nascent field of molecular biology. At a certain point, he became interested in understanding the connection between DNA and developmental biology. Or more simply put, how does DNA pass along the information that babies should have five fingers on their hands? And what goes wrong when a baby is born with six fingers? Looking for a simple organism to work with, Brenner was introduced by the MD and nematologist Ellsworth C. Dougherty to a tiny bacterial-feeder nematode that goes by the name of *Caenorhabditis elegans*. Beginning with Brenner, who was followed by many scientists worldwide, *C. elegans* became an important model for studies on genetics, developmental biology,

[6] A species, e.g., *Caenorhabditis elegans*, is a group of nematodes that evolved from a common ancestor. Hence, they share physical, physiological, genetic, and behavioral features.

human diseases, and the development of pharmaceuticals. Incidentally, the first animal to have its genome sequenced was *C. elegans*, two years before the sequencing of the human genome. For his contributions to science, Brenner was the co-recipient of nothing less than the 2002 Nobel Prize in Physiology or Medicine. We'll see in Chapter 5 how nematodes have been used as tools to monitor pollution in the soil and water; in industrial plants; in biomedical research; and for the biological control of agricultural and urban pests.

Chapter 6 brings two exciting topics: paleonematology and what I have dubbed astronematology. Nematodes evolved from an extinct, unknown invertebrate sometime in the late Proterozoic eon, around 550 million years ago (mya). Beginning at about 400 mya, nematodes have been preserved in amber (fossilized tree resin), rock deposits, coprolites (fossilized dung), and mummies, giving nematologists insights into nematode evolution and human biogeography. Shooting towards the future, we'll visit recent studies with nematodes in space and see how nematodes boarding the space shuttle Columbia survived the disastrous reentry into the atmosphere that killed seven astronauts onboard.

After grasping the importance of nematodes in Chapters 2-6, you'll see some more details about these ubiquitous invertebrates. In Chapter 7, a computer animation shows the main features of nematode morphology, with emphasis on adaptations that enabled nematodes to thrive in so many environments. This animation is narrated by a nematologist who devoted his scientific career to nematode morphology and its evolution, the University of California-Riverside emeritus professor, James G. Baldwin. Chapters 2-7 end with interviews with scientists that work with nematodes in different areas of science. They talk about their personal trajectory, area of expertise, challenges and expectations, and how important nematodes are for their career.

In Chapter 8, you'll learn more about nematode biology as we discuss the life cycle and behavior of some nematodes. Our journey into the exciting world of nematodes ends in Chapter 9, where you'll find links to scientific societies devoted to nematology and resources through which to learn more about these astonishing little critters. For instance, Scishow® has produced a very nice presentation about nematodes, which you can see at https://www.youtube.com/watch?v=vBWzrlCBhCM&t=38s

CHAPTER 2

NEMATODES AS PLAYERS IN ECOSYSTEMS WORLDWIDE

As we've seen in Chapter 1, nematodes are important in a wide range of fields. They are abundant in virtually all environments, where they thrive thanks to morphological and physiological adaptations. By feeding on other microorganisms or parasitizing virtually all groups of living beings, nematodes are relevant to the environment; agriculture; human health; veterinary; and basic and applied sciences. In the following chapters, we'll look into each of these areas, and learn to appreciate how nematodes impact humankind. The current concern of laypeople, scientists and governments with the Earth's climate change and biodiversity suggests that we should begin by understanding the role of nematodes in ecosystems.

Let's begin by recalling that life on Earth is largely dependent on sunlight. In a process called photosynthesis, plants, algae[1], and cyanobacteria[2] capture energy from sunlight and use it to convert carbon dioxide (CO_2) and water into energy-rich and carbon-rich compounds, with oxygen being released in the process. The energy retained in the carbon-rich compounds is then released to be used for the organism's needs. In ecological jargon, plants, algae, and cyanobacteria are the primary producers of organic (carbon-rich) compounds (Fig. 2-1).

