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UNIVERSITY OF | JYVÄSKYLÄ

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To my parents, V & V

ABSTRACT

The aims of the thesis were to test current trophic-dynamic models and to find essential features of microbial-based soil food webs in order to formulate a verbal trophic-dynamic model for them. To achieve the aims I carried out experiments in microcosms filled with sterilised litter-humus mixture. Into microcosms I established simplified soil food webs of various structure containing bacteria and fungi (1. trophic level), bacterivorous and fungivorous nematodes (2. level), and a predatory nematode (3. level). I found that the biomass of microbivores was limited by predation in these food webs, i.e., it was top-down controlled, whereas grazing had a varying and substantially smaller effect on microbial biomass. Fungal biomass appeared to be donor-controlled, i.e., limited by resources only, while bacterial biomass was affected by both resources and grazing. The limitation of microbivore biomass by the predatory nematode did not affect microbial biomass or production, i.e., trophic cascades of biomass or production control did not occur. Microbial respiration was, however, increased when grazers were added, and mineralisation of C and N was loosely correlated with microbivore biomass. Increased microbial production tended to increase biomass at all trophic levels, meaning that all levels were bottom-up controlled. Refuges for microbes and microbivores in soil possibly caused the strong bottom-up control of the two lowest levels. Differences in microbivore diversity of three-level food webs affected significantly trophic interactions and led to idiosyncratic, or unpredictable, changes in trophic-level biomasses and nutrient mineralisation. The idiosyncracy of changes between the diverse and simple food webs followed from differences in microbivore characters — in their efficiency in resource utilisation and vulnerability to predation and competition. Trophic-level dynamics also differed between the bacterial and fungal channels, for bacterial and fungal biomasses responded differently to both grazing and energy addition. An omnivorous nematode, feeding on both bacteria and fungivore, did not substantially change trophic-level dynamics when compared with a food web containing a bacterivore. The results contradict trophic-dynamic models that predict limiting factors — resource availability and predation — to alternate at adjacent trophic levels, and support models predicting all levels to be limited by both resources and predation. Moreover, the results give evidence of discernible energy channels in soils, weak effects of omnivory on trophic-level dynamics and difficulties in predicting the consequences of declining species diversity.

Key words: Bottom-up vs. top-down control; energy channel; microbes; mineralisation; nematodes; omnivory; soil food web; species diversity; trophic level.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals. I have personally written all papers and performed most of the work.

I   Mikola, J. & Setälä, H. 1998. No evidence of trophic cascades in an experimental microbial-based soil food web. - Ecology (in press).

II   Mikola, J. & Setälä, H. 1997. Productivity and trophic-level biomasses in a microbial-based soil food web. - Manuscript (submitted).

III   Mikola, J. & Setälä, H. 1997. Relating species diversity to ecosystem functioning — mechanistic backgrounds and experimental approach with a decomposer food web. - Manuscript (submitted).

IV   Mikola, J. & Setälä, H. 1997. Interplay of omnivory, energy channels and C availability in a microbial-based soil food web. - Manuscript (submitted).

V   Mikola, J. 1997. Soil microcosms, random replicates, and testing of ecological theory. - Manuscript (submitted).

1   TROPHIC-DYNAMIC TRADITION OF ECOLOGY

Theories are what allow us to make sense of what we see.
Immanuel Kant

1.1   Fundamentals of the tradition

To determine what limits the abundance of populations within food webs, and to link the dynamics of populations and ecosystem functioning are primary tasks of contemporary ecology (Hunter & Price 1992, Power 1992, Jones & Lawton 1995, Persson et al. 1996). The trophic-dynamic tradition (Oksanen 1991), introduced by Hairston et al. (1960), tackles these tasks by reducing the complexity of food webs into trophic levels, and further by coupling the interactions within and between the levels to the functional properties of ecosystems. In this thesis I discuss six central models of the trophic-dynamic tradition: i.e., those by Hairston et al. (1960), Oksanen et al. (1981), Pimm (1982; pp. 16-17), Carpenter et al. (1985), McQueen et al. (1986), and Arditi & Ginzburg (1989). The models represent variable degrees of formality, provide an array of predictions, and were originally developed for different systems, but they all use trophic-level dynamics to explain the control of populations within food webs (see Table 1).

1.2   Control of trophic-level biomass and productivity

Hairston et al. (1960) were the first to propose that the factor limiting a population depends on the trophic level the population belongs to. They stated that in terrestrial ecosystems containing three trophic levels — plants, herbivores and carnivores — the

populations of plants and carnivores are limited by resources and those of herbivores by predation. According to their idea, terrestrial ecosystems are primarily top-down controlled and the limiting factors, resources and predation, alternate at adjacent trophic levels. Later on this verbal model was extended to systems with a varying number of trophic levels and was supplemented with an ecosystem-level concept, primary productivity (Fretwell 1977, 1987, Oksanen et al. 1981). The principle of alternating limiting processes at adjacent trophic levels, with the uppermost level always being limited by resources, remained the cornerstone of the model by Oksanen et al. (1981). Models were further improved by demonstrating that, besides limiting the biomass at lower trophic levels, upper levels can also control the productivity of these levels by affecting nutrient cycling (Carpenter et al. 1985, McNaughton 1985, Carpenter & Kitchell 1988, McNaughton et al. 1989).

