



Linking soil food web structure to above- and belowground ecosystem processes: a meta-analysis

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Soil fauna can be an important regulator of community parameters and ecosystem processes, but there have been few quantitative syntheses of the role of soil fauna in terrestrial soil communities and ecosystems. Here, we conducted a meta-analysis to investigate the impacts of invertebrate soil micro- and mesofauna (grazers and predators) on plant productivity and microbial biomass. Overall our results indicate that an increase in the biomass of soil fauna increased aboveground plant productivity across ecosystems by 35% and decreased microbial biomass by 8%. In addition, we found no evidence for trophic cascades in terrestrial soil food webs, but the bacterivorous component of soil fauna influenced plant productivity and microbial biomass more than did the fungivorous component. Furthermore, changes in the biomass of soil fauna differentially affected plant productivity among plant functional groups: a higher biomass of soil fauna increased aboveground productivity by 70% in coniferous systems. However, in ecosystems dominated by legumes, a functional group with lower inorganic nitrogen requirements, there was no response of aboveground productivity to increases in the biomass of soil fauna. In sum, the results of this meta-analysis indicate that soil fauna help to regulate ecosystem production, especially in nutrient-limited ecosystems.

Soil food webs regulate nutrient flow in terrestrial soil ecosystems and control the nutrient supply available to plants, thereby linking below- and above ground processes (Wardle 2002). The interactions between soil microbial communities and plants are well documented (Knops et al. 2002, Reynolds et al. 2003, Chapman et al. 2006). A growing number of studies indicate that higher trophic levels in soil food webs (e.g. bacterial and fungal grazers and their predators) may also be important regulators of soil food web dynamics and thus strongly affect terrestrial ecosystem function. For example, the invertebrate soil fauna is likely a major control point for nutrient availability (and therefore plant productivity), as it regulates the balance between the immobilization of nutrients into microbial biomass, and nutrient release through grazing (Moore et al. 2003). Despite the apparent importance of soil fauna in individual experiments, there have been few quantitative analyses of the effects of altered biomass or community structure of soil fauna on processes across ecosystems. Thus, we do not know if there are generalizable effects of soil fauna across terrestrial ecosystems, or whether changes in soil fauna have highly variable effects across soil communities and ecosystems.

Difficulty in interpreting the influence of soil fauna on ecosystem processes within and across ecosystems may be due to the variation in body size, feeding preferences, and resource processing rates among different components of

soil fauna. In this study we focus on the soil micro- and mesofauna (animals < 2 mm), primarily microbial grazers (e.g. bacterivores and fungivores) and predators. The soil macrofauna also affects soil processes and plant productivity; earthworms in particular have strong effects on plants and soil processes (Scheu 2003, Edwards 2004, Uvarov 2009). Belowground herbivores also influence plant productivity and nutrient dynamics (van der Putten et al. 2001), but in this study we focus on the fauna that mainly interacts indirectly with plants. These non-herbivorous grazer and predator communities are diverse and abundant in soils, include multiple phyla (protozoans, nematodes, enchytraeids, collembolans, and mites) that differ by several orders of magnitude in body size, and numerous individual studies indicate the effects of the micro- and mesofauna on plant and soil productivity are significant and worthy of a quantitative review.

The division of soil fauna into grazing and predatory trophic levels allows the evaluation of the role of trophic cascades (where predators, by consuming grazers, increase microbial biomass) in shaping soil community structure. Previous experiments testing for top-down control of microbial biomass by grazers or the occurrence of trophic cascades have been inconclusive (Mikola and Setälä 1998a, Lenoir et al. 2007). Differences among experimental systems, community structure, and the degree of omnivory influence the

strength of trophic cascades (Wardle 2002). Though recent syntheses have reviewed trophic cascades in terrestrial auto-trophic and aquatic food webs (Chase 2000, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002, 2006), to our knowledge there are no quantitative reviews assessing trophic cascades in terrestrial detrital food webs.

Resource compartmentalization of detrital energy into bacterial and fungal decomposition pathways can further complicate trophic frameworks in soil food webs. Bacterial and fungal pathways differ significantly in decomposition rates, because energy and nutrients cycle more quickly through the bacterial than the fungal pathway – bacteria consume more labile carbon as compared to fungi (Hendrix et al. 1986, Moore et al. 1988). In addition, these decomposition pathways may be differentially regulated, with top-down control of bacterial activity and bottom-up control of fungal activity (Wardle and Yeates 1993). Thus, communities that are bacterial or fungal dominated may differ in their response to shifts in the biomass of soil fauna.

