SOIL BIOTA, SOIL SYSTEMS, AND PROCESSES

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GLOSSARY

domains The major divisions of the biota on earth, namely: Bacteria, Archaea, and the Eucarya.

ecosystem engineers The concept whereby members of the macrofauna (e.g., termites and earthworms) are actually moving parts of the soil volume for their own uses (e.g., making macropores, which permit flow of large amounts of water rapidly through the soil).

immobilization The process wherein nutrients are taken up or immobilized in litter and other organic detritus until later (usually weeks to months) in the decomposition process.

microfauna Animals that have high turnover rates, and live in water films in soils. Small mesofauna, such as nematodes, are also water-film dwellers.

larger Mesofauna and macrofauna live in pores in portions of soil profiles.

mineralization The availability of inorganic nutrients in the decomposition of organic detritus, occurring after the immobilization phase; see above.

organizing centers Soils are centers of history and activity in terrestrial ecosystems. See the legacy concept in forest ecology.

SOIL BIODIVERSITY is an intriguing, largely unappreciated facet of global biodiversity. There are many phyla, even "domains," within soils, which are largely unseen, making use of the uniquely diverse physicochemical complexity of soils, which is an intersection of mineral, organic, aquatic, and aerial habitats. Organisms have evolved in soils literally since pre-Cambrian times (more than 600 million years ago). They are still largely undescribed, and this is particularly true for the prokaryotes, which have awaited the development of new techniques to characterize them. By linking several organismal groups to major processes in global biogeochemistry, it is proving possible to appreciate the wide array and diverse nature of soil organism functions in the biosphere.

I. SOILS AS COMPONENTS OF ECOSYSTEMS

A. Soil-Forming Factors

Soils are an intriguing, relatively thin (often <1 m. depth) zone of physical-chemical and biological weathering of the earth's land surface. Soils are formed by

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an array of factors, namely climate, organisms, parent material, the extent of slope, and aspect (relief) operating over time (Fig. 1). These factors affect major ecosystem processes, such as primary production, decomposition, and nutrient cycling, which lead to the development of ecosystem properties unique to that soil type, as a result of its previous history. For example, a deep loess soil in Iowa, with a very fertile and deep surface or "A" horizon, containing considerable amounts of organic matter, will be very different from an "A" horizon developed in the Nebraska sandhills, with much greater porosity and lower water retention due to the nature of the sandy surface material. As noted in the soil-forming factors diagram (Fig. 1), the array of biota—namely microbiota, vegetation, and consumers (herbivores, carnivores, detritivores)—is influenced by soil processes and in turn has an impact on the soil system.

B. Poly-Phasic Nature of Soils, Influence on the Biota

Soils are perhaps the ultimate in interface media, located at the intersection of four principal entities: the atmo-

