The Functional Architecture of Soil Biodiversity: Chemical, Biological and Ecosystem Engineers

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Abstract

Soil biodiversity forms the foundation of ecosystem functioning by supporting an intricate assemblage of organisms responsible for decomposition, nutrient cycling, trophic regulation, and the modification of soil physical structure. Classifying these organisms into three functional groups, chemical engineers, biological engineers, and ecosystem engineers, provides a robust framework for evaluating their ecological contributions. Chemical engineers, primarily comprising bacteria and fungi, mediate key biochemical transformations and drive the breakdown of organic substrates, thereby enhancing the bioavailability of essential nutrients. Biological engineers, encompassing protists, nematodes, and diverse microarthropods, regulate population dynamics within the soil food web and exert cascading influences on nutrient turnover and ecosystem stability through their predatory and grazing activities. Ecosystem engineers including earthworms, termites, ants, isopods, moles, and plant root systems reshape soil architecture by promoting aggregation, altering pore networks, and redistributing resources, ultimately improving aeration and hydrological functioning. Importantly, many soil organisms perform multiple ecological functions, integrating processes across trophic hierarchies and temporal scales. A functional understanding of these
soil organisms perform multiple ecological functions, integrating processes across trophic hierarchies and temporal scales. A functional understanding of these
organismal roles provides critical insights into soil resilience, productivity, and the development of sustainable land management strategies, highlighting the primacy of functional diversity over mere taxonomic composition.

Keywords: Soil architecture; Functional groups; Sustainable land management; Soil resilience; Soil productivity.

Introduction

Soils contain an exceptionally wide variety of biological and chemical processes, which makes evaluating soil biodiversity a complex task. Because of this complexity, using overly broad or overly detailed categories can hinder meaningful assessment. Therefore, soil biodiversity is more effectively examined by concentrating on functional groups, which are fewer and more practical than the feeding groups traditionally applied in soil food-web models. These functional groups are fundamental to the functioning of ecosystems, because they drive processes essential for maintaining system stability. Their activities directly support key ecological functions, such as nutrient cycling, organic matter transformation, and

DOI: https://doi.org/10.5281/zenodo.17748145

soil structural development. As a result, they play a central role in ensuring the delivery of vital ecosystem services for plants, animals, and humans (Barrios, 2007). Functional groups are defined as sets of species that contribute in similar ways to major biogeochemical or biophysical processes at the ecosystem level. Each species within such a group performs comparable ecological roles, and together they influence fundamental soil processes. Through this collective action, they shape the overall performance and resilience of soil ecosystems. Since classifications may be based on different criteria and can vary depending on the level of detail needed, functional approaches often include several nested categories (Lavelle, 1997). To maintain clarity, this report therefore categorizes soil organisms into three broad functional types: those involved in transformation and decomposition, those responsible for biological regulation, and those acting as soil engineers. Each of these functional areas is carried out by a discrete group of soil organisms adapted for that purpose. The organisms within each category demonstrate similar functional capabilities and ecological effects. Consequently, every functional category represents a distinct and ecologically meaningful group within the broader soil ecosystem. Chemical engineers represent the group of soil organisms responsible for transformation and decomposition, and they include species that break down plant residues and other organic materials. Their activities are central to carbon cycling, and they also drive the conversion of major nutrients such as nitrogen, phosphorus, and sulfur into biologically usable forms. Through these combined processes, they form the foundation of many essential soil biogeochemical pathways. Biological regulators consist of organisms that help maintain population balance among soil-dwelling species, particularly through grazing, predation, or parasitism. This group plays a major role in regulating soil-borne pests and diseases, and their actions support both ecosystem stability and plant health. Ecosystem engineers include organisms that actively modify soil structure by creating pores, tunnels, or other biological architectures. They also enhance aggregation or physically redistribute soil particles, which collectively improves aeration, infiltration, and root penetration. Although this functional classification may seem simplified at first glance, it has proven to be highly effective for both scientific communication and practical analysis (Lavelle, 1997; Barrios, 2007). A major advantage of this system is that the activities of each functional group can be arranged along multiple nested spatial and temporal scales, ranging from small, short-term interactions to broad, long-term ecosystem processes. This scaling ability is possible because soil organisms are shaped by environmental conditions in ways that depend on their size and dispersal capacities. For example, chemical engineers are predominantly microorganisms, meaning their responses are usually driven by highly localized environmental factors. However, some may still undergo long-distance or long-duration movement through mechanisms such as passive dispersal or survival during dormant stages. Biological regulators are mainly mesofauna, while ecosystem engineers are typically macro fauna, and both groups are influenced not only by immediate local conditions but also by larger-scale spatial and temporal processes that operate at the landscape level over extended periods. As a result, this functional framework provides a practical lens for interpreting soil processes and can guide management decisions, including whether to target a specific functional group directly or indirectly through broader-scale

DOI: https://doi.org/10.5281/zenodo.17748145

interventions. It is also important to recognize that the functional roles assigned to organisms are not absolute, and many species can perform multiple functions depending on context. For instance, certain biological regulators or chemical engineers that produce sticky proteins may also act as ecosystem engineers by contributing to soil aggregation. Similarly, numerous plant pests such as herbivorous insects and nematodes are partially regulated by microbial natural enemies. Bacteria, although mainly viewed as chemical engineers because of their capacity for biochemical decomposition, also exhibit limited disease suppression abilities and can influence soil structure at small scales (Young and Crawford, 2004). Conversely, earthworms, classically described as ecosystem engineers, possess a modest ability to break down organic matter using specialized enzymes, linking them partly to transformation processes (Luck *et al.*, 2003). This section therefore provides concise descriptions of the principal organisms within each functional group, outlining their biology and the major soil-related roles they perform, while excluding functions unrelated to soil ecosystems, such as roles in human disease. It also explains the key biotic and abiotic factors that shape their ecology and influence their functional capacities. For clarity, only the major soil organism types within each functional group are described in detail, whereas other groups—such as archaea and viruses among chemical engineers, or organisms like millipedes, centipedes, beetles, caterpillars and scorpions are mentioned only when their relevance is necessary for explanation.

