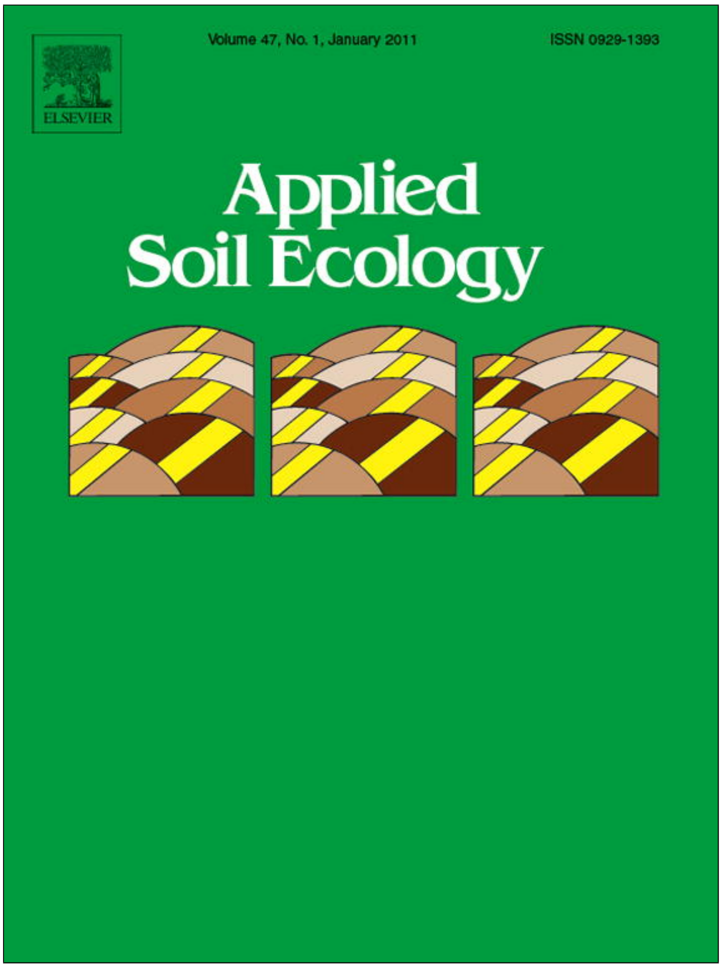

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Linking invertebrate communities to decomposition rate and nitrogen availability in pine forest soils

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ABSTRACT

Interpretation of biological indicators of soil quality depends on their ability to reflect ecological processes such as decomposition and nutrient mineralization. Mineral soils in pairs of relatively undisturbed and disturbed pine forests in each of three land resource regions of North Carolina (i.e., coastal plain, piedmont, and mountains) were monitored 15 times over two years. Abundance of nematodes in 35 families, collembolans in 8 families, and 16 other microarthropod taxa were enumerated. Nematodes were identified only in mineral soil whereas microarthropods were identified separately in litter and mineral soil. Rate (mg lost per day) of cellulose and wood decomposition were estimated based on weight loss of standardized substrates enclosed in litter baskets; available nitrate (NO_3^-) and ammonium (NH_4^+) were quantified in soil. Principal components analysis was performed on 59 invertebrate taxa to identify the taxa explaining the greatest proportion of variation in the monitored community. Soil microclimate and chemical properties were included as covariables. Canonical correlation was performed to quantify the relationship between soil invertebrate communities and indicators of ecological processes. Variation in soil N availability and decomposition rate was best explained when the two microfaunal communities, nematodes and arthropods, respectively, were examined separately. Nematode communities explained 2.3–6.9% of the variation in NO_3^- and NH_4^+ availability, indicators of N mineralization, in disturbed forests compared to 8.6–12.4% in undisturbed forests. In contrast, arthropod communities explained 11–14.8% of the variation in decomposition rate in disturbed forests compared to 2.8–14.3% in undisturbed forests. These results are the first to quantify, from a wide and realistic spatial variability in the environmental factors, the value of *in situ* soil microfaunal communities as indicators of soil processes, N availability and decomposition.

1. Introduction

For the past 60 years, ecological scientists have pursued an integrated definition and metric of soil quality (e.g., Howard, 1947; Brussaard et al., 1997). In the past 30 years, considerable attention has been given to soil invertebrates, such as nematodes and arthropods, demonstrating that these ubiquitous members of the soil community may be used as indicators of soil quality because they reflect ecological processes (Coleman, 2008). Changes in soil quality can serve as an indicator of change in the soil's structural and biological integrity and reflect degradation from environmental stresses (Wander and Drinkwater, 2000). Soil fauna affect soil carbon (C) and nitrogen (N) cycles through their interactions and effects on microbial biomass, inorganic and organic N pools, and soil organic matter pools (Yeates, 2003; Osler and Sommerkorn, 2007). For example, an estimated 20–30% of yearly litter input is consumed by the soil microarthropod community (Seastedt, 1984) and collembolans consume an estimated 6% of yearly litterfall (Van Straalen, 1989). In forest environments, where N may be limiting, soil fauna can make greater contributions than microbial communities to N mineralization through microbial grazing by soil fauna (Yeates, 2007). For example, abundance of total, bacterivorous, and fungivorous nematodes correlate positively with net N mineralization in forest soils (Forge and Simard, 2000). Collembolan fecal pellets contain 40 times more available nitrate (NO_3^-) than their food, and results in an estimated 2.4 times higher NO_3^- availability in forest litter, apart from any indirect effects such as increases in soil aggregate stability (Teuben and Verhoef, 1992).

Environmental disturbance can significantly and variably affect composition of soil nematode (Neher et al., 2005) and microarthropod (Barbercheck et al., 2008) communities. Disturbance of soil that changes physical, chemical and biological properties can have a cascading effect on other factors defining habitat, e.g., moisture, oxygen availability, and soil chemistry (Wall, 1999). For example, there is little evidence that rate of litter decomposition in forest ecosystems responds to disturbance such as harvest or

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fertilization in high elevation spruce-fir forests in British Columbia (Prescott et al., 2003). Likewise, disturbance did not affect decomposition rate of cellulose or balsa wood substrates in pine forests in North Carolina (Neher et al., 2003). Slow decomposition rates in forest soils are correlated with lower total N, electrical conductivity, and pH (Neher et al., 2003). In pine forests in North Carolina, soil microarthropod diversity, abundance of ants, and proportion of enchytraeids in the mesofauna differ between soils of different disturbance levels (Barbercheck et al., 2008). In British Columbia, Forge and Simard (2000) observed reduced abundance of fungivores in clearcuts compared with mature forests. In contrast, Neher et al. (2005) observed greater relative abundance of fungivores, and smaller abundance of bacterivores, in recently harvested compared to more mature pine forests in North Carolina. Alterations in soil food web structure can result in significant changes in decomposition processes (Setälä, 2002).

