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Author(s): Evelyn S. Wenk , Mac A. Callaham Jr ., Joseph J. O'Brien and Paul J. Hanson

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Soil Macroinvertebrate Communities across a Productivity Gradient in Deciduous Forests of Eastern North America

Evelyn S. Wenk[1], Mac A. Callaham Jr.[1,*], Joseph J. O'Brien[1], and Paul J. Hanson[2]

Abstract - Within the temperate, deciduous forests of the eastern US, diverse soil-fauna communities are structured by a combination of environmental gradients and interactions with other biota. The introduction of non-native soil taxa has altered communities and soil processes, and adds another degree of variability to these systems. We sampled soil macroinvertebrate abundance from forested sites in Missouri (MO), Michigan (MI), Massachusetts (MA), and New Hampshire (NH), with the objective of comparing community assemblages and evaluating the role of invasive earthworms along the temperature–productivity gradient represented by the sites. The primary detritivores encountered were earthworms and millipedes. Earthworms were collected only in MO and MI, and at much greater density in MO. Millipedes were found at every site except in MO, and at their highest mean density in NH. Warmer temperatures, higher litter productivity, and low Oa horizon depth (as found in MO) were correlated with high earthworm activity. Oa horizon depth was the greatest in NH, where the macroinvertebrate community was dominated (in terms of abundance) by predators and herbivores, not detritivores. Our results are suggestive of, and congruent with, the concept of earthworms as ecosystem engineers, as we found that the presence of non-native earthworm species was associated with significant differences in soil characteristics such as apparent rapid decomposition rates and reduced carbon storage in the Oa horizon.

Introduction

Macroinvertebrates make up an important part of the soil fauna in many forested ecosystems and are known to have significant influences on process-level phenomena such as decomposition and nutrient cycling where they are abundant (Coleman et al. 2004, Frelich et al. 2006). These organisms follow general patterns of community composition influenced by temperature and moisture gradients on large geographic scales (Coleman et al. 2004, Fierer et al. 2009, Peterson and Luxton 1982). At the continental scale in North America, latitudinal peaks in species richness can vary between Nearctic and Palearctic species for key taxa, and the introduction of non-native species has fundamentally changed soil faunal distributions (e.g., earthworms; Lilleskov et al. 2008). At a more local scale (e.g., meters to 10s of kilometers), land-use history and management practices can also affect soil macroinvertebrate communities (e.g., Callaham et al. 2003, 2006a). In fact, soil macroinvertebrate community structure is considered useful in terms of indicating disturbance and/or soil quality (Keith et al. 2012, Ponge et al. 2013, Ruiz et al. 2011). When considering previous

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[1]Center for Forest Disturbance Science, USDA Forest Service, Southern Research Station, 320 Green Street, Athens, GA 30602. [2]Environmental Sciences Division, Oak Ridge National Laboratory, PO Box 2008, Oak Ridge, TN 37831. [*]Corresponding author - mcallaham@fs.fed.us.

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investigations at both continental and local scales, it is notable that most of these are complicated by having evaluated soil macroinvertebrate communities across major differences in the vegetation or level of soil disturbance represented in samples (but see Kalisz and Powell [2000] for an important exception). Conspicuously absent, at least for North America, are studies examining the macroinvertebrate composition of soils under similar vegetation types (e.g., deciduous forest) across large geographic areas (e.g., 100s to 1000s of kilometers).

Earthworms (Oligochaeta) were extirpated from northern ecosystems following Pleistocene glaciations, and have been slow to recolonize glaciated soils due to their limited dispersal rates (Gates 1982, Hendrix et al. 2008, James 1995). In general, the result has been arthropod dominance of decomposer food webs throughout most northern hardwood forests in North America (Cárcamo et al. 2000, Suzuki et al. 2013). The introduction of non-native earthworms into these northern forests has occurred since European settlement of North America, and dispersal is now primarily driven by human activity in previously glaciated soils (Callaham et al. 2006b, Cameron et al. 2007, Costello et al. 2010). These non-native earthworms have been observed to cause dramatic reductions in litter and humus layers, and translocate C from surface litter into the A horizon (Bohlen et al. 2004, Eisenhauer et al. 2007, Frelich et al. 2006). Habitat modification by earthworms can also have significant effects on the rest of the soil invertebrate community (Cameron et al. 2013, McLean and Parkinson 2000, Migge-Kleian et al. 2006, Salamon et al. 2006) and vegetation (Frelich et al. 2006).

Saprophagous macroarthropods, such as millipedes (Diplopoda), are the primary macroinvertebrate detritivores in ecosystems without native earthworms (Cárcamo et al. 2000, Suzuki et al. 2013), and the effects of millipedes on nutrient cycling differ from those of earthworms. Soil respiration rates can be lower where millipedes are present, as compared to earthworms (Snyder et al. 2009), and some evidence suggests that the C:N of feces is lower for millipedes than for earthworms (Hedde et al. 2007). Earthworms and millipedes can also compete for food resources, particularly in situations where the earthworm species is invasive (Snyder et al. 2011).

Soil nutrient and energy cycling are known to be sensitive to composition and structure of the soil faunal community, and identifying the factors that affect distributions and abundances of soil fauna is necessary to understand how and why carbon cycling varies across a landscape. As part of a larger study examining soil organic matter dynamics at sites spanning a latitudinal and precipitation gradient in the eastern US, we sampled soil macroinvertebrates to evaluate potential relationships between these communities and the soil organic matter. To the best of our knowledge, only 1 other study (King et al. 2013) documented soil macroinvertebrate communities across a wide range of eastern North American forests. However, their sampling methods focused on social insects, whereas we focus first on describing the detritivore community, followed by the abundance of other macroinvertebrates, and place less emphasis on social insects. The primary objective for our study was to describe the soil macroinvertebrate communities within each site and to relate them to carbon cycling and environmental gradients using traditional community-ecology metrics.

