

A future for soil ecology ? Connecting the system levels: moving from genomes to ecosystems Opening Lecture to the XIII ICSZ “Biodiversity of soil organisms and ecosystem functioning”

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Abstract – As an introduction to the XIII ICSZ “Biodiversity of soil organisms and ecosystem functioning” the question is raised what contribution soil ecology has made to general ecology. Although the appearance of soil ecological papers in general ecological journals is limited, soil ecologists have had a major contribution to especially functional aspects of ecology like nutrient release and energy turnover mechanisms, perhaps partly due to the applied character of soil ecology. As a way forward it is suggested to unify further work and scientific discussions according to five research themes: 1. Combined spatial and temporal heterogeneity; 2. Scaling up from individual mobility via distribution patterns to bio-geography; 3. Structural and functional biodiversity: from gene-to ecosystem level; 4. Nutrient cycling/energy transfer at the micro- to macro-level; 5. Adaptability from bacteria to ecosystems: is there a mutual mechanism connecting genetic variation with ecosystems’ adaptive mechanisms? © 2001 Éditions scientifiques et médicales Elsevier SAS

micro- and macro-scale connections / nutrient cycling / organism adaptability / soil ecology / spatial and temporal heterogeneity

1. INTRODUCTION

In the present era of molecular biology, frequently felt as the enigmatic approach to biological research, it is often hard to understand the ultimate ecological consequences of these molecular mechanisms. To what extent are these generalizing and generic concepts helpful in understanding ecological structures and processes that always have been characterized by specification and diversification? Is it possible to forge the chain from molecular to ecosystem structures and ecosystem-processes? And to what extent are these insights helpful in a better and more sustainable protection of soils?

The first start for this introduction was a workshop of a group of soil ecologists in Lund (Sweden) end

2000 to discuss the way forward in the 21st century (see for an overview [27]). This has been put into a broader retrospective view to provide a jumping ramp which research lines and developments are the most promising and relevant for the future of soil ecology, given the need to protect soils because of their role as sustainable basis of terrestrial ecosystems.

Questions like ‘what is the functional role of enchytraeids in a coniferous forest floor’ are quite normal for soil ecologists. However, if we should ask the question: ‘What is the functional role of woodpeckers in coniferous forests’, it would be less recognisable as a sensible question for ecologists. This statement by Per Lundberg is an example of a general observation: why do soil(ecology) people always think and investigate in functional terms? Is it because of their roots, lying in agronomy and forestry? Is it because of the applied character of their research? Or is it just because it is hard to look into the opaque soil milieu and impossible during your studies to enjoy the aesthetic sight of flowered, winged and feathered fellow-creatures as above-ground-ecologists can do?

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2. WHAT HAS BEEN TYPICAL IN SOIL ECOLOGY FROM AN ECOLOGICAL PERSPECTIVE?

Some answers on these questions can be derived from an analysis of literature references.

A certain underestimation of soil ecological research is certainly not related to the level of research. Comparing soil ecological versus general ecological literature, Göran Bengtsson (personal comm.) concluded that the total scope of 'general ecology' and 'soil ecology' is quite similar, although there are differences in relative attention to different areas e.g. population or ecosystem oriented research. Thus for both groups there are clearly distinguishable periods in which research on particular issues received most attention; in approximate historical order: distribution problems, biodiversity, community issues and competition. From an analysis [4] of work on soil arthropods in a soil ecological (*Pedobiologia*) versus two general ecological journals (*Ecology* and the *Journal of Animal Ecology*) the most prominent difference was the lack of theory driven (hypothesis testing) research in soil ecology. In *Pedobiologia* 3 out of 44 papers were theory driven, whereas in *Ecology* and *J. of Animal Ecology* these were 17 out of 20 papers. Most of the papers in *Pedobiologia* were on ecology aspects, especially community ecology, while the two other journals had a much more even and wider range covering also individual and population level, as well as evolutionary aspects. Also when we assume/keep in mind that *Pedobiologia* is oriented on more factual and applied studies, it illustrates the statement that soil ecology is application driven.