The target audience of large-scale environmental monitoring programs is often policy makers who have little working knowledge of ecology or microscopic animals. As indicators, soil invertebrates reflect changes in soil quality from management practices and changes in policy. It is the relationships of bioindicators to soil function or ecological processes, rather than the taxonomic identity of a specific invertebrate, that is of primary concern. Two critical ecological processes that soil performs are decomposition and nutrient cycling. The contribution of invertebrates to these processes has been estimated in models (de Ruiter et al., 1993a,b, 1994; Osler and Sommerkorn, 2007), but few have quantified these relationships empirically (Crossley et al., 1992; Neher, 1999a).

The objective of the present study was to quantify the relationship between soil invertebrate communities and two indicators of soil function, decomposition rate and N availability, in pine forests across three land resource regions and two contrasting stand ages in North Carolina. We hypothesized that nematodes and microarthropods contribute significantly and variably to these ecological processes in forest soils and litter.

2. Materials and methods

2.1. Study sites and experimental design

This study is part of a larger project to identify invertebrate indicators of ecosystem condition and function, using physical disturbance as a proxy for ecosystem stress (Barbercheck et al., 2008; Neher et al., 2003, 2005). The aim was to include wide and realistic spatial variability in the environmental factors involved in influencing both the processes addressed and the soil fauna. We sampled paired sites with similar soil type and watershed in each of three ecosystems in each of three land resource regions (LRR) (i.e., coastal plain, piedmont, and mountains) in North Carolina, to represent relatively undisturbed and disturbed systems (Barbercheck et al., 2008; Neher et al., 2003, 2005; USDA-SCS, 1981) (Table 1). In this study, relatively young, disturbed forests had been harvested within the previous three years whereas relatively old, undisturbed forests had not been harvested for at least 50 years. For convenience, we will now refer to these sites as "disturbed" or "undisturbed" forests, respectively. The vegetation in undisturbed forests was dominated by trees, whereas the relatively disturbed forests were comprised of a mix of young trees, shrubs, forbs and grasses (Neher et al., 2003).

Samples were collected for soil invertebrates, ecological process, and soil properties at all sites seven to eight times per year for 2 years (1994: March, April, May, July, September, October, November; 1995: January, March, April, May, July, September, October, November) following Neher et al. (2003, 2005) and Barbercheck et al. (2008). Fifteen sampling dates allowed for comparison of invertebrates and processes at different time intervals with statistically acceptable sample sizes. For example, all sampling dates ($n = 76$) were available for concurrent or 0-month time lags. In contrast, 1-month time lags ($n = 40$) and 2-month time lags ($n = 54$) were possible for some date combinations but not all. For example, March samples could be compared with April for 1-month time lags and compared with May for 2-month time lags. No 1-month time lags were possible for July and November samples.

2.2. Soil samples

Because many soil characteristics are aggregated spatially, soil samples were collected using a systematic design. Two sets of soil samples were taken along two independent diagonal transects within a 2-ha area, with unique random starting points (Neher et al., 1995). Samples of mineral soil were collected using an Oakfield tube soil probe (2.5-cm diameter, 20-cm depth); litter layers in forest and wetland were sampled separately by hand. The soil or litter from each transect was pooled to form two composite samples comprised of 20 cores per site on each sample date. These samples were homogenized by hand in a bucket. Soil properties measured from each site included percentage soil organic matter (OM), pH, electrical conductivity (EC), and available NO_3^- and NH_4^+ (Neher et al., 2003). Daily means for soil temperature and moisture were recorded with Campbell 21X dataloggers using thermistors and gypsum blocks, respectively, with sensors placed at 20-cm depth to match the maximum depth of sampling invertebrates. Soil OM was determined by loss-on-ignition (Schulte et al., 1991). Soil pH and EC were measured according to Smith and Doran (1996). Available pools of N were extracted using potassium chloride and measured as the colorimetric net product of nitrogen mineralization. NO_3^- was determined by the method of Cataldo et al. (1975). The indophenol blue method was used to determine NH_4^+ availability (Keeney and Nelson, 1982). EDTA was added to the soil filtrate to prevent interference by calcium and magnesium ions.

2.3. Decomposition

Standardized substrates, that contained either predominantly cellulose or wood, were employed to quantify decomposition rate through 2 years (Neher et al., 2003). Round (2-cm diameter) disks of museum board (Strathmore, 100% cotton fiber, i.e., 100% cellulose, acid free and buffered with 2% calcium carbonate), and balsa wood (Midwest Co., 0.793 mm thick, 19.9% insoluble lignin, 0.42% soluble lignin, 77% cellulose) substrates does not necessarily mimic the complexity each type of decomposition processes in native materials, but they provide a standard means of comparison across sites.

To estimate rate of decomposition, three litter baskets (10 cm × 10 cm × 10 cm) constructed of galvanized hardware cloth (0.5 cm mesh) buried at each site along each of two transects at equal intervals (Blair et al., 1991; Neher et al., 2003). To install the baskets, a 10 cm × 10 cm × 10 cm cube of soil was removed so that the structure and litter layer of the soil were disturbed minimally. The cube of excavated soil was placed inside the basket and the baskets placed in the excavation hole so that the top of the basket was flush with the soil surface. After the baskets were placed in the soil, 20 disks each of museum board [mean initial weight (±SE) 184.7 mg (±0.39)] and balsa wood [mean initial weight 61 mg (±0.41)], dried at 70 °C and weighed, were placed between two 10 cm × 10 cm sheets of plastic window screen (1 mm mesh openings) to exclude predation by macrofauna. This decomposition substrate-screen "sandwich" was placed on the soil surface inside the basket and the lid of the basket closed to maintain structural stability. At every sample date, one disk each of museum board and balsa wood were removed from each basket and returned to the laboratory for immediate analysis. Museum board disks were retrieved

Table 1
Mean ± SE ($n = 30$) properties[a] of relatively disturbed (D, time since harvest < 3 years) and relatively undisturbed (U, time since harvest > 50 years) pine forest study sites in North Carolina.

