Diversity and Function of Soil Mesofauna

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CHAPTER 3

Diversity and Function of Soil Mesofauna

Deborah A. Neher and Mary E. Barbercheck

CONTENTS

INTRODUCTION

Diversity in natural communities of microbes, plants, and animals is a key factor in ecosystem structure and function. Agricultural ecosystems, however, are designed around one or several species of plants or animals. Reduction of diversity in agricultural systems, compared with that in natural ecosystems, is traditionally considered essential to increase production of food, forage, and fiber. For simplicity of

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Table 1 Hierarchy of Size and Abundance of Organisms Inhabiting Soil

Class	Example(s)	Biomass (g m^{-2})	Length (mm)	Populations (m^{-2})
Microflora	Bacteria, fungi, algae, actinomycetes	1–100	Not applicable	10^6–10^{12}
Microfauna	Protozoa	1.5–6.0	0.005–0.2	10^6–10^{12}
Mesofauna	Nematodes, enchytraeids, mites, Collembola	0.01–10	0.2–10	10^2–10^7
Macrofauna	Insects	0.1–2.5	10–20	10^2–10^5
Megafauna	Earthworms	10–40	20	0–10^3

Data from Dindal (1990) and Lal (1991).

management, biological cycles are sometimes replaced by fossil fuel-based products, e.g., synthetic fertilizers. Intense management practices that include application of pesticides and frequent cultivation affect soil organisms, often altering community composition of soil fauna. Soil biological and physical properties (e.g., temperature, pH, and water-holding characteristics) and microhabitat are altered when native habitat is converted to agricultural production (Crossley et al., 1992). Changes in these soil properties may be reflected in the distribution and diversity of soil mesofauna. Organisms adapted to high levels of physical disturbance become dominant within agricultural communities, thereby reducing richness and diversity of soil fauna (Paoletti et al., 1993).

Relationships between particular groups of organisms and management practices in agriculture can be studied under specific circumstances to define expected levels of diversity. The full diversity of soil communities has not been quantified for either agricultural or native ecosystems (Lee, 1991), and, in addition, the relationship between biodiversity and ecosystem function is not understood fully (Walker, 1992). Theoretically, this knowledge could be used to establish and maintain conditions that optimize beneficial effects of these organisms. Realistically, however, ideal conditions may be difficult to attain because of constraints imposed by agricultural production practices. We do not have sufficient knowledge to determine whether or not it is necessary, possible, or desirable to duplicate in agriculture the biodiversity that may be present in natural ecosystems.

This chapter examines the diversity and some of the functions of soil mesofauna in agricultural systems (Table 1). Most research on soil biota has focused on ecosystems such as forests and grasslands that are managed less intensively than agricultural or row crop systems. Ecologists have paid more attention to the role of micro- and mesofauna in ecosystem function, whereas agricultural scientists have focused on their role in nitrogen fixation and as pests and pathogens of crops. Our understanding of the role of soil organisms in agricultural systems is increasing, but more research is needed to elucidate their significance to crop production. Mesofauna occupy all trophic levels within the soil food web and affect primary production directly by root feeding and indirectly through their contribution to decomposition and nutrient mineralization (Crossley et al., 1992). Detailed reviews of the biology of soil fauna and their relationship to soil structure and ecological function are available (Wallwork, 1976; Swift et al., 1979; Freckman, 1982; Peterson and Luxton, 1982; Pimm, 1982; Seastedt, 1984; Dindal, 1990; Beare et al., 1992).

HABITAT

Unlike soil macrofauna (e.g., earthworms, termites, ants, some insect larvae), mesofauna generally do not have the ability to reshape the soil and, therefore, are forced to use existing pore spaces, cavities, or channels for locomotion within soil. Habitable pore space (voids of sufficient size and connectivity to support mesofauna) accounts for a small portion of total pore space (Hassink et al., 1993b). Microfaunal community composition becomes increasingly dominated by smaller animals as average pore volume decreases. Within the habitable pore space, microbial and mesofaunal activity is influenced by the balance between water and air. Maximum aerobic microbial activity occurs when 60% of the pore volume is filled with water (Linn and Doran, 1984). Saturation (waterlogging) and drought are detrimental to soil faunal communities because these conditions result in anaerobiosis or dehydration, respectively.

Populations and diversity of mesofauna are greatest in soil with high porosity and organic matter, and structured horizons (Andrén and Lagerlöf, 1983). Most biological activity occurs within the top 20 cm of soil which corresponds to the "plow layer" in agricultural soils. In uncultivated soil, mesofauna are more abundant in the top 5 cm than at greater depths in the soil. The organic horizon (O) is the area of accumulation of recognizable plant materials (high C:N ratio) and animal residues (low C:N ratio). The fermentation (F or O_1) layer consists of partially decomposed, mixed plant and animal debris permeated with hyphae of fungi and actinomycetes. The humus (H or O_2) horizon contains amorphous products of decomposition with the source unrecognizable. Eventually, organic matter from these horizons becomes incorporated into the mineral soil profile. Because cultivated agricultural systems often lack a distinct organic layer on the surface, one might expect diversity of soil biota to be less than in uncultivated or no-till soils (House et al., 1984).

