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TOWARD A COMPLETE SOIL C AND N CYCLE: INCORPORATING THE SOIL FAUNA

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Abstract. Increasing pressures on ecosystems through global climate and other land-use changes require predictive models of their consequences for vital processes such as soil carbon and nitrogen cycling. These environmental changes will undoubtedly affect soil fauna. There is sufficient evidence that soil fauna have significant effects on all of the pools and fluxes in these cycles, and soil fauna mineralize more N than microbes in some habitats. It is therefore essential that their role in the C and N cycle be understood. Here we introduce a new framework that attempts to reconcile our current understanding of the role of soil fauna within the C and N cycle with biogeochemical models and soil food web models. Using a simple stoichiometric approach to integrate our understanding of N mineralization and immobilization with the C:N ratio of substrates and faunal life history characteristics, as used in food web studies, we consider two mechanisms through which soil fauna can directly affect N cycling. First, fauna that are efficient assimilators of C and that have prey with similar C:N ratios as themselves, are likely to contribute directly to the mineral N pool. Second, fauna that are inefficient assimilators of C and that have prey with higher C:N ratios than themselves are likely to contribute most to the dissolved organic matter (DOM) pool. Different groups of fauna are likely to contribute to these two pathways. Protists and bacteria-feeding nematodes are more likely to be important for N mineralization through grazing on microbial biomass, while the effects of enchytraeids and fungal-feeding microarthropods are most likely to be important for DOM production. The model is consistent with experimental evidence and, despite its simplicity, provides a new framework in which the effects of soil fauna on pools and fluxes can be understood. Further, the model highlights our gaps in knowledge, not only for effects of soil fauna on processes, but also for understanding of the soil C and N cycle in general.

Key words: dissolved organic matter (DOM); Enchytraeidae; gross nitrogen immobilization; gross nitrogen mineralization; microarthropods; models; nematodes; protozoa; stoichiometry.

INTRODUCTION

Despite many years of research spent investigating the role of soil fauna in soil processes such as carbon and nitrogen cycling, we still lack a framework for understanding how and when soil fauna influence these processes. Such a model is essential if we are to predict the circumstances in which changes in assemblage structures will impact ecosystem processes. For example, recently considerable research focused on the consequences of increased species richness of soil fauna within functional groups on a number of soil processes (e.g.,

Laakso and Setälä 1999, Liiri et al. 2002, Cole et al. 2004). Without a framework, it is difficult to identify the pool or flux to test in such studies. Making these predictions is pressing because even though global climate change may affect soil C stocks directly (Bellamy et al. 2005) indirect effects through habitat change and therefore through changes in the soil biota are equally important (e.g., Briones et al. 2004).

Soil zoologists have long appreciated that soil fauna play key roles in regulating soil N cycling (e.g., Anderson et al. 1984, 1985, Coleman 1994), yet these roles have not been integrated into biogeochemical models (Seastedt 2000), although some of them are acknowledged (Schimel and Bennett 2004; Fig. 1a). Soil fauna affect all of the pools within the soil N cycle through their effects on microbial biomass, inorganic N pools, supply of dissolved organic matter (DOM), and

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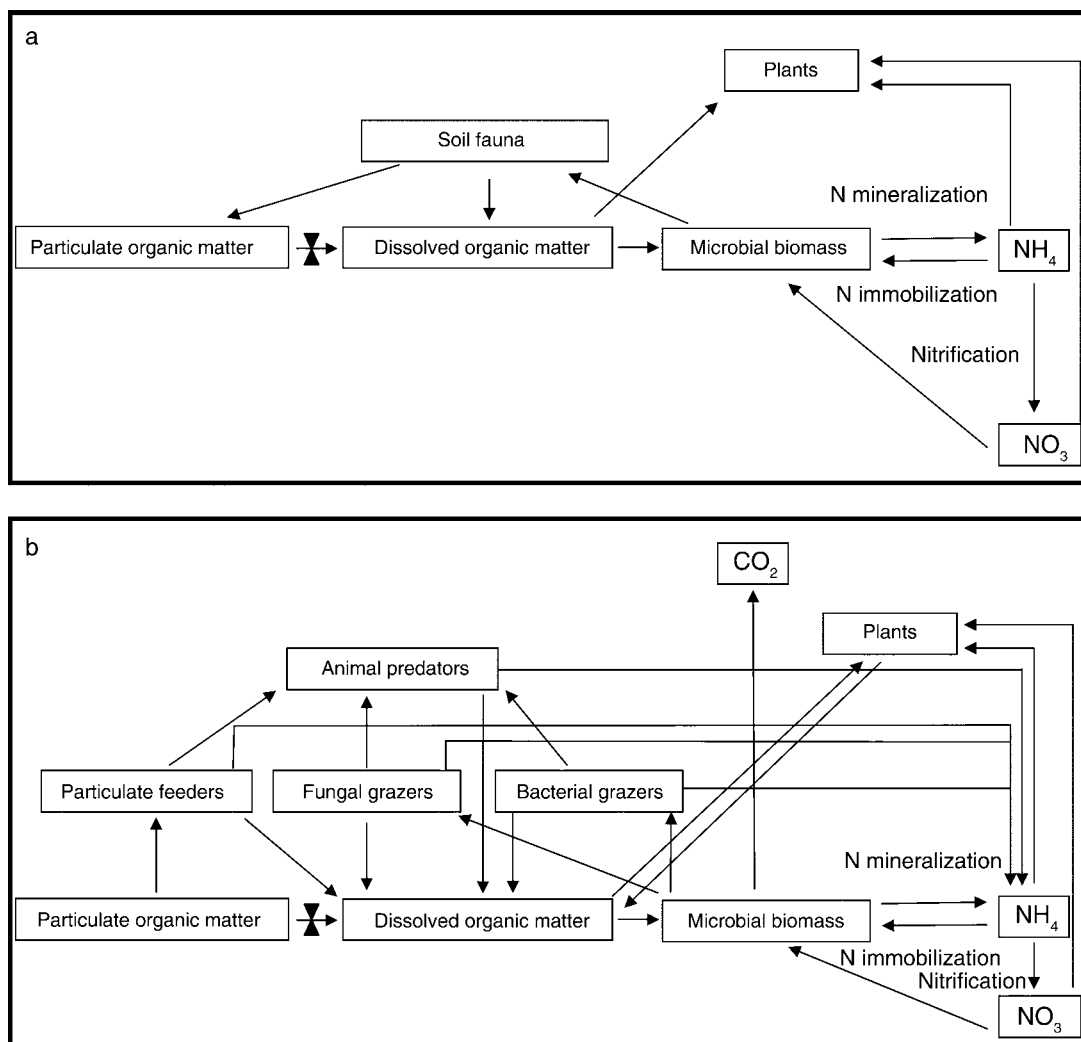


