

The Functional Roles of Forest Soil Arthropods: The Soil Is a Lively Place¹

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Abstract

Plant growth depends upon the activity of numerous types of organisms within the environment. The recycling of nutrients in the forest floor involves the interaction of a vast diversity of bacteria, fungi, protozoa, and invertebrates. Arthropods are integral to the initial shredding of the litter, which exposes nutrients to microbial digestion. Hundreds of California species either feed directly upon decomposer microorganisms or prey upon microbivorous taxa. Microbivory enhances the succession of microbial taxa with different enzymatic capabilities for processing soil resources. The final step of recycling, the entry of soil nutrients back into a root, is largely the result of invertebrates feeding upon microbes which have immobilized nutrients within the rhizosphere. Forest management practices can significantly alter soil foodwebs, which may in turn have significant effects on long-term soil productivity. Because arthropods facilitate a number of different soil processes, assays of soil arthropod abundance and community composition may prove to be useful in developing an understanding of the effects of forest management on nutrient cycles in forest soils.

Introduction

No one would deny that there is a formidable biological component to soils (Dindal 1990, Edwards and others 1988, Eisenbeis and Wichard 1987, Petersen and Luxton 1982). It is also undeniable that the fauna, microbes, and roots in healthy soils play a number of interactive functional roles (Benckiser 1997, Coleman and Crossley 1996, Fitter and others 1985). It is unfortunate, therefore, that as scientists and managers we are still rather naive in our understanding of soil ecology.

Can we delineate some of the most important functional roles played by the fauna in the soil? Can we associate these roles with individual species or groups of species? Can we devise simple cost-effective methodologies to evaluate both the effectiveness and the unintended nontarget effects of silvicultural practices (cool-burning, fertilization, herbicide application, compaction) on the integrity of soil ecosystems? We certainly can, but it will require the impetus of research managers and new collaborations between resource managers and university and government scientists.

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The Plant-Soil Interface: The Microbial Sheath

In natural ecosystems, plant roots do not function all by themselves. A growing body of research has demonstrated that nearly all plant species form symbiotic associations with fungi known as mycorrhizae. The majority of the absorptive surfaces of the roots of each mycorrhizal species are likely to be intimately involved in these symbioses. Less easy to quantify are the ensheathing populations of bacteria. The extent to which these neighboring microbes dominate the flow of nutrients into and out of plant roots is not generally appreciated.

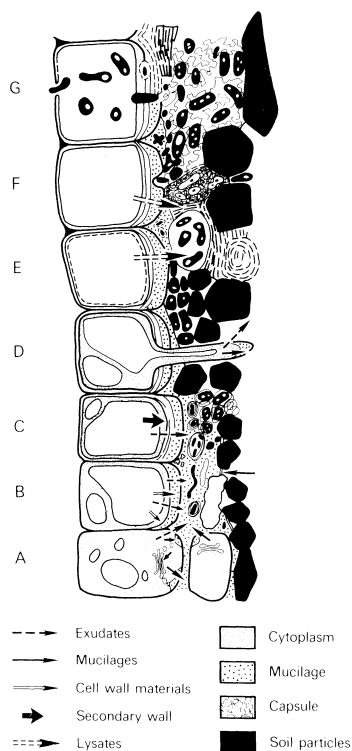


Figure 1—Stages in the life of a root surface cell and nearby rhizosphere. At A, the root cap zone, there is massive excretion of gel by the dictyosome vesicles into the rhizosphere. At B, the epidermal cells are emerging from beneath the root cap and beginning to extend; at this stage the cell is enclosed only by a primary wall. With cessation of longitudinal extension, the cell secretes a secondary wall (stage C) that the developing root hair must penetrate (stage D). With mechanical and microbial lysis of the cuticle, further mucilages are released into the soil. These organic materials together with the products of cell autolysis provide substrates for microorganisms, which proliferate in the rhizosphere (stage E). These microorganisms break down the primary wall (stage F) and invade the epidermis and cortex (stage G). At this stage the outer cortex ceases to function physiologically (Foster and others 1983).

