

Invited contribution  
**The soil food web: structure and perspectives**

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**Abstract**

This review outlines directions for future research in soil food web ecology. Two lines of research are considered to be most important: the adoption of new methodologies to investigate food relationships and the strengthening of experimentation to investigate the interaction strength between food web components. For a better understanding of food relationships molecular methods, particularly fluorescence in situ hybridization, and stable isotope methodology, including the analysis of variations in the abundance of  $^{13}\text{C}$  and  $^{15}\text{N}$ , are thought to be most promising. Implications of results of the studies which employed these methodologies for the structure and function of soil food webs are highlighted. © 2002 Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

*Keywords:* FISH; Food web; Soil ecology; Stable isotopes; Trophic interactions; Trophic structure

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**1. Introduction**

The major goal of ecology is to understand the dynamics of populations and communities. In animal communities this is fundamentally connected with food relationships and the resulting forces predators exert on their prey and vice versa. For depicting the complex array of feeding relationships in animal communities food webs have been invented. In their simplest form food webs picture links between species or feeding guilds (trophic species) in a binary way, i.e. by drawing arrows between prey and predator. These connectivity food webs are comparatively easy to construct and therefore are the most common found. They may help in visualizing principal relationships between species; however, they tell little about possible effects exerted by predators on prey or vice versa and therefore, are of limited value to understand structuring forces in food webs. An important step forward is including energy flow between trophic species in food webs, i.e. constructing energy flow webs. Particularly in soil ecology, energy flow webs received considerable attention [13,16,30]. In fact, the goal of

most soil food webs was to understand the impact of the soil community on decomposition processes and nutrient cycling [11,44]. It is of little surprise therefore, that most soil food webs have been constructed for arable systems, and hardly any more detailed energy flow webs exist for more natural communities like forests and natural grasslands.

In contrast to below-ground food webs, the major perspective of food webs of above-ground and of aquatic communities was to understand structuring forces between food web components, i.e. to uncover the relative strength of bottom-up vs. top-down forces [4,54]. Energy flow webs may give hints on whether predators may effectively control certain prey species, however, linking energy flow to the strength of coupling between predators and prey (interaction strength) is not straightforward. Therefore, for depicting interaction strength between food web components a third type of food webs, interaction strength webs, have to be constructed [43]. In contrast to energy flow webs, the basis of interaction strength webs is the per capita effect a predator exerts on its prey or vice versa. To be able to construct interaction strength webs it is necessary to base the predator impact on prey density, i.e. to calculate the predator per capita impact on prey [15,84].

Beside prey density, one of the crucial variables necessary for constructing interaction strength webs is the relative

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energetic contribution of the prey to the predator and the conversion efficiency of prey into predator production. This may be a fairly simple task in predators with a narrow prey spectrum but is hard to do for generalist predators with a wide spectrum of prey and in which the abundance of a specific prey may vary in time. In addition, the per capita effect of prey on predators strongly depends on whether juveniles or adults are consumed. All this adds to the extraordinary difficulty in estimating interaction strength in natural communities; it has been concluded, therefore, that interaction strength is extremely hard to delineate from descriptive food web studies [50,84]. This particularly applies to communities in which generalists and opportunistic feeders predominate, and exactly this is a very characteristic feature of soil animal communities [65].

Considering the tremendous difficulties soil food web ecologists are confronted with one may wonder how to proceed to better understand structuring forces in below-ground communities. The goal of this review is to outline my perspective which, despite a beginning highlighting problems, will emphatically stress that there are exciting prospects for major success in the near future. Two lines of research appear to be most important in that way: 1) a better understanding of the trophic structure of soil communities and of the feeding relationships between soil animal species (and microorganisms); and 2) to investigate interaction strengths between soil animal species using experiments of a hierarchy of complexity. There is an urgent need for incorporating new methodology for a better understanding of the trophic links between species and to shift from descriptive to experimental studies to uncover the structuring forces in below-ground food webs.

