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Author(s): Nigel E. Stork and Paul Eggleton

Source: *American Journal of Alternative Agriculture*, 1992, Vol. 7, No. 1/2, Special Issue On Soil Quality (1992), pp. 38-47

Published by: Cambridge University Press

Stable URL: <https://www.jstor.org/stable/44479649>

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# Invertebrates as determinants and indicators of soil quality

Nigel E. Stork and Paul Eggleton

**Abstract.** *Invertebrates are an integral part of soils and are important in determining the suitability of soils for the sustainable production of healthy crops or trees. We discuss the importance of the soil invertebrate fauna in relation to terrestrial habitats and global biodiversity as we understand it. We describe the role of the main invertebrate groups in soils, including earthworms, termites, springtails, and nematodes, and how they determine soil quality. Practical problems in dealing with the invertebrate fauna include sampling, taxonomy and availability of biological information on species. Various measures are available that use invertebrates to assess soil quality, each with its advantages and disadvantages. They include abundance, biomass, density, species richness, trophic/guild structure, food web structure, keystone species and ecosystem engineers. We propose the three most useful and practical of these as suitable to be combined with other biological (microbial) and non-biological (hydrological, physical, chemical) criteria into a single index of soil quality that might be used on a regional, if not international basis.*

**Keywords:** biodiversity, soil invertebrates, species richness, keystone species, earthworms, springtails, nematodes, termites

## Introduction

The soil is among the most complex habitat systems on the globe, yet its biological systems are poorly understood. It provides a living place for at least part of the life cycle of many animals, and the highly connective nature of foodwebs means that most, if not all, terrestrial organisms depend directly or indirectly on biological processes in the soil. Many small organisms, such as insects and other invertebrates, play a vital role in the production and maintenance of healthy soils, and therefore are key elements in the development of sustainable agriculture and forestry.

The central tenet of this paper is that invertebrates are an integral part of soil systems and that soil quality results at least in part from the interactions of soil with its

biotic community. To many soil invertebrate biologists this will seem a truism, given the extensive literature on this subject (e.g., Fitter et al., 1985; Edwards et al., 1988; Spence, 1985; Eselbeis and Wichard, 1987). To other biologists, however, and to most non-biologists, it is not so obvious. We review the ways in which invertebrates determine the nature of soil, and show how invertebrates can be used to assess human-induced changes in soil quality. We define "soil quality" as "the fitness of soils for the sustainable production of healthy, agriculturally important plants." This paper outlines the role of invertebrates in soil processes, suggesting how this role might be included in a general index of soil quality. This index would include physical and chemical measures, as well as other biological measures such as microbial activity. Consequently, we first outline the contribution of the soil fauna to biodiversity in general, emphasizing invertebrates. Second, we discuss the importance of the soil fauna in relation to the fauna of other terrestrial and aquatic

ecosystems. Third, we describe the most important invertebrate components and their role in soil processes. Fourth, we discuss problems of sampling, identification, and geographical distribution. Fifth, we consider how different measures of invertebrate biodiversity (biomass and abundance; species richness) and ecological complexity (trophic group analysis; food web studies; recognition of keystone species/ecosystem engineers) have been or could be used to indicate management-induced changes in soil quality. Finally, we suggest which of these measures are most practical. Because the field we cover is wide, we take a conceptual view and suggest broad approaches based on ecological and systematic theory.

## Invertebrate Diversity—the Baseline

Only a fraction of the species on earth have been named, but what fraction is a matter of great debate. We are not even sure how many species have been named already, although estimates range from 1.4 to 1.8 million (Stork, 1988; Stork and Gaston, 1990; May, 1990a,b). Insects comprise the largest single group of named species and attention has therefore focused on this group for estimates of total number of species on earth. Until the 1980s, most estimates for the number of insect species were between 1 and 3 million. Against this baseline, the 30 million tropical species suggested by Erwin (1982) created considerable renewed controversy. His method of estimating this figure, and the assumptions and extrapolation involved have been questioned by several authors. More recent estimates have been below 10 million (Stork, 1988; May, 1990a,b; Thomas, 1990; Gaston, 1991; Holloway and Stork, 1991; Hodkinson and Casson, 1991). Less

Biodiversity Division, Department of Entomology, The Natural History Museum, London SW7 5BD, United Kingdom.

attention has been paid to global estimates for other diverse groups of organisms, although Hawksworth (1991) suggests that there may be 1.5 million species of fungi. One group whose size is completely unknown are nematodes. Although fewer than 2000 species have been described, deep sea sediments and terrestrial samples suggest that the diversity of nematodes could equal or surpass that of insects (J. Lamshead, personal communication). In practice, species concepts for nematodes are far from clear.

