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Chronic nitrogen deposition alters the structure and function of detrital food webs in a northern hardwood ecosystem

Huijie Gan,[1,3] Donald R. Zak,[1,2] and Mark D. Hunter[1]

[1]*University of Michigan, Department of Ecology and Evolutionary Biology, 830 N University, Ann Arbor, Michigan 48109 USA*
[2]*University of Michigan, School of Natural Resources and Environment, 440 Church Street, Ann Arbor, Michigan 48109 USA*

Abstract. During the next century, atmospheric nitrogen (N) deposition is projected to more than double, potentially slowing litter decomposition by altering microbial community composition and function. If the flow of energy though detrital food webs is diminished by the slowing of decay under higher rates of atmospheric N deposition, this agent of global change could also negatively impact the abundance and composition of soil fauna. To test this hypothesis, we studied soil faunal communities in four sugar-maple-dominated forests that comprise a long-term N deposition experiment. To examine whether changes in soil faunal communities could then feed back to influence litter decay, litterbags with ^{13}C-enriched aspen litter were placed in the forest floor in one study site. The microbial community within the litterbags was characterized using PLFA analysis. Overall, long-term experimental N deposition reduced the abundance of microarthropods (ambient vs. experimental N deposition: 7844 vs. 4357 individuals/m^2, respectively; $P = 0.004$). We attribute this overall decline partly to the reduced energy flow entering the detrital food web, which has been documented in previous work in our system. Although there was no difference in microarthropod species richness between N deposition treatments, there was a shift in community composition within the most abundant group (Oribatida), indicating species-specific responses to N deposition. Experimental N deposition reduced the number of microarthropods colonizing litterbags by 41% ($P = 0.014$). This was associated with a reduction in ^{13}C mobilization from leaf litter into microbial biomass. Overall, this study demonstrates that chronic N deposition has a detrimental effect on the soil detritus food web, and that the negative effect may feed back to influence litter decay and ecosystem functioning.

Key words: decomposition; detrital communities; hardwood forests; microarthropods; microbial PLFA; N deposition; northern hardwood forest; oribatid mites; phospholipid fatty acid analysis.

Introduction

Global changes in climate and land use are affecting biodiversity in many ecosystems (Wolters et al. 2000), and this has triggered extensive research into the consequences of these anthropogenic forces for ecosystem functioning (Chapin et al. 1998, Diaz et al. 2006). The majority of experiments have focused on plants and animals living aboveground (Hughes 2000, Walther et al. 2002, Wu et al. 2011), whereas comparably less is known regarding belowground responses (Wardle et al. 1999, Blankinship et al. 2011). Most research into soil biotic responses to global change has focused on microbial communities, whereas the responses of soil fauna at higher trophic levels, such as nematodes, mites, and springtails, are less understood, but clearly mediate important functions that have ecosystem-level implications (Osler and Sommerkorn 2007, Sackett et al. 2010). For example, soil fauna can alter the physical environments of the soil through litter comminution and soil bioturbation (Lussenhop 1992), or can regulate the activity and population dynamics of the microbial community through grazing (Moore et al. 1988, Lussenhop 1992, Hassall et al. 2006). Moreover, significant links between soil fauna communities and decomposition rates have been observed in the field (Neher et al. 2012).

Anthropogenic nitrogen (N) deposition is a pervasive agent of global environmental change (Vitousek et al. 1997). Over the past 150 years, atmospheric N deposition has increased from 0.05–0.10 g N·m^{-2}·yr^{-1} prior to 1880 to 1.50–2.00 g N·m^{-2}·yr^{-1} in the early 1990s across large areas of the northern hemisphere; this rate is projected to double during the next century (Galloway et al. 2004). Atmospheric N deposition can stimulate net primary productivity in N-limited terrestrial ecosystems, thereby increasing ecosystem carbon (C) storage, albeit there is considerable debate regarding the extent of this stimulation (Nadelhoffer et al. 1999, Magnani et al. 2007). However, atmospheric N deposition also could increase ecosystem C storage by slowing plant litter decay and accelerating organic matter accumulation in soil (Carreiro et al. 2000, Frey et al. 2004). Although most studies of N deposition focus on

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[3] E-mail: huijgan@umich.edu

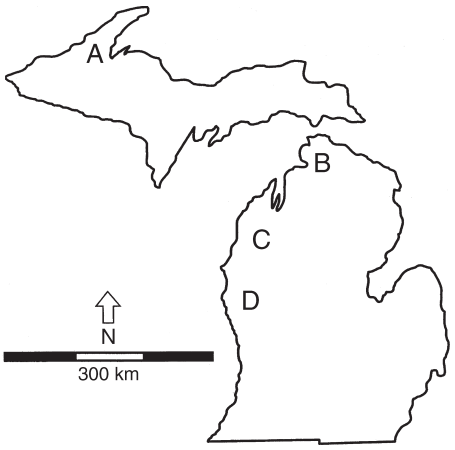

FIG. 1. Map of four study sites in the Great Lakes region in North America.

changes in the microbial community (Zak et al. 2011), the few studies that have been conducted suggest that soil fauna at higher trophic levels could also be affected by anthropogenic N deposition (Boxman et al. 1998, Xu et al. 2009, Eisenhauer et al. 2012). Shifts in microarthropod community composition, in response to experimental N deposition, can significantly reduce soil respiration and accelerate nutrient leaching in laboratory microcosms (Heneghan and Bolger 1996). However, our knowledge is incomplete regarding the in situ response of soil fauna to anthropogenic N deposition and potential feedbacks that could modify rates of litter decomposition.

