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ORIGINAL PAPER

Collembolans feeding on soil affect carbon and nitrogen mineralization by their influence on microbial and nematode activities

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Abstract We manipulated Collembola *Folsomia candida* Willem density and observed the density effect on carbon and nitrogen mineralization and on nematodes in microcosms filled with mineral soil. Collembolan densities were 0 (control), 25 (low), 100 (medium), and 400 (high) individuals per microcosm. The Collembola enhanced soil respiration and nitrogen mineralization rate in a density-dependent manner ($P<0.05$). The correlation between collembolan density and the metabolic quotient of microbes, qCO_2, was weakly positive ($r=0.44$, $P<0.05$). Collembola did not affect microbial biomass. These results suggested that enhanced carbon and nitrogen mineralization was an indirect effect of Collembola mediated by increased microbial activity. Collembola changed the C_{nema}/C_{mic} ratio, but only when present at the low density. Thus, Collembola had both positive and negative effects on the nematode population. The positive impact probably depends on the enhancement of microbial activity due to Collembola grazing behavior, while the negative effect appears to result from predation of nematodes.

Keywords Collembola · Mineral soil · Nitrogen mineralization · Microbial biomass · Feeding on nematode

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Introduction

Collembola constitute a large proportion of the soil mesofauna in some soil types where they appear to significantly affect nutrient flux. Microcosm experiments are very useful to study the effects of Collembola on nutrient cycling (Setälä and Huhta 1991; Bardgett and Chan 1999) and microbial composition (Hanlon and Anderson 1979; Bakonyi 1989; Hyvönen and Persson 1996).

Litter has been the preferred experimental substrate in studies on the interaction between Collembola and microbes, especially fungi (Hanlon and Anderson 1979; Bakonyi 1989; Bardgett et al. 1993), because of their high abundance in mor and moder type soils, and the fungivorous feeding habit of collembolans (e.g., Hunt et al. 1987). Thus, results of collembolan effects in the previous studies were mainly those of a litter system.

Collembola also inhabit mull type forest soils and sometimes reach high population densities in agricultural soils (Larink 1997). Kaneda and Kaneko (2002) found that low contents of organic matter in soil promoted growth of *Folsomia candida*, as carbon content generally decreases from the top layer to the mineral layer. For soil-dwelling Collembola, mineral soil systems appear to provide suitable living conditions. The ratio of fungal biomass to total microbial biomass in the litter layer is generally higher than in mineral soil, and the decomposition rate of organic matter in the litter layer is slower than in mineral soil (Holland and Coleman 1987). Thus, the energy flow would be quite different in litter and mineral soil. Therefore, Collembola probably affect nutrient cycling in different ways among litter and mineral layers by controlling the composition of the decomposer communities and, thus, the decomposition rates. Moreover, Lussenhop (1996) showed a significant collembolan role in agricultural systems.

Lussenhop (1996) studied the effects of collembolan density on nodule number and relative length of root infected by mycorrhizae in agricultural ecosystems, showing that Collembola mediated the effects of root symbionts (mycorrhizae and rhizobia) on leaf tissue nutrient concentration. At low availabilities of soil P, moderate collembolan densities enhanced mycorrhizal effects on plants, whereas high densities reduced these effects. These results demonstrated the critical function of Collembola for plant production. There is a need to better understand the effect of Collembola on nutrient cycling in mineral soil systems to completely understand the role of Collembola in soil ecosystems.

Although the effects of collembolan predation on nematode and protozoan communities have received little attention (example, Hunt et al. 1987; Bardgett and Chan 1999), Collembola are known to feed not only on bacteria and fungi but also mineral soil particles, organic matter, protozoa, and nematodes. Scheu and Setälä (2002) called these aggregated foods a resource unit. Collembola directly feed on nematodes (Gilmore 1970; Lee and Widden 1996), whereas they may stimulate nematode growth through enhancing microbial activity and biomass; thus, they may change microbivorous nematode biomass indirectly. As nematodes are also a key component in soil ecosystems, it is important to understand the linkage between Collembola and nematodes.