Functional Groups of Soil Organisms
Chemical Engineers (Transformers and Decomposers)

- Break down plant materials and organic substances
- Drive nutrient transformations of N, P, S and so on
- Mostly microorganisms responding to local environmental conditions
- Can disperse long distances passively or survive long periods through dormancy
- Mainly include bacteria, fungi and other microbes.

Example: Bacteria act primarily as chemical engineers but also show limited disease suppression and micro-scale engineering.

Biological Engineers

- Control soil organism populations through grazing, predation, parasitism
- Help regulate soil-borne pests and diseases
- Largely consist of mesofauna
- Affected by environmental processes at both local and broader spatial–temporal scales
- Microbial natural enemies partially regulate many plant pests, including herbivorous insects and nematodes.

Ecosystem Engineers

- Create and maintain soil structure, pore networks and biological channels
- Promote aggregation and movement of soil particles
- Often macrofauna, influenced by larger-scale environmental dynamics.

Example: Earthworms are classic ecosystem engineers but can also perform limited decomposition. Some organisms normally classed as biological regulators or chemical engineers may also act as ecosystem engineers by releasing sticky proteins or altering soil physical structure (Young and Crawford, 2004).

Chemical Engineers

Chemical engineers in soil ecosystems represent all microorganisms that drive the biochemical reactions responsible for organic matter decomposition. These organisms operate at the very base of the

DOI: https://doi.org/10.5281/zenodo.17748145

soil food web, performing both catabolic (breaking down complex compounds) and anabolic (rebuilding smaller units) processes that sustain nutrient turnover. Among them, bacteria and fungi are the dominant contributors; despite being the smallest soil inhabitants, they mediate over 90% of all energy flow within soil systems (Coleman and Crossley, 1996). This vast group also includes viruses, which are widely distributed in soils and capable of infecting an extensive array of hosts from bacteria and protozoa to plants and large animals. Their presence significantly influences microbial population dynamics, nutrient release following cell lysis, and genetic exchange within soil communities (Nannipieri and Badalucco, 2003).

Bacteria

Bacteria constitute a remarkably diverse assemblage of single-celled organisms that differ greatly in shape, physiology, and ecological strategy. Although most bacterial cells are less than 2 µm in diameter, their actual size range spans from 0.5–5 µm, presenting as spherical, rod-shaped, spiral, or filamentous forms (Figure 1). This morphological variation reflects their extraordinary metabolic and genetic diversity. They are widely recognized as the most species-rich and numerically abundant group on Earth (Torsvik and Øvreas, 2002), with global estimates reaching $4–6 \times 10^{30}$ cells, of which approximately 92% reside within soil and subsurface habitats. A single gram of soil contains roughly one billion bacterial cells and around 10,000 genetic lineages. Their biomass in temperate grasslands can reach 1–2 t/ha, an amount comparable to the mass of a cow, representing 3–5% of total soil organic matter (Killham, 1994).

Bacteria function primarily as aquatic organisms, occupying the water-filled micro-pores inside and between soil aggregates. Because most bacterial species lack effective locomotion, they anchor themselves to soil particles and organic residues, forming dense, structured communities known as biofilms (Donlan, 2002). These biofilms are complex ecological units comprising numerous bacterial species embedded in a self-produced matrix, where micro-colonies, channels, and cooperative behaviors develop. Their limited active movement means that bacterial dispersal relies principally on external forces—water movement, root elongation, soil fauna, and physical disturbances (Lavelle & Spain, 2001). Some species possess motility mechanisms, including flagella, gliding, twitching, or buoyancy changes, yet these only permit micrometer-scale repositioning. Consequently, bacterial mobility is extremely restricted, and more than 90% of soil bacteria remain in a dormant or inactive state because they cannot reach accessible substrates (Lavelle, 2002).

Bacterial functioning is strongly governed by soil moisture, which controls substrate diffusion, enzyme activity, and cell mobility. Their metabolic abilities span an enormous biochemical spectrum. Broadly, bacteria can be divided into: Heterotrophs, which obtain carbon from organic molecules. Autotrophs, which fix inorganic carbon and often perform nitrogen transformations. Bacteria engage in numerous mutualistic relationships with plants, benefiting both partners. Plants provide simple carbon molecules through root exudates, and bacteria supply fixed nitrogen, converting atmospheric N_2 into plant-available forms. The rhizobium-legume symbiosis is the most widely known example. Some strains are highly host-specific (e.g., soybean rhizobia), while others, such as rhizobium, can associate with multiple legume species. Other bacteria form symbioses with animals. For instance, some colonize earthworm

DOI: https://doi.org/10.5281/zenodo.17748145

nephridia, assisting in nitrogen recycling, while others attach to or reside inside fungal mycelia as mycorrhiza-helper bacteria, contributing to nutrient exchange and soil aggregation. Bacteria reproduce with exceptional rapidity population doubling can occur within minutes under optimal conditions (Eagon, 1962). They also possess a unique evolutionary advantage: horizontal gene transfer. Soil bacteria can take up extracellular DNA and proteins directly from their surroundings because soil particles protect and preserve these molecules (Khanna and Stotzky, 1992). Many bacteria can survive extreme environmental fluctuations UV radiation, heat, pressure, desiccation by forming endospores, metabolically inactive yet extraordinarily resilient structures. In this dormant state, bacteria can persist for decades or even centuries and also disperse great distances passively, contributing to their global ubiquity.