## 2. The trophic structure of below-ground communities

### 2.1. Aggregation of species to trophic groups

In food webs the basal entities usually are not biological species but feeding groups (guilds, trophic species) consisting of species which are assumed to be functionally equivalent, i.e. which depend on similar prey and therefore exert similar top-down forces on prey populations. Particularly in species-rich communities like the ones in soil, aggregating species to trophic groups is inevitable. However, aggregation of species is a controversial issue since for connectivity food webs it has been realized that food web properties may strongly depend on the degree of aggregation, i.e. on food web resolution [37,38]. Martinez et al. [39] stressed that the number of trophic species increases with sampling effort which was mainly due to the increase in intermediate species and not that of basal and top species.

In soil food webs species are almost uniformly aggregated according to taxonomic similarity assuming that higher taxonomic units represent feeding guilds

[6,14,30,60,88]. This is justified by referring to gut content analyses and morphological features; unfortunately, this approach inherits a multitude of difficulties. Soil animals are notoriously flexible in their diet; in fact, it may be difficult to assign a certain species to one trophic level. Depending on what food resources are available, collembolans and oribatid mites may feed on fungi, algae, amorphous detritus or even other soil animals thereby functioning as microbivores, herbivores, detritivores or even predators [3,35,36,55,59,78]. Particularly in detritivores which in their gut contain an amalgamation of different materials and organisms, it is virtually impossible to delineate which of the components form the basis of their diet [65]. For such important detritivores as earthworms it is still unclear on what they really live on. In contrast to previous assumptions that soil microorganisms form the major part of their diet [18], evidence is now accumulating that microorganisms in fact are of minor importance [20,83]. Certainly, we need more information on the diet of soil animals and this is where we may profit considerably from new methodical developments in the near future.

### 2.2. Promising methodologies

Immuno assays and ELISA techniques have been adopted to trace food relationships of some soil invertebrates, most importantly predators [7,25,34]. This certainly is a very useful approach which should be employed more frequently. However, due to problems in adopting this methodology to small organisms it is difficult to apply it for tracing food relationships between, for example, microbivores and fungi. With the development of new molecular methodologies this limitation is overcome. A particularly useful technique for tracing food materials in the gut of consumers is fluorescence in situ hybridization (FISH). This technique is now increasingly used to study the structure and dynamics of bacterial and fungal communities in situ [42,45,75]. Until today, however, only very few studies have employed this methodology to better understand food relationships in soil communities; a notable exception being the study of Fischer et al. [21,20]. Using probes targeting rRNA of eubacteria and  $\alpha$ -,  $\beta$ - and  $\gamma$ -subgroups of proteobacteria they did not find evidence for effective digestion of bacteria during the gut passage through *Lumbricus terrestris*. Surprisingly, this trend setting study apparently did not stimulate soil ecologists to take up the methodology and investigate food relationships of other soil invertebrates until today. The methodology has the power to open up the black box of microorganisms and may allow the tracing, for example, of specific species of fungi in the gut of microarthropods like collembolans and oribatid mites. Also, it may be adopted for tracing the prey spectrum of predators particularly small ones like gamasid mites. A particular advantage of the methodology is that it is applicable to even very small animals and it may therefore allow us to even