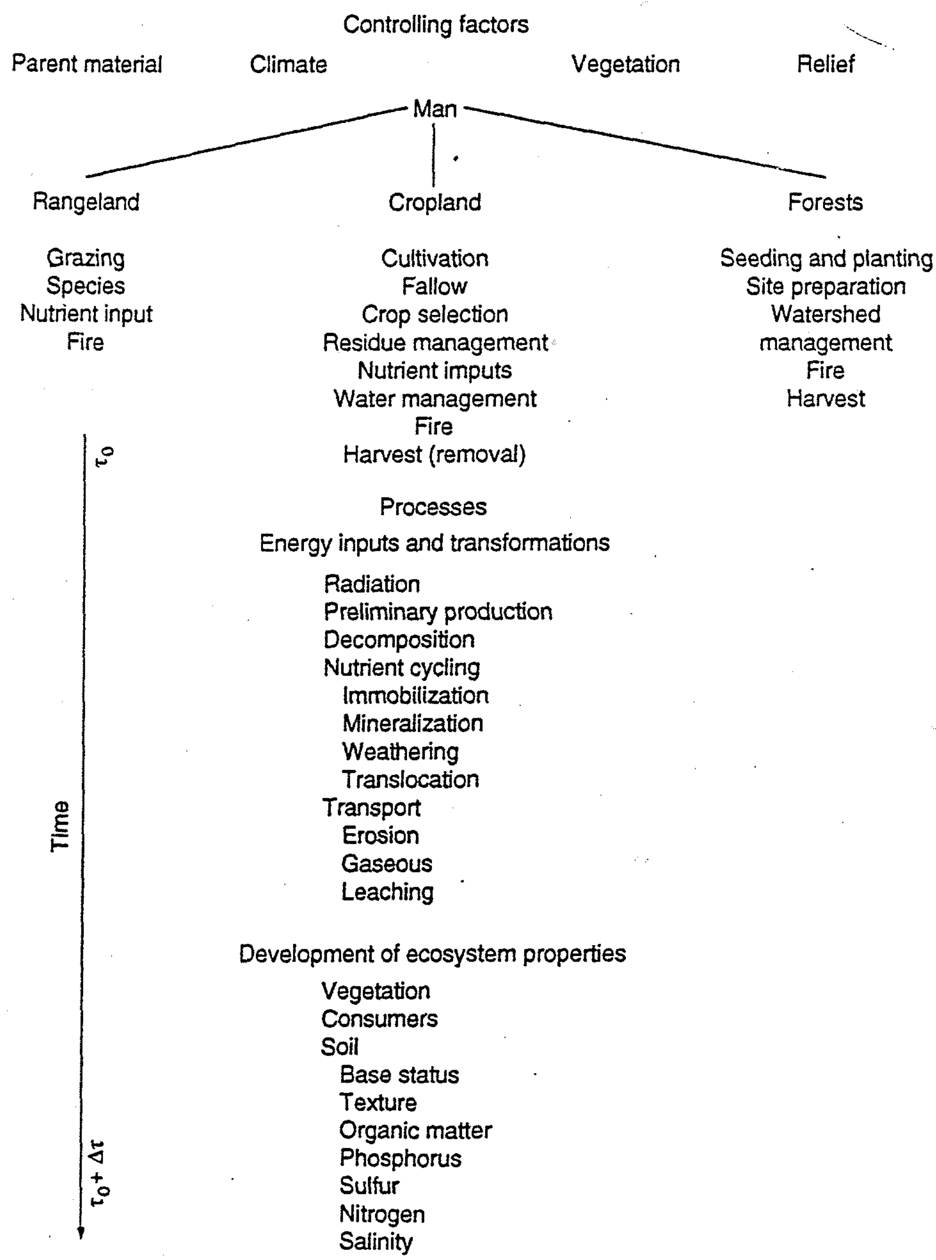

FIGURE 1 Soil-forming factors and processes, and the interaction over time. From Coleman *et al.* (1983) and Coleman and Crossley (1996).

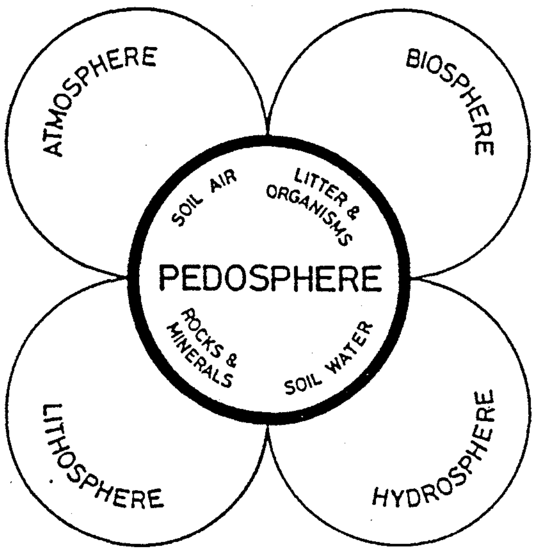

FIGURE 2 The pedosphere showing interactions of abiotic and biotic entities in the soil matrix. From Fitzpatrick (1984) and Coleman and Crossley (1996).

sphere, biosphere, lithosphere, and pedosphere (Fig. 2). Soils provide a wide range and variety of microhabitats, thus accommodating a very diverse biota. The microbes (bacteria and fungi) are found in numerous microsites, well–aerated or not; bacteria may thus respire either aerobically or anaerobically. There is an enormous amount of surface area (hundreds of m^2 per gram of soil) on the soil particles, which range in size classes from clays (0.1–2 μm in diameter), to silts (2–50 μm in diameter), and sands (0.05–2 mm diameter). Numerous microbes and micro- and meso-fauna (protozoa and nematodes) exist in water films on these particles and in or on the surfaces of microaggregates formed from the primary particles. In turn, the more mobile fauna, from collembola and mites (larger meso-fauna) to the macrofauna (earthworms, millipedes, ants, termites, and fossorial or earth-dwelling vertebrates), move through macro- and micro-pores in the soil. The macrofauna play a role in moving parts of the soil profile around and form many sorts of burrows and pores; they are often termed "ecological engineers."

II. SOILS AS ORGANIZING CENTERS IN ECOSYSTEMS

Soils may be viewed as the organizing centers for terrestrial ecosystems. Major functions such as ecosystem production, respiration, and nutrient recycling are controlled by the rates at which nutrients are released by decomposition in the soil and litter horizons and transported to the photosynthetic layers of the ecosystem. This is particularly true for less heavily managed, near-natural ecosystems, many of which occur on soils of relatively poor nutrient status. In these systems, mycorrhizas are often obligate partners in the obtaining of adequate nutrients for the growing plants. Mycorrhizas are known to be efficient at extracting nutrients from both mineral and organic sources, enabling plants to thrive in habitats that are considered poor in nutrients. We need to be aware of these and other mutualistic associations between microorganisms and roots, such as rhizobia and actinorrhizas, various root-associated symbiotic bacteria that facilitate the nitrogen fixation process on which the entire ecosystem often depends. These associations have arisen in soils over evolutionary time and are key to an understanding of ecosystem function.