A secondary objective for the study was to compare soil macroinvertebrate communities across sites, and to evaluate similarities and differences where observed. Our ultimate intent for this study was to contribute to the knowledge of relationships between native and introduced macroinvertebrates, and their potential effects on organic-matter cycling in eastern deciduous forests.

Materials and Methods

Study sites

We sampled soil macroinvertebrates in 4 broadleaf deciduous forests across the eastern US. The study sites spanned the range of forests found in this region, from cool, wet forests in the northeast, to a drier, cool forest in the upper Midwest, and a warmer and drier forest to the south (Fig. 1, Table 1). All study sites were located at AmeriFlux sites in the footprint of eddy-flux towers. The northern-most site was located at the University of Michigan Biological Station in northern Michigan (MI). Two sites were located in the northeastern US, one at Bartlett Experimental Forest in northern New Hampshire (NH), and one at Harvard Forest in central Massachusetts (MA). The southern-most site was located at Baskett Wildlife Research and Education Center in the Missouri Ozarks (MO). In June 2010, we sampled sites in the order MO, MI, NH, MA, beginning 2 June and finishing 9 June. In September 2010 we sampled sites in reverse order (MA, NH, MI, MO) beginning 10 September and finishing 19 September.

Soils in MI were well-drained, coarse-textured Rubicon or Blue Lake series Haplorthods, derived from deep lake-plain sand deposits. Soils in NH were well-drained, coarse loam-textured Berkshire series Haplorthods derived from granite and gneiss. MA soils were sandy loam-textured Gloucester series Dystudepts formed in glacial till. Soils from MO were of 2 types: silt loam-textured Weller series Hapludalfs derived from loess deposits, and clay loam-textured Clinkenbeard

Figure 1. Map of sampling locations in the eastern US. Sites were located at the Baskett Wildlife Research and Education Center, MO, University of Michigan Biological Station, MI, Bartlett Experimental Forest, NH, and Harvard Forest, MA.

series Argiudolls derived from limestone colluvium and residuum (details given in McFarlane et al. 2012).

Macroinvertebrate surveys

Prior to our soil macroinvertebrate surveys, 5 semi-permanent marked plots were established at each site for a separate, but closely related study (McFarlane et al. 2012). In the vicinity (within 5 m) of each of these plots, we selected 2 undisturbed locations in which to dig soil pits for invertebrate collection at each of 2 sampling times (June and September 2010), generating 4 soil pits per plot over the course of our study. With 5 plots per site, and 4 sites, we sampled a total of 80 soil pits. At each soil pit, we collected macroinvertebrates from a litter sample and a soil sample. First, we removed all leaf litter (including Oi and Oe material) from a 50 cm × 50 cm area, and then excavated soil (including the Oa horizon) from a 30 cm × 30 cm × 30 cm soil pit centered within the litter sample area. We placed litter and soil samples on separate plastic sheets and then hand-sorted each in the field for 1 person-hour. This time-limited approach to hand-sorting has been shown to be efficient, both in terms of numbers and biomass, for collection of soil macroinvertebrates (Schmidt 2001). During sorting, we broke fine roots and woody debris less than 2.5 cm diameter, soil clods, and aggregates into pieces smaller than 0.5 cm in diameter. All visible invertebrates larger than 0.5 cm in any one dimension were collected and preserved in 70% ethanol solution for transport to the USDA-FS Forestry Sciences Laboratory in Athens, GA. We documented the depths of soil genetic horizons for each pit before returning the soil to the pit where it originated, taking care to maintain the original horizonation as much as possible. We then returned the leaf litter to its original location. In June 2010, we marked each pit's location so as not to resample in the identical location in September.

Specimens were identified by the second author to the finest taxonomic resolution practical using keys of Schwert (1990) and Peterson (1967). He identified adult and pigmented juvenile earthworms to species, abundant insect orders to family, and other insects and arthropods to order or suborder. Because area based sampling

Table 1. Site characteristics at forest sites in Missouri (MO), Michigan (MI), Massachusetts (MA), and New Hampshire (NH). See text for data sources.

	MO	MI	MA	NH
Latitude	38.7441	45.5598	42.5377	44.0647
Longitude	-92.2000	-84.7138	-72.1715	-71.2880
Mean annual air temp (°C)	13.0	6.8	8.2	7.3
Mean annual precipitation (mm)	1037	608	1141	1300
Mean soil water content (m^3 m^{-3})	0.246	0.153	0.316	0.272
Mean Oa depth (mm)	0.5	37.5	56	69
Mean stand age (years)	82	84	86	104
Canopy species (% basal area)	*Quercus* (41), *Acer* (14), *Juniperus* (14), *Carya* (9)	*Populus* (38), *Acer* (26), *Betula* (10), *Pinus* (9), *Quercus* (8)	*Acer* (38), *Quercus* (21), *Tsuga* (13)	*Acer* (28), *Fagus* (20), *Betula* (17), *Tsuga* (17)
Litterfall (Mg C ha^{-1} $year^{-1}$)	1.65	1.24	1.06	0.97

(pit digging) is not ideal for sampling social insects such as ants and termites, we tallied these taxa for presence or absence only. All specimens are stored at the USDA-FS Forestry Sciences Laboratory in Athens, GA.

Site environmental data

We recorded litter and soil temperature at each plot using two temperature thermistors (Soil Moisture Smart Sensor and Temperature Smart Sensor, and HOBO data logger, Onset Computer Corporation, Bourne, MA) installed in the O-horizon and at 10 cm depth in the mineral soil. Soil moisture was recorded using probes (EC-5 soil moisture sensors ECHO probes, Decagon Devices, Inc., Pullman, WA) installed at a depth of 10 cm from the surface of the O-horizon. All temperature and moisture data were logged hourly at each plot from 2008 to 2011. Due to datalogger failure at some plots, we only used times with complete measurements for all 20 plots (~276 days, spanning May 2008–July 2009) in our analysis of environmental variables. Litterfall data were obtained from McFarlane et al. (2012). We measured Oa depth in September 2010 at each soil pit (40 measurements).