According to Lee [21], giving a qualitative historic overview on earthworm research, up to the 1950s earthworm research work was entirely confined to faunistics, phylogeny, biogeography and natural history, after 1950 ecologically related work started, mainly concerned with population biology. Only rather recently a more structural relation was made to the real environment for earthworms: the soil and its conditions, and at a larger scale land management. Satchell [28] states for research on earthworms that "this was not problem or policy driven but opportunistically as technology evolved in quite other fields; electron microscopy resulted in taxonomic revisions (although disputed by other scientists) which in turn contributed to understanding earthworm distribution in relation to tectonic plate movement". Satchell's example on taxonomy is interesting especially because the development of pure science at extremely small spatial scales has consequences for distribution problems at the global scale, hence connecting the different levels of biological organisation.

In conclusion soil ecology has its own territory and touches upon mainline ecological issues. However, soil ecological journals may have a somewhat limited penetration (Citation Index) and cross-reference to other journals.

3. WHY SHOULD SOIL ECOLOGISTS CONTRIBUTE LESS TO MAINSTREAM ECOLOGICAL THEORY; AND WHAT DO THEY HAVE TO OFFER FOR OTHER RESEARCH FIELDS

The observations of Bengtsson and Bot [1, 4] beg the question 'Why do soil ecologists contribute less to mainstream ecological theory? Is it again this applied perspective?'

Certainly this applied perspective is one of the main reasons. Irrespective of that it seems to be better to tackle the question the other way around: what special features have soil ecosystem researchers to offer to mainstream ecology? For example in 1972 Bouché [5] already proposed a concept of ecological categories for earthworms (anecic, epigeic, endogeic) which has been much later also adopted in other fields of ecology.

Also in general soil biologists have been leading in studies on nutrient cycles in terrestrial ecosystems, especially in relation to carbon, nitrogen and phosphorus fluxes. See for instance the whole series of 'green books' resulting from the International Biological Programme.

Soil ecology is featuring certainly not by easily observable and colourful looking organisms like butterflies; even the larger groups of organisms in soil are called cryptobiota (hidden organisms), not to mention the micro-organisms. Further, the black box that soils offer asks for specialised sampling and observation techniques and developing appropriate methodology is still a problem that needs much attention. On the other hand this offers a promising potential. In fact the recent development of new identification methodologies for micro-organisms already caused enormous progress, e.g. when we look at the recent observations on the diversity of bacterial strains [18, 23].

What soil ecologists do have to offer is:

- Their large and extensive experience in working with an extremely heterogeneous environment. This heterogeneity influences many of the processes. Many organisms, e.g. earthworms, moreover, create their own environment. This illustrates that in the soil, abiotic and biotic processes are closely interlinked and must be studied as such. Further, this heterogeneity taught us to work and think in maximum and minimum (sometimes extreme) conditions, next to the usual mean conditions.

- This combination of abiotic and biotic processes is typically illustrated by the case of bioavailability research. This comprises the physico-chemical availability of chemical compounds in the environment in relation to biological uptake mechanisms and internal transport to target organs. This sequential three-step approach has been worked out for soil contaminants in the framework of soil ecotoxicology, but was already a long-time topic in nutrient availability. Only when bioavailability is studied both from the perspective of physico-chemical availability and of biological uptake

and internal redistribution, this major issue in environmental standard policy can be solved properly [9].

– Their long-time tradition in multidisciplinary work. Microbiologists who are working together with ecologists, soil scientists, environmental chemists and modellers of transport-processes is a regular combination. As a consequence research on molecular and ecosystem processes are not that far apart in these kind of studies. To tackle such interacting complexity Setälä et al. [29] state in general terms: “Soils differ fundamentally from above-ground and aquatic ecosystems because of their immense biological and physico-chemical diversity and complexity, the dominant heterotrophic character of processes and the size of the organisms. In order to master this complexity modelling especially on decomposition processes will be helpful”. Recently a European Science Foundation programme has been started on ‘Food-web modelling for ecological assessment of terrestrial pollution’ [10].

