

# 1 · *Soil and Its Fauna*

Soils provide the foundation of human existence, with most of contemporary food, fuel, and fibre production being soil based, and the delivery of these goods is critical to human prosperity. The realisation that the future of the human population depends on healthy soils is by no means recent, dating back as far as work by Aristotle and later Charles Darwin. Wallwork (1976) formalised it when he wrote that '[i]t is now recognized that an ecological approach, through conservation, is the only way Man can exploit his natural resources without endangering their potential for future generations.' While this critical role of soils to human populations has long been recognised, our understanding of what makes soil function is still developing. Briefly described, it is now widely recognised that soil formation is a time-consuming process that depends on parent material, climate, topography, time, and the biota including soil fauna (Jenny 1941), and that a range of factors, both abiotic and biotic, governs ecosystem functioning (Bardgett 2005). In essence, the plants aboveground capture carbon (C) from the air through photosynthesis, which fuels the ecosystem, using nutrients and water retrieved from the soil to produce organic matter. A large part of the organic matter produced by plants ends up in the soil through plant root production, the release of root exudates or through allocation of C to microbial symbionts, or via deposits of leaf and woody material or animal faecal matter following herbivory. The microorganisms and fauna inhabiting the soil then recycle the plant-derived organic matter. The soil microbes can be considered the true 'engine' of the soils, governing most soil processes and accounting for some 80%–95% of all heterotrophic soil respiration, but direct and indirect interactions with the soil fauna have large implications for soil functioning. Indeed, the presence of certain species of soil fauna can fundamentally modify ecosystem structure and functioning.

The soil fauna, the lead character of this book, thus forms an essential component of the soil food web that is intimately linked to ecosystem functioning through both direct and indirect effects, ultimately

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influencing humans through the delivery of ecosystem services. A robust understanding of the current distribution of soil fauna, its contributions to ecosystem functioning, and responses to global changes is therefore critical to make informed predictions about the future state of our ecosystems and improved land use management. The soil fauna is also interesting to study in and of itself because of the astonishing diversity and abundance found belowground. Indeed, the recognition of this diversity of life found in soils prompted the popular phrase ‘the poor man’s rain-forest’ coined by Usher et al. (1979). It is now well established that our soils are teeming with life, representing a broad array of morphologies and life history strategies (Giller 1996; Figure 1.1), and that this biota is itself a critical component of what we term ‘soil’ (Jenny 1941). Indeed, a conservative estimate is that more than 360,000 species, approximately a quarter of all hitherto described living species, are soil or litter dwellers (Decaëns et al. 2006). This fauna can be broadly divided into ‘full-time’ and ‘part-time’ soil inhabitants, with the latter including many soil-dwelling insect larvae, mound-building insects, and vertebrates (Wolters 2001). However, strictly speaking we can define ‘true’ soil fauna as that which occupies and forages in soils or in the litter layer at least during part of its life cycle. This definition excludes many larger vertebrates that construct tunnels or colonies in soil but forage on vegetation or animals aboveground. This book will focus on the fauna that spends most, if not all, of its life in close association with soils, but the interactions with and impacts of other soil occupants will be discussed where pertinent to the understanding of soil fauna contributions to ecosystem functioning, distribution, or assemblage composition.

The diversity of soil fauna has long captured the attention of soil ecologists (Anderson 1975, Macfadyen 1962), particularly the question of what mechanisms allow so many species to co-exist within the soil matrix and how their activities influence our ecosystems. There are, however, still many unanswered questions relating to the biology, ecology, and biochemistry of soils prompting several prominent researchers to label soils as ‘a biotic frontier’ (André et al. 1994, Hågvar 1998). Our understanding of soil ecology is increasing at a rapid rate, but there is still a great need for new investigators in the field, and there are likely many significant novel insights yet to come. Indeed, the development of novel techniques, more sensitive equipment, and new analytical approaches hold great promise for substantial developments in the field of soil ecology, including a stronger characterisation of soil fauna assemblages and their contributions to ecosystem function. Despite the acknowledgement