Although we have no clear idea of global invertebrate diversity, we know more about their general patterns of distribution. Most diversity at the species level is found in terrestrial environments and greatest diversity occurs in the 5 to 7% of land covered by tropical forests. The indications are that for every temperate species there could be at least 5 to 10 tropical species, although a few groups show the reverse trend. At the regional or local level there are few data on the turnover of species in soil with distance, altitude and habitat, particularly for tropical soils.

The significance of the soil fauna is seldom recognized. In one study of lowland rain forest in Seram, Indonesia, there were more individuals and greater biomass of invertebrates in the top few centimeters of soil and leaf litter than in the canopy (Stork and Brendell, in press; Holloway and Stork, 1991). One of several assumptions that Erwin (1982) made in deriving his global estimate of 30 million species of tropical insects was that two-thirds of insect species are associated with the canopy of trees. Evidence from an intensive study of the beetle fauna (over 6000 species) of all habitats in one area of Indonesian rain forest suggests that this assumption is heavily biased toward the canopy and that most insects are ground based (P. M. Hammond, N.E. Stork, and M.J.D. Brendell, unpublished). Hammond (1990) found that 25% of this beetle fauna was associated with the soil/leaf litter for the major (feeding) part of their life cycle. Of the British insect fauna, arguably the best known in the world, probably 10% of the 22,000 species are closely associated with the soil and leaf litter, and possibly another 15% are loosely associated (e.g., many Lepidoptera pupate in the soil).

Clearly, the soil is very important for biodiversity. How vital that biodiversity is to the stable functioning of soils is unclear (see Castri and Younes, 1990, and below).

## ***Invertebrates in the Soil***

In this section we briefly discuss the kinds of invertebrates found in the soil, highlighting those that make the greatest contribution to soil quality and describing what is known of their role in soil processes. One classification into three groups derives from their size and the way they interact with their habitats (Anderson, 1988a).

- *Microfauna*. These are invertebrates of less than 100  $\mu\text{m}$ , mostly nematodes (along with Protozoa, which are outside the scope of this paper). Nematodes are associated with water films (2 to 5  $\mu\text{m}$  thick) on the surface of soil and organic particles, and water filled pores (20  $\mu\text{m}$  wide).
- *Mesofauna*. This diverse group of invertebrates are of sufficient size to overcome the surface tension of water on soil particles but are not large enough to disrupt the soil structure in their movement through soil pores (body width between 100  $\mu\text{m}$  and 2 mm). They include Acari (mites), Collembola (springtails), enchytraeid worms, small Diplopoda (millipedes), and many small larval and adult insects. Studies of the mesofauna have concentrated on springtails and mites. Many species of mesofauna are mycophagous and therefore affect fungal populations strongly.
- *Macrofauna*. This group consists of species large enough to disrupt the soil by their burrowing and feeding (2 mm to 20 mm wide). The most important taxa are Isopoda (woodlice), larger Diplopoda, earthworms, Isoptera (termites), Coleoptera (beetles), Diptera (flies), ants, and molluscs.

All three faunal types have a complex role in soil processes. In general, the micro- and mesofaunas appear to enhance microbial activity (Wright et al., 1989) and to accelerate decomposition (Christiansen et al., 1989; Setälä et al., 1988), as well as

mediating transport processes in the soil (Anderson, 1988b).

Springtails, earthworms, nematodes, and termites, are especially important in soil processes. Below, we summarize their contribution.

## ***Springtails***

Soil-dwelling springtails decompose plant residues (Kiss and Jager, 1987; Takeda, 1988). Larger species increase mineralization by selective feeding on fungi, while smaller species help in soil humification by non-selective scavenging and by mixing organic material and mineral soil particles (van Amelsvoort et al., 1988). However, grazing by some species may reduce VAM fungi (Rabatin and Stinner, 1988), and selective grazing by springtails certainly seems to affect the growth of certain litter-decomposing fungi (Newell, 1984a,b). Low levels of Collembola stimulate both fungal and bacterial growth, but higher levels may negatively affect fungal populations and reduce humification of the soil (Hanlon and Anderson, 1979).

## ***Earthworms***

The role of earthworms in soil turnover has long been recognized (Darwin, 1881; Lee, 1985). Up to 50% of aggregates in European soils may be weathered earthworm casts (Rushton, 1988), and soils worked by earthworms have higher pore volume, increased field water holding capacity, more water stable aggregates and higher infiltration rates than soils without earthworms or only with species active on the surface (Lee, 1983).