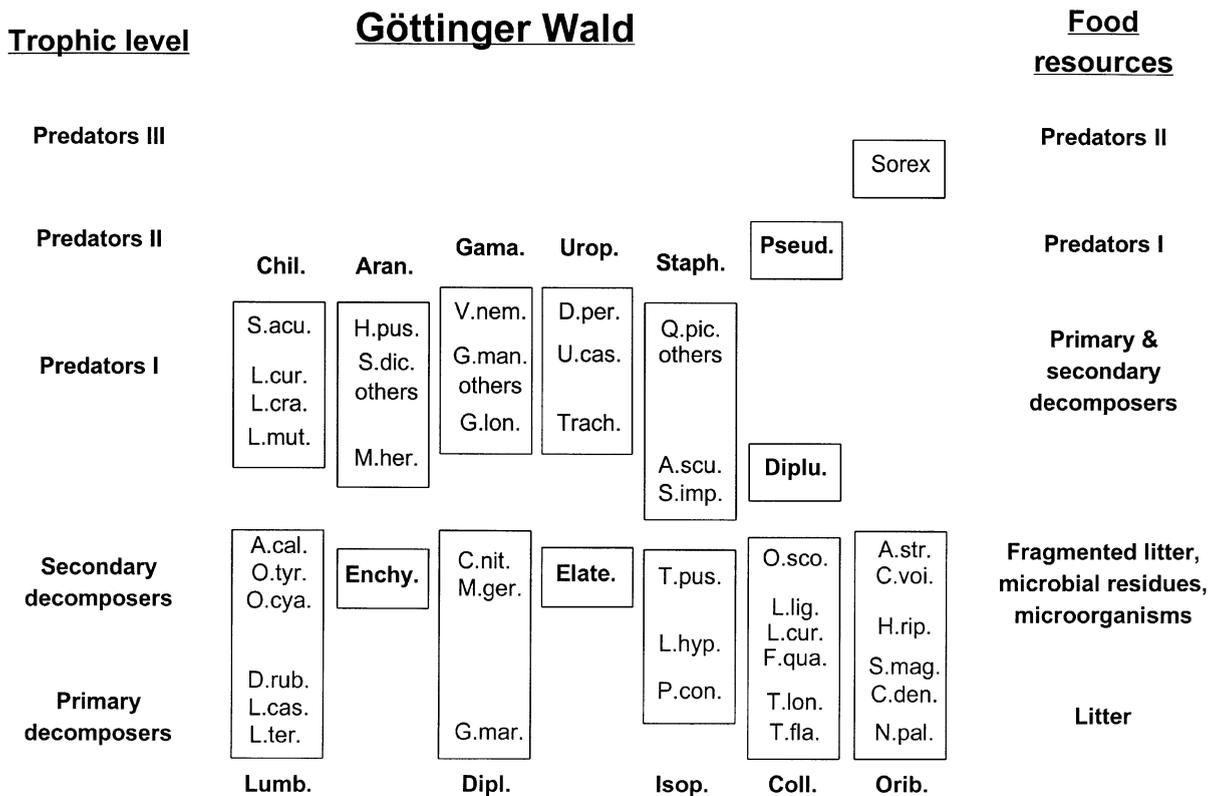


Fig. 1. Trophic structure of the decomposer community of a beech wood on limestone ('Göttinger Wald') as indicated by variations in the natural abundance of  $^{15}\text{N}$  in animal tissue (from Scheu and Falca [63]). Aran: Araneida; Chil: Chilopoda; Coll: Collembola; Dipl: Diplopoda; Diplu: Diplura; Elate: elaterid larvae (Coleoptera); Enchy: Enchytraeidae; Gama: Gamasina; Isop: Isopoda; Lumb: Lumbricidae; Orib: Oribatida; Pseud: Pseudoscorpionida; Staph: Staphylinidae (Coleoptera); Urop: Uropodina; for full species names see [63].

trace food materials in the gut of nematodes. This would be a very big step forward since, so far, for this keystone soil animal group, food relationships are delineated from morphological characters and laboratory feeding experiments only, and these form the bases for defining nematode trophic groups [86,89]. Like many other soil invertebrates, nematodes also appear to be generalist feeders and presumably opportunistically respond to food availability [85,86]. Therefore, there is an urgent need to prove nematode trophic grouping by in situ analysing their food relationships.

Gut content analyses using direct microscopy, electrophoretic studies and also molecular methods suffer an important shortcoming: they may uncover what animals fed on; however, delineating what was actually digested by the consumer remains speculative. For filling this gap another methodology which recently found considerable attention might be extremely valuable: the analysis of the natural variation in stable isotope content in animal tissue. The combined analysis of  $^{13}\text{C}$  and  $^{15}\text{N}$  is particularly promising since the first may allow the tracing of food material actually used for biomass production, while the second may allow one to judge the trophic position of a species [41,77]. This approach is about to become very popular in soil food