FIG. 1. (a) The new paradigm of soil N cycling (modified from Schimel and Bennett [2004]), and (b) a simplified representation of the interaction of soil fauna within the soil N cycle. There are no lines for faunal contributions to CO₂ production as they are considered to contribute little to overall soil respiration. In (b), lines for the return of biomass to the particulate organic matter pool are omitted for clarity. Double triangles on an arrow indicate the rate-limiting step in N mineralization and immobilization turnover (N MIT).

mass loss of organic matter (Fig. 1b). A number of studies also demonstrate an effect of soil fauna on fluxes such as microbial respiration, and faunal assemblage structure has been correlated with N mineralization and immobilization turnover (N MIT—the excretion and uptake of inorganic N by microbes; see Osler 2003 for a review). Yet frequently results from different studies are not consistent; undoubtedly due to the many disparate environments in which they are conducted and because the effects of numerous soil fauna groups have to be reconciled.

Here, we attempt to construct a framework that incorporates soil fauna into both the C and N cycle in soils. Our aim is to provide a framework that can be used to identify the pools and fluxes that fauna are likely to affect in different circumstances and hence facilitate

the incorporation of soil fauna into general models of the soil C and N cycle. We consider two mechanisms through which the fauna can directly affect the N cycle through excretion: first, through direct contributions of mineral N affecting net N mineralization, and second, through production of dissolved organic matter. The former mechanism has been appreciated for years (e.g., Anderson et al. 1985), but the latter has only been considered in terms of the C cycle and has not been linked to the N cycle within soil fauna studies (although see Fox et al. 2006). Discussion of the many roles that plants play in the C and N cycle (e.g., Knops et al. 2002, Chapman et al. 2006) and the interaction of soil fauna with these roles (see Bardgett 2005) is outside the scope of this paper; but we acknowledge that understanding

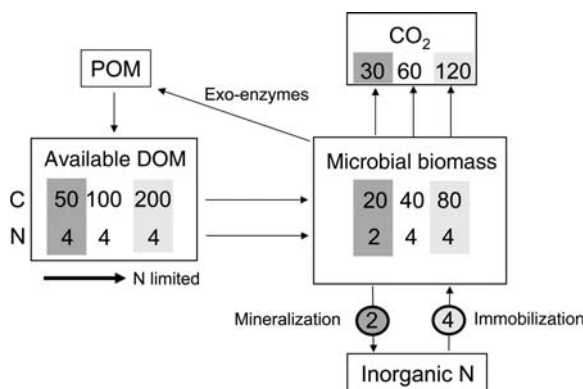


FIG. 2. Theoretical calculations of the C and N flux and microbial biomass that may result from DOM pools of varying C:N ratios. The C:N ratio of microbial populations was assumed to be 10:1. The potential effect of increasing DOM-C production is read from left to right within boxes. In the N-limited state, four units of N would have to be immobilized by the microbial biomass from the inorganic N pool to use all of the DOM-C available; hence the microbial biomass would contain eight units of N in total. When there is excess N, two units of N could be mineralized by the microbial biomass. No accounting for the cost of exo-enzyme production is made.

these roles is vital for developing a complete soil C and N model.

NITROGEN MODELS AND THE LINK BETWEEN C AND N DYNAMICS

Over the past decade a new paradigm of the N cycle has developed in which the supply of C- and N-containing monomers to microbial populations and the interaction between microbial populations and their predators has become central to the soil N cycle (Fig. 1a; Schimel and Bennett 2004). The key mechanism through which microbes access substrate is through the production of exo-enzymes that brings particulate organic matter (POM) into solution (DOM containing dissolved organic C and N, DOM-C, DOM-N), which serves as the source for microbial uptake of nutrients. The supply of labile DOM to the microbes is the rate-limiting step in N mineralization (Schimel and Bennett 2004). Central to N cycling is the process of gross N mineralization and immobilization turnover (N MIT) and net N mineralization is the balance of these two fluxes.

Schimel and Bennett (2004) present a complete model of how they expect N MIT to vary depending upon the soil N environment. In this model, microbes contribute little to N mineralization in environments where N is limiting, such as in boreal forests and tundra. As soil N supply becomes less limiting, more N is released from microbial populations and becomes a part of the inorganic N pool where it can be used by plants. This end of the scale is represented by agricultural environments and tropical forest.

