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# Transitory dynamic effects in the soil invertebrate community in a temperate deciduous forest: Effects of resource quality

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**Abstract**

The importance and strength of bottom-up forces in terrestrial soil systems are poorly understood. In contrast to aquatic systems, where trophic cascades and top-down forces dominate, it has been postulated that terrestrial systems are regulated mainly by bottom-up forces. We set up a 17 month field experiment to study the effects of addition of resources of different quality (wood, wheat bran, pet food, and glucose + phosphorous + nitrogen) on the soil micro-, meso- and macrofauna as well as on microbial biomass, ergosterol content and abiotic parameters (soil pH, water content, carbon and nitrogen content) in a beech forest (*Fagus sylvatica*) on sandstone. We hypothesized that bottom-up effects will be strong on lower trophic levels resulting in increased biomass of bacteria and fungi, and that this increase will propagate to higher trophic levels (microbivorous invertebrates, predators) but with decreasing intensity due to dampening of bottom-up forces at higher trophic levels by high connectivity, trophic-level-omnivory and generalist feeding. The results of the study in general did not support these hypotheses. Microbial biomass only moderately increased after resource addition, and while densities of several animal groups increased (lumbricids, nematodes, collembolans, gamasid mites, staphylinid beetles), densities of other groups declined (oribatid mites, prostigmate mites, lithobiids), and a large number of taxa remained unaffected (enchytraeids, diplopods, uropodine mites, pseudoscorpions, spiders). We conclude that (a) bottom-up forces are of limited importance in the soil system of temperate deciduous forests, (b) large primary decomposers, such as earthworms, do not depend on microorganisms as food but consume organic matter directly, (c) the link between microorganisms and microbivores, such as collembolans, is weak since collembolan density increased even though microbial biomass was unaffected, (d) habitat modification by ecosystem engineers, such as earthworms, is more important than resource availability for a number of soil invetebrates including prostigmate mites and centipedes, and (e) the soil food web in general is rather resistant responding little to changes in resource supply. The results also suggest that species which commonly are assigned to single trophic groups, such as collembolans, differently respond to changes of the base of the food web. Increased fungal biomass led to an increase in the density of *Folsomia quadrioculata* s.l. and *Isotomiella minor*, whereas the increased bacterial biomass was accompanied by an increase in density of *Ceratophysella denticulata* and *Isotoma notabilis*.


*Keywords:* Transitory dynamics; Bottom-up control; Oribatid mites; Collembolans; Nematodes; Earthworms; Gamasid mites; Staphylinids; Lithobiids

## 1. Introduction

Both bottom-up and top-down forces are structuring animal and plant communities, but it is debated which of these forces predominate in ecological systems and how strong they are (McQueen et al., 1989; Hunter and Price, 1992; Peterson et al., 1993; Moran and Scheidler, 2002). It is also disputed how far up in the food chain bottom-up cascades (sensu, Hunter and Price, 1992) extend and how

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strong effects from the top influence trophic levels at the base of the food web (Menge, 1992; Power, 1992; Strong, 1992; Halaj and Wise, 2001). It has been proposed that in aquatic systems top-down forces predominate forming trophic cascades (Paine, 1980, 1988; Carpenter et al., 1985) where predators function as indirect mutualists for food organisms of their prey (Schoener, 1993; Menge, 1995; Schmitz et al., 1997; Persson, 1999). Alterations at high trophic levels may be transferred to lower trophic levels without reduction in intensity (Townsend, 2003).

Top-down cascades also occur in terrestrial systems (Spiller and Schoener, 1990; Hunter and Price, 1992; Strong, 1992; Schmitz et al., 1997) including species-poor agricultural systems (Riechert and Bishop, 1990) but also complex and species-rich systems, such as temperate and tropical forests (Altegrim, 1989; Letourneau and Dyer, 1998) and soil communities (Strong et al., 1999). However, compared to aquatic systems, bottom-up cascades appear to dominate in terrestrial systems (White, 1978; Polis, 1994; Polis and Strong, 1996). Due to intraguild predation, omnivory and high connectivity terrestrial food webs buffer cascading effects (Polis, 1991; Hunter and Price, 1992; Strong, 1992; Mikola and Setälä, 1998; Halaj and Wise, 2002) and result in 'trophic trickles' rather than trophic cascades (Strong, 1992; Halaj and Wise, 2001; Dawes-Gromadzki, 2002; Dyer and Letourneau, 2003).