Mean forest stand age (in 2010) ranged from ~80 to ~100 years (Table 1; AmeriFlux 2013). Overstory species varied between sites (Table 1). The MO and MA sites were dominated by *Quercus* and *Acer*; the NH site was dominated by *Fagus*, *Acer*, and *Betula*; and the MI site by *Populus, Acer,* and *Betula* (AmeriFlux 2013). All forests contained a coniferous component, which ranged 9–17% basal area. Tree basal-area measurements were taken between 4 and 9 years prior to our sampling (AmeriFlux 2013).

Statistical methods

We summarized the invertebrate communities by calculating the mean abundance of individuals in each taxon per m^2 at each site. We also calculated the frequency of occurrence for each taxon at each site (# of pits present/total # of pits). We categorized taxa by functional group and calculated the proportion of the macroinvertebrate community in each functional group for each site.

To determine whether there were patterns in the variability in invertebrate community composition, we used nonmetric multidimensional scaling (NMS; McCune and Grace 2002) using PC-Ord (PC-Ord 2006). We created a site-species matrix listing the mean abundance of individuals per m^2 at each plot (plots = 20), and taxa that were found in at least 2 plots over the course of the study (taxa = 39). We modified the data and used species maximum relativized data in the ordination procedure and other community analyses. We used the Sorensen (Bray-Curtis) distance measure for the ordination, with a maximum of 250 iterations, and a stability criterion of 0.00001. Because axes in NMS are arbitrary, we used a varimax rotation prior to our vector analysis (see below). Ordination is most useful for visualizing community relatedness among sites, but Anderson (2001) suggests permutation-based non-parametric MANOVA (NPMANOVA) as a method of applying statistical inference for site comparisons. We used the PerMANOVA option in PC-ORD to conduct a one-way analysis of differences in community composition with site as the independent variable and the Sorensen (Bray-Curtis) distance measure as the dependent variable, using 4999 permutations. Pairwise comparisons *t*-tests ($\alpha = 0.05$) were used to test the null hypothesis of no difference in communities among sites.

In order to test for environmental drivers of any observed site differences, we applied a vector analysis to community composition using environmental variables derived from a factor analysis as independent variables and NMS site scores as the dependent variables. We chose to use an initial factor analysis because many of the environmental variables were collinear. By using the factor scores in our vector analysis we were guaranteed that our independent variables would be orthogonal. The 6 environmental measures used in the factor analysis were latitude, Oa horizon depth, litterfall, soil temperature, litter temperature, and soil water content. Environmental data collected at the soil-pit level was averaged by plot for this analysis. After regressing the NMS plot scores, we plotted vectors within the ordination space (a joint plot) where the direction of the vectors indicated the sign and magnitude of the regression coefficients and the lengths were scaled by the variance explained.

We generated rank–abundance curves for the invertebrate communities at each site to display relative species abundance. Abundance was calculated by summing all individuals collected at each site over both sampling dates (20 pits per site). We combined adults and larvae of the same taxon but kept soil and litter samples separate for rank abundance curves because of differences in the areal extent sampled. We used community and diversity indices to identify patterns in community assemblage across our sites (as in Callaham et al. 2006a). We calculated Shannon's diversity index (H'), species richness, and evenness (J') for each pit. To calculate H', we used the formula:

$$H' = \sum_{i=1}^{s} p_i * \ln(p_i)$$

where s is the total number of taxa collected, and p_i is the proportion of individuals that are taxon i relative to all individuals of all taxa collected for each pit. We calculated J' was calculated as:

$$J' = H' / \ln(s)$$

Percent similarity (PS) was calculated to determine the amount of overlap between each pair of sites using the formula:

$$PS = 1 - \sum_{i=1}^{s} \frac{| p_i - q_i |}{2}$$

where for all species i … s, p_i is the mean proportion of individuals that are taxon i in site p, and q_i is the mean proportion of individuals that are taxon i in site q.

We conducted analyses of variance (ANOVA), using PROC MIXED in SAS 9.3 (SAS Institute Inc. 2010) to compare diversity, richness, and evenness among sites, employing a separate model for each sampling time. We used a mixed model ANOVA, with sampling date as a random effect, to compare the abundances of specific taxa (e.g., earthworms, millipedes) among sites. For all ANOVAs, we used least squares means to make individual comparisons between sites.

Results

Invertebrate community distribution

We separated the sampled macroinvertebrate community into 55 unique taxa based on taxonomic relationship and developmental stage (i.e., immature or adult). The mean densities and proportion of pits in which all taxa occurred are displayed in Tables 2 and 3. The primary detritivores encountered were earthworms (Oligochaeta) and millipedes (Diplopoda). Earthworms were collected only from sites in MO and MI, and at much higher abundances in MO ($P < 0.01$; Fig. 2a). Millipedes

Table 2. Mean abundance of soil macroinvertebrates, excluding Insecta, expressed as number of individuals m^{-2} to a 30-cm depth, and proportion of total pits where each taxon was collected at each site ($n = 20$; means calculated on 2 pits x 5 plots x 2 dates). The functional group (fg) follows the taxon name (d = detritivore, h = herbivore, o = omnivore, ps = parasite, p = predator, s = scavenger, v = various, and w = woodborer). Site abbreviations are as in Table 1.

