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Response of soil invertebrates to disturbance across three resource regions in North Carolina

M. E. Barbercheck · D. A. Neher · O. Anas ·
S. M. El-Allaf · T. R. Weicht

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Abstract We evaluated the potential of soil microarthropods and enchytraeid worms to be useful as bioindicators of soil condition in forest, wetland, and agricultural ecosystems over a range of ecoregions. Selected mesofauna and soil characteristics in soil and litter in relatively undisturbed and disturbed examples of each of three ecosystems within each of three land resource regions were monitored over two years. Optimal times of year to sample these organisms as indicators of disturbance were April, May, July and September. No single measure reflected disturbance across all three ecosystems. Among forest sites, Simpson's diversity index, evenness, abundance of ants, and proportion of enchytraeids in the mesofauna differed between soils of different disturbance levels. Among agricultural sites, richness, evenness, abundance of mites, and proportions of collembolans and of enchytraeids in the mesofauna differed between disturbance levels. Among wetland sites, Shannon's and Simpson's diversity indices, richness based on the total mesofauna, and abundances of mites, diplurans, ants, and isotomid and onychiurid collembolans differed between disturbance levels. Covariates most frequently associated with abundance and diversity of the measured mesofauna were soil electrical conductivity, available N, organic matter, and pH. Canonical correspondence analysis provided information somewhat different to bivariate analysis. Using both approaches to examine soil and litter taxa that have distinctive responses to disturbance may help to identify candidate groups applicable for use in large-scale environmental monitoring programs.

Keywords Soil · Microarthropods · Collembola · Mites · Enchytraeids · Biological indicators · Environmental monitoring · Biodiversity · Wetlands

Introduction

Change in soil quality can serve as an indicator of change in the soil's structural and biological integrity and reflect degradation from environmental stresses

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M. E. Barbercheck
Department of Entomology,
North Carolina State University,
Raleigh, NC 27695, USA

D. A. Neher · O. Anas · S. M. El-Allaf
Department of Plant Pathology,
North Carolina State University,
Raleigh, NC 27695, USA

Present address:
D. A. Neher · T. R. Weicht
Department of Plant and Soil Science,
University of Vermont,
Burlington, VT 05405, USA

Present address:
M. E. Barbercheck (✉)
Department of Entomology,
The Pennsylvania State University,
University Park, PA 16802, USA
e-mail: meb34@psu.edu

(Wander and Drinkwater 2000). In many cases, we lack sufficient knowledge about the response of biotic communities to use them reliably to evaluate changes in the condition of natural resources and ecological systems (The H. John Heinz Center for Science, Economics and the Environment 2002; Herrick 2000; Lubchenco et al. 1991). Indicators that are useable across ecosystem boundaries would be especially valuable, and criteria for successful ecological bioindicators in large-scale monitoring programs have been examined (Neher et al. 1995). Measures of soil biology and function can be useful indicators of ecosystem condition (Chagnon et al. 2000; Neher et al. 2005; Parisi et al. 2005). Indicators that reflect relationships within biological communities, rather than enumeration of populations of a single functional or taxonomic group, can minimize the problem of considerable heterogeneity of populations within soil samples (Neher et al. 1995).

Soil organisms can be difficult to sample, process, and quantify, and often require highly skilled or trained personnel to identify or interpret. Even though soil organisms provide many critical ecosystem services, gaps in our knowledge of ecology and taxonomy limit our ability to broadly implement indicators based on them (Hawksworth and Ritchie 1993). In addition to incomplete taxonomy, there are a limited number of specialists to identify large numbers of samples that a large-scale assessment would require. Nevertheless, soil fauna provide different information than chemical and physical properties or microbial biomass. For example, other environmental and microbial variables (sand, clay, pH, fungal: bacterial biomass) predict less than 24% of the variation in soil nematode communities (Neher and Campbell 1994).

Environmental disturbance can be classified in many ways. For example, by type—chemical, physical, biological—that alters invertebrate communities in qualitatively and quantitatively different ways, and by characteristics of the disturbance, e.g., intensity, frequency, regularity and magnitude (Dyer and Letourneau 2003). The resulting disturbance regime can be characteristic of a system or site, e.g., annual fertility or chemical inputs in annual agricultural systems, grazing pressure (species, stocking rate, etc.) on pastures, or harvest of forests.