Klironomos and Kendrick (1995) showed *F. candida* was found over a wide range of soil depths, from the litter layer to 30 cm, and Faber (1991) defined *F. candida* as a hemi- and euedaphic Collembola which lives in raw humus and mineral soil. Therefore, it is reasonable to use *F. candida* in studying collembolan effects on nutrient cycling in mineral soil systems.

We manipulated collembolan density. Collembolan density fluctuates due to abiotic environmental factors and species interaction in soil. Additionally, nonlinear collembolan effects against their density were observed. For example, fungal respiration and mycorrhizal infection followed a bell-shaped response curve when plotted against collembolan density (Hanlon 1981; Gange 2000; Bakonyi et al. 2002). Thus, an investigation of the relationship between collembolan density and their impact intensity is necessary. A wide range of possible densities was used because collembolan number is sometimes more than 100,000 individual m^{-2} in agricultural systems (Larink 1997).

Materials and methods

Origin of test animal and soil

Two strains of *F. candida* were used. Strain 1 used for feeding experiments was obtained from Dr. M. Hasegawa (Showa University, Japan). Strain 2 was isolated from the soil of the arboretum of Shimane University (ca. 33 m above sea level, 35°28′N and 133°5′E) using a Tullgren funnel for microcosm experiments. The Collembola were cultured in an incubator at 22.5°C in the dark and fed with Baker's yeast. Soil material [Umbric Andosols according to Food and Agriculture Organization (FAO) classification] was collected from a deciduous broad-leaved forest, dominated by 35-year-old *Cornus controversa* Hemsley and *Zelkova serrata* (Thune.) Makino on the campus of Yokohama National University (57 m above sea level), Yokohama, Japan (35°28′N and 139°36′E).

Experimental procedures

Soil was collected from a 5 cm depth after removing the overlying organic layers. After coarse organic matter and stones were picked out, the soil was sieved (<2 mm) and defaunated by freezing for 24 h at −20°C. After thawing, the soil was inoculated with a suspension (10 ml per 1 kg) prepared by mixing 60 g sieved soil from the same site with 300 ml of deionized water. Glucose was added at 0.5 mg per 1 g soil in solution. The maximum water-holding capacity of the experimental soil was determined (Öhlinger 1995), and the actual water content was adjusted to 55% of this value by adding deionized water. After preparation, the soil samples were incubated for 7 days at room temperature.

Experimental systems

Collembolan feeding test

Nematodes were extracted from the soil to feed Collembola. This experiment was conducted using a sterol box (width 6 cm, height 3 cm) which was filled with a mixture of plaster of Paris and activated charcoal with a membrane filter on the surface of the substrate. Five nematodes were placed on the membrane filter and then ten Collembola of strain 1 were added. Seven of these boxes for each treatment were incubated at 25°C, and nematodes were counted 24 h after the Collembola had been introduced.

Collembolan effects on the soil system

Air-tight microcosms consisted of three layers that were made of a polycarbonate tube (10.6 cm diameter). The upper 2 cm layer was covered with a polycarbonate lid. The middle layer also was 2 cm high and had a gauze bottom to suspend a cup containing 30 ml of 1 N NaOH for soil respiration measurements, while the bottom layer was 7 cm high with a polycarbonate bottom. Thirty grams moist soil was put into the microcosm. Collembola (*F. candida*) were added at 0, 25, 100, and 400 individuals per microcosm

(zero, low, medium, and high density, respectively). There were six replicates of each microcosm experiment. The microcosms were kept at 20°C during the 10-day experimental period.