– The possibility, by using modelling approaches, to study these processes not just in a static but also in a dynamic way (see also the next comment). Paying more attention to the dynamic aspects of fauna dispersal could, moreover, provide possibilities to study recovery processes – after a physical or chemical disturbance – as a special form of natural succession processes and to pay attention to the combination of spatial and temporal distribution.

– Their habit of thinking in functional terms as illustrated by Hedlund [15] in foodweb-studies on fungal-springtail interactions. These interactions are characterised by pulses of activity after addition of food, which is the normal phenomenon under field conditions (e.g. litter-fall). What occurs in these foodwebs is a redistribution of resources, and the challenge is how to combine this pulse response with resource distribution as studied with foodweb models. Boddy [3] studying relations between saprotrophic fungi and other saprotrophs, and mycorrhizal fungi also advocated that more attention should be paid to these nutrient release mechanisms. As such she rightly claims that these interactions should be studied in soil, not on artificial laboratory media.

– Interlinked with this functional or activity approach is the experience of soil ecologists that the majority of organisms in the soil are inactive or in a resting stage. This especially holds for micro-organisms of which over 90% is normally resting, but also in soil faunal groups periods with high numbers and high activities are interlinked with periods with very small numbers and low activity [7]. So what is the importance/impact of structural diversity (of all species present) in relation to functional diversity (of only the active species)?

– In the biodiversity-discussion the issue of functional diversity is a typical soil ecological contribution to this worldwide debate. As Hopkin [16] formulated: “Are we using diversity as a probabilistic event because we cannot recognize the structure behind it? So next to species diversity (allowing the possibility of naming

entities) we should study functional and life-form (plasticity) diversity. And next to the study of fixed diversity ‘patterns’ we should study the total continuous process; because one of ecology’s prime interest is to describe and predict the probability of things happening”.

In conclusion: it is obvious and manifest that soil ecology has something special to offer. It looks across fences contrary to mainstream ecology in which physico-chemical aspects are ‘settled’ as environmental conditions instead of being crucial steering factors. It concentrates on functional aspects, especially related to pulse processes, and in this last aspect has close connections with ecology of streaming waters.

4. FROM MICRO-SCALE (MOLECULAR APPROACHES) TO MACRO-PROBLEMS (ECOSYSTEM-IMPACTS); HOW TO REALIZE THE CONNECTION BETWEEN THE LEVELS

In order to meet the challenges described above and to contribute to mainstream ecology, we have to go forward in an integrated way. The question phrased in the title of this paragraph defines such a way forward, which is not only a topic for soil ecology but for ecology in general. This integration not only means a combination of abiotic and biotic processes, in a static and dynamic, structural and functional way, but especially to provide ways to combine the molecular up to the ecosystem level approach. Like Satchell [28] already described: studying the consequences of taxonomic differences ultimately to the global level of world distribution, or the implications of earthworm burrowing behaviour for the physical structure of soils and the nutrient distribution in these soils and consequently for land management like Lee [21] mentioned. In both examples it is the combination of different fields of expertise that counts.

Therefore, I suggest in this context to define not so much research or expertise fields, but research themes that bring various specialisms together. These themes are primarily soil ecology-oriented, not so much focussed on soil zoology. Because one of the challenges for the future is to combine the benefits of a specialism like soil zoology with the credits of mutual cooperation with other research fields like microbiology and system-ecology. In this perspective I want to refer to [34] and to the theme of this conference “Biodiversity of soil organisms and ecosystem functioning”.

As a first ‘kick-off’ to enhance discussion during the XIII ICSZ and further on, I should like to suggest the following themes that will be briefly described in the framework of this introduction:

1. Combined spatial and temporal heterogeneity;
2. Scaling up from individual mobility via distribution patterns to biogeography;
3. Structural and functional biodiversity: from genes to ecosystem-level;

4. Nutrient cycling/energy transfer at the micro- to macro-level;

5. Adaptability from bacteria to ecosystems: is there a mutual mechanism connecting genetic variation with ecosystems' adaptive mechanisms?