Simple stoichiometry demonstrates the intimate link between soil C and N cycling through the microbial biomass (see Sterner and Elser [2002] for a complete

exposition of the application of stoichiometry to ecology). Chapin et al. (2002) provide an example where the C:N ratios of microbes are in the order of 10:1 and the microbes assimilate 40% and respire 60% of C. When C:N ratios of microbial food sources are below a threshold (less than $\approx 25:1$), there is excess N for the available C and this N is excreted as NH_4 (Fig. 2). Hence N is mineralized. When substrate exceeds the threshold, the microbes become increasingly N limited and N is retained in the microbial biomass or extracted from the inorganic pool, causing N immobilization (Fig. 2). Fig. 2 shows that in situations where there is a pool of available inorganic N, an increase in DOM-C may lead to greater CO_2 production by the microbes, greater gross N immobilization, and possibly increased microbial biomass. This is consistent with the study of Gibbs and Barraclough (1998) demonstrating that the addition of sucrose along with an organic N source, Rubisco, increased gross N immobilization and CO_2 production over treatments containing only the addition of Rubisco. It is also consistent with the correlation between gross N immobilization and CO_2 production in field soils described by Recous et al. (1999). Another interpretation of the apparent increase in microbial biomass with increasing DOM-C supply in Fig. 2 is that the microbes may have more C available for exo-enzyme production, which may liberate more DOM. The calculations in Fig. 2 take no account of the costs to the microbes of exo-enzyme production, which can be complex with differing resource supply (e.g., Allison 2005), or for the uptake or excretion of inorganic N. These costs may moderate any change in pool sizes and fluxes brought about as a consequence of increasing DOM production.

THE EFFECTS OF FAUNA ON C AND N DYNAMICS: PREDICTIONS FROM SOIL FOOD WEB MODELS

Parallel to the evolution of the new paradigm in N cycling has been the use of soil food web models to estimate the contribution of soil fauna to C and N cycling in different environments. These models simulate population dynamics in the soil food webs using life history parameters (feeding biology, assimilation efficiency, reproduction, and death rates) and the C:N ratios of predators and prey to produce estimates of contributions of different functional groups to net N mineralization and C mineralization (CO_2 production). The models are parameterized by direct observations of populations and quantification of net N mineralization through time (see Hunt et al. [1987] and de Ruiter et al. [1993] for full descriptions of the models). Experimental work supports many of the predictions of the food web models (Moore et al. 2003).

All food web studies suggest substantial roles for the soil fauna in N mineralization, with different faunal groups making important contributions to net N mineralization depending upon habitat. In the four different food webs from coniferous forests modeled by

TABLE 1. Life history parameters used in two published food web studies for different faunal groups; and values for C excreted, assimilated, and mineralized to CO₂, and N assimilated, and mineralized to NH₄, assuming 1 unit of input.

Faunal group	C:N ratio	Prey/excretion C:N ratio†	e_{ass}	C excreted	e_{prod}	C assimilated	N assimilated
Enchytraeids	5	10	0.25	0.75	0.40	0.10	0.025
Mites, fungal feeding	5.5	10	0.25	0.75	0.40	0.10	0.025
Nematodes, fungal feeding	5	10	0.30	0.70	0.40	0.12	0.03
Nematodes, fungal feeding‡	10	10	0.38	0.62	0.37	0.14	0.038
Oribatids, non Oribatids, Collembola, fungal feeding‡	8	10	0.50	0.50	0.35	0.18	0.05
Nematodes, predatory‡	10	10	0.50	0.50	0.37	0.19	0.05
Mites, predatory‡	8	10	0.60	0.40	0.35	0.21	0.06
Amoebae§	7	10	0.70	0.30	0.43	0.30	0.07
Amoebae, predatory	7	7	0.70	0.30	0.43	0.30	0.1
Nematodes, predatory	5	5	0.60	0.40	0.33	0.20	0.12
Microarthropods, predatory§	8	5	0.80	0.20	0.30	0.24	0.16
Enchytraeids	5	4	0.25	0.75	0.40	0.10	0.063
Mites, bacteria feeding	5.5	4	0.25	0.75	0.40	0.10	0.063
Nematodes, bacteria feeding	5	4	0.30	0.70	0.40	0.12	0.075
Mites, bacteria feeding‡	8	4	0.50	0.50	0.35	0.18	0.125
Nematodes, bacteria feeding‡	10	4	0.60	0.40	0.37	0.22	0.15
Amoebae§	7	4	0.70	0.30	0.43	0.30	0.175
Protozoa‡	7	4	0.95	0.05	0.40	0.38	0.238

Notes: C excreted is 1 minus the assimilation efficiency (e_{ass}); C mineralized and C assimilated are the consequence of the assimilation and production efficiency (e_{prod} ; see de Ruiter et al. [1993] for formulae). Percentage of N mineralized is the percentage of total N imbibed that is mineralized.

† The C:N ratio of what the fauna eat and therefore the C:N ratio of what they excrete.

‡ Parameters marked with this symbol are from de Ruiter et al. (1993). All others are from Schröter et al. (2003).

§ Symbol indicates that the prey C:N ratio for the group is not the exact value used in the food web models, as the group has a variety of prey with different C:N ratios.

Schröter et al. (2003), bacteria were estimated only to immobilize N. This was counteracted by net N mineralization by fungi and by large contributions to net N mineralization by testate amoebae. They estimated that fauna were more important for N than for C mineralization. Berg et al. (2001) also showed an immobilizing effect of bacteria and important contributions to N mineralization from amoebae, predaceous mites, and spiders in a Scots pine forest. In fact, the total contribution of soil fauna to N mineralization was greater than the contribution of fungi. Like Schröter et al. (2003) they estimated low contributions of fauna to C mineralization with the exception of enchytraeids. In contrast to these studies, de Ruiter et al. (1993) estimated net N mineralization by bacteria and fungi in seven food webs from grassland and arable agricultural fields. However, amoebae accounted for almost as much N mineralized as the microbes in all of the food webs, and in one food web, bacterial-feeding nematodes also made substantial contributions. Further, in pairs of treatments in their study, the relative contribution of soil fauna was higher in treatments where N availability might be expected to be less (integrated vs. conventional farming, no-till vs. conventional till, and zero vs. 120 kg N·ha⁻¹·yr⁻¹ added as fertilizer). These few studies therefore show consistency with biogeochemical models; in arable agricultural fields, microbes are most important for N mineralization, but in forest environments, where N may be more limiting, microbial contributions to net N mineralization decline and the contribution of

soil fauna to N mineralization through microbial grazing increases.