Land resource region	Forest type	Soil type	Vegetation history	N (μg/g)	EC (dS m^{-1})	SOM (%)	pH
Mountain	D	Clayey	Harvested in 1990; hilltop planted to white pine, *Pinus strobus*, in 1993	2.3 (±0.33)	0.05 (±0.006)	5.8 (±0.25)	4.8 (±0.09)
Piedmont	D	Sandy clay loam	Loblolly pine, *Pinus taeda*, planted 1992	1.7 (±0.11)	0.05 (±0.004)	6.7 (±0.13)	4.8 (±0.05)
Coastal Plain	D	Fine sandy loam	Loblolly pine planted in 1992	1.9 (±0.29)	0.06 (±0.006)	2.2 (±0.05)	4.7 (±0.07)
Mountain	U	Clayey	>90 year old white pine (dominant) with holly, *Ilex vomitoria*	2.4 (±0.27)	0.09 (±0.007)	4.9 (±0.15)	4.6 (±0.04)
Piedmont	U	Sandy clay loam	Loblolly pine planted in 1939	2.3 (±0.16)	0.08 (±0.008)	5.1 (±0.07)	4.9 (±0.22)
Coastal Plain	U	Fine sand	>80 year old longleaf pine, *Pinus palustris*, (dominant) with loblolly bay, *Gordonia lasianthus*	1.7 (±0.12)	0.07 (±0.002)	4.9 (±0.22)	4.2 (±0.06)

Adapted from Neher et al. (2003).

[a] EC, electrical conductivity; SOM, soil organic matter (Neher et al., 2003).

and weight loss estimated by differential moisture contents of substrates incubated at constant water potential (Herrick, 1995). Balsa wood disks were cleaned gently under running tap water with a soft toothbrush to remove adhering soil particles. Mass of substrate remaining was calculated as the difference between initial and final weight, expressed as a percentage of initial weight at each collection time. For convenience, when discussing decomposition rate of each substrate, we will refer to decomposition rate of balsa wood and museum board disks as wood and cellulose decomposition rate, respectively.

2.4. Nematodes

All soil samples were stored at 14 °C until nematode extraction to maintain community composition (Barker et al., 1969). Nematodes were extracted from soil only using a Cobb's sieving and gravity method (Ayoub, 1980), modified by triplicate passes through 710 μm, 250 μm, 150 μm, 75 μm, and 45 μm mesh sieves. The final pass through the sieves was followed by centrifugal-flotation, modified by using a 1:1 (v:v) sugar solution and centrifuging for 1 min (Neher and Campbell, 1994; Neher et al., 2005). Nematodes in each taxonomic family and trophic group recovered from 500 cm^3 of dry soil equivalent were enumerated and not corrected for extraction efficiency. A list of nematode genera observed within each taxonomic family was prepared for descriptive purposes (Neher et al., 2005). Nematodes were identified and enumerated by Mae Noffsinger (N & A Nematode Identification Service, Davis, CA).

2.5. Arthropods and enchytraeids

Separate 500 cm^3 aliquots of soil and litter from disturbed and undisturbed forest sites were placed in Tullgren funnels for five days during which microarthropods and incidental enchytraeids (Phylum Annelida, Subclass Oligochaeta) (hereafter for convenience referred to simply as “arthropods”) collected in 70% alcohol and 2% glycerol in vials for enumeration (Barbercheck et al., 2008). The extraction procedure targeted soil microarthropods and not enchytraeids (Panchenko, 2006). Even though the extraction procedure did not target enchytraeids, their numbers in our extractions were significant, and so are included here. Class Collembola were identified to family and all other arthropods were identified to class or order, depending on the organism.

2.6. Statistical analysis

Principal components analysis (PCA) was employed to identify the taxa explaining the greatest proportion of variation within the entire detected microinvertebrate community. Numbers of each taxon was transformed as ln $(x+1)$ prior to statistical analysis. Principal components analysis was performed using Canoco software version 4.5 (Ter Braak and Šmilauer, 2002). Software settings included interspecies correlation, species scores divided by standard deviation, no sample center, species center and standardize. Covariables of soil temperature, moisture, and chemical properties were included, as a third set of data, because they are associated with abundance and diversity of mesofauna (Barbercheck et al., 2008; Neher et al., 2005). For analysis, soil temperature and moisture were accumulated 1 month prior to sampling (Neher et al., 2003). Chemical properties were represented by pH, EC and OM. Treating physiochemical properties as covariables allows data to be adjusted for these secondary effects before quantifying associations between soil invertebrates and ecological processes.

Two types of correlations were performed: multivariatae canonical correlation and univariate, linear rank correlations. Correlations integrate direct and indirect contributions of biological activity and non-steady state dynamics. Direct effects include consumption, mineralization and dispersal of microbes. Indirect effects include trophic interactions and competition.

Multivariate canonical correlation procedures were used to quantify the relationship between microfaunal composition (nematodes and/or microarthropods) and ecological processes (available NO_3^- and NH_4^+, and rate of cellulose and wood decomposition) measured at 0, 1, or 2 months after taxa to evaluate potential time lag effects (Afifi et al., 2004). Invertebrate communities were expressed as PCA1 to PCA4 eigenvalues, providing parsimony to data without compromising information about community composition. Because of intercorrelation among variables within a canonical variable, canonical variable correlations rather than canonical variable coefficients were presented (Afifi et al., 2004). A Wilks' lambda statistic was used to test for significance of canonical correlations using the canonical correlation (CANCORR) procedure (SAS Version 9.1.3).

Univariate, linear rank correlations were performed to address two independent questions using the CORR (Spearman option because data were non-Gaussian in distribution) procedure (SAS Version 9.1.3). First, the correlation between soil invertebrate community composition (represented as PCA1 to PCA4) and ecological process indicator (nitrogen availability or decomposition rate) was computed. Second, the relationship between availability of nitrogen (NO_3^-, NH_4^+) and decomposition rate (cellulose, balsa wood) were determined. Correlations were performed between quantities of NO_3^- or NH_4^+availability at 5, 4, 3, 2, 1 and 0 months prior to decomposition rate of cellulose or wood to identify time lags between invertebrate community and ecological process indicators.