Adding earthworms to the soil can increase agricultural yields, at least in the temperate region (Rushton, 1988). Improved soil structure results from tunnelling and casting (Dexter, 1978). Tunnelling increases the air space in the soil, reducing erosion because of higher infiltration rates. This is important in the tropics, where high intensity rainfall causes heavy runoff (Aina, 1984). Surface casting promotes soil mixing. Earthworm casts increase the overall aggregate stability of the soil (Hopp and Hopkins, 1946; Blanchart et al., 1989). Where earthworms are not present, dense

mats of dead or decaying root material can build up at the soil surface, locking up nutrients. Earthworms also reduce soil crushing after heavy rainfall (Kladivko et al., 1986).

Earthworms are important in making phosphorus (Sharpley and Syers, 1976; Mackay et al., 1982), nitrogen (Svensson et al., 1986; Syers et al., 1979) and other nutrients available in the soil, while enhancing microbial activity within the cast material. They also may make the soil more suitable for springtails and other non-burrowing invertebrates by increasing the abundance of vertical pores (Marinissen and Bok, 1988). In the tropics megascolecid earthworms may significantly reduce the rate of decomposition of organic matter after clear felling of savannas and their subsequent cultivation. This may be important in reducing humus loss in cultivated land (Martin, 1991).

### **Nematodes**

Little is known of soil nematodes, largely because of their microscopic size, clumped distribution, and trophic variation (Freckman, 1982; Yeates, 1987). Phytophagous nematodes often reduce plant primary production. However, the situation is not simple. Feeding by plant parasitic nematodes reduces crop yields (Sykes, 1979), yet lower levels of activity may stimulate plant growth (Jones, 1957).

Often there is a positive correlation between total nematode abundance and primary productivity (or other correlates of primary productivity, such as levels of available phosphorus). Studies of plant growth suggest there is increased nitrogen mineralization in nematode grazed microcosms when the C:N ratio is low (Elliott et al., 1980; Yeates and Coleman, 1982). Soil nematodes may enhance decomposition by 16% in field soil and up to 30% in litter (Pradhan et al., 1988).

Microcosmal studies of the effects of manipulating populations of a few soil species suggest that fungal and bacterial feeding nematodes may stimulate microbial populations at low densities (Griffiths, 1986), but inhibit them at high densities. Such high densities of microbe feeding nematodes may be obtained after the application of insecticides that remove

nematophagous mites. Manipulation experiments have shown up to 40% reduction in decomposition in plots from which mites have been excluded in a desert ecosystem (Santos et al., 1981). This is thought to be due to a lack of predator pressure on cephalobid nematodes, which are bacterial grazers. With reduced mite predation, bacterial grazers may reduce populations of bacteria to a level where nutrients become immobilized in the soil. The same does not seem to apply to fungal feeding nematodes, which increase in abundance immediately after mite removal, but return rapidly to premanipulation levels. However, bacterial feeding nematodes may enhance nitrogen mineralization more effectively than fungal feeders, because fungi are efficient nitrogen mineralizers themselves, and this does not appear to be greatly enhanced by nematode grazing (Ingham et al., 1985). Bacterial feeding nematodes may be most effective in synergy with soil protozoa (Griffiths, 1986, 1989).

An important feature of nematodes is that they can enter cryptobiotic states and thus track temporal changes in microbial levels. Nematode populations are affected by soil structure. Population growth is lower in fine textured soil than in coarse textured soil (Elliott et al., 1980).

### **Termites**

Termites are a tropical/subtropical group of social insects occurring below 45° latitude. Often they are the dominant group by far in arid or semi-arid soils. Because some species can form vast colonies of millions of individuals, their effects on the soil can be considerable (Nye, 1955; Lee and Wood, 1971; Lobry de Bruyn and Conacher, 1990). Wood (1988) categorizes the main ways in which the soil is modified by termites as: physical disturbance of soil profiles; changes in soil texture; changes in the nature and distribution of organic matter; changes in the distribution of plant nutrients and hence changes in soil fertility; and construction of subterranean galleries. The importance of fungus-growing termites on litter turnover, soil fertility and global carbon cycling is only just beginning to be considered (Jones, 1990).

The construction of the sometimes huge nest and gallery systems by termites involves considerable movement of soil and litter (Collins, 1983). These structures are made of termite feces, saliva, and soil particles in a particular size range. Thus they may radically alter the texture and structure of the soil. Over long periods, large amounts of soil may be deposited on the surface and subsequently eroded (Bagine, 1984). Nutrient levels in soils can be altered by termites, particularly those species that forage for food and use symbiotic microfauna and microflora to break down plant materials (Collins, 1981; Coventry et al., 1988). Termites may concentrate organic nitrogen and carbon in their nests (Laker et al., 1984). The construction of subterranean galleries affects the soil water regime, increasing porosity, aeration and water infiltration. In one study in New Mexico, low vegetation cover areas treated with insecticide had significantly lower infiltration rates than untreated areas (Elkins et al., 1986), suggesting that subterranean galleries of termites enhance water infiltration and retention of topsoil.