[1] An introduction to algae can be seen at https://en.wikipedia.org/wiki/Algae
[2] An introduction to cyanobacteria can be seen at https://en.wikipedia.org/wiki/Cyanobacteria

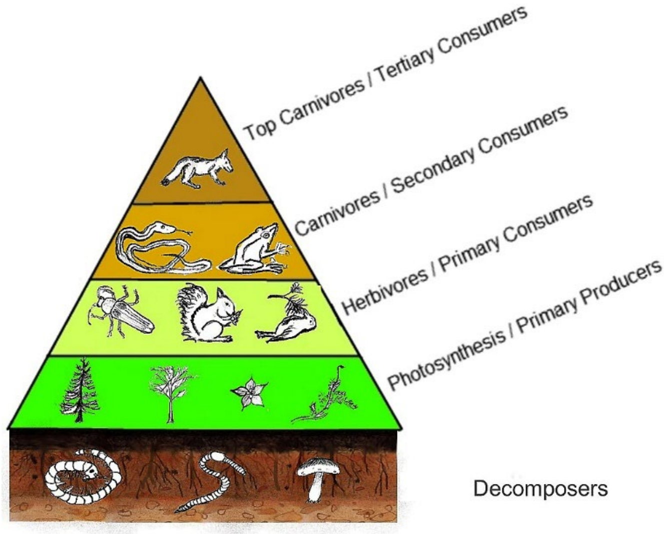

Fig. 2-1: A simplified trophic pyramid. Note that in the image decomposers and detritivores are not distinguished.

Going up in the trophic (nutritional) pyramid, most organisms not capable of performing photosynthesis consume the primary producers to obtain organic compounds, energy, and nutrients. These so-called herbivores include marine krill, termites, and livestock, among many other animal groups. In higher trophic levels, we have carnivores that eat herbivores (such as canines and felines), and carnivores that eat smaller carnivores (such as sharks and orcas). Eventually, the organic and inorganic compounds in all living forms must be recycled back. This is carried out by decomposers (mostly bacteria and fungi) and detritivores (invertebrates) that feed on feces and dead organisms. They break down complex molecules into simpler ones, making the nutrients necessary to life available again to the primary producers.

This nutrient cycle and energy flow sustains almost all forms of life on Earth (including humans), but it does not have the same dynamics all over the world. Scientists define an ecosystem as a collection of organisms (biota) that interact with physical and chemical (abiotic) features, resulting in a particular nutrient cycle and energy flow. For instance, a forest's soil and canopy are two distinct, spatially separated ecosystems. They have major differences in their biota and abiotic features, such as water content, temperature fluctuation, and incidence of ultraviolet radiation. Hence, their nutrient cycle and energy flow have distinctions too. Other ecosystems are not clearly separated in space, such as a freshwater river that empties into an estuary with brackish water, which opens into the salty ocean. These three ecosystems transition their biota, abiotic features, nutrient cycle and energy flow where they meet. Other examples of ecosystems include lakes, coral reefs, deserts, and caves.

Scientists have devoted a lot of effort to understanding these ecosystems, with different goals. For example, an agronomist may want to boost a biota-impoverished soil cultivated with field crops to improve their productivity. An ecologist may want to monitor an estuary used for navigation to alert for anthropogenic disturbances. And an oil-drilling company may want to assess the recovery of a marine ecosystem after an oil spill by monitoring the sea's continental shelf and nearby beaches. To understand an ecosystem, e.g., a forest soil, a scientist typically dissects it into parts. He/she characterizes the soil properties, such as texture and the amount of carbon (C) and nitrogen (N); measures how much C, N, and other elements enter and flow through the ecosystem; and identifies and/or quantifies the primary producers, herbivores, carnivores, and decomposers.

Because the whole biota of an ecosystem is typically diverse, the scientist chooses subsets to work on. He/she may assess the density of bacteria/µg of soil, the floristic (plant) composition, or the abundance of animals such as termites, frogs, or felines. These animals are very distinct in size, and so is their position in the trophic pyramid. Hence, ecologists group animals into the micro-, meso-, and macrofauna. The mesofauna—more often called meiofauna—comprise those animals whose body ranges between 0.01 and 1 mm in size[3], and which typically live in the tiny spaces amongst particles of soil or sediment deposited in lakes, rivers, estuaries, and oceans. The

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[3] The meiofaunal size limits are somewhat variable. Most scientists define meiofauna as the portion of the fauna that passes through a sieve with openings that measure 500 x 500 µm, but that is retained in a sieve of 44 x 44 µm.

meiofauna also inhabits moss and lichen mats on trees and rocks, and phytotelmata[4] (Fig. 2-2). Nematodes are part of the meiofauna.