Previous studies have reported that anthropogenic N deposition can have either beneficial or detrimental effects on detrital food webs. For instance, Sjursen et al. (2005) found increased microarthropod abundance in a subarctic ecosystem after application of NPK fertilizer, attributing this to the bottom-up effects of higher plant productivity. In contrast, N fertilization can reduce carbon allocation belowground to roots and rhizodeposition (Hogberg et al. 2010), thereby reducing energy availability in the soil environment. Moreover, anthropogenic N deposition can reduce rates of litter decay (Knorr et al. 2005, Zak et al. 2008), which can also reduce the energy entering the detritus-based food web. Both of these belowground responses to anthropogenic N deposition could negatively impact the soil microbial community, as well as higher trophic levels in the soil food web.

Here, we sought to understand the mechanisms by which chronic N deposition has influenced the dynamics of the detrital food web in soil. In a long-term field experiment consisting of four sugar maple (*Acer saccharum*) forest stands, chronic experimental N deposition has slowed plant litter decay and accelerated organic matter accumulation in forest floor and surface mineral soil (Pregitzer et al. 2008, Zak et al. 2008, Edwards et al. 2011). The slowing of plant litter decay has resulted from a decline in lignolytic extracellular enzyme activity, originating from the transcriptional down-regulation of fungal genes encoding these enzymes (Edwards et al. 2011). At the same time, microbial biomass had been reduced by 18% under experimental N deposition (DeForest et al. 2004). We were interested in determining whether soil fauna at higher trophic levels were also affected negatively by long-term experimental N deposition; we reasoned that a lower microbial biomass and the slowing of litter decomposition could plausibly reduce the flow of energy into the detrital food web. We focused on microarthropod groups involved in important soil processes, such as litter fragmentation and microbial grazing (collembola, oribatid mites), as well as mesostigmatic mites that, through their predation, are potential regulators of grazer abundance (Coleman et al. 2004). We hypothesized that (1) microarthropod communities are affected negatively by long-term N deposition, due to reduced energy flow entering the detrital food web; and that (2) the change in microarthropod communities further feeds back to slow litter decomposition. We tested these hypotheses by quantifying microarthropod populations in forest floors receiving ambient and experimental N deposition. Additionally, we placed litterbags containing ^{13}C-labeled leaf litter in one of the forest stands to determine whether chronic N deposition has compromised the ability of microarthropod communities to colonize and degrade new litter.

METHODS

Site description and experimental design

This long-term study of experimental N deposition consists of four sugar maple (*Acer saccharum*)-dominated northern hardwood forests in the Great Lakes region of North America (Burton et al. 1991). The sites are floristically and edaphically matched (>80% sugar maple on sandy soils), but they differ in climate along a north–south latitudinal gradient (Fig. 1). Within each study site, six 30×30 m plots were established in 1994; three plots receive ambient N deposition and the remaining three plots receive ambient plus 30 kg NO_3^--N·ha^{-1}·yr^{-1}. The additional NO_3^- is delivered over the growing season in six equal applications of solid $NaNO_3$ pellets; a 10 m wide buffer surrounds each plot, and it also receives the experimental treatments. More detailed descriptions of the study site can be found in Zak et al. (2008).

Microarthropod survey

Forest floor litter was collected in June 2009 in site B as an initial survey of microarthropod populations. Within each plot, a 10×10 cm PVC frame was placed randomly on the forest floor, and the O_i and Oe horizons were collected and placed in a plastic bag. In total, six samples were collected from each plot receiving either ambient ($n = 3$) or experimental N deposition ($n = 3$). All of the samples were transported to the lab in

coolers and placed in modified Tullgren funnels within 48 hours (Crossley and Blair 1991) to extract microarthropods. After the 5-day extraction, litter was placed in a 60°C oven for 24 hours for the subsequent determination of dry mass. A second microarthropod survey was conducted in May 2011 in all four study sites, using the same sampling and extraction scheme.

The extracted microarthropods were preserved in 70% ethanol, and three major groups (Mesostigmata, Collembola, and Oribatida) were enumerated under a microscope. For the second survey, those in the most abundant group (Oribatida) were further identified to genus or species based on the keys written by R. A. Norton and V. M. Behan-Pelletier (*unpublished data*) for use at the Ohio State University Summer Acarology Program.

Litterbag experiment

Litterbags (20×20 cm) were constructed using a layer of 1-cm polyester mesh to form the top of the bag and 1-mm fiberglass mesh on the bottom. The larger top mesh allowed for the free movement of invertebrates into the litter bags, and also reduced potential changes in microclimate created by the litterbags (Bradford et al. 2002). To quantify the active microbial community that relied on the litter inside the litterbags, 20 g of ^{13}C-enriched aspen litter (*Populus tremuloides*) was placed in each litterbag, representing new litter entering forest floor. We used aspen to produce ^{13}C-enriched leaf litter because sugar maple, the dominant species in our sites, is a slow-growing species that would not produce sufficient quantities of leaf litter for this experiment. The ^{13}C-enriched aspen litter was produced by pulse-labeling propagated ramets of one aspen genotype. Labeling was conducted in a field chamber during the 2008 growing season, and naturally senesced and abscised leaves were collected during autumn. The labeling chamber was similar to that used by Mikan et al. (2000).