		Abundance (individuals m^{-2})				Proportion of pits with taxon present			
Taxon	fg	MO	MI	MA	NH	MO	MI	MA	NH
Orthoptera, Gryllidae	d	-	0.20	-	-	-	0.05	-	-
Oligochaeta									
Aporrectodea caliginosa	d	82.11	2.22	-	-	0.95	0.10	-	-
Dendrobaena octaedra	d	-	0.76	-	-	-	0.10	-	-
Lumbricus spp.	d	51.98	5.53	-	-	0.95	0.45	-	-
Octolasion cyaneum	d	3.89	-	-	-	0.05	-	-	-
Unpigmented juveniles	d	110.10	0.20	-	-	0.95	0.05	-	-
Nematomorpha	ps	1.67	-	-	-	0.10	-	-	-
Gastropoda	h	3.92	3.20	1.16	0.80	0.50	0.60	0.20	0.20
Arachnida: Opiliones	p	-	-	0.40	0.40	-	-	0.10	0.10
Arachnida: Araneae	p	14.16	7.22	28.36	15.33	0.95	0.55	0.90	0.85
Isopoda	d	0.20	1.87	-	-	0.05	0.15	-	-
Diplopoda	d	-	2.71	3.87	15.42	-	0.20	0.45	0.70
Chilopoda: Geophilomorpha	p	4.33	1.36	19.22	6.04	0.35	0.25	0.75	0.60
Chilopoda: Lithobiomorpha	p	1.91	1.76	2.76	3.47	0.25	0.35	0.45	0.45

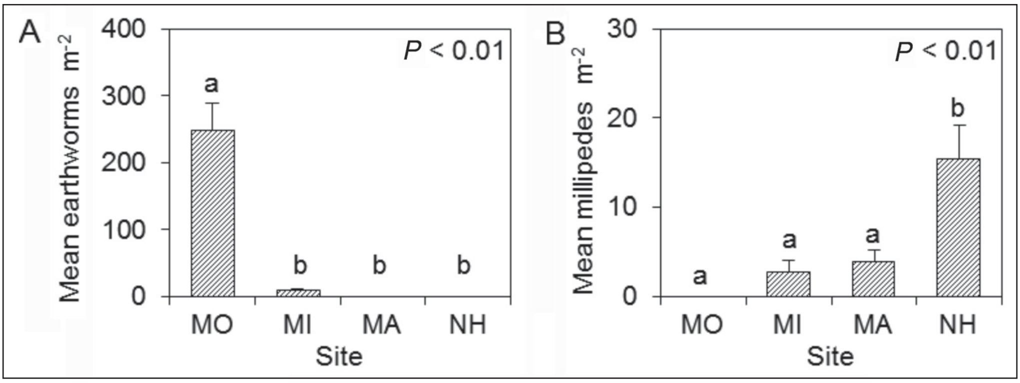

Figure 2. Mean (A) earthworm and (B) millipede abundances for soil and litter combined at 4 sites in the eastern US. Bars with different letters above are significantly different at α = 0.05; error bars represent the standard error of the mean. Note differences in y-axis scales. Site abbreviations are as in Figure 1.

Table 3. Mean abundance of soil insects, expressed as number of individuals m^{-2} to a 30-cm depth, and proportion of total pits where each taxon was collected at each site. The functional group follows the taxon name (abbreviations are as in Table 2). Site abbreviations are as in Table 1.

		Abundance (individuals m^{-2})				Proportion of pits with taxon present			
Taxon	fg	MO	MI	MA	NH	MO	MI	MA	NH
Orthoptera, Gryllidae	d	-	0.20	-	-	-	0.05	-	-
Orthoptera, other	h	0.20	-	-	-	0.05	-	-	-
Blattodea	o	3.51	-	-	-	0.40	-	-	-
Isoptera	d	N/A	N/A	N/A	N/A	0.15	-	-	-
Dermaptera	p	0.20	-	-	-	0.05	-	-	-
Hemiptera	h	0.20	0.20	1.40	-	0.05	0.05	0.30	-
Homoptera, Cicadidae	h	1.11	3.53	0.56	-	0.10	0.25	0.05	-
Homoptera, other	h	0.20	2.11	2.47	0.20	0.05	0.30	0.35	0.05
Neuroptera	p	-	-	0.20	-	-	-	0.05	-
Adult Coleoptera									
Cantharidae	p	-	0.56	-	-	-	0.05	-	-
Carabidae	p	24.22	0.76	2.60	3.27	0.70	0.10	0.40	0.50
Cicindellidae	p	-	-	-	0.20	-	-	-	0.05
Coccinellidae	p	-	0.20	-	-	-	0.05	-	-
Curculionidae	h	0.60	0.20	1.00	-	0.15	0.05	0.15	-
Elateridae	h	0.96	0.56	0.76	0.60	0.15	0.05	0.10	0.15
Scarabaeidae	h	2.51	2.47	1.16	0.56	0.30	0.30	0.10	0.05
Silphidae	s	-	0.20	-	-	-	0.05	-	-
Staphylinidae	p	2.62	2.27	1.91	2.56	0.25	0.2	0.30	0.20
other adult	v	1.11	3.11	-	-	0.10	0.25	-	-
Larval Coleoptera									
Alleculidae	d	6.51	0.56	2.22	0.56	0.20	0.05	0.20	0.05
Carabidae	p	1.51	0.76	0.76	0.76	0.15	0.10	0.10	0.10
Cerambycidae	w	-	-	-	0.20	-	-	-	0.05
Curculionidae	h	43.89	0.76	46.56	0.56	0.55	0.10	0.35	0.05
Dermestidae	s	-	0.20	-	-	-	0.05	-	-
Elateridae	h	5.00	18.02	37.53	25.98	0.25	0.85	0.90	0.70
Lampyridae	p	2.78	-	-	-	0.20	-	-	-
Scarabaeidae	h	20.24	30.56	2.98	-	0.55	0.75	0.10	-
Tenebrionidae	d	0.76	0.20	4.31	0.20	0.10	0.05	0.20	0.05
other larval	v	1.67	0.20	0.56	0.20	0.15	0.05	0.05	0.05
Adult Diptera									
Culicidae	ps	0.20	-	0.40	-	0.05	-	0.10	-
other adult	v	0.40	4.16	1.56	0.96	0.10	0.10	0.25	0.10
Larval Diptera									
Empidae	d	1.67	1.11	3.58	0.76	0.15	0.10	0.25	0.10
Fungivoridae	d	0.56	-	5.82	0.60	0.05	-	0.30	0.05
Tabanidae	d	0.56	-	-	0.20	0.05	-	-	0.05
Tipulidae	d	5.00	1.71	2.78	0.60	0.25	0.20	0.25	0.10
other larval	v	4.44	2.27	13.22	4.78	0.30	0.30	0.50	0.45
Adult Lepidoptera	v	0.20	-	-	-	0.05	-	-	-
Larval Lepidoptera	h	1.71	2.51	1.76	3.27	0.20	0.3	0.35	0.45
Hymenoptera, Formicidae	v	N/A	N/A	N/A	N/A	0.75	0.75	0.50	0.55
Hymenoptera, other	v	-	0.40	0.20	1.11	-	0.10	0.05	0.10
Insect pupae		7.82	0.76	3.98	2.47	0.40	0.10	0.40	0.35