web ecology [9,10,47,69,74]. The methodology has been proven to be a powerful tool to delineate feeding guilds in earthworms [9,69] and termites [8,33,74]. Recently, variations in the natural abundance of stable isotopes have been used to uncover the trophic structure of whole soil animal communities [57,63]. From their study on the trophic structure of the soil animal community of two beech forests of contrasting humus forms Scheu and Falca [63] concluded that microbivores and detritivores do not form distinct trophic levels, rather there appears to be a gradient from primary to secondary decomposers in most of the non-predatory soil animal groups including collembolans, earthworms, oribatid mites and millipedes (Fig. 1). A similar picture emerged for predators which did not form distinct trophic groups, rather most higher taxonomic units including centipedes, spiders, gamasid mites and staphylinid beetles appeared to consist of species forming a gradient from ones which predominantly feed on primary decomposers to others which predominantly feed on secondary decomposers. Overall, the results indicated that higher taxonomic units are only useful to depict very general trophic grouping, i.e. into predators and microbi-detritivores.

Despite the fact that the stable isotope approach is very promising, there are also limitations to this methodology. A limit of the methodology is set by the amount of nitrogen necessary for determination of  $^{15}\text{N}$  in a sample which, depending on the mass spectrometer used, needs to be between 5 and 20  $\mu\text{g N}$ . This limitation does not allow the determination of tissue  $^{15}\text{N}$  content in minute soil animals like nematodes. Even for collembolans or oribatid mites hundreds of specimens might have to be bulked to obtain a single reading. A major shortcoming of the methodology at present is that we have very little experimental proof to study to what extent  $^{15}\text{N}$  is really enriched per trophic level in soil animals. Therefore, the factor of 3.4  $\delta$  units indicated by the study of Wada et al. [77] remains unproven for soil invertebrates. Also, there is very little information on the variability in  $^{15}\text{N}$  data within species except for earthworms [67]. Furthermore, fractionation of  $^{15}\text{N}$  may vary with food quality as indicated by studies on locusts [81] and cladocerans [2]; in addition, the  $^{15}\text{N}$  content in animal tissue is known to change in starving animals [68,70]. Certainly,  $^{15}\text{N}/^{14}\text{N}$  ratios in animal tissue have to be interpreted with great care as stressed previously [22,26,79].

A peculiar feature of soil systems adds to this call for caution. In soils the content of  $^{15}\text{N}$  increases with soil depth which at least in part is due to the enrichment of  $^{15}\text{N}$  with decomposition of organic materials [46]. The differences in  $^{15}\text{N}$  content in organic matter is likely to transform into differences in  $^{15}\text{N}/^{14}\text{N}$  ratios in microorganisms and animal consumers;  $^{15}\text{N}$  concentrations in soil animals of different soil depths therefore cannot be translated into trophic positions in a straightforward way. Still,  $^{15}\text{N}/^{14}\text{N}$  ratios in soil animals may be extremely valuable to judge the nutritive importance of organic materials of different soil layers for soil microorganisms and soil invertebrates. In the study of Scheu and Falca [63],  $^{15}\text{N}$  content of organic matter strongly increased with soil depth in the mull humus beech forest investigated (Göttinger Wald). Interestingly, in none of the microbi-detritivores investigated did the  $^{15}\text{N}$  tissue content exceed that of the organic matter for 3–6 cm soil depth. Except for *Onychiurus scotarius*  $^{15}\text{N}$  tissue content in all the collembolan species studied was even below that of the bulk organic matter for 0–3 cm soil depth; this difference was even more pronounced for the hot water extractable organic matter (Fig. 2). Obviously, the organic matter incorporated into the mineral soil is of little importance for animal nutrition in that forest.

The increase in  $^{15}\text{N}$  enrichment with soil depth and the concomitant change in the base line of the food web in fact may help in delineating feeding guilds of soil invertebrates. To understand interaction strength between soil animal species it is necessary when defining feeding guilds to also consider the habitat, i.e. the soil layer, in which the species lives. It is evident that only those species can be tightly linked which colonize the same habitat. Including the soil layer a species lives in for defining feeding guilds in fact, has been proposed previously by Faber [19].