Fig. 2-2: A nematologist uses a pipette to collect nematodes that live in the water retained in a bromeliad.

With these ecology concepts in mind, let’s look at the nematodes. If someone knows nothing about nematode ecology, he/she might guess they impact ecosystems just because of their abundance. Estimates say that four out of five individual animals on Earth are nematodes, which colonize the widest spectrum of ecosystems among all animal groups. For example, nematodes represent 40-90% of the meiofauna that lives in the sediment of freshwater and marine ecosystems, where they reach densities of up to several thousand individuals/10 cm^2. Their predominance extends to soil too, which often contains millions of nematodes/m^2. In a recent study, scientists estimated that around the globe, 440 quintillion (4.4×10^{20}) nematodes live just in the upper 15 cm of soil (Fig. 2-3), but many nematodes colonize deeper in soils.

[4] Phytotelma (pl. phytotelmata) is a natural reservoir of freshwater and organic debris that fall into bromeliads, tree and bamboo holes, and pitcher plants.

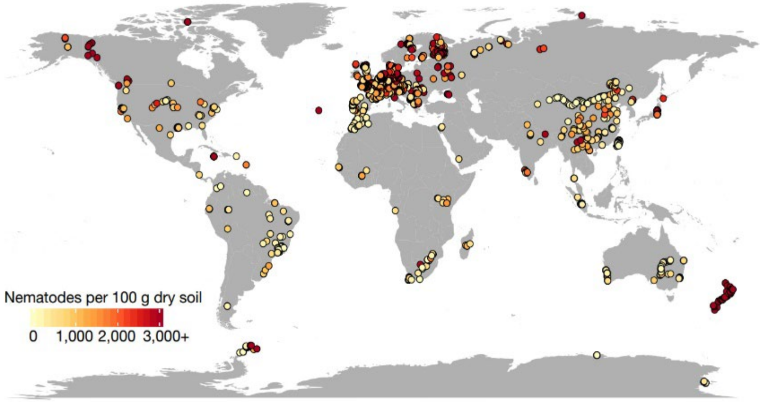

Fig. 2-3: Graphical representation of nematode density in 100 g of soil obtained from 6,759 samples collected worldwide.

It would be misleading not to mention that nematodes are less abundant in some ecosystems. Those with extremes in temperature; excessively dry; with only a temporary availability of liquid water; or with little input of organic matter have fewer nematodes, although they may still be the predominant component of the meiofauna. Such ecosystems include hot deserts, polar regions and caves. Nematodes have been found to be absent from cryoconite holes because of the permanent low temperatures of the water (Fig. 2-4).

Nematodes are abundant, but to appreciate their importance in ecosystems we need to look into yet another dimension—their diversity. As noted in Chapter 1, a group of nematodes that evolved from a common ancestor, sharing genetic, morphological, physiological, and behavioral features, is called a species. A collection of closely related species is grouped in a genus (plural, genera), and closely related genera are grouped in a family. All species arise at a specific point in time and place, but over time they may disperse and adapt to live in many locations. A case in point is the plant-parasitic genus *Meloidogyne*—the species *Meloidogyne incognita* occurs worldwide, while another species from the genus, *M. camelliae,* is only found in a few countries.

Fig. 2-4: Scientist drills through the frozen water of a cryoconite hole.

Worldwide, nematologists estimate that between 500,000 and 10 million nematode species exist, with only a small percentage of these already known to science. This discrepancy among estimates results from a series of scientific constraints[5], but even at the lower end of that spectrum nematodes are tremendously diverse. Most ecosystems are colonized by many nematode genera and species. For example, dozens of species may be found in a single square centimeter of freshwater or marine sediment. When nematologists sampled the soil of a tropical forest in Cameroon (West Africa)[6], they found a mean of 61 different species per 200 nematodes examined. This level of diversity is not exclusive to tropical forests, and can also be found in temperate forests and grasslands, and in the polar tundra.