Our overall objective was to determine if selected broad groups of soil microarthropods, enchytraeids and other invertebrates (Neher et al. 2005) differed consistently according to relative level of disturbance, and therefore could serve as potential bioindicators of soil condition across forest, wetland, and agricultural ecosystems. Our aim was to work within the framework of a large-scale environmental monitoring program, thus identifying one or two times of year that soil invertebrate communities are most likely to differ between levels of disturbance, and for differences to be robust enough to operate across different types of disturbance, and geographic differences in vegetation and soil type. We also wanted to use a level of taxonomic resolution and methodology that are sensitive to environmental change, yet approachable by non-specialists. To test this concept, we examined soil and litter microarthropod and enchytraeid worm populations in relatively disturbed and undisturbed sites multiple times per year concurrently with selected physical and chemical soil properties.

Materials and methods

Sample sites

We chose North Carolina as the initial study site because of its diversity of terrestrial ecosystems including wetlands, forests and land converted to agriculture. These systems are arranged spatially in a mosaic in three land resource regions (LRR) within the state, i.e., coastal plain, piedmont, and mountains, which represent geographic areas with unique soil type, topography, climate and water resources. We identified and sampled relatively undisturbed and disturbed sites paired with similar soil type in each of three ecosystems and three LRR (Table 1, Neher et al. 2003). This scale of resolution is recommended by Neher et al. (1998) as the finest necessary for establishment of reference comparisons for regional or national-scale monitoring programs.

Soil samples

Soil samples were collected at all 18 sites 15 times over 2 years, starting in March 1994 and ending in November 1995. 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

Table 1 Descriptions of relatively disturbed and undisturbed study sites in North Carolina[a] (adapted from Neher et al. 2003)

Ecosystem	Land Resource Region	Relative condition	Soil type	Vegetation history	N (μg g^{-1})	EC (dS m^{-1})	SOM (%)	pH
Forest	Mountain	Disturbed	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	Disturbed	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	Disturbed	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	Undisturbed	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	Undisturbed	Sandy clay loam	Loblolly pine planted 1939	2.3 (±0.16)	0.08 (±0.008)	5.1 (±0.07)	4.9 (±0.22)
	Coastal Plain	Undisturbed	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)
Wetland	Mountain	Disturbed	Loam	Cultivated > 45 years; corn, *Zea mays*, planted in 1993	7.7 (±1.96)	0.18 (±0.030)	5.0 (±0.12)	5.4 (±0.07)
	Piedmont	Disturbed	Fine sandy loam	Cultivated > 55 years; soybeans, *Glycine max*, planted in 1993	5.4 (±0.47)	0.16 (±0.010)	6.6 (±0.19)	5.6 (±0.08)
	Coastal Plain	Disturbed	Fine sandy loam	Cultivation history unknown; corn planted in 1993	16.8 (±2.62)	0.26 (±0.020)	18.3 (±0.93)	4.6 (±0.07)
	Mountain	Undisturbed	Loam	Undisturbed since 1968	3.6 (±0.38)	0.12 (±0.020)	8.4 (±0.15)	4.7 (±0.06)
	Piedmont	Undisturbed	Fine sandy loam	Planted to pines in 1960	4.5 (±0.19)	0.16 (±0.010)	9.0 (±0.13)	4.9 (±0.05)
	Coastal Plain	Undisturbed	Fine sandy loam	Closed canopy natural pond pine, *Pinus serotina*, woodland	3.6 (±0.28)	0.14 (±0.006)	41.6 (±2.9)	3.3 (±0.06)
Agriculture	Mountain	Disturbed	Coarse-loamy	Cultivated > 16 years; *Z. mays* planted in 1993	25.3 (±6.37)	0.28 (±0.040)	9.7 (±0.20)	5.5 (±0.11)
	Piedmont	Disturbed	Sandy clay loam	Cultivated > 55 years; wheat, *Triticum aestivum,* and soybean planted in 1993	6.4 (±1.16)	0.16 (±0.010)	3.7 (±0.15)	6.2 (±0.07)
	Coastal Plain	Disturbed	Fine sand	Cultivated > 50 years	2.7 (±0.76)	0.07 (±0.010)	1.6 (±0.28)	5.9 (±0.07)
	Mountain	Undisturbed	Coarse-loamy	Planted in fescue, *Festuca ovina,* and ladino clover, *Trifolium repens*, > 20 years	6.7 (±2.18)	0.19 (±0.020)	9.6 (±0.19)	6.6 (±0.09)
	Piedmont	Undisturbed	Sandy clay loam	Fescue pasture planted in 1959	3.7 (±0.36)	0.17 (±0.010)	4.8 (±0.17)	5.68 (±0.08)
	Coastal Plain	Undisturbed	Fine sand	Mixed pasture since 1956	4.3 (±0.98)	0.09 (±0.009)	2.8 (±0.11)	4.97 (±0.08)