TABLE 1   Central models of the trophic-dynamic tradition.

Model	Form of model	Characteristics of model
Hairston et al. 1960	verbal	• top-down control of trophic level biomasses • limiting factors (resources and predation) alternate at adjacent levels
Oksanen et al. 1981	mathematical	• *prey-dependent* prey-predator interactions • top-down control of trophic level biomasses • limiting factors alternate at adjacent levels • when productivity increases, stable-state biomass increases at resource limited levels only
Pimm 1982; pp. 16-17	mathematical	• levels are limited by resources only (=donor control)
Carpenter et al. 1985	verbal	• top-down control of *both* trophic level biomasses *and* productivity
McQueen et al. 1986	verbal	• all levels are limited by both resources and predation • top-down control is strongest at the top and bottom-up control at the bottom of food webs
Arditi & Ginzburg 1989	mathematical	• *ratio-dependent* prey-predator interactions • all levels are limited by both resources and predation • stable-state biomass responds to increasing productivity at all levels

In the Oksanen et al. (1981) model trophic interactions are represented by traditional prey-dependent prey-predator interactions (with logistic growth at the first level and Holling Type II functional responses at higher levels) in which the rate of consumption of preys by a predator is solely dependent on prey density. Prey-dependent trophic interactions give rise to the well-known prediction about the response of food web structure to increased primary productivity: that is, enrichment should lead to increased stable-state biomass at resource limited levels only, while the biomass at other levels should remain unchanged (Oksanen et al. 1981). Recently it has been argued, however, that prey-dependent interactions should be replaced by ratio-dependent interactions, in which the rate of consumption of preys by a predator depends also on the density of the predators (Arditi & Ginzburg 1989, Arditi et al. 1991, Hanski 1991, Ginzburg &

Akçakaya 1992, Akçakaya et al. 1995, McCarthy et al. 1995). Contrary to the basic prey-dependent models, which emphasise top-down control and alternating limiting factors, the ratio-dependent model by Arditi & Ginzburg (1989) predicts all trophic levels to be controlled by both resources and predation. Consequently, in ratio-dependent models stable-state biomass increases at all trophic levels with increasing productivity (Arditi & Ginzburg 1989). In the donor-control model by Pimm (1982; pp. 16-17) resources control biomass at all trophic levels whereas predation has no role in biomass control. Similarly to ratio-dependence, donor control leads to a simultaneous growth of biomass at all trophic levels after enrichment.

1.3 Species diversity, trophic interactions and ecosystem functioning

The loss of species has been documented in many ecosystems (Ehrlich & Wilson 1991, Pimm et al. 1995), and the consequences of declining species diversity are receiving increasing concern among ecologists (Schulze & Mooney 1994). Species diversity has never been explicitly incorporated in the trophic-dynamic tradition, however, and the trophic-dynamic models are therefore not usable to predict the influence of declining species diversity on trophic-level dynamics. On the contrary, trophic levels are in models principally assumed to be homogeneous, meaning that trophic levels should behave like single populations, and that all species occupying a trophic level should interact similarly with other levels (see however Hunter & Price 1992). Dynamics of heterogeneous trophic levels are known to differ from the dynamics of homogeneous levels (Leibold 1989, McCauley & Murdoch 1990, Leibold & Wilbur 1992, Abrams 1993), but since there is no evidence whether declining species diversity necessarily reduces the heterogeneity of trophic levels, trophic-dynamic models cannot predict whether diverse systems generally differ from simple systems with respect to trophic-level dynamics.

Changes in the functioning of ecosystems have, however, caused more anxiety among ecologists than the possible changes in the control of populations. An evidence of this concern are the three hypotheses recently formulated to elucidate the relationship between species diversity and ecosystem functioning: i.e., the redundant species hypothesis, the rivet hypothesis and the idiosyncratic response hypothesis (Lawton 1994, Lawton & Brown 1994, Vitousek & Hooper 1994, Johnson et al. 1996). The hypotheses provide testable predictions for the diversity-function relationship, but are still heuristic tools rather than real ecological theories (Lawton 1994). The problem is, how to link the interactions among populations to ecosystem functions, such as nutrient mineralisation or primary productivity, in order to provide mechanistic explanations for the hypotheses (Frost et al. 1995, Pace et al. 1995, Johnson et al. 1996). In this thesis I propose that the trophic-dynamic tradition can be applied when developing these hypotheses.

1.4 Energy channels and trophic interactions

An extreme type of heterogeneity within trophic levels is formed by channels through which energy and matter flow in an ecosystem. For instance, soil food webs are typically

composed of energy channels that originate from bacteria, fungi and plant roots, and merge at higher trophic levels (Moore & Hunt 1988, Wardle & Yeates 1993). Similarly to other types of heterogeneity, energy channels have a potential to complicate trophic-level dynamics if the nature of trophic interactions between the channels differs.

1.5 Omnivory and trophic interactions

Omnivores, or species feeding on several trophic levels, were earlier thought to be rare in food webs because omnivores make model food webs locally unstable (Pimm & Lawton 1978) and because real food webs seemed to have less omnivory than one could expect from chance (Pimm 1980, 1982). Due to this assumption the trophic-dynamic tradition paid little attention to omnivory (Oksanen 1991; see however Menge & Sutherland 1976, 1987). Recent surveys of food webs have, however, revealed that omnivores are common in various habitats (Moore et al. 1988, Sprules & Bowerman 1988, Hall & Raffaelli 1991, Polis 1991, Gunn & Cherrett 1993), and currently omnivores are suggested to form an important part of food webs, affecting also significantly trophic interactions (Polis et al. 1989, Polis & Holt 1992, Diehl 1993, Morin & Lawler 1995, Persson et al. 1996, Polis & Strong 1996).