Plants affect soil biota directly by generating inputs of organic matter above- and belowground and indirectly by the physical effects of shading, soil protection, and water and nutrient uptake by roots. Energy and nutrients obtained by plants eventually become incorporated in detritus which provide the resource base of a complex soil food web. Plant roots also exude amino acids and sugars which serve as a food source for microorganisms (Curl and Truelove, 1986). Soil mesofauna are often aggregated spatially which is probably indicative of the distribution of favored resources, such as plant roots and organic debris (Swift et al., 1979; Goodell and Ferris, 1980; Barker and Campbell, 1981; Noe and Campbell, 1985).

BIOLOGY AND ECOLOGY OF SOIL FAUNA

Soil mesofauna are often categorized by specific feeding behaviors, often depicted as microbial feeders. However, it should be emphasized that many organisms are at least capable of feeding at other trophic groups. As a result, omnivory in soil communities may be more prevalent than assumed previously (Walter et al., 1986; Walter, 1987; Walter et al., 1988; Walter and Ikonen, 1989; Mueller et al., 1990). Our discussion will focus specifically on nematodes, Collembola (springtails), and mites because they predominate in total numbers, biomass, and species of fauna in soil (Harding and Studdart, 1974; Samways, 1992).

Soil nematodes are relatively abundant (6×10^4 to 9×10^6 per m^2), small (300 µm to 4 mm) animals with short generation times (days to a few weeks) that allow them to respond to changes in food supply (Wasilewska, 1979; Bongers, 1990). Relative to other soil microfauna, trophic or functional groups of nematodes can be identified easily, primarily by morphological structures associated with various modes of feeding (Yeates and Coleman, 1982; Freckman, 1988; Bongers, 1990). Nematodes may feed on plant roots, bacteria, fungi, algae, and/or other nematodes (Wasilewska, 1979).

Mites and collembolans can account for 95% of total soil microarthropod numbers (Harding and Studdart, 1974). Soil mites occur mainly in three suborders. The suborder Oribatida (Cryptostigmata) comprises the numerically dominant group in the organic horizons of the soil. Members of the mite suborder Mesostigmata (Gamasida) are relatively large, active mites. The mite suborder Prostigmata (Actinedida) is a large and taxonomically complex group. Soil prostigmatids have more heterogeneous feeding habits than other mite suborders (see table in Kethley, 1990, for feeding habits). Prostigmatids are mostly fungal feeders and predators.

Collembolans are abundant and distributed widely. Collembolans have relatively high metabolic, feeding, and reproductive potential. Functional classification of collembolans (Christiansen, 1964; Bödvarsson, 1970; Verhoef and Brussard, 1990) can be based on gut content or shape of the mouthparts, which are adapted to the specific feeding habit (Swift et al., 1979). Because most forms of Collembola feed on decaying vegetation and associated microflora, the distribution of mycelia and spores of saprophytic fungi may be a major factor influencing the distribution of collembolans.

Other groups of arthropods that occur commonly in soil are pseudoscorpions, symphylans, pauropods, proturans, diplurans, and the immature stages of holometabolous insects (Dindal, 1990). Ants and termites can also be very numerous; however, these macroarthropods will not be considered here (Brian, 1978).

Plant Feeders

Plant-feeding nematodes can become abundant in agricultural ecosystems (Wasilewska, 1979; Popovici, 1984; Neher and Campbell, 1996). These nematodes may affect primary productivity of plants by altering uptake of water and nutrients. These abnormalities may result from changes in root morphology and/or physiology. For many agricultural crops, a negative relationship between crop yield and populations of plant-feeding nematodes, such as *Meloidogyne, Heterodera,* and *Pratylenchus* spp., has been observed (Mai, 1985; Barker et al., 1994). However, when entire nematode communities, including free-living nematodes, are examined, a positive association has been observed between plant biomass production and total nematode populations in grassland ecosystems (Yeates and Coleman, 1982). This relationship holds for plant production measured as harvested hay and root biomass (King and Hutchinson, 1976). A negative relationship between total nematode populations and plant productivity has been observed in tropical forests (Kitazawa, 1971). The relationship between soil nematode communities and row crop yield has yet to be determined.