were found at every site except MO, and at higher abundances in NH than other sites ($P < 0.01$; Fig. 2b). We found greater richness of beetle families in MI and NH, but the total abundance of beetles (larval and adult combined) was highest in MO and MA (Table 3). Total mean macroinvertebrate abundance (number of individuals per m^2; all pits + dates averaged, ± SE) was 416 (± 54) in MO, 195 (± 46) in MA, 107 (± 11) in MI, and 92 (± 16) in NH. The functional group with the greatest proportion of organisms varied by site, and was represented by the detritivores (64%) in MO, herbivores (including root feeders) in MI (60%) and MA (51%), and split equally between predators and herbivores in NH (36% each) (Table 4). The Curculionidae we collected were primarily soil-dwelling root feeders (D. Coyle, University of Georgia, Athens, GA, pers.comm.), and they are classified here as herbivores.

The variation in species composition was best explained by a 2-axis solution in the NMS ordination (stress level = 20.93, 70 iterations; Fig. 3). Axis 1 has an r^2 of 0.132 and axis 2 has an r^2 of 0.511. The NPMANOVA showed that there was a significant difference between sites ($F = 4.59$, $P < 0.01$). In the factor analysis, most of the environmental variables were strongly correlated, with only soil water content independent of the others (Table 5). Factor 1 explained 75% of the variance, and was positively correlated to litterfall, soil temperature, and litter temperature, and negatively correlated to latitude and Oa horizon depth. Factor 1 captures a N–S temperature-productivity gradient with higher temperature and productivity

Table 4. Variation in percentage of the macroinvertebrate community in each of four functional groups at four sampling sites in the eastern US. Values in parentheses are the mean number of individuals per m^2. Other functional group includes parasites, scavengers, omnivores, and taxa that were not identified to family. Site abbreviations are as in Table 1.

Site	Detritivore	Herbivore	Predator	Other
MO	64% (263)	20% (80)	13% (52)	3% (13)
MI	16% (17)	60% (64)	14% (15)	10% (11)
MA	12% (23)	51% (98)	29% (56)	8% (16)
NH	20% (18)	36% (31)	36% (32)	8% (7)

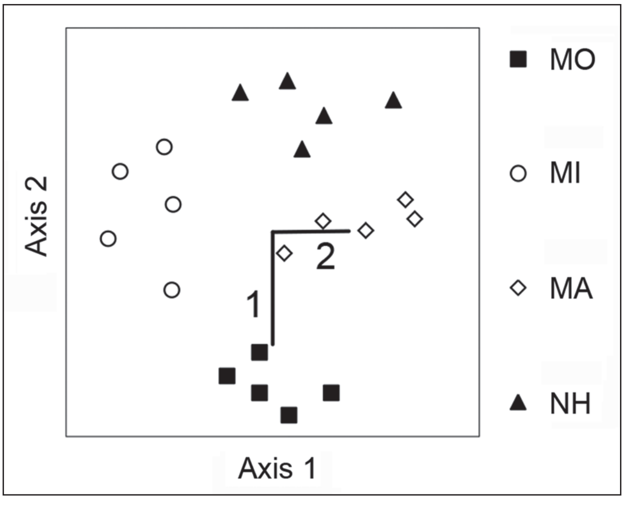

Figure 3. Ordination of plots in taxonomic space. Each plot point represents the mean of 4 pits; symbols indicate the geographic location of plots (MI = Michigan, NH = New Hampshire, MA = Massachusetts, and MO = Missouri). Vectors indicate the relative strength and direction of correlation of factor 1 (temperature/productivity) and factor 2 (soil water content) from the factor analysis; vector scaling is 100%.

towards the south. Factor 2 explained an additional 21% variance and was strongly positively correlated only to soil moisture. The joint plot (Fig. 3) shows that the temperature–productivity gradient drove the variation observed in Axis 2, while a soil-moisture gradient drove the site variation explained by Axis 1. Because the environmental vectors were essentially parallel to the NMS axes, these axes could be interpreted as temperature–productivity and soil-moisture gradients.

Diversity indices

The percent-similarity measures (Table 6) show that the MA and NH sites (geographically, the 2 sites closest to one another) had the most overlap, and the MO and NH sites (the 2 sites farthest apart) had the least overlap. The MI site, though a similar distance from the northeastern sites and MO, had more overlap with the northeastern sites, which were at similar latitude.