### **Other invertebrates**

Although not considered in detail in this paper, holometabolous insect groups such as Coleoptera (beetles) and Diptera (flies) are important in soils. Usually these are the groups with the greatest species richness but not always the greatest abundance or biomass. Many predatory and parasitoid soil insect groups are vital in the control of root feeding pest invertebrates (Clausen, 1940). Insects such as beetles and flies are particularly important in the breakdown of dung, carrion and leaf litter, and therefore return nutrients to the soil. Scarabaeid beetles may be especially important in this role (Greenslade, 1985; Kalisz and Stone, 1984).

Ants are found in most terrestrial habitats. Most are predators, and as such are a critical component of aboveground and soil communities. Ants, like termites, are social insects and their colonies have similar, but usually less spectacular, effects on the environment (Nye, 1955; Lobry de Bruyn and Conacher, 1990; Rogers and Lavigne, 1974). Many studies have shown the positive and negative impacts of ants



on different feeding groups of herbivorous insects and the close relationship that some plants have with particular species of ants. Less well known is the importance of ants in regulating the populations of other soil invertebrates.

Mites are important in the soil as fungivores, bacteriovores and nematode predators (Largerlof and Andren, 1988). Generalist fungivore mites may be important in nutrient mineralization from decaying roots (Arnold and Potter, 1987). They also are important in fragmenting litter, dispersing microbial spores, and stimulating microfloral activity.

Of non-insect groups, both Isopoda and Diplopoda are important as vectors of vesicular arbuscular mycorrhizal (VAM) fungi (Rabatin and Stinner, 1988). Isopods also may move litter deeper into the soil (Hassell et al., 1987).

Perhaps the most important contribution of invertebrates to soil structure is their feces. The fine structure of soils, and therefore many of its structural features that contribute to soil fertility, is largely determined directly (topsoil) or indirectly (mineral soil) by invertebrate fecal dynamics (see papers in the symposium volume edited by Spence, 1985; especially Pawluk, 1985; Rusek, 1985). For example, invertebrate fecal material was a significant component of all surface layers rich in organic matter in all regions of Canada (Pawluk, 1987). Decaying invertebrates may also contribute to nitrogen mineralization of the soil (Abrahamsen, 1990).

## **Problems in Studying Soil Invertebrates**

### **Sampling and extraction**

Sampling procedures are critical when assessing the abundance, biomass and species richness of invertebrates. Basic techniques have been described by Southwood (1978) and a good review of techniques applied to soil invertebrates is given by Edwards (1991). Different invertebrate groups usually require very different methods of sampling. This can cause

problems when comparing quantitative data collected in different ways (Schaefer and Schauer mann, 1990). For example, the abundance and biomass of termites are usually assessed by digging and hand sorting, while nematodes are extracted by very small soil core samples. Similarly, different research workers looking at the same invertebrate groups often fail to standardize their sampling protocols. A common source of error is variation in the depth and number of soil cores. Poor experimental design can lead to underestimation or even overestimation of groups that have patchy distributions.

Various extraction techniques are used to recover soil invertebrates. Most of these involve the movement of the animals through the soil, usually along behavioral gradients such as heat, light or chemicals (e.g., Tullgren-Berlese/ Kempson funnels). Others involve washing the animals from soil (e.g., Macfadyen apparatus). None of these techniques extract all the soil fauna, and some sample one group better than others. These problems have led to considerable variation in estimates of the numbers and biomass of soil invertebrates. Extraction techniques that drive living invertebrates through the soil are successful only when the temperature/light gradient is carefully controlled. The modified Kempson extraction process as used by Adis (1987), for example, takes 10 to 12 days. As a result, his estimates of arthropod abundance in rain forest soils in Brazil (Adis, 1988) are greater than those using more rapid methods of extraction (e.g., Stork and Brendell, in press).

Because of the problems of extracting the smallest invertebrates, (and perhaps because workers have fallen into the trap of believing that smaller means less significant), many authors have considered only the abundance of the macro and occasionally the mesofauna (e.g., Collins, 1980; Leakey and Proctor, 1987). The omission of the most abundant arthropod groups from abundance analyses may have serious consequences, particularly if such results are used to examine resource utilization and decomposition processes. In addition, data from larger arthropods often are difficult to interpret, because

these groups are found at lower densities and their characteristics have higher standard errors than for smaller arthropods.