PLACING SOIL FAUNA IN THE C AND N CYCLE

The focus of soil food web models upon C and N mineralization means that a critical pathway through which soil fauna may affect C cycling and N MIT is not addressed within the models (i.e., the effect of soil fauna on the quality and quantity of the DOM pool). As stated earlier, the production of labile DOM is the rate-limiting step in the N mineralization/immobilization process. Further, microbes may primarily be C limited in many environments (Wardle 1992), and hence effects on DOM-C production may have significant impacts upon the microbial biomass and consequently on the C and N cycle. Soil biologists are well aware of the role of soil fauna in C dynamics (see Bardgett 2005), but they have not integrated this with N MIT processes. Curiously, this is the role that Schimel and Bennett (2004) attribute to soil fauna in their diagram of the N MIT cycle (Fig. 1a), while they acknowledge other mechanisms elsewhere. This is all the more insightful because few studies have examined the effect of fauna on DOM supply (e.g., Cole et al. 2002, Liiri et al. 2002, van Vliet et al. 2004).

Experimental work clearly demonstrates that soil fauna affect the DOM pool. Both Cole et al. (2000) and van Vliet et al. (2004) found that enchytraeids increased soil DOM-C levels significantly. In the former study, this increase was associated with increased microbial respiration, while in the latter study, the effect of the enchytraeids was dependant upon soil type. Liiri

TABLE 1. Extended.

C mineralized to CO ₂	N mineralized to NH ₄	N mineralized (%)
0.15	0.005	5
0.15	0.007	7
0.18	0.006	6
0.24	0.024	24
0.33	0.028	28
0.32	0.032	32
0.39	0.034	34
0.40	0.027	27
0.40	0.057	40
0.40	0.080	40
0.56	0.130	65
0.15	0.043	17
0.15	0.044	18
0.18	0.051	20
0.33	0.103	41
0.38	0.128	51
0.40	0.132	53
0.57	0.183	73

et al. (2002) also show an effect of microarthropod species richness on DOM-C, although this effect was not apparent after the mesocosms in their experiment were stressed by drying. Litter bag studies demonstrate that the presence of microarthropods on organic matter substrates (i.e., particulate organic matter) increases mass loss by an average of 23% (Seastedt 1984). This effect is principally on mass loss of C and few studies find an effect of soil fauna on N loss from organic matter (Seastedt 1984). Schimel and Bennett (2004) consider the combination of mass loss and CO₂ production as sufficient to account for DOM-C supply. Therefore, the effects of soil fauna on mass loss of particulate organic matter (POM) and frequently on microbial respiration point to soil fauna facilitating DOM-C supply to microbes.

Using the parameters employed in food web models provides insight into how different soil fauna may affect the DOM and inorganic N pools. The key parameters are the C assimilation and production efficiency, the C:N ratio of the fauna, and the C:N ratio of their prey (Table 1). Within soil food web models, assimilation efficiency determines the amount of a food resource retained for growth and physiological maintenance, with the rest being excreted. The production efficiency describes the amount of assimilated C that is retained as biomass. These models assume that assimilation efficiency is the same for both C and N (e.g., Hunt et al. 1987), although this has not been demonstrated experimentally. Hence fungal-feeding fauna excrete material with a C:N ratio equivalent to fungi (usually 10:1 in food web models) and bacteria-feeding fauna excrete material with a C:N ratio equivalent to bacteria (usually 4:1 in food web models). Using these parameters, we see that there is a group of fauna that are efficient assimilators of C and N and hence excrete only small amounts, and due to their C:N ratios and that of their

prey, mineralize a very high proportion of the total N they ingest (Table 1). These fauna are either bacterial feeders or are predatory on other animals. For example, protozoa, bacterial-feeding nematodes and mites, as well as predatory mites fall in this group. Protozoa are primarily in the lower trophic groups that Laakso and Setälä (1999) considered most important for N mineralization. There is also a second group that assimilate C and N poorly and hence excrete a high proportion of ingested material and mineralize only a very small percentage of the N that they ingest. These are primarily fungal-feeding animals. Fauna such as enchytraeids, microarthropod microbivores, and fungal-feeding nematodes fall into this group (Table 1). Due to their low assimilation efficiency and their food source, this latter group should be excreting a proportionately large amount of material with a high C:N ratio, compared with the bacteria-feeding fauna. However, the solubility of feces from the fauna will ultimately determine their effect on the DOM pool. The buildup of enchytraeid or collembola excreta in some soils demonstrates that there is some recalcitrance in the feces of some fauna (see Dash 1990). Unfortunately there is a paucity of data on the C:N ratio of feces from soil fauna.

These two groups, efficient and inefficient assimilators, are essentially the fauna associated with the bacterial and fungal pathways, respectively; a distinction made in food web studies for many years (e.g., Hunt et al. 1987, Moore et al. 2003). However this is dependent upon the assignment of groups within particular studies. For example, de Ruiter et al. (1993) ascribe protozoa to the bacterial channel, while Schröter et al. (2003) consider them as panphytophagous, consuming both bacteria and fungi (Table 1). In such food webs, however, enchytraeids are part of three channels, feeding on bacteria, fungi, and directly consuming POM.