The constructed litterbags were transferred into the field in individual plastic bags. In total, 96 litterbags with aspen litter were placed in plots receiving ambient ($n = 3$) and experimental ($n = 3$) N deposition in site B during June 2009. In addition, 16 empty litterbags were placed on the forest floor to control for any external litter input to the litterbags. The Oi horizon was first removed, and the litterbags were secured to the top of the Oe horizon with steel pins; the original Oi horizon was then placed on top of each bag. Three supplementary litterbags were placed in the forest floor, as just described, but were immediately retrieved to estimate any loss during transportation.

Four litterbags from each plot were collected 2, 4, 12, and 16 months after placement in the field. Four empty litterbags were also collected on each date to estimate the mass of any external litter that had infiltrated litterbags. On each collection date, litterbags were placed in separate plastic bags in coolers and were transported to the laboratory within 24 hours. In addition, one soil core sample (5 cm diameter $\times$ 5 cm depth) underneath each litterbag was collected. Moreover, one forest floor sample outside the litterbags was collected from each plot. Both the soil and litter samples that were collected from outside the litterbags served as paired controls when comparing the microbial community inside bags (see *PLFA analysis*).

In the lab, the litterbags were cut open after the outside was carefully brushed, and any roots that had penetrated the litterbags were removed. The litter was then thoroughly homogenized. Approximately 75% of the field-moist litter was placed in modified Tullgren funnels to extract microarthropods (into 70% ethanol) over 5 days. The remaining litter was freeze-dried for phospholipid fatty acid (PLFA) analysis. The extracted microarthropods were sorted into three major groups including Mesostigmata, Collembola, and Oribatid mites; individuals were enumerated under a dissecting microscope and oribatid mites were further identified to species.

After microarthropod extraction, litter was oven-dried at 60°C and weighed to determine moisture content. The oven-dried litter was further ground into powder and combusted at 500°C to measure the ash-free dry mass. Five subsamples of the original litter were also combusted to determine the ash-free dry mass of the litter used in the beginning of the experiment. Litter mass loss during the field incubation was corrected for ash content, and mass loss values were expressed on an oven-dry, ash-free basis.

PLFA analysis

Phospholipids fatty acids (PLFAs) were extracted from the contents of each litterbag to determine microbial community composition, biomass, and ^{13}C content. Approximately 25% of the field-fresh litter from each litterbag was freeze-dried within 24 hours of collection. The litter samples in the forest floor outside the litterbags and the soil samples underneath the litterbags were also freeze-dried. About 1 g of freeze-dried litter (or 5 g of soil sample) was subjected to a solution containing 10 mL of CH_3OH, 5 mL of CH_3Cl, and 4 mL of PO_4^{-3} buffer to extract total lipids (White et al. 1979). A 21:0 internal standard (5 pmol) was added to each sample at the beginning of the extraction to determine the extraction efficiency. The extracted PLFAs were then separated by silicic acid chromatography. Isolated polar lipids were further subjected to an alkaline $CHCl_3$-CH_3OH solution to form fatty acid methyl esters (FAMEs; Guckert et al. 1985). Fatty acid methyl esters were separated using gas chromatography and quantified using a Finnigan Delta plus mass spectrometer with a GC/C III interface (Thermofinnigan, Bremen, Germany). Alongside the samples, a standard solution containing five common FAMEs (14:0, i15:0, 15:0, cy19:0, 18:1w7t) of known concentrations were analyzed after every fifth sample for quality assurance purposes. The concentration of sample

FAMEs was determined by a regression equation based on the standard FAMEs.

In total, 20 PLFA biomarkers were identified and grouped to bacteria, Actinobacteria, and fungi. The total PLFA abundance (nmol/g litter), after adjustment for extraction efficiency and extracted litter mass, was used as an indication of total viable microbial biomass. The ^{12}C:^{13}C ratio for each FAME was used to calculate the ^{13}C content of each group (μg ^{13}C/g litter), which was used to quantify the newly acquired C from the ^{13}C-enriched aspen litter.

Data analysis

The density of microarthropod groups in the forest floor was calculated in two ways. The first method combined the abundance of six subsamples within each plot and divided the sum by the total collected area (individuals/m^2). The second method employed the sum of the abundance within each plot divided by the total dried mass of the six subsamples (individuals/g dried litter). We also calculated the density-by-area abundance for the microarthropod groups inside the litterbags, based on the area of the litterbag (0.04 m^2) and the total dried mass of litter inside. Because the results from these two methods were highly correlated with each other, we present only the results of analyses of density-by-area data.

To test how experimental N deposition influenced the microarthropod community in the forest floor, we first used a Student's *t* test (unpaired) to analyze the first survey data (site B only). Three-way ANOVA (site, N treatment, and taxon group) was used to analyze the density data from the second survey (all four sites). The species richness of the oribatid community was assessed using individual-based rarefaction curves, and the 95% confidence zone was used to detect any difference between the N deposition treatments.

The species composition of the oribatid mite communities was represented in a community matrix using three different indices: relative abundance was calculated as the percentage of each species within each plot; presence or absence was the binary conversion from the raw abundance data; incidence of each species was the frequency of finding that species in six subsamples of that plot. The use of incidence data was to scale the original data to 0 (absence) to 6 (occurring in all six subsamples) to prevent bias of the dominant species or the rare species.

Bray-Curtis dissimilarity was calculated for these three community matrices, which were then subjected to nonmetric multidimensional scaling (nMDS) to visualize any differences in the species composition of oribatid mite communities (Kruskal and Wish 1978, Minchin 1987). To explore relationships between the compositional trends revealed by ordination and different N deposition treatments, we fitted the N deposition levels (ambient, 10 kg N·ha^{-1}·yr^{-1}; elevated, 40 kg N·ha^{-1}·yr^{-1}) to the nMDS space by rotational correlation (Dargie 1984), which is similar to a multiple linear regression of the environmental variables on the set of ordination axes. Statistical differences in community structure were also assessed using permutational multivariate analysis of variance (PerMANOVA; Anderson 2001). As the three different community matrices yielded similar results for the multivariate analysis, only the results from the incidence data are shown in the *Results* section.