5. COMBINED SPATIAL AND TEMPORAL HETEROGENEITY

Soil heterogeneity in combination with differences in numbers of soil animals has always attracted a lot of attention. But when you scan the literature it is studied either from a

temporal or a spatial perspective. Hardly ever is it studied in combination, although there are good reasons to do so. For it seems illogical that an increase in numbers over time and a consequent increase in variability in numbers should not also result in an increase in spatial variability. In this perspective it is not only the question whether temporal and spatial heterogeneity are interrelated but also how. Three possible relations can be postulated:

1. higher numbers result in stronger fluctuations both in space and time, hence these types of variability are linearly related;

2. spatial heterogeneity is just an extra tuning (adaptation to small changes in habitat conditions) on top of general temporal fluctuations (abundance);

3. spatial variation is greater than differences in time and a change in spatial distribution (the hotspots shift in place over time) will lead to homogeneity over longer time periods.

From a number of studies on soil arthropods [17, 32], we can conclude that there is a linearly related increase in temporal and spatial variability of populations of soil arthropods.

At a higher level of biological organisation: in forest soil animal communities or ecosystems, a similar phenomenon of a linearly related increase in temporal and spatial variability was observed, albeit for environmental conditions (soil moisture content). This relation occurred irrespective of the soil and litter types of these forests [32]. Some concepts developed at the still higher level of landscape ecology are very useful in general [17], and for soil scientists one of the most promising applications concerns geostatistics [11, 30]. When we move down to the level of micro-organisms, another picture is revealed [20]. The activities of the nitrifying bacteria measured as the amounts of nitrate and ammonium in the soil pore water showed a distinct greater spatial than temporal variability, the last one comprising the differences between the means for the consecutive samplings. This difference was explained by a possible role of specific items of the soil environment (moss and needles) in nitrification, which could be confirmed experimentally. This stresses the point that precise description and characterisation of environmental conditions is of ultimate importance in soil ecological research.

6. SCALING UP FROM INDIVIDUAL MOBILITY VIA DISTRIBUTION PATTERNS TO BIOGEOGRAPHY

Next to the intimate relation between environmental conditions and spatial distribution of soil animals, there is another crucial factor: behaviour. Soil animals can move, albeit sometimes rather slowly, and are consequently able to move around in a directed way and to make their own choices. Even soil organisms that disperse mainly passively can actively influence their own distribution, as shown for soil water bacteria. These show a selective dispersal patterns because they are passively transported in the groundwater but selectively adsorb to soil particles given e.g. the moisture conditions in the soil [1]. Therefore distribution of soil organisms always will include an individual impact. This has been well recognised with vertebrates in migration studies at the individual and population level of specific species and at the global level of the distribution of specific types of bird species). Also for surface-active animals there are ample examples, but for soil animals the examples are scarce, although according to Rusek (personal comm.) root feeding fauna groups like wireworms, *Melolonta* and tenebrionid larvae do show active horizontal migrations in search for food, especially in spring after the temperature inversion in soil.

With respect to dispersal mechanisms these can be purely diffuse, reactive or proactive. Dispersal and the resulting distribution pattern can be diffuse; just 'going with the wind'. It can respond to an external stimulus without an initiative and hence be re-active (like the passive dispersal plus selective establishing with the bacteria), or it can be an active but non-directed mobility in combination with selective establishment. In the case of proactive dispersal there is an active and directed dispersal plus a selective establishment. Sjögren [in 1] has observed that springtails make a distinct choice when offered a gradient of increasingly polluted soil. From field inventories we know that different springtail species do show a different sensitivity for heavy metals that is reflected in their horizontal distribution, as well as in the vertical distribution related to the heavy metal contamination profile in the soil (Eijsackers, unpublished information). Also earthworms clearly choose between Cu-contaminated and non-contaminated soil [6]. This had significant consequences for the active dispersal of earthworm species in 1 m² container with sections filled with grassland or Cu-contaminated vineyard soil. Consequently, field samplings in the same soils show numbers that are far lower in the contaminated vineyard soil than in the adjacent clean grassland soil (Eijsackers et al., in prep).

