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Review

Role of Arthropods in Maintaining Soil Fertility

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Abstract: In terms of species richness, arthropods may represent as much as 85% of the soil fauna. They comprise a large proportion of the meso- and macrofauna of the soil. Within the litter/soil system, five groups are chiefly represented: Isopoda, Myriapoda, Insecta, Acari, and Collembola, the latter two being by far the most abundant and diverse. Arthropods function on two of the three broad levels of organization of the soil food web: they are plant litter transformers or ecosystem engineers. Litter transformers fragment, or comminute, and humidify ingested plant debris, which is deposited in feces for further decomposition by micro-organisms, and foster the growth and dispersal of microbial populations. Large quantities of annual litter input may be processed (e.g., up to 60% by termites). The comminuted plant matter in feces presents an increased surface area to attack by micro-organisms, which, through the process of mineralization, convert its organic nutrients into simpler, inorganic compounds available to plants. Ecosystem engineers alter soil structure, mineral and organic matter composition, and hydrology. The burrowing by arthropods, particularly the subterranean network of tunnels and galleries that comprise termite and ant nests, improves soil porosity to provide adequate aeration and water-holding capacity below ground, facilitate root penetration, and prevent surface crusting and erosion of topsoil. Also, the movement of particles from lower horizons to the surface by ants and termites aids in mixing the organic and mineral fractions of the soil. The feces of arthropods are the basis for the formation of soil aggregates and humus, which physically stabilize the soil and increase its capacity to store nutrients.

Keywords: decomposition; detritus; ecosystem engineers; humus; litter transformers; mineralization; nutrients; pedogenesis; pedoturbation

1. Introduction

Soils originate and accumulate in a sequence of events that mark the stages of ecological succession, the development of biotic communities. Soil formation, or pedogenesis, involves a set of physical, chemical, and biotic processes. The properties of soils arise from the interactions of five basic factors: parent material, topography, climate, biota, and time [1].

In primary succession, soil formation begins with physical weathering of the rocky parent material, creating cracks and fissures, and fractionating it into finer particulate matter. Pioneer organisms, such as lichens, mosses, and liverworts, subsequently colonize the substrate, further breaking down the rock and incorporating detritus and organic compounds formed through photosynthesis and nitrogen fixation [2,3]. In the process, they stabilize and moderate the micro-environment, creating conditions favorable for later colonizers, eventually resulting in the establishment of higher plants and invertebrate animals. Over time, which may involve hundreds or thousands of years, soil structure builds and nutrient availability increases with the addition of metabolic wastes and other byproducts (plant litter, root exudates, feces), and the organisms' remains combined with the weathered mineral elements [4]. The process culminates in a steady state, in which the accumulation of organic matter is balanced by its decomposition to close or nearly close nutrient cycles [5,6]. As delimited by the depths at which biological influences are observed, a developed soil may be tens of meters thick [7].

Natural soils thus are an amalgam of materials of clastic and biological origin. They also have a significant living component; in fact, given the vast number of species present within soil, and the biomass they represent [8–12], a good-quality soil may itself be considered, in large part, living. Much attention historically has focused on the central role of earthworms in the soil system [13], and the activities of these animals have figured prominently in the public imagination. However, in terms of their abundance, diversity, and the variety of niches that they occupy, the arthropods also assume considerable significance in this environment.

Arthropods have long been recognized as important in the functioning of soil ecosystems, and a vast literature accordingly has accumulated. Much of the earlier literature, still relevant today, was cited in several classic treatises on the biology of soils published beginning in the 1950s [14–25]. Given the large volume of research that has been published, this review necessarily is limited in scope, and will be restricted to a survey of the principal roles played by arthropods in the processes that maintain soil fertility.

2. Soil Arthropods

Soils may harbor an enormous number of arthropod species, which may rival or exceed the numbers estimated to inhabit the canopies of tropical forests [26]. By one recent estimate, the soil fauna may represent as much as 23% of all described organisms, or about 360,000 species, with arthropods comprising 85% of that number [27]. However, accurate figures have been difficult to come by, hampered, at least in part, by limitations in sampling methodology [28]. Because of this, it has been suggested that, in some groups, the actual species richness may be an order of magnitude greater than the number of species that have been described [29].

Arthropods comprise a large proportion of the meso- and macrofauna of the soil, animals with body lengths ranging from about 200 μm to 16 cm or more [21,30,31]. Of the hemiedaphon and euedaphon, those organisms that live within the litter/humus boundary and lower in the soil profile [32], five groups are chiefly represented: Isopoda, Myriapoda, Insecta, Acari, and Collembola, the latter two being by far the most abundant and diverse. Species of Protura, Diplura, and Pauropoda are of lesser importance in the soil community [33–35], and have little influence on soil processes.

2.1. Microarthropods

This group consists principally of species of the acarine taxa Oribatida, Prostigmata, and Mesostigmata, and the Collembola. Large numbers of microarthropods are found in most soils [36,37] (Table 1), including those under cultivation [38,39], and these animals may be the dominant arthropods in a variety of environments from equatorial to polar regions and from temperate and tropical forests and grasslands to hot and cold deserts [34,40–43]. As part of the mesofauna, the microarthropods comprise the important middle links of soil food webs, serving, in their role as both predator and prey, to channel energy from the soil microflora and microfauna to the macrofauna on higher trophic levels [5].

2.1.1. Acari

The Acari of the soil includes members that feed on dead plant materials, as well as on the microflora (bacteria, fungi); in addition, species of Prostigmata and Mesostigmata may prey upon elements of the micro-and mesofauna (e.g., nematodes, collembolans, enchytraeid worms) [21,22,34]. The oribatids are the numerically dominant group of Acari in forest and grassland soils [42,44] and the most important in decomposition processes. Further discussion concerning the influence of Acari on soil processes thus will focus on this group, and it will henceforth be the acarine referent in discussions of the microarthropods.

