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Discussion paper

Use of enclosed model ecosystems in soil ecology: a bias towards laboratory research

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Abstract

Enclosed model ecosystems, or *microcosms*, have become a major research tool in soil ecology. Due to the speed, statistical power and mechanistic insights attainable with laboratory-based microcosm experiments, these have added considerably to our ecological knowledge. However, soil ecologists agree that, due to problems of scale and artificiality, microcosm research should be carried out in the context of appropriately scaled field model ecosystems (e.g. mesocosms). This paper aims at clarifying the terminology of enclosed model ecosystems as well as determining and discussing the frequency with which laboratory and field model ecosystems are used in current soil-ecological research. Among 92 model ecosystem studies published from 1993 to 1998 in soil biological journals, only 19 were performed in the field. Laboratory microcosms are, on average, significantly smaller and experiment duration is significantly shorter than in field model ecosystem studies. They are easier to maintain and allow for a larger number of experiments in a unit of time. We argue that the bias towards laboratory research is mainly caused by the growing demand for publications with high-impact ratings in an increasingly competitive scientific world and by the fact that an increasing emphasis is being placed on subjects where research can be carried out very quickly.

Keywords: Microcosm; Mesocosm; Enclosure; Scale; Reality; Publication impact factors

1. Introduction

Enclosed model ecosystems, often called *microcosms*, have become a major research tool in soil ecology because they are a method with which entire, yet simplified ecosystems can be studied and because they can be replicated for experimental studies at a reasonable cost (Beyers and Odum, 1993). They have been successfully used for studying the interactions among soil biota as well as between soil biota and plants and their effects on various ecosystem processes (Teuben and Verhoef, 1992; Verhoef, 1996; Laakso and Setälä, 1999).

Due to the speed, statistical power and mechanistic insights attainable with laboratory-based microcosm experiments, they have added considerably to our ecological knowledge. However, the study of laboratory microcosm behaviour is not a goal in itself. Microcosms can provide insights into how small, contained model ecosystems respond to certain manipulative treatments and can help to develop hypotheses about behaviour and functioning of real ecosystems. However, ultimately, the relevance of laboratory microcosm research for the field must be tested in the field. Thus, to be able to exploit their full potential as a research tool, laboratory microcosm studies must be placed in the context of appropriately scaled field studies (Carpenter, 1996). Odum (1984) suggested the use of a certain class of model ecosystems: he called for partially enclosed outdoor experimental set-ups to bridge the gap between laboratory microcosms and the large, complex, real-world macrocosm. He made the term *mesocosm* popular — it was originally coined by aquatic ecologists, e.g. Grice and Reeve (1982) — for a type of middle-sized experimental units where parts (populations) and wholes (ecosystem) can be investigated simultaneously.

This paper aims at clarifying several issues concerning the use of enclosed model ecosystems in soil-ecological research. First, we critically discuss the terminological confusion that has arisen around the mesocosm concept. Second, we point out the potential and limitations of laboratory microcosm research. Third, we determine the present abundance of laboratory and field model ecosystem