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[5] The following issues hinder more precise estimates of nematode diversity: **i)** the patchy distribution of nematodes results in great variation in the number of species found in different samples and surveys; **ii)** relatively few nematologists are experts in taxonomy; **iii)** there's no scientific consensus about species boundaries; and **iv)** many species cannot be easily distinguished from each other based on light microscopy only, which requires more refined (and expensive) techniques that most nematologists have no access to.

[6] Bloemers, G.F, Hodda, M. Lambshead, P.J.D. Lawton, J.H., and Wanless, F.R. 1997. The effects of forest disturbance on diversity of tropical soil nematodes. Oecologia, 111:575–582. https://doi.org/10.1007/s004420050274

Nematode diversity is lower in less favorable ecosystems, such as caves and polar regions. Furthermore, when a favorable ecosystem is heavily polluted or physically disturbed, many species are unable to cope with the new condition and disappear from the ecosystem. This change in the nematode community can be used to assess disturbance, pollution and recovery of an ecosystem, a possibility that we'll examine in Chapter 5.

The abundance and diversity of nematodes may lead you to assume that all species exist everywhere, and that nematodes have no limits in Nature. That's not true. Regional and local abiotic factors determine which species will thrive, such as rain and temperature regimes; availability of oxygen in the soil or sediment; and water salinity. Biotic factors also contribute to the range of a nematode species, such as availability of food, predation, and parasitism by fungi and bacteria. Moreover, man-made disturbances, such as forest clearance, mining, pollution, and soil plowing, also affect nematodes.

Nematologists are still working to fully understand how these complex factors interact and determine the distribution of nematode families, genera and species. Overall, it seems that most species have an ecosystem or regional adaptation. For example, a river that opens in an estuary, the nearby mangrove and beach, and the oceanic sediment are five contiguous ecosystems with distinct nematode communities, although several species may be found across these ecosystems. This ecosystem adaptation also occurs in soils (Fig. 2-5).

The abundance, diversity, and adaptation of nematodes hint to us that they must be an integral part of the ecosystems' nutrient cycle and energy flow. But how? This occurs mainly through their feeding. Nematodes feed on all members of the trophic pyramid, from the photosynthesizers to the top predators, exerting a negative or positive drive on their ecological role. Hence, nematodes interfere with the very processes that sustain life on Earth—primary production, herbivory, predation, decomposition, nutrient recycling, and energy flow.

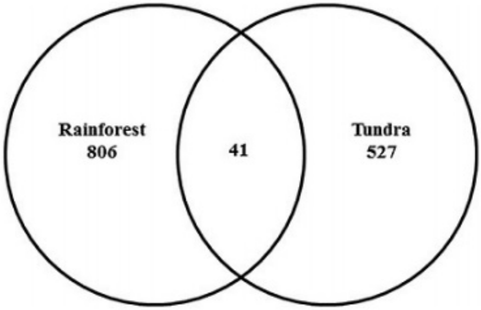

Fig. 2-5: Number of operational taxonomic units (~ species) of nematodes found exclusively or concomitantly in the soil of rainforest (in Malaysia) and tundra (in Svalbard, Norway).

Based on what nematodes feed on, they are categorized in trophic groups[7]. Plant-parasitic (also called plant-feeder) nematodes have in their mouth a stylet with which they pierce plant cells to withdraw nutrients, altering or destroying plant tissues as collateral damage. These nematodes may undermine plant growth and reproduction, as well as reducing plants' interaction with beneficial, symbiotic organisms, such as nitrogen-fixing bacteria. From an ecological perspective, plant-parasitic nematodes reduce the plants' primary production. Virtually all terrestrial and aquatic plants are parasitized by nematodes, in natural and agricultural ecosystems. The tremendous negative impact of nematodes on agricultural ecosystems is dealt with in Chapter 4.

Nematodes classified as unicellular eukaryote-feeders feed on microalgae, fungal spores, yeast, flagellates, ciliates and other protozoa. Their mouth may be equipped with structures to rupture their prey before swallowing it.

