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# INTERACTION BETWEEN SOIL FAUNA AND THEIR ENVIRONMENT

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## Abstract

Interactions between soil animals and their environment can be described in terms of positive and negative feed-back loops taking place in the build-up and steady-state of soil ecosystems, respectively. The size of animals determines the scale at which they interact with their physical and biotic environment. Nevertheless varying scales at which animals intervene in functional processes is not relevant to any hierarchical position within the ecosystem, due to symmetrical patterns in the relationships between microbes, animals, humus forms and vegetation types. The present knowledge has been reviewed and discussed to the light of an integrated view of the soil ecosystem, with a particular accent put on soil acidity.

## Introduction

During the last decade a considerable reappraisal has been made of the role of organisms and associate functions in forest ecosystems (1, 2). From agents helping in tree nutrition (symbiotic organisms) and recycling of primary production (decomposers) they passed to the status of full members of the forest ecosystem, acting side-by-side with trees to ensure its build-up and stability (3, 4, 5, 6). This is mainly due to the discovery of mutualistic relationships between soil organisms, their immediate environment, and major processes such as litter decomposition, root growth, and forest dynamics.

Mutualistic relationships may be expressed in terms of feed-back loops, a mathematical concept erected by Wiener (7) to describe interactions within systems of a high degree of complexity such as living organisms or self-regulating machines. When two sub-systems interact in a repressive manner, their interaction, called negative feed-back, leads to an equilibrium. This is a basic concept in homeostasis. On the contrary positive feed-back loops are characterized by a reciprocal stimulation or synergy between two sub-systems. This concept, firstly used to describe

biological systems, more especially nervous systems, has been successfully applied to ecosystems (1, 3).

Compared to biological systems, where negative feed-back loops (steady-state or buffer mechanisms) predominate, thus ensuring stability of the organism, ecological systems show phases of build-up followed by phases of collapse, also called aggradation and disintegration, respectively (1, 8, 9). Such shifts in ecosystem properties can be explained by positive feed-back loops, i.e. self-reinforcing mechanisms. Contrary to claims by Perry et al. (3), positive feed-back loops, despite their promising name, should not be considered as stabilizing forces for a given ecosystem. Rather, they force it definitely from one state to another; more precisely from a given temporary equilibrium (stabilized by negative feed-back loops) to another. As an example we can consider the role of phenolics in forest ecosystems. The polyphenol content of tree foliage is known to control the release of nitrogen in a mineral form during litter decomposition, i.e. the higher the amount of polyphenols, the slower the rate of nitrogen mineralization (10). The accumulation of recalcitrant forms of nitrogen (which are repellent to a lot of organisms) is due to the build-up of a layer of unincorporated organic matter (11). This creates locally acid conditions through slow oxydative processes involved in humification (12). These conditions favour acid-tolerant soil organisms which contribute in turn to increase the acidity of their environment, such as brown-rot fungi (13). This positive feed-back loop is itself reinforced by plant-soil relationships. It has been observed for a long time that when a plant species grew in moder humus, i.e. with a slow disappearance of litter and mostly epigeic fauna (arthropods, enchytraeids), it exhibited a higher content in phenolic substances than when growing in mull humus, i.e. with a rapid disappearance of litter and high earthworm activity (14). This increase in polyphenol content was experimentally demonstrated to be favoured by a decrease in nitrogen availability (15). Instead of stabilizing the forest ecosystem, this process, in the absence of further disturbance, can lead to a shift towards other ecosystems which are better adapted to nutrient-poor conditions, such as ericaceous heaths with mor humus, i.e. with poor faunal and microbial activity (5).

Negative feed-back loops (steady-state mechanisms) may be found, for instance in the ability of earthworms to buffer the pH of their immediate environment (16), due to amphoteric properties of their mucus (17). This points to the importance of changing constantly the scale at which processes should be studied if we want to understand the functioning and the fate of forest ecosystems (18, 19). We know now that mechanisms by which a soil animal is able to find suitable food and habitat within a space of, say, a few cubic centimeters (20), are as important for the fate of forest ecosysems as mechanisms which operate the growth and death of trees (19). The present paper will be focused on the feed-back processes (positive as well as negative) by which soil animals interact not only with their immediate

environment (the litter, the soil, and their inhabitants) but also with other compartments of forest ecosystems such as tree canopies.

## Macrofauna

### *Interactions between macrofauna species*

Most interactions between macrofauna and the soil environment concern mainly saprophagous animals, i.e. animals eating on litter or soil organic matter. The huge amount and variety of dead organic matter produced by forests, both above- and below-ground (21,22), and the amount and variety of microorganisms living in litter and underlying horizons (23), may explain why big-sized saprophagous invertebrates are to be found in such varied groups, with so strongly varying ecological requirements, such as molluscs, annelids and arthropods. Nevertheless the abundance and diversity of resources created by plant-microbe interactions cannot itself explain the diversity of macrofauna in forest soils.