Ecosystem properties, such as soil type, climate, plant community structure, and the intensity of herbivory can also influence soil communities, which may in turn influence ecosystem processes (Ruess et al. 1999, Bezemer et al. 2005, De Deyn and van der Putten 2005, Classen et al. 2006, 2007, Kardol et al. 2010). For example, soil nutrient availability as well as the nitrogen requirements of the established vegetation can regulate the response of an ecosystem to grazing by soil fauna (Moore et al. 2003). Increases in available nitrogen due to grazing on microbial communities may contribute more to inorganic nitrogen pools in nitrogen-limited soils than nitrogen-rich soils (Osler and Sommerkorn 2007). Certain components of soil fauna may also have a larger grazing impact on bacterial communities under warmer and wetter climates (Ruess et al. 1999, Kardol et al. 2010).

Here, we use meta-analysis to quantify the effects of the soil micro- and mesofauna (hereafter ‘soil fauna’) on key ecosystem parameters – above- and belowground plant productivity and soil microbial biomass. Plant biomass is a good integrator of ecosystem response and is measured in numerous studies, while changes in microbial biomass, also widely measured, can indicate the influence of soil fauna on organic matter decomposition and nutrient release. We pose four questions in this paper. (1) What are the effects of increases in the biomass of soil fauna on plant biomass, plant nitrogen concentration, and microbial biomass across all studies? (2) Does the number of trophic levels in the soil community alter the effects of soil fauna? (3) Does resource compartmentalization among microbial pathways alter the effects of soil fauna? (4) Do the effects of soil fauna vary among different plant and soil systems?

Methods

Study selection

We searched for published studies that assessed the effects of soil fauna on the following biotic response variables (Table 1): microbial biomass (quantified as microbial

Table 1. Meta-analysis data: response variables, number of studies collected, and number of observations extracted.

Response variable	No. of studies	No. of observations
Grazer biomass	4	16
Microbial biomass	20	75
Shoot biomass	37	122
Root biomass	31	102
Shoot N concentration	21	72
Root N concentration	10	25

carbon, through measures of respiration, and direct colony counts or hyphal measurements), plant (shoot and root) biomass, and plant (shoot and root) nitrogen concentration. Studies that manipulated predators (i.e. third trophic level) were used to evaluate the strength of trophic cascades, and we also compiled data on the response of grazers (second trophic level) from these studies. When possible, we calculated response variables from related data (e.g. calculate nitrogen concentration in shoots from total nitrogen in shoots and total shoot biomass). In March 2009 we searched Web of Science using search strings containing alternate combinations of the following terms: plant, collembola, nematode, protozoa, bacteria, fungi, microb* and rhizosphere. We performed an additional search using the search string ‘mite and plant’ in April 2010. We also located relevant studies by searching the references cited within each paper, as well as papers that subsequently cited the original papers found in our Web of Science searches. The searches produced 62 articles published from 1978 to 2008; all of these studies manipulated the biomass of particular components of soil fauna (grazers and/or predators) in a soil system that included a plant or plants. We found the criterion for the inclusion of plants in the study to be the most limiting factor for finding relevant studies. We did not find studies published earlier than 1978 that included plants when documenting the effects of changes in the biomass of soil fauna.

To be included in our meta-analysis, each study had to report at least one response variable of those we focused on in this meta-analysis, and the results had to be reported as treatment means. We did not include treatments that included earthworms in the manipulations, because ecosystem engineers, such as earthworms, have previously been shown to have large effects on above- and belowground processes and were beyond the scope of this study (Scheu 2003, Edwards 2004, Uvarov 2009). This analysis focuses on the other, often overlooked, components of belowground food webs. We also excluded studies where the biomass of the soil fauna was not manipulated successfully, or when freezing or insecticide treatments were used to reduce the biomass of the soil fauna but the success of the treatment was not measured (four studies). We excluded studies that added fungal grazers (i.e. collembolans) but did not provide fungal material other than mycorrhizae or quantify the growth of alternative fungi during the experiment (five studies). In the absence of other fungal species collembolans can disrupt the beneficial effects of mycorrhizae on plant growth (Warnock et al. 1982). However, collembolans often prefer grazing on non-mycorrhizal fungi (Klironomos and Kendrick 1995). After filtering the

articles based on the criteria listed above, we were left with 42 articles from which we extracted data (Supplementary material Appendix 1).