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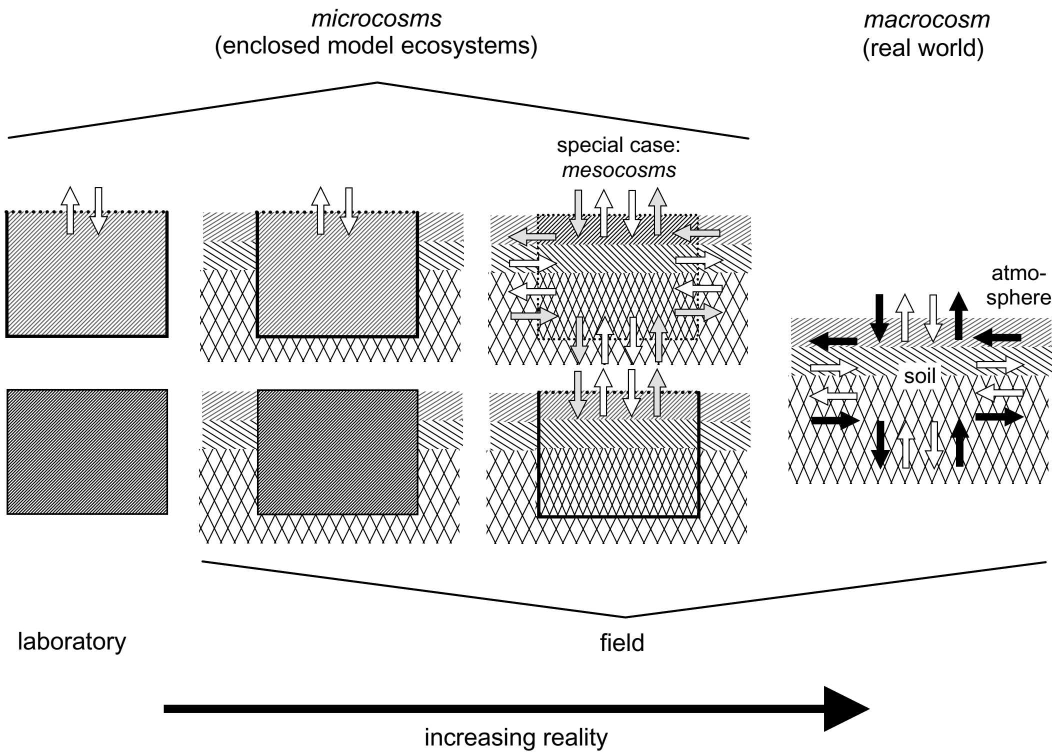

Fig. 1. Microcosms, mesocosms and the macrocosm ("real world"). White arrows, matter exchange (gas, water, nutrients); shaded arrows, controlled movement of soil animals; black arrows, unrestricted movement of soil animals. Upper and lower row of microcosms represent different degrees of permeability. Mesocosms are a special case of enclosed model ecosystems: they preserve the spatial characteristics of the environment (symbolised by different hatching for soil horizons); they allow for exchange of gas, water and nutrients with the environment (white arrows); and they allow for the controlled movement of soil animals between the mesocosm and the environment (shaded arrows). They are the microcosm type that most closely resembles natural conditions.

experiments by reviewing recent volumes of soil biological journals. Fourth, we attempt to identify possible reasons for the under-representation of field model ecosystem studies in soil ecology.

2. The term mesocosm

Odum (1984) provided a very brief definition limiting the use of the term mesocosm for bounded and partially enclosed outdoor experimental set-ups, that is, field enclosures with reduced or controlled input and output from and to its surrounding environment. Unfortunately, this definition is not very precise, and the examples he described — including plot trials in agricultural research under the mesocosm label — very soon created the impression that a mesocosm was simply just "any replicated experiment outside the laboratory" or even "any experiment (laboratory or field) with a larger size and higher spatial and/or organismic complexity than a typical microcosm". Elliott et al. (1986) removed soil cylinders from the field and placed them in a greenhouse, calling them mesocosms. This is in complete contradiction to Odum's definition: the cylinders were neither outdoor experimental set-ups nor were they partially enclosed (there was simply no surrounding environment with which a controlled exchange of soil organisms or matter could have taken place). Teuben and Verhoef (1992) understood soil mesocosms as microcosms placed in the field, throwing overboard the idea behind Odum's approach that a mesocosm should provide a degree of realism not possible in microcosm systems. In contradiction to this, Verhoef (1996) characterised mesocosms similarly to Elliott et al. (1986) as larger units taken directly from the field, but placed under controlled climatic conditions, completely neglecting Odum's mesocosm definition as field experimental set-ups with contact to their natural environment.