Populations of oribatids on the order of 10^5–10^6 individuals m^{-2} have been recorded in various forest types [34,45], with densities higher in coniferous than in deciduous soils [44]. However, in desert ecosystems, their numbers comparatively are much reduced [41], and their roles in the turnover of organic matter insignificant [46]. A major abiotic factor constraining the distribution of oribatids is adequate moisture, with the requisite soil humidity for euedaphic forms probably near saturation [47].

With more than 9000 species in 172 families, most of which inhabit the soil/litter system [48], the oribatids are considered the most successful of all soil arthropods. Species tend to exhibit low metabolic rates, slow development, lengthy life cycles, low numerical response capability, generally stable population densities [49], low fecundity, and iteroparity [50], traits suggestive of *K*-selection and probably influenced in part by the low nutritional quality of the diet. Parthenogenesis may be common, particularly in some families [51]. Life spans of one or two years appear to be common in oribatids in temperate soils [52]; three to five years have been reported for species in colder climates [53].

The feeding ecology of oribatids is diverse. Four main groups, based on modes of feeding, are commonly recognized: macrophytophages, which feed mainly on decaying higher plant material and rarely on fungi; microphytophages, those types feeding on fungi, bacteria, and other microflora;

panphytophages, which have an expanded diet breadth, including plant matter as well as fungi; and coprophages, the diet of which includes fecal material [54,55]. As the coprophagous habit probably is neither obligatory nor followed to the exclusion of other types of feeding, coprophages may reasonably be classed with the panphytophages [44]. However, the majority of oribatids are obligate or facultative fungivores [44,56]. These animals have been contributing to the breakdown of plant litter since early in the Pennsylvanian Epoch of the Carboniferous Period, perhaps 316 million years ago [57].

2.1.2. Collembola

Collembola (springtails) are hexapods formerly classified as primitively wingless insects [58], but now widely recognized as a lineage closely related to, but distinct from, the Insecta [59]. About 6500 species in 18 families have been described [60]. Like the oribatids, they also are extremely abundant in soil and leaf litter, with densities typically on the order of 10^4–10^5 individuals m^{-2} and, again, higher in coniferous forests [34], but are more numerous than oribatids in many soils [61]. Agricultural soils may be rich in Collembola [62]. Euedaphic species tend to be parthenogenetic and produce few offspring at a time over an extended reproductive period [60], life-history traits characteristic of animals living in stable environments. Average fecundity typically ranges between 50 and 100 eggs per female; depending on climate, there may be 1–4 generations annually [23]. Life spans of species living within the soil-litter system have been reported to range between 2 and 12 months or more [37,62]. Like soil-dwelling oribatids, euedaphic Collembola require a soil atmosphere approaching saturation [62].

The diet of Collembola is of considerable breadth, including moss protonema, bacteria, fungal hyphae and spores, algae, protozoans, arthropod feces, pollen, decaying plant materials and humus, other Collembola (living or dead), and stored products, and species are divided between those that masticate their food and those that are fluid feeders [62–64]. However, the majority of species are primarily or largely fungivorous [60].

2.2. Myriapoda

The Diplopoda (millipedes) and Symphyla are the most important myriapodous groups within the soil. About 12,000 species of millipede have been described and assigned to 2947 genera [65]. Millipedes are said often to be dominant arthropods in forest soils with a mull-type humus, also are numerous in deciduous forests with a mor humus formation, but are rare in coniferous forest mor [66]. They tend to be more abundant and diverse in calcareous soils, in fairly moist habitats, and typically in the upper soil horizons [67]. Densities of 1000–3000 m^{-2} have been recorded for various species [68]. Individuals may exhibit considerable longevity. Females of *Glomeris marginata* (Villers), for example, are known to live as long as 11 years [69]. Fecundity as high as 2000 eggs per female has been recorded in some species [68]. Most millipedes are detritivores, feeding on dead plant matter, such as leaf litter and wood, some also browsing on fungal mycelia. Trace fossils attributable to burrowing by millipedes, and including presumed fecal matter, have been found in strata of Late Ordovician (Richmondian) age, indicating that these animals have been active in soil processes for perhaps 445 million years [70].

The Symphyla are a rather small group of arthropods, with a reported 208 species in 13 genera and two families [71,72]. Populations, however, may be large in some environments, on the order of 10^3–10^4 individuals m^{-2}, and reach highest densities in cultivated soils [73]. Species also are common in grassland and forest soils. By one estimate, they may represent as much as 86% of the total myriapod population in some soils [74], but are often overlooked because of their small size and wide dispersion through the soil profile [75]. The group appears to reach its greatest diversity in warm temperate and tropical regions [76]. These animals are highly hygrotactic, and survive only in a soil atmosphere of 100% R.H. [77]. Symphyla are said to be extremely voracious, and will attack vegetable matter at an earlier stage of decomposition than will many other soil-inhabiting invertebrates [78].

2.3. Isopoda

These terrestrial crustaceans of the suborder Oniscidea are commonly known as woodlice or sowbugs. More than 3500 species in 518 genera have been described [79]. Despite their diversity, these animals are imperfectly adapted to a terrestrial existence. In particular, a set of structural (e.g., permeable cuticle) and physiological (gills) traits little modified from a marine ancestor means that the maintenance of water balance is of paramount importance to survival, and is largely achieved through behavioral means [80]. Isopods attain their greatest abundance in unmanaged temperate grasslands, numbers typically ranging from about 500–1000 m^{-2} [42]. A density of 7900 m^{-2} was estimated for *Trichoniscus pusillus* Brandt in scrub grassland in Britain, the maximum ever recorded for an isopod species [81]. Individuals tend to be long-lived, lifespans ranging from 1 to 2 years in semelparous species to 5 years in those exhibiting iteroparity [82]. The main dietary component is well-moistened detritus (leaves and wood residues), as well as their own feces, feeding on which permits the recycling of essential nutrients, such as inorganic copper [23]. Depending on species, breeding in temperate deciduous forests occurs during late spring to early fall when food resources are optimal (*i.e.*, abundant availability of partially decomposed litter) [83]. Fecundity of up to 250 eggs per female has been reported [82]. One to three generations per year appear to be typical.