Microarthropods rarely harm crop plants. However, soil mesofauna may become pests when a preferred food source is absent. Some Collembola, e.g., sminthurids and onychiurids, may feed on roots. For example, root-grazing injury on sugar beet is caused by *Onychiurus* spp. (Collembola) rubbing their bristled bodies against roots (Curl et al., 1988). However, root injury decreases if specific weed species and certain kinds and amounts of organic matter are present and, thus, provide the preferred microbial food supply. Few groups of soil mites are adapted to feeding on live plant tissues in soil. Some examples occur in the Tarsonemidae (Prostigmata) and Periohmanniidae (Oribatida). Most soil mites feed on plant material only after decomposition has begun. Often, increasing vegetational diversity and the quality and quantity of organic matter in soil increases potential benefits by soil mesofauna.

Microbial Feeders

Microbial-feeding mesofauna feed on fungi (including mycorrhizae), algae, slime molds, and bacteria by removing them from clumps of decaying material or soil aggregates (Moore and de Ruiter, 1991). Generally, bacterial-feeding nematodes such as Cephalobidae and Rhabditidae (Neher and Campbell, 1996) are abundant in agricultural ecosystems (Wasilewska, 1979; Popovici, 1984). Consumption of microbes by soil mesofauna alters nutrient availability by stimulating new microbial growth and activity plus releasing nutrients immobilized previously by microbes.

In general, fungal feeding is the dominant trophic function of microarthropods. Collembolan species have preferred food sources which are maintained even after the material has passed through the digestive tracts of other animals. For example, the collembolans *Proisotoma minuta* and *O. encarpatus* feed upon the soilborne fungal plant pathogen *Rhizoctonia solani* which causes damping-off disease on cotton seedlings (Curl et al., 1988). These collembolan species prefer feeding on the fungal pathogen in soil compared with the biocontrol fungi *Laetisaria arvalis, Trichoderma harzianum,* and *Gliocladium virens* (Curl et al., 1988). Additionally, collembolan species can distinguish and graze selectively on different species of vesicular-arbuscular mycorrhizae (Thimm and Larink, 1995).

Almost all oribatid mites are microbial feeders. Examples of microbial feeding also occur in the Mesostigmata (Ameroseiidae, Uropodidae) and Prostigmatida (Tarsonemidae, Nanorchestidae, Stigmaeidae Pygmephoridae, Eupodidae, and Tydeida). Although many microarthropods are microbial feeders, recent studies indicate that other arthropods are omnivorous and shift feeding behavior as food resources change (Walter, 1987; Mueller et al., 1990).

Omnivory

Omnivores add "connectedness" to the food web by feeding on more than one food source (Coleman et al., 1983). Omnivorous nematodes, such as some Dorylamidae, make up only a small portion of the total nematodes in agricultural ecosystems (Wasilewska, 1979; Neher and Campbell, 1996). They may feed on algae, bacteria, fungi, and other nematodes. Collembolans are often microbial feeders, but may also be facultative predators of nematodes (Snider et al., 1990). Mites that feed on both microbes and decaying plant material can be found in the oribatid mite families Nothridae, Camisiidae, Liacaridae, Oribatulidae, and Galumnidae. Coprophages, which ingest dung and carrion, including dead insects, are found among the oribatid families Euphthiracaridae, Phthiracaridae, Galumnidae, and Oppiidae.

Predators

Mesofauna may be predators or serve as prey for predaceous mites and other predators, such as beetles, fly larvae, centipedes, and spiders. Predatory nematodes feed upon all the other trophic groups of nematodes (Moore and de Ruiter, 1991) and represent only a small portion of the total nematodes in agricultural ecosystems (Wasilewska, 1979). Nematode predators (e.g., members of the orders Mononchida and Tripylida) and insect-parasitic nematodes (e.g., members of the families Steinernematidae, Diplogasteridae, Mermithidae) present in the soil may affect populations of their prey (Poinar, 1979; Small, 1987; Stirling, 1991).

Soil microarthropods can be important predators on small arthropods (e.g., proturans, pauropods, enchytraeids) and their eggs, nematodes, and on each other. Predation of insect eggs in agroecosystems may constitute a major influence of controlling microarthropod populations. Brust and House (1988) found that the mite *Tyrophagus putrescentiae* is an important predator of eggs of southern corn rootworm *Diabrotica undecimpunctata howardi* in peanuts. Chaing (1970) estimated that predation by mites accounted for 20% control of corn rootworms (*Diabrotica* spp.) and 63% control following the application of manure. Mite predation on root-feeding nematodes may be significant under some conditions (Inserra and Davis, 1983; Walter, 1988). For example, one adult of the mesostigmatid mite *Lasioseius scapulatus* and its progeny consumed approximately 20,000 *Aphelenchus avenae* on agar plates in 10 days (Imbriani and Mankau, 1983). Collembolan species may also consume large numbers of nematodes (Gilmore, 1970). For example, *Entomobryoides dissimilis* consumed more than 1000 nematodes in a 24-h period. Furthermore, collembolans may consume large numbers of insect-parasitic nematodes and, thus, affect the efficacy of these nematodes used as biological control agents of soil-dwelling insect pests (Epsky et al., 1988; Gilmore and Potter, 1993).