By their movements and feeding behaviour, saprophagous macrofauna transform various plant debris into compact aggregates, mixed or not with mineral matter, create cavities in the soil, make holes in dead leaves, wood and bark remnants, transport entire leaves or needles down to mineral horizons or defecate mineral matter within litter horizons (24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40). This activity creates a permanent movement of matter within the humus profile, associating food resources and habitats in a number of combinations which encourage a wide range of animal groups to cohabit and interact. This could explain why high densities of earthworms have been found constantly associated with high diversity and density of other saprophagous macrofauna such as slugs, woodlice and millipeds (41, 42, 43, 44, 45, 46).

The absence (egoism of species) or the existence of antagonistic/mutualistic relationships among animals of the same size, feeding on similar food resources (for instance decaying leaves or needles, or roots) has been debated (47, 48). Unfortunately few studies directly addressed this question, given the specialization of most soil zoologists for a given animal group if not for a given species.

By comparing earthworm communities present in above-ground ant nests with the surrounding soil and litter Laakso & Setälä (49) demonstrated that litter-dwelling earthworms, and more especially *Dendrodrilus rubidus*, were favoured to a large extent by the wetter environmental conditions and the abundance of food prevailing in ant mounds. The worms escaped predation by ants owing to the repellence of their mucus. No true mutualism was demonstrated but this study gave evidence that a combination of repulsion (earthworms to ants) and attraction (ants to earthworms) mechanisms may explain the observed co-occurrence of *Formica aquilonia* and *D. rubidus*.

By analysing gut contents of co-existing earthworm species, and comparing them with aggregates forming the mull A horizon into which they were living, Bernier (40) concluded to the existence of synergistic relationships between sympatric species. His results pointed to the contribution of several species of earthworms, occupying varying but strongly overlapping niches, to the building of the mull humus form. Such a mull profile was interpreted as the final result of their multiple interactions, thus confirming results obtained by Shaw & Pawluk (32) in laboratory experiments. Whether this scheme can embrace the activity of other mull-inhabiting macrofauna remains surprisingly an open question, although it has been postulated as the most realistic view by David (44). To answer definitively the question whether mull-inhabiting macrofauna other than earthworms are subordinate or not to earthworm activity necessitates experimental work, given the well-known limitations of co-occurrence data (50).

***Interactions between macrofauna and mesofauna***

The favourable action of saprophagous macrofauna upon mesofauna has been suggested by co-occurrence data in zones poor and rich in earthworms (51, 52, 53). This phenomenon has been experimentally verified only in a few cases (54, Salmon & Ponge, unpublished data). It appeared that the density of several microarthropod groups, mainly big-sized Collembola, was seemingly increased in the presence of living earthworms. Although Marinissen & Bok (51) claimed that the observed effects were due to changes in soil structure, nothing is known of the mechanisms actually involved in these interactions, given the number of ecological factors which can be affected by earthworm activity (55).

The vertical distribution of mesofauna is also influenced by macrofauna inasmuch as mull or moder humus forms can be attributed to a high or a low level of macrofaunal activity, respectively (46). Although a decrease in mesofaunal densities is generally observed from holorganic to hemorganic then to mineral horizons, A horizons of mull humus forms are more populated than corresponding horizons of moder humus forms (45, 56). This has been attributed to soil structure, in particular pore size (57, 58), and to the vertical distribution of organic matter (56, 59, 60). True mechanisms are poorly known apart from the positive geotropism of some endogeic species (58).

A strong relationship has been repeatedly observed between the distribution of most mesofaunal groups and humus forms and associated ecological factors (46, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72). This can be explained by i) the influence of macrofaunal activity on the distribution of mesofauna food resources and habitats, ii) the direct attraction of mesofauna for macrofauna (54, Salmon & Ponge, unpublished data), iii) the sensitivity of mesofauna to substrate acidity (73, 74, 75, 76), iv) the

influence of plant and microbial secondary metabolites (20, 77, 78, 79, 80, 81).

A few attempts have been made to find out reciprocal action of mesofauna (microarthropods, enchytraeids) upon macrofauna. This is possible only through experimental procedures, because unambiguous causal relationships are still more difficult to derive from field co-occurrence data than in the reverse case. Haukka (82) demonstrated that high densities of the enchytraeid *Enchytraeus albidus* were detrimental to growth and reproduction of the epigeic earthworm *Eisenia fetida* when these species were grown together in compost. This unexplained phenomenon, as well as differences in ecological requirements of these two oligochaete species, may contribute to understand the negative correlation which has been observed between enchytraeid and earthworm densities in forest soils (46, 83).

A more indirect action of mesofauna upon macrofauna is the burrowing of earthworm aggregates by enchytraeids. In mull humus, disintegration of earthworm hemorganic faeces by enchytraeids can be easily observed after earthworm exclusion (29, 84, 85). The comminution of earthworm aggregates (5 to 10 mm) into small enchytraeid faeces (10 to 50 µm) decreases bulk soil porosity (85). Given the stimulatory effect of soil compaction upon casting behaviour of the common anecic earthworm *Lumbricus terrestris* (37), a positive feed-back loop into which enchytraeid and earthworm species are involved can be postulated.