2.4. Termites

Termites are members of the Isoptera, an order with over 2600 described species in 281 genera [84]. These social insects are said to dominate soil arthropod assemblages across much of the dry tropics and into dry temperate regions, such as the Chihuahuan and Sonoran deserts of the southwestern United States [85], although they attain their highest diversity in the tropics [86]. Two broad groups of termites may be distinguished on the basis of diet [23]. Species that feed on humus, which are commonly found in tropical rain forests and build subterranean nests, depend entirely on partly decomposed plant matter in the soil. Wood- and litter-feeders, more abundant in savannas, nest either in the wood itself or in conspicuous above-ground structures. Termite nests are founded cooperatively by a male and female of the reproductive caste following a nuptial flight from the parent colony; the colony workforce that issues from this union consists of non-reproductive males and females [87]. Colony sizes of 3 million individuals have been reported from the tropics [88]. Ecological and life history traits or conditions that have contributed to termite social evolution include a tendency towards familial associations in cloistered, food-rich habitats; slow development; overlap of generations;

monogamy; iteroparity; high mortality risk attending dispersal by individuals; opportunities for nest inheritance by offspring remaining in the natal nest; and advantages of group defense [89].

2.5. Ants

Ants, comprising a single family, the Formicidae, within the order Hymenoptera, are the dominant arthropods in most terrestrial environments [90]. More than 12,000 species in 288 genera and 20 subfamilies have been described [91]. As in the termites, all species are social. Ants are efficient exploiters of food resources, and the evolution of cooperative foraging undoubtedly has been a key to their success [92]. The majority of ants are generalist predators and scavengers; a few species specialize in culturing fungi for food. Ant colonies essentially are female societies, in which a single individual, the queen, is responsible for reproduction, all other duties being performed by the sterile female worker caste; the sole contribution of males is as sperm donors during mating flights [90]. The ecological importance of ants has been examined in a recent review [93], which highlights the many ecosystem support services provided by these insects.

3. Functional Roles of Arthropods in Maintaining Soil Fertility

The term "soil fertility" denotes the degree to which a soil is able to satisfy plant demands for nutrients (including water) and a physical matrix adequate for proper root development, which is significantly influenced by biological processes. Arthropods function on two of the three broad levels of organization of the soil food web [94]: they are "litter transformers" or "ecosystem engineers." Litter transformers, of which the microarthropods comprise a large part, fragment, or comminute, and humidify ingested plant debris, improving its quality as a substrate for microbial decomposition and fostering the growth and dispersal of microbial populations. Ecosystem engineers are those organisms that physically modify the habitat, directly or indirectly regulating the availability of resources to other species [95]. In the soil, this entails altering soil structure, mineral and organic matter composition, and hydrology. Ants and termites are the most important arthropod representatives of this guild, the latter group having received the greater share of research attention [96].

3.1. Influence of Arthropods on Nutrient Cycling

Upwards of 90% of net terrestrial primary production ultimately may enter detritus food webs [97], where it is decomposed and recycled. Much of it originates in leaves and woody materials falling to the soil surface. However, the below-ground contribution to detrital mass has been estimated at 1.75 times that of all above-ground litter inputs, and roots may provide 2.3 times more nitrogen to the soil pool than all other inputs [98]. Plant litter is a mixture of labile substrates (e.g., sugars, starch) easily digested by soil biota, and other components (cellulose, lignins, tannins) more resistant to breakdown [5]. Decomposition of this material results from an interaction between physical and biological processes [99]. Litter first must be physically weathered before it becomes suitable for further degradation by the soil microflora and fauna. Fungi are the important initial colonizers of plant litter [100]. With increasing disintegration and solubilization of the substrate, bacteria increase in importance. After this initial microbiological phase, the breakdown process slows, and might come to a

halt altogether were it not followed by animal activity [101]. Saprophagous arthropods affect decomposition directly through feeding on litter and adhering microflora, thus converting the energy contained therein into production of biomass and respiration, and indirectly, through conversion of litter into feces and the reworking (re-ingestion) of fecal material, comminution of litter, mixing of litter with soil, and regulation of the microflora through feeding and the dissemination of microbial inoculum [11,102]. With the exception of some termite groups [103], only a small proportion of net primary production is assimilated by soil arthropods (e.g., <10% in oribatids, 4%–20% in millipedes and isopods [104,105]). Thus, the indirect influences of these consumers on decomposition and soil fertility are considered, in general, to be of greater importance [106,107].

The influence of the soil fauna on decomposition processes is greatest in the humid tropics, where plant litter decomposition occurs most rapidly. This is due largely to the actions of the microarthropods [108]. In cold temperate zones, rates of biological turnover are curbed by low winter temperatures and the slow breakdown of toxic plant secondary compounds [107]. However, most of the studies concerning the contribution of arthropods to nutrient cycling have focused on soils in temperate regions; comparatively little information is available from the tropics [109–111].

3.1.1. Litter Feeding and Comminution

A major contribution of arthropods to the decomposition and humification processes is through the comminution of plant debris [69,112–115]. The physical fragmentation involved destroys the protective leaf cuticle, exposes cell contents, and increases water-holding capacity, aeration, and downward mobility of particulate and soluble substances. Comminution of plant litter is brought about largely by the feeding activity of saprophagous animals, and, during passage through the digestive system, is accompanied by catabolic changes. The unassimilated residue from the communitive and catabolic processes is excreted as feces, typically smaller in size and of different chemical composition than the ingested food [11]. The plant matter passing out in feces also presents an increased surface area to attack by micro-organisms.