Measurements

Soil pH, total carbon, and nitrogen content of the initial soil were measured on the day the samples were taken. Soil total carbon and nitrogen content were determined using an NC ANALYZER (NC-95A, SHIMADZU, Kyoto, Japan). Soil pH was determined in a 2.5:1 (*v*/*w*) aqueous suspension. Microbial C was measured by the fumigation–extraction method (Vance et al. 1987) using 5 g (wet weight) of the soil. After fumigation with chloroform in the dark for 24 h, soil samples were transferred to 100-ml Erlenmeyer flasks and extracted with 50 ml 10% KCl for 30 min using a horizontal shaker at 170 rpm. The ratio of extract to soil (dry weight) was roughly 10:1 (*v*/*w*). The suspension was filtered, and organic C was determined using a total organic carbon (TOC) analyzer (TOC-5000A, SHIMADZU, Kyoto, Japan). Microbial C was calculated as the difference of extractable C in the fumigated and non-fumigated samples, using a conversion factor of 2.04 (Inubushi 1997). Dissolved organic carbon (DOC), ammonium, and nitrate were measured in the nonfumigated sample extracts. DOC was determined using the TOC-5000A analyzer. Nitrate was calculated from the difference of UV absorption at 210 nm before and after reduction of nitrate to nitrite (Kandeler 1995). Ammonium was measured using the indophenol-blue absorption (635 nm) method (Hidaka 1999). Soil respiration was measured by titration of 30 ml 1 N sodium hydroxide with 0.1 N HCl. The metabolic quotient, qCO_2 (μg CO_2–C respired h^{-1} μg^{-1} C_{mic}), was calculated from the biomass at the end of the experiment and the respiration data. The ratio of nematode carbon (C_{nema}) and microbe C (C_{mic}) was calculated according to Aescht and Foissner (1995). Nematode biovolume was estimated based on the average length and diameter of ten individuals collected at the end of the experiment. Microbial C, DOC, ammonium, nitrate, and nematode number were determined at the start and end of each experiment.

Statistical analysis

Chemical and biological soil characteristics were expressed on the basis of the oven-dry (105°C) weight. The nematode feeding test was analyzed using the Mann–Whitney test. The effects of collembolan density on soil respiration, nitrogen mineralization, and microbial biomass were evaluated by one-way analysis of variance (ANOVA), and Tukey–Kramer's honestly significant difference test. The effect of collembolan density on the C_{nema}/C_{mic} ratio was evaluated by the Kruskal–Wallis test and the Steel–Dwass significant difference test. Effects of collembolan and nematode densities on soil respiration rate, nitrogen mineralization rate, and qCO_2 were evaluated by regression analysis. The Steel–Dwass test was conducted using StatLight (Yukms, Tokyo, Japan), while all other tests were performed using Stat View 5.0J (SAS Institute, Cary, NC, USA).

Results

Collembola affected nematode number in the simply structured, basically two-dimensional environment provided in our experiments ($P<0.05$; Table 1). Nematode numbers were reduced by about 90% in 24 h when Collembola were present.

Initial soil pH, total carbon, and total nitrogen of the experimental soil were 5.82, 202 mg g^{-1} and 13.7 mg g^{-1}, respectively. Nematode numbers at the beginning were 19.5±1.6 g^{-1} (mean±SE $n=6$), and the means at the end of the experiments were 37.2±3.2 g^{-1} ($n=6$), 64.6±15.6 g^{-1} ($n=5$), 39.9±5.5 g^{-1} ($n=6$), and 46.3±7.9 g^{-1} ($n=6$) in the 0, 25, 100, and 400 collembolan treatments, respectively (mean±SE). DOC concentration at the beginning was 311±1 μg g^{-1} (mean±SE $n=6$), and the means at the end of the experiments were 306±12, 300±6, 299±7, and 311±5 in the 0, 25, 100, and 400 collembolan treatments, respectively (mean±SE $n=6$). The concentration of DOC did not change during the experiments irrespective of the treatment.

Collembola increased soil respiration depending on population density (Fig. 1); soil respiration in the high density experiment differed significantly ($P<0.05$) from all others. Collembola also accelerated nitrogen mineralization in a density-dependent manner (Fig. 2); there were significant ($P<0.05$) differences between the rate of nitrogen mineralization in the control and low-density tests, as compared to the medium- and high-density ones and between medium- and high-density experiments. The relationships between collembolan density to soil respiration and nitrogen mineralization showed a strong positive correlation ($r=0.87$, $P<0.05$ and $r=0.94$, $P<0.05$, respectively). Collembola, however, did not affect microbial biomass (Fig. 3), which tended to decrease towards the

Table 1 Number of nematodes remaining in the test chamber after 24 h with or without Collembola (mean±SD)

Collembola	With	Without
Nematode number ($n=7$)	0.43±0.79	4.57±0.53

The values are significantly different ($P<0.01$) in the Mann–Whitney test.