Omnivory is problematic for trophic-dynamic models because it violates the distinctness of trophic levels. For instance, models predicting limiting factors to alternate at adjacent trophic levels become irrelevant in communities where a consumer is able to limit biomasses of prey at two or more levels (Polis & Holt 1992, Persson et al. 1996). However, clear trophic-level dynamics have also been found in systems dominated by omnivores (Power 1990, 1995), and some authors argue that omnivory does not necessarily eliminate trophic-level dynamics in food webs (Hairston & Hairston 1997).

2 EXPERIMENTAL APPROACH, METHODOLOGICAL JUDGMENTS AND CONCEPTUAL ISSUES

Experiments are the only means of knowledge at our disposal. The rest is poetry, imagination.

Max Planck

2.1 Below-ground food webs and soil microcosms

Most models (see, e.g., Table 1) contributing to the trophic-dynamic tradition have been developed for aquatic and terrestrial above-ground systems (see, however, the recent contribution by Zheng et al. 1997). As a result, the trophic-dynamic tradition has not been utilised in below-ground studies although soil systems provide opportunities to relate interactions among populations to ecosystem-level processes, such as decomposition and nutrient mineralisation (Parmelee 1995, Bengtsson et al. 1996, Vanni & de Ruiter 1996, Zheng et al. 1997). In the heterotrophic soil food webs of my experiments (see Fig. 1), the first trophic level contained bacteria and fungi, the second trophic level microbivorous nematodes and the third level a predatory nematode. Only microbes were able to exploit the energy bound to detritus, and therefore produced the living organic material used by higher trophic levels (comparable to plants in autotrophic systems).

Microcosm experiments are of great value when studying soil systems. The nature of interactions between microbes and their grazers, and the connection between mineralisation and biotic interactions have, for the most part, been revealed with microcosm experiments (see reviews by Coleman et al. 1983, Verhoef & Brussaard 1990, Verhoef 1996). The microcosms I used were composed of glass vials and cellulose plugs that prevented the contamination by alien organisms. The vials were filled with 2 g of leaf-humus mixture, and before starting the experiments microcosms were gamma

radiated to sterilise the soil. I established food webs (Fig. 1) using organisms from pure cultures (microbes and microbivorous nematodes) and soil samples (the predatory nematode). Detailed descriptions of the methods and materials of the four experiments are presented in the original papers I, II, III and IV.
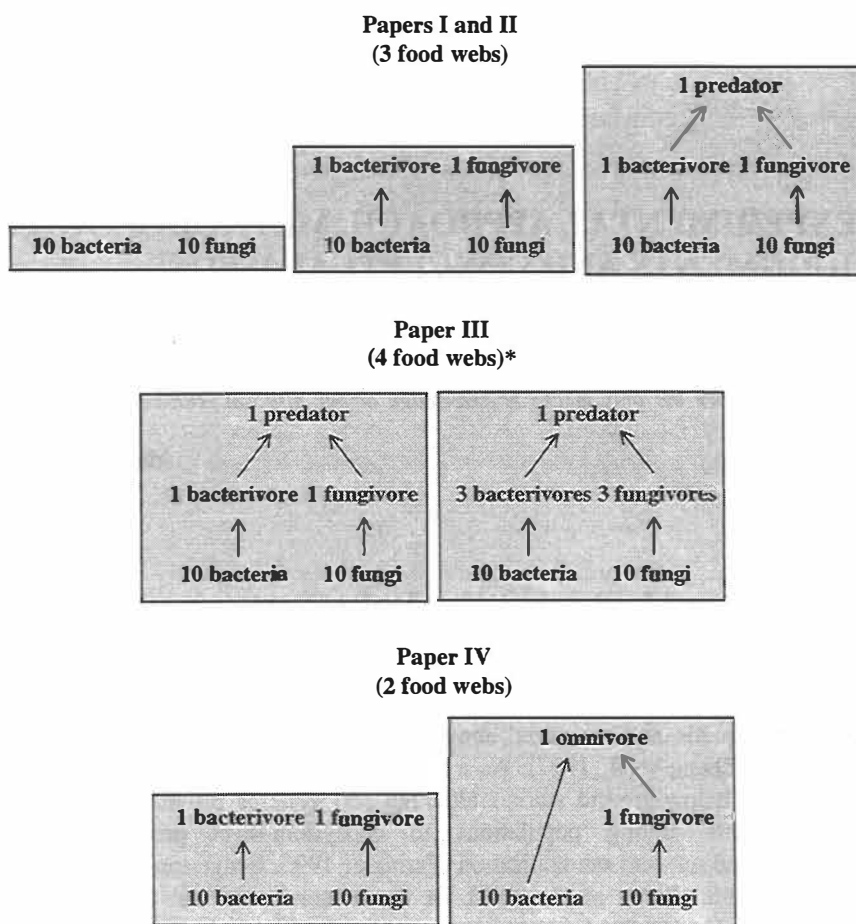

FIGURE 1   Graphical illustrations of the soil food webs used in the experiments of the original papers (*altogether three simple food webs with 1 bacterivore and 1 fungivore were established, each containing different microbivorous species). Arrows indicate feeding relationships.