## **Taxonomy and ecology**

Most soil faunas still are largely undescribed for most places on earth. This is particularly true of tropical sites. However, most invertebrate groups are well known and not difficult to separate. The difficulties usually lie at the species end of the scale. Indeed, many important groups, especially termites and nematodes, are taxonomically intractable (Greenslade, 1985). Taxonomists, an increasingly rare resource, too often produce keys that are designed for use by other taxonomists rather than by other biologists. The development of simple interactive computer identification systems, such as CABIKEY (CAB International, unpublished); PANKEY (Pankhurst, 1986, 1988); or COMTESA (Moldenke et al., 1991) should help reduce these problems and allow non-specialists to identify their own soil faunas. There is little ecological information for many species and accurate assessments are impossible in tropical regions, where a large part of the soil fauna may comprise species unknown to science.

## **Distributional factors**

The distribution of invertebrate groups varies considerably around the globe. Abiotic factors, latitude, and altitude are the most important influences on the composition and trophic structure of the soil fauna. Disturbance by humans also is important, although changes through disturbance often mimics those caused by natural processes. For example, plowing dries out the soil, making it less habitable for several hydrophilic groups, such as earthworms and nematodes (see below).

Abiotic factors clearly are important, especially extremes of humidity and temperature. Nematodes become inactive below soil water matric potentials of -0.4 MPa (Freckman et al., 1987), and earthworms probably require even higher water potentials. In the driest soils, only fungi and fungivorous mites appear to survive;

desert soil ecosystems may contain only these organisms for long periods (Whitford, 1989). The ability of mites to assume cryptobiotic states at low water matric potentials may explain this. Soil temperatures of 40°C and above are regularly attained in arid and semi-arid tropical and subtropical zones, and few animals other than some mites can withstand such temperatures (Whitford, 1989; Abdel-Galil and Darwish, 1987).

Differences in latitudinal diversity gradients for some groups, such as termites and earthworms, are reflected at least in food web structure if not trophic structure, with termites dominant in the tropics and earthworms in many temperate regions. Latitudinal gradients have been considered widely for many terrestrial and marine ecosystems but relatively rarely for soils (for a review of such studies see Petersen and Luxton, 1982). In many ways this is surprising given the low dispersal ability of many soil organisms and therefore their potential to be strongly constrained by historical biogeographical factors. How latitudinal gradients in soil taxa might change the nature and magnitude of soil processes mediated by invertebrates is unknown. However, there are hints that they could be extremely important (for example, the effect of earthworms introduced to New Zealand, O'Brien and Stout, 1978; see below). The major clades of some soil taxa may be found in very different parts of the world. Low-vagility groups such as earthworms are obvious examples. None of the five families of closely related holarctic earthworms are native to any other biogeographical region (Sims, 1982), although they have been dispersed by humans all over the world.

Altitude also constrains invertebrate populations. Leakey and Proctor (1987) showed that in Borneo the proportional biomass of annelids and diplopods dropped from lowland to upper montane forest, while rising for arachnids and cockroaches. On Volcan Barva in Costa Rica, some groups (Oligochaeta and adult Coleoptera) in soil and leaf litter decreased in biomass and density with increased altitude while others (Gastropoda, Araneae, Diplopoda, Symphyla, Dermaptera and larval Diptera) increased (Atkin and Proctor, 1988). Similar increases were found

for Oligochaeta, Isoptera and Chilopod on the slopes of Gunung Janing Barat (Brunei) while ants were most abundant and had highest biomass at a mid-altitude site.

### ***Invertebrate Measures of Change in Soil Quality***

The preceding sections demonstrate that invertebrates are not just passive inhabitants of the soil, but are active and integral constituents of soil systems. Their presence alters the physical and chemical structure of the soil and the rate and extent of soil processes. They are vital in determining soil quality for the production of healthy crops or forests, although the extent of this has been questioned (Anderson, 1987; Wright and Coleman, 1988). Soils that have poor hydrological, physical or chemical properties will inevitably have poor invertebrate communities. Many workers have used assessments of invertebrate communities to examine soil quality and the effect of human-induced changes such as deforestation or plowing. The loss of particular species may seem to have no direct impact on soil quality, but it may severely affect those species with more direct roles through food web interactions (see below). We must understand the structure of whole soil communities and how they are affected by different management practices. But how practical is the elucidation of such communities, and can we get the information we require from simple, easily sampled parameters? In this section we review various parameters, stressing both their theoretical power to explain soil invertebrate processes and their practicability.

#### ***Biomass, density and abundance***

Most invertebrate studies of management-induced changes in soil quality have measured biomass, density or abundance of invertebrates. Some general tendencies can be identified.