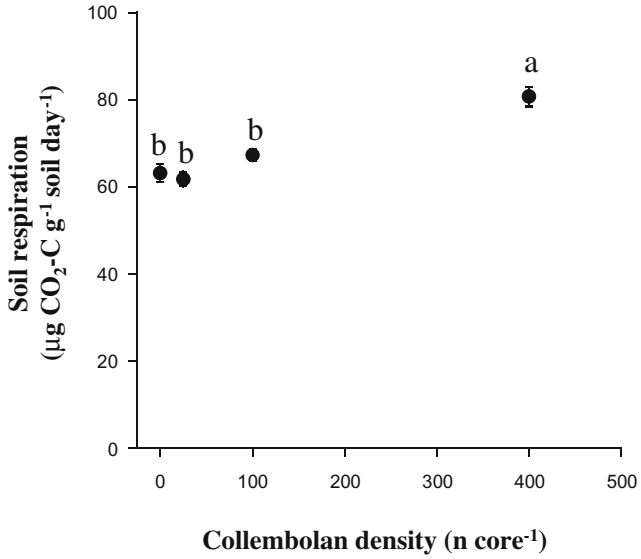

Fig. 1 Effects of collembolan density on soil respiration rate. Data are means±SE; n=6. Values highlighted by identical letters are not significantly different (P<0.05) in the Tukey–Kramer test

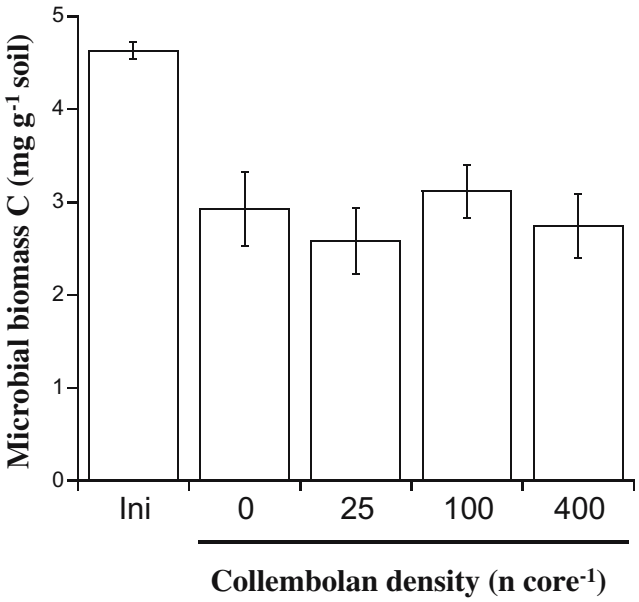

Fig. 3 Effects of collembolan density on microbial biomass. Data are means±SE; n=6. *F. candida* were added at rates of 0, 25, 100, and 400 individuals per microcosm. *Ini* Start of the experiment

end of the experiments in all treatments. A weak relationship was detected between qCO_2 and collembolan density (r=0.44, P<0.05). The C_{nema}/C_{mic} ratio peaked at low collembolan density (Fig. 4). No correlations were observed between nematode density at the end of the experiment and nitrogen mineralization or any biological parameters.