The different parameters for fauna groups and their prey from different food web models demonstrate the sensitivity of possible outcomes for C or N production from the soil fauna (Table 1). For example, the percentage of N mineralized for fungal-feeding nematodes calculated using the values of de Ruiter et al. (1993) is ~24%, while it is only 6% using values from Schröter et al. (2003; see Table 1). Darbyshire et al. (1994) demonstrate that the amount of NH₄ excreted by protozoa is highly sensitive to the C:N ratio of the food source. Predictions of contributions of faunal groups to N mineralization using food web models are also sensitive to microbial C:N ratio values (de Ruiter et al. 1993). Knowledge of the stoichiometry of different groups in different environmental circumstances is required to identify clearly taxa that contribute to inorganic N or DOM pools. Further, a complete assessment of how different soil fauna may affect the DOM pool requires calculation of feeding rates, using biomass and predation rates. However, this is an involved modeling exercise outside the scope of this paper.

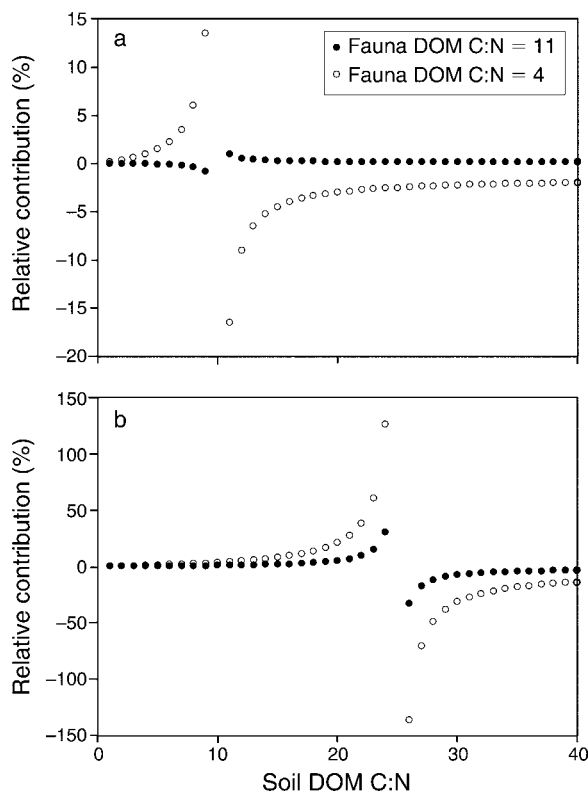


FIG. 3. Theoretical calculation of the relative contribution (percentage change in N mineralized or immobilized) from a 1% addition of DOM from faunal excretion with C:N ratio of either 4 (open circle) or 11 (solid circle) as soil DOM C:N changes. For the calculation it was assumed that there are 100 units of soil DOM-C, faunal excretion adds 1% more DOM-C, and the microbes have a production efficiency of 40% of C retained in biomass and 60% C respired. In (a) the microbial biomass has a C:N ratio of 4, such that the microbes mineralize N when the DOM C:N ratio is <10 and immobilize N when the DOM C:N is >10 . In (b) the microbial biomass has C:N of 10 such that the microbes mineralize N when the DOM C:N is <25 and immobilize N when DOM C:N is >25 . Note the different scale of the y-axis between (a) and (b).

POTENTIAL EFFECTS OF FAUNA ON C AND N DYNAMICS THROUGH DOM SUPPLY

The potential effects of faunal excretion on C and N dynamics through the DOM pool will be dependent upon its C:N ratio and the physiological parameters of the microbes. For the following discussion we term the optimum DOM C:N ratio for microbes as the value for which all available DOM-N is retained in the biomass. The central values in Fig. 2 (i.e., DOM C:N 25:1) would represent the optimum for the production efficiency and C:N ratio of the microbial biomass in that example. The relative effect of faunal contributions to N MIT through DOM input with C:N ratio above and below the optimum for microbes is shown in Fig. 3. To draw Fig. 3, we assumed that there were 100 units of soil DOM-C, faunal excretion added 1% more DOM-C (i.e., pool size becomes 101 C units), the microbial biomass

had a C:N ratio of either 4 (e.g., bacteria, Fig. 3a) or 10 (e.g., fungi, Fig. 3b), a production efficiency of 40% of C retained in biomass and 60% C respired, and that microbes use all available DOM-C. The relative contribution of fauna to N MIT was then calculated as the percentage difference in N mineralized or immobilized between 100 and 101 units of C being converted to microbial biomass, including the N contributed by the fauna in the 1 unit of DOM (0.25 and 0.091 units of N for fauna DOM C:N ratio of 4 and 11, respectively, in Fig. 3). The optimum DOM C:N ratio is 10 in Fig. 3a, hence mineralization occurs when soil DOM C:N ratio is <10 and immobilization occurs when it is >10 . Fauna excreting DOM with C:N ratio <10 (C:N = 4 in Fig. 3a) add more N than is required by bacteria to use the additional 1 unit of DOM-C provided, and consequently this N is mineralized (a positive relative contribution). When the soil DOM-N becomes limiting for the microbes (i.e., DOM C:N >10 in Fig. 3a), the bacteria use the additional DOM-N supplied by the fauna rather than immobilizing N from the inorganic pool, such that N immobilization is reduced (a negative relative contribution to N immobilization). In Fig. 3, the fauna excrete the same amount of DOM-N irrespective of the soil DOM C:N ratio. Hence the relative contribution of the DOM supplied by the fauna to N mineralization or immobilization is maximal as the soil DOM C:N ratio approaches the optimum for the microbes, as, at this point, the amount of N mineralized or immobilized by the microbes approaches zero. This same pattern occurs if fauna excrete DOM with C:N ratio >10 (excreted C:N = 11 in Fig. 3a). However, in this case, the DOM-N supplied by the soil fauna is less than required by the microbes to use all of the additional DOM-C supplied by the fauna, causing less mineralization at low soil DOM C:N ratio (<10 , a negative relative contribution to mineralization) and greater immobilization at higher soil DOM C:N ratio (a positive relative contribution to immobilization; Fig. 3a). The magnitude of the effects of DOM production by the fauna increases as the C:N ratio of the excreted material moves further away from the optimum for the microbes (compare the scale of the relative contribution axis between Fig. 3a and Fig. 3b) and as the quantity of DOM excreted by the fauna increases. It is important to note that, in this example, the DOM-C supplied by the fauna causes a 1% increase in CO_2 production while the relative effect on N MIT can be much higher than this when soil DOM C:N ratio is close to the optimum for the microbes (Fig. 3a, b).

