Soil fauna: occurrence, biodiversity, and roles in ecosystem function

Soil Microbiology, Ecology and Biochemistry

Coleman, D.C.; Geisen, S.; Wall, D.H.

https://doi.org/10.1016/B978-0-12-822941-5.00005-3

This publication is made publicly available in the institutional repository of Wageningen University and Research, under the terms of article 25fa of the Dutch Copyright Act, also known as the Amendment Taverne.

Article 25fa states that the author of a short scientific work funded either wholly or partially by Dutch public funds is entitled to make that work publicly available for no consideration following a reasonable period of time after the work was first published, provided that clear reference is made to the source of the first publication of the work.

This publication is distributed using the principles as determined in the Association of Universities in the Netherlands (VSNU) 'Article 25fa implementation' project. According to these principles research outputs of researchers employed by Dutch Universities that comply with the legal requirements of Article 25fa of the Dutch Copyright Act are distributed online and free of cost or other barriers in institutional repositories. Research outputs are distributed six months after their first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and / or copyright owner(s) of this work. Any use of the publication or parts of it other than authorised under article 25fa of the Dutch Copyright act is prohibited. Wageningen University & Research and the author(s) of this publication shall not be held responsible or liable for any damages resulting from your (re)use of this publication.

For questions regarding the public availability of this publication please contact openaccess.library@wur.nl

Chapter 5

Soil fauna: occurrence, biodiversity, and roles in ecosystem function

D.C. Coleman[*], **S. Geisen**[†], and **D.H. Wall**[‡]
[*]*Odum School of Ecology, University of Georgia, Athens, GA, USA;* [†]*Department of Plant Science, Laboratory of Nematology, Wageningen University, Wageningen, the Netherlands;* [‡]*Department of Biology and School of Global Environmental Sustainability, Colorado State University, Fort Collins, CO, USA*

Chapter outline

5.1 Introduction

Animals, a key group of heterotrophs in soils, shape bacterial and fungal biomass, activity, diversity, and community composition (Hättenschwiler et al., 2005). Many soil animals, which are mostly invertebrates and often referred to as "fauna," regulate nutrient cycling at ecosystem and global scales by feeding directly on plant materials and other organic substrates. The fragmentation or comminution of these materials enhances their decomposition. Comminution increases the surface area of plant structural materials and exposes cytoplasm, thereby enabling greater access by microbes. Decomposition is further

Soil Microbiology, Ecology, and Biochemistry. https://doi.org/10.1016/B978-0-12-822941-5.00005-3

accelerated, as the feeding activity of soil animals often results in the translocation of nutrients such as nitrogen (N) and phosphorus (P) from the soil to the substrate in the form of fecal material. Invertebrates consume bacteria and fungi, thereby directly cycling C and N and disseminating microbes from one organic source to another, as many microbes adhere to invertebrate exoskeletons and cuticles and survive passage through their digestive tracts (Coleman et al., 2012; Meier and Honegger, 2002).

Soil animals exist in food webs containing several trophic levels (Moore and de Ruiter, 2012). Some are herbivores, since they feed directly on roots of living plants, but most subsist on dead plant matter (saprophytes), the living microorganisms associated with it, or a combination of the two. Still others are carnivores or parasites. The structure of these food webs is complex, with many "missing links" only slowly being described (Geisen et al., 2019a; Scharroba et al., 2012; Scheu and Setälä, 2002; Walter et al., 1991).

5.2 Overview of faunal biodiversity in soils

The nature and extent of biodiversity in soils is impressively large (Coleman and Whitman, 2005; Fierer and Lennon, 2011; Jeffery et al., 2010; Whitman et al., 1998). Current estimates suggest that for most soil organism groups, a maximum of 10% of the existent species diversity is described (André et al., 2002; Geisen et al., 2019a). A potentially high degree of functional specialization may underlie this enormous diversity of soil life (Heemsbergen et al., 2004, Wurst and van der Putten, 2007). Species with similar biologies and morphologies (Coleman et al., 1993, 2004, 2018; Hendrix et al., 1986; Hunt et al., 1987) or ecological functions (Geisen et al. 2019a) are often grouped together for purposes of integration at the system level.

Soil fauna also may be characterized by the portion of their life cycle that is spent in the soil. Transient species, exemplified by the ladybird beetle, hibernate in the soil but otherwise live in the plant stratum. Gnats (Diptera) are temporary residents of the soil given that the adult stages live aboveground. Their eggs are laid in the soil and their larvae feed on decomposing organic debris. In some situations dipteran larvae are important scavengers. Cutworms are temporary soil residents, whose larvae feed on seedlings by night. Some nematodes that parasitize insects and beetles spend all or part of their life cycle in the soil. Periodic residents spend their life histories belowground, with adults, such as velvet mites, emerging to reproduce. Soil food webs are linked to aboveground systems, making trophic analyses much more complicated than in one subsystem alone (van der Putten et al., 2013; Wardle et al., 2004). Even permanent residents of the soil may be adapted to life at various depths within the soil profile.

A generalized classification by length and width illustrates a commonly used device for separating the soil fauna into size classes: microfauna, mesofauna, macrofauna, and megafauna. This classification encompasses the range from smallest to largest, i.e., from about 1 to 2 μm for some protists to 2 m for giant Australian earthworms (Moreira et al., 2009). Both faunal body lengths and widths are commonly related to their microhabitats (Fig. 5.1). Protists and the microfauna (rotifers, tardigrades, nematodes) inhabit water films. The mesofauna inhabit existing air-filled pore spaces and are largely restricted to existing spaces. Macrofauna have the ability to create their own spaces through their burrowing activities and, like the megafauna, can significantly influence gross soil structure (Lavelle and Spain, 2001; van Vliet and Hendrix, 2003).

The body size range among the soil fauna (grazers and predators) affects soil processes at a range of spatial scales. Three levels of participation have been suggested (Lavelle et al., 1995; Wardle, 2002): (1) "Ecosystem engineers," such as earthworms, termites, or ants, alter the physical structure of the soil itself, influencing rates of nutrient and energy flow (Jones et al., 1994); (2) "Litter transformers," the microarthropods, fragment decomposing litter and improve its availability to microbes; and (3) "Grazers and predators" directly consume bacteria, fungi (i.e., protist and nematode grazers), and microfauna (e.g., nematode and mite predators) and thus contribute significantly to the soil food web. These three levels operate on different size, spatial, and time scales (Fig. 5.2; Wardle, 2002).

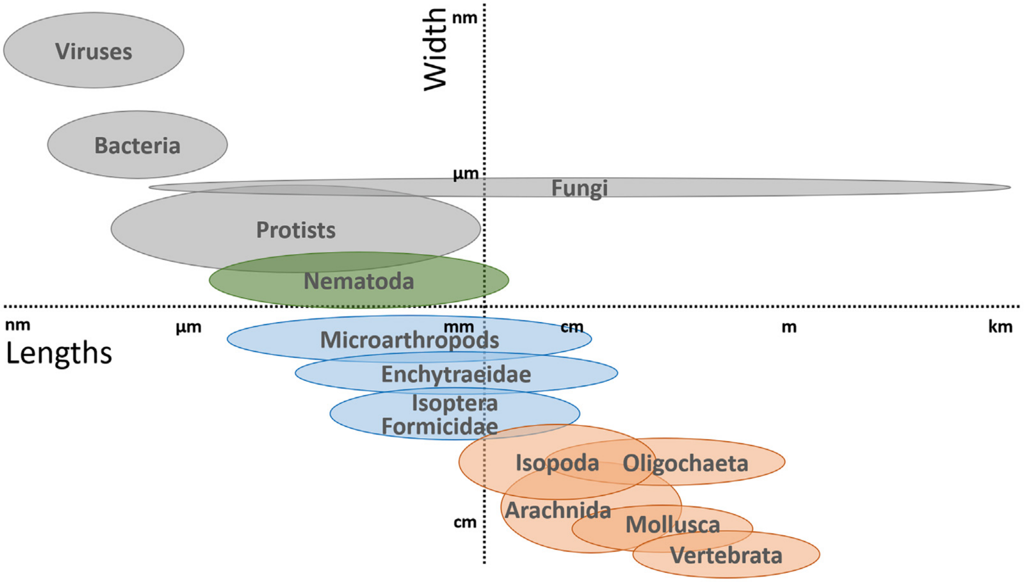

FIGURE 5.1 Size (body lengths and width) of all major groups of soil life showing the multidimensionality of size for large-scale categorization of soil organisms. Colours denote current large-scale classifications; Gray: microorganisms; Green: microfauna; Blue: mesofauna; Orange: macrofauna. *(Redrawn from Decaëns, 2010 and Swift et al., 1979.)*

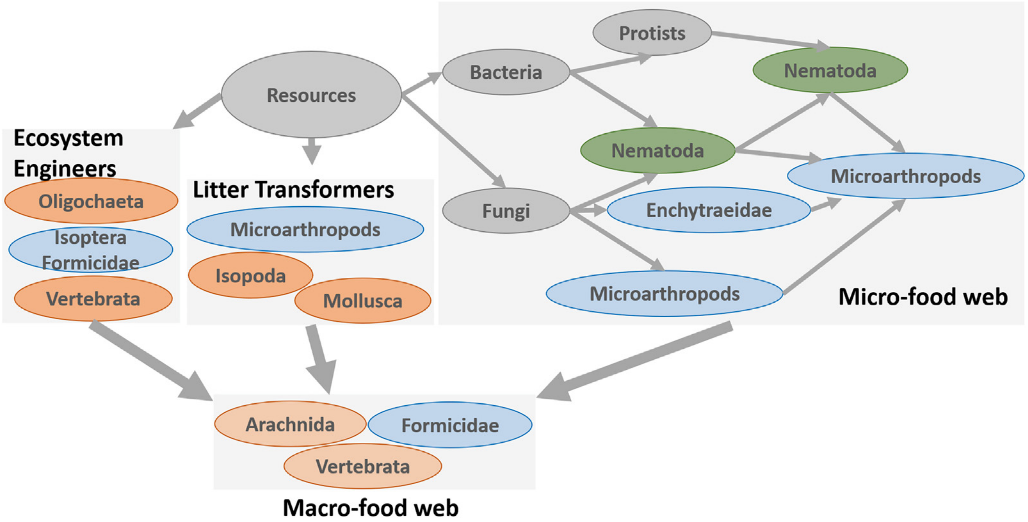

FIGURE 5.2 Organization of the soil food web into three categories — ecosystem engineers, litter transformers, and micro-food webs. *(Redrawn from Lavelle et al., 1995 and Wardle, 2002.)*

5.3 Protists: microbes among "fauna"

Protists can easily be called the problematic ones. They are not animals (Fig. 5.3) — hence no longer called protozoa (Adl et al., 2012) — but microbes (Caron et al., 2008). Similar to other microbes, a common feature of soil protists is that they can form highly resistant stages, called cysts, to survive adverse conditions (Geisen et al., 2018a). These cysts can remain for extended periods in the environment, as recently shown for those that were revived from millennial-old permafrost samples (Shmakova et al., 2016). Major taxonomic and phylogenetic revisions mainly based on molecular sequence information have resulted in major reshufflings of the eukaryotic tree of life (Adl et al., 2019) (Fig. 5.3). These insights have shown that many photosynthetic

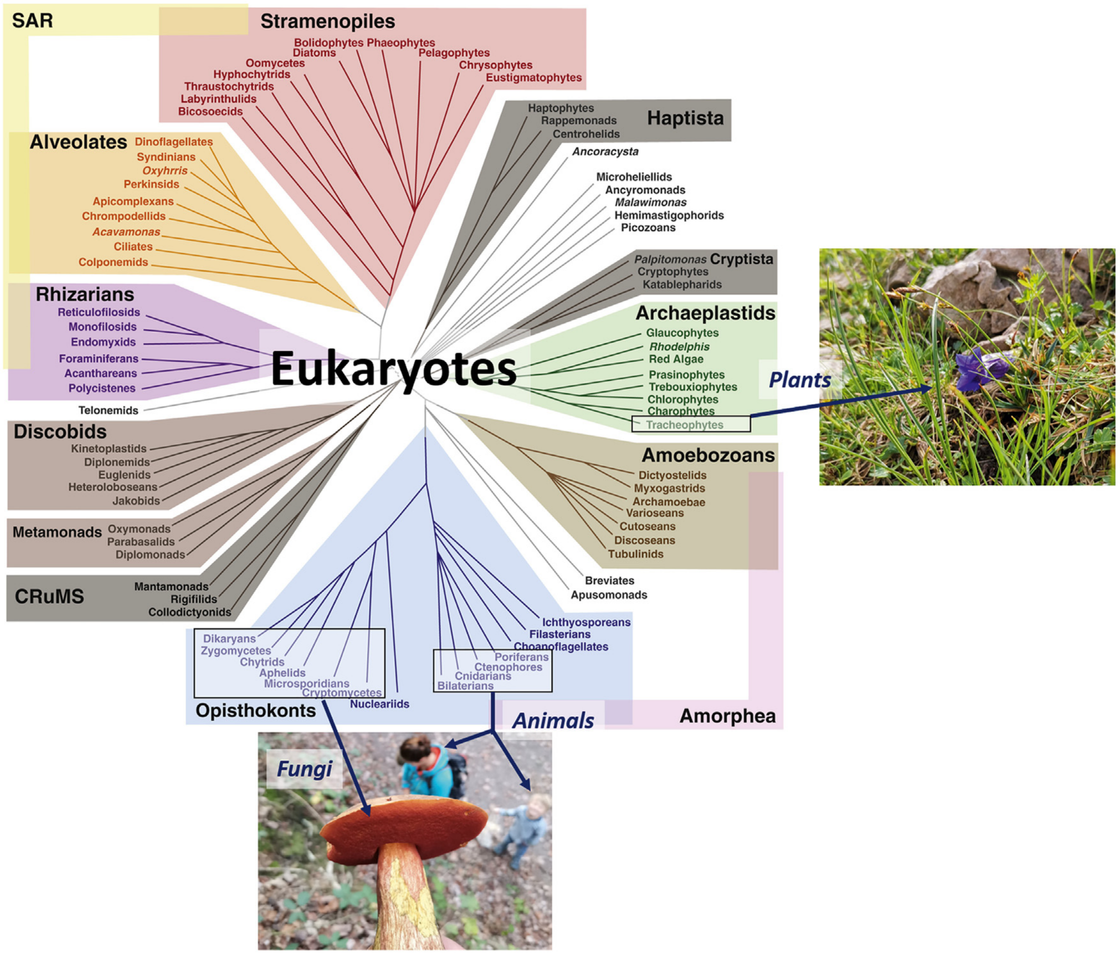

FIGURE 5.3 **Overview of the phylogenetic diversity of eukaryotes.** Multicellular organisms commonly considered to host most eukaryotic diversity, including animals, fungi, and plants, are shown in boxes. However, the remaining sections of the tree are made up of single-celled protists. *(Modified from Keeling and Burki, 2019.)*