Figure 1: Pictorial document of bacteria

Fungi

Fungi constitute a highly diverse and ancient lineage of organisms, ranging from microscopic yeasts to some of the planet's oldest and largest biological entities. They grow primarily as hyphae, fine multicellular threads that aggregate to form larger structures such as mycelial mats, rhizomorphs, moulds, and mushroom fruiting bodies (Figure 2). Over 80,000 species have been described as soil-associated, yet global fungal diversity is estimated at 1.5 million species. A single gram of soil can contain up to one million fungal individuals, and biomass may reach 2–5 t/ha in temperate systems. Because many fungi cannot be cultured and exist only as spores or microscopic hyphae, identifying soil fungal communities remains challenging. Some mycelia can extend astonishingly up to 200 meters per gram of soil (Bardgett et al., 2005).

Fungal hyphae penetrate soil pores, organic residues, roots, and even mineral surfaces by exerting substantial mechanical forces. Their high surface-area-to-volume ratio enables efficient nutrient uptake and growth within compact substrates. Although most exist as mycelial networks, some fungi persist as single-celled forms in moist or water-filled microhabitats. Fungi are heterotrophic, relying on organic carbon sources for growth. Their metabolic versatility allows them to decompose a vast array of organic materials—from simple sugars to highly resistant compounds such as lignin and cellulose. Many fungi participate in symbioses, the most important being mycorrhizal associations, which enhance plant nutrient uptake. Some species are parasitic on plants or other fungi, while others are predatory, capturing nematodes or amoebae using adhesive networks or constricting rings. A single plant may host multiple mycorrhizal fungi, each contributing differently to nutrient dynamics (Hawksworth, 1991).

Figure 2: Pictorial document of fungi

Function of Chemical Engineers

DOI: https://doi.org/10.5281/zenodo.17748145

Chemical decomposers, primarily bacteria and fungi, play indispensable roles in nearly all soil biochemical pathways. Their central function is the degradation of organic matter into plant-available nutrients through catabolic reactions. Decomposition occurs mostly under aerobic conditions near the soil surface, where microorganisms oxidize complex organic molecules, releasing energy, CO_2, nitrogen, and phosphorus. Simple compounds (e.g., sugars, amino acids) decompose rapidly, whereas complex molecules, cellulose, phenolics, waxes, break down more slowly. Lignin is the most resistant and is decomposed primarily by fungi. Mineralization transforms organic nutrients into inorganic ions such as NH_4^+, PO_4^{3-}, and SO_4^{2-}, essential for plant nutrition. Under anaerobic conditions, however, microorganisms convert nitrogen into organic acids and ammonia instead. Macro-decomposers, including earthworms and arthropods, also contribute by fragmenting plant residues, increasing surface area for microbial attack. Some decomposers additionally function as ecosystem engineers. For example, certain fungi secrete glomalin, a sticky glycoprotein that stabilizes soil aggregates and enhances soil structure (Purin and Rillig, 2007).

Biological Engineers

Biological Engineers represent a remarkably diverse assemblage of soil organisms, including protists, nematodes, and microarthropods, each contributing in unique ways to trophic regulation. Protists often act as highly efficient bacterial grazers, while nematodes occupy multiple trophic levels ranging from bacterial and fungal feeders to root herbivores and predators of other nematodes. Microarthropods, such as collembolans and mites, modulate fungal dynamics and influence litter fragmentation, thereby altering resource flow and microbial turnover. This group also encompasses various pathogenic, parasitic, and herbivorous organisms that regulate plant populations by suppressing plant growth, altering competition among plant species, or modifying nutrient allocation patterns. Their actions can limit the dominance of particular species and promote plant diversity, indirectly shaping microbial habitats and nutrient cycling pathways. Additionally, enchytraeids, commonly known as "pot worms," are included within this regulatory category. Although small and often overlooked, these organisms play an essential role in stimulating microflora through their feeding and burrowing activities. They accelerate nutrient mobilization, enhance microbial hotspots, and influence organic matter breakdown. In ecosystems where earthworms are scarce or absent, enchytraeids may also perform responsibilities similar to soil ecosystem engineers, modifying soil structure, redistributing organic material, and facilitating aeration and moisture retention. Through these combined activities, biological regulators ensure the functional integrity, ecological balance, and continuous resilience of the soil food web (Killham, 1994).