Scaling up from the individual, via the population to the community-level, establishment is an active choice to settle, reproduce and increase numbers. This will influence other populations leading to specific 'communities' – this last term suggesting some kind of

cooperation but it could well be some sort of living-apart-together. If such cooperation occurs, and for soil animals that is certainly the case, a functional perspective is added to the structural community-concept, which not intimately related to one of the components of the community (ephemeral) and related to system-characteristics and functional diversity. A very useful and extensive description of this functional scaling up is given in [19].

When we scale this up further to the biogeography-level human activities and large scale environmental impacts come into the picture as well. Introduction and further dispersal of earthworms in other continents primarily by man (but natural processes cannot totally be excluded) not only influences the community of endemic earthworms or similar groups (like *Microchaeta* species in Africa [25]), but also soil conditions and profiles. This has been shown especially for Australia and New Zealand [21], but also in South Africa [25], North America [26], and subantarctic islands [14]. At these scales man's impact on global processes (climate changes) but also at the landscape level (deforestation, fire) will have a major influence, too.

7. STRUCTURAL AND FUNCTIONAL BIODIVERSITY: FROM GENE- TO ECOSYSTEM LEVEL

Given Hopkin's comment about studying biodiversity also from a functional (life-form plasticity) perspective, 'classical' soil ecological studies should further elaborate on sequential processes in an intimate interaction between various organism groups. These should combine studies on broadly functional processes like litter fragmentation with studies on succession time sequences not only as natural phenomenon but also in the framework of recovery processes. By addressing the potential and variable activity (= mobility) of organisms, recovery processes of ecosystems after disturbance could be viewed as successional recolonisation (or secondary succession). This may lead to a better understanding of the resilience of an ecosystem after disturbance. Moreover, the concept of functional diversity (leagues as defined by Faber [12]), and Hopkin's plasticity concept could be used in this context, when looking especially at environmental resistance and sensitivity in relation to recovery.

A still remaining question in this context is in what way all this specialisation has been achieved when most of the organisms are in an non-active, resting stage in the soil.

At the ecosystem-level, ecosystem-models may be one way to connect the levels of biological organisation in this perspective [22]. As an alternative Boddy [3] sketched the potential of Artificial Neural Networks (ANNs) in ecological modelling at the molecular, species and system level. These ANNs could study

pattern recognition in a spatial and a temporal way, like for instance succession phenomena at various levels (molecular, litter degradation, 'classical' species succession, but also ecosystem succession).

8. NUTRIENT CYCLING/ENERGY TRANSFER AT THE MICRO- TO MACRO-LEVEL

Litter breakdown has been a classical issue in soil zoology, especially the cascade approach with a step-wise comminution and further mineralisation of litter by soil fauna and micro-organisms in an intimate interaction. This has been studied for various litter types, soil biota communities and ecosystems. The International Biological Programme (IBP) in the seventies has delivered a huge amount of excellent information; the well known series of green books.

From these studies the major role of soil animals becomes clear, initially in setting free nutrients for uptake by plant roots and for further mineralisation by micro-organisms. From a quantitative perspective the IBP-studies already clearly showed that micro-organisms play a dominant role in these breakdown processes, both with respect to nutrient releases and energy turnover (metabolism). Soil animals play a more catalysing role.

However, these IBP-studies also showed the consequences of mineralisation especially in relation to changed environmental conditions like cultivation of natural grasslands (e.g. prairies). When we compare the organic matter degradation and resulting loss in organic matter during the limited time lapse since cultivation of these grasslands started with studies about increase in organic matter content under different manuring practices, the loss is threatening soils. The question then becomes not how soil animals could improve mineralisation and nutrient release, but how difficult it will be to increase soil organic matter content and what role soil animals can have in conserving organic matter. This could be by maintaining soil aggregates and soil structure [8]. It is interesting to look at the results of the study on plant succession in relation to soil conditions and processes on small islands by Wardle and co-workers [33] from this perspective.