EC electrical conductivity, *SOM* soil organic matter (Neher et al. 2003)

[a] Values represent means and standard errors (± standard error; $n=30$)

within a 2 ha area, with a random starting point (Neher et al. 1995). Soil samples were collected using a soil probe (2.5 cm diameter, 20 cm depth); litter layers in forest and wetland sites were sampled separately by hand. Twenty soil cores were collected from transect 1 and 40 soil cores were collected from transect 2. The soil from each transect was pooled to form two composite samples which were separately homogenized by hand in a bucket. The composite sample from transect 2 was split into two subsamples so that variance within the site and within a sample could be quantified for each characteristic measured (Neher et al. 1995). Separate 500 cm^3 aliquots of soil (all sites) and litter (disturbed and undisturbed forest and undisturbed wetland sites) were placed in Tullgren funnels for five days during which microarthropods and enchytraeids (hereafter for convenience referred to as "total mesofauna") collected in 70% alcohol and 2% glycerin in vials for enumeration. Collembola were identified to family and all other microarthropods were identified to class or order, depending on the organism (Table 2).

Characteristics determined for the soil at each study site included percentage soil organic matter

Table 2 Abundances and frequencies of detection for organisms in soil (*n*=285) and litter (*n*=143) accumulated across 4 sampling dates (April, May, July, September) over two years (1994, 1995) for regions, ecosystems, and levels of disturbance combined

Taxon	Soil		Litter	
	Total numbers	Frequency (% of samples)	Total numbers	Frequency (% of samples)
Order Araneae	135	28.8	225	62.2
O. Acari	51,491	99.6	54,987	100.0
O. Pseudoscorpiones	30	7.4	79	26.6
O. Isopoda	1	0.4	9	2.1
Class Diplopoda	105	9.8	84	19.6
Cl. Chilopoda	34	9.5	49	19.6
Cl. Pauropoda	30	7.7	44	6.3
Cl. Symphyla	376	38.9	228	41.3
O. Protura	329	27.7	214	32.9
Fam. Hypogasturidae	8230	80.7	4415	88.1
F. Neanuridae	218	23.2	203	42.0
F. Onychiuridae	3431	74.4	1724	72.7
F. Cyphoderidae	58	1.8	3	1.4
F. Entomobryidae	2131	76.1	2010	84.6
F. Isotomidae	4863	62.1	4427	72.0
F. Oncopoduridae	0	0	2	0.7
F. Tomoceridae	10	2.8	75	14.0
F. Neelidae	40	5.3	33	10.5
F. Sminthuridae	338	28.4	121	24.5
O. Diplura	337	33.3	179	36.4
O. Isoptera	9	1.1	8	2.8
O. Dermaptera	13	3.9	11	5.6
O. Thysanoptera	337	86.7	322	89.5
O. Coleoptera adults	453	63.5	300	65.7
O. Coleoptera larvae	432	60.7	232	60.1
O. Diptera adults	304	46.7	174	49.7
O. Diptera larvae	785	49.1	337	44.8
O. Hymenoptera	1713	64.2	1229	80.4
Other arthropods	867	49.1	619	55.2
Cl. Oligochaeta	352	36.5	69	27.3

Soil samples were collected in all 18 locations, litter samples in nine.

(SOM), pH, electrical conductivity (EC), total available nitrogen (N) and texture (Table 1) (Neher et al. 2003, 2005). Daily means for soil temperature and moisture in all wooded sites (disturbed and undisturbed forests, undisturbed wetlands) were recorded with Campbell 21X dataloggers using thermistors and gypsum blocks, respectively, with sensors placed at 20 cm depth to match the depth of sampling invertebrates.