A significant amount of plant material may be involved. For example, as much as 20% of total annual litter input typically may be processed by the feeding activity of Collembola [116], a like proportion by that of oribatid mites [104], with about 3%–10% accounted for by Isopoda and Diplopoda [117–119], and up to 60% by termites [120]. Symphyla were estimated by Edwards [114] to contribute about 2% to annual litter turnover. Collins [121] suggested that the biomass processed by termites commonly might be 2 or 3 times greater than the actual amount of litter consumed, for example, that a "nest in the base of a moribund emergent tree…may consume or comminute only a few kg of wood, but if the tree is felled as a result, then up to 20 t (w.w.) of timber and its nutrient content will be made available for translocation into the decomposition subsystem of the forest floor". Consumption of pine needles by isopods (*Porcelio scaber* Latreille) ranged from 1–33 mg day^{-1}, depending on leaf toughness, highly decayed needles being preferred [122]. Depending on the species involved, their densities, and the botanical composition, the mean litter comminution by millipedes in European forests ranged from 59 to 719 mg dry weight m^{-2} day^{-1} [123]. Coprophagy is common in these arthropods, and may be crucial to ensuring proper nutrition. In one study, the feces of millipedes showed an increase in pH, from 5.5 to 7.7, over that of the litter ingested

and an 8-fold increase in moisture content, providing a favorable substrate for increased microbial, particularly bacterial, activity, which accelerated further decomposition [124]. The bacterial biomass and digestion products improved the nutritional value of fecal pellets, which, on reingestion, provided a source of readily assimilable nutrients. Because of the large quantities of litter that they process, millipedes often are among the most important contributors, of all soil invertebrates, to litter decomposition in moist, undisturbed habitats [42]. In habitats, in which earthworms are absent or rare, such as the acidic mor soils of coniferous forests, Collembola may assume a much greater role in the physical breakdown of organic matter [125].

3.1.2. Mineralization of Nutrient Elements

For nutrients to be available for uptake by plant roots, they must be present in the soil in inorganic form. Mineralization is the catabolic conversion of elements, primarily by decomposer organisms, from organic (*i.e.*, bound in organic molecules) to inorganic form, such as the generation of CO_2 in the respiration of carbohydrates and breakdown of amino acids into ammonium (NH_4^+) and ultimately nitrate (NO_3^-). The direct or indirect actions of arthropods in processing plant litter, which may be nutritionally poor or resistant to decomposition, increase available nutrient concentrations in the soil. Micro-organisms efficiently convert the low-quality, recalcitrant resources of plant litter, such as the structural polymers comprising cell walls, into living tissue with much narrower carbon: nutrient ratios and of higher food value for animals, providing a rich source of nutrients at low metabolic cost to the consumer [11]. A major proportion of the nutrients in the litter/soil system is concentrated and temporarily stored, or immobilized, in microbial biomass, and subsequently in consumers, particularly the microarthropods, ultimately to be liberated in feces and upon death [126,127].

The microbial mineralization of nutrients may be stimulated by arthropod grazing. Several studies [128] have demonstrated that grazing by Collembola has a strong stimulatory effect on fungal growth and respiration. Hanlon & Anderson [129,130] showed that carbon mineralization by fungi and bacteria in comminuted litter was enhanced by an optimal level of grazing by micro- and macroarthropods; increased grazing pressure above the optimum inhibited microbial respiration. Collembolan grazing on fungi can result in increased mobilization of available N and Ca, with implications for nutrient availability in particular environments, such as acidic forest soils, in which large nutrient pools tend to be immobilized in stores of accumulated organic matter [131]. Isopod (*P. scaber*) feeding on oak and alder litter colonized by the microflora increased microbial respiration 10- and 20-fold, respectively, over that in plots, in which isopods were absent, and resulted in increased availability of the macronutrients, C, N, P_2O_5-P, K^+, Mg^{2+}, and Ca^{2+}, in the topsoil, attributable to the increased availability of feces as substrates for further decomposition [132]. Arthropod grazing on the microflora also acts to regulate the rate of decomposition, preventing sudden microbial blooms [133], with the result that nutrients are mineralized and released from detritus, and made available for plant uptake, in a controlled and continuous fashion and their loss from the system minimized [134].

Arthropods also influence the distribution of microbial populations in the soil by transporting microbes or their propagules on or in their bodies. For example, Szabó *et al.* [135] found millipedes to have large numbers of conidia of *Streptomyces* spp. adhering to their cuticle, and dense populations of

gut bacteria of the Actinomycetales, Bacillales, and Enterobacteriales, which were spread in feces. Feces of the collembolan, *Pogonognathellus longicornis* (Müller), contained viable fungal spores (Dematiaceae) [63]. Hassall *et al.* [136] suggested that a major contribution of isopods to litter decomposition was their role in dispersing microbial (particularly bacterial) propagules in feces. The microflora have limited inherent capacities for movement, and may remain for long periods in inactive resting stages if local conditions are unsuitable for growth and reproduction, their contribution to soil metabolism in stasis. Thus, the faunal-mediated dispersal of these organisms to more favorable environments may serve to stimulate decomposition processes and increase the number of foci of microbial activity.

Significant amounts of K^+, PO_4^{3-}, N, Na^+, and Ca^{2+} may be stored in soil arthropod (Collembola, Oribatida, Isopoda, and Diplopoda) biomass [117,137,138], these animals constituting an important nutrient pool in the soil, which temporarily immobilizes ions and prevents them from being leached. Arthropod remains also may constitute a significant portion of the total pool of elements, particularly Ca, found in soil, rivaling that of the living standing crop [139]. Nutrients unassimilated from food by the soil fauna may become concentrated in feces in available form. For example, Teuben & Verhoef [138] found the feces of Collembola to contain more than 40 times more NO_3^- nitrogen than their food (fungi and algae) and concluded that the contribution of feces increased nitrate availability in the forest floor by a factor of 2.4. About 9% of the total nitrogen content in *Corylus* (Betulaceae) litter was returned to the soil as NH_3 in the feces of the millipede, *Glomeris marginata* [140]. Higher concentrations of nitrogen in feces than in food were reported for other species of *Glomeris* [141]. The feces of *Oniscus asellus* (L.) had higher concentrations of sulfur than the leaf litter on which the isopod fed [142]. Termite feces also were shown to constitute important pools of nitrogen and carbon, estimated at 2 and 59 kg ha^{-1}, respectively [143].