***Interactions between macrofauna and microfauna***

The action of macrofauna upon microfauna (protozoa, nematodes, tardigrades, pauropoda) has been poorly investigated. Indirect effects are mainly brought about by the building of humus forms by macrofauna. For instance the species distribution of nematodes will differ between humus forms (86, 87, 88, 89). Predation (90) as well as dispersal (91) of nematodes by earthworms have been observed in experimental microcosms with controlled fauna, and were attributed to casual contact. Nevertheless, attraction by freshly emitted woodlice faeces has been experimentally demonstrated for bacterivorous nematodes (Arpin, unpublished thesis). This was probably related with the strong bacterial development observed in fresh faeces of macrofauna (92), but attraction mechanisms remain unknown.

The action of microfauna upon saprophagous macrofauna has not been clearly demonstrated, except if we consider microfauna as a possible food for macrofauna, as previously stated, or in the case of mutualistic relationships involving bacteria, amoebae and earthworms (93), or even in infection diseases caused by parasitic protozoa (94). Unfortunately none of these studies was aimed at assessing the impact of microfauna upon macrofauna populations. This is possibly due to the prominence given to hierarchical concepts, i.e. lower-order levels, generally small-sized organisms, are thought to be controlled by higher-

order levels, generally big-sized organisms (1, 2, 6, 95).

***Interactions between macrofauna and vegetation***

Selective feeding on litter components has been demonstrated in a variety of litter-dwelling macrofauna living in woodlands such as woodlouse (34, 96, 97, 98, 99), millipeds (56, 96, 100), or earthworms (40, 101, 102, 103, 104). The presence of litter at the ground surface is also a prerequisite for a number of litter-consuming species which rapidly disappear after experimental litter deprivation (105, 106). These phenomena can be attributed to the need for proper food and habitat, within the limits of experimental conditions.

The palatability of litter has been often attributed to its content in polyphenols and amino-nitrogen, which proved negatively and positively correlated with consumption of a given litter type, respectively (102, 103, 107). Leaching of litter was demonstrated to increase its palatability only when of a long duration, and this effect was increased after previous grinding of the litter (102, 107), pointing to the presence of weakly soluble distasteful substances. Other experiments demonstrated the favourable influence of fungal or bacterial conditioning (34, 98, 99, 108, 109). Volatile compounds produced by fungi were demonstrated to help the woodlouse *Porcellio scaber* to detect its preferred food (109). Given the capability of earthworms to use odours as cues for finding their way (110) it is probable that olfaction is used by many groups to detect palatable litter.

If we try to make sense of this body of knowledge, it appears that, despite the fact that mechanisms may eventually change from one group to another, litter components where the stage of development of the decomposer community (ageing) has replaced distasteful tannin-protein complexes by more attractive nitrogen forms will be selectively eaten (10, 11, 111, 112, 113). Accordingly in the course of decomposition lignin is replaced by more attractive fungal mycelium (47, 114, 115, 116), and the toughness of leaf tissues is decreased. This latter change deserves special interest in the case of coniferous needles, known for their mechanical resistance to grinding (98).

The comparison of consumption and assimilation rates has indicated that, despite a more intense consumption of leaves or leaf parts previously conditioned by fungi (34, 98, 99, 102, 109, 117), this plant material had often lost most of its nutritive value, which resulted in lower assimilation rates (98). Thus a preference for a given food (choice) does not necessarily fit with nutrient requirements (need), which has been often neglected in theoretical studies on habitat selection (118).

Awaiting for further experiments on different animal groups, fungal odour could be one of the means by which animals find their preferred food before tasting or touching it. Consequences of

abovementioned processes in natural environments are that litter-consuming animals i) will move towards a particular stage of decomposition of litter along the humus profile, generally a few centimeters below the ground surface, ii) will make a choice between several litter components, for instance between leaves belonging to different botanical species, iii) may eventually disappear locally if proper food or habitat is absent at a scale exceeding the amplitude of their current horizontal and vertical movements. Only the latter process, fitting with hierarchical models (1, 2,6, 95), can be considered as an effective control of macrofauna by trees.

In a series of thirteen beech stands growing on acidic soils, Ponge et al. (46) observed that variations in the composition of soil fauna could be explained by mineral composition of beech litter, most litter-consuming macrofauna (typical of mull inhabitants) decreasing together with the richness of leaf litter in metals and alkaline earths. In this example changes in the mineral composition of beech litter could in turn be explained by geological and climatic influences. Similarly, selective effects of litter quality on earthworm communities have been observed by Muys & Lust (119) and Muys et al. (120). This could be explained by high mineral requirements of saprophagous macrofauna. These animals for instance lose a lot of calcium through the production of cutaneous mucus (121) or hardening of the cuticle (122, 123, 124), according to zoological groups.

The action of macrofauna upon vegetation can be appraised through changes in the environment of the root system effected by soil animals. Although a direct hormonal effect on plant growth of compounds extracted from earthworm faeces has been observed by Dell'Agnola & Nardi (125), most effects of soil macrofauna upon vegetation probably come from changes in nutrient availability and mechanical disturbance.