Data analysis

Criteria for optimal sample periods and candidate indicator taxa

We proceeded in several steps to determine the response of broad taxonomic groups, ratios among selected groups, and diversity measures to ecosystem and relative disturbance level. We chose the optimal time of year for sampling invertebrate populations by plotting means and standard error values for abundances and indices of interest through time. Criteria for determining optimal time of year for sampling invertebrate populations to discriminate relative level of disturbance included the period with the smallest variability in the calculated indices within relatively disturbed and undisturbed soils, greatest diversity of soil invertebrate communities within sites, and abundances of mesofauna between the 50th and 75th percentile of their annual maximum.

The criterion used for selecting particular groups of organisms for further analysis was detection in greater than 20% of the samples collected on the optimal sample dates. Although rare taxa can be among the first to become locally extinct as a result of habitat alteration, and therefore act as sensitive indicators, issues associated with interpreting rarity within the project time-frame (e.g., sampling and statistical issues; Link et al. 1994; Thompson 2006) were beyond the scope of this research. Therefore, groups of mesofauna that occurred in fewer than 20% of the samples will not be discussed.

Abundance

We determined the effect of relative level of disturbance and selected soil characteristics on abundance of mesofauna by restricting data analyses to samples collected in April, May, July and September (optimal sample periods). Data were analyzed as a nested design (Type II sums of squares) with fixed, independent variables defined as ecosystem type and disturbance nested within ecosystem; LRR was a random variable. Repeated measures analysis of covariance was performed using the MIXED procedure in SAS Version 8 (Cary, NC). Separate analyses were performed for two types of invertebrate populations (collembolans alone, total mesofauna including collembolans) as dependent variables. Covariates included SOM, pH, EC and N. A ln (x+c) transformation was used to normalize the variance of EC, N, and proportion SOM with c defined as 0.01, 0.1 and 0.01, respectively. Repeated measures analysis of covariance with single degree of freedom contrasts was performed for the forest soils with the additional covariates of temperature and moisture based on the accumulated units of temperature (°C) and moisture (MPa) for the seven days prior to sampling and estimating populations of the mesofauna (Neher et al. 2003). Hereafter, for convenience, the accumulated temperature and moisture units will be referred to as temperature or moisture.

For initial selection of candidate indicator groups, presence and abundance of microarthropods and enchytraeids were analyzed both as binomial and quantitative data. Binomial data were defined by assigning a group of mesofauna present as 1 and absent as 0 and performing a categorical analysis and a chi-squared statistic. Quantitative data defined as non-zero abundances of mesofauna were transformed as ln (x+0.1) and analyzed by a nested repeated measures analysis of covariance (as above) and an F statistic. Repeated measures analysis of covariance and categorical analysis were performed using MIXED and CATMOD procedures, respectively, in SAS Version 8 (SAS Institute 2000).

Diversity and similarity

Diversity of mesofauna was estimated using several indices, including: the Shannon diversity index; the Simpson diversity index; richness; and evenness (Hill 1973; Ludwig and Reynolds 1988; Neher et al. 2005). Data were analyzed as a completely nested design (Type II sums of squares) with fixed, independent variables defined as ecosystem type and disturbance nested within ecosystem; LLR was a random variable. Repeated measures analysis of covariance was performed using the MIXED procedure in SAS Version 8 (Cary, NC).

Jaccard and Morisita similarity indices were computed for each pair of experimental units among ecosystem types and disturbance levels using combined data from April, May, July and September for both years (Morisita 1959). Morisita indices were computed on median abundances of mesofaunal groups across April, May, July and September sampling times for each experimental unit. Both Jaccard and Morisita indexes have the advantage of relative independence from sample size and diversity (Ludwig and Reynolds 1988; Wolda 1981). Analysis of variance was computed with the MIXED procedure using SAS Version 8 (Cary, NC). The similarity index was used as the dependent variable to determine whether similarity was greater between levels of disturbance within each ecosystem than within a level of disturbance across ecosystems, and greater among than within an ecosystem type. Specific comparisons were quantified using single degree of freedom contrasts adjusted for Type I error. We calculated these indices based on presence or abundances of mesofauna groups detected and on proportions of mites, collembolans, and enchytraeids of the total mesofauna in the sample. Proportions were transformed by arcsine of the square root of (x+0.1) prior to analysis.