The  $^{15}\text{N}$  content of collembolans of the Göttinger Wald formed a gradient which spans over more than 6  $\delta$  units strongly indicating that the species have to be grouped into very different feeding guilds (Fig. 2). A similar pattern occurred for other microbi-detritivores. Overall, although the increase in  $^{15}\text{N}$  content with soil depth hampers a straightforward translation of  $^{15}\text{N}$  values into trophic groups, it may in fact be advantageous because it helps in understanding the relative importance of organic matter of different soil layers as a basal resource and it may help in aggregating species to meaningful feeding guilds to depict which species may be trophically linked. This is a big step forward for constructing interaction strength food webs.

### 2.3. Implications of stable isotope analyses for food web structure

So far there have been two studies which employed the analyses of variations in the natural abundance of stable isotopes to investigate the food web structure of soil animal communities; Ponsard and Arditì [57] focused on macrofauna whereas Scheu and Falca [63] included both macro and mesofauna. A major finding of both the studies was that predator species on average differ by more than one trophic level from prey species. Ponsard and Arditì [57] took this as evidence for intraguild predation, whereas Scheu and Falca [63] concluded that predators may preferentially feed on secondary decomposers (Fig. 3). Of course, these interpretations are not mutually exclusive; rather, it is likely that depending on the community investigated the one or the other might be closer to reality. Inherent in both views is that predators function as trophic level omnivores supporting the view that omnivory is very widespread in soil animal communities [23,52,65].

The view that predators predominantly feed on secondary decomposers implies that primary decomposers may be less affected by top-down forces than secondary decomposers. In fact, it has been hypothesized that size (e.g. in *Lumbricus terrestris*), production of deterrents (e.g. in *Glomeris marginata*) and mobility (e.g. in *Tomocerus flavescens*) of primary decomposers may contribute to make them less vulnerable to predation than secondary decomposers [63].

Before exploring the implications of this view in some more detail I will stress again that primary and secondary decomposers form a continuum of species feeding on detritus to those feeding predominantly on microorganisms; they do not form distinct trophic levels (see Fig. 1). For representing this gradient of trophic positions of microbi-detritivores it would certainly be better to adopt the approach of effective trophic levels, i.e. using decimals instead of integers to depict the trophic position of a species [12,48]. However, due to the limitations of the stable isotope approach (see above) this cannot be done with the available information.