Particularly in the drier, warmer areas of the world, termite foraging and other activities ensure efficient harvesting of litter and create conditions promoting microbial populations and the mineralization of organic compounds. For example, Buxton [144] reported that termites removed 91% of annual litterfall in tropical scrubland. Termites largely are dependent on gut symbiotes, flagellate protozoa and bacteria, for the digestion of the polysaccharides, such as cellulose and hemicelluloses, comprising a major portion of their food [88]. Those materials and others more resistant to breakdown, such as lignin, also may be processed externally by fungi and other microorganisms present in the nest [145], and converted into easily assimilable form. For example, the carbon to nitrogen (C:N) ratios of undecayed leaf litter and wood, typically 25–100:1 and 200–1200:1, respectively [146,147], are reduced by the white-rot *Termitomyces* fungi cultivated in the gardens of macrotermitine termites (Termitidae: Macrotermitinae) to values much closer to those of the tissues of the termites themselves (5–10:1 [85,148]). The termite colony thus is provided with organic matter relatively enriched in nitrogen. The fungal tissues fed upon by termites may be 38% protein or higher, and apparently are adequate for supplying the protein needs of the colony [149,150]. By feeding on these fungi, nutrients derived from plant litter ultimately are incorporated into termite biomass with high efficiency (e.g., > 50% assimilation of ingested N [151]). The end result of these nutritional adaptations is almost complete degradation of the plant materials originally collected by the termites, leaving very little residue [88]. Several termite species also are able to assimilate non-dietary nitrogen through fixation of atmospheric N by intestinal bacteria [152,153], and this source may provide a significant portion of the

nitrogen required by a colony [154]. Martius [155] estimated N-fixation by Amazonian rainforest species to be 115–145 g ha^{-1} year^{-1}. A major unresolved question is the fate of nutrients, particularly nitrogen (making up 6%–12% of tissues [156]), sequestered in termite bodies [143], although a substantial proportion must be returned to the ecosystem through predation [46,153], including the enormous mortality suffered by alate reproductives [103]. Lee [151] estimated nitrogen turnover via the predation pathway generally to range from about 1 to 25 kg ha^{-1}, and possibly to exceed 100 kg ha^{-1}, year^{-1}.

The nests of termites provide ideal conditions to support populations of a variety of microbial species instrumental in the mineralization of litter-derived nutrients [157]. The respiration of mound-building termites and their fungal comb was reported by Yamada *et al.* [158] to average around 10% of annual above-ground litterfall in dry tropical forest and savanna landscapes, and may exceed 20% when subterranean and other termite groups also are considered [159], a substantial mobilization of carbon. Mineralization of carbon by termite respiration in tropical rain forest was at lower rates, estimated at 1.0%–1.5% of annual litter production, and that by methane (CH_4) production considered negligible by comparison [155]. Termite-derived materials used in the construction of the nest center (hive or habitacle), galleries, and runways, such as carton, a mixture of excreta, soil mineral particles, and undigested, comminuted plant tissues, and saliva, may have appreciable nutrient content [88,160]. MacKay & Whitford [161] estimated the quantity of gallery carton deposited annually on the soil surface by subterranean termites in a North American desert ecosystem to be at least 2.6 tonnes ha^{-1}, accounting for a nitrogen input of 380 g ha^{-1}. Termite-modified soil incorporated into nests and other structures showed higher microbial activity [162] and was significantly higher, by several orders of magnitude in some cases, in NH_4^+ or NO_3^- nitrogen, Ca^{2+}, Mg^{2+}, K^+, and inorganic phosphorus [155,163–173] than surrounding, unmodified soil. Concentrations of available P in the mounds of *Procubitermes aburiensis* Sjöstedt were up to 76 times higher than in surrounding soil [174]. Mounds of two species of *Cubitermes* had up to 6 times the available P of adjacent soil, and also were significantly higher in available cations (Mg^{2+} and Ca^{2+}) and total N [175]. Those of Australian termitine and nasutitermitine species contained 2–7 times the nutrients (C, N, and exchangeable cations) as virgin soils [176]. Termite-modified soil also was significantly higher in organic matter and anions (HCO_3^-, Cl^-, SO_4^{2-}) than adjacent soil [177].

Termite nest material, which may originate from a network of chambers and tunnels of considerable areal extent (e.g., approaching 8000 m^2 [178]), ultimately is redistributed through weathering and erosion to enrich the surrounding soil [179]. Erosion rates may vary greatly, depending on the particular nest material involved and the intensity of rainfall, and may involve periods ranging from days to decades [161,180]. Aloni & Soyer [181] estimated the annual erosion rate by rainsplash of the mounds of *Cubitermes* spp. to be 3 tonnes ha^{-1}. Quantities of nutrients (in kg ha^{-1}) added annually to surrounding soil by erosion of macrotermitine mounds in East Africa were estimated by Pomeroy [182] to be: N (0.15–7.86), P (0.001–0.149), Ca (0.15–8.05), and K (0.05–2.54). The corresponding figure for N contributed by the mounds of Australian grassland species was an estimated 515 g ha^{-1}, 16% of the standing stock of soil inorganic nitrogen [171]. Material eroded from termite mounds and other structures may improve the fertility and productivity of nutrient-poor or highly weathered and degraded soils [183,184]. Aptly, termite nest material has been proposed as a soil amendment for crop production in agriculture [185].

Clearly, termites and their constructions function importantly in the replenishment of soil nutrients in natural ecosystems. The uniqueness of the involvement of termites in litter turnover and nutrient cycling was ably summed up by Lee & Wood [88] (p. 159): "The combination of foraging for food over a wide radius from the nest and returning it to the nest…intense degradation of the plant tissue collected, and use of the excreted end products of digestion for mound-building resulting in their removal from participation in the plant/soil system for long periods, sets termites apart from other soil animals in their influence on soil organic matter." Together with earthworms, they are thought to contribute more to litter breakdown than all other soil-inhabiting invertebrates [114].