2.2 Methodological value judgments

Ecology is full of methodological value judgments (Shrader-Frechette & McCoy 1993) and this thesis is not an exception. I therefore discuss the main judgments included in the experimental approach of the thesis.

Using microcosm food webs to simulate natural food webs is the first important methodological value judgment. To justify the use of microcosms, it is to be supposed that at least the main interactions, resource competition and predation, when occurring in microcosms, appropriately represent interactions occurring in the field. Main disadvantages of microcosm studies are that species diversity usually represents only a fraction of the diversity in the field, and that food webs seldomly achieve a stable state, thus breaking the common presupposition of stable-state food webs in mathematical models. On the other hand, the benefits derived from simplified model systems are also clear, i.e., exact measurements of processes and population dynamics which assure accurate tests of the ecological theory (see, e.g., Daehler & Strong 1996). Furthermore, since stable states seldomly occur anywhere else but in models, the unstable states of microcosm food webs cannot be considered highly artificial *per se*. Trophic-dynamic models have been successfully tested and developed in aquatic systems where equilibrium communities are neither usually attained (see, e.g., Carpenter & Kitchell 1988), implying that breaking the assumption of equilibrium — although undesirable — is not deleterious for the testing of trophic-dynamic models.

The second major methodological judgment concerns the estimation of microbial biomass in soil. I estimated the biomass of bacteria and fungi by measuring phospholipid fatty acid (PLFA) concentration in soil (see the method in Frostegård et al. 1991, Frostegård & Bååth 1996). The method is based on characteristic PLFAs in bacteria and fungi (reviewed by Vestal & White 1989, Tunlid & White 1992), which can be used as estimates for the biomass of these microbial groups. Critical questions for any indirect estimate of microbial biomass are: (i) whether the chosen estimate represents the proposed organisms only, and (ii) whether the estimate represents living biomass only.

To respond to the first question I determined PLFAs that would reliably represent the species of bacteria and fungi used in the experiments (see the species in I, III, IV). I made a preliminary experiment, in which I inoculated the species of bacteria and fungi as separate microbial groups into microcosms similar to those used in the main experiments. Three PLFA-analyses were then performed for both microbial communities during the following three weeks (four replicates each time), and those PLFAs whose amount increased only in the bacterial (16:1ω7t, cy17:0, 18:1ω7 and cy19:0) or only in the fungal community (18:2ω6 and 18:1ω9) were selected to represent bacterial and fungal biomass, respectively. I also took into consideration that after sterilization soil contains PLFAs bound to dead organic matter and, hence, measured how quickly these PLFAs decompose in soil. I determined the change in the amount of the selected four bacterial and two fungal PLFAs in fungal and bacterial communities, respectively, and found that the amount of the PLFAs did not decrease during a 3-wk incubation. Therefore, I assume that these stable PLFAs found in soil after irradiation do not interfere with *observing relative differences* in living microbial biomass between experimental treatments, as also suggested by Janzen et al. (1994), although they complicate *quantifying of absolute differences*.

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Using microbial respiration as an estimate of microbial productivity (I, II, IV) is the last main methodological judgment. The assumption of a positive relationship between microbial respiration and microbial productivity is based on numerous studies in soil systems, which imply that an increase in microbial respiration under non-stressed conditions is associated with an increase in microbial productivity (see Ingham et al. 1985, and references therein).

2.3 Defining the main concepts: top-down, bottom-up and donor control

In this thesis, I consider a trophic level to be top-down controlled if the biomass at the level depends on the presence of an adjacent higher level. Menge (1992) states similarly top-down control to "refer to situations where the structure (abundance, distribution, and/or diversity) of lower trophic levels depends directly or indirectly on trophic activities of higher trophic levels". Following the same logic, I call a level bottom-up controlled if the biomass at the level depends on the availability of its resources. Menge (1992) provides again a broader but consistent definition: "Bottom-up control refers to direct or indirect dependence of community structure on factors producing variation at lower trophic levels or in their resources". Finally, in a case the biomass at a level does not depend on the presence of an adjacent higher level, I consider the level to be donor-controlled [the same definition is achieved with Pimm's (1982) donor-control model]. Three circumstances thus may occur in food webs; (i) a trophic level is simultaneously bottom-up and top-down controlled (the relative importance of the two factors can vary), (ii) a level is purely top-down controlled, and (iii) a level is purely bottom-up controlled, i.e., donor-controlled. Alternatively, a trophic level can be defined to be donor-controlled also in a case its biomass depends on the presence of an adjacent higher level *if* the biomass does not depend on the higher-level *biomass* (DeAngelis et al. 1975, Chase 1996, Persson et al. 1996, Zheng et al. 1997). Because all formal donor-control models (DeAngelis et al. 1975, Pimm 1982, Chase 1996) make unrealistic and controversial assumptions about the characters of their food webs (Chase 1996, Persson et al. 1996), I define the concept of donor control simply to refer to situations where predators are unable to reduce the biomass of their prey. Importantly, since my definitions of the three concepts do not refer to any particular models, a trophic level can be considered bottom-up, top-down or donor-controlled irrespective of the mechanisms behind the control.