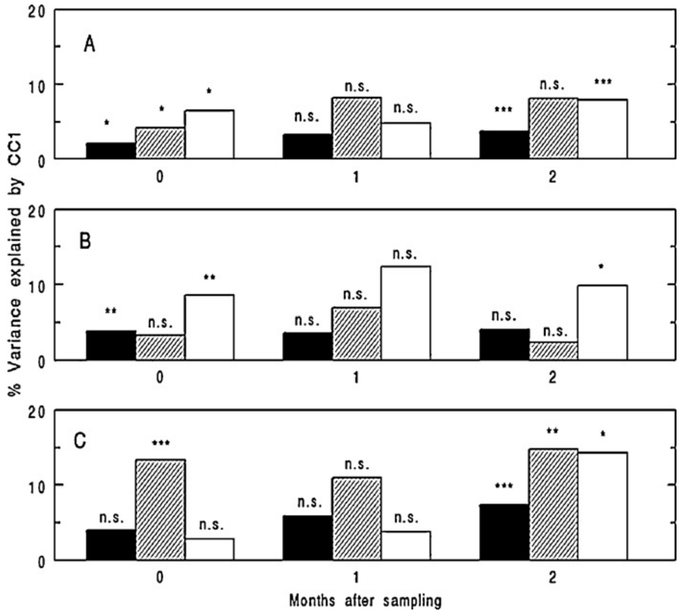

Fig. 1. Standardized variance explained by canonical correlation variable one (CC1) for the ability of (A) nematodes and arthropods to collectively explain available nitrogen (nitrate and ammonium) and decomposition rate (cellulose and wood), (B) nematodes to explain available nitrogen, and (C) microarthropods to explain decomposition rate. Communities were expressed as four PCA eigenvalues created while adjusting for soil moisture, temperature, pH, organic matter, and electrical conductivity. *P*-values for Wilks' Lambda statistics are illustrated (n.s.: $\geq$0.05, *: $\leq$0.05, **: $\leq$0.01, ***: $\leq$0.001) for each bar which represents a separate canonical correlation analysis of community composition and its' ability to explain nitrogen availability or decomposition rate at 0, 1, or 2 months later. Fill patterns represent forest disturbed and undisturbed pine forests pooled (black), disturbed forests only (hatched), and undisturbed forests only (white) in North Carolina.

3. Results

3.1. Invertebrate community composition

The first four PCA axes collectively explained 50% of the variation in taxa. Main weights in PCA1 were characterized by 12 nematode families, three collembolan families and three other microarthropod taxa (Tables 2 and 3). Nematode families explaining the most variance in PCA1 included Anguinidae, Aphelenchoididae, Cephalobidae, Criconematidae, Dorylaimidae, Longidoridae, Plectidae, Pratylenchidae, Prismatolaimidae, Rhabditidae, Tylenchidae, and Tylencholaimellidae (Table 2). Collembolan families explaining the most variance in PCA1 included the Entomobryidae, Hypogastruridae, and Isotomidae. Of the non-collembolan microarthropods, Acari (mites), Araneae (spiders), and ants (Hymenoptera: Formicidae) explained the most variance (Table 3).

3.2. Invertebrate correlations with soil nitrogen and decomposition

Variance of ecological process explained by soil invertebrates was greater when relatively disturbed and undisturbed sites were examined separately than pooled (Fig. 1). Further, more variance of an ecological process was explained by nematodes or arthropod rather than combined. Specifically, N availability was best explained by the nematode community and decomposition rate was best explained by litter and soil microarthropod community (Fig. 1).

Disturbance did not affect the availability of nitrogen (NO_3^- and NH_4^+ together were 1.7–2.3 μg/g in disturbed and 1.7–2.4 μg/g in undisturbed forests, respectively), but the percentage of variance explained by nematode communities of N availability, measured 0 and 2 months later, was greater in the undisturbed forests than in the disturbed forests (Fig. 1B). The first canonical correlation variable of nematode communities explained 2.3–6.9% of the variation in NO_3^- and NH_4^+ availability in disturbed forests compared to 8.6–12.4% in undisturbed forests.

The ability of microarthropod community to predict decomposition rate was greater in disturbed than undisturbed forests when decomposition rate was measured at the same time. Predictive ability was similar in both disturbed and undisturbed forests when decomposition rate was measured 2 months later (Fig. 1C). The first canonical correlation variable of arthropod communities explained 11–14.8% of the variation in decomposition rate in disturbed forests compared to 2.8–14.3% in undisturbed forests (Fig. 1C).

3.3. Soil nematodes

Nematodes extracted from forest soil were correlated with availability of NO_3^- and NH_4^+. The soil nematode community was characterized by PCA1 to PCA4 (Table 2). PCA1 or PCA2 correlated negatively or positively with NH_4^+ availability in disturbed forests, respectively (Table 2). NH_4^+ availability in disturbed forests was correlated positively with abundance of bacterivores (Alaimidae, Cephalobidae, Plectidae, Prismatolaimidae, Rhabditidae) and fungivores (Anguinidae, Aphelenchoididae, Diphtherophoridae, Tylenchidae), plant-parasites (Criconematidae, Hoplolaimidae, Trichodoridae, Tylenchulidae), and omnivores (Dorylaimidae). Two plant-parasite families (Longidoridae, Pratylenchidae) and one fungivore family (Tylencholaimellidae) decreased in abundance with an increase NH_4^+ in disturbed forests. PCA3 correlated positively with availability of NO_3^- in disturbed and undisturbed forests, and negatively with NH_4^+ in undisturbed forests. Nematode families with large eigenvectors within PCA3 were those typically associated with omnivorous and predaceous feeding behavior than was PCA1 or PCA2. Consistently, abundance of omnivores and predators increased with available NO_3^- in disturbed and undisturbed forests, and decreased with available NH_4^+ in undisturbed but not disturbed forests. PCA4 was not correlated significantly with either NO_3^- or NH_4^+ availability and was, therefore, not illustrated (Table 2).

3.4. Litter and soil arthropods

Arthropods extracted from forest litter or soils were correlated with decomposition rate of cellulose and wood (Table 3). PCA1 and PCA2 eigenvalues of litter or soil both correlated negatively with rate of wood decomposition in disturbed forests. Decreased rate of wood decomposition correlated positively with increased abundances of Isotomidae, Entomobryidae, Diplura, Acari, ants (Hymenoptera: Formicidae), and Diplopoda (millipedes) in both litter and soil. In litter (but not soil), decreased abundances of Tomoceridae, Araneae, and Isoptera correlated with faster rate of wood decomposition. In soil (but not litter), abundances of Hypogastruridae and adult Coleoptera correlated negatively with wood decomposition rate. PCA3 correlated positively with wood decomposition rate in disturbed forests only. Community PCA3 was characterized by increasing abundances of Neanuridae collembolans in litter and decreasing abundances of Coleoptera adults in soil. PCA4 correlated negatively with cellulose decomposition rate in disturbed and undisturbed forest, and wood decomposition rate in disturbed forest litter. PCA4 was characterized by increasing abundances of diplurans and millipedes (Diploda) in litter and soil.

3.5. Time lag between faunal abundance and ecological process

Availability of N (indicating net N mineralization) correlated linearly with nematode community composition (defined as PCA1 and PCA2 eigenvalues) more often at 2 than 1 or 0 months delay

Table 2
Principal component analysis (PCA) of soil nematode families and their correlation with available nitrate and ammonium in disturbed (D) and undisturbed (U) pine forests of North Carolina. Taxa in bold have species weights that exceed ±0.5 in PCA1 and/or ±0.4 in PCA2 and PCA3. The right four columns denote a direct or positive relationship (upward arrows) or inverse or negative relationship (downward-pointing arrows) between nematode families with relative large weights in PCA that were correlated significantly with nitrate or ammonium availability. Cells without arrows represent relationships that were not significant statistically ($P > 0.05$).