III. MAJOR SOIL PROCESSES

A. Decomposition: Immobilization and Mineralization

A very large proportion (greater than 90%) of the terrestrial net primary production is returned to the soil as dead organic litter. This litter, consisting of leaves, roots, and wood from trees and organic residues from agricultural fields, is decomposed on or in the soil, and the nutrients contained within it recycled for further use. The decomposition process drives complex food webs in the soil, with numerous interactions between the initial agents of decomposition, the bacteria and fungi, and the fauna which in turn feed on them.

Decomposition is the catabolism of organic compounds in plant litter and other organic detritus. Decomposition is principally the result of microbial activities; few soil animals have cellulases in their guts, which allows them to hydrolyze the celluloses in plant residues. The decomposition of organic residues involves the activities of a variety of soil biota, including both microbes and fauna, which interact conjointly in the process. For example, the initial breaking up of plant litter usually is conducted by the chewing and macerating action of both large and small animals. This initial breaking into smaller pieces, or "comminution," is a process that benefits the fauna, which derive nutritional benefit from the litter or microbes initially colonizing the plant material. The increased surface area and further inoculation of the smaller pieces enhances the microbial access to, and breakdown of, these tissues.

B. Nitrogen Cycle: Major Processes

Nitrogen enters the ecosystem via nitrogen fixation, in which the dinitrogen molecule (N_2) is separated into two nitrogen atoms, with considerable expenditure of energy and the assistance of the nitrogenase enzyme, to break the triple covalent bond. The atoms are ammonified and then used in the production of amino acids and proteins in the plant. Another avenue for nitrogen entry into soils is by lightning fixation, in which the extensive high-voltage energy in the lightning charge ruptures the dinitrogen molecule, hydrogens are attached, and then the ammonium is brought in by rainfall. As shown in Fig. 3, nitrogen is lost from the system via harvest and erosion of organic forms of N, it can be ammonified in decomposition, and then undergoes nitrification to nitrate (NO^{3-}), whereupon it can be taken up by biota, either plant roots or into microbial tissues. If there is adequate energy and low amounts of oxygen present, there can be denitrification, in which the nitrogen is lost as either nitrogen gas (N_2) or N_2O, nitrous oxide. For further details, consult textbooks on ecology or ecosystem studies.

The nitrogen cycle is of critical importance to biodiversity considerations, because key points in the cycle are dependent on relatively species-poor assemblages of microbes, including the nitrogen fixation and nitrification steps. There are only a few species of nitrogen fixing rhizobia, in the genera *Rhizobium* and *Bradyrhizobium*. The other principal nitrogen-fixing symbiont, the bacterium *Frankia* (Actinomycetaceae) forming the actinorrhiza (literally actinomycete-root), contains only a few species in the genus. However, approximately 194 plant species in eight families and four different subclasses of flowering plants have been identified as hosts. These plants share the general tendency to grow in marginal soils and play an important role as pioneer species in early successional habitats.

In the nitrification steps, noted earlier, there are only a few genera and species of nitrifiers. Most of them are autotrophic and quite sensitive to changes in soil pH. This means that these organisms may be unusually prone to being diminished or eliminated in regions where there is considerable acid rain.

IV. BIODIVERSITY IN SOILS

A. Evolutionary History

Soils, as we know them, with well-differentiated profiles, probably developed concurrently with the origin of a land flora in the early Devonian era, about 425 million years ago. The microorganisms that inhabit the soils, particularly the prokaryotic microbes such as the cyanobacteria, originated perhaps 3 billion years ago.