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[7] Nematologists have not yet come up with a unified classification of nematode trophic groups. I adopt the one by Moens, T. Traunspurger, W., and Bergtold, M. 2006. "Feeding Ecology of Free-living Benthic Nematodes". In Freshwater Nematodes – Ecology and Taxonomy, edited by Eyualem-Abebe, István Andrássy, and Walter Traunspurger, 105-131. Wallingford, CABI Publishing. Available at https://www.cabidigitallibrary.org/doi/pdf/10.5555/20063048500

Other nematodes are classified as predators, and they have a large mouth equipped with blades to rupture the prey that they swallow whole, or they use a stylet to puncture the prey and suck in their body contents. These nematodes can also scavenge on organic remains and absorb organic particles dissolved in the water. As low-level consumers, unicellular eukaryote-feeders and predator nematodes are preyed on by other invertebrates and fish (small species and juveniles of larger ones), thus transferring nutrients and energy up the trophic pyramid (Fig. 2-6).

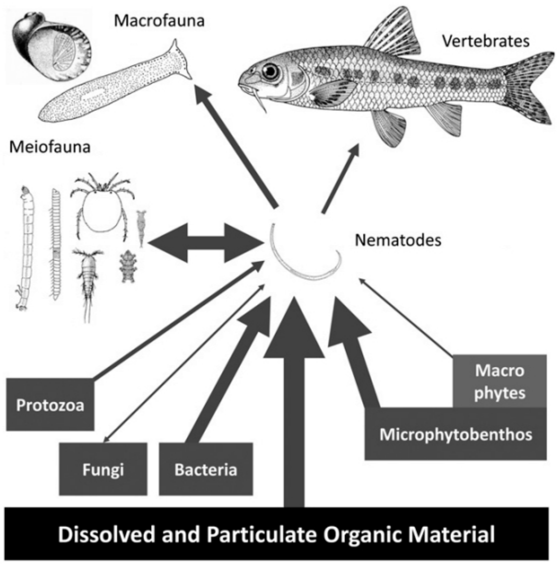

Fig. 2-6: Trophic interactions in freshwater ecosystems. The path of nutrients and energy is represented by the trajectory of the arrows. The arrows' width represents how often the interaction has been observed by scientists, not the quantity of food ingested.

Other nematodes are vertebrate- or invertebrate-parasites. These nematodes spend most of, or their entire life, inside their host, drawing nutrients from blood, cells, tissues, or food materials that are being digested by the host. Hosts include spiders, insects, fish, reptiles, amphibians, mammals (including humans), and several other groups[8]. Clinical signs and symptoms[9] caused by nematodes vary from none (the parasite may remain unnoticed by the host) to very serious, such as altering the host's normal behavior, or causing profuse bleeding, damage to vital organs, and death. Hence, nematodes may reduce the host's competitiveness, reproduction, dispersion, and life span. From an ecological perspective, parasitic nematodes affect the host's production, i.e., its normal growth, thus interfering negatively with its role in the ecosystem.

Bacterial-feeder nematodes are often the most abundant trophic group, and they are voracious. Ingham *et al.*[10] estimated that these nematodes eat almost four times their own weight in bacteria per day; Ferris *et al.*[11] calculated this relationship to be about 1.5-3.4; and Sohlenius[12] estimated that about 25% of the bacterial biomass in the soil of a coniferous forest was consumed by nematodes. This much feeding on bacteria suggests that nematodes have a negative effect on the ecological functions of bacteria. Actually, it is the opposite.

By eating a sizable part of the bacterial population, nematodes maintain that population's growth at an exponential rate, when the bacteria are most efficient in their ecological functions, be it decomposing organic matter for nutrient recycling, fixing atmospheric N to be used by organisms, or reducing nitrogenous compounds to return N back to the atmosphere (Fig.

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[8] Learn about nematodes parasitic on humans in Chapter 3; on farm animals in Chapter 4; and on invertebrates in Chapter 5.

[9] Clinical signs are measurable consequences of a disease or parasite, and they include bleeding, weight loss, and dehydration. They are distinct from symptoms, such as nausea, pain, and shortness of breath, which are perceived by the patient.