For the litterbag experiment, repeated-measures ANOVA was used to explore the effects of collection date and N deposition treatment on microarthropod density and the microbial PLFA composition inside the litterbags. We used nMDS to visualize the species composition of oribatid communities in the litterbags using the incidence data previously mentioned; statistical differences in community composition were assessed by PerMANOVA.

The remaining mass in the litterbags was scaled to percentage of the initial mass, and then was fitted to a first-order exponential decay equation ($A_t = e^{-kt}$), with A_t as the remaining mass at time t (Jenny et al. 1949). The decay constant k was estimated to represent the decay rate for each plot. Student's t test was used to compare the difference in decay rate of litterbags under different N deposition treatments.

Repeated-measures ANOVA was performed on IBM SPSS Statistics Version 19 (2011). The species rarefaction curves were generated using EstimateS version 8.2 (Colwell 2009). Multivariate analysis including nMDS and PerMANOVA were performed in package *vegan* (Oksanen et al. 2012) in R 2.15.1 (R Development Core Team 2012).

Results

Microarthropod surveys

The initial survey in site B (June 2009) revealed that the density of all three microarthropod groups was reduced by experimental N deposition. Oribatid mite density declined from 9722 ± 442 individuals/m^2 (mean ± SD) under ambient N deposition to 3833 ± 1551 individuals/m^2 under experimental N deposition ($P = 0.017$); this represented a 60% decline in density. Similarly, Collembola density under experimental N deposition (406 ± 200 individuals/m^2) was only 34% of that under the ambient treatment (1989 ± 362 individuals/m^2; $P = 0.044$). Finally, the density of Mesostigmata declined from 1289 ± 164 individuals/m^2 under ambient N deposition to 733 ± 116 individuals/m^2 under experimental N deposition ($P = 0.011$).

For the second survey in May 2011, three-way ANOVA revealed that all three microarthropods groups responded similarly to experimental N addition across all four study sites (Table 1, Fig. 2). Consistent with the results from the first survey, experimental N deposition reduced the overall density of microarthropods by 44% across four sites (Fig. 2). At the same time, the abundance of Mesostigmata was related positively with

TABLE 1. Analysis of variance (ANOVA) of the density of microarthropods in the forest floors and in the litterbags in northern hardwood forests in the Great Lakes region of North America.

Source of variation	df	SS	*F*	*P*
Forest floors				
Site	3	2.13	8.29	**<0.001**
Taxon	2	16.81	98.04	**<0.001**
Treatment	1	0.8	9.38	**0.004**
Site × Taxon	6	3.52	6.84	**<0.001**
Site × Treatment	3	0.38	1.48	0.233
Taxon × Treatment	2	0.24	1.38	0.262
Site × Treatment × Taxon	6	0.16	0.32	0.926
Residuals	48	4.12		
Litterbags				
Time	3	11.84	27.6	**<0.001**
Taxon	2	5.09	9.25	**0.004**
Treatment	1	2.27	8.23	**0.014**
Time × Taxon	6	2.61	3.05	**0.016**
Time × Treatment	3	1.96	4.57	**0.008**
Taxon × Treatment	2	0.05	0.03	0.913
Time × Taxon × Treatment	6	0.28	0.33	0.919

Note: The forest floor data were pooled from four study sites, and the litterbag data were pooled from four retrieval dates. Three-way ANOVA for forest floor data included site ($n = 4$), N treatment ($n = 2$), and taxon group ($n = 3$). Litterbag data were analyzed using repeated-measures ANOVA, with taxon group and N treatment as between-subject factors. Densities were calculated as the number of individuals per unit area and were log-transformed before analysis. Abbreviations: df, degrees of freedom; SS, sum of squares.

the abundance of Collembola and oribatid mites ($r^2 = 0.39$, $P < 0.01$). Despite the decline in overall density of microarthropods under experimental N deposition, the species richness of the oribatid community was comparable between N deposition treatments (Fig. 3), with the number of species being slightly lower under experimental N deposition (51 species) than in the ambient treatment (61 species).

However, different oribatid species responded differently to experimental N deposition, resulting in a change in the community composition (Table 2; PerMANOVA, $P = 0.01$). As seen in the nMDS ordination space in Fig. 4, oribatid communities from different sites were distinctly different along axis 1 (PerMANOVA, $P < 0.001$). At the same time, communities under experimental N deposition all clustered lower on axis 2, suggesting that experimental N deposition was causing similar changes in species composition (Table 2; site × treatment, $P = 0.514$). In addition, fitting the N deposition levels to the ordination space indicates that the elevated N deposition level is associated with mite communities represented at the lower end of axis 2 (Fig. 4; $R^2 = 0.309$, $P = 0.022$). Oribatid species that were only found (e.g., *Atropacarus striculus*, *Hypochthoninus rufulus*, *Platynothrus peltifer*) or were more abundant (e.g., *Fuscozetes fuscipes*) under experimental N deposition have relatively low scores on axis 2. In contrast, species with high scores on axis 2 are those only present (e.g., *Epidamaeus* spp., *Ommatocepheus* sp., *Pilogalumna* sp.) or more abundant (e.g., *Tectocepheus veltus*) under ambient deposition. A list of species with their nMDS