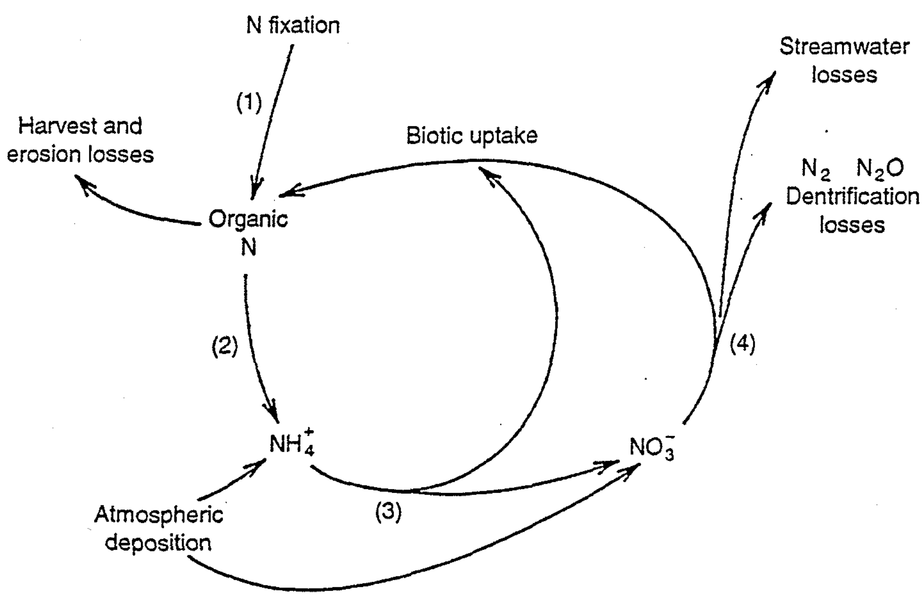

FIGURE 3 Inputs and outputs of N, which make up the intersystem transfers in an ecosystem. Numbers indicate groups of organisms active at a given stage of the *N* cycle. (1) Rhizobia, *Frankia*, (2) ammonifiers, (3) nitrifying bacteria, and (4) denitrifying bacteria. Denitrifying bacteria must compete with biotic uptake of NO_3 by other microbes and plants; thus the rate of nitrification sets an upper limit on denitrification losses. Streamwater losses represent the excess of available N over that taken up by biotic processes. Modified from Waring and Schlesinger (1985).

B. Diversity of Biota

Biodiversity is an inclusive concept, including a wide range of functional attributes in ecosystems in addition to being concerned with numbers of species present in the system. This differentiates it from the concept of species diversity, which is concerned with the identity and distribution of species in a given habitat or region.

Soil biodiversity is best considered by focusing on the groups of soil organisms that play key roles in ecosystem functioning. Spheres of influence (SOI) of soil biota are recognized, such as the root biota, the shredders of organic matter, and the soil bioturbators. These organisms influence or control ecosystem processes and have further influence via their interactions with key soil biota (e.g., plants). What is the extent of redundancy within functional groups within these SOI? Some soil organisms, such as the fungus and litter-consuming microarthropods, are very speciose. For example, there are up to 170 species in one Order of mites, Oribatida (members of the Arachnida, eight-legged arthropods), in the forest floor of one watershed in western North Carolina. The soil biota considered at present to be most at risk are some of the species-poor functional groups, such as specialized bacteria, that is, nitrifiers and nitrogen fixers (see diagram). Others include fungi forming mycorrhiza (literally fungus-root), a symbiotic association that benefits both plant and fungus, with the plant supplying high-quality carbon to the fungus, and the fungal hyphae exploring a greater volume of the soil, obtaining scarce mineral nutrients, particularly phosphorus. Other species-poor functional groups include macrofaunal shredders of organic matter (e.g., millipedes) and bioturbators of soils, which includes various types of earthworms and termites.

C. Three Great "Domains" of Organisms on Earth

All of life exists in three great "urkingdoms," or domains. These domains are (a) the *Bacteria* (eubacteria), which are the bacteria as generally considered; (b) *Archaea* (archaebacteria), which include the methanogens (methane-producers), most extreme halophiles (ones living in hypersaline environments), and hyperthermophiles (ones living in volcanic hot springs, and in mid-sea ocean hot-water vents); and (c) *Eucarya* (eukaryotes) (Fig. 4). The first two domains are prokaryotes, which are unicellular organisms, lacking a unit membrane-bound nucleus and other organelles, usually having their DNA in a single circular molecule. Eukaryotes, in comparison, consist of all of the organisms that have a unit membrane-bound nucleus and other organelles, such as mitochondria. Eukaryotic organisms are often multicellular. This scheme is based on an increasing body of evidence from ribosomal RNA (rRNA) phylogenies, that the archaebacteria are worthy of the same taxonomic status as eukaryotes and bacteria. As shown in Fig. 4, the universal rRNA tree develops from a postulated "cenancestor," leading to the relative positions of the three great domains.

1. Number of Species of Prokaryotes

Recent estimates of the number of prokaryotic species range from 100,000 to 10 million. Interestingly, the number of described species of bacteria in soil amount only to about 4000. This discrepancy is due largely to the fact that only a small proportion, usually less than 1%, of the bacteria present in soil or any other medium are amenable to culturing and subsequent microscopic observation.

It should be noted that, on the basis of the accepted criterion for separating taxa in microbial studies, which is a greater than 70% DNA homology, a mouse and a human would be considered as being in the same species. This leads to complications, as we shall see, in discussing the total amount of genetic diversity of all organisms, including the as-yet largely unknown diversity of Archaea and Eubacteria. The latter now are estimated to have an array of 36 kingdoms, which are genetically as diverse as the Kingdoms Animalia, Plantae, and Fungi in older classification systems.