PCA axis	1	2	3	Trophic group[b]	C–P value[b]	Nitrate		Ammonium	
						D	U	D	U
						3+[c]	3+	1–, 2+	3–
Nematode family									
Alaimidae	0.0764[a]	**0.4440**	–0.2526	B	4			↑	
Anatonchidae	–0.2203	0.0235	–0.1399	P	4	–	–	–	–
Anguinidae	**–0.5072**	–0.0880	0.0240	F	2			↑	
Aphelenchidae	–0.2854	0.3615	0.0468	F	2	–	–	–	–
Aphelenchoididae	**–0.6240**	–0.0065	–0.0644	F	2			↑	
Belondiridae	–0.0896	0.2668	–0.1305	O	5	–	–	–	–
Belonolaimidae	–0.1638	0.1510	–0.0293	PP	2	–	–	–	–
Cephalobidae	**–0.8837**	–0.0782	0.0151	B	2			↑	
Criconematidae	**–0.5242**	0.1748	0.2172	PP	3			↑	
Diphtherophoridae	0.1312	**0.6958**	–0.0017	F	3			↑	
Diplogasteridae	–0.1968	–0.0626	–0.0635	O	1	–	–	–	–
Dorylaimellidae	–0.1487	0.1593	**0.4926**	O	5	↑	↑		↓
Dorylaimidae	**–0.8052**	0.0119	–0.0732	O	4			↑	
Heteroderidae	–0.1167	0.1528	–0.3421	PP	3	–	–	–	–
Hoplolaimidae	–0.4181	**0.4351**	0.2052	PP	3			↑	
Ironidae	–0.0480	0.1879	**0.5282**	P	4	↑	↑		↓
Leptolaimidae	–0.1397	0.2659	**0.5095**	B	3	↑	↑		↓
Leptonchidae	–0.1799	0.1162	–0.1054	O	4	–	–	–	–
Longidoridae	**0.5307**	0.3041	–0.1097	PP	5			↓	
Monhysteridae	–0.1274	–0.0139	–0.0021	B	2	–	–	–	–
Mononchidae	–0.2913	0.0733	0.0376	P	4	–	–	–	–
Mononchulidae	–0.0398	0.3216	–0.3286	P	4	–	–	–	–
Mylonchulidae	–0.2127	–0.1793	–0.0703	P	4	–	–	–	–
Nygolaimidae	–0.0479	0.0603	–0.1981	P	5	–	–	–	–
Panagrolaimidae	–0.0708	–0.1270	–0.0220	B	1	–	–	–	–
Plectidae	**–0.6011**	–0.0597	–0.1921	B	2			↑	
Pratylenchidae	**0.6624**	0.3547	–0.1228	PP	3			↓	
Prismatolaimidae	**–0.5775**	0.1181	–0.1315	B	3			↑	
Rhabditidae	**–0.5690**	–0.0275	–0.0180	B	1			↑	
Rhabdolaimidae	–0.1030	0.3797	–0.3771	B	3	–	–	–	–
Seinuridae	–0.1437	–0.0508	–0.1685	P	2	–	–	–	–
Teratocephalidae	–0.1016	0.1948	0.0610	B	3	–	–	–	–
Trichodoridae	–0.2643	**0.5260**	0.1515	PP	4			↑	
Tripylidae	–0.2108	–0.0623	–0.3430	O	3	–	–	–	–
Tylenchidae	**–0.8838**	–0.0014	–0.0062	F	2			↑	
Tylencholaimellidae	**0.5521**	0.3965	–0.0690	F	4			↓	
Tylencholaimidae	–0.4093	0.0293	–0.1470	F	4	–	–	–	–
Tylenchulidae	–0.3023	**0.4263**	–0.0093	PP	2			↑	

[a] Eigenvector on principal component axis.

[b] B, bacterivore; F, fungivore; O, omnivore; P, predator; PP, plant-parasite. Nematode C–P index value (Bongers, 1990) is an indicator of nematode occurrence according to ecological succession, 1 (colonizer of relatively young, disturbed habitats) to 5 (persister in stable habitats).

[c] Principal Component axis with significant ($P \leq 0.05$) correlation coefficient. Eigenvalues were 0.1641, 0.0662, and 0.0446 explaining cumulative percentage variance of species data of 17.7, 24.9, and 29.7% for axes 1, 2, and 3 respectively.

(Table 4). When sampled at the same time (0 months), biota and processes correlated positively between nematode community PCA2 and NH_4^+ in disturbed forests. One month time delay measurements were significant statistically only in undisturbed forests; increased abundances of PCA3 nematode communities correspond with increased NO_3^- and decreased NH_4^+ availability. Two-month time delay measurements of N availability correlated significantly with PCA1 and PCA3 nematode communities. Specifically, increased PCA3 communities correlated positively with increased availability of NO_3^- and PCA1 communities correlated negatively with decreased availability of NH_4^+ in disturbed forests. PCA3 communities correlated negatively with availability of NH_4^+ in undisturbed forests.

Regardless of time of year that samples were collected, statistically significant correlation coefficients between arthropod community composition and decomposition rate occurred in disturbed forests. Correlation coefficients were more often significant statistically between decomposition rate of wood measured 0 and 2 months after microarthropods than decomposition rate measured 1 month later (Table 5). The only occurrence of significant correlation between microarthropod communities and decomposition rate of cellulose was apparent between arthropod PCA4 and decomposition rate 2 months later in both disturbed and undisturbed forests. Rate of wood decomposition decreased 0 and 2 months after an increased abundance of PCA1, PCA2, and PCA4 microarthropod communities. Increased PCA3 arthropod community abundance correlated positively with rate of wood decomposition at 0-month delay.

3.6. Time lag between soil N availability and decomposition rate

Two general patterns of the relationship between soil N availability and decomposition rate were revealed upon analysis. First, greater availability of soil N was correlated with faster decomposition rate of cellulose substrates and slower decomposition rate of wood substrates (Table 6). Second, NH_4^+ was correlated

Table 3
Principal component analysis (PCA) of soil and litter microarthropods and their correlation with decomposition rate of cellulose and wood in disturbed (D) and undisturbed (U) pine forests of North Carolina. Taxa in bold have species weights that exceed ±0.55 in PCA1 and/or ±0.45 in PCA2, PCA3, and PCA4. The right four columns denote a direct or positive relationship (upward arrows) or inverse or negative relationship (downward-pointing arrows) between microarthropod taxa with relative large weights in PCA axes that were correlated significantly with rate of cellulose or wood decomposition. Cells without arrows represent relationships that were not significant statistically ($P > 0.05$).