Roots larger than several millimeters in diameter serve to anchor the plant and transport water and water-soluble nutrients. Active physiological metabolism and uptake of nutrients are confined largely to the tips of fine roots. The growing tip of the rootlet secretes a wide variety of chemicals that are easily metabolizable carbohydrates (*fig. 1*; Foster and others 1983). These carbohydrates fuel rapid

bacterial growth and reproduction throughout the immediate vicinity of the rootlet (the rhizosphere). Fungal growth in the rhizosphere may be saprophytic, parasitic, or symbiotic. Symbiotic growth may form diverse compound structures, but two common forms predominate (Allen and others 1994). Fungal hyphae may completely envelop the rootlet with a thick covering (interwoven with the underlying root epidermal cells), thence radiating out for as much as several meters, often as individual fungal strands (ectomycorrhizae; *fig. 2*). Other fungi grow inward to penetrate through the cell wall of root cells, expanding into numerous pouches in direct contact with the plant cell membrane, simultaneously growing outward into the soil for several centimeters (endomycorrhizae; *fig. 3*).

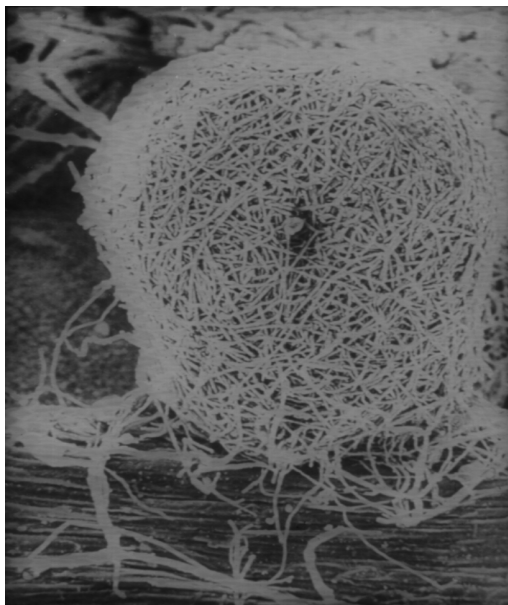


Figure 2—*Pinus strobus* root tip with ectomycorrhizal sheathing of *Pisolithus tinctorius* (Slide by James Trappe).

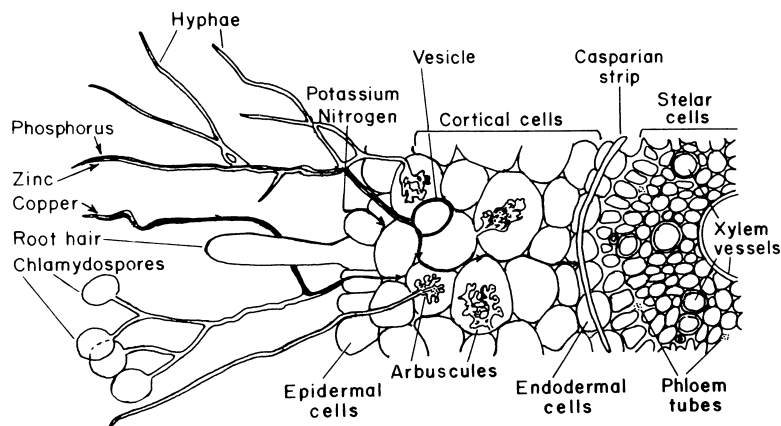


Figure 3—A typical endomycorrhiza showing hyphae extending beyond the root epidermis into the rhizosphere (Curl and Truelove 1986).

As a plant root matures, it is encased by a gelatinous sheath populated with bacteria and mycorrhizae (Curl and Truelove 1986, Foster and others 1983). As the outer epidermis ruptures, fine roots leak significant quantities of nitrogenous amines and micronutrients into the rhizosphere (*fig. 1*). In this manner the root provides large amounts of carbohydrates and smaller amounts of various other substances that facilitate microbial growth in the rhizosphere. Subsequently, bacterial and fungal metabolism produces catalytic exoenzymes, proteins secreted into the soil, which enzymatically degrade organic chemicals and alter inorganic chemicals. The majority of these soluble nutrients, which may be useful for plant growth, are probably captured by the bacteria or fungi within the rhizosphere. The root becomes encircled by microbes, and microbial metabolic levels far exceed that of the root itself.

Without fauna in the soil to graze upon bacteria and fungi, most of the nutrients would eventually accumulate in microbial tissue (Moore and others 1988).