Protists

Protists are unicellular eukaryotic organisms and represent the smallest members of the biological regulator group. Their typical size ranges from 10 to 50 μm, although some species may reach up to 1 mm. Protests (Figure 3) can achieve extremely high population densities, with up to 10^6 cells per gram of soil, and the total biomass in one hectare of soil can be roughly equivalent to the weight of two sheep. These organisms feed primarily on bacteria and fungi, making their abundance dependent on the availability of microbial prey. They require thin water films surrounding soil particles

DOI: https://doi.org/10.5281/zenodo.17748145

for survival and locomotion, highlighting the critical role of soil moisture in their activity. Consequently, protists are mainly found in the water layers around soil aggregates, where they can efficiently access nutrients and maintain mobility. Protists, one of the key groups of biological regulators, can be classified according to their modes of movement: ciliates move by beating their cilia like tiny oars, amoebae move by extending pseudopods, and flagellates swim by waving their flagella like a whip. They possess a high dispersal potential because they can form resistant or dormant stages that are passively transported by wind or water over long distances. Functionally, protists help regulate bacterial populations by surrounding and engulfing their prey and digesting them within vacuoles. They typically reproduce asexually through binary or multiple fission, although sexual reproduction may occur under environmental stress to allow genetic recombination. Their life cycle includes active and dormant phases, with cyst forms capable of surviving harsh conditions and long periods without water, nutrients, or oxygen, enabling rapid spread when conditions become favorable. The other major group of biological regulators are nematodes, or roundworms, which are tiny worms measuring about 0.5–1 mm in length and are extremely common in soils worldwide, often occurring at densities of 10–50 individuals per gram of soil (Bongers and Bongers, 1998).

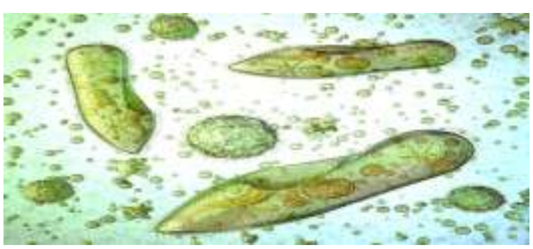

Figure 3: Pictorial document of protist

Nematodes

Nematodes (Figure 4) inhabit nearly all environments, including extreme habitats such as Antarctica and deep-sea trenches, and represent one of the most diverse animal groups, with over 80,000 species described and an estimated total of approximately 500,000 species. Nematodes, or roundworms, are ubiquitous in soils worldwide, with a preference for coarser, porous textures that allow movement through water films in pore spaces. They are generally unable to access the smallest pores and typically disperse only a few centimetres, although some species can migrate up to one metre per year or disperse passively via wind or by attachment to animals. Nematodes play essential roles in soil food webs and exhibit diverse feeding habits, including bacterivory, fungivory, algivory, root-feeding, predation on other nematodes and protists, and omnivory. Their feeding strategies vary according to diet; for example, fungal-feeding nematodes pierce fungal cell walls to extract contents, while predatory nematodes attach to the cuticle of prey and consume internal tissues. The distribution of nematodes in soil corresponds closely with the availability of their preferred prey, with bacterial and fungal feeders concentrated near microbial populations and root-feeders localized around susceptible plant roots. Reproduction is primarily sexual, with males generally smaller than females, though some species are hermaphroditic and retain self-fertilized eggs until hatching, occasionally resulting in juvenile cannibalism. Nematodes, like protists, possess the remarkable ability to enter a dormant state under unfavorable environmental conditions, such as high temperatures or drought. This desiccated, inactive form allows them to survive for extended periods, with some individuals documented to remain viable for over 40 years in preserved slide collections. This

DOI: https://doi.org/10.5281/zenodo.17748145

dormancy ensures their persistence in soil ecosystems and enables them to recolonize suitable habitats when conditions improve (Yeates, 2009).

Figure 4: Pictorial document of nematodes

Microarthropods

Microarthropods, another key group of biological regulators, are small invertebrates characterized by an external skeleton that provides structural support. They range in size from microscopic forms to a few millimetres and include diverse taxa such as springtails (Collembola), spiders, and mites. Springtails, the only wingless insects, typically measure 0.2–6 mm and possess specialized appendages, including a spring-like tail that facilitates jumping (Figure 5). Mites (Acaridae) are the most abundant arthropods in soil, with densities in forest soils reaching hundreds of thousands of individuals per square metre, though their small size—often only a few tens of micrometres—makes them easily overlooked. Currently, approximately 50,000 mite species are described, but estimates suggest that the group may include up to one million species. Collectively, micro arthropods contribute significantly to soil biomass, with one hectare of soil containing an equivalent mass comparable to four rabbits, highlighting their importance in soil ecological processes. Microarthropods, as a class of biological regulators, generally inhabit surface litter or remain confined to the upper layers of the soil due to their limited burrowing ability. Their small size enables them to navigate narrow pore spaces and root channels, allowing access to microhabitats that larger organisms can not exploit. Springtails, for example, often aggregate in groups and exhibit gregarious behavior mediated by secreted pheromones, which helps individuals avoid unfavorable conditions such as dry habitats, while mites display highly heterogeneous ecological adaptations depending on the species, ranging from surface dwellers to those inhabiting deeper soil layers. These organisms exhibit diverse feeding habits that contribute to their critical role in soil food webs. Most soil-dwelling micro arthropods are herbivores, fungal feeders, or predators. Predatory species consume nematodes or other microarthropods, with some acting as generalists feeding on multiple prey types, while others specialize in hunting a single prey species. Springtails and mites primarily feed on decaying plant material colonized by bacteria and fungi but may occasionally consume nematodes or other small invertebrates (Petersen and Luxton, 1982).