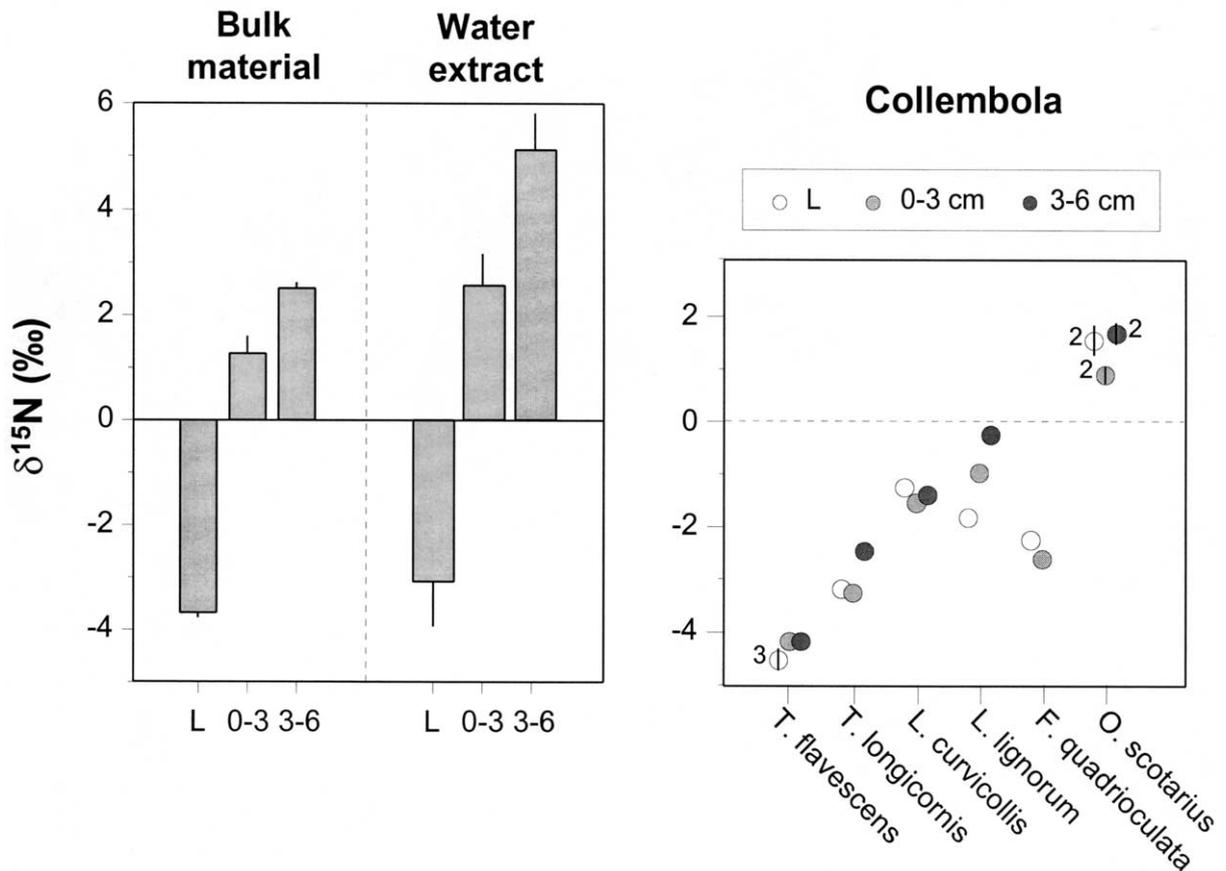


Fig. 2. The content of  $^{15}\text{N}$  in bulk and hot water extractable organic matter and in collembolan species of a beech wood on limestone (Göttinger Wald; modified from [63]); L, litter layer; 3 cm soil depth; 63–6 cm soil depth.

The view that the decomposer community consists of predators, primary and secondary decomposers with secondary decomposers being the intermediate level is reminiscent of a trophic cascade, cf. [51]; however, in contrast to trophic cascades the basal and intermediate level are not trophically linked (Fig. 3). Therefore, in this system preda-

tors do not function in destabilizing secondary decomposers because they do not share a common resource with them (cf. [17,29]). For depicting the trophic relationships in more detail plant residues and microorganisms have to be included (Fig. 4). In doing this, some interesting properties of below-ground food webs emerge. There appear to be two channels of energy transfer, the primary and the secondary decomposer channels (cf. [43]); the primary decomposer channel functions as a classic trophic cascade with three trophic levels; the secondary decomposer channel is much more complicated and includes omnivory, i.e. secondary decomposers feed on microorganisms and detritus and the latter they share with bacteria and fungi. Primary decomposers may compete with microorganisms for resources; primary and secondary decomposers are very indirectly linked trophically via fungi and bacteria; also, primary and secondary decomposers are indirectly linked by sharing common predators (apparent competition [28]). All these, of course, are extrapolated from a very much aggregated food web and therefore might be over simplistic. However, as indicated by theoretical analyses food webs may be much more 'lumpable' without losing their major properties

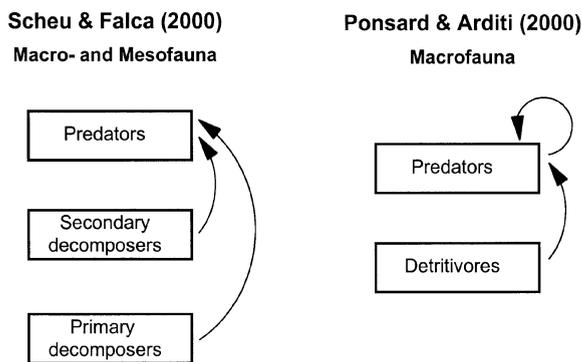


Fig. 3. Gross food web structure delineated from  $^{15}\text{N}$  natural abundance in soil animal tissue [57,63].