The Nature of Recycling

The Faunal Factor

From the plant's point of view, nutrient recycling must make available the limiting chemicals incorporated within the forest floor litter and provide a supply of required chemicals from the inorganic geologic substrate. Because plant roots are incapable of secreting enzymes to carry out these chemical transformations (Curl and Truelove 1986), plants are ultimately and completely dependent upon exoenzyme production by bacteria and fungi in the soil, and to a lesser degree upon the enzymes secreted within the digestive systems of soil-inhabiting fauna (from protozoa to vertebrates). Some abiotic chemical degradation occurs in the most extreme environments (deserts, bare rock surfaces), but these are exceptions to the general case of dependence upon microbial enzymatic degradation. Microbial degradation of resources within the soil matrix leads primarily to growth of microbes themselves because the potential absorptive surface area of microbes greatly exceeds that of roots. Thus, microbes can generally compete more efficiently for soluble nutrients. Microbial exoenzymes benefit plants only if some of the enzyme catalysis occurs directly next to a root tip or if mycorrhizal fungi directly share resources with the plant. Bacteria and fungi serve as a biological sponge in the soil, "immobilizing" or "pooling" nutrients from dead organic residues and the inorganic substrate by incorporating them into their own living biomass.

Soil fauna facilitate microbial growth and chemical degradation by:

- Shredding the dead plant parts in forest litter and burrowing into coarse woody debris.
- Moving either the resources or the microbial inocula in a continual homogenization of the soil.
- Improving the water-holding and oxygen-penetrating capabilities of the soil through the *geometry* and chemistry of their fecal pellets, which is soil itself.
- Enhancing the expression of the full range of chemical potentials of soil microbes by facilitating the succession of taxa with different exoenzymic capabilities.

- Liberating into the soil solution (also known as "mobilizing" or "mineralizing") the nutrients pooled within the microbial biomass of the rhizosphere by grazing upon the bacteria and fungi currently active around or within the microbial sheathing of physiologically active roots (Moldenke and others 1994, Seastedt 1984, Setälä and Huhta 1991, Visser 1985, Webb 1977).

Shredding and Burrowing

The half-life of different species of coarse woody debris on the forest floor is largely a function of the abundance and diversity of wood-boring insects (largely ambrosia, long-horned or metallic woodboring beetles) (Schowalter and others 1988). Boring insects carry microbial inocula and provide increased access for fungal attack (Ingham and Moldenke 1995). Often these beetles require the presence of actively growing fungi to concentrate limiting nutrients within the wood (Crowson 1981, Martin 1987).

Nutrients in dead leaves or needles are largely unavailable to most microbes. A bacterium in the leaf litter is analogous to a person in a pantry without a can opener. Eventually a person can beat a can open, but it is much more effective to have a can opener. The arthropod shredder is the bacterium's can opener. Bacteria and fungi will eventually use all of a dead leaf, but they are far more efficient if the leaf is shredded first. Shredders (i.e., millipedes, earthworms, sowbugs) crush vast quantities of plant cells from which they extract only the most readily available nutrients--the rest enter the normal soil recycling chain as the shredders defecate the crushed fragments (Hopkin and Read 1992). Passage through numerous shredding devices (the mouthparts of even much smaller organisms, i.e., penknife mites) is required before all the resources are finally available for complete enzymatic digestion (Dawod and FitzPatrick 1993). This process of continually refined shredding takes time, which accounts for the persistence of humus layers in the soil.

Transportation and Homogenization

People take mobility for granted until they become physically disabled. There may be 500 million bacteria in a teaspoon of forest soil, but each one is largely incapable of movement even though some bacteria have flagella that permit limited movement. Each bacterium needs diverse nutrients for growth and reproduction. From a bacterium's point of view, a resource that is several microns away is infinitely far away, because some other competitor is likely to be closer to the resource. There are several solutions: find a method of travel to cross the distance (hitchhike); have someone bring the resource to you; or hope that all your competitors between you and the resource already have enough of the resource and will not steal it before it diffuses back to you. Soil fauna fill the first two roles and provide a better chance of success for the bacterium.