The transformation of litter into macrofauna faeces and excreta was repeatedly demonstrated to increase element release and C/N ratio (33, 126, 127, 128, 129, 130, 131, 132). Some differences between zoological groups have been registered, for instance phosphorus availability was seen to be increased by earthworms but remained unaffected by slugs in an ecotron experiment (133). Similar effects were registered when soil was ingested by endogeic earthworms (134, 135).

The deposition of faecal material creates micro-sites which are favourable to the development of the root system of plants (127, 136), but also to fungal hyphae and bacteria (92, 127, 137, 138, 139, 140), bacteria being already stimulated to a great extent by mucus production within animal intestines (141, 142). Since most effects of faecal deposition and excretion are of a short duration (139), due to immobilization of nutrients by actively growing microflora or to leaching, the presence of roots in the vicinity of animal faeces may allow plants to uptake nutrients at the right place and at the right time they are

released by animals. This may explain why dramatic increases in nutrient availability observed in experiments with animals but without plants can be masked in the presence of plant roots (143).

Experiments with endogeic earthworms and birch seedlings demonstrated that the stimulatory effect of earthworms on seedling growth could be observed only in the presence of living worms (144). In the particular case of earthworms nitrogen fixation by free-living bacteria has been demonstrated to occur both in the hindgut (145) and in burrow linings (146), which may explain increases in nitrogenase activity observed in the presence of active earthworms (147).

Burying of plant parts and seeds (29, 148, 149, 150) and physical changes in the structure of the topsoil (28, 29, 32, 39, 151, 152, 153) have been demonstrated to influence the fate of plant communities (133).

Another possible mechanism by which soil macrofauna may influence the development of plant communities, as it has been observed in the regeneration of late-successional forest ecosystems (19, 150, 154), could be the release of phenolic toxicity (155, 156). This may occur directly, through chemical degradation of phenolic compounds during gut transit (157, 158), or indirectly through adsorption of these compounds to clay-organic complexes (159) which are present in casts deposited near or at the ground surface by soil-burrowing animals (36, 160).

***Interactions between macrofauna and abiotic factors***

Contrary to interactions between macrofauna species (prey-predator relationships excepted), interactions between macrofauna and their abiotic environment have been widely documented. Species which exhibit permanent or temporary burrowing activity, such as earthworms and millipeds, seem to be strongly influenced or even selected by mechanical features of the soil into which they dig, such as particle-size distribution (32, 109, 161, 162, 163, 164) and compaction (37), and also by chemical features such as acidity, water and oxygen tension (161, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175). They can influence in turn these features through their burrowing, casting, excreting and feeding activity (16, 28, 29, 32, 33, 37, 38, 141, 151, 153, 176, 177, 178, 179).

A reorganization of the soil structure, with disruption of ingested aggregates, has been observed during the earthworm gut transit (36, 39). Fluidification of the ingested soil and peristaltic movements of the intestine allow a close contact between bacterial colonies, humified organic matter and clay particles, using Van der Waals attraction energy (180). This attraction is further reinforced when the cast ages and dries (36). Consequences of this process are stabilization of organic matter (181, 182), increase in bulk density of soil aggregates (38, 179), appearance of stable bacterial microaggregates (36,39) and clay-humus assemblages (40, 152),

which form the bulk of the mull A horizon (183, 184, 185). This probably applies to American mull-forming millipeds as well (24, 186).

Homeostatic features of lumbricid activity indicate that these animals contribute to stabilize a lot of soil parameters through negative feed-back loops. Since pH (16), potassium availability (135) and macroporosity (37) were demonstrated to tend towards equilibrium values whatever the conditions prevailing at the start of experiments, it may be thought that at least some earthworm species are able to adapt their environment to their own requirements. This may help to explain the observed shifts from moder to mull associated with the passage from the pole stage to the full-grown stage of mountain forest stands following colonization by *Lumbricus terrestris* (150, 187). The impact of this process on the regeneration of Norway spruce (*Picea abies*) clearly indicates the participation of soil macrofauna to steady-state mechanisms taking place in late-successional forest stands (19, 188, see also Ponge, this issue).

## Mesofauna

### *The place of mesofauna in soil foodwebs*

The impact of mesofauna on its environment is often masked by that of bigger-sized animals such as saprophagous macrofauna, which dig the soil, pull plant debris, excrete, eat on plant debris and animal faeces, and defecate, at a scale overwhelming that of mesofauna individuals. In humus profiles with abundant macrofauna (mull humus) the physical impact of smaller-sized animals will thus be less apparent than in humus forms with abundant mesofauna but poor macrofauna (moder humus) where the deposition of faeces of small animals remains undisturbed (27, 183, 189, 190, 191, 192). This does not mean at all that the impact of mesofauna is negligible in mull humus.

The selection of mesofaunal groups, for instance by studying the recolonization of defaunated soil or litter enclosed in nets of varying mesh size, by enclosing or culturing animals in microcosms, may reveal a prominent contribution of mesofauna to decomposition and mineralization processes (193, 194, 195, 196, 197, 198, 199, 200, 201, 202, 203), and a strong impact upon microbial standing crop and activity (194, 204, 205, 206, 207, 208, 209, 210, 211), and soil structure (84, 85, 160), whatever the humus form. This may be achieved, too, by comparing nearby micro-sites where the activity of a given mesofaunal group varies greatly, as this is the case in and around fly larvae puparia (212).