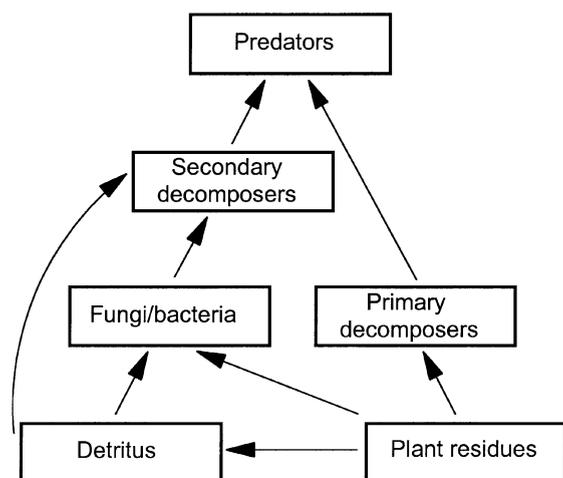


Fig. 4. Conceptual model of the below-ground food web distinguishing a primary decomposer and the secondary decomposer channel.

which particularly applies to communities in which there is much overlap in prey for predators and in predators for prey [72], as is certainly the case in soil communities.

The dual channel view of the below-ground food web implies that the decomposition process is notoriously flexible; assuming that primary decomposers are not effectively controlled by predators (see above), a weakening of the one pathway inevitably results in strengthening of the other. In fact, the very famous distinction of macrofauna dominated systems from mesofauna dominated systems can be easily delineated from this view. Hampering of macrofauna development due to, for example, soil acidity, as has often been documented [56,61], results in the strengthening of the secondary decomposer channel, i.e. in an increase in the density of fungal feeding collembolans and oribatid mites. Also, the assumption that primary decomposers compete with microorganisms for resources is supported by some studies [64]; however, there is very limited information on the subject [80]. Furthermore, there is evidence that secondary decomposers might in fact be more heavily controlled by predators than primary decomposers [26,27,31,62]. Again, however, the experimental proof is very limited. Certainly, the implications from descriptive food web studies need to be proven by experimentation and this is the last point I would like to elaborate in some more detail.

### 3. Uncovering interaction strength: experimentation

The prime role experiments play for uncovering causal relationships between food web components cannot be overemphasized. This primacy has long been realized by ecologists working above the ground [24,58,82], but appears to have been adopted more slowly by soil ecologists

as a review of journals like *Pedobiologia* indicates. As stressed above, a multitude of methods is now available to investigate links between soil animals and their food resources; however, all these methods fall short in uncovering the strength of these interactions in the field. To understand the relative importance of top-down and bottom-up forces experiments are indispensable [50,84]. In setting up experiments exploring these interactions soil ecologists face serious difficulties. Specific food web components are very hard to manipulate without serious side effects on soil structure, other soil organisms, nutrient status and other factors. A particular problem in soil is that food resources and habitat characteristics are intimately interwoven; detritivores live in their food resources [64]. To cope with these difficulties experiments of different complexity have to be employed.

Scheu et al. [66] distinguished assembly, reassembly and perturbation experiments (Fig. 5). The first investigate simple food web interactions in an artificial system where carbon and nutrient resources are provided. In these systems a known set of species are assembled or added to a microbial community of unknown diversity (e.g. adding protozoans or nematodes to a mixed culture of microorganisms). Control of resource supply to a limited number of species in a simplified habitat may allow a complete understanding of food web interactions; however, the significance of the relationships in the field remains largely unknown.

Including more natural conditions in respect to resources and habitat characteristics in experimental investigations is crucial to bridge the gap between the laboratory and the field. This has been widely attempted by employing more and more complex and sophisticated micro- and mesocosm systems [32,76]. In setting up micro- and mesocosm studies for investigation of soil food web interactions one is confronted with the difficulty that the organisms living in the soil materials to be used in the experiments have to be removed or killed in part or in total. In doing this procedures have to be used that leave habitat characteristics (physical and chemical soil properties) as intact as possible. Depending on the food web components to be re-established in the experimental systems soil materials have to be defaunated. Then a known set of organisms can be re-established (reassembly experiments; Fig. 5).