Multivariate analysis

Multivariate analyses were performed to explore the distribution of groups of mesofauna in relation to disturbance level and soil characteristics among ecosystems. A direct gradient procedure was performed with 'CANOCO' for Windows version 4.5 (ter Braak and Smilauer 2002). Site types (ecosystem, disturbance level) were treated as nominal (0,1) environmental variables. Soil chemical properties were treated as covariates, i.e., pH, SOM, EC, N. Abundances were transformed as ln (x+0.1) to normalize data prior to application of canonical correspondence analysis (CCA). A Monte Carlo permutation option was employed to determine the significance of the first axis. CCA results are displayed graphically with bi-plot scaling focused on inter-taxon distances, where vectors depict environmental variables and taxonomic groups are represented as points (centroids).

Results

Optimal sample period

Sample dates during the months of April, May, July, and September were most likely to discriminate between samples representing different levels of disturbance based on the criteria described in section 2.2.1 above. The measured soil mesofauna in samples collected in these months had the smallest variability in the calculated indices within relatively disturbed and undisturbed soils, greatest diversity within sites, and abundances between the 50th and 75th percentile of their annual maximum. Results reported are restricted to analyses of data from these sample dates unless otherwise indicated.

Abundance

Twenty-nine taxonomic groups were used in analyses to determine possible indicators of disturbance. Abundance pooled across all sample dates ("cumulative abundance") and frequency of detection, expressed as the percentage of samples of the total number of samples, varied among mesofauna groups, with mites (Acari) being most numerous and encountered most frequently (Table 2).

Ecosystem

Ecosystem had no significant effect on mean abundance of the total mesofauna in soil (F=1.90, df=2, 378, P=0.1510; Table 3) or litter (F=0.38, df=1, 192, P=0.5404; Table 4). For measured mesofauna in soil, ecosystem had a significant effect on the abundances of Acari, Diplura, and Hymenoptera (ants), isotomid collembolans, proportions of collembolans, mites and enchytraeids of the total, and the collembolan:mite ratio (Table 3). For measured mesofauna in litter, ecosystem had a significant effect on the abundances of onychiurid collembolans and symphylans (Table 4).

Disturbance

Relative level of disturbance had a significant effect on abundances of several groups of soil invertebrates (F=3.50, df=3, 378, P=0.0156; Table 3). Abundances of mesofauna that were detected in more than

Table 3 Means (±standard errors) of potential indicator invertebrate abundances (per 500 ml) and diversity indices in soil across LRR at study sites for April, May, July and September 1994 and 1995 in North Carolina[a]