Hence, the cascade approach not only holds for the detailed interaction between macro-, meso- and micro-comminutors, but also for the consequences at ecosystem, regional and global level. At the global level at present carbon-sequestration, the conservation of carbon in the organic pools in the soil, plays a prominent role within the climate debate. Instead of looking at the promotion of organic matter breakdown we have to look now where and when the process hampers, leading to an accumulation of organic matter.

9. ADAPTABILITY FROM BACTERIA TO ECOSYSTEMS: IS THERE A MUTUAL MECHANISM CONNECTING GENETIC VARIATION WITH ECOSYSTEMS' ADAPTIVE MECHANISMS?

For soil ecology it is the challenge to approach this problem not only at the population level, as done for springtails [24], but also at the genome and the ecosystem levels. Especially at the ecosystem level this is highly innovative and disputable as maintenance of a particular ecosystem structure over time has not been seen as a conserving characteristic of the ecosystem itself. And 'adaptation' of ecosystems to changed conditions the risk of semantic confusion as it has mostly been described in population dynamic terms like robustness and resilience.

To put molecular studies in a more general ecological framework, Tunlid [31] draws the parallel between molecular and ecological studies along three lines:

1. which signals control the various interactions between, for example, parasitic and saprotrophic growth phases, respectively, control microbial activities and interactions ?

2. which impact have these molecular signals on ecological interaction phenomenon, including microbial interactions on population dynamics in soil ?

3. which ecological significance has the high diversity of (redundant ?) genes in respect to species.

According to his analysis there is a surplus of genetical material that has no defined function, and quantification could give an indicative assessment of evolutionary impoverishment.

But genome studies could be applied also positively by defining which genomes trigger and control the various metabolic routes. Certain probes could be used to indicate a family of enzymes, and these functional genomes could be used to better investigate metabolic control theories.

Moving to the other end of the biological stairway, we also should study (eco)systems in a dynamic way, asking ourselves (as Jan Bengtsson did) questions like:

- Is the structured internal order of ecosystems or vegetation patterns just probability or is there a fixed pattern which can be maintained; so is there some kind of heritability of ecosystems?

- Are there positive feedbacks in soil part of the ecosystems as seen in above ground terrestrial systems (e.g. herbivory effects and nutrient cycling)?

Is there also selection and adaptation at the ecosystem level? [2].

When we look at ecosystems they show a particular internal organisation, which may have a rather broad range. This organisation is primarily steered by environmental conditions. When conditions are changing, the system pattern may stay as it is for a long time, but suddenly may switch and result in another system type. What triggers these switches is still not known, just as we do not know what factors steer the maintenance

of the system structure. From studies on soil formation on similar soils but with different vegetation types (tree species) we know that plant species, and thus litter composition, play a crucial role. The increase in earthworm numbers in liming experiments caused a change in litter fragmentation and thus in profile type (from mor to mull). Hence, also soil animals can cause this flip-over from one ecosystem type to another [2].

Put into the framework of general ecological theory these phenomena can also be described in terms of resilience or stability of the ecosystem. Then the maintenance of a specific structure is covered, but not the step-switch to another system-structure as described for the liming experiment.

10. A PLEDGE FOR (MORE) ECOSYSTEM ORIENTED RESEARCH IN SOIL ZOOLOGY

A pledge for a return to ecosystem research is not so much prompted by the present major interest in molecular processes, but by the way mankind is dominating ecosystems. We are selecting and changing ecosystems without really knowing what are the 'maintaining rules' for ecosystems and, hence, the long-term consequences or more precisely the *ecologically* relevant long terms. In this context, it is interesting to refer to a comment made by Franz [13] already in 1973 about the genetics of the landscape. "Genetische Bodentypen und Bodenbiozönosen lassen sich nicht in einfacher Weise zur Deckung bringen, wenn auch zwischen Bodenbiozönosen und Bodentypen eines bestimmten Landschaftsbereiches gesetzmässige Zusammenhänge bestehen" (genetic soil types and soil communities cannot be easily classified when there is also a clear relation between soil organism communities and soil types at the landscape level).