organisms ("algae" *sensu lato*) are phylogenetically intermingled with heterotrophic organisms ("protozoa" *sensu lato*) and that mixotrophs can live photo- and heterotrophically (Geisen et al., 2018a). Commonly used morphologically distinguishable groups, amoebae and flagellates, were shown to be paraphyletic (Geisen et al., 2018a) (Fig. 5.3). Today, morphotype-based investigations are rarely performed, and although they may still provide ecologically relevant information on protistan community changes (Geisen et al., 2014), they have mostly been replaced by phylogenetically informed analyses based on sequencing data (Geisen and Bonkowski, 2018). This phylogenetic view shows that most cultivated soil protists are placed in the eukaryotic supergroups Amoebozoa (most amoebae), Rhizaria (most flagellates and amoeba-flagellates), Discoba (amoebae and flagellates), and Alveolata (ciliates) (Adl et al., 2019; Geisen et al., 2018a). Sequence-based analyses have also revealed several other groups as being common soil protists, such as parasites in the Apicomplexa (Bates et al., 2013; Geisen et al., 2015; Oliverio et al., 2020). Apicomplexans represent up to 50% of all protists in some tropical forests, leading Mahé et al. (2017) to speculate that protists might be key controllers of animal biodiversity. Phototrophic protists that are major carbon fixers are also common in soils (Oliverio et al., 2020).

5.3.1 Methods to study soil protists

Different techniques can be applied to study soil protists (Geisen and Bonkowski, 2018), including traditional morphology-based investigations and molecular techniques. Morphological investigations suffer from profound biases as the most abundant soil protist groups cannot directly be observed due to their small size and transparent body shapes, and their primary use is to determine and quantify ciliates and testate amoebae (Foissner, 1999). Cultivation-based methods, such as the most probable number technique used in many studies, focus only on well-cultivable taxa (Berthold and Palzenberger, 1995; Darbyshire et al., 1974). The last decades have brought in a wealth of novel molecular tools to study protists, with high-throughput sequencing as the current method of choice (Geisen and Bonkowski, 2018). Yet, further study is needed to standardize and optimize the information gained from molecular protistan surveys, as issues including primer biases do not allow a cumulative investigation of soil protistan diversity (Geisen et al., 2019a). There are currently no molecular approaches available that provide biomass or abundance data, essential information necessary to answer many ecological questions beyond diversity estimates (Fig. 5.4)

5.3.2 Ecology of protists

Soil protists are diverse in many ways; their sizes can range from a few micrometers to many centimeters as in the case of network-forming myxomycetes as the largest cells on earth (Geisen et al., 2017). Protist sizes can reflect adaptations to specific environments and indicate specific habitat niches. Smaller taxa inhabit all soil pore sizes and can penetrate into tiny pores in the soil matrix, while larger taxa, including testate amoebae and ciliates, are found in larger soil pores in the upper soil or litter layers. Smaller protists are more abundant than larger ones, with small flagellates (but also amoebae) dominating soil protistan communities (Finlay et al., 2000). Many factors, other than soil pore sizes, determine protist distribution and community composition. Soil moisture appears to be the main determinant of protistan communities at small and large spatial scales (Bates et al., 2013; Geisen et al., 2014; Oliverio et al., 2020). Other factors such as pH and organic carbon content also contribute to the structure of soil protistan communities (Dupont et al., 2016; Oliverio et al., 2020). The use of fertilization for soil management has directly

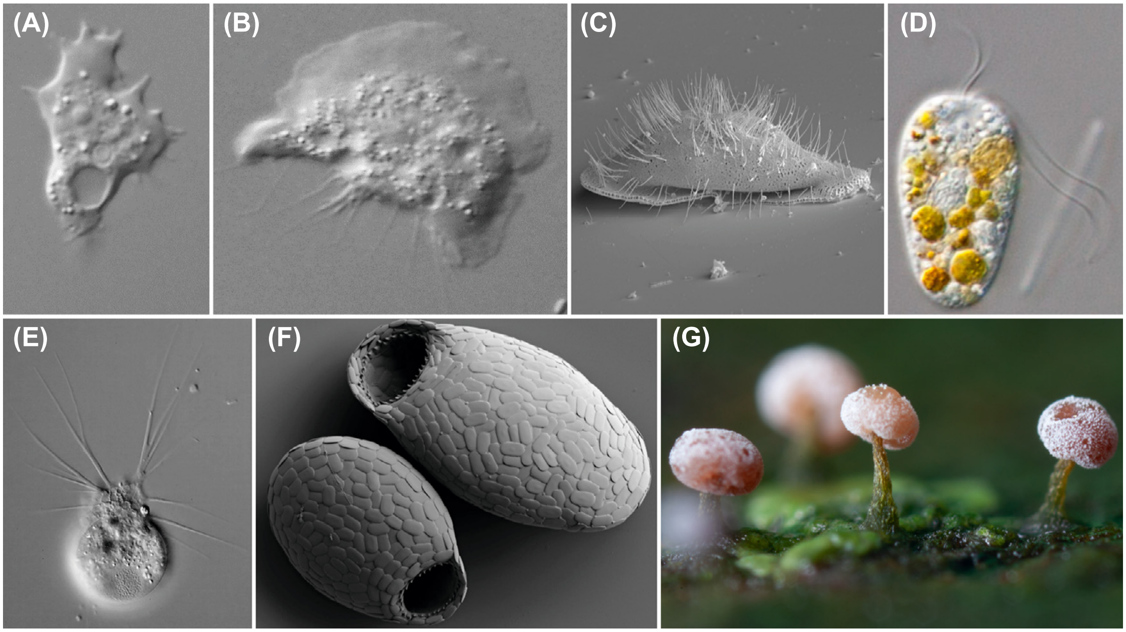

FIGURE 5.4 Morphology of common soil protists. (a–c) amoebae; (a): *Acanthamoeba* sp., (b): *Flamella* sp.; (c): *Cochliopodium vestitum*); (d): the flagellate *Viridiraptor invadens*; (e–f): testate amoebae (e): *Lecythium hyalinum*; (f): *Corythion* sp; (g): a slime mold that builds fungal-like multicellular fruiting structures from aggregated single-celled amoebae. *(Pictures with permission from Stefan Geisen (a–b), Eckhard Völcker, Steffen Clauß (c–f), and Maries Elemans (g).)*

affected soil protists (Lentendu et al., 2014), resulting in significant changes over those found in other groups of soil microorganisms (Zhao et al., 2019). Plants shape protistan communities (Hünninghaus et al., 2019; Sapp et al., 2018), with protists being the soil biodiversity group that increases the most with an increase in plant diversity (Scherber et al., 2010).

5.3.3 Ecological relevance of protists

Protists are not only influenced by plants, but in turn, affect plant performance. In fact, the ecology of protists is immense, such as shown by their diversity of feeding modes. While the majority of protists feed on bacteria, others feed on fungi, and are omnivores, phototrophs, animal parasites, or plant pathogens (Dupont et al., 2016; Geisen, 2016; Oliverio et al., 2020). Through these trophic interactions, protists serve as an immensely important intermediate level for nutrient transfer to higher trophic levels (de Ruiter et al., 1995). Through trophic feeding interactions, protists liberate nutrients, particularly N, which acts as a fertilizer to boost plant growth (Bonkowski, 2004). However, protists select for their preferred prey items (Geisen et al., 2016). However, protists are not *per se* plant-beneficial as several plant pathogenic protistan groups exist, among them plasmodiophorids and oomycetes (Schwelm et al., 2018). These protists have traditionally been considered fungi due to the presence of convergent features, such as the formation of hyphae and presence of easily dispersed fruiting bodies (Beakes et al., 2012). Due to different physiological and biochemical features, including nonchitinous cell walls as well as those based on phylogenetic analyses, plasmodiophorids and oomycetes are now unambiguously placed as nonfungal organisms among protists (Adl et al., 2019). Protists affect plant growth depending on the presence of keystone species (pathogens) and the overall community composition. For example, the community composition of protists may be a reliable determinant of plant performance at the seedling establishment stage, indicating that certain protistan communities can guarantee plant health while others can predict plant disease during later stages of plant growth (Xiong et al., 2020).

Protists generally increase microbial activity and therefore may stimulate other microbial-driven ecological processes in soils (Geisen et al., 2018a). For instance, decomposition, and therefore C release to the atmosphere, is potentially increased through protist predation of microbes (Geisen et al., 2020). Heterotrophic protists may even contribute to the increase of the stable soil C fraction through predation on bacteria and fungi, as microbial-derived C represents the major fraction of recalcitrant C in soils (Liang et al., 2019). Specific protist species, as well as the composition of protistan communities, might also serve as responsive indicators for environmental change or soil quality, as they often respond more dramatically to changes compared to other groups of soil microorganisms including bacteria and fungi (Foissner, 1999; Zhao et al., 2019).

5.4 Microfauna

Soils, litter layers, and moss layers or biocrusts, especially those with high periodic water saturation, are environments in which soil microfauna inhabit thin water films. Nematodes, which are the most abundant microfauna group in soils, are covered in more detail below. Rotifers and tardigrades can reach abundances of above 100×10^4 m^{-2} to a depth of 10 cm in forest topsoils (Ito and Abe, 2001; Sohlenius, 1979). Both groups contain members of diverse functional feeding groups that have different mouth and ingestion apparatuses (Wallace, 2002). Tardigrades feed on bacteria, yeasts, and protists but also on rotifers and plants (Schill et al., 2011). Tardigrades can be major predators of nematodes (Hyvönen and Persson, 1996), including root-feeding nematodes, that can suppress nematode-induced root damage (Sánchez-Moreno et al., 2008). Tardigrades are preyed on by microarthropods (Hyvönen and Persson, 1996). Tardigrades, rotifers, and nematodes have a matchless ability to survive the most severe environmental conditions − for example, desiccation in soils, as they have the capacity to enter into an anhydrobiotic stage (Iglesias Briones et al., 1997; Kutikova, 2003). This adaptation allows microfauna to be present even in the driest soils that only sporadically receive water input. The ecology of rotifers (see below) and tardigrades in soils is still poorly understood (Wallace, 2002).

5.4.1 Rotifera

These small (0.05−3 mm long) fauna are typically only found in soils and other environments containing an abundance of water films (Segers, 2007). Rotifers exist in leaf litter, mosses, lichens, and even more extreme environments, such as wet soils of the Antarctic Dry Valleys (Segers, 2007; Treonis et al., 1999).

Rotifers are characterized by being transparent and having a three-part body: (1) an anterior ciliary structure or a ‘crown’ with cilia, (2) a body wall that appears to be pseudo-segmented (lorica), and (3) a feeding apparatus with strong muscles and jaws. More than 90% of soil rotifers are in the order Bdelloidea, or worm-like rotifers. Life history features include the construction of a shell, which may have particles of debris and/or fecal material adhering to it. Some rotifers will use the empty shells of Testacea, the thecate amoebae, to survive. The parthenogenic Bdelloidea are vortex feeders, creating currents of water that bring food particles, such as unicellular algae or bacteria, to the mouth for ingestion. The importance of these organisms is largely unknown, except as having roles in biogeochemical cycling. They are extremely diverse globally (Robeson et al., 2009, 2011), reaching abundances exceeding 10^5 m^{-2} in moist, organic soils (Wallwork, 1970). Rotifers are extracted from soil samples and enumerated using methods similar to those used for nematodes (see the following section), but morphological identification has been stymied because they can only be identified while alive and active (Segers, 2007).

5.4.2 Nematoda

The phylum Nematoda contains aquatic nematodes or roundworms, which are among the most numerous and diverse of the multicellular organisms found in any ecosystem. It has been estimated that four of every five animals on Earth are nematodes (Bongers and Ferris, 1999), with the total number of nematodes in soils estimated to be $4.4 \pm 0.64 \times 10^{20}$ (van den Hoogen et al., 2019). Nematodes are important belowground parasites and pathogens of plants with effects on net primary productivity (NPP) and organic matter decomposition (Wall et al., 2012). Nematodes have a very early evolutionary origin among the Eukarya, likely in the Cambrian explosion about 550 million years ago (Blaxter et al., 1998; dos Reis et al., 2015).

The overall body shape is cylindrical, tapering at the ends. Nematode body plans are characterized by a “tube within a tube” (alimentary tract/the body wall). They have a complete digestive system or an alimentary tract, consisting of a stoma or stylet, pharynx (or esophagus), and intestine and rectum, which opens externally at the anus. The reproductive structures are complex, and sexes are generally dimorphic. Many species are parthenogenetic, producing only females. Nematodes are highly diverse, with estimated species numbers at a million (Geisen et al., 2019b). Due to their enormous abundances, high species richness, and functional diversity (Fig. 5.5), nematodes are used as indicators of soil quality (Bongers, 1990; Domene et al., 2011; Ferris and Bongers, 2006; Ferris et al., 2001; Vervoort et al., 2012; Wilson and Kakouli-Duarte, 2009).

5.4.2.1 *Methods to study soil nematodes*

Nematodes are extracted from soils using a variety of techniques, either active or passive, each having distinct advantages and disadvantages (Geisen et al., 2019b). The most used approaches take advantage of their aquatic nature, along with gravity, and require ideally hundreds of grams of soil submerged in water to provide reliable information on nematode communities. The Baermann funnel method has many modifications and consists of soil being placed on a tissue or filter paper on a screen (sieve or window screen) at the large mouth of a funnel that is hanging vertically. The funnel is filled with water and closed off with a rubber tube clamped at the funnel base. The nematodes actively move through the soil and down through the water to the funnel base, where they are collected for examination (Hooper, 1970). These methods provide unbiased information on the activity of organisms, as they are based on the animal’s movement.