2. Biomass and Numbers of Bacterial Species on Earth

This figure is vastly underestimated. We are just now delineating the overall genetic makeup of isolates taken from soils, which are determined by the use of molecular probes. The total numbers of bacteria on earth in all habitats is truly staggering: $4–6 \times 10^{30}$ cells, or 350 to 550 petagrams of Carbon. One petagram is 10^{15} g, or one billion metric tonnes. The amount of the total that is calculated to exist in soils is approximately 2.6×10^{29} cells, or about 5% of the total on earth. A majority of bacteria exist in oceanic and terrestrial subsurfaces, especially in the deep mantle regions, extending several kilometers below the earth's surface.

3. Viruses as Quasi-Organisms

Viruses are quasi-organisms, not included in the three domains. Viruses are RNA or DNA molecules contained within protein envelopes. Viral particles are metabolically inert, carrying out neither biosynthetic nor respiratory functions. They multiply only within host cells, by inducing a living host cell to produce the necessary

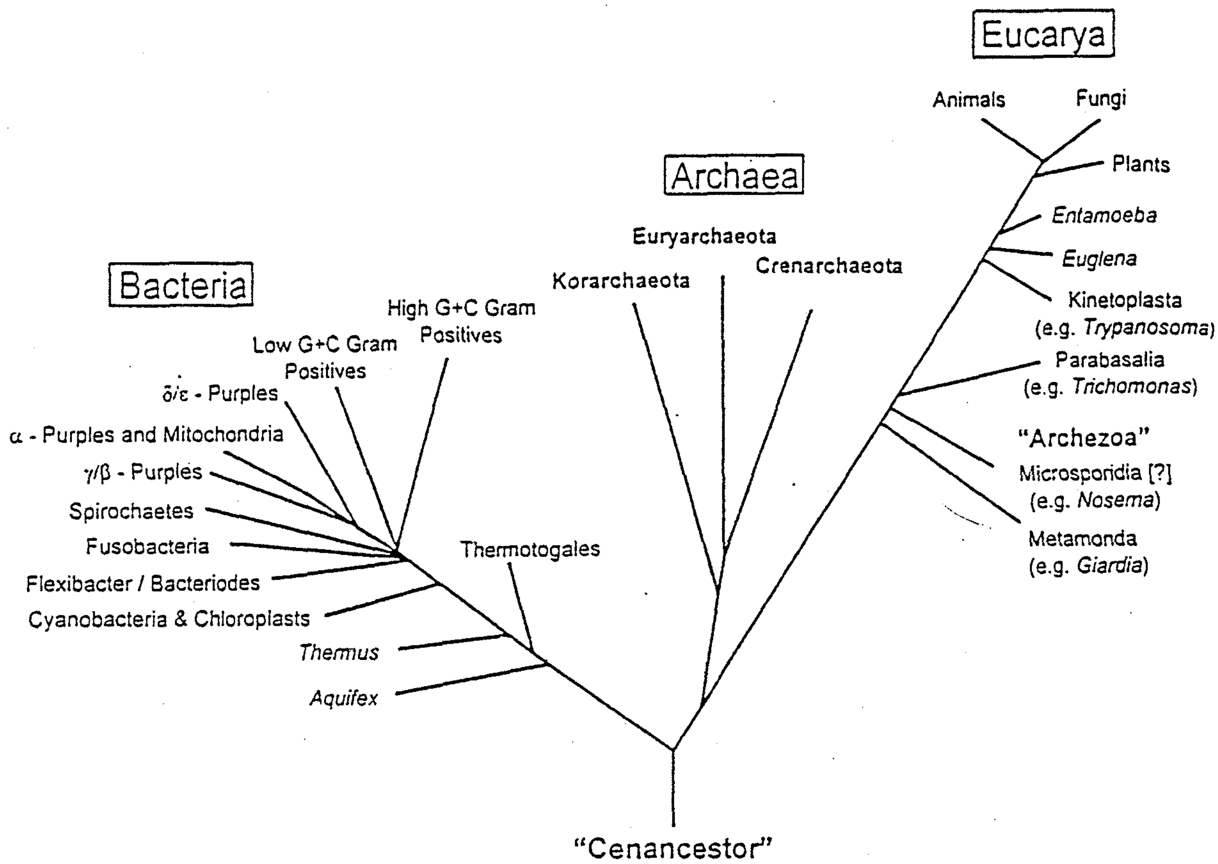

FIGURE 4 Schematic drawing of a universal rRNA tree showing the relative positions of evolutionary pivotal groups in the domains *Bacteria, Archaea,* and *Eucarya.* The location of the root (the cenancestor) corresponds to that proposed by reciprocally rooted gene phylogenies. The question mark beside the Archezoa group Microsporidia denotes recent suggestions that it might branch higher in the eukaryotic portion of the tree. (Branch lengths have no meaning in this tree.) From Brown and Doolittle (1997).

viral components. Once assembled, the replicated viruses escape from the cells. Viruses infect all sorts of animals, plants, and microbes. Viruses parasitizing bacterial cells are commonly called bacteriophages, or simply phages. Although little is known about the ecology of viruses, they can persist in soils for many years and decades. Some research on viruses in deserts showed that they were inactivated in soils at acid pH levels between 4.5 and 6. There is little information on the overall species diversity of viruses in soils. Current estimates are 5000 species known and perhaps 130,000 in existence.