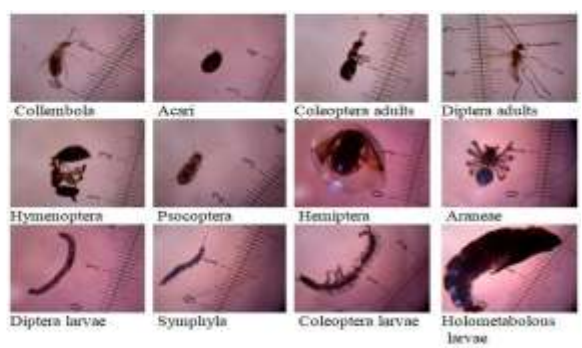

Figure 5: Pictorial document of microarthropods

Functions of Biological Engineers

Functionally, biological regulators act as integrators within soil food webs, connecting the activities of chemical engineers with higher trophic levels both

DOI: https://doi.org/10.5281/zenodo.17748145

spatially and temporally. By feeding on microbial populations and modulating microbial activity during digestion, they regulate the dynamics of lower trophic levels. Microbial activity continues within the faecal pellets of these invertebrates, which are sometimes re-ingested, thereby exploiting released substrates. Predatory, parasitic, and mutualistic interactions exert top-down control over microbial populations, stimulating prey growth at low predator densities and suppressing populations at high densities. This regulatory mechanism often exerts a stronger influence on microbial populations than resource availability itself and can cascade to affect the abundance, biomass, and productivity of lower trophic levels. However, the outcomes of such regulation are highly context-dependent, as soil food webs are dynamic and sensitive to environmental disturbances and changes in species composition. Protists and nematodes, as key biological regulators, play a crucial role in soil ecosystem functioning through their predatory activities. By feeding on microorganisms, they help fragment organic matter and disperse both decomposers and nutrients throughout the soil, effectively increasing the surface area of organic substrates available for microbial decomposition. This activity indirectly enhances nutrient availability, as nutrients that would otherwise remain immobilized within microbial biomass become accessible to plants and other soil organisms. Research also suggests that increased complexity in soil food webs, driven by interactions among biological regulators and other trophic levels, can accelerate nutrient mineralization and potentially boost overall ecosystem productivity (Setala and Huhta, 1991).

Beyond their influence on nutrient cycling, biological regulators exert significant indirect effects on aboveground biodiversity. By modulating plant presence, growth, and chemistry, protists, nematodes, and other regulators can influence interactions between plants and herbivorous pests or pathogens. Consequently, this functional group is pivotal for maintaining semi-natural ecosystems, promoting sustainable agriculture, and supporting forestry management. Through these indirect pathways, they affect plant abundance, control the spread of invasive species, and mitigate outbreaks of pests and diseases in crop systems. Such integrative functions highlight their importance not only in soil trophic dynamics but also in shaping broader ecosystem resilience and productivity. The spatio-temporal distribution of biological regulators is shaped by multiple environmental gradients, including soil type, moisture availability, and land-use practices. For example, springtail populations in agricultural landscapes often correlate with large-scale gradients in soil carbon and the type of cultivation practiced, while nematode distributions can be strongly influenced by soil disturbance and resource availability, as species must recolonize nutrient-rich patches from adjacent areas to survive under fluctuating conditions. Interestingly, even at smaller spatial scales within fields, aggregated patterns of nematode populations (6–80 m) have been observed, demonstrating that soil food web components can maintain structured distributions despite homogenizing influences such as monoculture or tillage (Robertson and Freckman, 1995). These fine-scale patterns underscore the importance of considering spatial heterogeneity in soil when modeling ecosystem processes and understanding the linkages between soil populations and ecosystem functions. At micro-scales, heterogeneity in soil structure and chemical properties is perceived differently by

DOI: https://doi.org/10.5281/zenodo.17748145

microorganisms, such as protists, emphasizing the role of environmental variation in shaping organismal interactions. At macro-scales, passive dispersal mechanisms, including wind and water transport, enable widespread distribution of certain species, such as springtails across the Arctic, highlighting the interplay between local ecological processes and long-distance dispersal in maintaining biological regulator populations. At any given moment, only a fraction of the total species within soil ecosystems is actively participating in biological processes, as activity is largely restricted to those organisms capable of exploiting the resources currently available. The activity of biological regulators, therefore, tends to occur in pulses, closely following temporal patterns of resource availability. Their growth and reproduction typically peak during periods when resources are abundant, such as immediately after the addition of organic matter to soil, but decline sharply when conditions become suboptimal. For example, bacteria-feeding protists and nematodes exhibit maximal population growth during the first few weeks after organic matter input, after which the majority of protist species enter dormant, resting stages by forming cysts to survive adverse conditions (Ekelund and Rønn, 1994).

In essence, when resources become scarce, many biological regulators prioritize temporal adjustment of their activity over spatial movement. This ability to enter dormant or low-activity states ensures the survival of species through unfavorable conditions, allowing them to respond rapidly to future pulses of resource availability. Such dynamic temporal patterns are critical for sustaining nutrient cycling, soil ecosystem stability, and the overall functioning of soil communities over time.

Ecosystem Engineers

Ecosystem engineers are organisms that actively modify their environment in ways that influence other organisms, primarily through their mechanical and structural activities. In the soil, these engineers are capable of creating durable organo-mineral structures and networks of pores by moving through, mixing, and manipulating the soil—a process broadly termed bioturbation. Among the most significant soil ecosystem engineers are earthworms, termites, ants, and plant roots, which collectively contribute to soil formation, aggregation, aeration, and nutrient distribution. Interestingly, ecosystem engineering is not limited to macrofauna or vertebrates; microorganisms and fungi can also modify soil structure. For instance, arbuscular mycorrhizal fungi release glomalin and other exudates that promote soil aggregation, while fungal hyphae physically enmesh soil particles, binding them together into stable aggregates. Even bacteria, though microscopic, contribute to soil structure by producing extracellular polymeric substances that help stabilize aggregates. Together, these biological activities from microorganisms to large vertebrates demonstrate the multi-scale influence of soil ecosystem engineers on physical, chemical, and biological soil properties, thereby shaping the habitat and resources available for other soil biota (Scheu, 2001).