Discussion

Collembola increased nitrogen mineralization, soil respiration, and qCO_2 in a density-dependent fashion. On the other hand, microbial C remained unaffected. Thus, Collembola increased microbial activity without significant changes in microbial biomass. Numerous studies have evaluated faunal effects on soil ecosystems by comparing normal and defaunated soil (e.g., Ingham et al. 1985; Setälä and Huhta 1991; Bradford et al. 2002), whereas relatively few have addressed the effects of soil faunal density on soil properties. Because population densities in the soil are controlled by abiotic environmental factors as well as by species interactions, manipulating densities in studies of faunal effects is important for a realistic assessment of

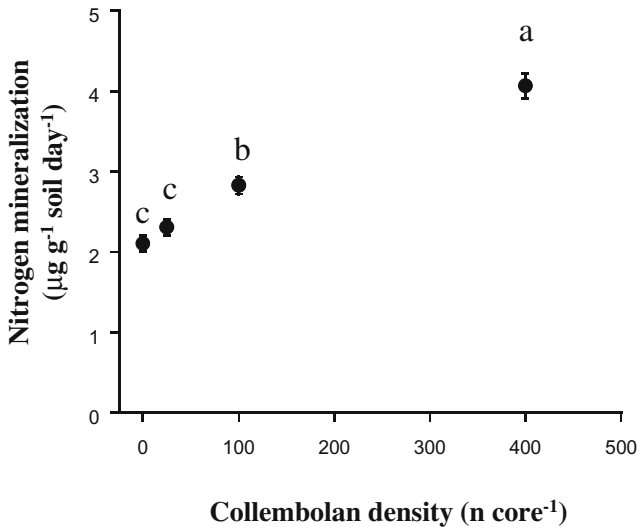

Fig. 2 Effects of collembolan density on nitrogen mineralization rate. Data are means±SE; n=6. Values highlighted by identical letters are not significantly different (P<0.05) in the Tukey–Kramer test

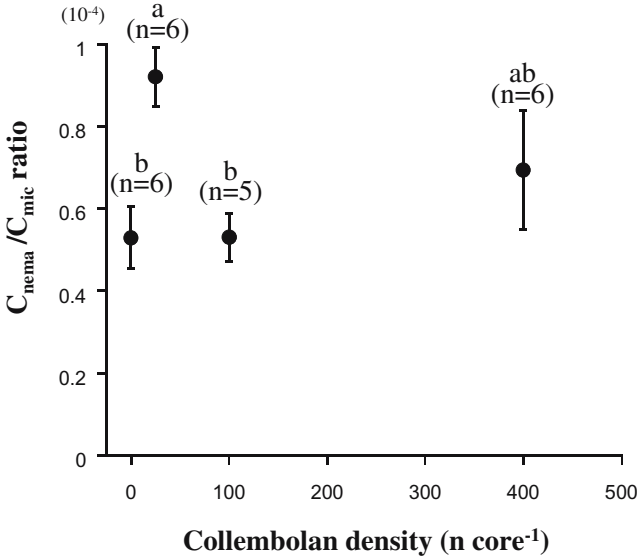

Fig. 4 Effects of collembolan density on the ratio of nematode C to microbial biomass C. Data are means±SE. The *numbers in parentheses* denote sample size. Values highlighted by identical letters are not significantly different (P<0.05) in the Steel–Dwass test

faunal effects on plant growth in the field. In this study, collembolan effects on nitrogen and carbon mineralization were positively correlated with the insects' density, while the C_{nema}/C_{mic} ratio changed in a nonlinear way.

In previous studies, the impact of Collembola on nitrogen mineralization appeared to be mediated by their effects on microbial community structure, fungal age, substrate conditions, etc (Visser et al. 1981; Seastedt 1984; Teuben 1991). In many studies, Collembola enhanced nitrogen mineralization (Ineson et al. 1982; Anderson et al. 1983; Cragg and Bardgett 2001), whereas a decrease in nitrogen mineralization by Collembola was also reported (Visser et al. 1981; Teuben 1991). Collembola are thought to accelerate the immobilization of nutrients in microbes by enhancing microbial activity through grazing. In this study, the enhancement of nitrogen mineralization in the presence of Collembola might be detectable only because of decreasing microbial biomass in all treatments, as increasing microbial biomass tends to increase nitrogen immobilization rates. Although nematodes that feed on bacteria and fungi promote nitrogen cycling (Ingham et al. 1985; Huixin et al. 2001; Okada and Ferris 2001), we found no correlation between nematode density at the end of the experiment and nitrogen and carbon mineralization rates. Collembola might affect microbial activity and resource unit community structure by feeding on the resource unit. Therefore, the effects of Collembola on nitrogen mineralization were more pronounced than those of nematodes in our experiment.