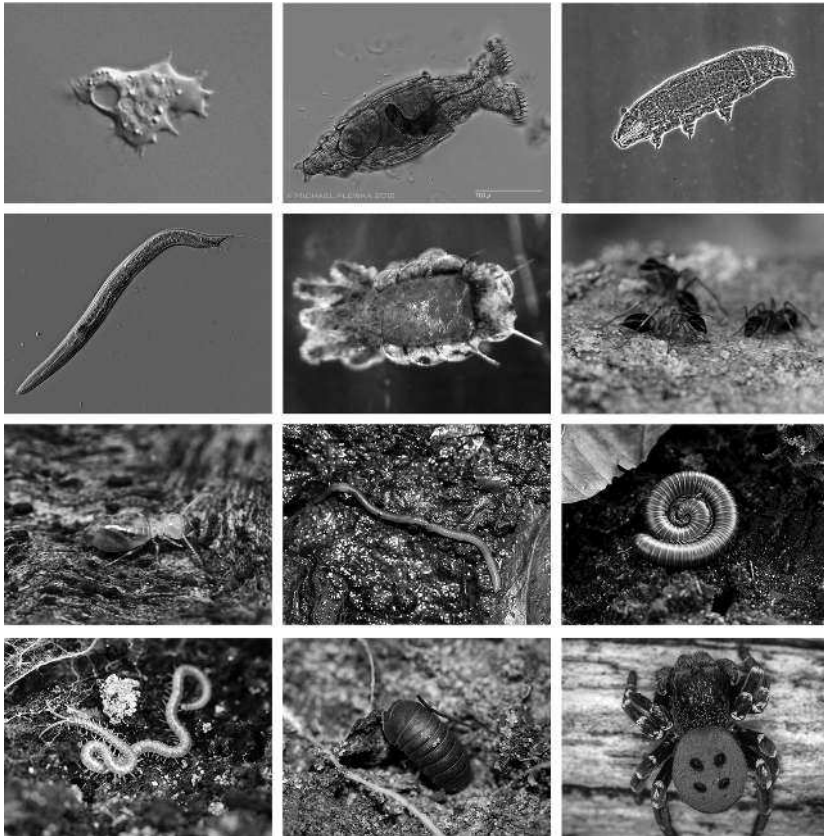


Figure 1.1 Examples of some common soil-associated fauna. Top panel (from left): Protozoa (*Acanthamoeba* sp.; courtesy of Stefan Geisen); the rotifer *Mniobia magna* (Rotifera; courtesy of Michael Plewka, Hattingen, Germany); the Antarctic tardigrade *Mesobiotus polaris* (Tardigrada). Second panel from top (from left): the nematode *Caenorhabditis elegans* (Nematoda; courtesy of Michael Plewka, Hattingen, Germany); oribatid mite (Acari: Oribatida); ant (Hymenoptera: Formicidae). Second panel from bottom (from left): termite (Isoptera); earthworm (Annelida: Megadrilacea); millipede (Myriapoda: Diplopoda). Bottom panel (from left): centipede (Myriapoda: Chilopoda); woodlouse (Isopoda); the spider *Eresus sandaliatus* commonly known as ladybird spider (Aranae; courtesy of Kenneth Tinnesen). Photos by the author unless noted otherwise.

of the astonishing diversity found belowground and its contribution to ecosystem services, there has to date been limited concern about the possible loss of soil biodiversity and the consequences for the future of soils (Veresoglou et al. 2015, Wolters 2001). Soil fauna has also been of more direct value to humans by providing a significant source of protein

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throughout history, and many indigenous peoples still consume a broad variety of soil-dwelling animals including earthworms, insect larvae, and termites (Decaëns et al. 2006). Indeed, Alfred R. Wallace described this phenomenon more than 150 years ago (Wallace 1853). Still, this is rarely taken into account when the value of soil fauna is considered today. I hope this book will pique interest in soil fauna assemblages and their role in ecosystems and encourage the development of stronger frameworks to promote the explicit consideration of soil fauna in conservation and land management more broadly.