PCA axis	1	2	3	4	Decomposition rate			
					Cellulose		Wood	
					D	U	D	U
					4–[b]	4–	1–, 2–, 3+, 4-	
Litter arthropods								
Neanuridae	0.4700[a]	−0.1989	**0.5327**	−0.001			↑	
Tomoceridae	0.2751	**0.4642**	0.3828	−0.2243			↓	
Isotomidae	**0.5896**	0.2010	0.0542	−0.1551			↓	
Entomobryidae	**0.6099**	−0.0185	0.1472	−0.1615			↓	
Neelidae	0.3024	0.1984	0.1360	0.0636	–	–	–	–
Sminthuridae	−0.3688	0.4402	0.2331	−0.0614	–	–	–	–
Protura	0.5113	0.1152	0.2605	0.2284	–	–	–	–
Diplura	0.4284	−0.2502	0.2532	**0.4553**	↓	↓	↓	
Acari (mites)	**0.8445**	−0.1756	0.0226	−0.0730			↓	
Araneae (spiders)	**0.5625**	−0.1806	0.1823	0.1526			↓	
Isoptera (termites)	0.0892	**0.5341**	−0.2414	0.2913		↑	↓	
Coleoptera larvae	0.5332	−0.1085	0.3666	0.1505	–	–	–	–
Coleoptera adults	0.5178	0.2854	−0.0242	0.0668	–	–	–	–
Diptera larvae	0.4730	0.3322	0.3614	0.0837	–	–	–	–
Diptera adults	−0.2672	0.3330	0.3025	0.0087	–	–	–	–
Hymenoptera (ants)	**0.5898**	−0.2667	0.1937	0.1475			↓	
Chilopoda	0.3133	0.1524	0.2787	−0.0942	–	–	–	–
Diplopoda (millipedes)	0.1478	0.1769	0.0583	**0.5092**	↓	↓	↓	
Symphyla	0.4052	−0.4107	0.1419	0.2577	–	–	–	–
Dermaptera	0.0874	0.4025	−0.1009	−0.0152	–	–	–	–
Oligochaetes	0.3315	0.2856	0.2638	−0.0899	–	–	–	–
Pseudoscorpionida	0.3760	0.3700	0.1396	−0.1514	–	–	–	–
Others	0.4260	−0.0982	0.0231	−0.0771	–	–	–	–
Soil arthropods								
Onychiuridae	0.0150	0.2572	−0.1676	0.3045	–	–	–	–
Hypogastruridae	**0.7008**	−0.4105	−0.1709	−0.0981			↓	
Neanuridae	0.3998	−0.1941	0.2170	−0.0194	–	–	–	–
Tomoceridae	0.2623	0.2704	0.1475	−0.3868	–	–	–	–
Isotomidae	**0.5634**	0.3349	−0.2287	0.0168			↓	
Entomobryidae	**0.5738**	−0.1574	−0.2274	−0.2187			↓	
Cyphoderidae	−0.0691	0.0401	−0.0497	−0.1112	–	–	–	–
Sminthuridae	0.2155	0.1689	−0.2200	−0.1270	–	–	–	–
Protura	0.4434	0.1529	−0.1145	0.1006	–	–	–	–
Diplura	−0.0987	0.0947	0.1894	**0.5306**	↓	↓	↓	
Thysanura	0.0327	0.1203	−0.0999	0.0198	–	–	–	–
Acari (mites)	**0.8005**	−0.0260	−0.3284	−0.1348			↓	
Araneae	0.2526	−0.1957	0.0270	−0.0146	–	–	–	–
Coleoptera larvae	0.4521	0.1665	−0.2627	0.1486	–	–	–	–
Coleoptera adults	0.3510	−0.1009	−**0.4803**	0.0921			↓	
Diptera larvae	0.4727	0.3182	−0.2305	0.1340	–	–	–	–
Diptera adults	0.3142	0.1174	−0.0938	0.2124	–	–	–	–
Hymenoptera (ants)	**0.6469**	−0.0654	−0.1248	−0.0678			↓	
Chilopoda	−0.5160	0.1337	0.2206	0.2444	–	–	–	–
Diplopoda (millipedes)	0.1637	0.1663	−0.4274	**0.4807**	↓	↓	↓	
Pauropoda	0.1496	0.3628	−0.2580	−0.0064	–	–	–	–
Symphyla	0.5238	−0.1358	−0.1308	0.1020	–	–	–	–
Dermaptera	−0.0336	−0.1781	−0.3270	−0.0895	–	–	–	–
Oligochaetes	0.3548	0.2071	−0.0264	−0.3578	–	–	–	–
Pseudoscorpionida	0.3109	0.1177	−0.1009	−0.1901	–	–	–	–

[a] Eigenvector on principal component axis.

[b] PCA axis with significant ($P \leq 0.05$) correlation coefficient. Eigenvalues were 0.1875, 0.0623, 0.0543, and 0.0442, explaining cumulative percentage variance of species data of 20, 26.8, 32.6, and 37.4% for axes 1, 2, 3 and 4, respectively.

with decomposition rate more often than with NO_3^- (Table 6). Faster rate of cellulose decomposition corresponded with greater availability of NH_4^+ in undisturbed forests (alone or in combination with disturbed forests) 4 months earlier. Slower rate of wood decomposition corresponded with greater availability of NH_4^+ in undisturbed forests (alone or in combination with disturbed forests) 5 and 0 months earlier. There was no significant relationship between rate of decomposition of cellulose or wood and NH_4^+ availability in disturbed forests alone.

4. Discussion

Few field studies have quantified relationships between soil invertebrate communities and soil processes in general (Crossley et al., 1992; Neher, 1999a), but the present study suggests that variation in soil N availability and decomposition rate are best explained when the two faunal communities, nematodes and arthropods are examined separately. When both processes and groups of invertebrates are combined, high variation results in a

Table 4
Spearman rank correlation coefficients between nematode community composition (PC axes 1–4) and availability of soil ammonium (NH_4^+) or nitrate (NO_3^-) at sampling (T0), one (T1) and two (T2) months after sampling nematode communities in disturbed (D) and undisturbed (U) pine forests in North Carolina. Degrees of freedom are listed for each group of comparisons between nematode community composition and number of months later that nitrogen was measured.

Nematode community	Nitrogen form	Forest type	Time lag[a]		
			T0	T1	T2
PC axis	NO_3^-	D	*df* = 90	*df* = 90	*df* = 48
1			0.064	0.052	0.117
2			0.055	−0.084	−0.231
3			0.029	0.028	0.298*
4			0.055	0.002	−0.044
PC axis	NO_3^-	U	*df* = 90	*df* = 90	*df* = 48
1			−0.009	−0.107	0.190
2			0.154	0.189	−0.064
3			−0.162	0.245*	0.247
4			0.057	0.045	−0.007
PC axis	NH_4^+	D	*df* = 66	*df* = 90	*df* = 48
1			−0.091	−0.115	−0.397**
2			0.243*	−0.054	0.028
3			−0.150	0.038	−0.228
4			−0.102	0.171	0.122
PC axis	NH_4^+	U	*df* = 66	*df* = 90	*df* = 48
1			−0.175	−0.155	−0.184
2			−0.145	−0.044	0.122
3			−0.032	−0.210*	−0.486***
4			−0.159	−0.150	−0.124

[a] All 15 sampling dates allowed for comparison of invertebrates and processes sampled on the same day (T0). In contrast, T1 and T2 were possible for some date combinations but not all. For example, March samples could be compared with April for T1 and compared with May for T2. Zero T1 were possible for July and November samples.