Following extraction, nematodes are identified morphologically under an inverted or dissection microscope. While enumeration and even functional placement can be done after a short training, taxonomic identification to family or genus level remains an expert task and requires a substantial commitment of many hours per sample. Alternatively, qPCR approaches can be conducted to estimate abundances of targeted taxa with specific primers (Vervoort et al., 2012). Use of high-throughput

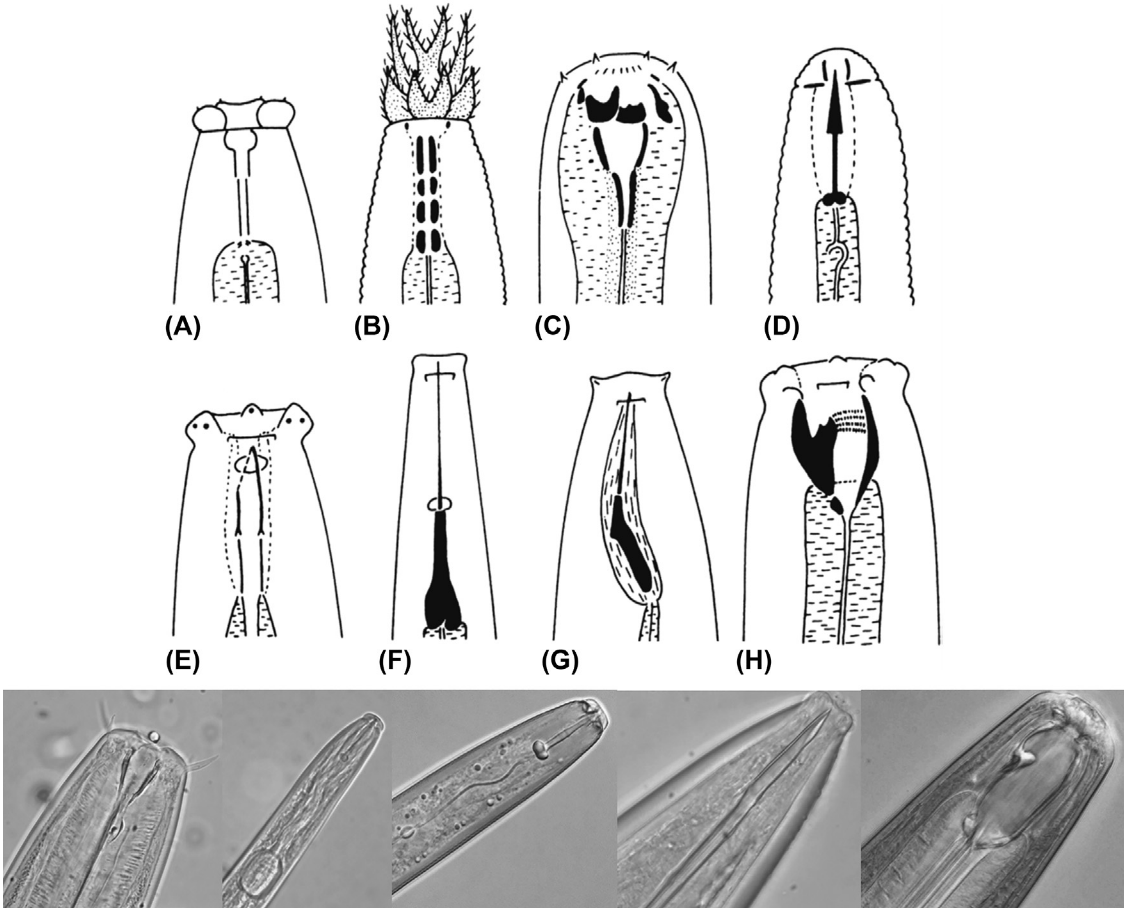

FIGURE 5.5 **Head structures of a range of soil nematodes.** (a) *Rhabditis* (bacterial feeding); (b) *Acrobeles* (bacterial feeding); (c) *Diplogaster* (bacterial feeding, predator); (d) tylenchid (plant feeding, fungal feeding, predator); (e) *Dorylaimus* (feeding undetermined, omnivore); (f) *Xiphinema* (plant feeding); (g) *Trichodorus* (plant feeding); (h) *Mononchus* (predator). Lower row shows real images of a bacterial-feeding *Epitobrilus steineri*, a fungal-feeding *Aphelenchoides* sp., a plant-feeding *Pratylenchus crenatus*, an omnivore *Dorylaimus stagnalis*, and a predator *Mononchus* sp. *(With permission from Yeates and Coleman, 1982.)*

sequencing for high-resolution taxonomic profiling of nematode communities is increasingly done (Geisen et al., 2018b). There are still some biases with this approach, as sequence abundances cannot be used directly to infer species abundances (Griffiths et al., 2018); however, relative sequence abundance closely reflects relative species biomasses (Schenk et al., 2019). Nematode functioning can be assessed based on a priori knowledge of feeding preferences, growth rates, etc. More exact information on trophic positions can be obtained using fatty acid markers or profiles (Kühn et al., 2018). Stable isotope-based techniques are used to predict feeding patterns, especially when combined with high-resolution taxonomic identification tools such as high-throughput sequencing techniques (Crotty et al., 2012; Geisen et al., 2019b). The method of choice to determine nematode communities depends on the availability of experts, time, and techniques. Ideally, a combination of methods is employed to obtain information on abundances, community structure, and feeding preferences of soil nematode communities.

5.4.2.2 Nematodes in soil food webs

Soil nematode abundance generally decreases with increasing soil depth and distance from plants, as many soil nematodes are largely concentrated in the litter layer or rhizosphere, or where organic matter accumulates. Nematodes also move vertically in soils toward plant roots, but the distance of movement is dependent on nematode species, in addition to soil type, temperature, and moisture. In deserts nematodes are associated with plant roots to depths of 15 m, as are mites and other biota (Freckman and Virginia, 1989); the nematode *Halicephalobus mephisto* was recovered from soils 3 km deep (Borgonie et al., 2011).

Nematodes have several dispersal methods and are transported with plants, soils, and other invertebrates, and by wind and water; some of these methods involve survival mechanisms. Wallace (1959) noted that local movement of nematodes was optimum when soil pores were half drained of free water. Elliott et al. (1980) noted that the limiting factor for nematode survival often hinges on the availability and size of soil pore necks, which enable passage between soil pores. Yeates et al. (2002) measured the movements, growth, and survival of three genera of bacterial-feeding soil nematodes in undisturbed soil cores maintained on soil pressure plates. Interestingly, nematodes showed significant reproduction in water-filled pores above 1 μm in diameter.

Nematodes feed on a wide range of foods, with general trophic groupings including bacterial feeders, fungal feeders, plant feeders, predators, and omnivores. In most cases these trophic groups can easily be determined using morphological features, particularly anterior (stomal or mouth) structures (Fig. 5.5) (Moore and de Ruiter, 2012; Yeates and Coleman, 1982; Yeates et al., 1993). Plant-feeding nematodes have a hollow stylet that pierces cell walls of higher plants. Some species are facultative plant feeders, feeding occasionally on plant roots or root hairs. Others, recognized for their damage to agricultural crops and forest plantations that include root-knot and cyst nematodes, are obligate parasites of plants and feed internally or externally on plant roots. The effect nematodes have on plants is generally species specific and host plant specific and can include alterations in root architecture, water transport, plant metabolism, or all of these.

5.4.2.3 Ecology of soil nematodes

We are rapidly increasing our understanding of the main determinants of the biogeography of soil nematodes. Griffiths and Caul (1993) found that nematodes migrated to “hot spots” of decomposing grass residues where there were considerable amounts of labile substrates and microbial food sources. At the global level and at large spatial scales, soil texture, sand content, and soil organic matter (SOM) levels are key determinants of nematode abundances and community composition (Song et al., 2017; van den Hoogen et al., 2019). The presence of plants obviously is the key determinant for the abundance of plant parasites (van den Hoogen et al., 2019), while even the identity of plant species affects abundances and nematode community composition (Wilschut et al., 2019). Like most soil organisms, nematodes are enriched in topsoils and the rhizosphere compared to root-free bulk soil (Ingham et al., 1985). Nematodes can occur at a depth of 15 m in deserts (Freckman and Virginia, 1989) and can even be found in soils of several kilometers’ depth (Borgonie et al., 2011).

Evidence suggests nematodes have similar patterns to larger aboveground animals, with their diversity peaking in the tropics (Li et al., 2020; Porazinska et al., 2012). Other studies reported highest nematode diversity in temperate zones (Song et al., 2017), or with nematode diversity being similar in tropical and polar regions (Kerfahi et al., 2016).

Nematode communities are useful bioindicators of soil quality (Bongers, 1990; Ferris and Bongers, 2006; Ferris et al., 2001; Vervoort et al., 2012). Intense management increases the ratio of bacteria to fungi leading to higher abundances of bacterivorous nematodes. Disturbance, such as plowing, especially decreases larger nematode species, such as predators, that reproduce more slowly than their smaller bacterivore counterparts, leading to an even stronger reduction in the ratio between bacterivorous taxa to omnivores and predators. As such, it was shown that biomass of trophic groups declines and that the diversity of nematodes is reduced by intensive agricultural practices (Tsiafouli et al., 2015). However, this seems to depend on the abiotic surroundings, as agricultural practices can even stabilize nematode communities and increase diversity in harsh environments (Li et al., 2020). Some plant parasitic nematodes are endemic to a region or country and, when dispersed with soil elsewhere, may result in crop damage and quarantine regulations to prohibit the species. For example, the potato cyst nematode, *Globodera rostochiensis*, originated in Central America and was transported with potatoes globally. Quarantine regulations, *Globodera*-resistant potato varieties, and noncrop rotations have successfully limited the nematode in the United States to areas in New York. The causative agent of the pine wilt disease, *Bursaphelenchus xylophilus*, a native of the United States that spread in the 1990s with wood shipped to Europe, is a quarantined pest in many countries.

5.5 Mesofauna

5.5.1 Microarthropods

Many microarthropods feed on fungi and nematodes, thereby linking microfauna and microbes with the mesofauna (Chamberlain et al., 2006). Microarthropods in turn are prey for macroarthropods, such as spiders, beetles, ants, and centipedes, thus bridging a connection of nutrients cycled to the macrofauna and to further identification of food webs in soils. Large numbers of microarthropods (mainly mites and collembolans) are found in most types of soils, and like nematodes, a square meter of forest floor may contain hundreds of thousands of individuals representing thousands of species. They have a significant impact on decomposition processes and are important reservoirs of biodiversity.

Mites and collembola are characterized as mesofauna and live in soil air-filled pore spaces. They are typically enumerated by extracting them from soil samples using drying rather than water to drive the organisms out of the soil. Variations of the Tullgren funnel, which uses heat to desiccate the sample and force the arthropods into a collection fluid, or flotation in solvents or saturated sugar solutions, are followed by filtration (Edwards, 1991).

Microarthropod densities vary seasonally within and between different ecosystems. Temperate forest floors with large organic matter content support high numbers of microarthropods (33−88,000 m^{-2}), with coniferous forests having in excess of 130,000 m^{-2}. Tropical forests, where the organic layer is thin, contain fewer microarthropods (Coleman et al., 2004, 2018; Seastedt, 1984). Tillage, fire, and pesticide applications typically reduce populations, but recovery may be rapid, with microarthropod groups responding differently. These effects of disturbance on abundance and diversity can be variable for many groups of soil animals, such as nematodes, collembola, and earthworms. In the spring forest leaf litter may develop large populations of collembolan “snow fleas” (*Hypogastrura nivicola* and related species).

Considerable progress has been made in determining the details of trophic (feeding) interactions in microarthropods, particularly for the oribatid mites. Stable isotope techniques have provided new information on the diet of mites over time — the ^{13}C and ^{15}N stable isotope signatures of mite gut contents and tissues enable the assignment of oribatid mites into feeding guilds (Pollierer et al., 2009; Schneider et al., 2004). An alternative approach uses a morphological analysis of mite chelicerae (chewing mouth parts). In cases of ambiguous trophic relationships the dietary preferences are then further resolved through isotope analyses (Perdomo et al., 2012). Chamberlain et al. (2006) used a combination of fatty acid gut analysis with compound-specific C isotope analysis to show that two collembolan species consumed nematodes. The study of the fate of DNA from two prevalent species of soil nematodes, eight species of oribatid mites, and one Mesostigmatid determined that these organisms acted as either predators or scavengers on soil nematodes (Heidemann et al., 2011). More recently, Crotty and Adl (2019), using ^{13}C and ^{15}N enrichment, established trophic cascades in microcosms containing an Ascomycetous fungus and single or multiple species of fungivorous microarthropods (the collembolan *Lepidocyrtus curvicollis*, an astigmatid *Tyrophagus putrescentiae*, and the oribatid *Oribatula tibialis*). A mesostigmatid predator *Hypoaspis aculeifer* provided an upper trophic level in this trophic cascade.

The cold hardiness of certain microarthropods, such as collembola in the genus *Tullbergia mediantarctica*, is impressive. Fox (2020) notes that this springtail has survived more than 30 onslaughts of ice sheets over the rocky slopes of the Transantarctic Mountains in far southern Antarctica. They have survived in temperature regimes occasionally colder than −40°C, with their genomes unchanged over 5 million years’ time. Perhaps *Tullbergia* reproduce parthenogenetically, thus enabling them to persist successfully without the complications of mating in an extreme environment.

5.5.2 Enchytraeids

Species from 19 of 28 genera of enchytraeids, small unpigmented oligochaetes, are found in soil. The remainder occur primarily in marine and freshwater habitats (Jeffery et al., 2010, Schmelz and Collado, 2010a,b; van Vliet, 2000). The Enchytraeidae are thought to have arisen in cool temperate climates, where they are commonly found in moist soils rich in organic matter. Identification of enchytraeid species is difficult, but genera may be identified by observing internal structures through the transparent body wall of specimens mounted on slides. Molecular tools are slowly finding their way into enchytraeid species identification, revealing profound numbers of cryptic species. However, molecular barcode regions are not fully assigned, and diversity analyses currently remain based on morphological tools (Schmelz et al., 2017).