Our meta-analysis included only articles published in English. We also included only articles published in peer-reviewed journals, and did not search for data in theses, conference proceedings, or other sources that were unlikely to be peer reviewed. This was for two reasons. First, we used the peer-review process as a benchmark as to the quality of the data. Second, we did not feel we could comprehensively locate all unpublished studies on this topic. However, meta-analyses may be influenced by publication bias against smaller studies showing non-significant results (Peters et al. 2006). A funnel plot, plotting effect size versus sample size, can be used to detect publication bias, as there will be fewer studies with small sample sizes that have non-significant results. We tested for evidence of publication bias by quantitatively evaluating funnel plots through regressing, for each response variable, the effect size of individual studies versus the inverse sample size of the study (Peters et al. 2006). A significant non-zero slope indicates that the funnel plot is asymmetrical and there may be publication bias. Regression of funnel plots of each response variable showed no evidence of publication bias (Supplementary material Appendix 1). Differences in duration of the individual experiments could have also been a confounding factor that altered effect sizes among experiments. We determined whether there was a significant relationship between experimental duration and effect sizes, evaluating significance through randomization and resampling of the independent variable (999 iterations) (Gurevitch and Hedges 1999, Rosenberg et al. 2000). The duration of studies ranged from 12 to 561 days, but length of study had no significant relationship with the magnitude of the effect size (Supplementary material Appendix 1).

Data extraction

For each of the response variables (Table 1) we extracted mean responses of control and treatment groups from tables and scanned figures using DataThief III ver. 1.5 (Tummers 2006). In our analysis, the 'treatment' groups were those containing a relatively higher biomass of the manipulated component of the soil fauna, and the 'control' group was the treatment containing a lower biomass of the manipulated component of the soil fauna.

Each unique faunal-addition and control treatment interaction was classified as one observation in our dataset. In some of the studies multiple treatments shared a control treatment, resulting in non-independence of these observations. However, the selection of one treatment over the others would have been arbitrary. We felt it was more important to retain data from treatments that varied in species and functional group composition, as well as complexity, rather than make unjustified exclusions (Englund et al. 1999, Hungate et al. 2009). For replicates where there were multiple measurements over time we used only the data from the final sampling date. In studies where different replicates were used to monitor the change in a response variable over time (i.e. full factorial design incorporating time), we recorded the data from all observations. The number of

studies and number of observations from which data were extracted for each response variable are listed in Table 1.

Meta-analyses

Calculating effect sizes

For each observation we converted the ratio between the control and treatment means into an individual effect size, using the natural log of the response ratio (LRR): $\ln(\text{treatment/control})$ (Hedges et al. 1999). A positive effect size indicates a positive effect of increased biomass of soil fauna and a negative effect size indicates a negative effect of increased biomass of soil fauna on the response variable of interest.

We estimated the mean effect size (grand mean effect size for all studies combined) for all of the studies within a group by calculating the mean of the individual effect sizes from the studies in the group. We calculated the variance (and confidence intervals) around this mean effect size using bootstrapping (999 iterations) because the majority of studies did not include measures of variation for the mean (Rosenberg et al. 2000). For each group of studies, the mean effect size was considered significant (< 0.05) if the 95% confidence intervals of the mean effect size did not overlap with zero. Figures present mean effect sizes (LRR) and 95% confidence intervals. For each group of studies we also report the effects of increased biomass of soil fauna using the non-log transformed data, which allowed us to translate the mean effect size (LRR) into a mean percent change from control (for the group of studies: $(\sum(100 \times \text{study treatment mean}/\text{study control mean}))/\text{number of studies in group}$), a metric that provides a more intuitive understanding of the effects of changes in the biomass of soil fauna.

What are the effects of increases in the biomass of soil fauna on plant biomass, plant nitrogen concentration, and microbial biomass across all studies?

We calculated the mean effect size of each response variable incorporating observations from all 42 studies (grand mean effect size). These grand means indicate whether there are generalizable effects of changes in the biomass of soil fauna across the wide variety of experimental systems represented by the studies. After this overall assessment, we investigated in more detail what specific characteristics of the study systems were the main drivers of the responses to changes in the biomass of soil fauna.

Does the number of trophic levels in the soil community, resource compartmentalization, or plant/soil type alter effects of soil fauna?

To determine what aspects of communities altered the effect size of an increased biomass of soil fauna on the response variables, we separated the data into groups according to three ecological categories, and performed three additional meta-analyses to compare the mean effect sizes among groups. The categories were:

1. Number of trophic levels: we defined microbial biomass as the first trophic level, microbial grazers as the second trophic level, and predators as the third trophic level. Groups: (1) manipulation of second trophic level (grazers only) or (2) manipulation of third trophic level (predators).