* $P \le 0.05$.

** $P \le 0.01$.

*** $P \le 0.001$.

weaker correlation signal. In this study, soil nematode and soil and litter arthropod communities are correlated with soil N availability and decomposition rate, respectively. Available nitrogen was correlated with nematode community composition in undisturbed but not disturbed forests. Perhaps, the greater proportion of bacterivorous nematodes in undisturbed forests at least partly explains the positive correlation with available nitrogen in those soils. In contrast, decomposition rate was better explained by microarthropod

Table 5
Spearman rank correlation coefficients between arthropod community composition (PC axes 1–4) and decomposition rate or museum board (cellulose) or balsa wood (wood) at sampling (T0), one (T1) and two (T2) months after arthropod communities in disturbed (D) and undisturbed (U) pine forests in North Carolina. Degrees of freedom are listed for each group of comparisons between arthropod community composition and number of months later that decomposition rate was measured.

Arthropod community	Decomposition rate	Forest type	Time lag[a]		
			T0	T1	T2
PC axis	Cellulose	D	*df* = 76	*df* = 40	*df* = 54
1			0.007	−0.292	0.014
2			0.237	−0.019	0.142
3			0.222	0.052	0.175
4			−0.065	−0.094	−0.303*
PC axis	Cellulose	U	*df* = 76	*df* = 40	*df* = 54
1			0.158	0.103	0.131
2			−0.021	0.176	0.221
3			−0.106	0.170	0.107
4			−0.108	0.088	−0.486***
PC axis	Wood	D	*df* = 75	*df* = 40	*df* = 53
1			−0.310**	−0.154	−0.400**
2			−0.313**	−0.252	−0.529***
3			0.260*	0.125	−0.143
4			−0.357**	−0.052	−0.372**
PC axis	Wood	U	*df* = 76	*df* = 40	*df* = 54
1			−0.192	−0.308	0.089
2			0.143	0.117	−0.086
3			−0.188	−0.121	0.102
4			0.058	0.026	0.013

[a] All 15 sampling dates allowed for comparison of invertebrates and processes sampled on the same day (T0). In contrast, T1 and T2 were possible for some date combinations but not all. For example, March samples could be compared with April for T1 and compared with May for T2. Zero T1 were possible for July and November samples.

* $P \le 0.05$.

** $P \le 0.01$.

*** $P \le 0.001$.

Table 6

Spearman rank correlation coefficients between availability of soil ammonium (NH_4^+) or nitrate (NO_3^-) at same time (T0) or months prior (T-1 through T-5) to rate of decomposition of museum board (cellulose) or balsa wood (wood) in disturbed (D) and undisturbed (U) pine forests separately, or combined (D + U) in North Carolina. Degrees of freedom are listed for each group of comparisons.[a]

	Time lag	Spearman rank correlation coefficients					
		T-5	T-4	T-3	T-2	T-1	T0
	Decomp Rate	*df* = 36	*df* = 48	*df* = 36	*df* = 54	*df* = 40	*df* = 76
NO_3^-							
D + U	Cellulose	−0.13	−0.16	−0.06	−0.08	0.02	−0.01
D	Cellulose	0.04	−0.03	0.23	−0.12	0.06	0.09
U	Cellulose	−0.14	−0.24	−0.32	−0.03	−0.06	−0.05
D + U	Wood	−0.15	0.01	−0.16	−0.03	−0.02	0.04
D	Wood	−0.11	0.20	0.12	0.13	−0.02	0.27*
U	Wood	−0.09	−0.09	−0.42*	−0.11	−0.02	−0.08
NH_4^+							
D + U	Cellulose	0.03	0.30**	−0.25*	0.00	0.05	0.08
D	Cellulose	−0.1	0.10	−0.24	−0.07	−0.15	0.06
U	Cellulose	−0.28	0.57***	−0.20	0.12	0.23	0.18
D + U	Wood	−0.40***	−0.03	−0.14	−0.12	−0.26*	−0.23**
D	Wood	−0.21	0.01	−0.33	−0.26	−0.24	−0.17
U	Wood	−0.47**	−0.01	0.15	0.07	−0.18	−0.25*

[a] All 15 sampling dates allowed for comparison of invertebrates and processes sampled on the same day (T0). In contrast, T-1 to T-5 comparisons is possible for some date combinations but not all. For example, May samples could be compared with April for T-1 and compared with March for T-2.

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

community composition in disturbed than undisturbed forests. Joo et al. (2006) found that even though microarthropods were correlated positively with mass loss of needle litter, they had no significant effect on the amounts of nitrogen immobilized in the litter. Based on our experimental design, it is difficult to differentiate between the effects of disturbance and/or more time for niche partitioning and adaptation. However, younger forests comprised predominantly of grasses, forbs, and shrubs, had more heterogeneous surface litter readily accessible for decomposition than did older forests comprised of mature conifers. Mass loss is often increased when litters of different species are mixed (Gartner and Cardon, 2004).

4.1. Nitrogen

The percentage of variation explained by nematode taxa and availability of N in pine forests of this study surpasses previous estimates of the contributions of nematode communities to net N mineralization in another pine forest system (Berg et al., 2001, 2004). However, these observed linkages are the result of different measurements. Berg et al. (2001) estimated the direct contribution of N mineralization assuming a steady state model (Hunt et al., 1987). Our results support observations that bacterivorous nematodes are net NH_4^+ excretors resulting from higher C:N ratios than their prey. In contrast, fungivorous nematodes have similar C:N ratios with their prey excreting less NH_4^+ (Bouwman et al., 1994; de Ruiter et al., 1993b). Further, nematode communities correlated with available N at 0 and 2 months into the future. These results indicate that biological activities by the standing nematode community are indicators of current and future available N.

Three omnivore-predators, Ironidae, Leptolaimidae and Dorylaimellidae, were the only nematode taxa to correspond both with NO_3^- and NH_4^+ availability. This observation could be explained by a trophic cascade in which predators are responding to the increase of bacterivores (Ettema, 1998; Wardle and Yeates, 1993). There are inherent time delays between omnivore-predators, responses to an increased availability of bacterivores, which increase in abundance after grazing and assimilating bacteria. The 2-month delay between abundance of nematode communities and availability of N in this study was less than the 3 or 6 months reported previously (Neher, 1999b; Wardle et al., 1995; Yeates et al., 1993). However, the sampling frequency was greater in this than in the other studies.