ECOSYSTEM PROCESSES

Micro- and mesofauna contribute directly to ecosystem processes such as decomposition and nutrient cycling in complex and interactive ways (Swift et al., 1979).

Bacteria, actinomycetes, fungi, algae, and protozoa are primary decomposers of organic matter. These microorganisms are involved directly with production of humus, cycling of nutrients and energy, elemental fixation, metabolic activity in soil, and the production of complex chemical compounds that cause soil aggregation.

Microbial-grazing mesofauna affect growth and metabolic activities of microbes and alter the microbial community, thus regulating decomposition rate (Wasilewska et al., 1975; Trofymow and Coleman, 1982; Whitford et al., 1982; Yeates and Coleman, 1982; Seastedt, 1984) and nitrogen mineralization (Seastedt et al., 1988; Sohlenius et al., 1988). Nematodes feed on bacteria and fungi on decaying organic matter, but not on the organic matter itself. Nematode species with a buccal stylet (spearlike structure) feed on cell contents and juices obtained by piercing the cellular walls of plant roots or fungal mycelium. Other species have no stylets and feed on particulate food such as bacteria and small algae (Vinciguerra, 1979). Microarthropods fragment detritus and increase surface area for further microbial attack (Berg and Pawluk, 1984). For example, collembolans and mites may enhance microbial activity, accelerate decomposition, and mediate transport processes in the soil. Even when they do not transform ingested material significantly, they break it down, moisten it, and make it available for microorganisms.

There is evidence that plants benefit from increased mineralization of nitrogen by soil mesofauna. Shoot biomass and nitrogen content of plant shoots grown in the presence of protozoans and nematodes were greater when compared with plants grown without mesofauna (Verhoef and Brussard, 1990). Soil fauna are responsible for approximately 30% of nitrogen mineralization in agricultural and natural ecosystem soils. The main consumers of bacteria are protozoa and bacterial-feeding nematodes which account for 83% of nitrogen mineralization contributed by soil fauna (Elliott et al., 1988). Nematodes also excrete nitrogenous wastes, mostly as ammonium ions (Anderson et al., 1983; Ingham et al., 1985; Hunt et al., 1987). Collembola excrete nitrate in concentrations 40 times more than their food source (Teuben and Verhoef, 1992). Furthermore, large collembolan species increase mineralization by selective feeding on fungi, whereas smaller species aid in the formation of humus by nonselective scavenging and mixing of the mineral and organic fractions of soil (van Amelsvoort et al., 1988). Microfauna constitute a reservoir of nutrients. When microfauna die, nutrients immobilized in their tissues are mineralized and subsequently become available to plants.

Soil fauna transport bacteria, fungi, and protozoa (in gut or on cuticle) across regions of soil and, thus, enhance microbial colonization of organic matter (Seastedt, 1984; Moore et al., 1988). For example, Collembola and sciarid fly larvae transmit root-infecting fungi and fungal parasites (Anas and Reeleder, 1988; Whipps and Budge, 1993). Microarthropods are surrounded by and, therefore, may disseminate propagules of insect-parasitic fungi including *Beauveria* spp., *Metarhizium* spp., *Paecilomyces* spp., and *Verticillium* spp. and facultative pathogens of insects in the genera *Aspergillus* and *Fusarium* spp. Under laboratory conditions, Collembola and mites transport spores of the insect-parasite *M. anisopliae* (Zimmerman and Bode, 1983). The impact of insect-parasitic fungi on natural populations of microarthropods is unknown.

VALUE OF DIVERSITY

Diversity in form and function of biotic communities results in the formation of spatial and temporal heterogeneity of organisms that contributes to the overall function of the ecosystem. Individual taxa may have multiple functions, and several taxa may appear to have similar functions. However, function may not necessarily be redundant, because taxa performing the same function are often isolated spatially, temporally, or by microhabitat preference (Beare et al., 1995). Biodiversity allows organisms to avoid intense competition for food or space, decrease invasion and disruption, and maintain constancy of function through fluctuating environmental conditions.

Various measures of diversity are available to describe soil invertebrate communities including abundance, biomass, density, species richness, species evenness, maturity indexes, trophic/guild structure, and food web structure. Indexes of diversity, which include elements of richness (number of taxa) and evenness (relative abundances), can be applied at scales ranging from alleles and species to regions and landscapes. Diversity indexes do not reveal the taxonomic composition of the community. For example, a community composed entirely of exotic species could have the same index value as a community composed entirely of endemic species. Therefore, a diversity index, by itself, does not predict ecosystem health or productivity.