The sloppy use of the term mesocosm in the soil-biological literature is not unique. Inconsistent use of definitions has been identified as a serious impediment to progress in ecology (cf. McIntosh, 1999) and many concepts face the risk of being garbled to the point of oblivion (cf. the critical papers by Hurlbert, 1997; Lawton, 1997; Wilson, 1999). Ecology is a scientific discipline overloaded with jargon (Peters, 1991). If the term *soil mesocosm* continues to be used arbitrarily instead of referring to a well-defined methodological concept, it will remain as only another ambiguous word in the overflowing body of ecological jargon and, consequently, should be dropped. In its place, the more comprehensive term *ecological microcosm* or *enclosed* *model ecosystem* should be used in scientific communication, accompanied by a closer description of the actual design. For example, Beyers and Odum (1993) embrace all kinds of contained model ecosystems — from few-millilitre test tubes to Biosphere 2 — under the common label ecological microcosm (though providing specific names for certain types of microcosms). We would argue, however, in accordance with the definition put forth by Odum (1984), that a particular methodological approach to the construction of model ecosystem justifies the use of the specific label *soil mesocosm*. We think that soil mesocosms differ from other types of ecological microcosms in certain fundamental features:

1. Soil mesocosms are pieces cut out of real-world ecosystems. The experimental units are taken directly from the field (soil cylinders, monoliths) and differ from other kinds of microcosms since they preserve (a) the entire community of soil organisms and (b) the full small-scale spatial complexity of the habitat (soil pores, humus layers, etc.). While microcosms are typically composed arbitrarily by adding single elements (substrate, specimen of animal species, microbial inoculum, etc.), mesocosms aim at preserving the original field conditions.
2. Soil mesocosms are placed in the field and, thus, are exposed to the natural fluctuations of the physical environment (temperature, moisture, light conditions, etc.), rather than to the typically maintained conditions in the laboratory (constant temperature or temperature cycle, etc.).
3. Soil mesocosms are partially enclosed. They are open to a certain extent to their environment and — depending on the aim of the study and on the kind of mesocosm boundary — allow for the exchange of matter and energy with the atmosphere and the surrounding soil (gas exchange, precipitation, organic matter supply through fresh detritus, lateral migration of soil biota, etc.). Thus, the experimental units are interwoven in the same net of biotic and abiotic relationships with their surroundings, as is the case with undisturbed soil.
4. Treatments in soil mesocosms are subtractive or perturbative. While treatments in microcosms are defined by the addition of single items to an experimental unit, mesocosm units are treated as otherwise undisturbed wholes by subtraction of the variables under question (e.g. by excluding animals of a certain size-class) or by perturbation (e.g. by providing a stress factor).
5. Mesocosms allow for longer, larger-scale experiments than are possible in the laboratory. However, metric dimensions in space and time alone do not define a mesocosm: a contained laboratory model ecosystem under constant conditions and designed for an earthworm experiment might still be larger and run longer than a partially enclosed field model ecosystem designed for the study of soil micro- or mesobiota.

The combination of the features (1)–(5) outlined above ensures a degree of reality that cannot be easily achieved by other types of microcosms (Fig. 1). We suggest the use of the term soil mesocosm as defining the set-up between simplistic soil microcosms and natural macrocosms, providing that the conditions above are fulfilled. This is in agreement with the use of the term mesocosm in other fields of ecological research: Boyle and Fairchild (1997) characterise mesocosms in ecotoxicology — indicating some difference in terminology in the designation of microcosms and mesocosms — as "outdoor semi-controlled ecosystems" that include "natural species assemblages" and that are subject to the "vicissitudes of regional weather, natural recolonisation, interspecific interactions, disease, and other factors."

Mesocosms have already been used successfully in soil ecology, for example in studying the effects of soil mesofauna on microbial activity and community structure (Vedder et al., 1996; Kandeler et al., 1999) and on nutrient supply (Zechmeister-Boltenstern et al., 1998) in spruce forest soil.

3. Potential and limitations of laboratory microcosms

The role of enclosed model ecosystems in ecological research has been disputed in recent years (e.g. Beyers and Odum, 1993; Lawton, 1995; Carpenter, 1996; Fraser and Keddy, 1997). The main points of criticism are:

1. Ecological systems do not have one single characteristic scale, research must instead be carried out at a range of different scales (including microcosms). Scale has been recognised as an important determinant of patterns and processes observed in natural ecosystems (Levin, 1992). The choice of scale for an experiment can, thus, heavily affect the observed ecological dynamics: scaling up from the microcosm scale to larger scales appears to be questionable, since community structure (species interactions controlling ecological processes) and biophysical components (micro-relief, soil organic matter, ion exchange capacity, buffering fluxes of energy and matter, etc.) may not increase along the same dimensions (Anderson, 2000). Particularly in aquatic ecology, scale has been the primary factor of concern when discussing the significance of microcosm research (Frost et al., 1988; Petersen et al., 1999).
2. The relevance of the results of laboratory microcosms for the extrapolation to the field situation is unclear due to their low degree of reality, namely the artificially low complexity of both spatial structure and community composition maintained in standard laboratory microcosms as compared with the field situation. For example, Leonard and Anderson (1991) showed that, in spatially complex laboratory systems, the interaction between a Collembolan species and a fungus was reversed compared with spatially simple systems. Mebes and

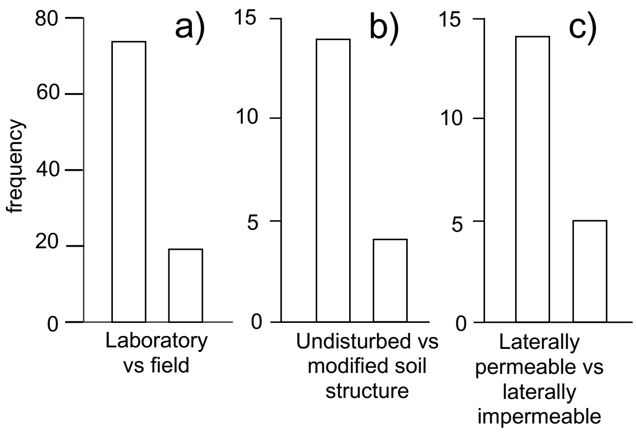

Fig. 2. Number of model ecosystem studies published in five soil ecological journals from 1994 to 1998: (a) number of studies carried out in the laboratory (left) and in the field (right); (b) number of field model ecosystems with undisturbed (left) or modified (right) soil structure; (c) number of field model ecosystems with laterally permeable (left) or impermeable (right) borders.

> Filser (1998) demonstrated in a laboratory microcosm study that different single Collembolan species lead to different patterns of N mobilisation and immobilisation. Earthworms in laboratory microcosms exhibited different relationships between CO_2 production and body weight when kept under constant or diurnally fluctuating temperature regimes (Uvarov, 1998). These few examples demonstrate that the outcome of a laboratory microcosm study is potentially predetermined by the investigator's choice of experimental conditions. Thus, laboratory microcosms are valuable research tools when these problems are treated as research questions by themselves (Lawton, 1996), such as the role of size, community composition or spatial complexity in ecological interactions; they are, however, of little value for extrapolation to the field.

Thus, laboratory microcosm studies should be incorporated into research programs with appropriately scaled field studies to assess the correspondence between microcosm and natural system behaviour (Carpenter, 1996). Although this point has also been stressed by soil ecologists (Verhoef, 1996), soil-ecological research has very rarely combined model ecosystem studies at the laboratory and at the field level (e.g. Teuben and Verhoef, 1992).

4. Frequency of use of laboratory and field model ecosystems

Soil ecologists agree that field model ecosystem research is important and necessary for scientific progress (Elliott et al., 1986; Teuben and Verhoef, 1992; Verhoef, 1996). But how much research is actually performed by using mesocosms (or similar systems)? We screened five volumes (1994–1998) of the journals *Soil Biology and Biochemistry*, *Biology and Fertility of Soil*, *Applied Soil Ecology*, *Pedobiologia* and the *European Journal of Soil Biology* to obtain some idea of how frequently model-ecosystems have been used recently in soil ecology. We included papers focusing on interactions in the context of an ecosystem, thereby excluding papers reporting on growth studies, toxicity tests or similar experiments that characterise physiology or behaviour of single species or single trophic levels. We also excluded litterbag studies and replicated field studies that were plot trials rather than model ecosystems (for example, experimental manipulation of leaf-fall by roofs). Separate experiments carried out in the same model ecosystem facility or published in the same paper were counted separately.