4. Numbers and Biodiversity of Eukaryotes

a. Fungal Diversity

Fungi are multicellular eukaryotes that are found in many habitats worldwide. They have long, ramifying strands (hyphae), which can grow into and explore many microhabitats, and are used for obtaining water and nutrients. The hyphae secrete a considerable array of enzymes, such as cellulases, and even lignases in some specialized forms, decomposing substrates *in situ,* imbibing the decomposed subunits and translocating them back through the hyphal network. Fungi are very abundant, particularly in undisturbed forest floors in which literally thousands of kilometers of hyphal filaments will occur per gram of leaf litter.

Fungi are still little-described, with possibly less than 5% of them known to Science (69,000 described; perhaps 1,500,000 in existence (Table I)). This is largely because of the fact that so many fungi are associated with tropical plants and animals, and these in turn have not been described.

As noted earlier, the roles of mycorrhizas in soil systems are being increasingly viewed as central to much of terrestrial ecosystem function. The total number of mycorrhizal species may be just 1000 or 2000, but they are essential to the growth and reproduction of numerous families of plants. Recent experimental studies have noted that species richness, namely with large versus small numbers of species of Arbuscular

TABLE I

Comparison of the Numbers of Known and Estimated Total Species Globally of Selected Groups or Organisms

Group	Known species	Estimated total species	Percentage known
Vascular plants	220,000	270,000	81
Bryophytes	17,000	25,000	68
Algae	40,000	60,000	67
Fungi	69,000	1,500,000	5
Bacteria	3,000	30,000	10
Viruses	5,000	130,000	4

Source: Hawksworth (1991).

mycorrhiza, has a positive impact on plant primary production in macrocosms of North American old fields (fields undergoing succession and not intensively managed).

b. Microfauna

The unicellular eukaryotes, or Protoctista, include a wide range of organisms, which are more often called protozoans. These include the flagellates, naked amoebae, testacea, and ciliates (Fig. 5). These organisms range in size from a few cubic micrometers in volume to larger ciliates, which may be up to 500 micrometers in length and 20 to 30 micrometers in width. Protozoa are quite numerous, reaching densities of from 100,000 to 200,000 per gram of soil. Bacteria, their principal prey, often exist in numbers up to 1 billion per gram of soil. All of these organisms are true water-film dwellers and become dormant or inactive during episodes of drying in the soil. They can exist in inactive or resting stages for literally decades at a time in very exeric environments.

About 40,000 extant protozoan species have been described, but many more undoubtedly are awaiting scientific discovery. Foissner (1997) notes that about 360 protozoan species per year are being discovered. In an extensive survey of soils from Africa, Australia, and Antarctica, in some cases nearly half of the total species described were new to science. This was particularly true in Africa, where of 507 species identified, 240 of them, or 47%, were previously undescribed. Even in a more extensively investigated region, Australia, 43% of the total of 361 species were new to science. In Antarctica, 95 species were described, with only 14, or 15%, being unknown.

Because many habitats have been uninvestigated yet, and the isolation procedures are still imperfect, from 70 to 80% of all soil ciliates may yet be unknown. This high proportion may hold true for the other protozoan groups as well.

c. Mesofauna

i. Nematodes Nematodes feed on a wide range of foods. A general trophic grouping is bacterial feeders, fungal feeders, plant feeders, and predators and omnivores. Anterior (stomal or mouth) structures can be used to differentiate general feeding or trophic groups. The feeding categories are a good introduction, but feeding habits of many genera are complex or poorly known. For example, some genera in immature phases will feed on bacteria and then become predators on other fauna once they have matured. Because of the wide range of feeding types and the fact that nematodes seem to reflect ages of the systems in which they occur (e.g., annual versus perennial crops, or old fields and pastures and more mature forests), they have been used as indicators of overall ecosystem condition. This is a growing area of research in soil ecology, and one in which the intersection of community analysis and ecosystem function could prove very fruitful. Current species described total some 5000, and upward of 20,000 may exist.

ii. Collembola Collembolans, or "springtails," are primitive Apterygote (wingless) insects. They are called "springtails" because many of them have a spring-like lever, or furcula, which enables them to move many body lengths away from predators by use of it, in a springing fashion. Collembolans are ubiquitous members of the soil fauna, often reaching abundances on 100,000 or more per square meter. They occur throughout the soil profile, where their major diet is decaying vegetation and associated microbes (usually fungi). However, like many members of the soil fauna, collembolans defy placement in exact trophic groups. Many collembolan species will eat nematodes when those are abundant. Some feed on live plants or their roots. One family (Onychiuridae) may feed in the rhizosphere and ingest mycorrhizae or even plant pathogenic fungi.