Debates concerning relationships between biodiversity and ecosystem stability became popular in the 1960s and 1970s. MacArthur (1955) was the first to argue that complex systems are more stable than simple systems. In the early 1970s, May (1972; 1973) used mathematical models to argue that diverse communities were less stable than simple systems. Today, some conclude that relatively simple, short food webs that exhibit little omnivory or looping are more stable than longer food webs with much omnivory or looping. A short food web is one with few trophic levels (Polis, 1991). Others hypothesize that high linkage is responsible for making food webs unstable, i.e., stability can develop if numbers of species increase but not if omnivory increases (Pimm et al., 1991; Lawton and Brown, 1993). It is clear from this ongoing debate that it is impossible to generalize the relationship between biodiversity and ecosystem stability. Besides, none of the theories has been tested adequately for application to soil communities.

Factors affecting diversity within trophic groups of the detritus food web include altitude, latitude (Procter, 1984; Rohde, 1992), predation in the presence of strong competitive interactions (Petraitis et al., 1989), and disturbance (Petraitis et al., 1989; Hobbs and Huenneke, 1992). For example, the pervading theory is that the greatest species diversity is found in the tropics and that diversity decreases with increasing latitude (Rohde, 1992). However, the opposite is true for free-living nematodes. Free-living nematodes are more diverse and abundant in temperate than in tropical regions (Procter, 1984; 1990). Nematodes are tolerant of harsh conditions at high latitudes but are not competitive against more-specialized soil fauna in the tropics (Petraitis et al., 1989).

At smaller scales, predators may promote species diversity among competing prey species when they feed preferentially on exceptionally competitive prey (Petraitis et al., 1989). Disturbance also plays a role with the "intermediate disturbance hypothesis" suggesting that taxonomic diversity should be highest at moderate levels of disturbance (Petraitis et al., 1989; Hobbs and Huenneke, 1992). Disturbance is defined as a cause (a physical force, agent, or process, either abiotic or biotic) that results in a perturbation (an effect or change in system state relative to a reference state and system) (Rykiel, 1985). If disturbance is too mild or too rare, then soil communities will approach equilibrium and will be dominated by fewer taxa that can outcompete all other taxa. However, attainment of steady-state equilibria in agricultural or natural ecosystems is uncommon (Richards, 1987). If disturbance is common or harsh, only a few taxa that are insensitive to disruption will persist, therefore decreasing biodiversity (Petraitis et al., 1989). For example, Prostigmatid mites in the Eupodidae, Tarsonemidae, and Tydeidae are among the most abundant in cultivated agroecosystems and their numbers increase rapidly in response to disturbances such as cultivation (Crossley et al., 1992).

AGRICULTURAL DISTURBANCES

Disturbance can alter the diversity of an ecosystem (Atlas, 1984) directly by affecting survivorship of individuals or indirectly by changing resource levels (Hobbs and Huenneke, 1992). Sometimes, diversity measurements reflect the result of disturbance caused by pollution and/or stress. For example, taxonomic diversity of microinvertebrate communities was less in polluted or disturbed than in unpolluted or undisturbed agricultural sites (Atlas et al., 1991). Pollution eliminates sensitive species, reducing competition so that tolerant species proliferate (Atlas, 1984).

The successional status of a soil community may also reflect the history of disturbance. Succession in cropped agricultural fields begins with depauperate soil which acts like an island to which a series of organisms immigrate. First, opportunistic species, such as bacteria and their predators, are colonists of soil. Subsequently, fungi and their predators migrate into the area (Böstrom and Sohlenius, 1986). Microarthropods, such as collembolans, mites, and fly maggots, can colonize nearly bare ground and rise quickly in population density. Top predator microarthropods, such as predaceous mites and nematodes, become established later and may have a function similar to keystone predators in other community food webs (Elliott et al., 1988). Finally, macro- and megafauna, such as earthworms, millipedes, slugs, centipedes, wood lice, sow bugs, and pill bugs, join the soil community (Strueve-Kusenberg, 1982).

Succession can be interrupted at various stages by agricultural practices, such as cultivation and applications of fertilizer and pesticide (Ferris and Ferris, 1974; Wasilewska, 1979). Such interruptions reduce diversity and successional "maturity." Maturity indices are based on the principles of succession and relative sensitivity of various nematode taxa to stress or disruption of the successional sequence (Bongers, 1990). Indices that describe associations within biological communities, such as a maturity index, are less variable than measures of abundance of a single taxonomic or functional group and are, thus, more reliable as measures of ecosystem condition (Neher et al., 1995).