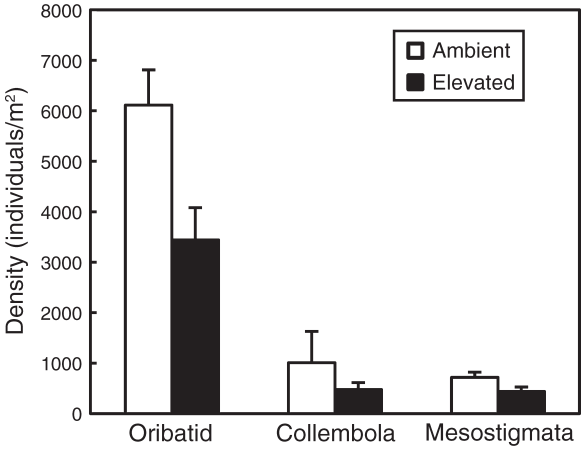

FIG. 2. Density (mean + SE) of Oribatida, Mesostigmata, and Collembola in the forest floor, averaged across four study sites, under ambient and elevated N. Three-way ANOVA indicated that density of Oribatida, Mesostigmata, and Collembola was significantly lower under experimental elevated N deposition ($P = 0.004$).

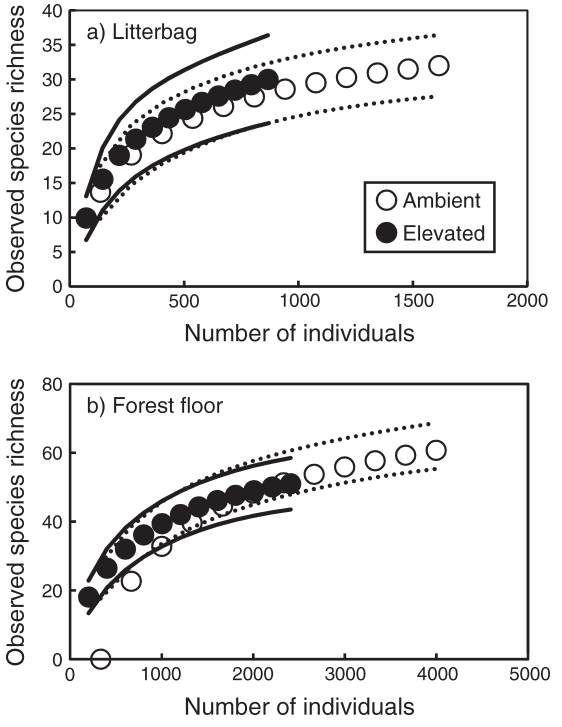

FIG. 3. Rarefaction curves of oribatid mite communities (a) inside the litterbags and (b) in the forest floors. The forest floor data were pooled from four study sites, and the litterbag data were pooled from four retrieval dates. The solid lines indicate the 95% confidence zones for the rarefaction curve of ambient N plots; the dotted lines indicate 95% confidence zones for the rarefaction curve of elevated N deposition plots. Replicate times = 500.

TABLE 2. PerMANOVA analysis of the species composition of oribatid mite communities in the forest floor or that inside the litterbags.

Source of variation	df	SS	F	R^2	P
Forest floor					
Treatment	1	0.19	2.40	0.07	**0.010**
Site	3	1.22	5.13	0.42	**<0.001**
Treatment × Site	3	0.23	0.97	0.08	0.514
Residuals	16	1.27	0.44		
Total	23	2.92			
Litterbag					
Treatment	1	0.54	3.13	0.11	**0.001**
Time	1	0.69	4.01	0.14	**<0.001**
Treatment × Time	1	0.27	1.55	0.05	0.140
Residuals	20	3.45	0.70		
Total	23	4.94			

Note: The incidence of the species, calculated as the frequency of encountering that species in the six subsamples within each plot, was used in the community matrix. The forest floor data were from the second microarthropod survey across four sites; the litterbags data were pooled from four retrieval dates. For PerMANOVA analysis, Bray-Curtis index was used and permutation times = 2000. Abbreviations: df, degrees of freedom; SS, sum of squares.

scores and their association with the N treatments can be found in Appendix A: Table A1.

Litterbag results

Aspen litter decayed rapidly, with an average of 17% of initial mass remaining after 16 months. Comparison of the decay constant k indicated that there was no difference between mass loss rates of litter under ambient and experimental N deposition (Fig. 5; $P = 0.434$).

Similar to the results from the forest floor, the density of microarthropods in the litterbags was lower under experimental N deposition (Fig. 6; treatment effect, $P = 0.014$). The populations also varied among the retrieval dates (Table 1; time effect, $P < 0.001$), wherein oribatid mite densities were greater during the two summer collection dates (August 2009 and June 2010), and Mesostigmata and Collembola densities declined through time (Fig. 6; time × taxon interaction, $P = 0.016$). There was a positive relationship between the densities of Mesostigmata and Collembola, even after accounting for the time effect (partial regression, time as covariate; $R^2 = 0.51$, $P = 0.021$). Although the number of oribatid species in the litterbags was similar between N deposition treatments (Fig. 3), oribatid community composition varied between N deposition treatments (Table 2; treatment effect, $P = 0.001$).

PLFA analyses

Total microbial biomass (represented by total PLFA abundance) in the forest floor outside the litterbags and in the soil underneath the litterbags was very similar among four retrieval dates and did not differ between the ambient and experimental N deposition treatments (Appendix B: Fig. B1). Similarly, the total microbial biomass inside the litterbags did not differ between the ambient and experimental N deposition treatments (Fig. 7a), although the total biomass was slightly lower in the second year (time effect, $P = 0.027$).