Overgrazing was observed in litter systems at high population densities of Collembola (Hanlon and Anderson 1979; Ineson et al. 1982; Andrén and Schnürer 1985; Bardgett et al. 1993), which decreased hyphal covering of the substrate surface (Andrén and Schnürer 1985) and soil respiration (Bardgett et al. 1993). In some of these studies, collembolan densities were higher than those of this study. While collembolan densities were similar, our results on soil respiration contrast with those of Bardgett et al. (1993). This might be due to differences in the substrates used and the composition of the decomposer communities. Bardgett et al. (1993) used litter substrate and only fungi as decomposers; in our study, mineral soil served as the substrate, and the decomposer community was more complex, including bacteria, fungi, protozoa, and nematodes. Collembola increased bacterial biomass and decreased fungal biomass in a microcosm experiment using a litter system (Hanlon and Anderson 1979). Differences in bacteria and fungi mortality may occur because hyphae are severely damaged physically by foraging Collembola, whereas spores of fungi and bacteria remain largely unaffected. Spores and bacteria have been observed in collembolan fecal pellets (Borkott and Insam 1990; Lussenhop 1992; Thimm et al. 1998); this suggests that these are not digested by Collembola. Fungi are important decomposers in litter systems, whereas bacterial activities are more important in mineral soil systems (Beare et al. 1992; Lavelle and Spain 2001). Collembola selectively graze on hyphae (Moore et al. 1987; Kaneda and Kaneko 2004); selective feeding on bacteria was also reported (Thimm et al. 1998). In contrast to Collembola ingesting hyphae, animals that feed on bacteria and protozoa also take up mineral particles. Collembola probably access their food organisms more easily in litter than in mineral soil systems due to the structure of the substrate. Therefore, microorganisms in mineral soil might be protected from collembolan predation to some extent, which may explain the differences in the results from experiments using different substrates.

Collembola significantly decreased nematode number in the feeding experiments, which is consistent with previous studies (Brown 1954; Gilmore 1970; Walter et al. 1988; Gilmore and Potter 1993; Lee and Widden 1996). However, the feeding experiment was a simple system, as in other feeding studies (example Walter et al. 1988; Lee and Widden 1996); we chose this system for testing whether Collembola feed on nematodes or not. Using a soil/vermiculite mixture as a three-dimensional substrate, Gilmore (1970) showed that Collembola decreased nematode numbers similarly as they did in a two-dimensional system. In addition, Lee and Widden (1996) reported that *F. candida* preferred bacteria-feeding nematodes to the fungus *Cladosporium cladosporioides*, which was preferred by *F. candida* to other fungal species in Klironomos et al. (1992). In our microcosm experiments,

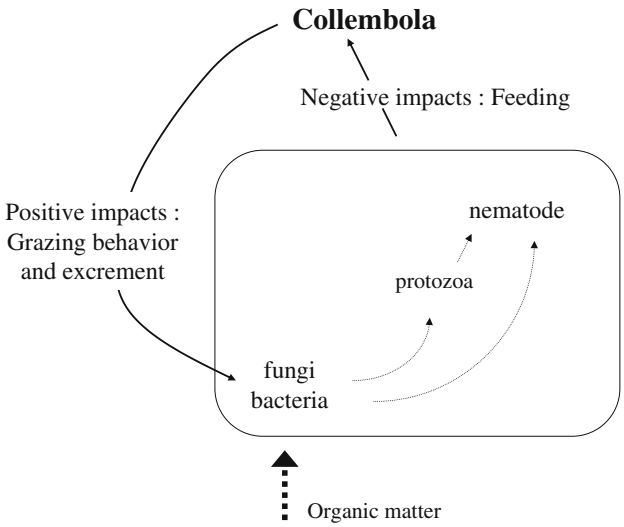

Fig. 5 Diagram showing positive and negative effects of Collembola on nematodes. Collembola have a negative influence on nematodes on which they prey. On the other hand, the foraging activity of Collembola might remove the deadlock between competing fungi, while their excrements stimulate the growth of bacteria and fungi on which nematodes feed. *Broken arrows* represent material fluxes; *solid arrows* denote collembolan effects on nematodes