With this in mind, the aim of this chapter is to provide an overview of the development of soil fauna ecology as a field of research, describe soils as a habitat for soil fauna, and introduce the main groups of soil fauna. Chapter 2 covers the contributions of this fauna to ecosystem processes. I define soil fauna broadly to include the heterotrophic, unicellular, eukaryotic Protozoa as part of the soil microfauna. The Protozoa are ubiquitous in soils and play a key role in carbon (C) and nutrient cycling but are rarely discussed in conjunction with bacterial, fungal, or Archaeal assemblages. I also include examples of ‘part-time’ soil fauna, i.e. fauna that spends only part of its life cycle in soil, where it is deemed to be particularly relevant to the functioning of the soil and plant communities, or when it influences the distribution of other soil fauna.

### 1.1 A Brief History of Soil Fauna Ecology As a Field of Research

Naturalists have long had a keen interest in the organisms that inhabit soils, both because of the interesting nature of the organisms found in soils and because it has been known for centuries that the functioning of soils itself is underlain by the intricate interactions between the myriad of organisms that live within. For example, although the ability of the earthworm *Lumbricus terrestris* to modify its environment was described in detail by Darwin (1881), even Aristotle understood the contributions of earthworms to organic matter decomposition (Edwards and Lofty 1977). Understandably, the investigations of soil fauna and its role in ecosystems were initially focused on the larger soil fauna because of the difficulties of observing the smaller soil fauna. Indeed, the vast majority of the soil fauna diversity was recognised only after the Dutch businessman and scientist Antoni van Leeuwenhoek modified the microscope to view biological samples in the late 1600s. He went on to describe a range of ‘animalcules’ using this design, including several types of soil microfauna

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that we now know are common in soil, such as protists, rotifers, and tardigrades. Soil fauna ecology as a field of research has progressed rapidly since then, particularly since the beginning of the twentieth century.

Early work by the Danish biologist C. F. Bornebusch on the fauna of forest soil, particularly oak and beech, outlining the differences in relative abundance of key soil fauna groups (Bornebusch 1930) has since been validated by more recent work (Wallwork 1976). Similarly, feeding activity of collembolans was explored in the early twentieth century by Macnamara (1924), providing the first insights into soil food web interactions. While Protozoa were discovered by the users of the early microscopes, the field of soil ‘protistology’ did not begin in earnest until the early twentieth century when a few seminal studies began to unravel the importance of protozoans in soils through work undertaken in Rothamsted, England (Wilkinson et al. 2012). Later work by Weis-Fogh (1948) and Petersen and Luxton (1982) in consolidating contemporary knowledge of soil biota across biomes was hugely important to our understanding of belowground assemblages. The diversity and distribution of soil fauna, and its contributions to ecosystem functioning, have since these publications been the topic of several books, including *The Diversity and Distribution of Soil Fauna* by Wallwork (1976), *The Biology of Soils: A Community and Ecosystem Approach* by Bardgett (2005), and the third edition of *Fundamental of Soil Ecology* by Coleman et al. (2018). These books and others synthesise the literature and have provided great insight into the world belowground and the role of soil fauna in our ecosystems. They therefore helped to frame soil fauna ecology as a field of research and have substantially shaped the approaches we use today. While this book will cover some of the topics presented in these works where they intersect with soil fauna assemblages, I would implore anyone interested in soil ecology to revisit these books for a broader perspective. They also provide an interesting perspective into how our understanding of soil ecology has changed over time beyond the following overview.