Eight families of collembolans occur in soils. Many collembolans are opportunistic species, capable of rapid population growth under suitable conditions. Eggs are laid in groups. Collembolans become sexually mature with the fifth or sixth instar, but they continue to molt throughout life. Although many species are bisexual, some of the common species are parthenogenic, consisting of females only. Collembolan "blooms" are a phenomenon of late winter or early spring, when some species may appear in large numbers on the surface of snow banks, on the surface ice of pond water, or on

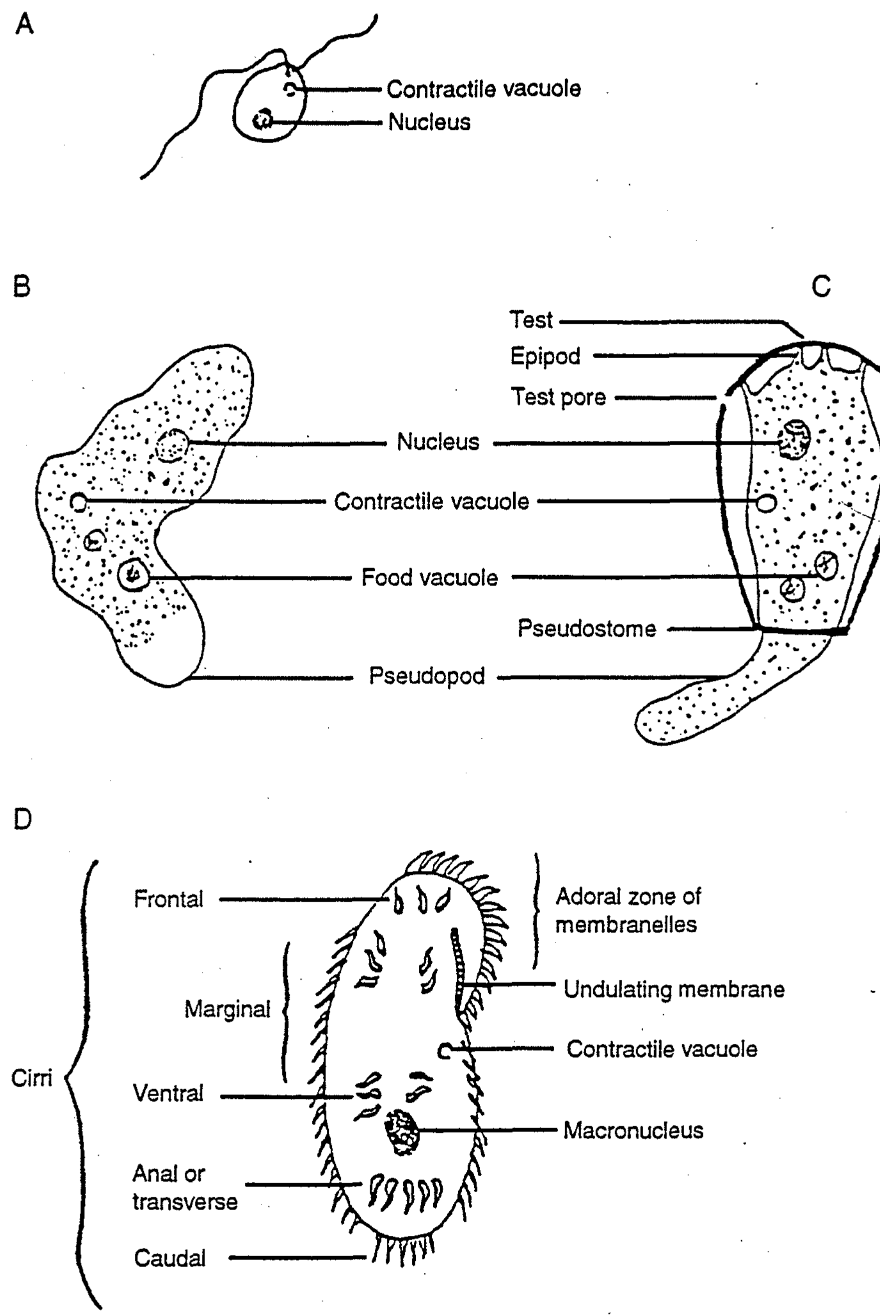

FIGURE 5 Morphology of four types of soil Protozoa: (a) flagellate (*Bodo*), (b) naked amoeba (*Naegleria*), (c) testacean (*Hyalosphenia*), and (d) ciliate (*Oxytricha*). From Coleman and Crossley (1996).

lichen-covered granite outcrops. There are some 6500 described species and possibly more than 10,000 in existence.

iii. Mites (Acari) The soil mites, Acari, are chelicerate arthropods related to the spiders. They are often the most abundant microarthropods in many types of soils. A 100-g sample may contain as many as 500 mites representing nearly 100 genera. This diverse array includes participants in three or more trophic levels, with varied strategies for feeding, reproduction, and dispersal.