2. Microbial pathway: the pathway(s) in which the manipulated soil fauna fed. Groups: (1) bacterial, (2) fungal, or (3) both bacterial and fungal.
3. Plant/soil group: in the majority of reviewed experiments, plants were planted in soils from their native ecosystem, (e.g. tree species with native forest soils, grasses and legumes in either arable or grassland soils). Groups: (1) conifers, (2) deciduous plants (i.e. non-leguminous angiosperms), (3) grasses or (4) legumes.

We established that there had to be a minimum of ten replicates per group for it to be included in a meta-analysis. For each ecological category, we calculated the mean effect size (LRR) and bootstrapped 95% confidence intervals as above (Rosenberg et al. 2000). We then compared the mean effect sizes among groups using a χ^2 -test of within and between group heterogeneities (Rosenberg et al. 2000). We report the χ^2 -test statistic for between groups (Q_b), the degrees of freedom, and the p-value. Note that these meta-analyses evaluate statistical significance in two ways: (1) whether a particular treatment significantly affects the response variable of interest, as indicated by whether a mean effect size is significantly greater than or less than zero (signified by non-overlap of confidence intervals with zero). (2) Whether the mean effect sizes of different groups within an ecological category (listed above) are significantly different from each other (as indicated by p-value of χ^2 -test).

We used Metawin ver. 2.0 (Rosenberg et al. 2000) to perform all meta-analyses.

Results

Studies

The 42 studies used in these meta-analyses manipulated a broad variety of soil micro- and mesofauna under various experimental conditions (Supplementary material Appendix 1). The most frequently manipulated taxa were protozoa (primarily grazers), nematodes (grazers and predators), collembolans (grazers), and mites (grazers and predators).

What are the effects of increases in the biomass of soil fauna on plant biomass, plant nitrogen concentration, and microbial biomass across all studies?

The grand mean effect sizes, incorporating data from all 42 studies representing a wide range of experimental conditions, showed that overall, a higher biomass of soil fauna had significant positive effects on plant productivity, both above- and belowground, and negative effects on microbial biomass (Fig. 1). These grand mean effect sizes translate to, for treatments with a higher biomass of soil fauna compared to control treatments, a mean 35% increase in aboveground plant biomass, a mean 25% increase in belowground biomass, and a mean 8% reduction in microbial biomass. There were no significant overall effects of changes in the biomass of soil fauna on shoot or root nitrogen concentrations (Fig. 1).

Does the number of trophic levels in the soil community alter the effects of soil fauna?

We did not detect a trophic cascade from predators to microbial biomass, or find any general effects of trophic cascades

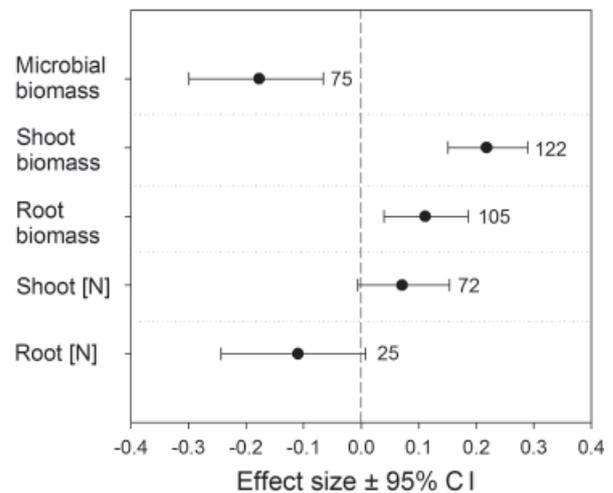


Figure 1. Overall effects of soil fauna on biotic variables. Means and 95% confidence intervals of the effects of increased biomass of soil fauna on measured response variables (N = nitrogen). The number to the right of the confidence interval indicates the number of observations for each variable.

on plant productivity. Predators significantly reduced the density of grazers, translating into a mean reduction of grazers by 20% in treatments containing predators relative to those without (Fig. 2). However, this decrease did not cascade further through the food web. Soil communities with a higher biomass of soil fauna, containing either two or three trophic levels, reduced microbial biomass by approximately 10% (Fig. 3). However, the reduction in microbial biomass did not differ among treatments with two or three trophic levels ($Q_b = 0.051$, $DF = 1$, $p = 0.67$). There was also no significant difference in the magnitude of the increase of shoot biomass ($Q_b = 0.15$, $DF = 1$, $p = 0.30$) or root biomass ($Q_b = 0.017$, $DF = 1$, $p = 0.75$) between the two trophic level groupings (Fig. 2). The only response variable that depended on the number of trophic levels in the faunal manipulations was shoot nitrogen concentration: in treatments with a higher biomass of soil fauna and three trophic levels there was a 60% increase in shoot nitrogen concentration compared to the control treatments. This was a significantly higher increase in shoot nitrogen concentration than occurred in treatments with higher biomass of soil fauna but that contained only two trophic levels ($Q_b = 1.45$, $DF = 1$, $p = 0.001$) (Fig. 2).