In situ observation of the activity of mesofauna may also allow to evaluate their place in soil foodwebs, such as for instance in rhizotrons (48). More indirect methods, by counting, weighing, and measuring the assimilation and turnover rate of elements in different animal groups, may help to evaluate the role of mesofauna in the cycling of nutrients (122, 123, 124, 213, 214, 215, 216, 217, 218, 219, 220, 221).

Some particular substrates, too hard or unpalatable to macrofauna, are consumed by mesofauna only, thus allowing their faeces to accumulate locally. This is the case of decaying wood (222, 223, 224), bark (47, 140), coniferous needles and leaf petioles (140, 225, 226, 227, 228), and mosses (47). The particular place of oribatid mites in the tunnelling of hardest substrates such as bark, coniferous cones and needles has been highlighted (229, 230), and even quantified (231, 232, 233). These animals may be followed by other groups such as enchytraeid worms, which tunnel in turn the conditioned substrate and ingest faeces of the former group in a successional pathway (Ponge, this issue). Interactions between different mesofauna species may be explained by direct positive or negative influences (234, 235, 236, 237), but also by changes operated in a given substrate before another species can consume or colonize it (140, 238).

***Interactions between mesofauna and microorganisms***

Compared to saprophagous macrofauna, which influence soil respiratory activity and mineralization through direct litter or soil processing, a different impact of non-predatory mesofauna upon microflora may be found through its grazing activity, for instance by releasing nutrients immobilized in microbial biomass (223, 239). The release of nutrients immobilized by microflora in a form more available for vegetation, such as for instance the excretion of mineral nitrogenous compounds by microbivorous fauna, will stimulate the development of microflora, which will in turn stimulate populations of microbial-feeders. Nevertheless, such positive feed-back loops were never observed on the field, given the buffering effects exerted by soil nutrient levels when depletion thresholds are reached (240, 241, 242, 243).

Both growth stimulation and predation of soil microorganisms may compensate each other (203), or the balance between them may be affected by animal densities (194, 195, 243, 244, 245, 246), which may result in unexpected phenomena. For instance the absence of a net effect of mesofauna on soil respiration (carbon mineralization) can keep pace with a strong increase in nitrogen mineralization (247). In this connection the growth of tree seedlings may be stimulated by mesofauna despite of a strong reduction in the biomass of symbiotic as well as non-symbiotic microflora under their grazing influence (211).

Given our knowledge of turnover rates of nitrogen it has been calculated that a noticeable part of mineral nitrogen is produced by animals grazing on microflora, which excrete nitrogen as urea or ammonia, rather than by soil microorganisms themselves, which immobilize it (248, 249, 250, 251). This could explain why the feeder root system of plants fits so exactly the vertical distribution of soil animal activity whatever the humus form (252).

The question which arises in the light of these highly demonstrative experimental studies is their bearing on natural conditions, where heterogeneity is high, both in time and space, and composition of mesofaunal communities highly variable (253). Leonard & Anderson (254) demonstrated that when using spatially heterogeneous (porous) substrates for rearing the Collembolan *Folsomia candida* together with the fungus *Mucor plumbeus*, results may be quite opposite to that obtained with a smooth surface without any refuge for the fungus. Such importance of refuges for microflora, for instance inside decaying plant debris, may explain why no effect of grazing on fungal communities was found in some experiments using coniferous needles (255).

The impact of fluctuating factors, such as moisture and temperature, on the temporal and spatial distribution of mesofauna (256, 257, 258, 259, 260, 261, 262, 263, 264, 265, 266, 267, 268), may have a decisive influence on overall mineralizing effects (269). Species-specific effects have been demonstrated with phylogenetically related animals belonging even to the same trophic group or guild (201), or by manipulating the composition of complete mesofauna communities (270). Thus better knowledge of mechanisms would be desirable before a clear picture of environmental effects of mesofauna could be drawn.

Mechanisms by which mesofauna may have a noticeable impact on microflora are manyfold. Predation has a direct impact on the density of viable fungal spores and mycelia (208, 271, 272, 273, 274, 275, 276), and of bacterial microaggregates (185). Besides, the vertical and horizontal distribution of microflora (bacteria, fungi and microalgae) and their ability to colonize new substrates are affected to a great extent by transportation of viable propagules on the integument and in faeces of mesofauna (277, 278, 279, 280, 281, 282, 283).

Direct, non nutrient-based, effects of grazing by mesofauna on growth patterns of microfungi have been demonstrated by Hedlund et al. (284). These authors observed that grazing by the Collembolan *Onychiurus armatus* induced a shift from the common mode of growth of *Mortierella isabellina* in the absence of fauna (short, highly sporulating hyphae) to fast-growing non-sporulating hyphae. A similar phenomenon has been observed in cultures of the fungus *Dendryphiella vinosa* under the influence of grazing by the mite *Tyrophagus putrescentiae* (Reisinger, unpublished thesis). This might partly explain, besides nutritional effects (285), the stimulation of fungal development which has been repeatedly observed under the influence of grazing at low faunal densities, at least in gnotobiotic conditions (194, 282).