Overall, the microbial PLFAs inside the litterbags were highly enriched by ^{13}C, compared to those outside the litterbags. The average ratio of ^{13}C:^{12}C of PLFAs in the forest floor was 0.012, whereas this ratio inside the litterbags averaged 0.035. Although the total microbial PLFAs were similar, the lower ^{13}C:^{12}C ratio led to a significantly lower ^{13}C content of microbial PLFAs under experimental N (Fig. 7b; $P = 0.03$), and all three microbial groups (fungi, Actinobacteria, and bacteria) responded similarly (taxon × treatment effect, $P = 0.259$). At the same time, the ^{13}C content of the microbial PLFAs declined over time ($P < 0.001$).

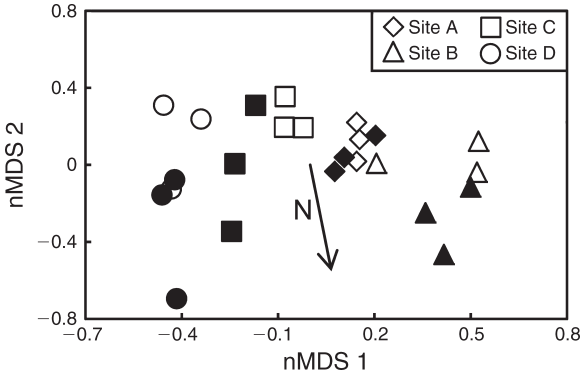

FIG. 4. The nonmetric multidimensional scaling (nMDS) ordination of the oribatid mite communities in the forest floor. The arrow indicates the direction of increasing N deposition ($R^2 = 0.309$, $P = 0.022$). Symbol shapes designate different sites. Symbols are open for ambient N deposition plots and solid for elevated N deposition plots.

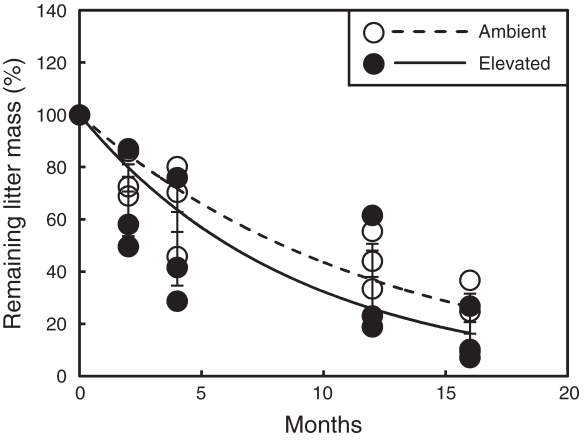

FIG. 5. Mass loss rates (mean ± SE) of aspen litter inside the litterbags over time. Litter mass loss did not differ between the ambient plots and the elevated N deposition plots ($P = 0.434$). The lines are best fit to the first-order exponential decay equation on the average of the ambient deposition (open circles, dashed line) and the elevated treatment (solid circles, solid line).

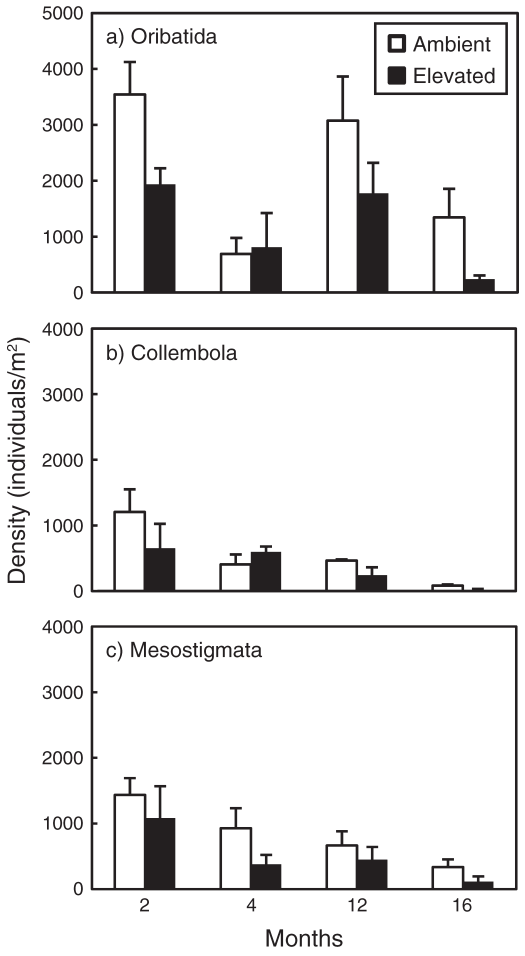

FIG. 6. Density (mean + SE) of microarthropods (Oribatida, Collembola, and Mesostigmata) inside the litterbags. Repeated-measures ANOVA indicated a decrease in their density in litterbags under elevated N deposition (treatment effect, $P = 0.014$).

Interestingly, the ^{13}C content of soil microbes underneath the litterbags did not increase until the last retrieval date, suggesting a time lag in the mobilization of ^{13}C-labeled aspen litter from the litterbags (Appendix B: Fig. B2).