The remaining meta-analyses combine the treatments that manipulate both trophic levels, and the general term 'soil fauna' refers to this combination of trophic levels.

Does resource compartmentalization among microbial pathways alter the effects of soil fauna?

When studies were divided into groups based on microbial pathway (bacterial, fungal, or both), the reduction of microbial biomass and increase in plant productivity due to a higher biomass of soil fauna was mainly driven by experiments that manipulated bacterial grazers. Increases in the biomass of bacterial grazers reduced microbial biomass by 11% (Fig. 3). This decrease, however, did not significantly differ from the effect of fungivores and combined grazers on microbial biomass ($Q_b = 0.76$, $DF = 1$, $p = 0.22$).

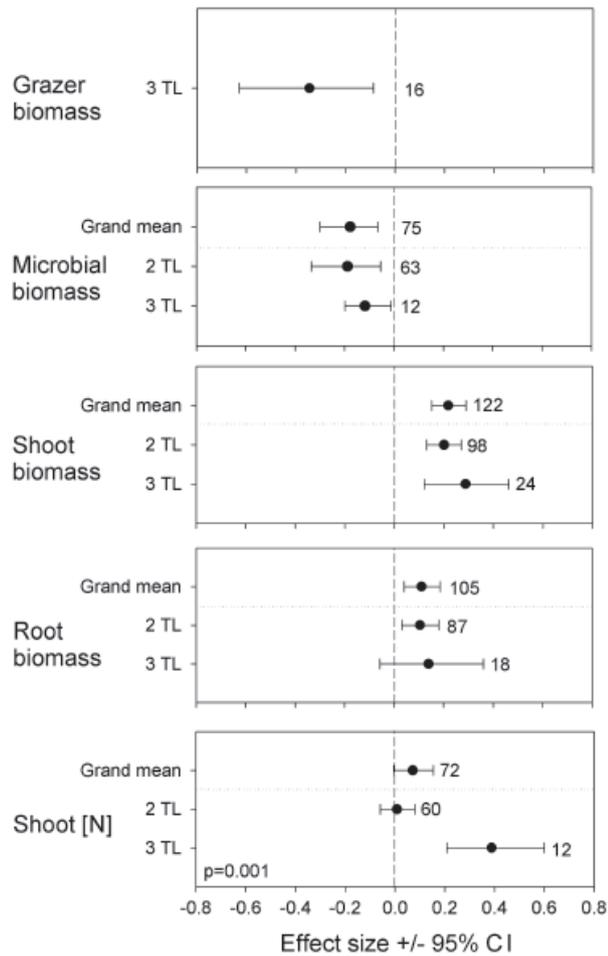


Figure 2. Testing for trophic cascades in the soil food web. Mean effect size (LRR) and 95% confidence intervals of the effects of increased biomass of soil fauna comprising 2 (no predators) or 3 (with predators) trophic levels (TL) on measured response variables (N = nitrogen). Response variables that have significantly different mean effect sizes among groups with a different number of trophic levels have the p-value at the left of the chart (complete p-values are provided in text). The number to the right of the confidence interval indicates the number of observations in each group.

Increased biomass of all grazer groups increased shoot biomass, but comparison among grazer groups indicated that bacterial grazers increased shoot biomass significantly more (48%) than did fungal grazers (20%), while soil communities containing both bacterial and fungal grazers caused an intermediate increase in shoot biomass (38%) ($Q = 1.0$, $DF = 1$, $p = 0.04$). Soil communities with a relatively higher biomass of both bacterial and fungal grazers increased shoot nitrogen concentration by 43% (Fig. 3), and this increase was significantly greater than the effect of bacterivores on shoot nitrogen concentration, but not greater than the effect of fungivores ($Q_b = 1.1$, $DF = 1$, $p = 0.004$).

Do the effects of soil fauna vary among different plant and soil systems?