Ant nests also may contain higher concentrations of nutrients than surrounding soil. Large amounts of organic matter from plant and animal (prey, carrion) sources accumulate in refuse dumps within nests. This material, combined with metabolic wastes and secretions from the ants themselves, which may become incorporated into nest soil, undergoes decomposition and mineralization by the microflora, leading to an accumulation and local concentration of nutrients [186]. For example, mounds of several ant species (mainly of the genera *Formica*, *Lasius*, and *Myrmica*) sampled in tallgrass prairie were significantly higher in exchangeable cations, such as Ca^{2+}, Mg^{2+}, and K^+, and in trace elements (Fe, Mn, Zn) than in soil without mounds [187]. Nests of species within the same genera, investigated by Czerwiński *et al.* [188], contained generally higher amounts of available P and K (P_2O_5, K_2O), as well as exchangeable cations (Ca^{2+}, Mg^{2+}, K^+, Na^+), and showed higher levels of microbial activity, than in uninhabited, control soil. A similar pattern was reported for mounds of the fire ant, *Solenopsis invicta* Buren, which were significantly higher in organic matter and concentrations of P, K, Ca, and Mg than in surrounding soil [189]. Baxter & Hole [190], Beattie & Culver [191], and Culver & Beattie [192] also found markedly higher concentrations of available P and K in ant mounds than in the surrounding soil. Mound soil was 3 times higher in NO_3^- and 28 times higher in NH_4^+ than ant-free soil [193]. The concentrations of available N were 600%–800%, and those of PO_4-P 200%–300%, higher in nests of the harvester ant, *Pogonomyrmex barbatus* (Smith), than in surrounding soil; organic matter content also was 25%–35% higher in the ant-modified soil [194]. Corresponding values were similar for nests of the slave-making species, *Formica sanguinea* Latreille [195]. The organic matter content of soil worked by ants was reported by Shrikhande & Pathak [196] to be 1.5 times greater than that of control soil. The increases in nutrient (e.g., cation) and organic matter content likely are factors influencing the generally observed shift in pH values towards neutral in ant-modified soil [197].

Particularly in infertile soils with low organic matter content and low rates of decomposition, predators, such as ants, speed the return to the soil of nutrients concentrated in the tissues of other animals [186]. This singular contribution of ants to organic matter turnover was recognized and emphasized more than a century ago by Wheeler [198]. A similar process results from the activities of those groups indirectly herbivorous in diet. The leaf-cutting attine ants (Myrmicinae: Attini), for example, are considered the chief agents for introducing organic matter, in the form of discarded fungus gardens, into the nutrient-poor soils of the New World tropics, this material then becoming available to other organisms for further decomposition [199]. After colony death, the enriched soil in the nests of these species serves as a locus for colonization by various plant species, and may act as an accelerator of succession, promoting a shift in the character of the vegetation from pasture to woodland [200]. The activities of this tribe of ants clearly facilitate the decomposition of plant

materials and promote nutrient cycling. Farji-Brener & Tadey [201] concluded that the magnitude of the contribution of leafcutter ants to soil fertility was among the highest of any animal group.

3.2. Influence of Arthropods on Soil Structure

Biology plays a major role in the stabilization of soil structure [202]. Among the more biologically significant attributes of soil are the spatial organization of soil particles, and of the pore spaces and voids among them, the combination of the particles into aggregates, and the stability of the aggregates in water [203]. A favorable soil structure ensures adequate nutrient retention, aeration, and water-holding capacity below ground, facilitates root penetration, and prevents surface crusting and erosion of topsoil. Arthropods affect the structural properties of soils in various ways.

3.2.1. Soil Mixing and the Development of Pores and Voids

Biotic pedoturbation refers to the displacement or mixing of soil material through the actions of organisms [204]. In general, the mesofauna are not considered important in this process because they are too small to move most soil particles (although some Collembola and oribatid mites are said to make active "microtunnels" in the soil matrix [205]); these animals instead rely on existing cracks and crevices, and the channels and spaces created by the larger fauna to aid their mobility within the soil [202]. The subterranean network of tunnels and galleries that comprise termite and ant nests plays an important role in enhancing aeration and water infiltration through the soil profile, increasing water storage, and retention of top soil. Termites have been reported to work the soil to depths of 50 m or more [206]. The heaps of accumulated old nest material of an *Anoplotermes* species in Amazon floodplain forest had infiltration rates more than 27 times higher than in surrounding, unmodified soil [207]. In experimental studies, Elkins *et al.* [208] and Whitford [209] found plots, from which subterranean termites had been eliminated, to have significantly reduced water infiltration and storage, and increased runoff and sediment flow (bedload) compared to plots populated with termites. Mando and colleagues [210–212] showed that active encouragement of termite activity through the application of surface mulches significantly improved the hydraulic properties of degraded soils. Under such conditions, soil, in which termites (*Macrotermes subhyalinus* [Rambur] and *Odontotermes* sp.) were active, had infiltration rates ranging from 2 to 6 to above 9 cm^3 s^{-1}, 2–3 times those in soil without termites [213]. Infiltration rates around the nests of four abundant species of ant averaged 120 mL min^{-1}, more than 3 times as rapid as through the surrounding farmland soil [214]. The infiltration pathways and sinks provided by ant nests limited post-fire hill-slope erosion by reducing overland water flow rates following heavy rainfall events [215]. Experimental crop yield increased 36% and infiltration rates 3-fold in plots supporting ant and termite populations over those in plots, from which the insects had been excluded [216]. The system of chambers and galleries comprising ant and termite nests, which increases the porosity of soil, improving aeration and water infiltration, together with the organic matter (from feces, salivary and other secretions, food remnants [217,218]) accumulating therein, which enhances water-holding capacity, creates an environment favorable for the penetration of plant roots [186,219].