In below-ground systems, bottom-up forces appear to dominate (Ponsard et al., 2000), however, few studies have investigated if resources or consumers are more important (Slobodkin et al., 1967; Heal and Dighton, 1985; Hunt et al., 1987). The main argument for the dominance of the resource control is that litter does not accumulate and therefore the systems need to be bottom-up controlled (Hairston et al., 1960). However, this argument is only valid for saprophytic bacteria and fungi and for animals that feed directly on decomposing litter (Anderson and Domsch, 1978; Wardle, 1992; Gallardo and Schlesinger, 1994); it does not apply for animals feeding on bacteria, fungi and algae or for higher level consumers. Bottom-up forces have been reported to structure the density and community structure (=species richness and dominance) of some groups of the soil macrofauna in a mull beech forest (Göttinger Wald, Germany; Scheu and Schaefer, 1998) but not to affect the density and community structure of the soil mesofauna in the same experiment (Maraun et al., 2001). Presumably, the increase in earthworm density indirectly affected the soil mesofauna via competition for resources and habitat destruction in that experiment (Maraun et al., 2003b). These effects of large ecosystem engineers, such as earthworms, alter the whole soil food web and may override bottom-up and top-down forces. Therefore, we set up an experiment in an acidic beech forest where earthworms are scarce to avoid the possibility that experimentally increased densities of these large detritivores override trophic responses. By adding resources with different nitrogen content we investigated the role of resource quality for controlling the soil invertebrate community. The resources included wood, a mixture of glucose, nitrogen and phosphorous, pet food and wheat bran ranging in C-to-N ratio from 1080 to 18. A shortcoming of bottom-up experiments is often the way in which resources are added. If resources are added as particulate materials (Judas, 1990; Chen and Wise, 1997), the amount of resources is increased but also the size of habitable space making the separation of these two effects difficult. We therefore added the resources as powder which was dissolved in water to minimize habitat changes and hypothesized that resources with high C-to-N ratios will predominantly promote the fungal food chain, whereas resources with low C-to-N ratios will predominantly promote the bacterial food chain. We investigated the response of the three major components of the soil food web to the addition of resources: microorganisms, animal decomposers (Lumbricidae, Diplopoda, Collembola, Oribatida, certain taxa of Nematoda) and predators (Staphylinidae, Aranaeida, Lithobiidae, Pseudoscorpionida, Prostigmata, Uropodina, Gamasina, certain taxa of Nematoda).

## 2. Materials and methods

### 2.1. Study site

The study site is located 50 km northwest of Göttingen in the Solling forest, a 135-yr-old beech forest (*Fagus sylvatica* L.) in Lower Saxony (Germany). In the forest the herb layer is poorly developed and consists mainly of *Luzula luzuloides*, *Avenella flexuosa*, *Oxalis acetosella* and *Polytrichum* mosses (Ellenberg et al., 1986). The Solling is a mountain range of about 400 $km^2$ at 500 m a.s.l. Parent rock is red sandstone which at the study site is covered with a loess layer of about 1 m. The soil type is an acidic Cambisol with the humus form moder. Litter and soil pH are low (3.0 and 3.4, respectively). The average annual precipitation is 1045 mm and the average annual temperature is 6.5 °C (Ellenberg et al., 1986). The experiment was conducted at a fenced site where trees have not been harvested during the last 40 years.

### 2.2. Experimental design and sampling

In April 1997 circular experimental plots of 1 $m^2$ were established in the forest using plastic fences of 40 cm height. The fences were dug into the soil to a depth of 5 cm. Five treatments were established: watered control (ctr), wood, CNP (addition of carbon, nitrogen and phosphorous), pet food (pf) and wheat bran (wb). The CNP medium consisted of glucose, $NH_4NO_3$ and $NaH_2PO_4$ dissolved in 6 l of deionised water. The amount of C, N and P in the CNP solution added was equivalent to five times the annual litter input (1120 g C, 36 g N, 2 g P). The organic materials