We found a significant difference in H' between sites in September ($P = 0.03$) but not in June ($P = 0.65$) (Fig. 4, Table 7). In September, MO had a significantly higher H' than NH. Species richness varied between sites in both June ($P = 0.003$) and September ($P = 0.001$). Species richness was lowest in NH at both sampling times. J' was not significantly different between the sites at either sampling time, but in MA and NH there was a significant increase in J' between June and September (MA: $P = 0.011$, NH: $P = 0.044$), suggesting decreasing dominance of the community by a few taxa, over the course of the season.

Rank–abundance curves (Fig. 5) showed that all sites had soil invertebrate communities dominated by few taxa. MI and NH, the northern-most sites, had the fewest number of taxa represented by 10 or more individuals in samples, for both litter and soil. The highest numbers of individuals in any 1 taxon were found at the

Table 5. Factor loadings of environmental variables, analogous to Pearson's correlation coefficients. * signifies loadings that were used to interpret and name the factors.

	Factor 1: temperature–productivity	Factor 2: soil water content
Latitude	-0.8929*	-0.3996
Litterfall	0.9582*	-0.2198
Oa Depth	-0.8970*	0.2830
Soil water content	-0.0482	0.9809*
Soil temp	0.9896*	0.0923
Litter temp	0.9932*	0.0641
Eigenvalue	4.4881	1.2628
% total variance explained	74.8	21.05

Table 6. Percent similarity of the soil macroinvertebrate community between study sites in Missouri (MO), Michigan (MI), Massachusetts (MA), and New Hampshire (NH).

	MO	MI	MA	NH
MO	-	0.36	0.37	0.25
MI		-	0.48	0.47
MA			-	0.66
NH				-

2 southern-most sites: MO and MA. In MO soil samples, the taxa represented by over 100 individuals were both non-native earthworms—*Lumbricus* spp. and *Aporrectodea caliginosa* (Savigny). In MA litter samples, the taxon with the highest rank abundance was spiders (Araneae).

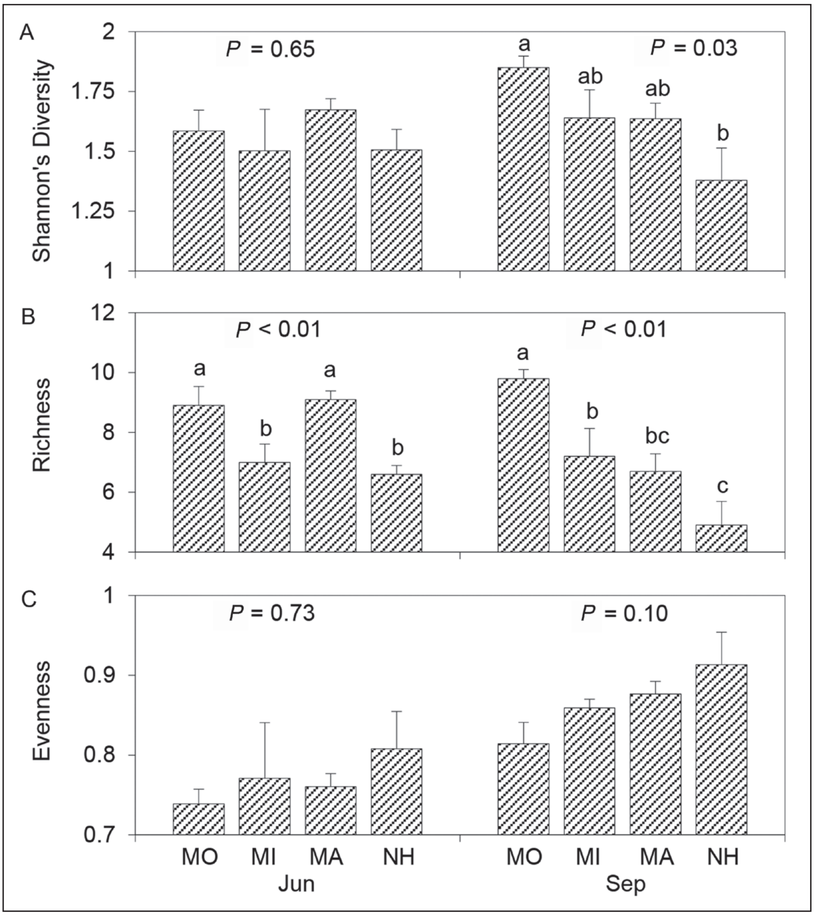

Figure 4. (A) Mean Shannon's diversity, (B) mean taxonomic richness, and (C) mean evenness of soil macroinvertebrate communities at four sites in the eastern US. in June and September 2010. Levels of significance are shown at α = 0.05, error bars represent the standard error of the mean. Site abbreviations are as in Table 1.

Table 7. F-table for all ANOVAs used in analyzing soil macroinvertebrate data.

Effect	DF	*F* value	$P_r > F$
Earthworm abundance	3	38.83	<0.01
Millipede abundance	3	11.35	<0.01
Total abundance	3	25.33	<0.01
Shannon's diversity			
June	3	0.56	0.65
September	3	3.83	0.03
Taxonomic richness			
June	3	6.9	<0.01
September	3	8.49	<0.01
Evenness			
June	3	0.43	0.73
September	3	2.45	0.10