Bacterial and fungal inocula can be carried either on the outer body surfaces of invertebrates or in their intestinal tracts (Anderson 1988, Visser 1985). In general, the number of spores carried phoretically is directly proportional to the surface area of an organism. The viability of ingested inocula is generally proportional to the time it requires to pass through the length of the gut (Anderson 1975). Well-fed individual invertebrates have high percentages of viable inocula in their feces, whereas poorly

fed individuals produce feces with minimal viable inocula. The best-known transporters of both organic substrates and microbial inocula are anecic earthworms (species that feed largely on the soil surface, defecate deep in the soil, and construct extensive tunnels in the rooting zone) (Lavelle 1988).

Building the Fabric of the Soil

Kubiena (1938) at the University of Iowa was the first American to carefully document the contribution of different invertebrates to the microstructure of the soil. Pawluk (1985) at the University of Alberta has recently documented the invertebrate biogenic characteristics of all natural Canadian soils. Thin-section photography has revealed that the humus, A-layer, and much of the litter and B-layers are mostly invertebrate feces (*fig. 4*). Living between (and sometimes within) these feces are the occasional roots, microbes, protists, and invertebrates, together with scattered undigested dead plant and animal material (Bal 1982, Rusek 1985). The content of the feces can be largely organic (litter consumers), inorganic (deep soil endogeic earthworms), or heterogeneous mixes (mobile millipede coprovores). Only in soils with very low organic content (deserts) or frequent disturbance (annual row crop agriculture) do invertebrate feces fail to be the predominant structural elements (Pawluk 1985).

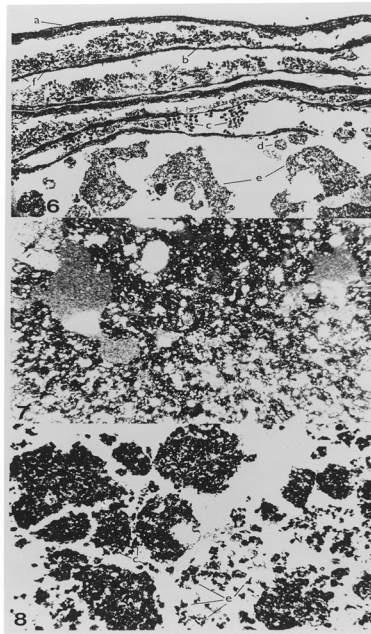


Figure 4—Thin sections of Bohemian oak soils. Top: oak leaves partially metamorphosed into feces by Collembola (f), Enchytraeidae (b), oribatid mites (c). Below the leaves are droppings of fungus-gnat larvae (d) and the epigeic earthworm *Dendrobaena rubida*. Middle: soil fabric of mineral soil composed entirely of feces of endogeic earthworms. Bottom: Droppings of epigeic earthworms near surface of a mull soil subsequently partially disintegrated by enchytraeids (e) and Collembola (c) (Rusek 1985).

The size, shape, and percentage of organic content in the feces control many physical and chemical properties of different soil types (Martin and Marinssen 1993). A matrix of large fecal pellets promotes macropore formation, facilitating aeration and infiltration. Dense mixes of small feces promote wettability and refugia from predators. The majority of soil-dwelling arthropod species probably feeds principally upon the fungi growing on the surface of fecal pellets (Anderson 1975). As they graze on the hyphae they often physically abrade the pellets themselves, exposing additional nutrients to microbial attack.

Each time an annelid worm or arthropod ingests solid food it secretes copious carbohydrate lubricants (mucus). These carbohydrates do act as energy sources for intestinal microbes, but in most instances the mucus ultimately surrounds and embeds the fecal material as well (Edwards and Lofty 1972, Lee 1985). When the content of the fecal material is largely inorganic, as it is for most deep-dwelling earthworms, this input creates a branching "drilosphere" throughout the soil of additional resources and subsequent microbial growth (Barois and others 1993, Bouche 1975).

The feces of earthworms are continually reingested to exploit the nutrients filtered from the soil solution by microbial populations. Thin-section soil micrographs document that soil structure is dominated by invertebrate feces, but it is the largely unstudied rate of re-consumption that drives the turnover of the embedded nutrients.

Microbial Succession

There may be as many as 40,000 kinds of microbes in a single teaspoon of soil (Tiedje 1994). These different microbes exhibit a wide variety of chemical capabilities (Fox 1994, Hawksworth 1991, Palleroni 1994). This level of specialization for resources is mediated by the fauna. The vast majority of microbes is inactive at any given time; only the subset of species capable of using the actual specific chemical composition of resources currently available is metabolically active (Lavelle 1994). As such species grow, and consequently change the chemistry of the remaining resources, the fauna consume them (presumably after most of them have reproduced), which permits other species to succeed them.