The thrust delivered by numerous dual leg pairs, together with the calcified head capsule and leverage provided by the labrum, collum, or a flat back in some species, enable millipedes to force

their way between closely packed soil particles and excavate burrows [68,69]. These animals also may contribute indirectly to increasing water infiltration by consuming dead and decaying root systems, thereby opening channels within the soil [220]. The isopod, *Helleria brevicornis* Ebner, is known to excavate vertical burrows in soil up to 10 cm deep [23].

Jacot [221] identified millipedes as one of the groups instrumental in mixing organic matter with the mineral soil. Oribatids also are thought to contribute to the deep mixing of organic material by their movements to, and deposition of feces in, lower layers of the soil profile [36]. Similarly, the tendency for symphylans to move rapidly up and down the soil profile serves to distribute their feces widely throughout the soil [78]. Fecal materials are major constituents contributing to the formation of stable soil aggregates (see discussion below), which are important in maintaining adequate water infiltration and drainage [222].

The activities of ants and termites below ground may have a significant influence on the particle size distribution within the soil. In particular, the selective removal of the finer and smaller soil particles from lower in the profile may result in a greater contrast in texture between the A (topsoil) and B (subsoil) horizons, with implications for abiotic pedogenic processes, such as the development of suspended water tables or an increase in the redox potential within the soil, which affects nutrient availability and the capacity of the soil to support vegetation [223]. Early on, Shaler [224] suggested that, in moving particles upwards through the soil profile, because they are more widespread than earthworms, ants, in the aggregate, had a much greater influence on soils. This view largely has been supported by a sizeable body of research over the ensuing years [225], which indicates global rates of ant-mediated pedoturbation of *ca.* 10 tonnes ha^{-1} year^{-1}. In some areas, the rate of transfer of soil to the surface by ants is significantly higher than that via earthworm casting [215]. Construction of the average leafcutter ant (*Atta* sp.) nest may require the excavation of up to 23 m^3 of soil [201] weighing approximately 40 tonnes [199]. Sudd [226] found that ants of various temperate-zone and tropical species were capable of moving to the surface from 35 mg to more than 1100 mg of soil per nest day^{-1}. Lyford [227] estimated that at least 60 g m^{-2} of soil in a New England (USA) forest were transferred annually by ants from the B horizon to the surface in the process of mound building, and suggested that the entire A horizon (25–46 cm thick) of some of the virgin brown podzolic soils of the region was the product of such pedoturbation over a period of 3000–4000 years. An estimated 6 m^3 (7.4 tonnes dry weight) of soil ha^{-1} was moved by ants (*Formica cinerea* Mayr) from the B horizon to the surface to form the upper parts of extant mounds in a North American prairie [190]. Bulk density (a function of porosity and organic matter content) of the deposited material was significantly lower than that of the surrounding soil (~0.29–0.53 *vs.* 1.04 g cm^{-3}). Nest building by *Atta cephalotes* (L.) in a tropical forest resulted in displacement to the surface of an estimated 460 tonnes of subsoil ha^{-1} over the average colony's lifespan [228]. The authors concluded that leafcutter ants played a major role in soil genesis and development in areas of the New World tropics. In a soil that contained traces of old nests at different levels, Béique & Francœur [229] also showed that ants brought a considerable amount of material from the B horizon to the surface, thus restoring to the root zone of plants nutrients that had previously washed down through the soil profile.

Termite mounds often are abundant in tropical regions, numbering in excess of 1000 ha^{-1} and representing, in aggregate, many tonnes of soil [88]. In regions, in which mounds are numerous, an estimated 1 tonne or more ha^{-1} of mineral soil from the lower horizons was deposited on the surface

annually [169,230]. The estimated amount of soil brought to the surface by subterranean termites in a temperate desert was somewhat lower, at about 750 kg ha^{-1} year^{-1}, and included a rich clay component [170]. The nest-building activity of termites was calculated to result in pedoturbation of a 20–37-cm-thick layer of soil in 1000 years, contributing significantly to soil turnover [181].

Other arthropod groups have demonstrated prodigious earth-moving abilities, which may contribute importantly to soil formation. For example, the dry clay (so-called takyr) soils of arid regions of southeastern Russia, which contain large amounts of gypsum and salts, were reported by Dimo [231] to be extensively worked by desert isopods of the genus *Hemilepistus*. At an estimated population density of 1.4 million individuals ha^{-1}, the animals were deemed capable of transporting, from a depth of up to 1 m to the surface, 5–6 tonnes of soil, of a different granulometrical and chemical composition, annually. As a result, the improved topsoil was able to support a more diverse and dense vegetation.

3.2.2. Formation of Soil Aggregates

Soil aggregates, or peds, the basic units of soil structure, are formed by natural processes, commonly involving the activity of organisms [8,232]. Fecal pellets, combining fine mineral particles with undigested organic matter, are the major contribution of invertebrates to the formation of soil aggregates [205,233]. Mucilaginous substances, byproducts of microbial decomposition, bind the feces with other soil components into stable microstructures [202,234]. These organomineral complexes are substrates, on which inorganic nutrients may become adsorbed and so available to plants [23]. The resulting humus, an amorphous colloidal material comprising partially decomposed organic matter that makes up topsoil and increases the soil's capacity to store nutrients (e.g., cations) and prevent their rapid leaching, thus is largely derived from animal feces [235–241]. The humus of well-developed soils represents a significant pool of macronutrients, such as N, P, K, Ca, and Mg, which may be stored in amounts exceeding 1 tonne ha^{-1} [242]. It also is involved in chelation reactions, which aid in the micronutrient nutrition of plants, buffers the soil against rapid changes in pH, and supports an abundance and diversity of micro-organisms, promoting increased mineralization activity [243].