The Enchytraeidae are typically 10 to 20 mm in length and are anatomically similar to the earthworms, except for the miniaturization and rearrangement of features. They possess setae (with the exception of one genus) and a clitellum in segments XII and XIII, which contain both male and female pores. Sexual reproduction in enchytraeids is hermaphroditic and functions similar to that in earthworms. Cocoons may contain one or more eggs, and maturation of newly hatched individuals ranges from 65 to 120 days depending on species and environmental temperature (van Vliet, 2000). Enchytraeids also display asexual strategies of parthenogenesis and fragmentation, which enhance their probability of new habit colonization (Dósza-Farkas, 1996).

5.5.2.1 Methods to study enchytraeids

Enchytraeids are typically sampled in the field using cylindrical soil cores of 5 to 7.5 cm in diameter. Large numbers of replicates may be needed for a sufficient sampling due to the clustered distribution and spatial heterogeneity of enchytraeid populations (van Vliet, 2000). Extractions are often done with a wet-funnel technique, similar to the Baermann funnel extraction used for nematodes. In this case soil cores are submerged in water in the funnel and exposed for several hours to a heat and light source from above; enchytraeids move downward and are collected in the water below.

5.5.2.2 Distribution and abundance of enchytraeids

Enchytraeids are distributed globally from subarctic to tropical regions. Keys to the common genera are presented by Schmelz and Collado (2010a,b) and Schmelz et al. (2017). Enchytraeid densities range from 1000 to a high of 140,000 individuals m^{-2}, depending on ecosystem type and management practice (van Vliet et al., 1995). Vertical distributions of enchytraeids in soil are related to organic horizons. Up to 90% of populations may occur in the upper layers in forest and no-tillage agricultural soils (Davidson et al., 2002). Seasonal trends in enchytraeid population densities appear to be primarily associated with moisture and temperature regimes (van Vliet, 2000).

In more acidic soils with reduced earthworm abundances, enchytraeids have significant effects on SOM dynamics and on soil physical structure. Enchytraeids affect soil structure by producing fecal pellets, which, depending on the animal size distribution, may enhance aggregate stability in the 600 to 1000 μm aggregate size fraction. In organic horizons these pellets are composed mainly of fine, highly decomposed organic matter particles, but in mineral soils, organic matter and mineral particles may be mixed into fecal pellets with a loamy texture. Davidson et al. (2002) estimated that enchytraeid fecal pellets constituted nearly 30% of the volume of the surface horizon in a Scottish grassland soil. Encapsulation or occlusion of organic matter into these structures may reduce decomposition rates by protecting organic matter from microbial attack.

5.5.2.3 Food sources of enchytraeids

Enchytraeids ingest both mineral and organic particles, although typically of smaller size ranges than those of earthworms. Finely divided plant materials, often enriched with fungal hyphae and bacteria, are a principal portion of the diet of enchytraeids. Microbial tissues are probably the fraction most readily assimilated because enchytraeids lack the gut enzymes to digest more recalcitrant SOM (Jeffery et al., 2010; van Vliet, 2000). Didden (1990, 1993) suggested that enchytraeids feed predominantly on fungi, at least in arable soils, and classified a community as 80% microbivorous and 20% saprovorous. The mixed microbiota that occur on decaying organic matter, either litter or roots, are probably an important part of the diet of these creatures. The remaining portions of organic matter, after the processes of ingestion, digestion, and assimilation, are excreted and become part of the slow-turnover pool of SOM. Mycorrhizal hyphae have been found in the fecal pellets of enchytraeids from pine litter (Ponge, 1991). Enchytraeids probably consume and further process larger fecal pellets and castings of soil macrofauna, such as collembolans and earthworms (Rusek, 1985; Zachariae, 1964). Thus fecal contributions by soil-dwelling invertebrates provide feedback mechanisms affecting the abundance and diversity of other soil-dwelling animals.

5.6 Macrofauna

5.6.1 Macroarthropods

Larger insects, spiders, myriapods, and others are considered together under the appellation "macroarthropods." Typical body lengths range from about 10 mm to as much as 15 cm for centipedes (Shelley, 2002). The group includes a mixture of various arthropod classes, orders, and families. Like the microarthropods, the macroarthropods are defined more by the methods used to sample them than by measurements of body size. Large soil cores (10 cm diameter or greater) may be appropriate for euedaphic (dwelling within the soil) species. Arthropods can be recovered using flotation techniques (Edwards, 1991); however, hand sorting of soils and litter, though time consuming, yields better estimates of population size than flotation. Capture-mark-recapture methods have been used to estimate population sizes of selected macroarthropod species, but the method is problematic due to inadequate recoveries of organisms during resampling (Southwood, 1978). Pitfall traps have been widely used to sample litter- and surface-dwelling macroarthropods. This method collects arthropods that fall into cups, filled with preservative (e.g., antifreeze), and whose rims are flush with the soil surface. Absolute population estimates are difficult to obtain with pitfall traps, but the method yields comparative estimates when used with caution. Many of the macroarthropods are members of the group termed "cryptozoa," a group consisting of animals that dwell beneath stones or logs, under bark, or in cracks and crevices. Cryptozoans typically emerge at night to forage, and some are attracted to artificial lights. The cryptozoa fauna is poorly defined but remain useful for identifying a group of invertebrate species with similar patterns of habitat utilization. Due to the well-established expertise on morphological species identification, molecular tools are only slowly emerging to study cryptozoans (Deiner et al., 2017).

Termites and ants in particular are important movers of soil, depositing parts of lower strata on top of the litter layer (Fig. 5.6). Emerging nymphal stages of cicadas may be numerous enough to disturb soil structure. Larval stages of soil-dwelling scarabaeid beetles sometimes churn the soil in grasslands. These and other macroarthropods are part of the group that has been termed ecological engineers (Jones et al., 1994). Some macroarthropods participate in both above- and belowground parts of terrestrial ecosystems. Many macroarthropods are transient or temporary soil residents and thus form a connection between food chains in the "green world" of foliage and the "brown world" of the soil. Caterpillars descending to the soil to pupate or migrating armyworm caterpillars are prey to ground-dwelling spiders and beetles. Macroarthropods may have a major influence on the microarthropod portion of belowground food webs. Collembola, among other microarthropods, are important food items for spiders, thus providing a macro- to microfauna connection. Other macroarthropods, such as cicadas, emerging from soil may serve as prey for some vertebrate animals (Lloyd and Dybas, 1966), including endangered vertebrate species (small mammals) (Decaëns et al., 2006), thus providing a link to the larger megafauna. Among the macroarthropods, there are many litter-feeding species, such as millipedes, that are significant consumers of leaf, grass, and wood litter. The decomposition of vertebrate carrion is largely accomplished through the actions of soil-dwelling insects (Payne, 1965).

Litter-feeding millipedes harbor a gut microbiota that is distinctly different from that of the ingested organic substrate of leaf litter. Using denaturing gradient gel electrophoresis (DGGE), Knapp et al. (2009) found a stable, indigenous microbial community in the gut of the millipede *Cylindroiulus fulviceps* in abandoned alpine pastureland. Its gut microbiota was dominated by Gamma- and Delta-proteobacteria and resisted dietary changes even during a varied dietary intake.

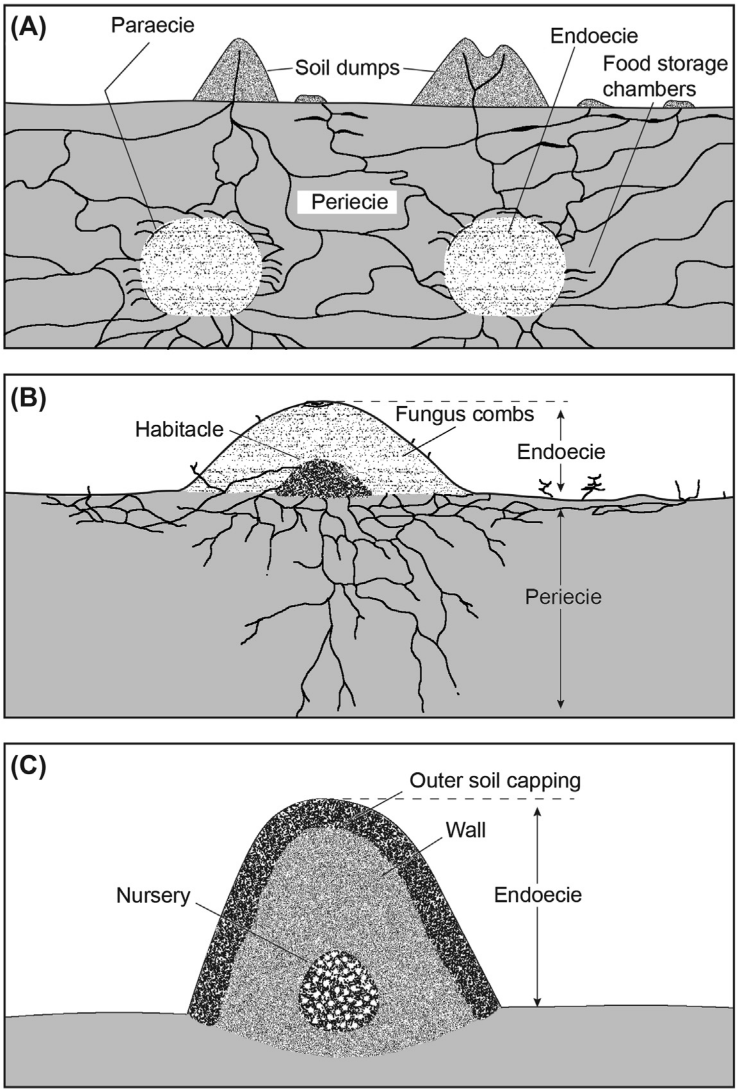

FIGURE 5.6 **Termite mounds.** Diagrammatic representation of different types of concentrated nest systems: (a) *Hodotermes mossambicus*, (b) *Macrotermes subhyalinus*, and (c) *Nasutitermes exitiosus. (With permission from* Lee and Wood, 1971*.)*

A more general aspect of arthropod feeding biology is addressed by the study of enzymatic roles in the digestion of plant cell walls, in particular, cellulose and lignin. Considered over evolutionary time, insects were more active in the "brown world" of decomposition of plant tissues on or in the soil, until the development of herbivory, possibly coinciding with the origin of the Angiosperms c. 160 million years ago. Some of the earliest orders of insects to arise, such as the Isoptera (Termites), have approached the problem of development of cellulases by developing symbiotic associations with protists in their hindguts

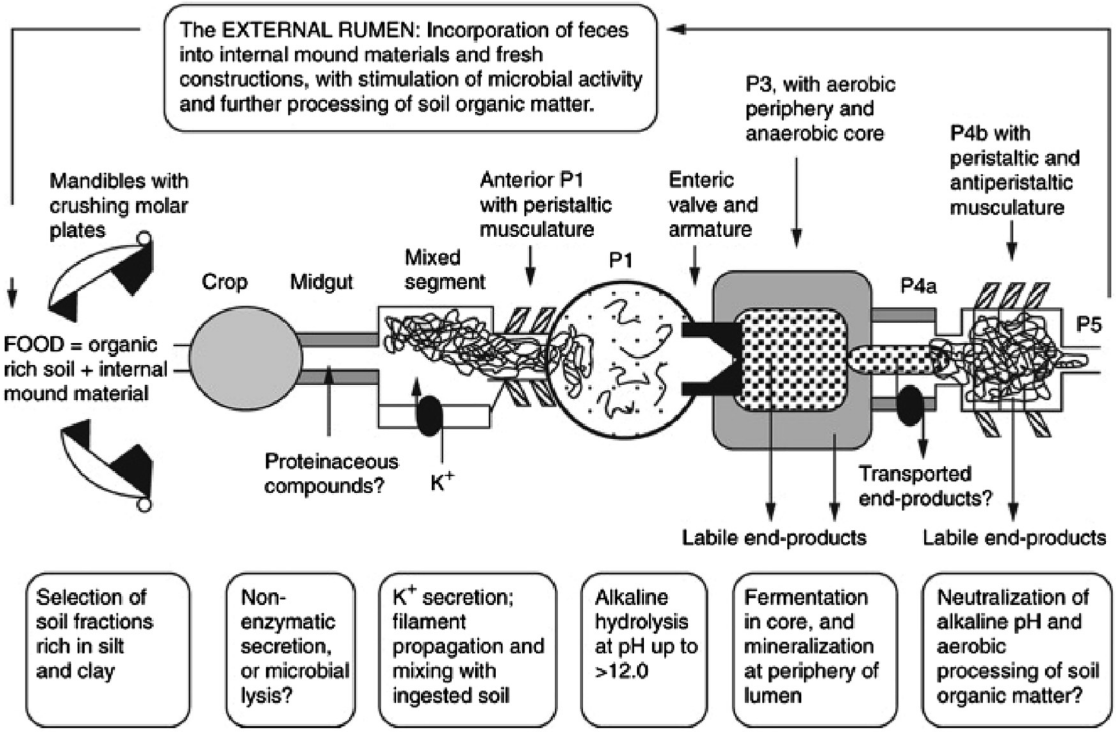

FIGURE 5.7 **Hypothesis of gut organization and sequential processing in soil-feeding Cubitermes-clade termites.** The model emphasizes the role of filamentous prokaryotes, the extremely high pH reached in the P1, and the existence of both aerobic and anaerobic zones within the hindgut. *(From Brauman et al. (2000).)*

(the more primitive termite families) or their own endogenous cellulases (Termitidae) (Calderón-Cortés et al., 2012) (Fig. 5.7). Significantly, the combined synthesis and activity of cellobiohydrolases and xylanases effectively degrade lignocellulose in the termite hindgut (Gilbert, 2010). The development of endogenous cellulases and in some cases laccases occurred in numerous insect families, including several in the order Coleoptera, and a few Lepidoptera and Diptera (Calderón-Cortés et al., 2012).