Soil fauna biomass often drops with increased agricultural usage in pastures and arable land. For example, earthworm populations drop significantly under plowing (Edwards and Lofty, 1982; Christensen et al., 1987; Rushton, 1988; Garceau et al.,

1988; Cavalli, 1989). Nakamura (1988) showed that direct drilling and rotary digging reduced the abundance of Enchytraeidae (Annelida), oribatid and other mites, springtails and other invertebrates in a Japanese arable andosol, while the application of an organic mulch increased it. Stinner et al. (1988) showed that under no-tilled treatments, the abundance of mites and springtails was higher than with conventional plowing. Studies in North Dakota also showed a higher abundance of springtails in no-tilled versus tilled soils, but the effect on mites was the opposite (Boles and Oseto, 1987). Compaction of soils by tractors also reduces invertebrate biomass and abundance (Aritajat et al., 1977).

High maintenance conditions (fertilizer, herbicide and insecticide treatments) result in greater abundance and biomass of invertebrates. For example, the abundance of oribatid mites on Kentucky bluegrass turf increases under high maintenance conditions (Arnold and Potter, 1987) and mites, springtails, isopods and diplopods also were more abundant after the application of lime fertilizer and organic manure in Brazil (Luizao, 1985). Reclaimed sites tend to show rapid increases in invertebrate biomass and abundance (e.g., Hutson, 1980).

Woodland areas tend to support a higher biomass of soil invertebrates than grassland. In a *Fraxinus americana* plantation in Quebec, the population density of edaphic mites, springtails, insects and other soil arthropods dropped under tillage and harrowing (Tousignant et al., 1988). The average abundance of mites and insects decreased by half, and that of springtails was reduced by 88%. This may be correlated with a drop in the humidity of the soils. Another study on mixed forest in Ontario showed that both whole tree and conventional harvesting reduced the arthropod fauna considerably. Oribatei, Prostigmata and Mesostigmata were found in significantly greater numbers in uncut plots than harvested plots. Whole tree harvesting has less effect on soil arthropods than conventional tree harvesting (Bird and Chatarpaul, 1986). Earthworm numbers also drop on deforested land (Krishnamoorthy, 1985; Dunger, 1988), although in some temperate coniferous forests,

earthworms may be absent (Shaw et al., 1991). Similar depression of invertebrate abundance and biomass occurs in felled and cultivated tropical forests (Lasebikan, 1975; Critchley et al., 1979; Badejo and Lasebikan, 1988; Dangerfield, 1990) and subtropical forests (Abe and Watanabe, 1983).

Correlation between the abundance of invertebrates and various soil factors has often been used to indicate differences in soil quality. Van Straalen et al. (1988), for example, showed that the abundance of oribatid mites and sminthurid springtails decreased in Dutch coniferous forests as the C:N ratio increased and the Mn concentration decreased. Similarly, a positive correlation was found between the mite *Tetranychus curcubitacearum* and nitrogen levels in a field in Egypt (Hoda et al., 1986). Springtail and mite densities often are positively correlated with humidity and negatively correlated with temperature (Jam et al., 1986; Hutson and Veitch, 1987). Pollutants at sub-lethal levels can change springtail species composition (Bengtsson and Rundgren, 1988). Finally, there are clear physical and chemical influences on earthworm distribution (Lavelle, 1988a). Calvin and Diaz-Cosin (1985, 1986) show the influence of pH, soil texture and C:N ratio on earthworm abundance.

Total abundance, biomass and density represent simple variables that can be measured independent of the difficulties involved in recognizing factors at the species or microsite level (Anderson et al., 1985). However, these measures can be variable and represent "snapshots" in time. Although seasonal changes in abundance and biomass can be considerable, for invertebrates these parameters do not fluctuate as rapidly and as dramatically under minor changes in soil temperature or moisture content as they do for microorganisms such as bacteria and fungi. These measures, however, tell us little about community structure and nothing about the likely course of future soil processes. King et al. (1985), for example, compared springtail populations in natural and improved pastures in Australia and showed that although abundance rose under improved pasture, the overall species richness dropped. In addition, species composition changed,

with many more introduced than endemic springtail species present in the improved pasture. Clearly, abundance measures can be misleading about invertebrate-mediated soil processes. So, is species richness better for this purpose?