The fecal pellets of Collembola readily agglomerate and form water-stable aggregates in soil [244]. Strong interparticle cohesive forces within fecal pellets contribute to their persistence [245]. Feces of Collembola and other microarthropods constitute a significant proportion of the humic material in developing sand dunes, and are thought to contribute to dune consolidation and stabilization by binding sand grains into larger aggregates [246]. The fecal pellets of Collembola are central to the formation and persistence of the microstructure in some arctic, alpine, and other weakly developed soils [247]. Organomineral micro-aggregate structures from the feces of soil-feeding termites also are thought to aid in increasing structural stability and porosity of tropical soils [248,249]. In areas of high termite activity, these micropeds may comprise 20% of the soil matrix [250].

Arthropod feces generally play a larger role in the formation of the moder and mor types of humus [30,238] and in the formation of primitive soils (rendsinas, rankers [251]). However, although earthworms generally are considered to predominate in the development of mull-type soils [6], arthropods, such as millipedes, also may contribute substantially to these or to mull-like formations [252,253]. (By contrast, a lack of millipedes, as well as earthworms, in the mor soils of coniferous forests is thought to be one of the main reasons for the slow decomposition of pine

needles [68].) The volume of feces contributed may be considerable. For example, collembolan populations, at densities typical of forest soils, were estimated to produce around 175 cc of fecal pellets m^{-2} annually [254], equivalent to the formation of a soil layer of roughly 0.2 mm in depth [255]. Production of fecal pellets by desert isopods (*Hemilepistus reaumuri* [Audouin & Savigny]) ranged from 2 to 41 g m^{-2} year^{-1}, depending on site conditions (primarily moisture regime), subsequently to be redistributed and mixed with soil during rainfall events [256]. Striganova [257] (cited in [42]) estimated that annual millipede consumption of litter in woodland would result in deposition of a layer of fecal pellets 0.5–1 cm thick on the soil surface. On rocky sites, millipedes (Glomeridae) may facilitate the process of succession by consuming the detritus accumulating in cracks and depositing their excrement there, providing a substrate favorable for the colonization of higher plants [23].

Table 1. Approximate abundance (number m^{-2}) of hemi- and euedaphic arthropods in different soils [11,42,90,258–265].

Body-Size Group [5]	Taxon	Soil Type					
		Tundra (arctic alpine)	Mor (boreal forest)	Mull (warm temperate forest)	Temperate Grassland (prairie)	Tropical Savanna	Tropical Forest
Mesofauna	Microarthropoda	100,000	400,000	40,000	25,000	2000	15,000
	Symphyla	0	3000	600	1000	2000	800
Macrofauna	Diplopoda/Isopoda	0	500	1000	500	<1	400
	Formicidae	0	50	3000	1000	2000	800
	Isoptera	0	0	1000	1000	4000	5000

4. Conclusions

Soils are integral parts of ecosystems, and are maintained in a fertile state largely through the actions of their constituent biota. Fertility is a function of a soil's capacity to provide plants not only with essential nutrients for growth and reproduction, but also with a physical matrix that facilitates root growth and respiration, and maintains its structural integrity against erosive forces. Arthropods influence soil fertility in two principal ways. First, they promote the decomposition of plant litter directly, by converting it into their own tissues, and indirectly, by transforming it physically and chemically into substrates amenable to further degradation. The higher assimilation efficiencies of termites allow these animals to convert a greater proportion of ingested litter directly into biomass than is possible for other soil arthropods, whereas the main contribution of the Collembola, Oribatida, Myriapoda, and Isopoda to nutrient cycling is via the indirect route, as secondary decomposers, conditioning litter, through comminution and passage through the gut, for further breakdown by the microflora. The nests of termites and ants, with their incorporated fecal materials, waste dumps, or fungal gardens, also provide rich substrates for the microbial degradation and mineralization of organic matter. The end result of these processes is the conversion of complex organic molecules into simpler, inorganic forms that can be used by plants. Arthropod grazing on microbial populations also may serve to regulate the availability of nutrients to plants, ensuring their release in a controlled and continuous manner and minimizing their loss from the root zone.

The second major way, in which arthropods contribute to the maintenance of soil fertility, is through their effects on the physical structure of the soil. Ants and termites are the pre-eminent earth

movers in many regions of the world, and may surpass earthworms in this capacity in some cases. The pedoturbation resulting from their activities brings substantial amounts of subsoil to the surface, increasing the mineral content of the topsoil and providing sites for ion exchange in the root zone. The tunneling and burrowing of arthropods provide channels for air passage and water infiltration, and also serve to mix organic matter into the upper soil layers. The feces of arthropods serve as nuclei for the accretion of soil aggregates, basic units of a soil's structure and important in maintaining its integrity, and are a significant factor in the formation of humus, which contributes to water and nutrient retention in the soil.

This review has attempted to establish and emphasize the importance of arthropods as beneficial members of the soil fauna. Such recognition may largely be absent from the public imagination. There appears to be little appreciation of the key roles of arthropods as providers of essential ecosystem services, particularly those involving the breakdown and recycling of dead plant matter. As a case in point, perhaps second only to earthworms, termites contribute more to plant litter breakdown than all other soil invertebrates, and termites are the main agents of degradation, among the soil fauna, of the highly recalcitrant materials (cellulose, lignin) making up wood. Yet these insects routinely are maligned and their status as pests greatly exaggerated. For example, a series of commercial spots currently (July 2013) appearing on North American television, which advertises the services of a leading pest control company, depicts impossible, nightmarish creatures (none of which resembles, even remotely, an insect or any other arthropod) demolishing houses and declares in an ominous tone that "termites are monsters." Such an assertion is preposterous, and is unfortunate in its perpetuation of a myth. The benefits provided by termites in breaking down woody materials, which otherwise would accumulate on the landscape and persist for long periods of time, and speeding the return of their nutrients to the soil system, undoubtedly far outweigh any costs they impose as structural pests. In the unimaginable absence of these and other arthropods, their activities, and the processes that they influence, soils unquestionably would be impoverished, and, in some regions of the world, in which important elements of the fauna, such as earthworms, are rare or absent, might fail to support other than only the most highly simplified communities.

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Conflicts of Interest

The author declares no conflict of interest.

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