Earthworms

Earthworms are elongated, segmented invertebrates that can range in size from just a few millimetres to several tens of centimetres in length, essentially functioning as a tubular digestive system (Figure 6). Their morphology is highly adapted for burrowing and processing soil, allowing them to ingest soil and organic matter while simultaneously creating channels and pores that enhance aeration and water infiltration. In many ecosystems, earthworms constitute

DOI: https://doi.org/10.5281/zenodo.17748145

a substantial portion of the soil fauna biomass, often accounting for up to 50% in temperate grasslands and reaching as high as 60% in temperate forest soils, highlighting their dominant role in soil structure formation and nutrient cycling. Earthworms comprise several thousand species worldwide, classified into five main families. In Europe, North America, and Western Asia, the family Lumbricidae is the most prevalent, with approximately 220 recognized species. Earthworms are obligate burrowers that ingest soil, expelling it either onto the surface or into the tunnels they create. Locomotion occurs through coordinated muscular contractions that alternately shorten and extend the body, aided by mucus secretions that lubricate the soil, enabling them to travel several metres within their burrows. Functionally, earthworms play a critical role in soil processes, particularly in the decomposition of organic matter. They are herbivorous and categorized into three ecological groups: epigeic worms dwell in leaf litter or compost and have limited effects on soil structure; endogeic worms live and feed within the topsoil, largely consuming plant material; and anecic worms construct deep semi-permanent burrows while foraging on surface litter, mixing it with soil. The earthworm gut acts as an active microbial reactor, selectively activating dormant microorganisms and producing casts rich in nutrients such as ammonium (NH_4^+) and phosphate (P), thereby enhancing soil fertility. Reproductively, most earthworms are hermaphroditic, possessing both male and female reproductive organs, but they still require mating to exchange sperm and fertilize their eggs. A minority of species reproduce via parthenogenesis, which facilitates rapid colonization and occasional invasiveness. Earthworms generally take about one year to reach maturity, although only 20–30% survive to adulthood. Large, deep-soil dwelling species may live for several years, reflecting their significant ecological role as long-term ecosystem engineers (Ekelund and Rønn, 1994).

Figure 6: Pictorial document of earthworms

Termites

Termites are small social insects, typically ranging from 0.5 to 2 cm in length depending on species and caste (Figure 7). They are eusocial, living in colonies that can contain up to one million individuals. While termites are most abundant in tropical regions, they can inhabit nearly any environment where soil does not completely freeze during winter. Globally, nearly 3,000 termite species have been described, but in Europe, fewer than ten species occupy natural habitats, with only a subset living primarily in the soil. Subterranean termites primarily live and reproduce in soil, sometimes several metres below the surface, though certain colonies construct nests inside fallen trees or other aboveground structures. Termite nests are highly elaborate, composed of soil, mud, chewed wood or cellulose, saliva, and faeces, forming a protected environment that maintains optimal humidity through water condensation. Within these nests, tunnel-like galleries allow termites to move efficiently, regulate air flow, and maintain a stable balance of oxygen and carbon dioxide, ensuring suitable microclimatic conditions for colony survival. Both individual termites

DOI: https://doi.org/10.5281/zenodo.17748145

and entire colonies generally remain confined within their territorial boundaries or near available food resources, limiting long-distance movement. They are key detritivores in terrestrial ecosystems, contributing critically to soil nutrient cycling. They digest cellulose, a complex polysaccharide that forms the structural component of plants and is indigestible to most other organisms, including humans. Their diet predominantly consists of dead plant material such as wood and leaf litter, and in some cases, animal dung. Additionally, some species ingest mineral-rich soil along with partially decomposed plant material, while fungus-growing termites cultivate fungal gardens on chewed plant substrates, which enhances the decomposition of organic matter and improves nutrient availability. By processing large quantities of organic and mineral material, termites facilitate soil formation, enhance porosity, and indirectly promote microbial activity (Lavelle and Spain, 2001).

Termites are eusocial insects living in highly organized colonies composed of distinct castes specialized for particular roles. Colony establishment begins with a reproductive pair: a queen and a king. Over time, mature colonies can expand to include several hundred to several million individuals. The queen, the central reproductive individual, produces a small number of eggs initially (10–20 per day) but can lay thousands per day as the colony grows. Thousands of worker termites maintain the nest, tend to the queen, gather food, and care for larvae. Soldiers, equipped with large mandibles and powerful jaws, serve as defenders to protect the nest and the colony from predators and intruders. This caste system ensures the efficient division of labor, survival, and long-term persistence of the colony. The lifespan of termites varies among castes. Most worker and soldier termites live only a few weeks, performing their roles within the colony before dying. In contrast, the reproductive pair—the queen and king—can live for several years, ensuring the long-term continuity and stability of the colony (Ekelund and Rønn, 1994).

Figure 7: Pictorial document of e termites

Ants

Ants are small, eusocial insects, ranging in size from approximately 0.75 to 52 mm, and, like termites, they live in complex colonies with highly organized social structures. They have successfully colonized almost every terrestrial ecosystem on Earth, demonstrating exceptional ecological adaptability. This global success is largely due to their diverse life strategies, cooperative behavior, and ability to modify habitats and exploit a wide range of resources (Figure 8). Ant colonies often build elaborate nests, forage efficiently, and display division of labor among specialized castes, which contributes to their resilience and ecological impact. Ants, similar to termites, are eusocial insects that live in structured colonies comprising distinct castes of individuals. Their life cycle begins with an egg, which develops through complete metamorphosis, including larval and pupal stages, before emerging as an adult. Colony size varies widely depending on the species and age, ranging from just a few individuals in newly established colonies to several million in mature colonies. The lifespan of ants is highly

DOI: https://doi.org/10.5281/zenodo.17748145

ISSN NO-2584-2706

variable and is influenced by both species and caste. Worker ants typically live for a few months to a year, while queens, responsible for reproduction, can live for several years, sometimes exceeding a decade in certain species. This longevity allows queens to maintain and expand colonies over long periods, ensuring the continuity of their social structure (Lavelle and Spain, 2001).