3 TROPHIC-LEVEL DYNAMICS IN MICROBIAL-BASED SOIL FOOD WEBS

If at any future time the facts are ascertained, then credence should be given to the direct evidence of the senses rather than the theories.

Aristotle

3.1 Aims of the thesis

The main objectives of this thesis were to test current trophic-dynamic models and to find essential features of microbial-based soil food webs in order to draw up a trophic-dynamic model for them. Specifically, I tried to clear up the importance of resources and predation in limiting trophic level biomasses and productivity in microbial-based soil food webs (I, II, IV), and to clarify the effects of omnivory (IV) and energy channels (I, II, IV) on trophic-level dynamics. Moreover, I aimed to provide mechanistic backgrounds for the hypothesised relationships between species diversity and ecosystem function, and to test both the suggested mechanisms and the hypotheses using a soil food web (III).

3.2 Control of trophic-level biomasses and microbial productivity

3.2.1 Top-down control

The models by Oksanen et al. (1981) and Carpenter et al. (1985) predict the biomass and productivity of trophic levels to be top-down controlled in food webs, and the top-down control to manifest itself as cascading trophic interactions. In the microbial-based soil

food webs of the studies described in this thesis the occurrence and strength of top-down control depended on the trophic level concerned, for microbial biomass was with variable success limited by the microbivores, whereas the predatory nematode constantly limited the biomass of the microbivores (I, II). Furthermore, no trophic cascades of biomass limitation occurred in any experiment, i.e., although the biomass of microbivores was reduced by the predatory nematode, this did not lead to an increasing microbial biomass (I, II). Trophic cascades of productivity control neither occurred. Microbivores generally increased microbial productivity when compared with pure microbial communities, but adding the third trophic level had no effect on productivity although the predator limited the biomass of microbivores (I, II).

The results match earlier findings in soil food webs. Third-level predators have usually reduced the biomass at the second trophic level, both in microcosms (Allen-Morley & Coleman 1989, Martikainen & Huhta 1990, Setälä et al. 1991, Brussaard et al. 1995) and in the field (Santos et al. 1981, Elkins & Whitford 1982, Parker et al. 1984), whereas the response of microbes to grazing has varied greatly. When grazed, the biomass of bacteria and fungi has either remained unchanged (Brussaard et al. 1995), decreased (Woods et al. 1982, Ingham et al. 1985, Allen-Morley & Coleman 1989) or increased (Bååth et al. 1981, Bengtsson & Rundgren 1983, Griffiths 1986, Faber et al. 1992, Hedlund & Augustsson 1995), which suggests trophic cascades of biomass control to be irregular in microbial-based soil food webs. One reason for the absence of trophic cascades is the high turnover rate of microbes (I). When energy is easily available, microbes can utilise the nutrients liberated by animals and increase their turnover rate, which results in an unchanged microbial biomass in spite of continuous grazing by microbivores.

In accord with my results (I, II), the respiration of microbes is frequently found to increase when the second trophic level is added into microbial communities, infering that nutrients excreted by animals are vital for continuous activity of microbes (reviewed, e.g., by Coleman et al. 1983, Ingham et al. 1985). In addition to microbivores, herbivores are also known to be able to increase the productivity of their resources by speeding up nutrient cycling (McNaughton 1985, Sterner 1986). Microbial- and plant-based food webs thus demonstrate that upper trophic levels are able to control the productivity at the first level, and that models lacking this indirect top-down control (such as Oksanen et al. 1981) may not properly predict biomass limitation or functioning in food webs. However, my results also show that even the model including nutrient cycling (Carpenter et al. 1985) cannot adequately explain the control of productivity in soil food webs. This is mainly because the model emphasises trophic cascades which seem to be absent in microbial-based food webs.

Mineralisation of C and N was loosely correlated with the biomass of microbivores (I, II), although exceptions for this rule were observed (III). Since the predatory nematode controlled the biomass of microbivores, mineralisation of C and N was also partly top-down controlled (I, II).

3.2.2 Bottom-up and donor control

According to the Oksanen et al. (1981) model, enrichment leads to increased biomass at trophic levels limited by resources, while biomass at other levels remains constant. The models by Arditi & Ginzburg (1989) and Pimm (1982; pp. 16-17) predict biomass to increase at all levels when productivity is increased, the former due to ratio-dependent

and the latter due to donor-controlled trophic interactions. In my microbial-based soil food webs higher microbial productivity tended to increase biomass at all trophic levels regardless of the number of levels present in the food web (II, IV). Simultaneous increase of biomass at all trophic levels does not support models with alternating limiting factors at adjacent trophic levels (i.e., Hairston et al. 1960, Oksanen et al. 1981, Carpenter et al. 1985), but on the contrary, is in accordance with models that predict all levels to be limited by resources (i.e., Pimm 1982, McQueen et al. 1986, Arditi & Ginzburg 1989, and several modified prey-dependent models).