DISCUSSION

After 17 years of experimental N deposition, the abundance of both detritivores (Oribatida and Collembola) and predaceous mites (Mesostigmata) has declined in forest floor, suggesting that a reduction in decay under experimental N deposition has decreased energy flowing through the soil food web. This finding directly contrasts to previous studies, in which positive effects on soil fauna have been found under N fertilization. This discrepancy may arise from the fact that those ecosystems are either young, developing forests (Berch et al. 2006), grasslands (Van der Wal et al. 2009), or heathland (Sjursen et al. 2005), in which enhanced productivity under N deposition has directly increased plant litter production. Such an increase would provide additional substrate for soil fauna, thereby increasing energy available to the soil food web (Berch et al. 2009). In our study system, net primary productivity has also increased under experimental N deposition, but has been allocated to stem production, rather than leaf or fine-root litter production (Burton et al. 2004, Zak et al. 2011). It appears that equivalent litter production under ambient and experimental N deposition, combined with reduced decay under experimental N deposition, has decreased the amount of energy available to fuel organisms at high trophic levels in the soil food web. Our observations, in combination with the studies just described, indicate that changes in plant litter production and its rate of decay can both be important controls of soil fauna communities under N deposition.

Consistent with our observations, detrimental effects of anthropogenic N deposition on soil fauna have been reported from various ecosystems. For example, Eisenhauer et al. (2012) found that the abundance of predatory nematodes and the species richness of nematodes and microarthropods were reduced in a long-term (13-year) grassland study under experimental N deposition. They attributed this decline to decreases in rhizodeposition. Other evidence of the negative effects of anthropogenic N on soil fauna has been observed in

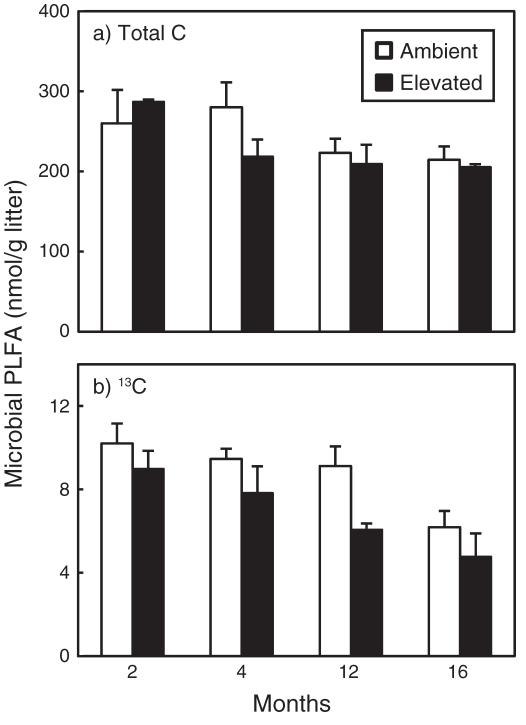

FIG. 7. (a) Total C and (b) ^{13}C content (mean + SE) of microbial PLFAs (phospholipid fatty acids) inside the litterbags. Although the total microbial biomass did not differ between the N treatments (total C, $P = 0.56$), the ^{13}C content declined over time ($P < 0.001$) and was consistently lower in the elevated N deposition treatment (^{13}C, $P = 0.03$).

boreal spruce forests (Lindberg and Bengtsson 2006), lodgepole pine forests (Berch et al. 2006), and subtropical forest (Xu et al. 2007). However, the amounts of N added in the aforementioned studies were much higher ($\geq$100 kg N·ha^{-1}·yr^{-1}) than those in our experiment (30 kg N·ha^{-1}·yr^{-1}); such high levels of N could result in soil acidification, base cation depletion, and the mobilization of Al^{3+}, all of which are detrimental to soil fauna (Matson et al. 2002). Such changes in soil chemistry have not occurred in our experiment, because soils are newly developed in calcareous glacial drift; soil pH, salt concentrations, and cations remain unchanged (Zak et al. 2008, Patterson et al. 2012). In contrast, litter decomposition has slowed due to the inhibition of lignolytic activity, resulting in an accumulation of organic matter in forest floor and surface soil (Pregitzer et al. 2008, Zak et al. 2008). The thickening of forest floor could potentially provide increased living space for soil fauna; however, declines in their densities suggest that these microarthropods are not limited by habitat availability. Rather, the positive relationship between the Mesostigmata and their prey (oribatid mites and Collembola) suggested that the decline in Mesostigmata was due to the decline in their food resources (oribatid mites and Collembola), which in turn was a bottom-up effect from the inhibition of microbial activity and litter decomposition under long-term experimental N deposition.

In spite of the decline in overall abundance, we did not observe a change in species richness of the most abundant group (Oribatida) under experimental N deposition (Fig. 3), which contrasts with other studies (Eisenhauer et al. 2012). However, it is difficult to compare the results among studies, because some provide only broad taxonomic resolution (Eisenhauer et al. 2012) and most studies do not quantify sampling effort (i.e., rarefaction analysis), which is crucial to understand whether the majority of species have been encountered. In our study, we did observe fewer species under elevated N deposition; however, rarefaction analysis indicates that species richness should converge between N treatments with additional sampling.