The choice mesofauna may operate between different microorganisms has been repetitively established (286, 287, 288, 289, 290, 291, 292, 293, 294, 295, 296, 297). Such choices may modify the composition of microbial communities, for instance they may displace equilibrium levels

between competing fungal strains, at least in experimental conditions (206, 209, 298, 299). As abovementioned, when microorganisms may escape predation by animals (which is a realistic view, at least in forest soils), such effects may totally disappear (255).

Much more specificity appears in choice experiments than when rearing animals on single cultures (208, 231, 288, 290, 291, 297, 300). Some microbial species may reveal toxicity or imped the reproduction of animals consuming them or even influence their life habits (77, 288, 295, 296, 300, 301). Discrepancies between choices and needs were revealed by Walsh & Bolger (291). They demonstrated on the Collembolan *Onychiurus furcifer* that *Trichoderma* spp., the least preferred fungi in choice experiments, were nevertheless the best suited for growth and reproduction when animals were forced to feed only on them. This may have a bearing on the respective place of mesofauna and microflora. When animals graze upon microflora, choose between microbial strains, or disseminate them, we can say at first sight that they control microflora. When some microbial strain locally kills animals or impeds their reproduction or force them to abandon an elsewhere favourable micro-site, then we can say that microflora controls mesofauna as well. In fact both are interacting and thus their effects cannot be hierarchized.

The results of mesofauna-microflora interactions, which are controlled by genetically-fixed or acquired mechanisms, vary according to local and casual circumstances. This points to strong discrepancies between choices, needs, and actually observed relationships, and may raise doubts to the bearing of some brilliant experimental results to field conditions. For instance the Collembolan *Pseudosinella alba* was found to eat preferentially on fungal spores when reared on laboratory cultures, although gut contents of field-collected animals were made only of small hyphal pieces (208). The plasticity of food diets of mesofauna has been underlined by several authors (47, 240, 302, 303), and shifts from microbivory to carnivory (304), or the reverse (48),were observed. This indicates that most interrelationships between soil resources and mesofauna are elastic rather than tight connections, as underlined by Gunn & Cherrett (48).

Relationships between mesofauna and microflora may be considered as homologous to those prevailing between macrofauna and litter types, similar mechanisms being even probably in use when an animal selects a food or colonizes a substrate. The role of fungal odour as an attractant has been demonstrated for springtails grazing on fungi (79) as well as for woodlouse feeding on leaf litter (109). Sensitivity to substrate acidity has been demonstrated both for mesofauna and macrofauna (76). Nevertheless conspicuous differences may exist, mainly due to differences in the size of animals (202).

Litter offers more space and available food than the underlying soil for big-sized animals, and

it protects them from predation and desiccation by help of its laminated structure. It can be postulated that this is not so important for smaller-sized animals, which are able to move and feed in pores of the underlying mineral soil and in the rhizosphere. Circumstantial evidence can be found by comparing the effects of litter deprivation on both macrofauna and mesofauna. Although litter-consuming macrofauna was suppressed after a few months without any litter at the ground surface (106), few quantitative and qualitative changes were observed in mesofauna living commonly in litter (305).

***Interactions between mesofauna and abiotic factors***

The influence of soil pH and related factors on the distribution of mesofauna species has been repetitively observed in a variety of taxonomic groups, using collections in varying soil and vegetation conditions (46, 62, 63, 66, 67, 69, 70, 71, 267, 306, 307, 308, 309). This influence has been established at the species level (vicariant species) as well as at wider taxonomical levels. For instance the Collembolan *Pseudosinella mauli* replaces the phylogenetically-related *Pseudosinella alba* at pH level below 5 (63, 67, 71). At the genus level, the same author observed a replacement between *Onychiurus* and *Protaphorura*. At a higher-order level enchytraeids were favoured over other mesofauna groups in dysmoder humus forms, i.e. moder humus forms with a thick OH horizon. In this humus form, often confounded with mor under the general name raw humus, they compose the main part of soil fauna (46).

Despite of the wide occurrence of the influence of soil acidity (pH or related factors) on soil animal communities (72), this phenomenon has not been explained satisfactorily. We may suspect a common factor acting separately on different species or groups of species or on the contrary tight connections between members of the soil animal community. In the latter case this would drive the faunal composition towards one of two possible combinations (or strategies), for instance mull and moder humus forms (46, 187). External factors or casual events may cause a shift in the species composition, further strengthened by positive feed-back loops. The first hypothesis (separate action of external factors) is based on the egoism of species, the second one on strong mutualistic interactions. Present knowledge cannot ask this disputed question.

During the last two decades a number of field and laboratory experiments have been performed on the biological aspects of soil acidification, given the interest of this concept for the understanding of damages to forest ecosystems caused by man activity (e.g. plantation of exotic trees, management practices, acid rains, greenhouse effect). Mineral compounds (310, 311, 312, 313, 314, 315, 316, 317, 318, 319, 320, 321, 322, 323, 324, 325, 326, 327, 328) and organic compounds (320, 321, 326) have been used to manipulate pH of soil and litter, and litter inputs

have been artificially increased or decreased (305, 329).