Four suborders of mites occur frequently in soils: the Oribatei, Prostigmata, Mesostigmata, and Astigmata. Occasionally, mites from other habitats are extracted from soil samples. These include, for example, plant mites (also called spider mites), predaceous mites normally found on green vegetation, and parasites of vertebrates or invertebrates. The most numerous ones are the true soil mites. The oribatid mites (Oribatei) are the characteristic mites of the soil and are usually fungivorous or detritivorous. Mesostigmatid mites are nearly all predators on other small fauna, although a few species are fungivores and may become numerous at times. Astigmatid mites are associated with rich, decomposing nitrogen sources and are rare except in agricultural soils. The Prostigmata contains a broad diversity of mites with several feeding habits. Very little is known of the niches or ecological requirements of most soil mite species, but some interesting information is emerging. For further details on the life-history characteristics of these interesting animals, refer to Coleman and Crossley (1996). About 20,000 species have been described and possibly in excess of 80,000 exist.

d. Macrofauna

i. Termites Termites (Isoptera) are one of the major ecosystem "engineers" particularly in tropical regions. Termites are social insects with a well-developed caste system. By their ability to digest wood, they have become economic pests of major importance in some regions of the world. Termites are arranged in five different families. The termites in a more primitive family, the Kalotermitidae, possess a gut flora of protozoans, which enables them to digest cellulose. Their normal food is wood that has come into contact with soil. Many species of termites construct runways of soil, or along root channels, and some are builders of large, spectacular mounds. Members of the phylogenetically advanced family Termitidae possess a formidable array of microbial symbionts (bacteria and fungi, but not protozoa), which enable them to process and digest the humified organic matter in tropical soils and to grow and thrive on such a diet.

Although termites are mainly tropical in distribution, they occur in temperate zones and deserts as well. Termites are often considered the tropical analogs of earthworms since they reach large abundances in the tropics and process large amounts of litter. Termites parallel earthworms in ingestive and soil turnover functions. The principal difference is that earthworms egest much of what they ingest in altered form (that enriches microbial action), whereas termites can transfer large amounts of soil/organic material into building nests and mounds (carbon sinks). More than 2000 species of termites have been described, and probably up to 10,000 exist.

ii. Earthworms The earthworm fauna of North America is surprisingly poorly known, given the importance of these animals to soil processes and soil structure. Much of the evidence for earthworm effects on soil processes comes from agroecosystems and involves a small group of European lumbricids (family Lumbricidae in the order Oligochaeta). In North America, south of the southern limit of the Wisconsinan glaciation, several native genera exist. However, exotic (often peregrine European lumbricids) earthworm species have been introduced into much of this area following human population changes and colonizations. Impacts of exotic earthworms on native species are not well understood, although there is evidence that when native habitat is destroyed and native earthworm species extirpated, exotic earthworms colonize the newly empty habitat. As more extensive studies are carried out, it is becoming clear that earthworms are present in a wide variety of tropical as well as temperate ecosystems.

Earthworms have important roles in the fragmentation, breakdown, and incorporation of soil organic matter (SOM). This affects the distribution of SOM and also its chemical and physical characteristics. Changes in any of these soil parameters may have significant effects on other soil biota, by changing their resource base (e.g., distribution and quality of SOM, microbes, or microarthropods) or by changing the physical structure of the soil. Recent evidence indicates that earthworm activities impact the communities of other soil biota through their effects on the chemical and physical characteristics of SOM, causing changes in oribatid species richness and microarthropod abundances. It is probable that earthworm-induced changes in the microbial and microarthropod communities will also have impacts both higher and lower in the soil food web. Some 3650 species of earthworms have been described and possibly as many as 8000 exist.

V. CONCLUSIONS

It is apparent that a large proportion of the biota associated with soils are as yet undescribed, with the most extreme cases being the bacteria and fungi. However, of even somewhat more extensively studied groups, such as Oribatid mites, more than half remain unknown to science. Therefore, it is premature to give even a rough estimate of the total numbers of species that occur in many of these taxa, as such large percentages of the total number of organisms are skill unknown. It is incumbent on the rising generation of ecologists and biologists to develop more innovative ways to describe, catalog, and understand the myriad patterns and processes in the biosphere, which are due in large part to the actions of the biota. It is hoped that some of the observations in this chapter, plus the insights offered by the references cited in the bibliography, will encourage this effort.

See Also the Following Articles

ARCHAEA, ORIGIN OF • BACTERIAL BIODIVERSITY • EUKARYOTES, ORIGIN OF • FOOD WEBS • FUNGI • NITROGEN AND NITROGEN CYCLE • SOIL CONSERVATION

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