Soil systems are especially suitable to study these kinds of rules because it is easy to change from population and ecosystem level and, hence to relate population and ecosystem level. Moreover, soil systems are easily to be manipulated for these kinds of approaches due to small spatial scales and short life cycles.

These questions open a window to issues like: how to make ecosystems evolutionarily more stable, which traits to be selected in this context, and how to prevent conflicting selection pressures at different levels of biological organisation. Soil zoological research not only has a functional role in this type of research, it also provides a window to general ecology.

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REFERENCES

- [1] Bengtsson G., Dispersal, heterogeneity, and resilience: challenging soil quality assessment, in: Van Straalen N.M., Løkke H. (Eds.), *Ecological Risk Assessment of Contaminants in Soil*, Ecotoxicology series 5, Chapman and Hall, London, 1997, pp. 191–212.
- [2] Bengtsson J., Disturbance and resilience in soil animal communities, *European J. Soil Biol.* 38 (2002), in press.
- [3] Boddy L., Interspecific combative interactions between wood-decaying basidiomycetes, *FEMS-Microbiology-Ecology* 31 (2000) 185–194.
- [4] Bot J., Soil arthropods and ecological theories, MSc-Report, Dept. Animal Ecology and Ecotoxicology, Vrije Universiteit, Amsterdam, 1995.
- [5] Bouché M.B., *Lombriciens de France*. Ecologie et Systématique, Institute National de Recherche Agronomique, Paris, 1972.
- [6] Eijsackers H., Effecten van koperhoudende varkensmest op regenwormen en op de kwaliteit van grasland, *Landbouwkundig Tijdschrift* 93 (1981) 307–314.
- [7] Eijsackers H., Bund C.F., van de, Doelman P., Ma W.C., Aantallen en fluctuaties van het bodemleven (Numbers and activities of soil life), Report RIN 88/33, Arnhem, 1988.
- [8] Eijsackers H., Zehnder A.J.B., Litter decomposition: a Russian matryoshka doll, *Biogeochemistry* 11 (1990) 153–174.
- [9] Eijsackers H., Soil ecotoxicological risk assesment: how to find avenues in a pitch dark labyrinth, *Archiv. of Toxicol. (Suppl. 20)* (1998) 83–96.
- [10] ESF-programme, Food-web modelling for ecological assessment of terrestrial pollution, European Science Foundation, Strasbourg, 2001.
- [11] Ettema Ch.H., Rathbun S.L., Coleman D.C., The importance of patch dynamics for soil Nematode species coexistence: Implications for diversity-function analysis, in: Rusek J. (Ed.), Abstracts, XIII. International Colloquium on Soil Zoology, Ceske Budejovice, 14 – 18 August Icaris Ltd, Praha, 2000, p. 4.
- [12] Faber J.H., Functional classification of soil fauna: a new approach, *Oikos* 22 (1991) 110–117.
- [13] Franz H., Die Geschichte der Bodenzoologie und ihre Einbeziehung in die bodenkundliche Forschung, in: Vanek J. (Ed.), *Progress in Soil Zoology*, Academia Publ. House, Prague, 1973, pp. 13–23.
- [14] Frenot Y., Introduced populations of *Dendrodrilus rubidus* ssp. (Oligochata: Lumbricidae) at Corzet, Kerguelen and Amsterdam islands: effects of temperature on growth patterns during the juvenile stages, *Soil Biol. Biochem.* 24 (1992) 1433–1439.
- [15] Hedlund K., Tritrophic interactions in a soil community enhance decomposition rates, *Oikos* 88 (2000) 585–591.
- [16] Hopkin S., Life and death (mostly death) to the soil. Contribution to Workshop ‘Facing the 21st Century’, Lund, Sweden 11-12 Dec, 1999.