[10] Ingham, R.E. Trofymow, J.A. Ingham, E.R., and Coleman, D.C. 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecological Monographs, 55:119-140. https://doi.org/10.2307/1942528

[11] Ferris, H. Venette, R.C., and Lau, S.S. 1997. Population energetics of bacterial-feeding nematodes: carbon and nitrogen budgets. Soil Biology and Biochemistry, 29:1183-1194. https://doi.org/10.1016/S0038-0717(97)00035-7

[12] Sohlenius, B. 1979. A carbon budget for nematodes, rotifers and tardigrades in a Swedish coniferous forest soil. Ecography, 2:30-40. https://doi.org/10.1111/j.1600-0587.1979.tb00679.x

2-7). In ecological jargon, nematodes enhance the nutrients' turnover performed by the bacteria, i.e., the rate at which nutrients are recycled back to the environment over time or over its total pool.

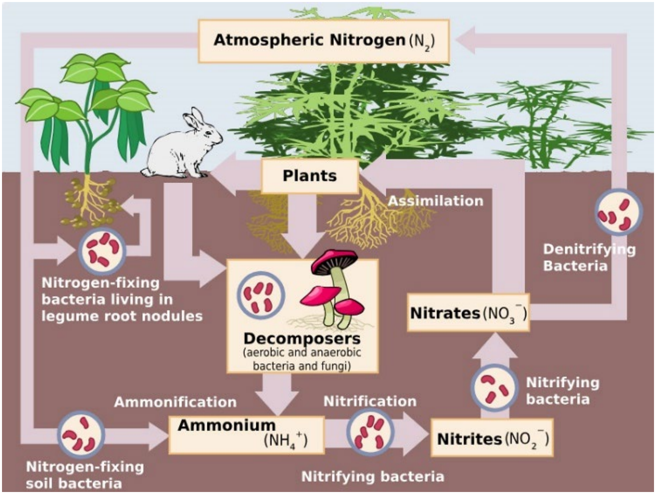

Fig. 2-7: The different groups of bacteria involved with the nitrogen cycle in Nature.

The same occurs with decomposing fungi. Fungal-feeder nematodes use their stylet to pierce fungal hyphae[13] and suck in their content. Nutrient turnover by decomposing fungi is also enhanced by nematodes. Some fungal-feeder nematodes may, nonetheless, negatively affect mycorrhizal fungi, which establish mutually beneficial symbiosis with plants.

A couple more feeding strategies exist in the phylum Nematoda, but they do not receive specific classifications. One is found in the insect-parasitic family Mermithidae. Mermithids spend part of their life embedded in the host's hemolymph, the nutrient-rich fluid that bathes all organs and serves as the insect's circulatory system. Because the nematode lives surrounded by the hemolymph, it absorbs nutrients directly through its cuticle, the thin coat (not a proper skin) that surrounds the nematode body (see more about

[13] A hypha (pl. hyphae) is a filamentous, branching structure used by many fungi to colonize the environment.

nematode morphology in Chapter 7). Other nematode groups also absorb at least part of the nutrients through the cuticle.

Another feeding strategy with no specific classification is found in nematodes that have developed symbiosis with bacteria, which enables them to live in oceanic hydrothermal vents and deep in wetland sediments. In these locations, oxygen and sunlight are scarce or non-existent, and sulfide may accumulate. Sulfide is a substance poisonous to oxygen-breathing organisms. The nematode carries the symbiotic bacteria around its body or within its gut, through oxic and sulfidic sediment regions. This allows the bacteria to oxidize sulfide to sulfate, and to use the energy liberated in this reaction to produce its organic compounds. The nematode benefits from eating part of the bacterial population, and from being protected against sulfide-poisoning. The dynamics of this symbiosis is less clear for nematodes that carry the bacteria inside their gut.

One might think that in any given ecosystem, countless nematodes fight each other for the supply of host plants, fungi, bacteria, or other food sources, perhaps leading to the survival of the fittest species only. But that is not what is found in undisturbed, natural ecosystems, in which the nematode community is typically diverse, and often shows no major contrast in the abundance of different genera and species. The dynamics for this relative equilibrium in the nematode community are still a matter of study for nematologists devoted to ecology. What scientists know is that nematodes are genetically variable, with considerable distinction amongst closely related species, and amongst individuals within a single species.