Although the rate of microbial grazing by soil fauna in different soil types remains largely unquantified, such grazing rates may be very high (Coleman and Crossley 1996, Visser 1985). More than 200,000 individual fungivorous arthropods can inhabit every square meter of conifer forest soil on average (Moldenke 1990, Petersen and Luxton 1982). The most frequently occurring fungivorous arthropods are oribatid mites, endeostigmatid mites, and springtails. The fungivorous springtail, *Onychiurus*, is the prime determinant of the fungal community composition of a conifer soil in Scotland (Newell 1984). By preferentially consuming a fast-growing species, it keeps fungal diversity high; when *Onychiurus* is removed, a single fungal species predominates, representing 90 percent of the fungal biomass.

Microbial Grazing and Consumption of Microbes

Plant growth depends upon nutrient uptake by the roots. When nitrogen, either as NO_3 or NH_4 ions, is released as an enzymatic byproduct into the soil solution, how does it enter a root? Since the carbon:nitrogen ratio of bacteria and fungi is very low compared to that of the plant material and organic matter they "eat," these organisms

act as accumulators ("sinks") of nitrogen. Bacteria growing within the rhizosphere mucigel have ample supplies of labile carbon. They require nitrogen and other soluble nutrients that are being drawn toward the root as water enters the root's vascular system.

A large fraction, perhaps most, of the nitrogen in growing plants enters a root as the result of fauna grazing the microbes in the rhizosphere (de Ruiter and others 1993, Moore and others 1988). As rhizosphere-grazers (the protozoa, rhabditid nematodes, bacteria- and fungus-feeding mites, and springtails) scrape bacteria and fungi off the root surface and consume them, they defecate (Kuikman and others 1990). Some of the nitrogenous byproducts in these feces can penetrate the disturbed microbial sheaths of the roots. As long as the populations of microbial grazers do not get too dense, they stimulate mycorrhizal growth and exoenzymic activity (Finlay 1985).

Two studies substantiate this interpretation. First, a culture of fungi, bacteria, protozoa, and nematodes from native grassland soil was incubated in a microcosm, and the rate of nitrogen mineralization was estimated by intermittent drainage of soil water (Hunt and others 1987). When biocides were added to kill the protozoa and nematodes grazing on microbes, mineralization rate decreased by more than 82 percent.

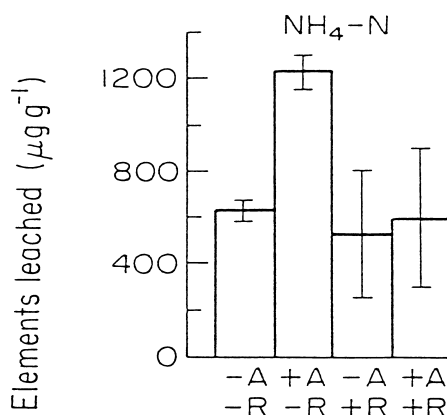


Figure 5—Total ammonium released as leachate from microcosms with 6-week incubation under four experimental treatments. A = arthropods; R = roots of oak seedlings; + = presence; - = absence. Incubation with arthropods alone mineralized significantly more nitrogen (Anderson and others 1985).

Second, normal soil profiles of English oak forests containing natural populations of soil microbes and protozoa were reconstituted in the laboratory (Anderson and Ineson 1982, Anderson and others 1985). Nitrogen mineralization was monitored in the leachate, and a base rate for microbes in the absence of any plant roots or arthropods was established (*fig. 5*). Addition of a growing oak seedling did not affect the rate. The oak root cannot directly cause mineralization, and it can act only as a passive sponge. Addition of an arthropod shredder greatly enhanced nitrogen mineralization. The increased rate of nutrient mineralization was directly

correlated with the biomass of shredders added (relatively independent of specific taxon). Surprisingly, synchronous addition of both oak seedling and arthropod shredders resulted in no detectable difference from the basal rate of nitrogen leaching with only microbes present. The "missing" nitrogen that should have leached in their combined presence manifested itself in an increased rate of seedling growth (more than fourfold higher than in the absence of arthropods).