This brings us to the conundrum of distribution patterns of soil fauna. As our knowledge of the diversity belowground increases, so does our understanding of the possible ‘true’ distribution of these organisms. At a global scale we recognise and describe broad patterns of species distributions in the field of biogeography, which originated as a field of research in the mid-eighteenth century, building on the early discovery by the French naturalist Georges-Louis Leclerc, Comte de Buffon (1707–88), that groups of organisms differ between geographical regions. Earthworms were similarly noted very early on to have achieved greater

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distribution than what was expected (Beddard 1912, Eisen 1900), indicating that human activities have long been modifying soil fauna assemblages. The origin of the biogeography of microfauna as a field dates back to the mid-nineteenth-century work by Christian Gottfried Ehrenberg, who noted that the ciliate fauna differed between mountain ranges (described in Heger et al. 2011). Biogeography has had a significant impact on ecology through the study of similarities, and dissimilarities, of fauna and flora of different patterns of the Earth. Early on it was recognised that the contemporary distribution of organisms did not reflect the current position of Earth's landmasses, giving rise to the hypothesis that these must have been placed differently in the past. However, this was against the paradigm that Earth's landmasses were fixed in position. A German meteorologist, Alfred Wegener, who recognised the discrepancies between the distribution of flora and fauna and global geography, challenged this idea in 1912. He posed that continents changed position over time through the process of 'continental drift' (see Chapter 4). Hence, biological evidence provided early indications of a heretofore unrecognised process. The acceptance of continental drift as a phenomenon was, however, not fully accepted until much later in the 1960s after geological data provided further supporting evidence given the initial reluctance to consider the idea more carefully. In terms of contemporary distribution patterns of flora and fauna the focus is generally on 'ecological biogeography'. That is, in very broad terms, why are species where they are, what restricts them from colonising other areas, why are there more species in some areas than others, what are the relationship with climate, topography, soil, latitude, etc.? By contrast, 'historical geography' addresses questions related to constraints on species ranges at geological timescales touching on evolutionary and phylogenetic relationships, influence of past geography and climate, and dispersal. For a more in-depth description of the evolution of biogeography as a field I encourage the reader to consult Cox et al. (2016). However, it is essential to recognise ecological and historical biogeography as important drivers of the patterns we observed today.

It is now evident that soil fauna assemblages are highly variable through both time and space. The next logical question is then, how does belowground variability in assemblage structure and composition influence ecosystem functioning? The progress in understanding the contribution of soil fauna to ecosystem functioning has largely been spurred by critical developments in the field, causing leaps in knowledge at particular times. As described in Huhta (2007) limited effort was



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made to quantify the role of soil fauna to ecosystem functioning until the era of litter bag studies began in the late 1950s. The litter bags were used to manipulate the soil fauna assemblages by limiting the access of organisms above certain sizes, for example, excluding macrofauna using mesh sizes of 2 mm diameter, or macrofauna and mesofauna by using smaller mesh sizes sometimes in combination with various biocides to exclude specific taxa, or conversely by containing soil fauna within the bags themselves (e.g. enchytraeids, Standen 1978). The contribution of the excluded (or contained) fauna particularly to litter decomposition could then be quantified by comparing the treatments with and without the fauna. The method has been criticised due to certain shortcomings, such as not accounting for litter mass loss due to fragmentation, changes in the microclimate, and unrealistic removal of soil fauna (see the discussion in Kampichler and Bruckner 2009; Chapter 2), but has provided significant insights into the contribution of soil fauna to ecosystem processes particularly in the early applications and is still a popular and useful approach to address certain questions. Early reviews of the method thus concluded that soil meso- and macrofauna contribute significantly to litter decomposition processes but had mixed effects on mineralisation processes (Edwards et al. 1970, Seastedt 1984).

Another period of significant progress in soil fauna ecology occurred during the International Biological Program from the late 1960s to the mid-1970s that had the main aim of quantifying patterns of metabolism, energy flow, and productivity among biomes (Huhta 2007). It provided new insight into soil food webs, with one of the main findings that the soil fauna decomposer assemblages generally had somewhat lower than expected impacts, usually less than 10% of all material assimilated (Petersen and Luxton 1982), on energy flows. However, these estimates largely exclude the contribution of protozoans due to technical constraints, and several studies provided evidence that the contribution of this group could be substantial, possibly exceeding that of all other soil fauna combined (Macfadyen 1963, Persson et al. 1980). Soil microcosm approaches have similarly provided substantial insights into ecosystem functioning but were not adopted to address questions related to soil fauna contributions until the early 1960s (Patten and Witkamp 1967). Since then, however, many key findings have been based on micro- or mesocosm approaches, with a particularly large interest in such studies in the 1980s and 1990s (Huhta 2007). These systems have allowed researchers to manipulate the soil food web to investigate effects on C and nutrient cycling, plant growth, and ecosystem function more broadly, and