5.6.2 Oligochaeta (earthworms)

Earthworms are the most familiar and, with respect to soil processes, often the most important of the soil fauna. The importance of earthworms arises from their influence on soil structure (e.g., aggregate or crumb formation, soil pore formation) and the breakdown of organic matter (e.g., fragmentation, burial, and mixing of plant residues) (Carpenter et al., 2008).

Invasive earthworms are now colonizing less disturbed and even pristine forested habitats of the glaciated portions of North America (Cameron et al., 2007; Frelich et al., 2006; Hale et al., 2005). The history of road construction in northern boreal forests is a strong predictor of the extent of earthworm invasion, and the distance of a particular forested habitat from active agriculture is directly related to earthworm invasion (Cameron and Bayne, 2009). The modern era of earthworm research began with

Darwin's (1881) book, "The Formation of Vegetable Mold through the Actions of Worms, with Observations of Their Habits," which called attention to the beneficial effects of earthworms. Since then, a vast literature has established the importance of earthworms as biological agents in soil formation, organic litter decomposition, and redistribution of organic matter in the soil (Edwards, 1998; Hendrix, 1995; Lavelle and Spain, 2001).

Earthworms are classified within the phylum Annelida, class Oligochaeta. Species within the families Lumbricidae and Megascolecidae are ecologically the most important in North America, Europe, Australia, and Asia. Some of these species have been introduced worldwide by human activities and now dominate the earthworm fauna in many temperate areas. Any given locality may be inhabited by only native species, all exotic species, a combination of native and exotic species, or no earthworms at all. Relative abundance and species composition of local fauna depend greatly on soil, climate, vegetation, topography, land use history, and especially past invasions by exotic species.

5.6.2.1 Earthworm distribution and abundance

Earthworms are native to habitats where soil water and temperature are favorable for at least part of the year, while in North American forests they have now been introduced and become invasive. They are most abundant in forests and grasslands of temperate and tropical regions and least so in arid and frigid environments, such as deserts, tundra, or polar regions. Earthworm densities in a variety of habitats worldwide range from 10 to 2000 individuals m^{-2}, the highest values occurring in fertilized pastures and the lowest in acid or arid soils (coniferous or sclerophyll forests). Typical densities from temperate deciduous or tropical forests and certain arable systems range from 100 to over 400 individuals m^{-2}, representing a range of from 4 to 16 g dry mass m^{-2}. Earthworms are also highly diverse, with at least 7000 described species and many more awaiting description (Phillips et al., 2019). Intensive land management (especially soil tillage and application of toxic chemicals such as soil and plant pesticides) often reduces the density of earthworms or may completely eliminate them. Conversely, degraded soils converted to conservation management often show increased earthworm densities after a few years (Curry et al., 1995; Edwards and Bohlen, 1996).

5.6.2.2 Biology and ecology

Earthworms are often grouped into functional categories based on their morphology, behavior, and feeding ecology and their microhabitats within the soil (Lavelle, 1983; Lee, 1985). Epigeic and epiendogeic species are often polyhumic, meaning they prefer organically enriched substrates and utilize plant litter on the soil surface and C-rich upper layers of mineral soil. Polyhumic endogeic species inhabit mineral soil with high organic matter content (3%), such as the rhizosphere, while meso- and oligohumic endogeic species inhabit soil with moderate (1−3%) and low (1%) organic matter contents, respectively. Anecic species exploit both the surface litter as a source of food and the mineral soil as a refuge. The familiar *Lumbricus terrestris* is an example of an anecic species, constructing burrows and pulling leaf litter down into them. The American log worm (*Bimastos parvus*) exploits leaf litter and decaying logs with little involvement in the soil, making it an epigeic species. Epigeic species promote the breakdown and mineralization of surface litter, whereas anecic species incorporate organic matter deeper into the soil profile and facilitate aeration and water infiltration through their formation of burrows.

5.6.2.3 Influence on ecosystems and soil processes

Earthworms, as ecosystem engineers (Lavelle et al., 1998), have pronounced effects on soil structure as a consequence of their burrowing activities as well as their ingestion of soil and production of castings (Lavelle and Spain, 2001; van Vliet and Hendrix, 2003). Casts are produced after earthworms ingest mineral soil or particulate organic matter, mix and enrich them with organic secretions in the gut, and then deposit the material as a slurry lining their burrows or as discrete fecal pellets. Excretion of fecal pellets can occur within or upon the soil, depending on the species. Turnover rates of soil through earthworm casting range from 40—70 t ha^{-1} y^{-1} in temperate grasslands (Bouché, 1983) to 500—1000 t ha^{-1} y^{-1} in tropical savannas (Lavelle et al., 1992). While in the earthworm gut, casts are colonized by microbes that begin to break down SOM. As casts are deposited in the soil, microbial colonization and activity continue until readily decomposable compounds are depleted. Mechanisms of cast stabilization include organic bonding of particles by polymers secreted by earthworms and microbes, mechanical stabilization by plant fibers and fungal hyphae, and stabilization due to wetting and drying cycles and age-hardening effects (Tomlin et al., 1995). Mineralization of organic matter in earthworm casts and burrow linings produces zones of nutrient enrichment compared to bulk soil. These zones, referred to as the "drilosphere," are often sites of enhanced activity of plant roots and other soil biota (Lavelle et al., 1998). Plant growth-promoting substances have also been suggested as constituents of earthworm casts. Many earthworm castings from commercial vermicomposting operations are sold commercially as soil amendments to improve soil physical properties and enhance plant growth (Edwards and Shipitalo, 1998).

Earthworm burrowing in soil creates macropores of various sizes, depths, and orientations, depending on species and soil type. Burrows range from about 1 to 10 mm in diameter and constitute among the largest of soil pores. Continuous macropores resulting from earthworm burrowing may enhance water infiltration by functioning as bypass flow pathways through soils. These pores may or may not be important in solute transport, depending on soil water content, the nature of the solute, and chemical exchange properties of the burrow linings (Edwards and Shipitalo, 1998). Earthworm burrows in agricultural systems can lead to groundwater contamination with pesticides and fertilizers (Edwards and Shipitalo, 1998).

Despite the many beneficial effects of earthworms on soil processes, some aspects of earthworm activities may be undesirable (Lavelle et al., 1998; Parmelee et al., 1998). Detrimental effects include: (1) removing and burying of surface residues that would otherwise protect soil surfaces from erosion; (2) producing fresh casts that increase erosion and surface sealing; (3) increasing compaction of surface soils by decreasing SOM, particularly for some tropical species; (4) riddling irrigation ditches, making them leaky; (5) increasing losses of soil N through leaching and denitrification; and (6) increasing soil C loss through enhanced microbial respiration. Earthworms may transmit pathogens, either as passive carriers or as intermediate hosts, raising concerns that some earthworm species could be a vector for the spread of certain plant and animal diseases. The net result of positive and negative effects of earthworms, or any other soil biota, determines whether they have detrimental impacts on ecosystems (Lavelle et al., 1998). An effect, such as mixing of O (litter [L], fermentation [F], and humification [H] zones, also called Oi, Oe, and Oa zones, respectively) and A horizons (top of the mineral soil surface, containing the preponderant amount of organic matter), may be considered beneficial in one setting (e.g., urban gardens) and detrimental in another (e.g., native forests) (Edwards, 1998).

5.6.3 Formicidae (ants)

Formicidae, the ants, are probably the most significant family of soil insects due to the very large influence they have on soil structure. Ants are numerous, diverse, and widely distributed from arctic to tropical ecosystems. Ant communities contain many species, even in desert areas (Whitford, 2000), and local species diversity is especially large in tropical areas. Populations of ants are equally numerous. About one-third of the animal biomass of the Amazonian rainforest is composed of ants and termites, with each hectare containing in excess of 8 million ants and 1 million termites (Hölldobler and Wilson, 1990). Furthermore, ants are social insects, living in colonies with several castes.

Ants are major predators of small invertebrates. Their activities reduce the abundance of other predators such as spiders and carabid beetles (Wilson, 1987). Ants are ecosystem engineers, moving large volumes of soil, much as earthworms do (Hölldobler and Wilson, 1990). Ant influences on soil structure are particularly important in deserts where earthworm densities are low. Given the large diversity of ants, identification to species is problematic for many, but Wheeler and Wheeler (1990) offer keys to subfamilies and genera of the Nearctic ant fauna. See also Ellison et al. (2012).

5.6.4 Isoptera (termites)

Along with earthworms and ants, termites are the third major earth-moving group of invertebrates. Termites are social insects with a well-developed caste system. Through their ability to digest wood, they have become economic pests of major importance in some regions of the world (Bignell and Eggleton, 2000; Lee and Wood, 1971). Termites are highly successful, constituting up to 75% of the insect biomass and 10% of all terrestrial animal biomass in the tropics (Bignell, 2000; Wilson, 1992). While termites are mainly tropical in distribution, they occur in temperate zones as well. Termites have been called the tropical analogs of earthworms since they reach large abundances in the tropics and process large amounts of litter. Termites in the primitive families, such as Kalotermitidae, possess a gut flora of protists, which enables them to digest cellulose. Their normal food is wood that has come into contact with soil. Most species of termites construct runways of soil and some are builders of spectacular mounds. Members of the phylogenetically advanced family Termitidae do not have protistan symbionts but possess a formidable array of microbial symbionts (bacteria and fungi) that enable them to process and digest the humified organic matter in tropical soils (Bignell, 1984; Breznak, 1984; Pearce, 1997). A generalized sequence of events in a typical Termitinae soil-feeder gut emphasizes the role of filamentous prokaryotes, the extremely high pH reached in the front of the hindgut, and the existence of both aerobic and anaerobic zones within the hindgut (Brauman et al., 2000).

Three nutritional categories include wood-feeding species, plant- and humus-feeding species, and fungus growers. The last group lacks intestinal symbionts and depends upon cultured fungi for nutrition. Termites have an abundance of unique microbes living in their guts. One study of bacterial microbiota in the gut of the wood-feeding termite *Reticulitermes speratus* found 268 phylotypes of bacteria (16S rRNA genes, amplified by PCR), including 100 clostridial, 61 spirochetal, and 31 Bacteroides-related phylotypes (Hongoh et al., 2003). More than 90% of the phylotypes were found for the first time, but it is unknown if they are active and participating in wood decay. Other phylotypes were monophyletic clusters with sequences recovered from the gut of other termite species. Cellulose digestion in termites, which was once considered to be solely due to the activities of fungi and protists and occasionally bacteria, has now been demonstrated to be endogenous to termites. Endogenous cellulose-degrading enzymes occur in the midguts of two species of higher termites in the genus *Nasutitermes* and in the Macrotermitinae (which cultivate basidiomycete fungi in elaborately constructed gardens) as well (Bignell, 2000).

In contrast to C-degradation by termites, only prokaryotes are capable of producing nitrogenase to fix N_2, which occurs in the organic matter-rich, microaerophilic milieu of termite guts. Some termite genera have bacteria that fix relatively small amounts of N, but others, including *Mastotermes* and *Nasutitermes*, fix from 0.7 to 21 g N g^{-1} fresh wt. day^{-1}. This equals 20 to 61 μg N per colony per day, which would double the N content if N_2 fixation was the sole source of N and the rate per termite remained constant (N content of termites assumed to be 11% on a dry weight basis) (Breznak, 2000). Some insight into the roles of soil-feeding termites in the terrestrial N cycle has been provided by Ngugi and Brune (2012), who measured significant denitrification in the hindguts of two genera of soil-feeding termites ranging from 0.4 to 3.9 nmol h^{-1} (g fresh wt.)$^{-1}$ N_2O, providing direct evidence that soil-feeding termites are a hitherto unrecognized source of this greenhouse gas in tropical soils. For an extensive exposition of the role of termites in the dynamics of SOM and nutrient cycling in ecosystems worldwide, refer to Bignell and Eggleton (2000). An overview of omics research in termites is covered by Scharf (2015).

A profound demonstration of the potential for termites to regulate ecosystem stability/resilience is described by Ashton et al. (2019), where termites were responsible for mitigating the effects of drought on an entire tropical forest ecosystem. In this study the presence of termites was associated with higher soil moisture during drought conditions, which in turn was associated with faster decomposition rates (and attendant nutrient supply rates), ultimately resulting in greater seedling survival among rainforest plants. These results emphasize the importance of soil fauna in the stability (or even persistence) of an ecosystem under stress.

5.7 Roles of soil fauna in ecosystems and societal impacts

Evidence on how soil fauna will respond to environmental change and how shifts in soil faunal abundance, diversity, and community composition will influence aboveground processes has advanced considerably (see Cheeke et al., 2012; de Vries et al., 2012, 2020; Rillig et al., 2020; Wall et al., 2012). Loss of species due to varying management practices, soil erosion, pollution, and urbanization, and the resulting effects on ecosystem function and services are becoming widely recognized and are related to larger issues of biodiversity loss, desertification, and elevated greenhouse gas concentrations (Koch et al., 2013). This has resulted in international attention to the importance of soils beyond agricultural soils and, in particular, to soil biodiversity, as now summarized in the FAO report on soil biodiversity (FAO et al., 2020). We are now able to answer basic questions about soil fauna including such topics as whether there are cosmopolitan vs. endemic fauna species; what the local and global biogeographic distribution and range of faunal species is; what the factors influencing the distribution of key species are; and whether the loss of species affects ecosystem function (Veresoglou et al., 2015; Wall et al., 2012). Food web ecology, with its emphasis on community assembly and disassembly, has the potential to act as an integrating concept across conservation biology and community and ecosystem ecology as well as for provision of ecosystem services (de Vries et al., 2012; Moore and de Ruiter, 2012; Thompson et al., 2012; Wall et al., 2012).

Global experiments and syntheses have continued to address the quantification of the role of soil fauna in ecosystem processes and, in particular, have led to increased evidence for the faunal contribution to C cycling. Global multisite experiments show that soil fauna are key regulators of decomposition rates at biome and global scales (Makkonen et al., 2012; Powers et al., 2009; Wall et al., 2008). García-Palacios et al. (2013) conducted a meta-analysis on 440 litterbag studies across 129 sites to assess how climate, litter quality, and soil invertebrates affect decomposition. This analysis showed that fauna were responsible for a ∼27% enhancement, on average, of litter decomposition across global and biome scales.