Since the predatory nematode systematically reduced the biomass of microbivores (I, II), the simultaneous increase of biomass at all levels cannot be merely explained by donor-controlled trophic interactions. The unability of the microbivores to reduce the biomass of microbes (I, II), however, resembles donor control. Increased turnover rate, which probably is the main explanation for the constant microbial biomass, has not been considered to be a mechanism producing donor-controlled interactions (see DeAngelis et al. 1975, Pimm 1982, Chase 1996), and the formal donor-control model by Pimm (1982; pp. 16-17) predicting prey biomass not to depend on the presence of predators cannot be used when donor control is based on increased turnover rate. Nevertheless, increased microbial biomass in soil food webs after energy additions may be a reflection of donor-controlled microbial biomass.

Prey refuges, predator aggregation and predator interference are stated to be mechanisms leading to ratio-dependent trophic interactions (Arditi & Ginzburg 1989, Akçakaya et al. 1995). Prey refuges most probably exist in all soil systems, for microbes are known to partly grow in small soil pores inaccessible to protozoans and nematodes (Elliott et al. 1980, Rutherford & Juma 1992, England et al. 1993). Furthermore, as the diameter of the microbivores also was considerably smaller than the diameter of the predatory nematode in my experiments, a substantial part of microbes and microbivores probably lived in soil pores inaccessible to their respective predators, i.e., in circumstances capable to give rise to ratio-dependent prey-predator interactions (II). In addition to ratio-dependent models, a diverse assemblage of modified prey-dependent models has been constructed to explain the simultaneous growth of biomass at adjacent trophic levels (see, e.g., Diehl et al. 1993, Abrams 1994, Persson et al. 1996). For instance, when spatial heterogeneity of predator abundance, or prey refuges, is included in prey-dependent models, the models can account for the simultaneous increase of predator and prey biomass (Scheffer & de Boer 1995). Consequently, both the modified prey-dependent models (e.g., Scheffer & de Boer 1995) and the ratio-dependent model (Arditi & Ginzburg 1989) could provide an explanation for the results, but without further experiments it is impossible to infer which way is the correct one to model trophic-level interactions in microbial-based soil food webs. In any case, my results are in agreement with earlier studies showing that enhanced productivity frequently gives rise to increasing biomass at all trophic levels regardless of their location within food chains (McQueen et al. 1986, McNaughton et al. 1989, Pace & Funke 1991, Ginzburg & Akçakaya 1992, Rosemond et al. 1993, Schmitz 1993, Balciunas & Lawler 1995, Osenberg & Mittelbach 1996, Proulx et al. 1996, Brett & Goldman 1997).

McQueen et al. (1986) proposed a trophic-dynamic model for plant-based fresh-water pelagic systems. Their hypothesis states that top-down regulation of trophic levels is strongest at the top of the food web and weakens with every step down, and that bottom-up regulation is strongest at the bottom of the food web and weakens with every step up. My results support the McQueen et al. (1986) hypothesis notably well. Energy

addition, or bottom-up control, affected the biomass most significantly at the two lowest trophic levels (II, IV). Predation, or top-down control, limited clearly biomass at the second trophic level, but not uniformly biomass at the first trophic level (I, II). It seems that trophic interactions at the top and bottom of microbial-based soil food webs differ with respect to the ability of resources and consumers to affect each other's biomass, which suggests that models using uniform trophic functions to represent all trophic interactions within a food web fail in their predictions.

3.3 Microbivore diversity, trophic interactions and system functioning

I propose that the trophic-dynamic tradition, together with the concept of niche, can be applied when developing mechanistic backgrounds for the three hypotheses formulated to describe the diversity-functioning relationship — i.e., the redundant species, the rivet and the idiosyncratic response hypothesis (see Lawton 1994, Lawton & Brown 1994, Vitousek & Hooper 1994, Johnson et al. 1996). My reasoning is the following: if remaining species can modify their niches as other species disappear, productivity within their trophic level remains unchanged, whereas in the absence of niche modification productivity decreases. Decreased productivity within a trophic level reflects in the biomass and productivity at other levels as predicted by the trophic-dynamic models. Changes in biomass and productivity finally bring about changes in ecosystem functioning. In the redundant species hypothesis remaining species can modify their niches, and so functioning remains unchanged. In the predictable change hypothesis (my counterpart for the rivet hypothesis, see paper III), and in the idiosyncratic response hypothesis remaining species cannot modify their niches, which leads to predictable and unpredictable changes in functioning, respectively. Unpredictable changes are due to differences in the characters of species or due to indirect interactions between populations.

I tested the hypotheses and the suggested mechanisms using a soil food web with three trophic levels: microbes, microbivorous nematodes and a predatory nematode. I established one diverse (containing 3 bacterivores and 3 fungivores) and three simple (each containing 1 bacterivore and 1 fungivore) food webs (Fig. 1), and found that trophic-level biomasses varied in a idiosyncratic way between the diverse and the simple food webs, thus suggesting idiosyncratic responses also in functioning. The unpredictability of biomass results followed from the differences in microbivore characters — efficiency in resource utilisation and vulnerability to predation and competition. Changes in microbial respiration and total mineralisation of C and N, i.e., in the functioning of the system, were also idiosyncratic rather than redundant or predictable, although idiosyncracy was not as clear as in the case of trophic-level biomasses. Based on the results, it seems that predicting accurately the influence of declining species diversity on trophic-level dynamics and ecosystem processes is difficult unless the characters of species and the nature of their interactions are known. Supporting this idea, some recent studies have shown ecosystem processes to depend more on plant species and functional group composition than on plant species and functional group diversity (Wardle et al. 1997b, Hooper & Vitousek 1997).