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have provided substantial insight into the diversity–functioning relationship belowground. Most of the early studies found limited effects of species richness *per se*, with the main effects being driven by functional traits or by keystone species (Filser 2003, Huhta et al. 1998, Laakso and Setälä 1999b). Later reviews have supported these initial findings but suggest that there is a bit more to it and that the loss of soil biodiversity including fauna can substantially impact ecosystem functioning, particularly when the impacts on multiple functions are considered over temporal and spatial scales (de Graaff et al. 2015, Nielsen et al. 2011a).

Similarly, in the 1960s soil sterilisation using  $\gamma$ -irradiation was applied as a novel tool to address soil ecological questions, both in the field and in the laboratory, with David C. Coleman and colleagues largely pioneering this work. For example, they sterilised soil cores collected in the field, subsequently inoculating these with individual fungal strains, and then placed them at field sites and followed the colonisation of soil fauna, rationalising that mite and springtail species that colonised soil cores with individual fungi showed a preference for these (Coleman and Macfadyen 1966). They also used  $\gamma$ -emitting  $^{65}\text{Zinc}$  radioisotopes to label soil fungi in the field and subsequently tracked the radioactive compounds as they moved through the soil food web to delineate soil fungal food webs (Coleman and McGinnis 1970). Since these early experiments, the use of stable isotope approaches, including stable isotope labelling, particularly using  $^{13}\text{C}$ ,  $^{15}\text{N}$ , and, more recently,  $^{18}\text{O}$ , have become more common and have provided substantial insight into the structure of soil food webs and potential food sources of soil fauna (see Chapters 2 and 3).

The latest substantial leap forward relating to the ecology and biogeography of soil fauna relied on the development of molecular sequencing approaches. These approaches were initially used in soils to investigate microbial assemblage composition but were soon adapted to the larger eukaryotic soil fauna as well (see Chapter 3 for a broader discussion of the application of molecular approaches to investigate soil fauna assemblages). The main advantages of sequencing approaches lie in their ability to provide higher resolution than morphological characteristics, thus allowing us to gain further insight into phylogenetic relationships, better distinguish closely related taxa, or provide insight into cryptic species complexes; with some limitations more recent high-throughput sequencing approaches can even provide whole assemblage fingerprints. However, getting relative abundance data from sequencing approaches remains a significant obstacle for multicellular taxa, which generally restricts us to using presence/absence data only or matching more



focused sequencing approaches with abundance data gathered through quantitative polymerase chain reaction (PCR) assays, or by more ‘old school’ morphological counting. Moreover, we are yet to define robust species delineation protocols for soil fauna based on molecular tools. This is not a problem where reference sequences are known, but the existing databases are far behind.

## 1.2 Soil As a Habitat

To understand the complexity and diversity of soil fauna assemblages and how they are distributed through space and time it is necessary to consider the constraints imposed on soil fauna by soil as a habitat. Soil is a highly complex, three-dimensionally heterogeneous habitat consisting of mineral particles, air- and water-filled pores, as well as decomposing and living organic matter, including the soil biota itself. The mineral component can be characterised based on the relative size distribution of particles (Figure 1.2), with the particle size increasing from clay (0.000–0.002 mm) to silt (0.002–0.02 mm) to fine sand (0.02–0.2 mm) and coarse sand (0.2–2 mm), and the chemical characteristics of the mineral components. Soil texture exerts a significant control on soil structure and associated traits, such as water infiltration and water holding capacity. The chemical characteristics of the mineral component depend strongly on parent material, but also on geophysical and biological processes, and soil type and origin therefore moderate the availability of nutrients essential to plants and soil organisms. Soil structure is also greatly influenced by organic input of plant and animal origin. Indeed, the distribution of decomposing organic material and plant roots strongly influences the distribution and activity of soil biota, including the fauna, within the soil horizon but also contributes to distribution of soil fauna at larger scales (Beare et al. 1995). The authors recognised five ‘arenas’ of particular high biological activity in soils: the porosphere, the drilosphere, the rhizosphere, the detritosphere, and the aggregatosphere, while Lavelle and Spain (2001) identify another area of activity – the termitosphere.