Although the total number of oribatid mite species did not differ between the N deposition treatments, species-specific responses resulted in a shift in community composition (Fig. 4). Overall, there were 16 species absent under experimental N deposition, whereas five species (*A. striculus*. *H. rufulus*, *P. peltifer*, and two *Xylobates* species) occurred exclusively under experimental N deposition. Moreover, it should be noted that species in the same genus can respond differently to experimental N deposition. For instance, *Tectocepheus veltus* and *T. minor* are two closely related and morphologically similar species that are often found in temperate regions (Laumann et al. 2007). *T. veltus* is dominant in many ecosystems (Fujikawa 1988, Fujita and Fujiyama 2001), but its relative abundance declined under experimental N deposition. In contrast, the relative abundance of *T. minor* increased under experimental N deposition (Appendix A). The minor species (*T. minor*) had also been found to dominate *T. veltus* in crop fields, which the authors attributed to the higher migration ability of *T. minor* and its ability to utilize different microhabitats (Fujita and Fujiyama 2001). In our case, we are unable to provide an ecological explanation for this response because the autecology of these species (especially *T. minor*) is largely unknown. Changes in energy flow or changes in fungal community composition under experimental N deposition (Edwards et al. 2011) may alter the competitive ability of mites that have different preferences for fungal species (Mitchell and Parkinson 1976). We expect that species that rely more on fungal hyphae in their diets will be more negatively affected by N deposition than those that rely more on detritus or other food items. Indeed, the accumulation of organic matter on the forest floor may even benefit species that feed predominantly on litter. Consistent with this expectation, many of the species detrimentally affected by experimental N deposition (Appendix A), including species in the genera *Epidamaeus* (Kaneko 1988), *Eremaeus* (Mitchell and Parkinson 1976), *Carabodes* (Schneider et al. 2004), and *Galumna* (Neena and Haq 1989), feed predominantly on fungal hyphae (Luxton 1972). On the other hand, the three species that only occurred under experimental N deposition rarely feed on fungi. For example, *Atropacarus striculus* and *Platynothrus peltifer* are primary decomposers that feed predominantly on litter, an insight derived from their ^{15}N:^{14}N natural abundance (Schneider et al. 2004) and their lack of chitinase to degrade fungal cell walls (Siepel and De Ruiter Dijkman 1993); *Hypochthoninus rufulus* has been reported to be an omnivore that feeds mostly on dead animals (Siepel and De Ruiter Dijkman 1993, Schneider et al. 2004). Another omnivore (*Fuscozetes fuscipes*; Wallwork 1958) also increased in its relative abundance under experimental N deposition.

We expected that reductions in the densities of soil fauna under experimental N deposition would then reduce subsequent litter decomposition, completing a feedback process between litter and soil fauna. Our data are in partial support of this prediction. First, presumably because of their lower densities in natural litter, fewer microarthropods colonized our experimental litterbags under experimental N deposition. Various studies have observed that microarthropod communities can accelerate the recovery of fungal communities after disturbance (Maraun et al. 1998*a*), stimulate extracellular enzyme activity, and increase microbial respiration (Kaneko et al. 1998, Wickings and Grandy 2011). Such simulating effects may arise because microarthropods can: (1) fragment litter, exposing more surface area for microbial activity; (2) disperse fungal spores and hyphae on their body surface; and (3) graze on fungal hyphae and simulate metabolism of microorganisms (Behan et al. 1978, Lussenhop 1992). Therefore, the lower densities

of microarthropods under experimental N deposition could result in lower microbial activity that feeds back to reduce litter decay. However, our results provided mixed evidence for this prediction. Although we did observe a lower ^{13}C content of microbial PLFAs inside the litterbags, we did not observe any change in total microbial biomass or litter decay rate in litterbags under elevated N deposition. Typical limitations of litterbag experiments (e.g., no control over litter fragments that were lost from the bags) may have reduced the statistical power necessary to detect any difference in decay rates between treatments. Nevertheless, the lower ^{13}C contents of microbial PLFAs may suggest that the ability of the microbial community to utilize new litter was reduced, which may have resulted, in part, from lower microarthropod activity. That is, reduced litter fragmentation and a lower surface area for microbial attack may have reduced the amount of litter ^{13}C assimilated by the saprotrophic microbial community. Additionally, changes in the oribatid community could potentially alter the composition of the microbial community by selective feeding (Mitchell and Parkinson 1976, Maraun et al. 1998*b*) with consequences for mobilization of ^{13}C from the litter.

Ecological implications

By combining field surveys and a litterbag experiment, we have demonstrated that chronic N deposition has a detrimental effect on a detritus-based food web, which may have diminished the ability of saprotrophic organisms to metabolize fresh litter. This finding argues that soil food webs may not be buffered against global change stressors as previously thought (i.e., elevated CO_2, increased temperature, and so forth). Functional redundancy has been assumed to be a common feature of soil fauna (Wolters 2001), and it is believed to be the reason why changes in species composition may have little influence on decomposing litter (Liiri et al. 2002). However, there is evidence that environmental stress can produce changes in the abundance and activity of soil fauna, with important consequences for nutrient and carbon cycling (Heneghan and Bolger 1996, Briones et al. 2009). For example, some microarthropod groups failed to recover after intense agriculture management, leading to slower organic matter decay in abandoned agricultural areas (Siepel 1991). In our study, the decline in the overall abundance of microarthropods would presumably reduce litter fragmentation for saprotrophic microorganisms potentially contributing to the declining rate of belowground C cycling observed in our system. This suggests a possible feedback mechanism wherein the inhibition of lignolytic activity under experimental N deposition reduces the energy entering the detritus-based food web, which detrimentally affects the soil fauna; the decline in soil fauna activity would then feed back to inhibit the ability of microorganisms to decompose new litter. Our results suggest that future rates of atmospheric N deposition could alter the composition and function of soil food webs, wherein the slowing of microbial decay initiates a cascading negative effect on higher tropic levels, culminating in the greater storage of C in soil organic matter.

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Supplemental Material

Appendix A

Oribatid mite species present in this study and their species scores from nMDS analysis (*Ecological Archives* A023-069-A1).

Appendix B

Figures for microbial phospholipid fatty acids (PLFAs) outside the litterbags (*Ecological Archives* A023-069-A2).