A higher biomass of soil fauna increased conifer shoot biomass by 70%, deciduous shoot biomass by 50%, and grass shoot biomass by 24% (Fig. 4). The impact of a higher biomass of soil fauna on these plant groups was significantly

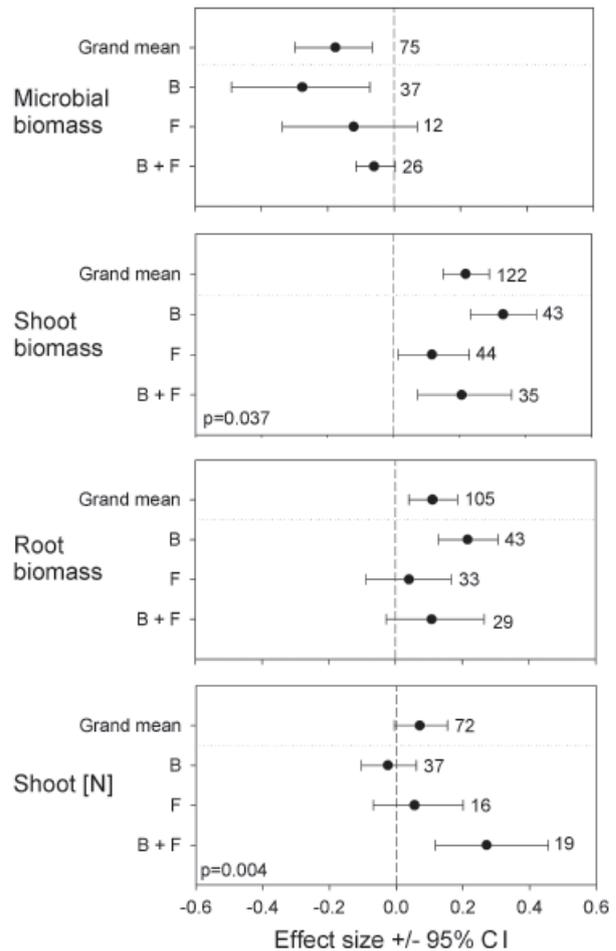


Figure 3. Effects of manipulating the biomass of soil fauna in different microbial pathways. Mean effect sizes and 95% confidence intervals of the effects of increased biomass of soil fauna (all trophic levels) from the bacterial pathway (B), the fungal pathway (F) or both pathways (BF) on response variables (N = nitrogen). Response variables for which microbial pathway groups have significantly different mean effect sizes have the p-value at the left of the chart (complete p-values are provided in text). The number to the right of the confidence interval indicates the number of observations in each group.

greater than the effect size for legume shoot biomass ($Q_b = 1.8$, $DF = 1$, $p = 0.008$), which showed no response to changes in the biomass of soil fauna.

Discussion

Our results indicate that, across terrestrial ecosystems, soil fauna can regulate soil food webs and have strong effects on above- and belowground processes. Our study yielded four major conclusions: (1) increases in the biomass of soil fauna increased plant productivity and decreased microbial biomass across ecosystems. The largest response was for aboveground plant biomass, where average biomass increased by 35%. (2) Trophic cascades in soil food webs are not common. (3) Aboveground plant biomass increased significantly more (28%, on average) in ecosystems dominated by bacterial grazers than by fungal grazers. (4) The response of aboveground plant biomass

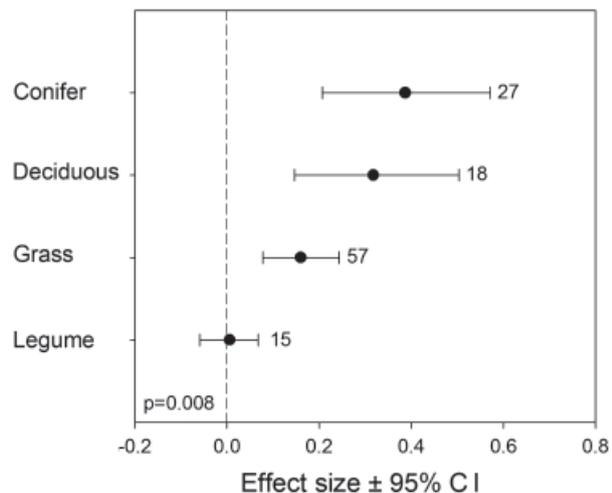


Figure 4. Plants from a variety of ecosystems respond differently to soil fauna. Means and 95% confidence intervals of the effects of increased biomass of soil fauna (all trophic levels) on shoot biomass from experiments containing different plant and soil types. The p-value at the left of the chart indicates the significance of among group comparisons (complete p-values are provided in text). The number to the right of the confidence interval indicates the number of observations in each group.

to changes in the biomass of soil fauna varied among different plant and soil types. In treatments with a higher overall biomass of soil fauna (both bacterivores and fungivores), aboveground biomass in coniferous ecosystems increased by 70%, whereas an increase in the biomass of soil fauna did not alter biomass in nitrogen-fixing leguminous ecosystems.