The relationship between species diversity and ecosystem function has previously been studied mainly with plant communities (Naeem et al. 1996, Tilman et al. 1996, 1997, Hooper & Vitousek 1997, but see Naeem et al. 1994), without much consideration on the effects of plant diversity on other trophic levels. My results, however, show that declining diversity at one level can considerably affect the biomass at other trophic levels. When diversity of microbivores declined, not only their own biomass but also biomasses at other trophic levels were affected. Importantly, changes in biomass at one level also reflected in the functional parameters mainly accounted for by other levels.

3.4 Trophic-level dynamics in separate energy channels

At the bottom of the food webs the distinctness of the fungal and the bacterial channels was clearly discernible, for the two microbial groups responded differently to both microbivore grazing and energy addition (I, II, III, IV).

Fungivores could not reduce the abundance of fungi (I, II), whereas bacterial biomass was variably affected by their grazers; lowered in one experiment (II) and not affected in another (I). The species composition of fungivores had no effect on fungal biomass (III), while bacterial abundance was significantly affected by the species composition of their grazers (III, IV). Fungal biomass thus appeared to be clearly donor-controlled, whereas bacterial biomass was partly controlled by the bacterial feeding nematodes. Supporting my results, Wardle & Yeates (1993) concluded that fungi are limited by competition and bacteria by nematode grazing in cultivated soils. They suggested the difference to be mainly caused by the defences against grazing which fungi owe more than bacteria.

The effect of energy additions on bacterial and fungal biomass depended on the amount of energy supplied. When a modest amount of additional energy was provided, the biomass of both groups increased (II), whereas with greater amount of energy, fungal biomass increased and bacterial biomass decreased (IV). Greater amount of energy led to an extremely small concentration of ammonium-N in soil, in which conditions fungi seemingly were competitively superior to bacteria, and thus the only group able to benefit from the additional energy (IV). Similarly, Bååth et al. (1978) found that fungal biomass could be increased in soil by glucose additions, whereas both glucose and nitrogen were required to increase the biomass of bacteria.

My results give evidence of different trophic-level dynamics in the bacterial and fungal channel. The two channels differ at the bottom of food webs, i.e., with respect to interactions between microbes and their resources, and microbes and their grazers, whereas they do not differ with respect to interactions between microbivores and their predators. Consequently, the results are in good accordance with earlier conclusions about energy channels in soil food webs (Moore & Hunt 1988, Wardle & Yeates 1993), and show the importance of acknowledging food web compartments when applying trophic-dynamic models in soil systems.

3.5 Effects of omnivory on trophic-level dynamics

To study omnivory I established two food webs: the first contained fungi, bacteria, a fungivorous nematode and a bacterivorous nematode, and the second fungi, bacteria, the fungivore and an omnivorous nematode feeding on both the bacteria and the fungivore (Fig. 1, IV). The basic difference between the food webs thus was the number of trophic levels within the fungal channel; two in the presence of the bacterivore and three in the presence of the omnivore.

The omnivore did not considerably change trophic-level dynamics in the food web (IV). Firstly, its influence on the biomass and dynamics of the fungivore population did not reflect in the biomass of fungi. Secondly, the fungal channel did not respond differently to the increased productivity in the two food webs although the number of trophic levels within the channel differed. However, the omnivorous feeding habit seemed to reduce the grazing pressure of the omnivore on bacterial biomass as compared with the bacterivore. The results show, as Hairston & Hairston (1997) suggested, that omnivory does not necessarily eliminate trophic-level dynamics in food webs, and that food webs containing omnivores may produce similar trophic-level dynamics to food webs made up of distinct trophic levels.

3.6 Generality of results?

Studies seeking the diversity-functioning relationship have recently raised a question, how to select species for treatment levels to represent different food web structures. Studies using non-randomly selected sets of species to represent diversity levels (e.g., Naeem et al. 1994) have been argued to be unable to distinquish the effect of species diversity *per se* from the effect of specific species combinations (André et al. 1994, Huston 1997). In response to this criticism, randomly selected dissimilar replicates within diversity levels have become common in biodiversity studies (see Naeem et al. 1996, Tilman et al. 1996, 1997, Wardle et al. 1997a).

The difficulty of separating the effect of a particular species combination from the effect of a food web characteristic exists in all studies inquiring into the effects of structural changes in food webs. Most food web studies, apart from the biodiversity studies, would therefore benefit from randomly selected replicates (V). The idea of random replicates, as a methodological improvement in experimental food web ecology, emerged not until I performed the experiments included in this thesis, and consequently had no influence on my experimental set-ups. When weighed afterwards, the generality of my results would have improved if the replicates had been created randomly from the available pool of species (10 bacteria and 10 fungi, 3 bacterivores and 3 fungivores), especially as the characters of species, and indirect interactions between species, appeared to greatly affect trophic interactions (III).

4 FORMULATION OF A TROPHIC-DYNAMIC MODEL FOR MICROBIAL-BASED SOIL FOOD WEBS

Whenever one lights upon more exact proofs, then we must be grateful to the discoverer, but for the present we must state what seems plausible.

Aristotle

Based on the results of this thesis the following verbal trophic-dynamic model for microbial-based soil food webs can be formulated:

1. Microbial productivity increases when microbial grazers are added.

2. Changes in the biomass at the third or higher levels of a food web have no cascading effects on the biomass and productivity at the microbial level, whereas increase in microbial productivity leads to increased biomass at all trophic levels.