4.2. Decomposition

Many microarthropods feed directly on litter and the microbes associated with it, fragmenting litter and dispersing microbes in the process. Seastedt (1984) estimated that arthropods consume 20–30% of the yearly litter input and have large effects on decomposition rate. Existing food web models suggest that mites do not make a large contribution to N availability because they focus on net mineralization without consideration of immobilization (de Ruiter et al., 1993a; Hunt et al., 1987). Osler et al. (2004) hypothesize that mite community structure relates to N immobilization. Immobilization can also occur as N is incompletely digested and deposited as fecal material (Prescott, 2005). Arthropod fecal material can be recalcitrant, become incorporated into soil aggregates, or become coated with organic material and clay minerals that can slow rate of decay (Prescott, 2005).

Soil microarthropods explain more variation associated with decomposition rate of cellulose in undisturbed than disturbed forests. The taxa correlate with rate of cellulose decomposition contrasted those correlated with wood degradation. Positive associations between soil microfauna, such as oribatid mites, with degradation of cellulose may relate to carbohydrases produced by endemic microflora in their gut or the animal itself (Siepel and de Ruiter-Dijkman, 1993). Tomocerid collembolans and Diplopoda (millipedes) prefer high quality forest litter (Bertrand and Lumaret, 1992; Moya-Laraño and Wise, 2007). Fast rates of cellulose decomposition degrade the litter quality, which may at least partly explain why numbers of Diplopoda decrease with faster cellulose decomposition.

All microarthropods, except neanurid collembolans, correlate negatively with rate of wood decomposition. Lignin degradation is an endothermic chemical process catalyzed predominantly by white rot fungi (Dix and Webster, 1995). These fungi contribute to lignin decomposition through the production of lignin peroxidase, manganese peroxidase, and/or laccase that can decompose portions of the lignin molecule (Hatakka, 1994). A negative association of arthropod groups with rate of wood decomposition may be direct, by feeding on fungi associated with the decomposition of wood, or indirect, through predation on decomposer organisms (Hunter et al., 2003; Moya-Laraño and Wise, 2007).

Collembolans play essential roles in the detrital food web by consuming both primary materials and decay organisms, and by serving as high quality prey items for arthropods such as spiders and ground beetles (Wise et al., 1999). Larger species, for example, those in the family Tomoceridae, are primary decomposers and feed directly on litter material and the adhering fungi and bacteria. Smaller species, e.g., in the families Onychiuridae, Hypogastruridae, and Isotomidae, are fungal, algal, or diatom feeders. Entomobryid collembolans are predominantly fungivores (Chahartaghi et al., 2005). Nematodes may be important food sources for some species (Huhta et al., 1998), and opportunistic scavenging of dead invertebrates is common. In our study, isotomid, entomobryid, tomocerid, and hypogastrurid collembolans correlated negatively with wood decomposition rate, suggesting that direct feeding on fungi by these organisms may contribute to this negative relationship. Collembola form a significant proportion of the diets of ground-dwelling spiders, ground beetles (Carabidae), rove beetles (Staphylinidae), mesostigmatid mites, ants, diplurans, and other predacious arthropods (Hopkin, 1997; McBrayer and Reichle, 1971). We speculate that an indirect effect of spiders and other arthropod predators on the rate of decomposition, whether positive or negative, may correlate with altering the manner that collembolans interact with fungi, a major resource for Collembola and an abundant primary decomposer in forest leaf litter. In trophic-cascade experiments in forest leaf litter, primarily tomocerids or entomobryids increase in response to reduced densities of spiders (Lawrence and Wise, 2000, 2004).

The feeding structures of neanurid collembolans differ from the other collembolans in that they lack a molar plate. Most species of Neanuridae have stylet- or crochet-hook-like mandibles, suggesting a diet consisting of liquid or engulfed micro-organisms (Adams, 1979; Greenslade et al., 2002). Based on ratios of stable isotopes of N, Chahartaghi et al. (2005) suggested that at least some Neanuridae feed on a high protein animal diet. Berg et al. (2004) reports a lack of chitinase activity, necessary to digest fungal cell walls, in *Neanura muscorum* and characterizes this species as an opportunistic herbo-fungivore or predator. Given that the abundance of neanurids in our study is related positively to the rate of wood decomposition, we hypothesize that those detected in our study do not include white rot fungi as a major portion of their diet, or, alternatively, these collembolans may have been preying upon organisms that consume white rot fungi.

4.3. Relationship between soil N availability and decomposition rate

Soil fauna contribute to all pools and fluxes of soil C and N cycle (Osler and Sommerkorn, 2007). Correlations in this study were apparent more often between decomposition and available NH_4^+ than available NO_3^-. This finding supports Prescott et al. (2003) who observed no relationship between soil NO_3^- availability in clear-cuts with decay rate. Temporal variability in soil C and the coupling of soil C with N content in forest soils is expected (Wardle, 1998). N is often a limiting nutrient for microbial activity and, thus, decomposition of organic substrates. In this study, increased availability of N often preceded detectable changes in decomposition rate by 3–5 months. Greater availability of soil N correlates positively with faster decomposition rate of cellulose substrates and slower decomposition rate of wood substrates. This linkage between N and substrate-specific decomposition rate supports conclusions from previous studies that used extra-cellular soil enzymes to characterize the functional roles of microbes (Carreiro et al., 2000; Knorr et al., 2005). Those authors found additions of N increased microbial cellulose activity, while simultaneously reducing ligninolytic enzyme activity, explaining both increased cellulose decomposition and decreased wood decomposition.

5. Conclusions

Our results quantify the relationship of specific faunal groups as indicators of decomposition and N availability in soil. Correlation among soil mesofauna to vital ecological processes is a necessary first step to justify their implementation as biological indicators for environmental monitoring. In our analyses, association of invertebrate communities was greater with N availability or decomposition rate when measured two, compared with one, months later. These results suggest that food web models may be improved by addressing spatial and temporal partitioning, population dynamics, taxon-specific parameters and interactions such as compensatory growth resulting from grazing or predation. Often, soil food web models are based on functional groups (de Ruiter et al., 1994). The association of specific taxonomic groups with soil N availability and decomposition rate suggests the need to clarify community composition changes and links to the C and N cycle processes in space and through time to better understand the effects of disturbance and change on ecosystem function. Assessment of broad taxonomic groups with ecological processes provides insights more detailed than previous reports (e.g., Hunt et al., 1987). However, further research is needed to establish more quantitative relationships of specific groups, especially among arthropods, to better understand the roles of soil fauna in C and N cycles.

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