- [17] Jepson P.C., Scale dependency in the ecological risks posed by pollutants: is there a role for ecological theory in risk assessment ? in: Van Straalen N.M., Løkke H. (Eds.), *Ecological Risk Assessment of Contaminants in Soil*, Ecotoxicology series 5, Chapman and Hall, London, 1997, pp. 175–189.
- [18] Kowalchuk G.A., Gerards S., Woldendorp J.W., Detection and characterization of fungal infections of *Ammophila arenaria* (Marram grass) roots by denturing gradient gel electrophoresis of specifically amplified 18S rDNA, *Appl. Environ. Microbiol.* 63 (1997) 3858–3865.
- [19] Lavelle P., Bignell D., Lepage M., Soil function in a changing world: the role of invertebrate ecosystem engineers, *Eur. J. Soil Biol.* 33 (1997) 159–193.
- [20] Laverman A., Zoomer R., Verseveld H., van Verhoef H., Temporal and spatial variation in nitrogen transformations in a coniferous forest, *Soil Biol. Biochem.* 32 (2001) 1661–1670.
- [21] Lee K.E., Some trends and opportunities in earthworm research or: Darwin’s children – the future of our discipline, *Soil Biol. Biochem.* 24 (1992) 1765–1771.
- [22] Moore J.C., Ruiter P.C. de, A food-web approach to assess the effects of disturbances on ecosystem structure, function and stability, in: Van Straalen N.M., Løkke H. (Eds.), *Ecological Risk Assessment of Contaminants in Soil*, Ecotoxicology series 5, Chapman and Hall, London, 1997, pp. 157–171.
- [23] Ohkuma M., Kudo T., Phylogenetic diversity of the intestinal bacterial community in the termite *Reticulitermes speratus*, *Appl. Environ. Microbiol.* 62 (1996) 461–468.
- [24] Posthuma L., Effects of toxicants on population and community parameters in field conditions, and their potential use in the validation of risk assessments methods, in: Straalen N.M., van Løkke H. (Eds.), *Ecological Risk Assessment of Contaminants in Soil*, Ecotoxicology series 5, Chapman and Hall, London, 1997, pp. 85–123.
- [25] Reinecke A.J., The ecology of earthworms in southern Africa, in: Satchell J.E. (Ed.), *Earthworm ecology*, Chapman and Hall, London, 1983, pp. 195–207.
- [26] Reynolds J.W., The status of earthworm biogeography, diversity, and taxonomy in North America revisited with glimpses into the future, in: Edwards C.A. (Ed.), *Earthworm Ecology*, St. Lucie Press, Boca Raton, US, 1998, pp. 15–34.
- [27] Rundgren S., Andersson R., Brinkmark L., Gustafsson K., Josefsson M., Torstensson L. (Eds.), *Integrated Soil Analysis Ambio XXVII* (1) (1998) 2–78.
- [28] Satchell J., Take the money – call the tune, *Soil Biol. Biochem.* 24 (1992) 1193–1196.
- [29] Setälä H., Haimi J., Siira-Pietikanen A., Sensitivity of soil processes in northern forest soils: are management practices a threat ? *Forest Ecol. Management* 133 (2000) 5–11.

- [30] Stein A., Bekker R.M., Blom J.C.H., Rogaar H., Spatial variability of earthworm populations in a permanent polder grassland, *Biol. Fertil. Soils* 14 (1992) 260–266.
- [31] Tunlid A., Molecular biology: a linkage between microbial ecology, general ecology and organismal ecology, *Oikos* 85 (1999) 177–189.
- [32] Vegter J., Coexistence of forest floor Collembola, PhD Thesis Vrije Universiteit Amsterdam, 1985.
- [33] Wardle D.A., Zackrisson O., Hörnberg G., Gallet C., The influence of island area on ecosystem properties, *Science* 277 (1997) 1296–1299.
- [34] Wardle D.A., Giller K.E., The quest for a contemporary ecological dimension to soil biology, *Soil Biol. Biochem.* 28 (1997) 1549–1554.