Biodiversity Is "Politically Correct," But Are So Many Kinds Really Needed?

We estimate that there are probably 200-250 species of soil arthropods per square meter and 2,500 per square kilometer of western coniferous forest soil⁵ (Parsons and others 1991). There are dramatic changes in the soil fauna as one compares north-facing versus south-facing slopes, young stands and mature forest, and pine forest and oak forest.⁶ Among all of this diversity, are there certain species that may perform special roles?

The Unique Role of the Macroshredder

Different ecosystems throughout the world are characterized by fundamentally different soil chemical and physical properties. The fundamental chemical differences result largely from the geologic substrate, but the physical attributes (the development of horizons, the microporosity, structure, and wettability) are largely a result of the biota.

Most of the California and Oregon conifer forest soil is what Europeans call a "mor" soil, with rather distinct strata separating litter, humus and mineral soil (Klinka and others 1981). In perennial Valley Grassland soil (called "mull"), on the other hand, there is rapid incorporation of organic materials into the subsoil and consequently an indistinct separation of organic and inorganic layers within the rooting zone. Mull soils are created largely by the activity of earthworms, a critical subset of which are called anecic worms (*fig. 6*). Anecic worms have vertical burrows and take living or dead leaves from the surface to feed upon and excrete deep in the soil (Lavelle 1988). In the conifer forest, characterized by few earthworms, earthworms have horizontal burrows. Consequently, there is little mixing between the upper soil layers, resulting in a mor structure. A majority of the species of invertebrates living in our forest soils are either fungivorous or predaceous. Very few species fill the functional role of large-bodied (> 5 mm) detritus consumer or macroshredder.

In Oregon forests the millipede *Harpaphe* is the principal macroshredder (Moldenke 1990). In northern California ponderosa pine forests it is the spirobolid millipede (Moldenke 1992). These two keystone species regulate the rate of initial shredding of fallen leaf resources. The more common the millipede, the thinner the litter layer becomes and the faster it is metamorphosed into humus. Our own investigations throughout the Northwest have shown that macroshredder populations decrease along a latitudinal gradient along the West Coast conifer belt of North America: California has significant populations of both earthworms and millipedes;

⁵ Unpublished data on file at Department of Entomology, Oregon State University, Corvallis, OR 97331.

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Oregon has dense populations of millipedes but scant earthworms; mainland British Columbia possesses few millipedes and no earthworms; Alaska has no macroshredders at all. The litter layer builds up more rapidly as you go north, because of the absence of macroshredders. In Alaska, for example, litter decomposition is so slow under conifer forests that as the forests age, the insulating litter layer passes a critical point and permafrost results. Shredding of forest floor litter in Alaska is left only to the microshredder mites and springtails, and, as a consequence of slower activity, much of the ecosystem nutrient supply becomes immobilized in the permafrost and forest growth becomes extremely slow (Flanagan and van Cleve 1977).

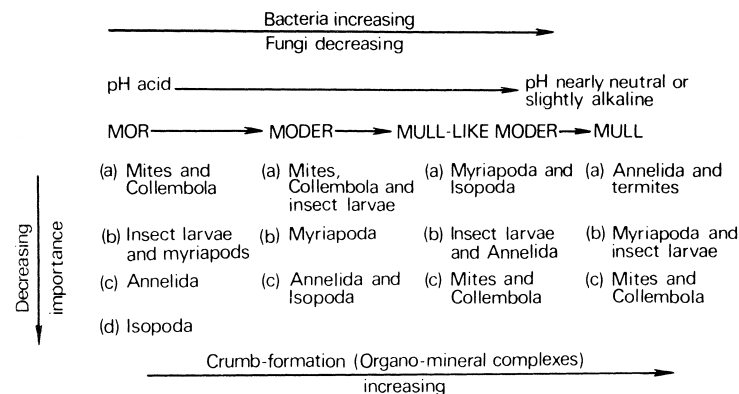


Figure 6—Soil categories, pH, and biota responsible for soil structure (Wallwork 1970).