Soil Texture and Compaction

Soil texture may impose physical restrictions on the ability of fauna to graze on microbes; therefore, texture may play a role in faunal-induced mineralization of microbial carbon and nitrogen (van Veen and Kuikman, 1990). Carbon and nitrogen mineralization is generally faster in coarse than in fine-textured soils. In clay soils, organic material is protected physically from decomposers by its location in small pores. In sandy soils, organic matter is protected by its association with clay particles (Hassink et al., 1993a). Nematodes and microarthropods are often less abundant in heavy clay soil than in sandy or peat soil (van de Bund, 1970; Zirakparvar et al., 1980; Verma and Singh, 1989). Euedaphic species such as collembolans in the Onychiuridae and mesostigmatid mite *Rhodacarus roseus* are especially rare in clay soil (Didden, 1987).

Mesofauna are affected adversely by soil compaction (Aritajat et al., 1977a,b). Wheel-induced compaction reduces soil porosity, which is accompanied by a decrease in microbial biomass carbon and the density of Collembola (Heisler and Kaiser, 1995). Collembolans avoid narrow pores to protect their waxy surface from damage (Choudhuri, 1961). Wheel traffic decreased the density of collembolans and predatory mites by 30 and 60%, respectively, compared with noncompacted soil. The number of species was also reduced by compaction (Heisler, 1994).

Cultivation

Cultivation affects biogeochemical cycling by physically rearranging soil particles and changing pore size distribution, patterns of water and gas infiltration, and gas emission (Klute, 1982). Tillage disrupts soil aggregates, closes soil cracks and pores, and promotes drying of the surface soil. Soil fauna become sparse in top layers of cultivated soil because moisture content fluctuates widely and the original pore space network in this layer is destroyed. These physical alterations of the surface layers of soil may persist for many years after cultivation has ceased.

Soils managed by conventional — or reduced — tillage practices have distinct biological and functional properties (Doran, 1980; Hendrix et al., 1986). Plant residue is distributed throughout the plow layer in fields managed with conventional tillage. Under these conditions enhanced by cultivation, organisms with short generation times, small body size, rapid dispersal, and generalist feeding habits thrive (Steen, 1983). These soils are dominated by bacteria and their predators such as nematodes and astigmatid mites (Andrén and Lagerlöf, 1983; Yeates, 1984; Hendrix et al., 1986; Beare et al., 1992) and are considered in an early stage of succession. Oribatid and mesostigmatid mites decrease while other groups such as prostigmatid mites and Collembola tolerate, but do not benefit, from cultivation (Crossley et al., 1992). However, prostigmatid mite communities can be more diverse, containing both fungal- and nematode-feeding taxa in cultivated soils (van de Bund, 1970). Many microarthropods have omnivorous feeding habits in systems cultivated frequently (Beare et al., 1992).

Conservation — or no-till — practices generate more biologically complex soils than conventional tillage; however, in general, no-tillage cultivation does not appear to result in greater concentrations of microarthropods than conventional tillage except under drought stress (Perdue and Crossley, 1989). However, many studies comparing tillage effects are short term. Our knowledge about tillage effects may change as more long-term studies are implemented. Reduced tillage leaves most of the residue of the previous crops on the soil surface, and results in changes in physical and chemical properties of the soil (Blevins et al., 1983). Surface residues retain moisture, dampen temperature fluctuations, and provide a continuous substrate which promotes fungal growth. The increased fungal abundance can be attributed to the ability of fungi to translocate nutrients from soil into surface residues, their tolerance of lower pH and water potentials that often occur in surface residues, and their ability to penetrate and use large detritus particles (Hendrix et al., 1986; Holland and Coleman, 1987). Relative abundances of fungi and their predators, such as nematodes and many microarthropods groups (e.g., uropodid mesostigmatid mites; tarsonemid, eupodid, tydeids, and pygmephorid prostigmatid mites; oribatid mites) (Walter, 1987), in no-till soils represent a more mature successional state than one dominated by bacteria (Yeates, 1984; Böstrom and Sohlenius, 1986; Hendrix et al., 1986; Holland and Coleman, 1987; Neher and Campbell, 1994). Fungal feeding by microarthropods may stimulate microbial growth and enhance decomposition and nutrient immobilization (Seastedt, 1984). However, nutrient mineralization rates are relatively slow with stratification of debris and soil; nutrients are immobilized inside plant debris on the soil surface (Hendrix et al., 1986; Holland and Coleman, 1987).

Fertilization

Fertilization may influence the population abundance or composition of mesofaunal communities in soil. The outcome is a result of factors such as fertilizer quality and/or quantity (Verhoef and Brussard, 1990). Fertilization may, thus, affect the abundance and diversity of soil mesofauna directly or indirectly. These changes in community composition may, in turn, influence ecosystem function.