Because nematodes are genetically variable, they vary in their life span, prolificity, resistance to environmental stress, and susceptibility to parasitic fungi and bacteria, amongst other characters. Moreover, an ecosystem, say, a forest soil, is highly heterogeneous and dynamic at the microscopical level. Hence, nematodes face ever-changing favorable and unfavorable factors, such as availability of food, pH, salinity, and natural enemies. This likely evens out the conditions for many species, allowing their coexistence and diversity.

Scientists also know that we need better understanding of nematode-feeding biology. Studies have shown that bacterial-feeder nematodes can discern and select different species of bacteria, and that some predator nematodes prefer some types of prey over others. Moreover, each plant-parasitic nematode species has a specific host range, all other plants being resistant to it. In other words, there are minutiae in the nematodes' feeding preferences and diet that nematologists still do not understand, and that do not fit the simplistic classification of trophic groups.

Therefore, a forest soil, with millions of different fungi, bacteria, invertebrates, and plants, is a vast "menu" that serves the preferences and needs of thousands of nematode species. Apparently, each of these species occupies a specific niche and has a function in the ecosystem. In ecological jargon, it seems that nematode species have little redundancy amongst them. This is why nematologists believe that high nematode diversity contributes to the good functioning of ecosystems.

This is not to say that nematodes collaborate with each other, or that they don't compete for resources. Nematologists know that plant-parasitic nematodes may compete for the same host, sometimes with one species replacing the other. Nematodes that are parasitic on vertebrates and invertebrates also interfere with each other in the same host. But on a large scale, nematode species, genera, and trophic groups are present and diverse in most ecosystems worldwide.

In addition to their feeding activity, nematodes contribute to ecosystems' functioning by other means. Bacterial-feeder nematodes ingest more bacteria than their nutritional need of N. They excrete this excessive N as ammonium, increasing the soil content of mineral N by up to 20%. This large output of ammonium is readily absorbed by plants for their growth, and by nitrifying bacteria that recycle N back to the atmosphere. Therefore, nematodes have a significant, indirect contribution to Earth's N cycle, in terrestrial and aquatic ecosystems. Furthermore, a recent study estimated that the global population of soil nematodes breathe at least 1.32 gigatons of carbon into the atmosphere per year. Hence, the contribution of nematodes to the global carbon cycle is considerable.

Most nematodes migrate constantly in the soil, marine and freshwater sediments, and biofilms[14]. In sediments, they produce a vast net of micro burrows that contribute to oxygen and nutrient permeation, favoring microorganisms. Nematodes also excrete through glands and cuticle mucilaginous substances to which bacteria, fungi and other microorganisms attach themselves. During nematode migration, those substances are shed, serving to stabilize the burrows, and as a substrate for the microorganisms that are dispersed along the burrows.

In conclusion, nematodes are an integral part of the Earth's ecosystems. In their abundance and diversity—of species and feeding strategies—nematodes connect to all levels of the trophic pyramid. They reduce primary and secondary production; enhance nutrient and energy transfer between trophic levels by being predator and prey; and indirectly enhance organic matter decomposition and nutrient cycles. The growing awareness of and interest in nematodes as players in natural and agricultural ecosystems are reflected in the increasing number of scientific articles, reviews, book chapters, and books on the subject (Fig. 2-8).

All forms of life—nematodes included—should be valued simply for their existence and their esthetic and/or spiritual value. Nonetheless, there is a strong utilitarian view that emphasizes ecosystems and their biota as providers of "services", defined through a human-centered perspective and for the benefit of humans. Under this view, an ecosystem, such as a forest, provides recreation for urban dwellers and resources for local communities; is a repository of genetic resources and C "sequestered" from the atmosphere; participates in nutrient cycles; and retains most of the rainfall, gradually releasing it through streams and rivers, thus reducing the frequency and intensity of seasonal floods. Preserving ecosystems and their biota has become important to society.

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[14] A biofilm or microbial mat is a community of microorganisms that stick to each other and often also to a biotic or abiotic surface. These organisms are embedded in a slimy matrix that is composed of extracellular polymeric substances. For more information, see https://en.wikipedia.org/wiki/Biofilm