The formulation in food web studies, where fauna excrete material with a C:N ratio equivalent to their food source means only bacterial-feeding and predatory fauna should be excreting material with a C:N ratio less than the optimum for the bacterial community, and hence be causing increased mineralization from the microbial biomass. In our example, fungal feeders excreting material with a C:N ratio of 10 would have

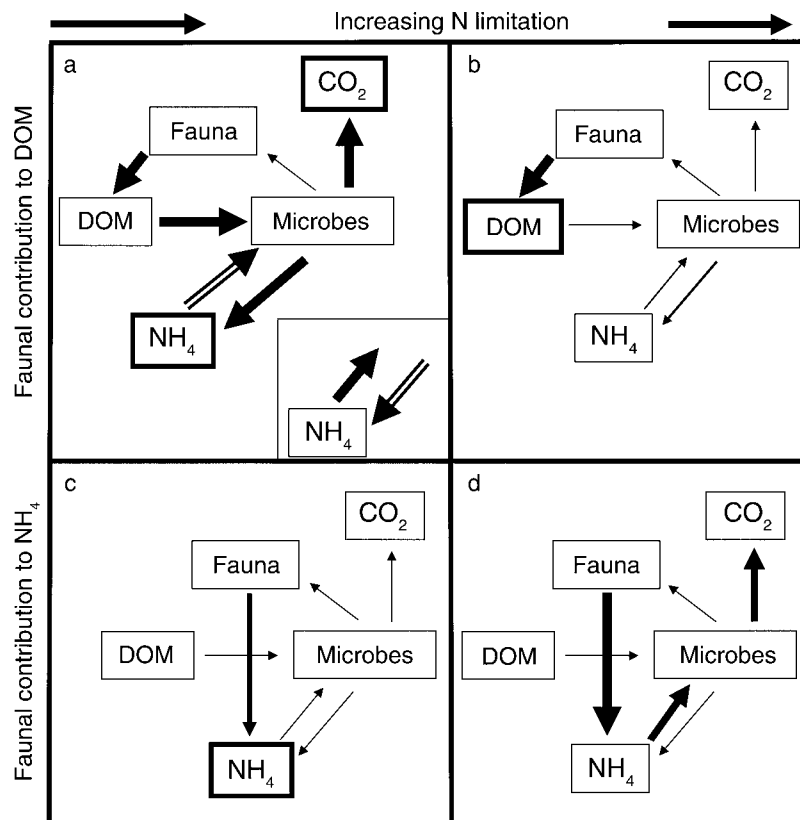


FIG. 4. A framework for understanding the relative contributions of fauna to the DOM and inorganic N pools, CO_2 production, and gross N fluxes in soils with increasing N limitation. An open arrow indicates a decrease in the process rate caused by the fauna; thickened solid arrows indicate a positive effect of faunal contribution to the soil C and N cycle; and thickened boxes represent pools that may be affected by the fauna. In panel (a), fauna contribute DOM with C:N ratios below the optimum for microbes while, in the inset, the faunal DOM-contributed C:N ratio is above the optimum for microbes. The decrease or increase in process rates associated with N MIT in panel (a) is dependant upon soil DOM C:N ratios. In (b), microbes are unable to use increased DOM availability due to low soil N levels, and hence DOM accumulates. In (d), microbes are immobilizing N and soil fauna release NH_4 through grazing on the microbial biomass while, in (c), microbes tend to mineralize N and hence relative faunal contributions to the inorganic N pool are less.

no impact on N MIT from the bacteria (Fig. 3a) as this is exactly the optimum C:N ratio for the bacteria, so that all of the DOM-N excreted by the fauna is retained in the biomass. This prediction will change if the physiological parameters of the bacteria are altered (e.g., production efficiency changed to 30% instead of 40%). This prediction may also change if the assumption in food web models that assimilation efficiency is the same for both C and N is incorrect, and N is preferentially assimilated over C, in which case fungal feeders may then excrete material with a higher C:N ratio than is optimal for bacteria. All fauna should, however, have similar effects on fungal mineralization for which the optimal soil DOM C:N ratio is on the order of 25:1 (Fig. 3b).

A FRAMEWORK TO INCORPORATE SOIL FAUNA INTO THE SOIL C AND N CYCLE

Using this formulation, we can now construct a framework for the effects of excretion by soil faunal on

C and N cycling (Fig. 4). Where the microbial community is N limited, microbes assimilate rather than release N (Fig. 4b, d). In these situations, the effect of fauna that increase soil DOM production may do little for N dynamics as microbial populations are already N limited and consequently are unable to use more DOM (Fig. 4b). Consequently, the soil DOM pool may increase. While the microbial community is N limited, grazing on the microbial population by fauna releases N and the contribution of the fauna to net N mineralization may be relatively high (Fig. 4d). However, the microbes may readily assimilate the NH_4 excreted by the fauna such that no increase in the inorganic N pool will be apparent, although it may be reflected through increased immobilization rates from the inorganic N pool and increased CO_2 production.