Nutrients applied to agricultural soils may be derived either from fossil fuels or plant and animal waste products. Nutrients are available in both forms, but organic amendments also contain microbes and their respective food resources. Additions of mineral fertilizers decrease populations of oribatid (cryptostigmatid) and prostigmatid mites, and root- and fungal-feeding, omnivorous and predaceous nematodes (Sohlenius and Wasilewska, 1984). Numbers of root-feeding nematodes may increase with increased nitrogen fertilizer (Wasilewska, 1989). Populations of astigmatid mites (Andrén and Lagerlöf, 1983) and bacterial-feeding nematodes (Sohlenius and Wasilewska, 1984) increase with additions of mineral fertilizer, but even more so when soils are fertilized with manure which simultaneously adds organic matter and microbes (Andrén and Lagerlöf, 1983; Weiss and Larink, 1991). However, in Dutch polder soil, abundances and biomass of nematodes, mites, and Collembola were similar between fields fertilized with manure, crop residues, and green manure and those field soils amended with crop residues and synthetic fertilizer (van de Bund, 1970).

Mesofauna aggregate around manure and plant litter (van de Bund, 1970). Populations of fungal-feeding nematodes (Weiss and Larink, 1991), potworms

(Enchytraeids), collembolans, and sometimes mesostigmatid mites increase with applications of manure (Andrén and Lagerlöf, 1983). Fratello et al. (1989) examined the effects of seven types of organic fertilizer on the microfauna in alfalfa fields. The reactions of populations of microarthropods to the different treatments varied with sample date, illustrating the highly complex interactions that occur in the soil. Poultry manure, sheep manure, worm compost, autoclaved urban sludge, urban sludge, vetch green manure, or straw were added to soil to provide a common level of 4% organic matter. Straw was the only additive that did not depress mite populations. Fewer mites and Collembola were found in plots treated with autoclaved urban sludge than those treated with non-autoclaved urban sludge.

The quality of plant and animal wastes as nutrient sources may be altered by composting. For example, applications of aged compost can increase suppression of plant pathogens by increasing the effectiveness of biocontrol agents. The plant-pathogenic fungus *Rhizoctonia solani* may cause damping-off disease in soil when fresh or immature compost material high in cellulose content is added. However, in aged compost, cellulose is degraded and the biocontrol fungus *Trichoderma* spp. can parasitize the pathogen effectively, thus suppressing disease (Chung et al., 1988).

Large doses of mineral or manure fertilizers can harm mesofauna because of toxicity (e.g., anhydrous ammonia) or high osmotic pressure due to salt (Andrén and Lagerlöf, 1983). The repellent nature of ammonium can affect soil invertebrates adversely (Potter, 1993). The potential for toxic effects can be decreased by applying composted manure and sludge (Ott et al., 1983). However, accumulation of heavy metals from repetitive sludge applications may kill omnivorous and predaceous nematodes (Weiss and Larink, 1991).

Fertilization affects soil microflora and, thus, indirectly impacts soil mesofauna by changing their food resources (Weil and Kroontje, 1979). Additions of nitrogen may acidify soil and inhibit microbial growth and activity. Nitrogen may also affect the quality of microbes as a food source for mesofuana. Booth and Anderson (1979) grew two species of fungi in liquid media with 2, 20, 200, or 2000 ppm nitrogen and determined the fecundity of the collembolan *Folsomia candida* while feeding on the fungi. Fecundity increased with increasing nitrogen content up to 200 ppm. *F. candida* did not show a preference for feeding on fungi with a greater or lesser nitrogen content.

The effect of fertilization on microarthropod species diversity and abundance within taxa and the subsequent impact on decomposition and nutrient mineralization processes are not well understood. For example, synthetic fertilizers increase nematode diversity, but applications of manure decrease nematode diversity (Wasilewska, 1989). The mechanism(s) explaining the differences are not understood. Applications of synthetic nitrogen fertilizer on Swedish arable soils growing spring barley (*Hordeum distichum* L.) changed community composition, but not numbers and biomass of nematodes, Collembola and mites (Andrén et al., 1988). Within a given environment, increased densities of microarthropods have been correlated with increased foliage, root and microbial productivity (Lussenhop, 1981), or increased food resource via fertilization. It is not known at what scale of resolution soil faunal communities respond to changes in ecosystem function.

Pesticides

Pesticides are an integral part of modern farming practice. Pesticides can enter the soil by a variety of routes, e.g., intentional application, spillage, overspraying, runoff, aerial transport with soil, or leaching. Organic matter plays a major role in the binding of pesticides in soil. Fulvic and humic acids are most commonly involved in binding interactions. Pesticides or their degradation intermediates can also be polymerized or incorporated into humus by the action of soil microbial enzymes (Bollag et al., 1992).

Soil fumigation with general biocides such as methyl bromide decreases microbial populations and nearly eliminates nematodes (Yeates et al., 1991). Although recovery occurs, population densities may not return to prefumigation levels even after 5 months (Yeates et al., 1991). Fumigation with general biocides return the successional status of soil to that of a depauperate soil matrix that can only be inhabited by primary colonists. However, within 60 weeks after soil fumigation and manuring, a progression of colonization by early successional species followed by more-specialized, later successional taxa can be observed (Ettema and Bongers, 1993).