F. candida would also feed on nematodes in a mineral soil environment.

In contrast, Hyvönen and Persson (1996) and Huhta et al. (1998) suggested that fungivorous microarthropods and/or *F. candida* decreased, but never increased, nematode populations in raw humus forest soil in microcosm experiments. In our experiments, the C_{nema}/C_{mic} ratio was increased at the low collembolan density but not at the high density. Thus, Collembola appeared to have positive effects on the nematode population. The biomass of nematodes feeding on bacteria or fungi is known to be larger in the rhizosphere, in which more easily metabolized substrates are present than in other microenvironments (Ingham et al. 1985). Bacteria-feeding nematode biomass was increased by the addition of glucose (Anderson et al. 1981) and correlated with microbial biomass as well as probably microbial activity. In the present study, Collembola presence increased the soil respiration rate and qCO_2, indicating an enhancement of microbial activity. These collembolan effects on microbes are a plausible mechanism for positive impact of Collembola on nematodes. In the experiments of Hyvönen and Persson (1996) and Huhta et al. (1998), fungivorous arthropods and *F. candida* decreased, but never increased, nematode densities. The density of fungivorous arthropods in the study by Hyvönen and Persson (1996) was 143 g^{-1} soil at the beginning of the experiment and more than 100 g^{-1} soil during and at the end of the experiment (Huhta et al. 1998). These densities are substantially higher than that detected in our study, opening the possibility that positive effects of Collembola on nematodes escaped detection in the older study.

As summarized in Fig. 5, Collembola predation negatively influenced nematode density but also had an indirect positive impact by their grazing behavior and excrements. Deadlock, that is, a stagnation of fungal growth due to a balance between competing species, was mostly observed under oligotrophic conditions in in vitro experiments (Stahl and Christensen 1992). Even if microarthropods do not feed on fungi, their motile activity may lead to hyphal damage (Lussenhop 1992). Collembola may enhance fungal activity by breaking the deadlock between interacting fungal species through grazing and walking. As Collembola may also stimulate bacterial and sugar fungal activity by excreting high nutritional substrates, they indirectly promote free-living nematode growth. This stimulation of the soil food web may be the mechanism by which the insects led to increased nematode populations. However, the adverse effects of collembolan feeding on nematodes especially at medium and high densities might counter the Collembola's stimulating effects.

Density compensation between bacterivorous and fungivorous nematodes was demonstrated by perturbation studies (e.g., Ruess et al. 1996, 2001); soil acidification and biocide exposure led to species loss but not to significant modifications of total abundance (Ruess et al. 1996, 2001). K-strategists, such as omnivores and predators, decreased, while opportunists increased after perturbations (Ruess et al. 1996, 2001). On the other hand, nematode populations are thought to be regulated by predatory nematodes, mites, and Collembola (Allen-Morley and Coleman 1989; Hyvönen and Persson 1996; Mikola and Setälä 1998; Laakso and Setälä 1999). Our results are consistent with these studies; although Collembola do not feed exclusively on nematodes, they affected the nematode population when they were present at medium and high densities.

In the previous studies, which were conducted mainly using litter systems, carbon mineralization had a bell shape response curve and decreasing trend in relation to collembolan density in some studies (Hanlon and Anderson 1979; Hanlon 1981; Bardgett et al. 1993), while nitrogen mineralization had variable relationships between collembolan density (Teuben and Roelofsma 1990; Teuben 1991; Bardgett et al. 1993). Likewise, negative impacts of Collembola on nematodes were only observed (Hyvönen and Persson 1996; Huhta et al. 1998). In this experiment using a mineral soil system, we showed that collembolan effects on nitrogen and carbon mineralization were positively correlated with the insects' density, while the C_{nema}/C_{mic} ratio changed in a nonlinear way. In addition, this study found a positive impact of Collembola on nematodes when Collembola were at a low density.

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