Agricultural practices affect many of the key functional and structural attributes of ecosystems in several ways: the transformation of mature ecosystems into ones that are in a managed developmental state is induced by tillage operations and other activities, such as applying fertilizers and pesticides. These manipulations have the potential to shift the elemental balance of a system, decrease species diversity, and alter the soil food web (Cheeke et al., 2012; Moore and de Ruiter, 2012). Conventional tillage practices alter the distribution of organic material and affect the rate of formation of micro- and macroaggregates in the soil profile. This has a profound effect on the turnover rates of organic matter that is associated with the aggregates (Elliott and Coleman, 1988; O'Brien and Jastrow, 2013; Six et al., 2004), as well as affecting ecosystem services (Cheeke et al., 2012). de Vries et al. (2012) showed that grassland, fungal-based food webs were more resilient than agricultural fields with bacterial-dominated food webs and provided evidence for management options that enhanced ecosystem services. Cock et al. (2012) provide evidence for manipulating soil invertebrates to benefit agriculture and to enhance ecosystem services, such as biological control and C sequestration. Their focus includes successful case studies in sustainable agriculture. Koch et al. (2013) bring attention to the global policy impact of land degradation and loss of soils, biodiversity and ecosystem services, and its implications for food security. Soil fauna continue to be an exciting research field, linking aboveground systems to belowground diversity and function, as well as to environmental issues at local to global scales (Cock et al., 2012; Wall, 2004; Wall et al., 2012).

5.8 Summary

Soil fauna may be considered very efficient means to assist microbes in colonizing and extending their reach into the horizons of soils worldwide. Their roles as colonizers, comminutors, and engineers within soils have been emphasized, but new technologies and global environmental issues are yielding new questions about how to manipulate soil fauna for the long-term sustainability of soils. The demand for taxonomic specialists for all groups of soil biota is increasing as we currently recognize that molecular information alone is insufficient for many studies. Stable isotope technologies are being used with more precision to reveal the transfer of C and N through soil food webs and elucidate the role of each trophic group. This technique is clarifying that soil faunal species hitherto thought to be within one trophic group are not, thus leading to research about the structure and resilience of soil food webs. Information on the biogeography of soil fauna, their latitudinal gradient patterns, and their relationship to aboveground hot spots and to land management strategies, as well as their taxonomic status and natural history, will be critical for understanding how bacteria, archaea, fungi, protists, and soil invertebrates interact and respond to multiple global changes (Fierer et al., 2012; Wall et al., 2001, 2008; Wu et al., 2011). For example, soil invertebrates can be invasive species, which, depending on the species, can affect soil C sequestration, soil fertility, and plant and animal health, resulting in economic and ecosystem change. We feel protection of known biodiversity in ecosystems clearly must include the rich pool of soil species. This is because data for some of these species individually and collectively indicate tight connections to biodiversity aboveground, major roles in ecosystem processes, and provision of ecosystem benefits for human well-being (Wall, 2004; Wall et al., 2005; Wardle et al., 2004). Additionally, climate envelopes (e.g., niche dimensions of climate tolerance ranges) can be developed as more is known about soil species identity, activity, and geographic ranges, aiding in the development of land management practices and projections for the functioning of tomorrow's ecosystems under climate change. For further reading on the roles of fauna in soil processes, see Coleman (2008), Coleman et al. (2012; 2018), Geisen et al. (2019a; b), Nielsen (2019), and Wall et al. (2012).

References

Adl, S.M., Simpson, A.G.B., Lane, C.E., Lukeš, J., Bass, D., Bowser, S.S., et al., 2012. The revised classification of eukaryotes. J. Eukaryot. Microbiol. 59, 429–514.

Adl, S.M., Bass, D., Lane, C.E., Lukeš, J., Schoch, C.L., Smirnov, A., et al., 2019. Revisions to the classification, nomenclature, and diversity of eukaryotes. J. Eukaryot. Microbiol. 66, 4–119.

André, H.M., Ducarme, X., Lebrun, P., 2002. Soil biodiversity: myth, reality or conning? Oikos 96, 3–24.

Ashton, L.A., Griffiths, H.M., Parr, C.L., Evans, T.A., Didham, R.K., Hasan, F., et al., 2019. Termites mitigate the effects of drought in tropical rainforest. Science 363 (6423), 174–177. https://doi.org/10.1126/science.aau9565.

Bates, S.T., Clemente, J.C., Flores, G.E., Walters, W.A., Parfrey, L.W., Knight, R., et al., 2013. Global biogeography of highly diverse protistan communities in soil. ISME J. 7, 652–659.

Beakes, G.W., Glockling, S.L., Sekimoto, S., 2012. The evolutionary phylogeny of the oomycete "fungi". Protoplasma 249, 3–19.

Berthold, A., Palzenberger, M., 1995. Comparison between direct counts of active soil ciliates (Protozoa) and most probable number estimates obtained by Singh's dilution culture method. Biol. Fertil. Soils 19, 348–356.

Bignell, D.E., 1984. The arthropod gut as an environment for microorganisms. In: Anderson, J.M., Rayner, A.D.M., Walton, D.W.H. (Eds.), Invertebrate-Microbial Interactions. Cambridge University Press, Cambridge, pp. 205–227.

Bignell, D.E., 2000. Introduction to symbiosis. In: Abe, T., Bignell, D.E., Higashi, M. (Eds.), Termites: Evolution, Sociality, Symbioses, Ecology. Kluwer Academic, Dordrecht, pp. 189–208.

Bignell, D.E., Eggleton, P., 2000. Termites in ecosystems. In: Abe, T., Bignell, D.E., Higashi, M. (Eds.), Termites: Evolution, Sociality, Symbioses, Ecology. Kluwer Academic, Dordrecht, pp. 363–387.

Blaxter, M.L., De Ley, P., Garey, J.R., Liu, L.X., Scheldeman, P., Vierstraete, A., et al., 1998. A molecular evolutionary framework for the phylum Nematoda. Nature 392, 71–75.

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

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol. Evol. 14, 224–228.

Bonkowski, M., 2004. Protozoa and plant growth: the microbial loop in soil revisited. New Phytol. 162, 617–631.

Bonkowski, M., Clarholm, M., 2012. Stimulation of plant growth through interactions of bacteria and protozoa: testing the auxiliary microbial loop hypothesis. Acta Protozool. 51, 237–247.

Borgonie, G., Garcia-Moyano, A., Litthauer, D., Bert, W., Bester, A., van Heerden, E., et al., 2011. Nematoda from the terrestrial deep subsurface of South Africa. Nature 474, 79–82.

Bouché, M.B., 1983. The establishment of earthworm communities. In: Satchell, J.E. (Ed.), Earthworm Ecology: From Darwin to Vermiculture. Chapman & Hall, London, pp. 431–448.

Brauman, A., Bignell, D.E., Tayasu, I., 2000. Soil-feeding termites: biology, microbial associations and digestive mechanisms. In: Abe, T., Bignell, D.E., Higashi, M. (Eds.), Termites: Evolution, Sociality, Symbioses. Kluwer Academic Publishers, Dordrecht, pp. 233–259.

Breznak, J.A., 1984. Biochemical aspects of symbiosis between termites and their intestinal micro-biota. In: Anderson, J.M., Rayner, A.D.M., Walton, D.W.H. (Eds.), Invertebrate-Mirobial Interactions. Cambridge University Press, Cambridge, UK, pp. 209–231.

Breznak, J., 2000. Ecology of prokaryotic microbes in the guts of wood- and litter-feeding termites. In: Abe, T., Bignell, D.E., Higashi, M. (Eds.), Termites: Evolution, Sociality, Symbioses, Ecology. Kluwer Academic Publishers, Dordrecht, pp. 209–231.

Calderón-Cortés, N., Quesada, M., Watanabe, H., Cano-Comacho, H., Oyama, K., 2012. Endogenous plant cell wall digestion: a key mechanism in insect evolution. Annu. Rev. Ecol. Evol. Syst. 43, 45–71.

Cameron, E.K., Bayne, E.M., 2009. Road age and its importance in earthworm invasion of northern boreal forests. J. Appl. Ecol. 46, 28−36.

Cameron, E.K., Bayne, E.M., Clapperton, M.J., 2007. Human-facilitated invasion of exotic earthworms into northern boreal forests. Ecoscience 14, 482−490.

Caron, D.A., Worden, A.Z., Countway, P.D., Demir, E., Heidelberg, K.B., 2008. Protists are microbes too: a perspective. ISME J. 3, 4−12.

Carpenter, D., Hodson, M.E., Eggleton, P., Kirk, C., 2008. The role of earthworm communities in soil mineral weathering: a field experiment. Mineral. Mag. 72, 33−36.

Chamberlain, P.M., Bull, I.D., Black, H.I.J., Ineson, P., Evershed, R.P., 2006. Collembolan trophic preferences determined using fatty acid distributions and compound-specific stable carbon isotope values. Soil Biol. Biochem. 38, 1275−1281.

Cheeke, T., Coleman, D.C., Wall, D.H. (Eds.), 2012. Microbial Ecology in Sustainable Agroecosystems. CRC Press, Boca Raton.

Cock, M.J., Biesmeijer, J.C., Cannon, R.J., Gerard, P., Gillespie, D., Jiménez, J., et al., 2012. The positive contribution of invertebrates to sustainable agriculture and food security. CAB. Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour. 7, 1−27.

Coleman, D.C., 2008. From peds to paradoxes: linkages between soil biota and their influences on ecological processes. Soil Biol. Biochem. 40, 271−289.

Coleman, D.C., Whitman, W.B., 2005. Linking species richness, biodiversity and ecosystem function in soil systems. Pedobiologia 49, 479−497.

Coleman, D.C., Hendrix, P.F., Beare, M.H., Cheng, W., Crossley Jr., D.A., 1993. Microbial and faunal dynamics as they affect soil organic matter dynamics in subtropical agroecosystems. In: Paoletti, M.G., Foissner, W., Coleman, D.C. (Eds.), Soil Biota and Nutrient Cycling Farming Systems. CRC Press, Boca Raton, pp. 1−14.

Coleman, D.C., Crossley Jr., D.A., Hendrix, P.F., 2004. Fundamentals of Soil Ecology. Elsevier, San Diego.

Coleman, D.C., Vadakattu, G., Moore, J.C., 2012. Soil ecology and agroecosystem studies: a dynamic world. In: Cheeke, T., Coleman, D.C., Wall, D.H. (Eds.), Microbial Ecology in Sustainable Agroecosystems. CRC Press, Boca Raton, pp. 1−21.

Coleman, D.C., Callaham, M.A., Crossley Jr., D.A., 2018. Fundamentals of Soil Ecology, third ed. Elsevier, Academic Press, London.

Crotty, F.V., Adl, S.M., 2019. Competition and predation in soil fungivorous microarthropods using stable isotope ratio mass spectrometry. Front. Microbiol. 10, 1274. https://doi.org/10.3389/fmicb.2019.01274.

Crotty, F.V., Adl, S.M., Blackshaw, R.P., Murray, P.J., 2012. Protozoan pulses unveil their pivotal position within the soil food web. Microb. Ecol. 63, 905−918.

Curry, J.P., Byrne, D., Boyle, K.E., 1995. The earthworm population of a winter cereal field and its effects on soil and nitrogen turnover. Biol. Fertil. Soils 19, 166−172.

Darbyshire, J.F., Whitley, R.E., Graebes, M.P., Inkson, R.H.E., 1974. A rapid micromethod for estimating bacterial and protozoan populations in soil. Rev. Ecol. Biol. Soil 11, 465−475.

Darwin, C., 1881. The Formation of Vegetable Mould, through the Action of Worms. John Murray, London.

Davidson, D.A., Bruneau, P.M.C., Grieve, I.C., Young, I.M., 2002. Impacts of fauna on an upland grassland soil as determined by micromorphological analysis. Appl. Soil Ecol. 20, 133−143.

Decaëns, T., 2010. Macroecological patterns in soil communities. Glob. Ecol. Biogeogr. 19, 287−302.

Decaëns, T., Jimenez, J.J., Gioia, C., Measey, G.J., Lavelle, P., 2006. The values of soil animals for conservation biology. Eur. J. Soil Biol. 42, S23−S38.

de Ruiter, P.C., Neutel, A.M., Moore, J.C., 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269, 1257−1260.

de Vries, F.T., Liiri, M.E., Bjornlund, L., Bowker, M.A., Christensen, S., Setälä, H.M., et al., 2012. Land use alters the resistance and resilience of soil food webs to drought. Nat. Clim. Change 2, 276−280.

de Vries, F.T., Griffiths, R.I., Knight, C.G., Nicolitch, O., Williams, A., 2020. Harnessing rhizosphere microbiomes for drought-resilient crop production. Science 368, 270−274.

Deiner, K., Bik, H.M., Mächler, E., Seymour, M., Lacoursière-Roussel, A., Altermatt, F., et al., 2017. Environmental DNA metabarcoding: transforming how we survey animal and plant communities. Mol. Ecol. 26, 5872−5895.

Didden, W.A.M., 1990. Involvement of Enchytraeidae (Oligochaeata) in soil structure evolution in agricultural fields. Biol. Fertil. Soils 9, 152–158.

Didden, W.A.M., 1993. Ecology of Enchytraeidae. Pedobiologia 37, 2–29.

Domene, X., Chelinho, S., Campana, P., Natal-da-Luz, T., Alcañiz, J.M., Andrés, P., et al., 2011. Influence of soil properties on the performance of *Folsomia candida*: implications for its use in soil ecotoxicology testing. Environ. Toxicol. Chem. 30, 1497–1505.

dos Reis, M., Thawornwattana, Y., Angelis, K., Telford, M.J., Donoghue, P.C.J., Yang, Z., 2015. Uncertainty in the timing of origin of animals and the limits of precision in molecular timescales. Curr. Biol. 25, 2939–2950.