A total of 92 experiments met our criteria. The vast majority (73) of model ecosystem studies were conducted in the laboratory (microcosms), only 19 were conducted in the field (mesocosms and similar systems) (Fig. 2a). Among the latter, eight model ecosystems correspond to the mesocosm type defined above by partially enclosing soil cores or monoliths while leaving its structure undisturbed. Five systems were prepared by forcing metal or plastic screens into the soil, thus preventing lateral exchange of matter and biota with the surrounding soil; four systems were composed of mixed or sieved substrate (Fig. 2b and c).

5. Reasons for the under-representation of field model ecosystems

Why do soil ecologists prefer to study model ecosystems in the laboratory rather than in the field despite the frequently expressed desire for controlled field experiments? Possibly soil ecologists simply do not need them. While screening the journals for microcosm and mesocosm studies, we found a number of experiments that dealt with the analysis of soil ecosystems in a plot-trial style. While aquatic ecologists are forced to enclose water bodies because of the mobility of their medium, soil ecologists often find it sufficient to demarcate plots due to their target organisms' restricted lateral movement in soil. However, plot-trials could not be found more often than field model ecosystem studies; that is, even when stating that field model ecosystems are not necessary for certain soil-ecological questions, laboratory microcosms are still considerably over-represented. Possibly the requirements for teamwork in mesocosm or field level studies can be provided only by larger laboratories. We think that the main reason why soil ecologists are tempted to work mainly in the laboratory is caused by the current conditions of scientific work. Carpenter (1996) in his critique of microcosm experiments addresses a number of issues: costs for construction and maintenance of microcosms can be modest, so they are attractive for theses; microcosms keeps the staff on campus, where the administration would

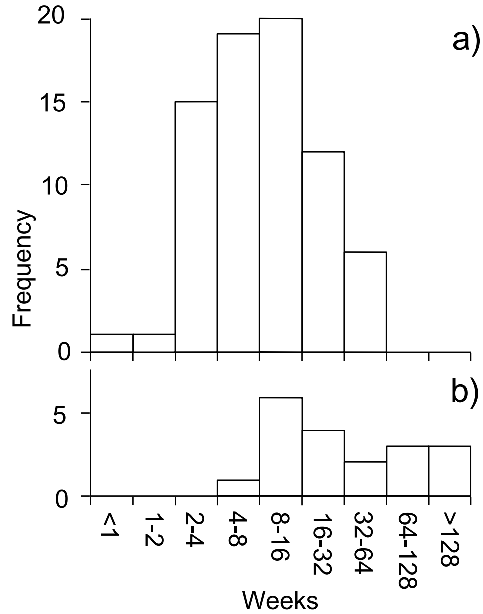

Fig. 3. Duration of laboratory (a) and field (b) model ecosystem studies published in five soil ecological journals from 1994 to 1998.

like them to be; and, most important, microcosms provide rapid results to meet publication goals for career development.

We compared the duration of the 92 studies of our review: model ecosystem studies in the laboratory lasted between 1 and 57 weeks with a median duration of 8.6 weeks; studies in the field were significantly longer, with a range of 5.7–224 weeks and a median of 27.5 weeks (Mann–Whitney $U = 266$, $P < 0.001$) (Fig. 3). Consequently, during an average field model ecosystem study, three laboratory microcosm experiments may be run. Also the size in terms of their volume (and hence the feasibility of running several experiments in parallel) of model ecosystems differed significantly: laboratory systems ranged from 0.02 to 32.6 l (median: 0.94 l), field systems from 0.5 to 10^7 l (median: 18.3 l) (Mann–Whitney $U = 164.5$, $P < 0.001$) (Fig. 4). The duration of studies and expense for maintaining larger experimental units multiply the number of results per unit of time that can be gained by laboratory microcosm studies — in disfavour of field studies — and, consequently, may be processed into manuscripts. A larger number of studies per unit time increases the chance of obtaining "good results", that is, results that confirm an expected relationship between biota or ecosystem processes. Moreover, the probability of detecting significant treatment effects is higher in microcosms than in mesocosms, since the contribution of species to processes are progressively masked as observations are made over larger scales: the smaller the number of species in a low-scale experiment, the more apparent is their particular function (Anderson, 2000).