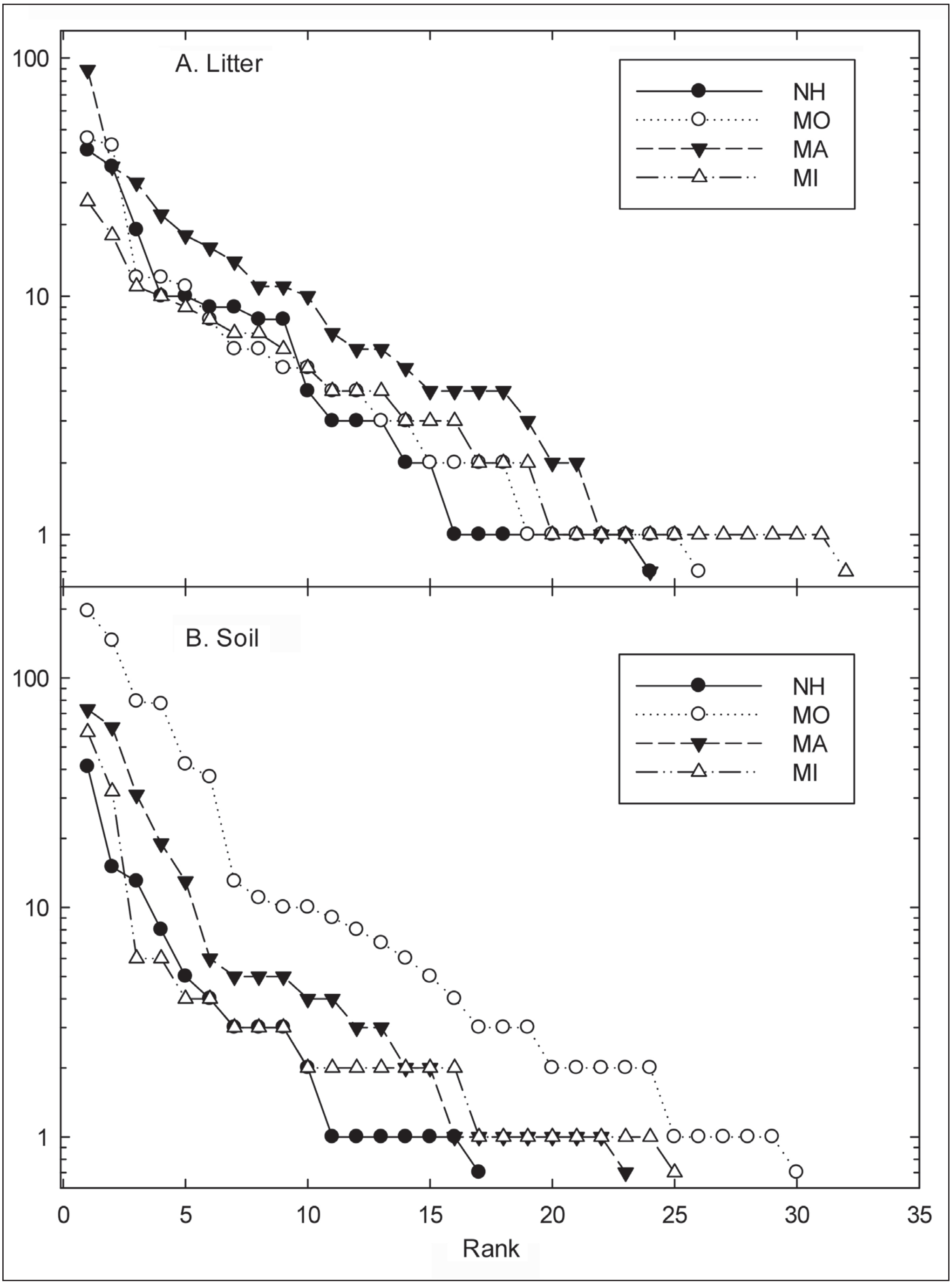

Figure 5. Rank-abundance curves for (A) litter and (B) soil-dwelling macroinvertebrates at 4 sites in the eastern US. Abundance equals the total number of individuals of each taxon collected at each site from a total of 20 pits per site. Note: y-axis is log scale. The point where a curve drops below 1 indicates the rank level at which no further taxa were collected for the site. Site abbreviations are as in Figure 1.

Discussion

Several soil invertebrate taxa are known to be most abundant in temperate deciduous forests (e.g., earthworms and millipedes), and decrease in abundance towards the tropics or as the coniferous forest component increases (Fierer et al. 2009, Peterson and Luxton 1982). While the structure of the soil invertebrate communities we observed may be related to trends that vary over much larger geographic areas, we posit that other factors (invasive species, productivity, temperature) had important effects on the soil invertebrate community structure, given that our sampling was carried out in relatively similar deciduous forest vegetation.

Among our study sites, productivity was highest in the south, with the highest mean temperature and litterfall and fastest SOM C turnover time (McFarlane et al. 2012) at the southern-most site. Other studies have observed a positive correlation between belowground faunal biomass and net primary productivity (McNaughton et al. 1989). We sampled abundance, not biomass, but we observed a positive correlation between belowground invertebrate abundance and productivity.

The largest difference in the detritivore community composition between our sites was related to the non-native earthworm component. The earthworm population density in MO was over 25 times the density we found in MI, and we sampled no earthworms at all in MA or NH. All adult earthworms we collected were non-native species. MO was also the only site where O horizon depth was close to zero. Earthworms can have significant effects on the organic layer, causing little differentiation between mineral and organic horizons (Schaefer and Schauermann 1990, Teuben and Smidt 1992), and reducing the thickness of the organic layer (Kuperman 1996, Snyder et al. 2011). Non-native earthworms have been documented in all 4 of the states (Reynolds 1995) in which we sampled. Invasions of non-native species are the result of anthropogenic activity and propagule pressure (Callaham et al. 2006b, Colautti et al. 2006, Su 2013). Non-native earthworms are present at sites farther north near the Great Lakes and St. Lawrence River in Canada, and throughout interior Canada (Dymond et al. 1997, Moore and Reynolds 2003, Reynolds 1995, Wironen and Moore 2006), and so all 4 sites are within their range; thus, their absence may not be due to unsuitable habitat or even an absence of introduction. It is possible they are present in such low densities in our sample areas that we did not detect them in NH and MA.