Dósza-Farkas, K., 1996. Reproduction strategies in some enchytraeid species. In: Dosza-Farkas, K. (Ed.), Newsletter on Enchytraeidae. Eotvos Lorand University, Budapest.

Dupont, A.O., Griffiths, R.I., Bell, T., Bass, D., 2016. Differences in soil micro-eukaryotic communities over soil pH gradients are strongly driven by parasites and saprotrophs. Environ. Microbiol. 18, 2010–2024.

Edwards, C.A., 1991. The assessment of populations of soil-inhabiting invertebrates. Agric. Ecosyst. Environ. 34, 145–176.

Edwards, C.A. (Ed.), 1998. Earthworm Ecology. St. Lucie Press, Boca Raton.

Edwards, C.A., Bohlen, P.J., 1996. Earthworm Biology and Ecology. Chapman & Hall, London.

Edwards, W.M., Shipitalo, M.J., 1998. Consequences of earthworms in agricultural soils: aggregation and porosity. In: Edwards, C.A. (Ed.), Earthworm Ecology. CRC Press, Boca Raton, pp. 147–161.

Elliott, E.T., Coleman, D.C., 1988. Let the soil work for us. Ecol. Bull. Copenhagen 39, 23–32.

Elliott, E.T., Anderson, R.V., Coleman, D.C., Cole, C.V., 1980. Habitable pore-space and microbial trophic interactions. Oikos 35, 327–335.

Ellison, A.M., Gotelli, N.J., Farnsworth, E.J., Alpert, G.D., 2012. A Field Guide to the Ants of New England. Yale University Press, New Haven.

FAO, ITPS, CBD, GSBI, EC, 2020. State of Knowledge of Soil Biodiversity – Status, Challenges and Potentialities, Full Report. FAO, Rome.

Ferris, H., Bongers, T., 2006. Nematode indicators of organic enrichment. J. Nematol. 38, 3–12.

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

Fierer, N., Lennon, J.T., 2011. The generation and maintenance of diversity in microbial communities. Am. J. Bot. 98, 439–448.

Fierer, N., Leff, J.W., Adams, B.J., Nielsen, U.N., Bates, S.T., Lauber, C.L., et al., 2012. Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. PNAS USA 109, 21390–21395.

Finlay, B.J., Black, H.I.J., Brown, S., Clarke, K.J., Esteban, G.F., Hindle, R.M., et al., 2000. Estimating the growth potential of the soil protozoan community. Protist 151, 69–80.

Foissner, W., 1999. Soil protozoa as bioindicators: pros and cons, methods, diversity, representative examples. Agric. Ecosyst. Environ. 74, 95–112.

Fox, D., 2020. Extreme survivor. Sci. Am. 322 (4), 50–57.

Freckman, D.W., Virginia, R.A., 1989. Plant-feeding nematodes in deep-rooting desert ecosystems. Ecology 70, 1665–1678.

Frelich, L.E., Hale, C.M., Scheu, S., Holdsworth, A.R., Heneghan, L., Bohlen, P.J., et al., 2006. Earthworm invasion into previously earthworm-free temperate and boreal forests. Biol. Invasions 8, 1235–1245.

Gao, Z., Karlsson, I., Geisen, S., Kowalchuk, G., Jousset, A., 2019. Protists: puppet masters of the rhizosphere microbiome. Trends Plant Sci. 24, 165–176.

García-Palacios, P., Maestre, F.T., Kattge, J., Wall, D.H., 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecol. Lett. 16, 1045–1053.

Geisen, S., 2016. The bacterial-fungal energy channel concept challenged by enormous functional versatility of soil protists. Soil Biol. Biochem. 102, 22–25.

Geisen, S., Bonkowski, M., 2018. Methodological advances to study the diversity of soil protists and their functioning in soil food webs. Appl. Soil Ecol. 123, 328–333.

Geisen, S., Bandow, C., Römbke, J., Bonkowski, M., 2014. Soil water availability strongly alters the community composition of soil protists. Pedobiologia 57, 205–213.

Geisen, S., Tveit, A.T., Clark, I.M., Richter, A., Svenning, M.M., Bonkowski, M., et al., 2015. Metatranscriptomic census of active protists in soils. ISME J. 9, 2178–2190.

Geisen, S., Koller, R., Hünninghaus, M., Dumack, K., Urich, T., Bonkowski, M., 2016. The soil food web revisited: diverse and widespread mycophagous soil protists. Soil Biol. Biochem. 94, 10–18.

Geisen, S., Mitchell, E.A.D., Wilkinson, D.M., Adl, S., Bonkowski, M., Brown, M.W., et al., 2017. Soil protistology rebooted: 30 fundamental questions to start with. Soil Biol. Biochem. 111, 94–103.

Geisen, S., Snoek, L.B., ten Hooven, F.C., Duyts, H., Kostenko, O., Bloem, J., et al., 2018a. Integrating quantitative morphological and qualitative molecular methods to analyze soil nematode community responses to plant range expansion. Methods Ecol. Evol. 9, 1366–1378.

Geisen, S., Mitchell, E.A.D., Adl, S., Bonkowski, M., Dunthorn, M., Ekelund, F., et al., 2018b. Soil protists: a fertile frontier in soil biology research. FEMS. Microbiol. Revs. 42, 293–323.

Geisen, S., Vaulot, D., Mahé, F., Lara, E., de Vargas, C., Bass, D., 2019a. A User Guide to Environmental Protistology: Primers, Metabarcoding, Sequencing, and Analyses. bioRxiv, p. 850610.

Geisen, S., Briones, M.J.I., Gan, H., Behan-Pelletier, V.M., Friman, V.P., de Groot, G.A., et al., 2019b. A methodological framework to embrace soil biodiversity. Soil Biol. Biochem. 136, 107536.

Geisen, S., Hu, S., dela Cruz, T.E.E., Veen, G.F., 2020. Protists as catalyzers of microbial litter breakdown and carbon cycling at different temperature regimes. ISME J. 15, 618–621. https://doi.org/10.1038/s41396-020-00792-y.

Gilbert, H.J., 2010. The biochemistry and structural biology of plant cell wall decomposition. Plant. Physiol 153, 444–455.

Griffiths, B.S., Caul, S., 1993. Migration of bacterial-feeding nematodes, but not protozoa, to decomposing grass residues. Biol. Fertil. Soils 15, 201–207.

Griffiths, B.S., de Groot, G.A., Laros, I., Stone, D., Geisen, S., 2018. The need for standardization: exemplified by a description of the diversity, community structure and ecological indices of soil nematodes. Ecol. Indic. 87, 43–46.

Hale, C.M., Frelich, L.E., Reich, P.B., Pastor, J., 2005. Effects of European earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, USA. Ecosystems 8, 911–927.

Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst. 36, 191–218.

Heemsbergen, D., Berg, M.P., Van Hall, J., van Hal, J.R., Faber, J.H., Verhoef, H.A., 2004. Biodiversity effects on soil processes explained by inter-specific functional trait dissimilarity. Science 306, 1019–1020.

Heidemann, K., Scheu, S., Ruess, L., Maraun, M., 2011. Molecular detection of nematode predation and scavenging in oribatid mites: laboratory and field experiments. Soil Biol. Biochem. 43, 2229–2236.

Hendrix, P.F. (Ed.), 1995. Earthworm Ecology and Biogeography in North America. CRC Press, Boca Raton.

Hendrix, P.F., Parmalee, R.W., Crossley Jr., D.A., Coleman, D.C., Odum, E.P., Groffman, P.M., 1986. Detritus food webs in conventional and no-tillage agroecosystems. Bioscience 36, 374–380.

Hölldobler, B., Wilson, E.O., 1990. The Ants. Belknap Press, Cambridge, MA.

Hongoh, Y., Ohkuma, M., Kudo, T., 2003. Molecular analysis of bacterial microbiota in the gut of the termite *Reticulitermes speratus* (Isoptera; Rhinotermitidae). Fems. Microbiol. Ecol. 44, 231–242.

Hooper, D.J., 1970. Extraction of free-living stages from soil. In: Southey, J.F. (Ed.), Laboratory Methods for Work with Plant and Soil Nematodes. Ministry of Agriculture, Fisheries and Food, London, UK, pp. 5–30.

Hünninghaus, M., Dibbern, D., Kramer, S., Koller, R., Pausch, J., Schloter-Hai, B., 2019. Disentangling carbon flow across microbial kingdoms in the rhizosphere of maize. Soil Biol. Biochem. 134, 122–130.

Hunt, H.W., Coleman, D.C., Ingham, E.R., Ingham, R.E., Elliott, E.T., Moore, J.C., et al., 1987. The detrital food web in a shortgrass prairie. Biol. Fertil. Soils 3, 57–68.

Hyvönen, R., Persson, T., 1996. Effects of fungivorous and predatory arthropods on nematodes and tardigrades in microcosms with coniferous forest soil. Biol. Fertil. Soils 21, 121–127.

Iglesias Briones, M.J., Ineson, P., Piearce, T.G., 1997. Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. Appl. Soil Ecol. 6, 117–134.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecol. Monogr. 55, 119–140.

Ito, M.T., Abe, W., 2001. Micro-distribution of soil inhabiting tardigrades (Tardigrada) in a sub-alpine coniferous forest of Japan. Zool. Anz. 240, 403–407.

Jeffery, S., Gardi, C., Jones, A., Montanarella, L., Marmo, L., Miko, L., et al., 2010. European Atlas of Soil Biodiversity. European Commission, Publications Office of the European Union, Luxembourg.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Keeling, P.J., Burki, F., 2019. Progress towards the tree of eukaryotes. Curr. Biol. 29, R808–R817.

Kerfahi, D., Tripathi, B.M., Porazinska, D.L., Park, J., Go, R., Adams, J.M., 2016. Do tropical rain forest soils have greater nematode diversity than High Arctic tundra? A metagenetic comparison of Malaysia and Svalbard. Glob. Ecol. Biogeogr. 25, 716–728.

Knapp, B.A., Seeber, J., Podmirseg, S.M., Rief, A., Meyer, E., Insam, H., 2009. Molecular fingerprinting analysis of the gut microbiota of *Cylindroiulus fulviceps* (Diplopoda). Pedobiologia 52, 325–336.

Koch, A., McBratney, A., Adams, M., Field, D., Hill, R., Crawford, J., et al., 2013. Soil security: solving the global soil crisis. Glob. Policy 4, 434–441.

Kühn, J., Richter, A., Kahl, T., Bauhus, J., Schöning, I., Ruess, L., 2018. Community level lipid profiling of consumers as a tool for soil food web diagnostics. Methods Ecol. Evol. 9, 1265–1275.

Kutikova, L.A., 2003. Bdelloid Rotifers (Rotifera, Bdelloidea) as a component of soil and land biocenoses. Biol. Bull. Russ. Acad. Sci. 30, 271–274.

Lavelle, P., 1983. The structure of earthworm communities. In: Satchell, J.E. (Ed.), Earthworm Ecology: From Darwin to Vermiculture. Chapman & Hall, London, pp. 449–466.

Lavelle, P., Spain, A.V., 2001. Soil Ecology. Kluwer Academic, Dordrecht.

Lavelle, P., Blanchart, E., Martin, A., Spain, A.V., Martin, S., 1992. Impact of soil fauna on the properties of soils in the humid tropics. In: Lal, R., Sanchez, P.A. (Eds.), Myths and Science of Soils of the Tropics. SSSA Special Publications, Madison, WI, pp. 157–185.

Lavelle, P., Lattaud, C., Trigo, D., Barois, I., 1995. Mutualism and biodiversity in soils. Plant Soil 170, 23–33.

Lavelle, P., Pashanasi, B., Charpentier, F., Gilot, C., Rossi, J.P., Derouard, L., et al., 1998. Large-scale effects of earthworms on soil organic matter and nutrient dynamics. In: Edwards, C.A. (Ed.), Earthworm Ecology. St. Lucie Press, Columbus, Ohio, pp. 103–122.

Lee, K.E., 1985. Earthworms: Their Ecology and Relationships with Soils and Land Use. Academic Press, Sydney.

Lee, K.E., Wood, T.G., 1971. Termites and Soils. Academic Press, London.

Lentendu, G., Wubet, T., Chatzinotas, A., Wilhelm, C., Buscot, F., Schlegel, M., 2014. Effects of long-term differential fertilization on eukaryotic microbial communities in an arable soil: a multiple barcoding approach. Mol. Ecol. 23, 3341–3355.

Li, X., Zhu, H., Geisen, S., Bellard, C., Hu, F., Li, H., et al., 2020. Agriculture erases climate constraints on soil nematode communities across large spatial scales. Glob. Change Biol. 26, 919–930.

Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial necromass contribution to soil organic matter. Glob. Change Biol. 25, 3578–3590.

Lloyd, M., Dybas, H.S., 1966. The periodical cicada problem. I. Population ecology. Evolution 20, 133–149.

Mahé, F., de Vargas, C., Bass, D., Czech, L., Stamatakis, A., Lara, E., et al., 2017. Parasites dominate hyperdiverse soil protist communities in Neotropical rainforests. Nat. Ecol. Evol. 1, 0091.

Makkonen, M., Berg, M.P., Handa, I.T., Hättenschwiler, S., van Ruijven, J., van Bodegom, P.M., et al., 2012. Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. Ecol. Lett. 15, 1033–1041.

Meier, F.A., Honegger, R., 2002. Faecal pellets of lichenivorous mites contain viable cells of the lichen-forming ascomycete *Xanthoria parietina* and its green algal photobiont, *Tebouxia arboricola*. Biol. J. Linn. Soc. 76, 259–268.

Moore, J.C., De Ruiter, P.C., 2012. Soil food webs in agricultural ecosystems. In: Cheeke, T., Coleman, D.C., Wall, D.H. (Eds.), Microbial Ecology of Sustainable Agroecosystems. CRC Press, Boca Raton, pp. 63–88.

Moreira, F.M.S., Huising, E.J., Bignell, D.E., 2009. A Handbook of Tropical Soil Biology: Sampling and Characterization of Belowground Biodiversity. Earthscan, London, UK.