The Big Tree and the Tiny Springtail: Physical Size Is Not Necessarily an Adequate Measure of Importance

In the French Alps, oak forests growing on clay soils are tall, provide good timber, grow vigorously throughout the year, produce large annual crops of leaves that are shed in the fall, and are associated with soils characterized by a thin litter and a thick humus layer (Kilbertus and Vannier 1981). Oaks on sandy soils, however, are stunted, grow few leaves during an annual season, and are associated with soils with deep litter and very thin humus layers.

Decomposition of oak leaves is largely limited by the presence of high concentrations of phenols. These phenols can polymerize into a macromolecule that fills the entire digestive system, as either a caterpillar ingests a green oak leaf or a millipede ingests a dead leaf. This polymerization impedes digestive enzymes from supplying nutrients and reduces consumption of additional resources (Schultz 1989).

Springtails of the genus *Tomocerus* are abundant on clay soils but are scarce on sandy soils. *Tomocerus* is uniquely able to feed on the fungi growing on the decaying oak leaves because it can prevent the phenol chain reaction from occurring. *Tomocerus* fills its midgut with inorganic clay particles from the mineral soil in which it resides during the hot dry daytime. When it surfaces in the evening to feed, the phenols are bound to the charged clay particles. This adaptation allows *Tomocerus* to thrive and indirectly benefits the entire community by detoxifying the phenols within its feces. Litter resources on clay soils are rapidly incorporated into

microbial biomass, but the insufficiency of clay particles on the sandy soils retards decomposition. Consequently a large percentage of the nutrients are locked up in the dead litter layer and are not available to the ecosystem on sandy soil (Kilbertus and Vannier 1981).

Management Applications

Can Invertebrates Be Useful?

Soil arthropod biodiversity can be useful as indirect assays of ecosystem function or productivity, or as direct estimators of ecosystem responses to differing management protocols.

Soil Compaction: A Foodweb Research Example

A number of techniques have been developed to ameliorate compacted soils. "Subsoiling" (subsurface fracture of compacted soil with restricted surface disruption) is currently being used throughout the Pacific Northwest. Studies of the impacts of subsoiling on biotic processes are generally lacking. We took soil samples from a ponderosa pine (*Pinus ponderosa*) forest in the Deschutes National Forest, Oregon, in an area that had been harvested several times over a 20-year period with partial cuts and machine piling.⁷

Table 1—*Characteristics of soil foodweb composition under ponderosa pine forests in Deschutes National Forest, Oregon. Fungal and bacterial biomass expressed as $\mu\text{g/g}$ dry weight soil; density of nematodes per gram dry weight soil; density of arthropods per $25 \times 25 \text{ cm}^2$. Arthropod density pooled from both horizons.*

Condition	Soil depth	Total fungal biomass	Active fungal biomass	Active bacterial biomass	Total nematode density	Total arthropod density
	cm	$\mu\text{g/g}$	$\mu\text{g/g}$	$\mu\text{g/g}$	number	number
Control forest	0-5	718.5	12.5	6.0	20.4	581
	15-20	548.5	1.3	3.4	5.7	
Compacted skid trail	0-5	540.7	9.2	9.4	175.6	556
	15-20	349.7	1.9	6.2	45.5	
Subsoiled skid trail	0-5	495.1	11.5	7.4	20.4	534
	15-20	295.4	4.5	4.7	19.0	

Results indicated the following scenario of events. Initial compaction caused by the use of skid roads removed approximately one-third of the soil fungal biomass (*table 1*). Fungi inhabiting the deeper layer of soil remained largely metabolically active. This fungal demise led to the stimulation of soil bacteria by 1.5- to 2.0-fold, and an 8- to 9-fold increase in predominantly bacteria-feeding nematodes. Total

⁷ Unpublished data on file at Sisters Ranger District, Deschutes National Forest, USDA Forest Service, Sisters, OR 97759.

arthropod densities remained constant (*table 1*), but the species composition shifted from a community overwhelmingly dominated (78 percent) by fungivorous mites to one with a large component of bacterivores (11 percent) and predators (9 percent) of bacteria-feeding nematodes (*fig. 7*).