	Ecosystem									
	Forest		Agriculture		Wetland		Covariates			
	Disturbed	Undisturbed	Disturbed	Undisturbed	Disturbed	Undisturbed	pH	EC DS m^{-1}	SOM %	Total N μg g^{-1}
Total arthropods										
Total arthropods $^{\text{n.s.}, **}$	9.29 (±1.75)	7.38 (±0.78)	6.43 (±1.08)	7.95 (±1.08)	9.77* (±1.31)	86.05 (±24.27)	ns	*** pos	*** pos	** pos
Shannon **, ***	0.87 (±0.05)	0.99 (±0.04)	0.79 (±0.04)	0.83 (±0.05)	0.77* (±0.03)	0.99 (±0.04)	*** neg	ns	ns	ns
Simpson $^{\text{n.s.}}$, ***	0.55* (±0.03)	0.48 (±0.02)	0.54 (±0.02)	0.57 (±0.03)	0.58* (±0.02)	0.47 (±0.02)	** pos	** pos	ns	** neg
Richness ***, ***	9.38 (±0.43)	9.97 (±0.29)	6.63* (±0.33)	8.19 (±0.31)	7.79* (±0.27)	10.21 (±0.35)	*** pos	*** pos	ns	*** neg
Evenness*, ***	0.62* (±0.02)	0.66 (±0.02)	0.73* (±0.02)	0.61 (±0.02)	0.63 (±0.02)	0.68 (±0.02)	ns	*** neg	ns	*** pos
Acari*, **	6.75 (±1.500)	4.67 (±0.685)	3.78* (±0.819)	5.72 (±1.047)	6.93* (±1.176)	60.72 (±19.07)	ns	*** pos	*** pos	* pos
Diplura*,*	0.040 (±0.009)	0.037 (±0.012)	0.015 (±0.006)	0.044 (±0.016)	0.027* (±0.009)	0.065 (±0.016)	*** pos	ns	*** pos	ns
Diptera adults$^{\text{n.s., n.s.}}$	0.012 (±0.003)	0.045 (±0.010)	0.009 (±0.003)	0.028 (±0.005)	0.045* (±0.012)	1.09 (±0.406)	ns	ns	*** pos	ns
Hymenoptera (ants)*,***	0.097* (±0.020)	0.270 (±0.055)	0.09 (±0.06)	0.521 (±0.190)	0.0234* (±0.007)	0.995 (±0.260)	ns	ns	*** pos	ns
Collembola only										
Total Collembola	2.09 (±0.36)	1.95 (±0.19)	1.53 (±0.21)	1.33 (±0.19)	2.31* (±0.25)	20.99 (±5.63)	ns	ns	*** pos	ns
Shannon $^{\text{n.s., n.s}}$	0.87 (±0.06)	0.83 (±0.05)	0.77 (±0.05)	0.88 (±0.05)	0.81 (±0.04)	0.97 (±0.05)	ns	*** pos	ns	* neg
Simpson $^{\text{n.s., n.s.}}$	0.52 (±0.03)	0.54 (±0.03)	0.56 (±0.03)	0.49 (±0.03)	0.54 (±0.02)	0.47 (±0.02)	ns	*** neg	ns	* neg
Evenness $^{\text{n.s., n.s.}}$	0.74 (±0.02)	0.68 (±0.02)	0.71 (±0.03)	0.78 (±0.02)	0.73 (±0.02)	0.72 (±0.02)	ns	* pos	ns	ns
Isotomidae**,*	0.450 (±0.110)	0.426 (±0.071)	0.477 (±0.212)	0.265 (±0.103)	0.583** (±0.129)	9.51 (±3.07)	ns	ns	*** pos	ns
Onychiuridae$^{\text{n.s.}}$,**	0.529 (±0.179)	0.419 (±0.098)	0.206 (±0.045)	0.211 (±0.040)	0.417*** (±0.085)	1.57 (±0.46)	ns	** pos	*** pos	ns
Proportion of total community										
Collembola ***, **	0.33 (±0.03)	0.32 (±0.03)	0.43* (±0.03)	0.24 (±0.03)	0.36 (±0.04)	0.37 (±0.02)	** pos	*** neg	ns	** pos
Mites$^{*, \text{n.s.}}$	0.57 (±0.04)	0.55 (±0.03)	0.51 (±0.03)	0.61 (±0.04)	0.57 (±0.04)	0.52 (±0.03)	ns	*** pos	ns	ns
Enchytraeids**, *	0.003* (±0.001)	0.005 (±0.001)	0.014* (±0.005)	0.003 (±0.001)	0.02 (±0.004)	0.01 (±0.002)	ns	ns	ns	ns
Collembola: Mite**$^{, \text{n.s.}}$	0.37 (±0.04)	0.37 (±0.03)	0.39 (±0.04)	0.30 (±0.03)	0.38 (±0.04)	0.43 (±0.03)	* pos	*** neg	ns	** pos

Significance level for each main effect: n.s., *, **, *** where n.s. $p > 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, determined by repeated measures analysis of covariance. Superscript positions: ecosystem, disturbance main effects. Means in data columns followed by * are significantly different ($p < 0.05$) between relative disturbance levels within an ecosystem. Pos = positive association of covariate with the measure of abundance or diversity, neg = negative association. EC: Electrical Conductivity, SOM: Soil organic matter.

20% of soil samples and differed significantly ($P < 0.05$) by level of disturbance but not by ecosystem included total arthropods (wetland only) and total collembolans (wetland only) (Table 3). Abundances of mesofaunal groups that were detected in more than 20% of litter samples and differed significantly ($P < 0.05$) between levels of disturbance but not ecosystem included total arthropods, total Collembola, Acari, hypogastrurid collembolans, Hymenoptera (ants), adult Diptera, the proportions of mites and collembolan of total arthropods, and the collembolan: mite ratio (Table 4).