3. The biomass of fungi and top predators is mostly limited by resources, whereas the biomass of bacteria and intermediate trophic levels, e.g., microbivores, is limited by both resources and predation.

4. Declining species diversity of microbivores leads to idiosyncratic changes in trophic interactions and nutrient mineralisation, at least in food webs with a moderately low number of species.

YHTEENVETO

Trofiatasojen vuorovaikutukset ja säätely maaperän mikrobipohjaisissa ravintoverkoissa

Tutkimusteni tarkoitus oli maaperän ravintoverkkoja apuna käyttäen kokeellisesti testata vesi- ja maaekosysteemeihin kehitettyjä trofiatasojen vuorovaikutuksia kuvaavia malleja. Tarkoitukseni oli lisäksi etsiä maaperän mikrobipohjaisten ravintoverkkojen olennaisia piirteitä, joiden avulla voisin hahmotella niitä kuvaavan sanallisen trofiatasomallin. Käytin kokeissa yksinkertaisia mikrokosmoksia, jotka oli rakennettu lasipullosta ja pullon sulkevasta selluloosatulpasta. Täytin mikrokosmokset puolilleen humuksen ja koivunlehtikarikkeen seoksella, joka oli säteilytetty maassa luonnostaan elävien eliöiden tappamiseksi. Perustin humuksen ja karikkeen seokseen yksinkertaisia ravintoverkkoja orgaanista ainetta hajottavista bakteereista ja sienistä (1. trofiataso), niitä syövistä sukkulamadoista (2. trofiataso) ja muita sukkulamatoja syövästä sukkulamatopedosta (3. trofiataso).

Havaitsin kokeissa, että saalistus sääteli mikrobeja syövien sukkulamatojen biomassaa, kun taas mikrobien biomassaan laidunnus vaikutti vähemmän ja vaihtelevammin. Sienten biomassaa sääteli ainoastaan resurssien saatavuus mutta bakteerien biomassaa rajoitti myös laidunnus. Vaikka sukkulamatopeto pystyi rajoittamaan mikrobinsyöjien biomassaa, tällä ei ollut vaikutusta mikrobibiomassaan tai -tuotantoon. Toisin sanoen, ylimmän tason vaikutus toisen trofiatason biomassaan ei heijastunut alimmalle tasolle. Kun mikrobinsyöjät laidunsivat mikrobeja, mikrobihengitys oli suurempaa kuin mikrobien kasvaessa yksin, ja lisäksi hiilen ja typen mineralisaatio oli keskimäärin sitä suurempaa mitä suurempi oli mikrobinsyöjien biomassa. Lisääntynyt mikrobituotanto johti suurempaan biomassaan kaikilla trofiatasoilla. Maan rakenteen mikrobeille ja mikrobinsyöjille tarjoamat suojapaikat todennäköisesti vähensivät saalistuksen merkitystä kahden alimman tason säätelyssä ja korostivat näiden tasojen selvää resurssirajoitteisuutta. Mikrobinsyöjien lajistollisen monimuotoisuuden muutos vaikutti trofiatasojen välisiin vuorovaikutuksiin ja johti trofiatasojen biomassojen ja ravinnemineralisaation epäennustettaviin muutoksiin. Lajidiversiteetin pienenemisen epäennustettavat seuraukset johtuivat mikrobinsyöjien ravinnonhyödyntämistehokkuuden, kilpailukyvyn ja saalistuksensiedon eroista. Trofiatasojen väliset vuorovaikutukset olivat erilaiset bakteereista ja sienistä alkavissa energiakanavissa, sillä sekä laidunnus että energian saatavuus vaikuttivat eri tavalla bakteerien ja sienten biomassaan. Omnivori sukkulamato, joka pystyi bakteerien ohella syömään myös muita sukkulamatoja, ei merkitsevästi vaikuttanut trofiatasojen biomassoihin tai vuorovaikutuksiin, kun tilannetta verrattiin yhteisöön, jossa omnivorin tilalla oli ainoastaan bakteereja syövä sukkulamato.

Kokeitteni tulokset ovat ristiriidassa niiden trofiatasojen vuorovaikutuksia kuvaavien mallien kanssa, jotka ennustavat resurssien saatavuuden ja saalistuksen vaihtelevan rajoittavana tekijänä peräkkäisillä trofiatasoilla, ja tukevat malleja, joissa kaikkien tasojen biomassaa rajoittavat sekä resurssien saatavuus että saalistus. Lisäksi tulokset antavat viitteitä maaperässä olevista selkeästi eriytyneistä energiakanavista, omnivorian vähäisestä vaikutuksesta trofiatasojen vuorovaikutuksiin ja vaikeudesta ennustaa lajiston köyhtymisen seurauksia.

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Original papers

I

No evidence of trophic cascades
in an experimental microbial-based soil food web

by

Juha Mikola and Heikki Setälä

Ecology (in press), 1998

II

Productivity and trophic-level biomasses
in a microbial-based soil food web

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Manuscript (submitted)

III

Relating species diversity to ecosystem functioning
— mechanistic backgrounds and experimental approach
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IV

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V

Soil microcosms, random replicates,
and testing of ecological theory

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