Earthworm invasions often occur in waves, with epigeic species being the first to arrive, and endogeic and anecic species invading only after the organic layer has already been reduced (Eisenhauer et al. 2007, Hale et al. 2005, James and Hendrix 2004). Once stable populations of endogeic and anecic species establish, the forest floor does not recover. We observed a greater abundance of endogeic earthworms (*Aporrectodea caliginosa* and *Octolasion cyaneum* (Savigny) [Blue Worm]) in MO, and a greater abundance of epigeic earthworms (*Lumbricus rubellus* Hoffmeister [Red Earthworm] and *Dendrobaena octaedra* (Savigny)) in MI (where the O horizons were thicker). One possible explanation is that the MO site has been invaded by non-native earthworms longer than the MI site. Our observation may also reflect the differences in earthworm communities observed across temperature gradients.

As temperature increases, earthworms can feed on SOM at lower concentrations because of increased mutualistic digestion from gut microbial activity; thus, the relative abundance of endogeic species increases at warmer sites (Lavelle et al. 1995). Additionally, we found a seasonal variation in epigeic earthworms. At both sites there were more epigeic earthworms in June than in September. It is possible that a reduction in the organic layer during the season, or drier overall conditions in late summer, may be responsible for the observed reduction in epigeic earthworms.

The presence of earthworms may have helped produce not only the fast SOM-C turnover rate observed in MO, but also the faster SOM-C turnover rate observed in MI relative to NH and MA (McFarlane et al. 2012). Decomposition rates are generally lower when moisture is limited (Collison et al. 2013, Riutta et al. 2012) and temperatures are lower (Gholz et al. 2000), but MI did not have the longest SOM-C turnover times—instead, the northeastern sites did (McFarlane et al. 2012). We suggest that at our sites decomposition was influenced more strongly by the presence of non-native earthworms than by precipitation or temperature. This observation is in line with other recent studies indicating that local factors may be more influential to decomposition rates than simple climate characteristics (Bradford et al. 2014, Wall et al. 2008).

Millipedes were present at all sites except MO, and they dominated the detritivore community at the NH site. Millipedes are primarily epigeic (Hopkin and Read 1992), and millipede survival is lower when litter and Oe/Oa horizon material is absent or reduced (David et al. 1991, Snyder et al. 2013), such as by non-native earthworms (Snyder et al. 2011). The shallower Oe/Oa horizon depth at the MO and MI sites, attributable to the greater earthworm abundances at these sites, may have resulted in less habitat and food resources for millipedes, as hypothesized in Snyder et al. (2011) and observed in Snyder et al. (2013). The absence of millipedes from our samples at the MO site was unexpected, and invites further scrutiny. In a study conducted in upland broad-leaf forest habitat close to the current study (within 40 km of our sampling site), Dowdy (1968) reported 14 species of millipedes in litter and soil occurring at average densities of ~23 individuals per square meter. Further information about millipedes in the forests of Missouri is scarce, but there are more recent reports of certain species occurring in the state (McAllister et al. 2005, Shelley et al. 2006), and there is no reason to expect that millipedes would not be represented in the fauna at our sampling site. It is possible that non-native earthworm abundances have increased significantly since Dowdy's study, and the absence of millipedes from our study site may be a direct consequence of this invasion.

The detritivore community in MA was dominated by larval Diptera and Coleoptera, in comparison to NH, which was dominated by millipedes. Though these sites had several similarities (no earthworms, thicker Oa/Oe horizon depth) compared to the other sites, there were also differences (MA was warmer, drier, and more productive and had a different tree community). Larval Diptera have shown a preference for deciduous forests over coniferous in boreal Canada (Paquin and Coderre 1997), and an increase in litter supply was shown to have a positive effect on Diptera (Hövemeyer 1989) and Coleptera larvae (David et al. 1991). These relationships may have helped to generate the differences in detritivore communities we observed, but additional research would be necessary to identify the mechanisms behind community structure at each site.

While some of the most notable differences in the invertebrate community between sites was due to detritivores, predators and herbivores were more abundant than detritivores at the northern sites and deserve further examination. Lindberg et al. (2002) found that drought conditions negatively affected the relative abundance of predators, and similarly, we found that the 2 driest sites, MO and MI, had the fewest predators. Predators can make up an increasing component of the invertebrate community as one transitions into coniferous and older forests (Paquin and Coderre 1997), but the sites in our study varied only by at most 22 years in stand age and 8% in percent coniferous basal area. The coniferous forest component was represented by a different species, *Tsuga canadensis* (L.) Carrière (Eastern Hemlock), in MA and NH, though, and it is possible that the accompanying difference in litter composition affected the predator communities. Predator–prey relations also may have impacted the invertebrate communities we observed. For example, Carabidae, which are known to consume earthworms (Eitzinger and Traugott 2011, King et al. 2010), were found at their highest density in MO.

Herbivores reached their highest relative abundances in MI and MA, though total herbivore abundance in MO was similar to MA and MI. The most-abundant herbivores we collected were Curculionidae, Elateridae, and Scarabaeidae larvae. Soil invertebrate herbivore communities can be influenced by vegetation (Frederick and Gering 2006) and soil texture (Carpaneto et al. 2010, Davis 1996), but much of the research on root-feeders is from agricultural and otherwise managed systems (e.g., Johnson and Murray 2008, Johnson et al. 2010). As our results show, forest soils are home to diverse herbivore communities; however, additional research in this area is needed to help clarify what biotic and abiotic factors are responsible for producing these communities.

Several of the patterns we observed across the 4 sites included in this study relate to known effects of abiotic gradients and biotic interactions, and provide some insight into transitions that may occur with predicted climate change (IPCC 2013) and increasing densities of non-native invasive species (e.g., Ricciardi 2007). We predict that as Palearctic earthworms invade new sites, or their abundances increase, faster SOM-C turnover rates and a reduction in the litter layer will result. Further impacts may include reduced abundances of other detritivores due to competition for limited resources with earthworms. The community assemblages we describe here are important as examples of the wide variety of soil macroinvertebrate communities found throughout the range of eastern deciduous forests.

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