Ngugi, D.K., Brune, A., 2012. Nitrate reduction, nitrous oxide formation, and anaerobic ammonia oxidation to nitrite in the gut of soil-feeding termites (*Cubitermes* and *Ophiotermes* spp.). Environ. Microbiol. 14, 860–871.

Nielsen, U.N., 2019. Soil Fauna Assemblages. Cambridge University Press, Cambridge, U.K.

O'Brien, S.L., Jastrow, J.D., 2013. Physical and chemical protection in hierarchical soil aggregates regulates soil carbon and nitrogen recovery in restored perennial grasslands. Soil Biol. Biochem. 61, 1−13.

Oliverio, A.M., Geisen, S., Delgado-Baquerizo, M., Maestre, F.T., Turner, B.L., Fierer, N., 2020. The global-scale distributions of soil protists and their contributions to belowground systems. Sci. Adv. 6, eaax8787.

Parmelee, R.W., Bohlen, P.J., Blair, J.M., 1998. Earthworms and nutrient cycling processes: integrating across the ecological hierarchy. In: Edwards, C.A. (Ed.), Earthworm Ecology. St. Lucie Press, Boca Raton, pp. 123−143.

Payne, J.A., 1965. A summer carrion study of the baby pig, *Sus scrofa* Linnaeus. Ecology 46, 592−602.

Pearce, M.J., 1997. Termites: Biology and Pest Management. CAB International, Wallingford, UK.

Perdomo, G., Evans, A., Maraun, M., Sunnucks, P., Thompson, R., 2012. Mouthpart morphology and trophic position of microarthropods from soils and mosses are strongly correlated. Soil Biol. Biochem. 53, 56−63.

Phillips, H.R.P., Guerra, C.A., Bartz, M.L.C., Briones, M.J.I., Brown, G., Crowther, T.W., et al., 2019. Global distribution of earthworm diversity. Science 366, 480.

Pollierer, M.M., Langel, R., Scheu, S., Maraun, M., 2009. Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios (N-15/N-14 and C-13/C-12). Soil Biol. Biochem. 41, 1221−1226.

Ponge, J.F., 1991. Food resources and diets of soil animals in a small area of Scots pine litter. Geoderma 49, 33−62.

Porazinska, D.L., Giblin-Davis, R.M., Powers, T.O., Thomas, W.K., 2012. Nematode spatial and ecological patterns from tropical and temperate rainforests. PLoS One 7, e44641.

Powers, J.S., Montgomery, R.A., Adair, E.C., Brearley, F.Q., DeWalt, S.J., Castanho, C.T., et al., 2009. Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. J. Ecol. 97, 801−811.

Rillig, M.C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C.A., Buchert, S., Wulf, A., et al., 2020. The role of multiple global change factors in driving soil functions and microbial biodiversity. Science 366, 886−890.

Robeson, M.S., Costello, E.K., Freeman, K.R., Jeremy Whiting, J., Adams, B., Martin, A.P., et al., 2009. Environmental DNA sequencing primers for eutardigrades and bdelloid rotifers. BMC Ecol. 9, 25.

Robeson, M.S., King, A.J., Freeman, K.R., Birky Jr., C.W., Martin, A.P., Schmidt, S.K., 2011. Soil rotifer communities are extremely diverse globally but spatially autocorrelated locally. PNAS USA 108, 4406−4410.

Rusek, J., 1985. Soil microstructures − contributions on specific soil organisms. Quaest. Entomol. 21, 497−514.

Sánchez-Moreno, S., Ferris, H., Guil, N., 2008. Role of tardigrades in the suppressive service of a soil food web. Agric. Ecosyst. Environ. 124, 187−192.

Sapp, M., Ploch, S., Fiore-Donno, A.M., Bonkowski, M., Rose, L.E., 2018. Protists are an integral part of the *Arabidopsis thaliana* microbiome. Environ. Microbiol. 20, 30−43.

Scharf, M.E., 2015. Omic research in termites: an overview and a roadmap. Front. Genet. https://doi.org/10.3389/gene 2015.00076.

Scharroba, A., Dibbern, D., Hunninghaus, M., Kramer, S., Moll, J., Butenschoen, O., et al., 2012. Effects of resource availability and quality on the structure of the micro-food web of an arable soil across depth. Soil Biol. Biochem. 50, 1−11.

Schenk, J., Geisen, S., Kleinboelting, N., Traunspurger, W., 2019. Metabarcoding data allow for reliable biomass estimates in the most abundant animals on earth. MBMG 3, e46704.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., et al., 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468, 553−556.

Scheu, S., Setälä, H., 2002. Multitrophic interactions in decomposer food-webs. In: Tscharntke, B., Hawkins, B.A. (Eds.), Multitrophic Level Interactions. Cambridge University Press, Cambridge, UK, pp. 223−264.

Schill, R.O., Jönsson, K.I., Pfannkuchen, M., Brümmer, F., 2011. Food of tardigrades: a case study to understand food choice, intake and digestion. J. Zoolog. Syst. Evol. Res. 49, 66−70.

Schmelz, R.M., Collado, R., 2010a. A guide to European terrestrial and freshwater species of Enchytraeidae (Oligochaeta). Soil Org 82, 1−176.

Schmelz, R.M., Collado, R., 2010b. Checklist of taxa of Enchytraeidae (Oligochaeta): an update. Soil Org. 87, 149−153.

Schmelz, R.M., Beylich, A., Boros, G., Dózsa-Farkas, K., Graefe, U., Hong, Y., et al., 2017. How to deal with cryptic species in Enchytraeidae, with recommendations on taxonomical descriptions. Opusc. Zoolog. Budapest 48, 45−51.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., et al., 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios (15N/14N). Soil. Biol. Biochem. 36, 1769−1774.

Schulz-Bohm, K., Geisen, S., Wubs, E.R.J., Song, C., de Boer, W., Garbeva, P., et al., 2017. The prey's scent − volatile organic compound mediated interactions between soil bacteria and their protist predators. ISME J. 11, 817−820.

Schwelm, A., Badstober, J., Bulman, S., Desoignies, N., Etemadi, M., Falloon, R.E., et al., 2018. Not in your usual top 10: protists that infect plants and algae. Mol. Plant Pathol. 19, 1029−1044.

Seastedt, T.R., 1984. The role of microarthropods in decomposition and mineralization processes. Annu. Rev. Entomol. 29, 25−46.

Segers, H., 2007. Annotated checklist of the rotifers (Phylum Rotifera), with notes on nomenclature, taxonomy and distribution. Zootaxa 1−104.

Shelley, R.M., 2002. A synopsis of the North American centipedes of the order scolopendromorpha (Chilopoda). V. Museum. Nat. Hist. Mem. 5, 1−108.

Shmakova, L., Bondarenko, N., Smirnov, A., 2016. Viable species of Flamella (Amoebozoa: variosea) isolated from ancient arctic permafrost sediments. Protist 167, 13−30.

Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of the research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics. Soil Tillage Res. 79, 7−31.

Sohlenius, B., 1979. A carbon budget for nematodes, rotifers and tardigrades in a Swedish coniferous forest soil. Holarctic Ecol. 2, 30−40.

Song, D., Pan, K., Tariq, A., Sun, F., Li, Z., Sun, X., et al., 2017. Large-scale patterns of distribution and diversity of terrestrial nematodes. Appl. Soil Ecol. 114, 161−169.

Southwood, T.R.E., 1978. Ecological Methods with Particular Reference to the Study of Insect Populations. Chapman, London.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley.

Thompson, R.M., Brose, U., Dunne, J.A., Hall Jr., R.O., Hladyz, S., Kitching, R.L., et al., 2012. Food webs: reconciling the structure and function of biodiversity. Trends Ecol. Evol. 27, 689−697.

Tomlin, A.D., Shipitalo, M.J., Edwards, W.M., Protz, R., 1995. Earthworms and their influence on soil structure and infiltration. In: Hendrix, P.F. (Ed.), Earthworm Ecology and Biogeography in North America. CRC Press, Boca Raton, pp. 159−183.

Treonis, A.M., Wall, D.H., Virginia, R.A., 1999. Invertebrate biodiversity in Antarctic dry valley soils and sediments. Ecosystems 2, 482−492.

Tsiafouli, M.A., Thebault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., et al., 2015. Intensive agriculture reduces soil biodiversity across Europe. Glob. Change Biol. 21, 973−985.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., et al., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194−198.

van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., et al., 2013. Plant-soil feedbacks: the past, the present and future challenges. J. Ecol. 101, 265−276.

van Vliet, P.C.J., 2000. Enchytraeids. In: Sumner, M. (Ed.), Handbook of Soil Science. CRC Press, Boca Raton, pp. C70−C77.

van Vliet, P.C.J., Hendrix, P.F., 2003. Role of fauna in soil physical processes. In: Abbott, L.K., Murphy, D.V. (Eds.), Soil Biological Fertility − A Key to Sustainable Land Use in Agriculture. Kluwer Academic, Dordrecht, pp. 61−80.

van Vliet, P.C.J., Beare, M.H., Coleman, D.C., 1995. Population dynamics and functional roles of Enchytraeidae (Oligochaeta) in hardwood forest and agricultural systems. Plant Soil 170, 199−207.

Veresoglou, S.D., Halley, J.M., Rillig, M.C., 2015. Extinction risk of soil biota. Nat. Commun. 6, 8862−8872.

Vervoort, M.T.W., Vonk, J.A., Mooijman, P.J.W., Sven, J.J., Van den Elsen, S.J.J., Van Megen, H.H.B., et al., 2012. SSU ribosomal DNA-based monitoring of nematode assemblages reveals distinct seasonal fluctuations within evolutionary heterogeneous feeding guilds. PLoS One 7 (10), e47555.

Wall, D.H., Snelgrove, V.R., Covich, A.P., 2001. Conservation priorities for soil and sediment invertebrates. In: Soule, M.E., Orians, G.H. (Eds.), Conservation Biology: Research Priorities for the Next Decade. Island Press, Washington, DC, pp. 99−123.

Wall, D.H. (Ed.), 2004. Sustaining Biodiversity and Ecosystem Services in Soil and Sediments. SCOPE No 64. Island Press, Washington, DC.

Wall, D.H., Fitter, A., Paul, E., 2005. Developing new perspectives from advances in soil biodiversity research. In: Bardgett, R.D., Usher, M.B., Hopkins, D.W. (Eds.), Biological Diversity and Function in Soils. Cambridge University Press, Cambridge, UK, pp. 3−30.

Wall, D.H., Bradford, M.A., St John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E., et al., 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Glob. Change Biol. 14, 2661−2677.

Wall, D.H., Bardgett, R.D., Behan-Pelletier, V., Herrick, J.E., Jones, H., Ritz, K., et al. (Eds.), 2012. Soil Ecology and Ecosystem Services. Oxford University Press, Oxford, UK.

Wallace, H.R., 1959. The movement of eelworms in water films. Ann. Appl. Biol. 47, 366−370.

Wallace, R.L., 2002. Rotifers: exquisite metazoans. Integr. Comp. Biol. 42, 660−667.

Wallwork, J.A., 1970. Ecology of Soil Animals. McGraw-Hill, London.

Walter, D.E., Kaplan, D.T., Permar, T.A., 1991. Missing links: a review of methods used to estimate trophic links in soil food webs. Agric. Ecosyst. Environ. 34, 399−405.

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press, Princeton.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629−1633.

Wheeler, G.C., Wheeler, J., 1990. Insecta: hymenoptera formicidae. In: Dindal, D.L. (Ed.), Soil Biology Guide. Wiley, New York, pp. 1277−1294.

Whitford, W.G., 2000. Keystone arthropods as webmasters in desert ecosystems. In: Coleman, D.C., Hendrix, P.F. (Eds.), Invertebrates as Webmasters in Ecosystems. CAB International, Wallingford, UK, pp. 25−41.

Whitman, W.B., Coleman, D.C., Wiebe, W.J., 1998. Perspective. Prokaryotes: the unseen majority. Proc. Natl. Acad. Sci. USA 95, 6578−6583.

Wilschut, R.A., Geisen, S., Martens, H., Kostenko, O., de Hollander, M., ten Hooven, F.C., et al., 2019. Latitudinal variation in soil nematode communities under climate warming-related range-expanding and native plants. Glob. Change Biol. 25, 2714−2726.

Wilson, E.O., 1987. Causes of ecological success - the case of the ants - the 6th Tansley lecture. J. Anim. Ecol. 56, 1−9.

Wilson, E.O., 1992. The Diversity of Life. Norton, New York.

Wilson, M.J., Kakouli-Duarte, T., 2009. Nematodes as Environmental Indicators. CABI Press, Wallingford, UK.

Wu, T., Ayres, E., Bardgett, R., Wall, D., Garey, J., 2011. Molecular study of worldwide distribution and diversity of soil animals. Proc. Natl. Acad. Sci. USA 108, 17720−17725.

Wurst, S., van der Putten, W.H., 2007. Root herbivore identity matters in plant-mediated interactions between root and shoot herbivores. Basic Appl. Ecol. 8, 491−499.

Xiong, W., Song, Y., Yang, K., Gu, Y., Wei, Z., Kowalchuk, G.A., et al., 2020. Rhizosphere protists are key determinants of plant health. Microbiome 8, 27.

Yeates, G.W., Coleman, D.C., 1982. Role of nematodes in decomposition. In: Freckman, D.W. (Ed.), Nematodes in Soil Ecosystems. University of Texas Press, Austin, pp. 55−80.

Yeates, G.W., Bongers, T., Degoede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera − an outline for soil ecologists. J. Nematol. 25, 315−331.

Yeates, G.W., Dando, J.L., Shepherd, T.G., 2002. Pressure plate studies to determine how moisture affects access of bacterial-feeding nematodes to food in soil. Eur. J. Soil Sci. 53, 355−365.

Zachariae, G., 1964. Welche bedeutung haben enchytraus in waldboden? In: Jongerius, A. (Ed.), Soil Micromorphology. Elsevier, Amsterdam, pp. 57−68.

Zhao, Z.-B., He, J.-Z., Geisen, S., Han, L.-L., Wang, J.-T., Shen, J.-P., et al., 2019. Protist communities are more sensitive to nitrogen fertilization than other microorganisms in diverse agricultural soils. Microbiome 7, 33.