Predator-induced trophic cascades in soil food webs are not widespread

Strong (1992), and others (Halaj and Wise 2001, Shurin et al. 2002) have suggested that community-level trophic cascades are primarily found in particular aquatic food webs, and are less common in aboveground terrestrial food webs. Our quantitative review of soil food webs suggests that predator-induced trophic cascades in terrestrial soil food webs are not common. More specifically, although having more predators reduced grazer density by 20%, overall there was no subsequent shift in microbial biomass or plant productivity.

Only a handful of experiments have directly tested for predator-induced trophic cascades in soils; these studies were not included in our meta-analyses because plants were not included in the experimental design (Santos et al. 1981, Mikola and Setälä 1998a, Laakso and Setälä 1999, Lenoir et al. 2007). However, the results from these studies suggest that trophic cascades may not be a general phenomenon because the occurrence of cascades often depends on environment and resource availability. For example, Mikola and Setälä (1998a) and Laakso and Setälä (1999), using soils from mature pine and mixed forests in central Finland, found no evidence of trophic cascades from predators to microbial biomass, although predators did reduce grazer biomass. In contrast, Lenoir et al. (2007), working with soils from a Swedish Scots pine stand, found trophic cascades occurred

when the soils were nitrogen-limited, but not in soils that had been fertilized with nitrogen. Santos et al. (1981), working with desert soils, found that predatory mites controlled the populations of nematode bacterivores, and the resulting cascade decreased bacterial populations and slowed the rate of litter decomposition. In this case, the dry soils may have contributed to the outcome of interactions between bacterivores and bacteria. Similarly, in forest litter, predators cause trophic cascades affecting fungal biomass under dry conditions, but not under wet conditions (Lensing and Wise 2006). This rainfall dependent trophic cascade results from slower growth rates of fungal communities under dry conditions, causing grazing to have a more substantial impact on microbial populations. Thus, abiotic factors like resource availability, precipitation, and soil moisture may play a key role in determining whether trophic cascades are important for shaping microbial community structure and associated soil processes.

If indeed trophic cascades are more common under dry or nitrogen-limited conditions, then in environments exposed to increasing drought or nutrient depletions, control of nutrient cycling may shift partially to higher trophic levels. Although experiments manipulating drought, temperature, or nutrient status have found that the community composition of soil fauna shifts with changes in moisture (Lindberg et al. 2002, Kardol et al. 2010), resource supply (Cole et al. 2005, Antoninka et al. 2009), temperature (Briones et al. 2009, Castro et al. 2010, Kardol et al. 2010), and climate (Wall et al. 2008, Kardol et al. 2010), the effects of these perturbations on trophic cascades could be more widely tested. However, our data support previous work suggesting that high community diversity and turnover, large numbers of interactions, and high rates of omnivory in soil communities all contribute to a general scarcity of trophic cascades (Cousins 1987, Strong 1992, Thompson et al. 2007).

Bacterial grazers have a larger impact than fungal grazers

When we grouped the data by grazer decomposition pathway (bacterial, fungal, both), we found that an increased biomass of bacterial grazers had a significant negative impact on microbial biomass, and a significantly larger impact on plant productivity than did a higher biomass of fungal grazers. The negative effect of bacterial grazers on microbial biomass suggests top-down control of bacterial biomass. Conversely, we found that fungal grazers did not affect microbial biomass, supporting the regulation of fungal community growth by resource availability (Mikola and Setälä 1998b, Wardle 2002, Moore et al. 2003). The lack of top-down control of fungi due to compensatory growth in response to grazing is well documented (Wardle 2002). Relative to fungal grazers, a higher biomass of bacterial grazers led to an increase in shoot biomass, suggesting a stimulation of nutrient availability with bacterial grazing, and a concomitant increase in plant productivity. These changes in plant biomass support work by Moore et al. (2003) and Osler and Sommerkorn (2007) who predicted that the bacterial component of soil fauna will have a greater positive effect on nitrogen availability than the fungal component of soil fauna. In general, bacteria consume more labile (lower

C:N ratio) organic matter than fungi, and therefore the rate of nutrient turnover tends to be faster in the bacterial pathway than in the fungal pathway (Moore et al. 2003). At the same time, bacteria themselves have a lower C:N than fungi, and the consumption of bacteria by grazers results in the excretion of more mineralized nitrogen from bacterivores than fungivores (Osler and Sommerkorn 2007).