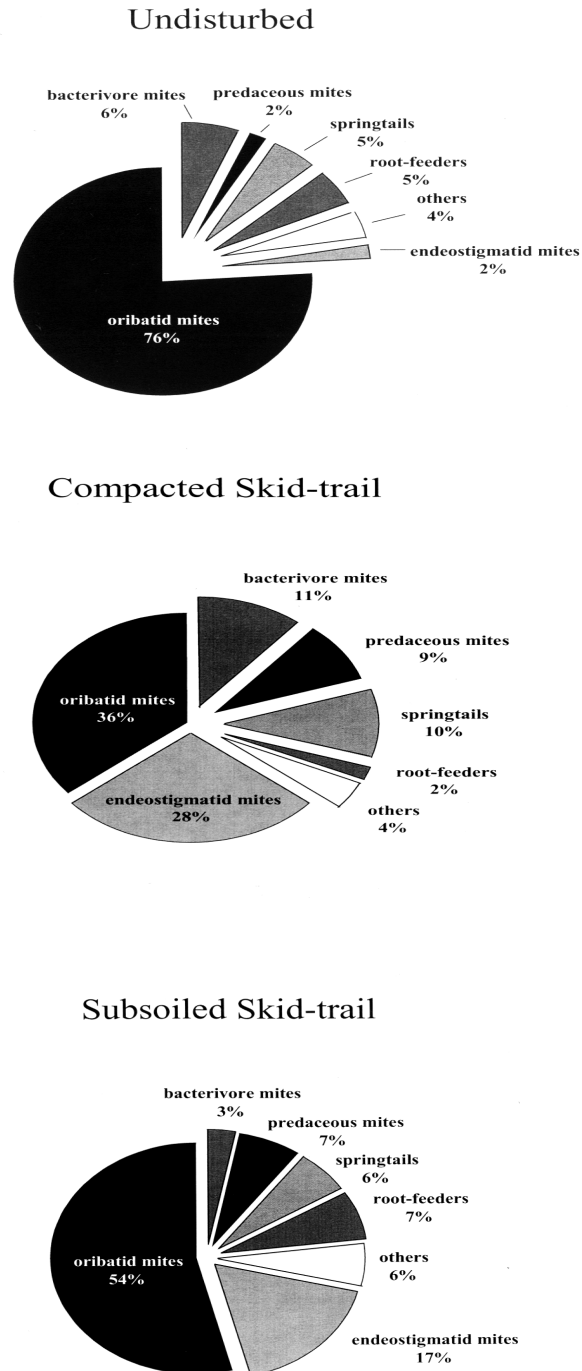


Figure 7—Arthropod community composition in undisturbed and skid-trail soils of ponderosa pine forests in Deschutes National Forest.

Subsoiling continued to reduce total fungal biomass but did enhance the active component within both soil layers (*table 1*). This shift of increased fungal activity accompanies a decrease in active bacterial biomass and an enormous decrease in bacteria-feeding nematodes. It is likely, though we did not examine for it directly, that the active fungi in both the compacted and subsoiled cores was largely saprophytic, whereas that in the adjacent noncompacted forest floor was predominantly ectomycorrhizal. Total arthropod density did not change, but subsoiling resulted in a species composition far more similar to the fungivore-dominated noncompacted forest floor (*fig. 7*).

We conclude from these data on skid trails and a parallel study on compacted landings that compaction: shifts the entire foodweb to one that utilizes primarily bacteria (rhabditid nematodes, gamasid mites); reduces the general size categories of soil inhabitants (rhabditids in place of tylenchids; oppioids and endeostigmatids in place of ceratozetoids; and shifts their life history towards short-lived species (oribatids shift to endeostigmatids and springtails).

In this example, arthropods provided a useful indicator for determining the effects of subsoiling as a management option, but the ability to understand the results was greatly enhanced by expanding the breadth of the analysis to include soil microbes and nematodes.

Conclusion

Arthropods open up spatial and temporal scales of examination that reveal something about how an ecosystem works--scope and knowledge that are unavailable with the usual analyses. Soil chemical and physical properties are usually examined with soil cores. But soil cores inherently contain information limited to one random point and only one instant of time. Tree-ring analysis, on the other hand, reveals different information about soils. Think of the level of understanding we need between these contrasting, conventionally explored scales.

Arthropods that live in the soil perform a number of critical soil functions. Soil is made mostly of the feces of arthropods. Microbe-grazing by arthropods mineralizes nutrients to complete the nutrient recycling process. We need to study arthropods for their own sakes, as well as for their indicator roles of additional soil processes being carried out at ever finer scales of resolution.

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