Experiments closest to the field situation are perturbation experiments. In perturbation experiments a single or a few species, food web components or resources (food items, CO<sub>2</sub>, nutrients, habitable space, etc.) are manipulated in the field (added or removed) and the response of the community is observed. Due to their close link to the field situation perturbation experiments are a very powerful tool in uncovering the way species are connected in nature. Two types of perturbation experiments have been distinguished [5]: pulse perturbations where the system is perturbed once and the community is left to respond, and press perturbations where perturbations are repeated to keep a response variable at a

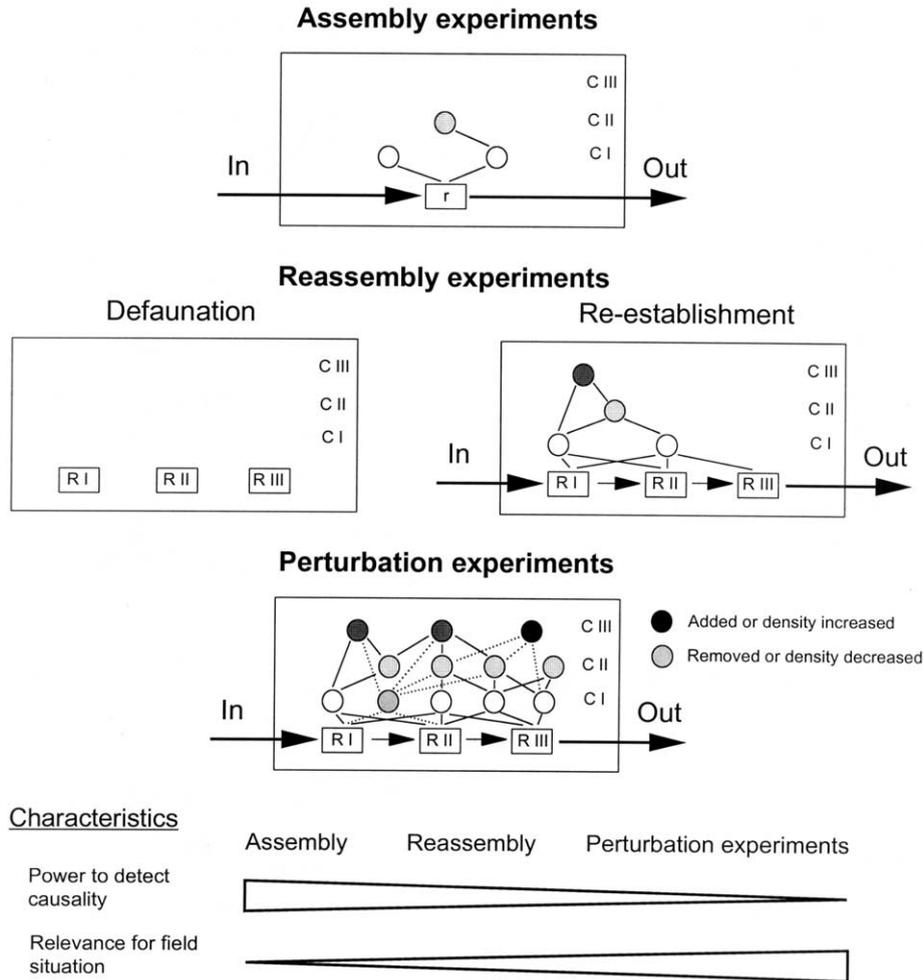


Fig. 5. Types of experiments to investigate soil food web interactions with two major inherent characteristics. CI, CII, CIII: consumer levels; r: artificial food resource; RI, RII, RIII: food resources (soil organic matter) changing due to the activities of decomposer organisms (from [66]).

certain level. As already stressed, manipulation of species and resources is exceptionally difficult in decomposer communities. Also, there may be serious difficulties in understanding the causalities responsible for observed changes in density of certain food web components. Due to the complexity of food web interactions and the associated large number of possible indirect effects (cf. [1,40,41,49,73]) tracking down biologically meaningful explanations is “complicated, challenging, fraught with peril” [87]; still, the experimental approach is the most promising for getting a deeper understanding of the structuring forces of real communities [24,50,53,71]; as stressed before [66], it is essential for a closer integration of soil ecology into general ecology to adopt this approach as the main tool for exploring food web relationships in soil communities. Soil ecologists certainly should respond to the quest for a contemporary ecological dimension in soil biology [79] by fostering experimentation.

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