### **Species richness**

Species richness has been used in many soil studies. For example, the number of species of earthworms fell from eight to three in a Canadian deciduous forest after tree felling and plowing (Garceau et al., 1988). Similar results have been found for earthworms in woodland and grasslands in India (Krishnamoorthy, 1985), for earthworms and termites in primary forest converted to improved pasture in Peru (Lavelle, 1988b), and for mites and Collembola in primary and burnt secondary forest in central Amazonia (Adis, 1988). In addition, mite and collembola species richness change with pH (Hagvar, 1987). Occasionally, some groups become more species rich in poorer soils. Braithwaite et al. (1988), for example, found that species richness for termites rose when various measures of soil quality declined in Kakadu National Park, Australia. This may be due to the absence of competitors in poor soils, so that termite species richness increases as the overall community is impoverished.

An advantage of species richness is that it provides a broad measure of the complexity of communities and perhaps their resilience to change. Its disadvantage lies in the practical difficulty of distinguishing invertebrate species and the little that it reveals about species interactions. However, species richness has the potential to tell us more about invertebrate communities and soil quality than straight biomass, density or abundance. The following approaches go beyond simple taxonomic biodiversity measures and attempt to get at ecological complexity and interactions directly.

### **Trophic group diversity**

A simple ecological classification of soil trophic structure reflects the common resources that different species use: primary producers (green plants), her-

bivores, predators and decomposers. Although many studies of soil invertebrates examine biomass, abundance, or species richness, few take into account the trophic arrangement of soil communities. In practice, trophic analysis of the soil fauna is very difficult because it requires knowledge of the biology of individual species or groups of similar species. It is not enough to show changes in species richness of taxa chosen at high taxonomic levels if such levels embrace species with a wide range of trophic responses to differing soil conditions. Nematodes, for example, input into soil processes at almost every trophic level. Some workers have argued that studies of particular taxonomic groups tells us very little, because of the convergence in trophic function of phylogenetically unrelated organisms and the divergence in trophic behavior of related taxa (e.g., Walter et al., 1988 for predatory soil arthropods). However, this has not been proven or examined for most groups, and taxonomy may be a useful predictor of ecological function if the right taxonomic levels are chosen for investigation (Gauld, 1986).

Despite these problems, trophic group structure is increasingly analyzed in impact assessments of management practices on soil communities. A particularly useful method is to examine groups of species that use the same trophic level resource but in different ways. These have been termed functional groups or guilds (see also, in the context of soil guilds, the "league" concept of Faber [1991]). A few examples are given below.

The number of earthworm guilds (functional groups) fell from four in tropical forest to one in cultivated land in Peru (Lavelle, 1988a,b). In the temperate region, plowing buries leaf litter and sward, thus removing the food of one guild of earthworms (those that form permanent burrows and forage on the surface), and destroying the habitat of another (those that live in the leaf litter and sward). A third guild (those that live and feed entirely within the soil) increase in biomass and abundance (Rushton, 1988).

Several authors have shown that the composition of nematode guilds differs according to the nature of soil in which they are found (Ingham et al., 1989; Boag,



1988; Arpin et al., 1986). For example, Arpin and Ponge (1986) show how guild structure changes between a *Pinus sylvestris* plantation and a mixed *P. sylvestris* and *Quercus petrae* plantation, because of less disturbance in the mixed woodland. Braithwaite et al. (1988) demonstrated considerable variation in the number of species of different guilds of termites and related this to soil quality and other factors (see above).

An interesting aspect of trophic group studies is the uncertain effect that pesticides, which are intended to kill specific taxonomic groups, have on community structure. A nematocide kills nematodes regardless of their trophic position and disrupts the whole community if functional redundancy is low (discussed shortly). Insecticide treatment of a maize system led to increased oribatid mite density but consistently lowered mesostigmatid mite density, with uncertain community consequences (Stinner et al., 1988).

Trophic studies show that some systems recover slowly from depauperation, if at all. Studies of beetle assemblages in Wyoming (Parmenter and MacMahon, 1987) suggest that the difference in trophic structure between undisturbed and reclaimed soil sites are so great that the original trophic structure might take many years to return.

Of fundamental importance both to studies of species richness and to trophic analysis is the concept of "functional redundancy." How far can a community be reduced before it begins to lose its trophic cohesion? How many units (i.e., species) can a system lose before trophic groups are lost, harming soil quality? What is the minimum number of species required for the soil community to survive as a significant contributor to soil quality? How well can stressed communities regenerate? We need to answer these questions before the connection between biodiversity and soil quality can be adequately assessed.