When N availability increases (Fig. 4a, b), the effect of fauna increasing soil DOM production may enable microbes to take up more DOM. If the microbial community rapidly assimilates the DOM, a faunal effect

on the DOM pool may not be apparent by looking at the pool size but rather may be expressed by greater CO_2 production. Irrespective of the size or C:N ratio of the DOM pool, fauna that contribute to the DOM pool by excretion should cause an increase in CO_2 production when there is sufficient N for the microbes to use the increased C supply (Fig. 4a). The consequences of DOM excretion by soil fauna for N MIT will then be dependant upon the C:N ratio of the excrement, the optimum C:N ratio of the microbial population, and the soil DOM C:N ratio (Fig. 3). Where the C:N ratio of the excreted DOM is below the optimum for the microbes (most likely in relation to bacterial feeders) the overall change in DOM quality caused by the fauna should lead to increased mineralization or reduced immobilization, and therefore potentially increase the size of the NH_4 pool (Fig. 4a). In contrast, if the DOM excreted has a C:N ratio above the optimum for the microbes, the change in DOM caused by the fauna could lead to increased immobilization or reduced mineralization, and therefore potentially reduce the size of the NH_4 pool (Fig. 4a, inset). As soil N availability increases, the microbial contribution to the inorganic N pool increases. Hence, direct contributions of fauna to the inorganic N pool are relatively less, although this may still be a significant contribution to net N mineralization, as soil food web models demonstrate (Fig. 4c).

Inefficient assimilators, principally fungal feeders, have the potential to contribute greater quantities of DOM relative to bacterial feeders. This makes it more likely that their effects on microbial respiration (CO_2 production) through DOM supply will be detectable. Further, as these fauna are excreting material of a quality that may be close to the optimum for bacterial populations, they have the greatest potential to excrete DOM that may be above the optimum C:N ratio for bacteria. This would occur, theoretically at least, if there is differential assimilation between C and N in these fauna. Such DOM excretion would lead to decreases in the inorganic N pool through either decreased mineralization rates or increased immobilization rates (Fig. 4a, inset). In contrast, the more efficient assimilators (bacterial feeders) may contribute only small amounts to the DOM pool and hence detection of effects on microbial respiration may be more difficult. However, a small contribution of DOM with a low C:N ratio has the potential to have relatively large impacts on N MIT and therefore on inorganic N pools (open symbols in Fig. 3).

The formulation in Fig. 2 demonstrates that increases in DOM may lead to increases in microbial biomass. However, the soil fauna responsible for altering DOM C:N ratio is also feeding upon the microbial biomass, as are other fauna. Hence, we may not see an increase in microbial biomass with changes in soil fauna communities, and consequently this pool is not highlighted in Fig. 4. However, soil fauna grazing on one community (e.g., fungi) may be contributing DOM to other components of the microbial community (e.g., bacteria).

Therefore they may cause a decrease in fungal biomass and either an increase or no change in bacterial biomass. To this end, Kaneko et al. (1998) found that a mite, *Oppiella nova*, decreased fungal biomass and increased respiration. Likewise, Cole et al. (2002) found that enchytraeids decreased fungal biomass, increased DOM-C, but had no effect on plant growth (see also the discussion by Bardgett and Chan [1999] of interactive effects of fungal-feeding Collembola and bacterial-feeding nematodes). Understanding this balance between changes in microbial biomass with grazing vs. faunal effects on inorganic N supply and DOM production is extremely important, as the microbial population exerts such a strong influence on N MIT and therefore on plant nutrient availability.

The framework presented here points to particular fauna affecting different fluxes in different environments that helps to identify the particular pools and fluxes that specific fauna will affect within an environmental context. This should facilitate greater understanding of the role of soil fauna in the C and N cycle but may require the use of new techniques. While microbial respiration has been measurable for some time, techniques for determining gross N fluxes have only been developed relatively recently, and tractable methods for determining DOM-N flux are not yet available (Schimel and Bennett 2004). The DOM pool is highly dynamic: available forms of DOM-N may be used within hours (Jones 1999) and DOM-C is rapidly replenished following leaching (e.g., Judd and Kling 2002). However, the majority of this C may be from older soil C stocks that are of a quality not easily used by microbial populations. Measuring CO_2 production and quantifying DOM simultaneously may help to identify the effects of soil fauna on DOM supply. The same inorganic N pool size may be the consequence of quite different summations of gross N mineralization and gross N immobilization. Hence, soil fauna may affect C and N fluxes dramatically but show no indication of affecting net N mineralization rates.

The discussion by Cole et al. (2002) of the disparate results of their study in comparison with those of Bardgett and Chan (1999) provides an excellent example of the applicability of this model. Cole et al. (2002) added enchytraeids to microcosms constructed using soil from a blanket peat bog, where NH_4 levels were in the order of $100 \mu\text{g N/g dry mass}$. The enchytraeids decreased microbial biomass (principally fungal biomass) and increased DOM-C but had no effect upon nutrient availability or plant nutrient content (e.g., Fig. 4b). Bardgett and Chan (1999) conducted a similar experiment but in organic soils with NH_4 levels on the order of $12 \text{ mg N/g dry mass}$, at least at the start of the experiment, and using bacterial-feeding nematodes and fungal-feeding Collembola. In this case, the presence of the collembolans either on their own or in combination with the nematodes increased soil NH_4 (e.g., Fig. 4a, c). Cole et al. (2002) speculated that the differential effect of

the fauna between these two experiments was a consequence of the higher C:N ratio of their soil compared with that used by Bardgett and Chan (1999), which may have resulted in the remaining microbial populations rapidly assimilating any available N released through enchytraeid activity. This interpretation agrees with the proposed model (Fig. 4b). Another possibility is that the assimilation efficiency of the enchytraeids and the quality of their food source in the mesocosms was insufficient to affect inorganic N supply. As the enchytraeids appeared to be feeding on fungi, food web parameters predict they will contribute to the DOM pool but may have little effect on N mineralization (e.g., Table 1; solid symbols in Fig. 3).