Figure 8: Pictorial document of ant

Isopods

Isopods are a diverse and globally distributed group of crustaceans, encompassing more than 10,000 described species. They possess segmented bodies and exhibit considerable size variation, ranging from as small as 0.5 mm to several tens of centimetres (Figure 9). Isopods inhabit a variety of environments, including soil, leaf litter, and aquatic habitats, and they play important roles in decomposition and nutrient cycling within ecosystems. Isopods occupy a range of habitats, from aquatic environments to fully terrestrial ecosystems. The suborder Oniscidea, comprising approximately 5,000 species, represents the most successful group of crustaceans to colonize terrestrial environments. These terrestrial isopods, commonly known as sowbugs or pill bugs, are typically found in the litter layers of soils, where they inhabit moist microhabitats that provide shelter and food. Their adaptation to land has allowed them to become key components of detritus-based food webs. Isopods primarily function as detritivores, consuming decomposing organic matter and contributing to nutrient cycling in soils. In doing so, they act as ecosystem engineers by producing stable faecal pellets that can influence soil structure and microbial activity. Their ecological role can be particularly pronounced in arid or desert environments, where isopods contribute significantly to organic matter breakdown and soil stabilization (Yair 1995). While most species are detritivorous, some may adopt herbivorous, carnivorous, or even parasitic feeding strategies, highlighting their ecological versatility. Isopods reproduce sexually, with distinct male and female individuals engaging in mating behaviors that ensure the continuation of populations within their habitats. The average lifespan of most isopod species is approximately two years, although some individuals have been recorded to survive up to five years under favorable conditions, reflecting their resilience in variable environments (Ekelund and Rønn, 1994).

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Figure 9: Pictorial document of Isopod

Moles

Moles are small, fossorial mammals uniquely adapted for life underground. Measuring roughly 15 cm in length, they possess cylindrical bodies, a hairless, pointed snout, and highly specialized forelimbs for digging. Their eyes are small and covered, and external ears are absent, adaptations that minimize resistance while moving through soil (Figure 10). Moles play significant roles as ecosystem engineers by aerating soil, mixing organic and mineral components, and creating burrow networks that influence soil structure and hydrology. Moles are fossorial mammals that spend

DOI: https://doi.org/10.5281/zenodo.17748145

nearly their entire lives underground, inhabiting an extensive network of permanent and semi-permanent tunnels. The permanent deep burrows form complex systems that can extend over hundreds of meters at variable soil depths. These tunnels serve multiple purposes, including long-term feeding and nesting, sometimes accommodating several generations of moles. Nest chambers are typically spherical and lined with dry plant material to provide insulation and comfort. The majority of mole tunnels, however, are shallow, measuring 3–4 cm in diameter, and are distributed across their hunting grounds. These surface tunnels are generally short-lived and may only be reused sporadically. Moles prefer to construct their burrows in elevated, well-drained areas while hunting in soils that are shaded, cool, moist, and rich in prey, such as earthworms and insect larvae. Surface tunneling is most commonly observed in newly cultivated fields, light sandy soils, or shallow soils, where prey density is high. Deeper tunnels are employed during extreme environmental conditions, such as droughts or low temperatures, providing refuge and stable microclimates for the moles. Moles are voracious predators, primarily feeding on earthworms but also consuming other small soil invertebrates, including insect larvae, particularly during the summer months. They exhibit extraordinarily high metabolic demands, consuming between 70% and 100% of their body weight daily. To satisfy these energy requirements, moles actively excavate soil, forming molehills as they extend their tunnel networks at a rate of approximately 30 cm per hour. Moles employ both trapping and hunting strategies to capture prey. They can intercept organisms falling into their tunnels or actively pursue and extract prey from the soil. Their saliva contains toxins that paralyze earthworms, enabling them to store prey in underground “larders” for later consumption; in some cases, these larders have contained up to 1,000 earthworms. Through these activities, moles not only regulate soil invertebrate populations but also contribute to soil aeration and mixing. Moles are solitary for most of the year, with males and females occupying exclusive territories. During the breeding season, males expand their territories extensively in search of females. Mating typically results in litters of three to four offspring in spring. Juvenile moles remain in the maternal nest for approximately six weeks before dispersing aboveground, a phase that exposes them to significant predation risk. The average lifespan of moles is generally under three years, though some individuals may survive up to six years. Predation by owls, buzzards, stoats, domestic cats, and dogs significantly affects mole populations, and anthropogenic factors, including vehicular traffic and habitat disturbance, further contribute to mortality (Lavelle and Spain, 2001).