Broad-spectrum insecticides that are applied for the control of insect pests can be toxic to predaceous and parasitic arthropods. A single surface application of chlorpyrifos reduced populations of predatory mites in plots of Kentucky bluegrass for 6 weeks and similar applications of isofenphos reduced populations of non-oribatid mites, Collembola, millipedes, and Diplura for as long as 43 weeks (Potter, 1993). Densities of Collembola were lower in aldicarb-treated soil than in untreated soil, but only the collembolans in the suborder Arthropleona were influenced negatively, whereas Symphypleona were not affected or occurred in higher numbers in soil treated with aldicarb (Koehler, 1992). Mesostigmatid mites did not occur at the site for the first 2 months after treatment, and their abundance was reduced for 6 months. After 3 and 4 years, abundance was similar in treated and untreated soil. Koehler (1992) noted a change in species composition associated with aldicarb treatment and categorized three groups of reaction. The most sensitive organisms were absent from 9 months to 1 year after application; other groups showed no reaction to treatment, or a positive reaction. Surface-dwelling microarthropods appeared to be affected less negatively than were soil-dwelling microarthropods.

Badejo and Van Straalen (1992) tested the effects of atrazine on the growth and reproduction of the collembolan *Orchesella cincta*. The lethal concentration (LC_{50}) for atrazine was estimated at 224 μg/g atrazine in food. Mortality and molting frequency increased with increasing concentrations of atrazine. The no observed effect concentration (NOEC) on egg production of *O. cincta* was 40 μg/g. Based on data for five collembolan species, 2.7 μg/g was estimated to be the hazardous concentration for 5% of soil invertebrates, which corresponds to the recommended field rate of 2.5 μg/g. House et al. (1987) investigated the impact of seven herbicides on miroarthropods and decomposition. No effect of any herbicide was observed on numbers of microarthropods, but decomposition of wheat straw was more rapid in soils without than with herbicide.

Generally, phenoxy acetic acid herbicides (e.g., 2,4-D, 2,4,5-T, 2-methyl-4-chlorophenoxyacetic acid) do not depress soil fauna directly with toxic effects, but indirectly through reduced vegetation and smaller additions of organic matter to soil (Andrén and Lagerlöf, 1983). Simazine, a triazine herbicide, is deleterious to most soil fauna (Edwards and Stafford, 1979).

Certain compounds such as the fungicide benomyl and its conversion product carbendazim have negative effects on soil biota even in low concentrations (Andrén and Lagerlöf, 1983). Applications of the fungicide captan to field soil reduce the abundance of saprophytic fungi and fungal-feeding mites compared with untreated field soil (Mueller et al., 1990).

CONCLUDING REMARKS

There are many other factors that influence diversity and function in agricultural soils. Greater diversity and later successional communities of soil fauna such as nematodes are found in soils with perennial crops compared with soils with annual crops (Ferris and Ferris, 1974; Wasilewska, 1979; Freckman and Ettema, 1993; Neher and Campbell, 1994). Root growth is more extensive and less ephemeral with perennial than with annual crops. Differences between soils with perennial (e.g., meadow fescue *Festuca pratensis* L.) and annual (e.g., barley) crops may be less pronounced for perennial crops younger than 3 years old than more mature crops (Böstrom and Sohlenius, 1986).

In fields where annual crops are grown, the diversity of soil fauna is increased with management practices such as crop rotation, polycultures, crop mixtures, trap crops, and intercropping. For example, populations of oribatid (cryptostigmatid) and prostigmatid mites and springtails were greater in soils with crop rotation than without (Andrén and Lagerlöf, 1983). However, diversity of nematode communities in soils in intercropping systems of yellow squash (*Cucurbita pepo* L.) and cucumber (*Cucumis sativa* L.) with alfalfa (*Medicago sativa* L.) or hairy indigo (*Indigofera hirsuta* L.) were not greater consistently than monocultures (Powers et al., 1993). The lack of consistent difference in diversity was attributed to fluctuations in diversity occurring within the growing season. Further studies are needed to elucidate the role of faunal diversity in soils with heterogeneous cropping systems.

Agricultural systems are complex, and most research studies have focused on single factors in an effort to reveal underlying mechanisms. This results in a lack of understanding of how multiple environmental and biotic factors interact to affect soil biodiversity and function. As interest in reducing fossil fuel–based inputs increases, reliance on natural cycles and processes will increase. We should allow the soil to work for us and not work against it (Elliott and Coleman, 1988). More research is needed to determine the impact of multiple and interacting management practices on biodiversity, nutrient cycling, pest populations, and plant productivity. With this information, we can maximize our ability to tailor agricultural practices to optimize crop productivity while positively affecting beneficial soil organisms and the functions they perform.

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