OUTLOOK

The framework developed here is theoretical, and although it can already be corroborated by some experimental data sets, it requires further validation through both modeling and experimental approaches. The framework could be assessed further by including the contribution of the soil fauna to the DOM pool in food web models, to assess the importance of fauna for N cycling through this mechanism. This will require some development of the food web models. Presently only one model allows the C:N ratio of the substrate to be dynamic (Hunt and Wall 2002) and inputs of DOM from soil fauna will change the C:N ratio of the "substrates" used by the microbes. It is well known that the models are very sensitive to the C:N ratios used throughout the models (de Ruiter et al. 1993). Knowledge of the solubility of excreta is also required to parameterize a model, and this may also help to determine if the assumption in soil food web models that C and N are assimilated with equal efficiency is valid.

New techniques using stable isotopes and biomolecules will be useful to parameterize models in different environmental contexts in the future (Moore et al. 2004). Assimilation efficiencies used in food web models are derived from a few studies conducted in the 1970s. The development of stable isotope tracing into faunal pools will facilitate determining these efficiencies and the feeding sources of different fauna in a greater array of environmental circumstances (e.g., Albers et al. 2006). Stable isotopes also help to clarify the feeding groups to which various fauna belong. For example, using natural abundance ratios of ^{15}N , Schneider et al. (2004) show that some oribatid mites are predatory on other soil fauna. This changes the classification of this group that is usually isolated within a microbe-feeding guild in soil food web models. Further, one of the groups they identify as predatory, the Oppiidae, are some of the most persistent (Osler and Beattie 1999) and dominant oribatids across habitats (Maraun and Scheu 2000). Hence, their role within the N mineralization process may not have been well-modeled in the past. Further, feeding biology may change with habitat and ontogeny

(Behan-Pelletier and Hill 1983) and fauna have preferences for particular components of the microbial biomass (e.g., Maraun et al. 1998a) such that the effect of specific fauna on processes may be variable in different circumstances. Stable isotopes, and use of lipid analysis in combination with stable isotopes (e.g., Russ et al. 2005), may be efficient methods for determining these changes rather than through time consuming studies of gut contents.

We have considered potential effects of soil fauna on the C and N cycle in a nebulous soil matrix context. Applying the model to their effects on specific substrates (i.e., particulate organic matter [POM]) is far more difficult. In this more complex case, taking account of the cost of exo-enzyme production and the quality of the DOM liberated by the microbes becomes very important. The effects of soil fauna on decomposition rates are most apparent on poorer quality POM (Seastedt 1984, Couëteux et al. 1991, Tian et al. 1995). Fig. 3b indicates that DOM supplied by fauna when soil DOM C:N ratio is in the region of 25:1 leads to either increased N mineralization or decreased immobilization. This may, in fact, represent an N source that facilitates fungal production of exo-enzymes, which have a very high N requirement (Allison 2005), and hence enable increased decomposition. Further, the fauna have other effects on the decomposition of substrates that are not a consequence of the consumption of microbes. For example, fauna are able to transport microbes and other materials within the soil matrix (Anderson 1988, Maraun et al. 1998b), and direct feeding on the substrate can radically transform it physically (e.g., Webb 1991). Even the carcasses of animals (i.e., their contribution to soil POM) can affect C and N dynamics (e.g., Perez-Moreno and Read 2001, van Vliet et al. 2004).

Finally, the fact that the contribution of fauna to the N cycle has not been integrated into biogeochemical models may be due to the process involved in calculating N fluxes. Models for calculating gross N mineralization (e.g., Mary et al. 1998, Müller et al. 2004) work on a mass balance approach that assumes all mineralization and immobilization is driven by microbes but takes no account of microbial biomass or respiration (other than in terms of N immobilized in organic forms). Hence, predictions of soil N supply derived using microbial N MIT data have to be reconciled with observed inorganic N pools and microbial biomass through longer periods of time (Murphy et al. 2003). However, direct contributions of soil fauna are never accounted for. This is perfectly reasonable based on the short-term incubations required to determine fluxes. Accounting more fully for faunal contributions to soil C and N cycling becomes most pressing when systems are managed for utilitarian ends (see, e.g., Janzen 2006). In these cases, probable changes to soil fauna communities brought about through management (e.g., an altered tillage regime) may be important for outcomes for C and N cycling. Further, taking greater account of fauna contributions

to the C and N cycle may lead to more accurate predictions of soil N supply than are currently made using either biogeochemical or food web based models (e.g., de Ruiter et al. 1994, Garnier et al. 2003).

CONCLUSIONS

In conclusion, it is clear that the effects of soil fauna on soil C and N cycling occur through all pools and fluxes associated with the process. We have presented a framework that can help to integrate the soil fauna into models of these processes and assist in targeting measurements on appropriate processes in relation to the fauna in manipulative experiments. Validation of the model is required and this will need efforts from a range of different disciplines. The framework is potentially of use to soil chemists and zoologists to interact as, to date, they have tended to work in parallel and consequently their models fail to capture all of the processes and possible outcomes of interactions in these vital processes.

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