### Food webs

Conventional trophic analysis takes a simplistic view of species interactions (for understandable pragmatic reasons). In reality, species of organisms are linked in webs of interactions that can be extremely

complex. Many such food webs have been studied and described, particularly those for simple, species-poor systems such as treehole communities (Pimm et al., 1991). Few food webs have been constructed for soil communities. However, conceptual models have been proposed. For example, Hendrix et al. (1986) drew diagrams of possible food webs associated with tillage and non-tillage systems. They suggested that tilled systems are dominated by disturbance-adapted bacteria with high metabolic rates, while non-tilled systems are dominated by fungi. The structure of these food webs suggests that decomposition is faster in the tilled system and that nutrient loss from the soil therefore is greater. Food web structure is important because the rate at which populations recover from disasters may well be dependent on food chain length (Pimm, 1982). Removal of individual species from food webs is likely to have unpredictable effects depending on the position they occupy and the number and abundance of dependent organisms. Long term studies are required to understand the effects of changes in food web structure.

### Keystone species and ecosystem engineers

The idea that some species are more important for the structure of communities than other species (or groups of species) has attracted some support (Paine, 1969). These "keystone" species usually are very abundant or of considerable biomass (e.g., oak trees in an oak woodland). Alternatively, if they are small or less abundant, they play a critical role in a food web (e.g., euglossine bees and brazil nut trees). However, occurrence of keystone species is uncertain outside aquatic ecosystems (Krebs, 1985) and there seems no easy way to identify possible keystone species in the very complex soil environment.

A related and perhaps more useful idea is that of "ecosystem engineers" (C.G. Johns and J.H. Lawton, unpublished manuscript). Certain groups of organisms, sometimes even single species, may "engineer" environments for many other organisms and thus form the bedrock of communities. In soil, groups that might be considered ecosystem engineers are earthworms (predominantly in temperate

regions), termites and ants (predominantly in tropical regions).

In temperate regions, earthworms make a major contribution to soil structure, and thus to soil community stability and soil quality. The introduction of earthworms to New Zealand (Stockdill, 1982) appears to have increased the annual flux of C from 300 to 1000 kg ha<sup>-1</sup>, while mean residence time of organic compounds has decreased from 180 to 76 years (O'Brien and Stout, 1978).

Certain species of termites have been identified as potential keystone species (Redford, 1984). Termitaria have a higher nutrient content than the surrounding soil, and provide habitats for many other organisms, even when the termites have abandoned them (Salick et al., 1983).

### International Measures of Soil Quality-Ranking Parameters

The need for a global assessment of land degradation, highlighted by the UN conference on the Human Environment, was acted upon by the Food and Agriculture Organization, which established an international set of standards of soil types. This paper was presented at a meeting on the Assessment and Monitoring of Soil Quality convened to investigate the possibility of establishing some simple measures of assessing soil quality. Several physical, chemical and biological factors contribute to the quality of soils and ultimately to the nutritional value of crops. Measurement and monitoring of soil quality therefore has to take these factors into account. A simple index of soil quality might include three invertebrate measures as well as two or three each of hydrological, chemical, physical and microbiological characteristics of the soil. Of the various biological criteria that have been discussed above, those that are selected must reflect the nature of the particular soil in question and the region. Earthworms may be a key group for temperate regions, but termites may be more appropriate for drier tropical or subtropical soils. (Note, however, that earthworms can be very important in wet tropical soils, e.g., Aina, [1984].) These criteria also must be easy and cheap to determine. We have discussed how



ecological factors must be taken into account through consideration of trophic, guild, or food web structure. We suggest the following as a priority list of measurable biological criteria for invertebrates:

**1. Keystone species or ecosystem engineers.** Where such groups can be identified unambiguously, their abundance, biomass and density may represent the best criteria for quickly and effectively assessing the invertebrate contribution to soil quality.

**2. Taxonomic diversity at the group level.** Assessment of the abundance, biomass and density of all soil invertebrates at the order/class level will provide a simple indication of the ecological complexity of the soil community.

**3. Species richness of several dominant and perhaps more taxonomically tractable groups of invertebrates.** Again, this will indicate the ecological complexity of the soil community.

Inevitably, these three measures will provide only a simple guide to soil quality. We echo the conclusion of Anderson (1988a) that the real obstacle to evaluating the invertebrate contribution to soil quality is a "lack of understanding of the links between gross soil processes and the structure of soil organism communities." If we are to understand these processes, then at least one or two major, in-depth studies of the community structure (e.g., Schaefer and Schauermaun, 1990) and of the interactions of invertebrates with each other and with micro organisms and their soil environment must be attempted.

**Acknowledgments.** NES thanks the organizers of the Workshop on the Assessment and Monitoring of Soil Quality, including Bob Papendick, John Haberern, and Carole Piszczek, for the invitation to participate, and the Rodale Institute for financing the visit. We are grateful to Joe Anderson, Anne Baker, David Bignell, Richard Brown, Chris Lyal, Bill Sands, Tony Russell-Smith and an anonymous referee for commenting on early drafts of this paper.

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