Figure 10: Pictorial document of mole

Plant Roots

Roots are critical ecosystem engineers, significantly influencing soil structure, nutrient cycling, and microbial activity. The total biomass of roots in soil can rival or even exceed aboveground plant biomass (Figure 11), highlighting their pivotal role in stabilizing soils, creating channels for water and air movement, and facilitating interactions between soil organisms and

DOI: https://doi.org/10.5281/zenodo.17748145

plants. Root growth and turnover contribute to soil aggregation and organic matter inputs, indirectly supporting the activities of both chemical engineers and biological regulators in terrestrial ecosystems. Roots are the belowground structures of plants that serve two primary functions: anchoring the plant to the soil and absorbing water and nutrients. Short-lived, thin roots are primarily responsible for nutrient and water uptake, while larger, perennial roots provide structural stability by firmly anchoring the plant. Root systems exhibit a wide variety of shapes and sizes, ranging from shallow to deep, and consist of coarse roots (greater than 2 mm in diameter), which function like branches and are generally long-lived, and fine roots, which are short-lived and specialized for resource absorption. Roots tend to grow in directions that offer favorable conditions for aeration, nutrient availability, and moisture. Roots perform two primary functions: absorbing water and inorganic nutrients, and anchoring the plant in the soil. In addition, roots often serve as storage organs for food and nutrients, and can produce or store chemicals that protect plants from herbivores and pathogens. The soil region immediately surrounding roots, known as the rhizosphere (approximately 2 mm from the root surface), is highly dynamic and biologically rich. Roots release organic compounds called root exudates, which, together with nutrient and water uptake, create a unique environment that differs significantly from the bulk soil. Microorganisms feed on these exudates, attracting larger soil organisms, so that microbial density in the rhizosphere can be up to 500 times higher than in surrounding soil. Furthermore, many plants form symbiotic relationships with fungi or bacteria, enhancing their uptake of nitrogen, phosphorus, and water. Plant roots are highly dynamic. Root hairs typically live only a few days, while other fine roots may turn over within days or weeks. Only the larger, anchoring roots can persist for the life of the plant (Stanton, 1988).

Figure 11: Pictorial document of plant roots

Function of Ecosystem Engineers

Unlike biological regulators, the influence of roots as ecosystem engineers is primarily non-trophic. Their key role lies in modifying the soil environment through physical movement and the construction of organo-mineral structures with specific physico-chemical properties, which can significantly influence soil structure, nutrient distribution, and water dynamics. Some organisms primarily classified in other functional groups can also act as ecosystem engineers. For example, soil microorganisms, although mainly functioning as chemical engineers in decomposition, can influence soil structure. Bacteria and fungi exude sticky substances, such as polysaccharides and proteins, which bind soil particles into aggregates, thereby improving soil structural stability (Lavelle 1997). While their engineering effect is generally less pronounced than that of dedicated ecosystem engineers, it contributes to soil formation and function. Similarly, large biological regulators, such as springtails and mites, also perform minor engineering functions. By grazing on microbes and excreting nutrient-rich faeces, they create structures in organic matter where microorganisms can thrive. These structures may temporarily enhance mineralisation, although they can also limit aeration and water storage over longer

DOI: https://doi.org/10.5281/zenodo.17748145

periods, thereby affecting decomposition and nutrient cycling (Cole, 2002). Organic

acids leached from these structures can further influence long-term soil processes.

Summary of the characteristics of the three soil functional groups

The table below presents a scheme of the soil organisms' characteristics (Turbé et al., 2010).

Table 1: Summary of the characteristics of the three soil functional groups

Characteristics	Chemical Engineers	Biological Engineers	Ecosystem Engineers
Main Organisms	Bacteria, fungi	Protists, nematodes, mites, springtails (Collembola)	Ants, termites, earthworms, plants roots
Function	Organic matter decomposition, mineralisation, nutrients release, pest control, toxic compounds degradation	Regulation of microbial community dynamics, faecal pellet structures, mineralisation, nutrient availability regulation (indirect), litter transformation and organic matter decomposition	Creation and maintenance of soil habitats; transformation of physical state of both biotic and abiotic material, accumulation of organic matter, compaction of soil, decompaction of soil, soil formation
Body size	0.5-5 µm (bacteria) 2-10 µm (fungal hyphae diameter)	2-200 µm (protists) 500 µm (nematodes) 0.5-2 mm (mites)	0.1-5 cm (ants) 0.3-7 cm (termites) 0.5-20 cm (earthworms)
Density in soil	10^9 cells/g of soil (bacteria) 10 metres/g of soil (fungal hyphae)	10^6 g/soil (protists) 10-50 g/soil (nematodes) 10^3-10^5 per m^2 /soil(mites) 10^2-10^4 m^2/soil (springtails)	10^2-10^3 m^2/soil (ants) 10-10^2 m^2/soil (earthworms)
Resistance to environmental stresses	High (cysts, spores)	High (Protist, nematodes) Intermediate (mesofauna)	Low
Ability to change the environment	Highly restricted to micro environments	Intermediate	High

Conclusion

Soil functional architecture is central to ecosystem functioning, with chemical engineers, biological regulators, and ecosystem engineers each contributing distinct yet interrelated roles. Chemical engineers drive organic matter decomposition and nutrient transformations, supporting foundational biochemical pathways. Biological regulators modulate soil food webs, controlling microbial populations and facilitating nutrient availability, while ecosystem engineers shape the physical environment, enhancing soil structure and resource distribution. Many organisms exhibit multifunctionality, bridging categories and demonstrating the dynamic and context-dependent nature of soil biodiversity. This functional perspective allows for a more targeted understanding of soil processes across spatial and temporal scales, informing ecosystem management

DOI: https://doi.org/10.5281/zenodo.17748145

and conservation strategies. Recognizing and integrating the contributions of these functional groups is essential for maintaining soil health, promoting sustainable agriculture, and ensuring the continued provision of ecosystem services in both natural and managed landscapes.

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