Some results of acidification and liming experiments were in agreement with observations done in natural conditions. This is the case for the increase in density of the Collembolan *Willemia anophthalma* and *Mesaphorura yosii* observed after artificial acidification of the forest floor with diluted sulphuric acid (319). These species are strongly acidophilic according to Ponge (63, 67, 71), Hågvar & Abrahamsen (69) and Pozo (308). In other cases unexpected results were obtained, such as a decrease in densities of the acidophilic enchytraeid *Cognettia sphagnetorum* after acidification of the ground floor with sulphuric (310, 316), nitric (318), or oxalic acid (326). Lime addition decreased its densities similarly. This contradictory result can be explained by the sensitivity of *C. sphagnetorum* to ion concentration and other related properties of soil solutions such as osmotic pressure or electric conductivity (320, 330). Field experiments with varying chemicals demonstrated that pH itself was not responsible for the variations which were observed in faunal assemblages following acid treatments (327).

Litter deprivation impoverishes the soil, at least in the first top centimeters, and thus causes a decrease in microarthropod densities, as this has been observed experimentally (305, 329) and in natural forest floors with topographic irregularities (331, 332). Nevertheless litter addition (by doubling or tripling the normal litter input) does not decrease the pH level and does not mimic moder humus forms (305, 329). In natural conditions Garay (331) observed that there was a threshold under which increases of litter input did not affect microarthropod densities. Above this threshold, a strong depletion was observed in most microarthropod populations, spatially associated with the development of white-rot colonies in litter. This is consistent with our present knowledge of the biology of white-rot fungi, which need a threshold in the thickness of undecayed litter to start their colonial development (333).

Laboratory experiments, using pH buffer compounds, were used to test preferences of animals towards more or less acidic substrates (73, 76) or to study the effects of different pH levels on important metabolic activities (74, 75). Several authors recently suggested using them as bioindicators of soil acidification (76, 334). Although this can be supported by abovementioned field and laboratory observations, we nevertheless question this use given the complexity of what is called soil acidification. Soil acidity must be defined not only by the amount of protons in soil solutions or on exchange sites, but also by the amount of free and exchangeable $Al^{3+}$ ions, which are potentially toxic to plants and animals (335). Organic acids such as phenolic acids are also known for their toxicity to plants (336, 337), fungi (338, 339,340), and soil animals (80). Some aliphatic and phenolic acids, and even larger assemblages such as fulvic acids, may chelate metals and alkaline earths and thus are

active agents of podzolisation (341, 342, 343). All these aspects of soil chemistry and biochemistry should be included in the concept of soil acidity.

Multiple aspects of forest ecology and management are strongly related to soil acidity and many small-scale effects are intermingled into larger-scale phenomenons such as changes in humus forms, which are of prime relevance to soil acidification (344, 345, 346, 347). For instance the passage from mull to moder humus form, i.e. from macrofauna- to mesofauna-dominated soil animal communities (in biomass) involves a concomitant decrease in the mineralization rate of organic matter (83), a higher residence time of organic matter before it can be incorporated with mineral matter (187), and an increase in fungal standing crop (348) thus in the production of organic acids with a high chelative power such as oxalic acid (349). The increase in the weathering (dissolution) of minerals due to prominent fungal activity (350), which would normally compensate for soil acidification (351), may not benefit at all for soil organisms and roots when these become restricted to ectorganic horizons.

If interactions between species are the driving force in the above mentioned shifts in soil animal communities, then nothing can be inferred from soil mesofauna concerning pH levels, or other aspects of soil acidity, except in natural or near-natural conditions to which these animals have been adapted for a long time. Only in this case interactions between species or groups have time enough to shape the animal community. In laboratory experiments with acidified (sulphuric acid) or limed OH horizon, Hågvar (352) observed that acidification favoured the growth of the Collembolan *Mesaphorura yosii* but only in the case where a complete mesofauna was present. When the same species was cultured in defaunated humus (without reinoculation by other fauna) this species grew at a lower rate in acidified, compared to limed and control conditions, thus pointing to strong interactions between animal species during the development of acid-tolerant or acid-intolerant communities.

## Microfauna

Although a number of laboratory and field experiments have been conducted on nematodes (269, 353, 354, 355, 356, 357, 358, 359, 360, 361), protozoa (93, 355, 362, 363, 364, 365, 366, 367), and total microfauna (202, 368, 369), the interaction between microfauna and their immediate environment is far from being clearly understood, at least in natural conditions. Due to their small size and liquid faecal material, these animals do not participate actively in the building of the soil fabric and in litter comminution. Rather, their small size and more specialized feeding habits make them more susceptible to interact with microflora. It has been observed that the onset of bacterial decomposition of needle litter was largely due to the penetration of internal tissues by protozoa, nematodes, and rotifers, before bigger-sized animals could intervene (228, 370).