The porosphere (*sensu* Vannier 1987) represents the system of pores of varying sizes, constructed through both physical and biological activity that is occupied by the soil biota. Larger types of soil fauna such as earthworms and some species of enchytraeids (Didden 1993, Hamilton and Dindal 1983) can physically engineer the soil structure, but most soil biota are dependent on pre-existing pores as their habitat. The drilosphere (*sensu* Hamilton and Dindal 1983) refers to the activity of

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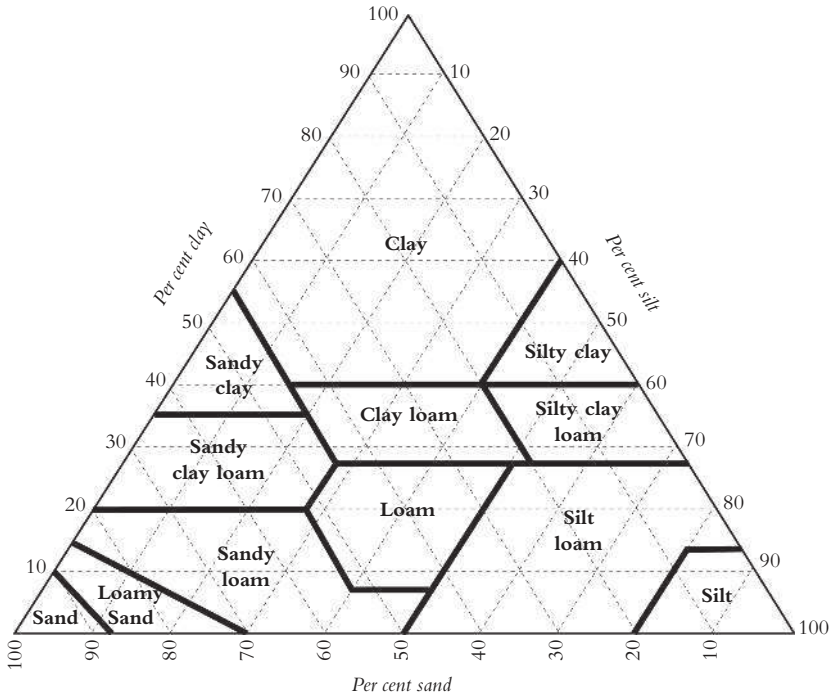


Figure 1.2 Soil texture is classified based on particle size distribution, specifically clay (0.000–0.002 mm), silt (0.002–0.02 mm) and fine sand (0.02–0.2 mm), and coarse sand (0.2–2 mm).

Modified from USDA (1951).

earthworms, both the formation of mounds and vertical distribution of fragmented litter, which leads to the formation of hotspots of organic materials (Maraun et al. 1999). During growth, several forms of organic compounds, such as sugars and amino acids, are ‘leaked’ from plant roots, which stimulate microbial activity (Feldman 1988). The rhizosphere, a term coined by Hiltner (1904), refers to the zone around the root where microbial and faunal activity is stimulated by plant influences, including exudates that comprise a significant proportion of plant photosynthetically derived C (Lavelle and Spain 2001). The zone of recognisable litter from plants composes the detritosphere, which is also sometimes referred to as the litter system. Both the quantity and quality of the litter can influence the biological assemblages that occur in the litter layer (Beare et al. 1995). Finally, the term aggregatosphere refers to the aggregations of particles in soils formed through physical, chemical, and biological processes (Lee and Foster 1991). Lavelle and Spain (2001)