Plant and soil type interact with effects of soil fauna

Theoretical models predict that plant species and soil type (Knops et al. 2002, Chapman et al. 2006) are important ecological parameters interacting with soil fauna to affect microbial biomass, nitrogen availability and plant productivity. Plant functional group affects nitrogen availability in soils, because in general there is a negative relationship between nitrogen availability and the lignin:N of the leaf litter contributing to soil organic matter (Wedin and Tilman 1990, Scott and Binkley 1997). Such a relationship predicts that initial nitrogen availability should be highest in grass-dominated ecosystems, intermediate in deciduous-dominated ecosystems, and lowest in coniferous ecosystems. Correspondingly, soil fauna will also differentially affect soil nitrogen availability. Increases in the biomass of soil fauna and grazing on microbial biomass should have a greater impact on nitrogen availability in nitrogen-limited soils (Osler and Sommerkorn 2007), because faunal-released nitrogen provides a relatively larger contribution to the inorganic nitrogen pool. We suggest that differences in initial soil nitrogen availability among studies may account for some of the variation in the response of plant productivity to the increased biomass of soil fauna seen in this meta-analysis. Our results indicate that the increase in plant biomass with a higher biomass of soil fauna was greatest for nitrogen-limited plant/soil systems (i.e. conifers), and the response of plant biomass became lower for plant/soil systems with higher nitrogen availability (i.e. deciduous plants, followed by grasses). This relationship was consistent for legumes, which as nitrogen fixers, did not respond to increases in the biomass of soil fauna and any associated changes in nitrogen availability (Fig. 2).

We cannot assess the causal relationship between the decrease in microbial biomass and increase in plant biomass. A decrease in microbial biomass can benefit plants, as bacteria and fungi may compete with plants for nutrients in soils with low nitrogen availability (Kaye and Hart 1997), and some bacteria and fungi are pathogenic to plants. However, microbes also benefit plants by breaking down organic matter and increasing the nitrogen available for plant uptake. Indeed, the successful cycling of nutrients in soils depends on this relationship (Wardle 2002). The decrease in microbial biomass seen in our meta-analysis does not necessarily indicate a functional decrease in microbial activity, because microbial activity can increase as a result of grazing on dead or dying microbial matter (Hanlon 1981). In addition, grazers can also alter the microbial community to favour species that produce plant growth hormones or increase nutrient cycling (Bonkowski 2004, Mao et al. 2007). Finally, soil fauna may be affecting plant growth through other indirect mechanisms. Grazers and other components of soil fauna excrete mineralized nitrogen (Teuben and Verhoef 1992) and

transport microbes and inorganic materials through the soil (Anderson 1988).

Several lines of evidence support our hypothesis that soil fauna increases soil nitrogen availability and that this is the primary mechanism for increases in plant productivity seen in our meta-analysis. First, legumes did not show a response to the increased biomass of soil fauna, whereas plants that are more dependent upon mineralized nitrogen in the soil (e.g. conifers, deciduous plants, and grasses) did. Second, comparison between the effects of increased biomass of soil fauna on plant biomass indicated there was a relatively higher increase in shoot biomass than root biomass, consistent with increases in nutrient availability (Davidson 1969). Third, bacterial grazers had a greater effect on plant productivity compared to fungivores. Nitrogen cycles more quickly through the bacterial pathway, and bacterivores tend to excrete waste with a lower C:N ratio than fungivores. We were not able to estimate the direct effects of soil fauna on soil nitrogen availability because there were not consistent measurements of soil nitrogen availability across experiments. We recommend that future experiments manipulating soil food web structure assess changes in nutrient cycling by tracking organic and inorganic nitrogen pools in soil, microbial biomass, and plant biomass.

Conclusions

Changes in the biomass of soil fauna alter plant productivity and soil microbial biomass and there is predictable variation in these effects that arises from the resource compartmentalization of components of soil fauna, and plant and soil type.

We recognize that interactions among community structure and abiotic factors (e.g. nutrient availability, temperature, moisture) will change the effects of soil fauna in ways we did not explore in this meta-analysis. In addition, the studies in this meta-analysis were done in mesocosms, and results may differ under more complex field conditions and in ecosystems that include other components of soil fauna such as earthworms, macroarthropods, and herbivores. However the results of this meta-analysis emphasize the importance of non-herbivorous soil micro- and mesofauna in regulating plant productivity and microbial communities in terrestrial ecosystems, and provide generalizations and hypotheses that can help guide future experimental research. Understanding the control points connecting aboveground and belowground communities, and the mechanisms that influence their interdependence, provides insight on how ecosystems function as well as how disturbances, like global change, may influence these interactions (van der Putten et al. 2009).

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Supplementary material (available online as Appendix O18728 at www.oikos.ekol.lu.se/appendix). Appendix 1.