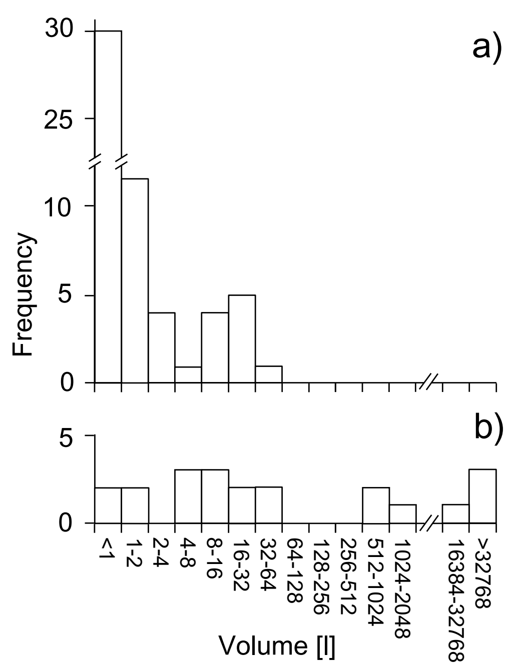

Fig. 4. Size of experimental units in laboratory (a) and field (b) model ecosystem studies published in five soil ecological journals from 1994 to 1998.

It is the experience of many researchers that it is more difficult to publish a paper when there are statistically non-significant differences between experimental treatments. The resulting "file-drawer problem" (non-significant results are less frequently published than significant ones) has been identified as a serious impediment to scientific progress and has also been discussed in the context of ecological research (Csada et al., 1996; Bauchau, 1997). We conclude that soil ecologists tend to carry out research that can guarantee publishable results to a certain degree rather than involve themselves in time-consuming experimental field studies of complex systems that may fail in delivering significant treatment effects.

It is not our aim to blame soil ecologists for neglecting the frequently expressed need for replicated field studies. We believe that the strong bias towards simple and short laboratory experiments is imposed on them by the growing demand for high-impact ratings for publications in an increasingly competitive scientific world. In a review on the advantages and disadvantages of impact factors, Kokko and Sutherland (1999) noticed a trend that increasing emphasis is placed on subjects where research can be carried out very quickly. In their opinion, this is of considerable concern for ecology, where long-term studies are a fundamental part of the science. We completely agree with this view. We think that this may also be the reason for another observation made during our journal screening: the overwhelming number of experimental field studies in soil ecology are still carried out by the use of litterbags, a method which was introduced by Bocock and Gilbert (1957) and is more than 40 years old. Litterbags, like microcosms, can be cheap, easy to maintain and replicable in large numbers and, thence, allow the collection of more results per unit of time than complex mesocosm systems. Litterbags, however, suffer from similar disadvantages and limitations as microcosms: they create an artificial environment with high local concentration of food and shelter for various soil biota (thus influencing spatial and temporal scales of ecological processes) and with biotic and abiotic conditions differing from the surrounding soil and litter layers (e.g. inhibitory effects on certain fungal structures, St. John, 1980). Thus, litterbags are valuable research tools for addressing a restricted range of ecological questions (e.g. measurement of litter disappearance rates in systems with high seasonal supply of aboveground organic matter), but they receive much more attention and application than they deserve. Like microcosms, they should also be embedded in a context of appropriately scaled field studies.

In conclusion, laboratory microcosms are a valuable tool in soil-ecological research when problems of scale and reality (e.g. size of model ecosystems, community composition) are treated as research questions for themselves. However, laboratory microcosm research alone is not sufficient for judging the role of species interactions in the field. Field experiments with model ecosystems (preferably mesocosms) are severely needed, since they allow for research on larger spatial and temporal scales in experimental units that resemble the natural conditions much more closely. The frequent use of simple, easy-to-maintain and inexpensive experimental set-ups in the laboratory (microcosms) and the field (litterbags) reminds us of the lad who lost his key in the dark doorway, but looks for it under the street-lamp because there is more light over there. In the long term, soil ecologists are well advised not to choose their research instruments according to convenience or to the demands for high-impact ratings, but according to the demands of the core questions of their science. Otherwise we face the danger of ending in a blind alley where "work in artificially enclosed environments generates beautifully replicated, well-controlled studies of artefacts — that is of processes that do not occur in the field" (Lawton, 1999).

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