The prominence of microfaunal densities in most forest soils (371), and high metabolic and biomass turnover rates of smallest animals (372), make them contributing greatly to fundamental processes such as mineralization of carbon and nitrogen (354, 365, 367). This occurs mainly through the net stimulatory effects of predation during short phases of active reproduction of microbes and may become insignificant or may reverse during phases of microbial stasis (354, 365).

A model of plant nutrition including the grazing activity of microfauna has been built for plants with root hairs, based on microcosm data (249). The main interest of this model was to include labile processes, such as the short development of a bacterial colony in a given micro-site, into continuous processes taking several weeks to achieve, such as the exploration of a given volume of soil by a root system. Nevertheless the passage from gnotobiotic laboratory to eubiotic field conditions is rather difficult due to the need for proper experimental devices allowing observation or manipulation of microfauna. Exclusion of bigger-sized animals by enclosing defaunated litter in nets with mesh size as small as 48 µm allows the entry of undesired juvenile enchytraeids and microarthropods, which will rapidly become members of mesofauna within the time of the experiment, thus impeding clear separation of microfaunal from mesofaunal influence (202).

The direct observation of animals gave valuable information about the feeding habits of nematodes (373, 374) and protozoa (375). For instance the seasonal inclusion of a bacterial diet in the food regime of predatory nematodes has been demonstrated (374), thus confirming the application to the field of observations made in laboratory cultures by Yeates (376). This has greatly improved our knowledge of real foodwebs (255, 377).

The action of environmental conditions upon microfauna has been described too, although poorly explained at least in field conditions. Changes in the balance between bacteria and fungi, which are controlled by both pH and litter accumulation, are reflected in the distribution of specialized trophic groups, such as bacterial- and fungal-feeding nematodes (358, 356, 360, 378, 379), which makes them a useful tool for acidification studies. As this has been observed in macrofaunal and mesofaunal animal groups the distribution of nematode and protozoa species may change according to soil type and humus form (86, 89, 380, 381, 382), and changes in morphological features of ubiquitous species have been also registered according to humus form (87, 88). These animals, which are mostly living in water films surrounding soil and litter particles, are highly sensitive to the water regime of the soil (356, 383), and the absence of tunnelling activity and comminution of the soil matrix make them strongly dependent on available space (384).

## Pathways for future research

Soil organisms, living in darkness at the bottom of higher plants, have been long-time neglected, being considered as accessory members of terrestrial ecosystems. Now there is increasing evidence that they play a key role in most processes taking place at the forest ecosystem level (19). Examination of research trends over the last twenty years gives evidence of a marked diversification in methods and objectives. Inventories, which were considered as most successful tools for the appraisal of population dynamics, nutrient cycles, and other functional features of ecosystems, have not been abandoned, but rather have been enriched with functional studies, based on the understanding of processes, together with a better knowledge of life habits and food regimes.

Antagonisms, attractions, stimulations, are functional links between organisms which may be considered as the result of long-term evolution (adaptation and coevolution). DNA-coded ecological interactions could thus be considered as a basis for a hypothetical organization of ecosystems, assumed to be stabilized by negative feed-back loops, as within an organism. In the soil, mull, moder, and mor humus forms (385) can be hypothesized to be the result of multiple interactions involving both soil organisms (animals, free and symbiotic microbes) and plants, which have evolved together in the course of earth history (1, 3, 4, 5, 386).

If this hypothesis is true then unexpected events, such as the appearance of foreign organisms, or new toxic substances, or other disturbances to which organisms are not adapted for a long time, may generate an increase in positive against negative feed-back loops, thus destabilizing ecosystems when a tolerance threshold is reached. Man activity, by increasing the frequency of chaotic events (travels, manipulation of gene material, pollution, etc...), which organisms have not memorized in their gene material and thus cannot anticipate and counteract, may contribute to the disorganization of most ecosystems. If the alternative hypothesis is true, i.e. if negative (stabilizing) feed-back loops are absent or scarce at the scale of the ecosystem, then such chaotic events would not increase anything else than the normal level of ground noise.

The knowledge of mechanisms prevailing in biotic interactions is a prerequisite for a sound prediction of the fate of most ecosystems in an increasingly changing world. Among such mechanisms, those involving soil organisms are more difficult to establish given the hidden nature of the soil. Despite these inherent difficulties future research on soil ecology should try to focus more on symmetrical relationships between soil organisms and their proximate or remote environment.

In the above review few references were done to negative feed-back loops, i.e. to buffering mechanisms ensuring the stability of the soil

ecosystem. This is because few of them have been understood to the present date. Ulrich (386) described the different buffer ranges of weathering minerals. Gourbière (333) explained the regulation of litter thickness by thesholds in use and depletion of ressources by white-rot fungi. The amphoteric nature of the mucus excreted by earthworms (17) may play a prominent role in the buffering of soil pH in mull humus forms. Despite these stabilizing mechanisms most above described interactions are positive feed-back loops which may explain build-up or disintegrative phases rather than equilibrium phases.

Thus there is an urgent need for exploring symmetrical interactions between soil animals and their environment if we want to measure the degree of organization of the soil ecosystem, and thus to predict its capability to face the chaotic influence of mankind and other disturbing influences.

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