Diversity in soil

Ecosystem

In soil, Shannon's diversity index, richness, and evenness differed among forest, agriculture and wetland soil ecosystems (Table 3). Mean richness in forest, agriculture and wetlands were 9.7, 7.4, and 9.0, respectively.

The only statistically significant difference due to ecosystem for any of the diversity indicators for forest and undisturbed wetland litter was evenness based on collembolan families (Table 4).

Disturbance

Several diversity indices differed between relatively disturbed and undisturbed soils within an ecosystem, but none were significant in every ecosystem (Table 3). Among forest sites, Simpson's diversity index differed between disturbance levels. Among agricultural sites, richness and evenness based on the total mesofauna differed between disturbance levels. Among wetland sites, Shannon's and Simpson's diversity indices, and richness differed between disturbance levels (Table 3).

In forest litter, significant differences in diversity based on relative level of disturbance were observed for richness based on the total mesofauna, and Shannon's and Simpson's diversity indices based on collembolan families (Table 4).

Similarity

According to Morisita similarity index values, the soil communities among ecosystems were less similar than between disturbance levels within an ecosystem. Morisita and Jaccard indices of similarity did not indicate differences in similarity between forest and wetland soils, or between undisturbed and disturbed soils (Table 5).

Environmental covariates

All of the measured soil characteristics were significant covariates for at least some of the abundances and calculated diversity indices in the three ecosystems and two relative levels of disturbance (Table 3). In soil, EC, available N, SOM, and pH covaried with 12, 9, 8, and 6 of the 19 abundance and diversity measures, respectively (Table 3).

In forest soils (disturbed and undisturbed forest, undisturbed wetland), temperature units accumulated for 7 d before the sample date were associated positively with total arthropod and enchytraeid abundance, Shannon's and Simpson's diversity measures based on total mesofauna, Simpson's diversity index based on Collembola and proportions of mites in the measured mesoafauna; and negatively with the proportions of Collembola and enchytraeids of the measured mesofauna and the Collembola:mite ratio (Table 6). Soil moisture units accumulated for 7 d before the sample date were associated positively with total mesofauna abundance but negatively with Shannon diversity values.

Multivariate analysis

Disturbed and undisturbed soils within an ecosystem were associated more closely than soils among ecosystems (Fig. 1). Soil chemical properties tended to be associated with specific ecosystems. For example, total available N and EC correlated positively with agricultural soils (i.e., disturbed and undisturbed agriculture, disturbed wetland converted to agriculture). Disturbed and undisturbed forests were negatively correlated with EC. Undisturbed wetland soils correlated positively with SOM and negatively with soil pH.

Soil mesofauna varied among ecosystem types and disturbance levels within ecosystem (Fig. 1). For example, mites, entomobryid and sminthurid collembolans, dipteran and coleopteran larvae, and enchytraeids were associated with agricultural sites. Onychiurid and isotomid collembolans, coleopteran

Table 4 Mean (± standard error) invertebrate abundances (numbers per 100 ml litter) and diversity indices based on total measured mesofauna, Collembola only, and proportions of candidate indicators across LRR, and disturbance levels in forest and wetland litter for April, May, July and September 1994 and 1995 in North Carolina

Measure	Forest		Wetland
	Disturbed	Undisturbed	Undisturbed
Total Arthropods$^{\text{n.s., ***}}$	71.64 (±12.18)	137.82 (±18.587)	91.45 (±13.619)
Total Collembola $^{\text{n.s., ***}}$	8.44 (±1.22)	29.51 (±3.38)	16.88 (±1.74)
Hypogastrurid Collembolans $^{\text{n.s.,***}}$	2.308 (±0.521)	10.97 (±1.83)	5.337(±0.915)
Onychiurid Collembolans $^{\text{*,**}}$	1.004 (±0.237)	4.59 (±0.995)	1.683 (±0.379)
Symphyla $^{\text{***,***}}$	0.125 (±0.030)	0.787 (±0.145)	0.054 (±0.015)
Protura $^{\text{*,***}}$	0.087 (±0.029)	0.723 (±0.249)	0.096 (±0.027)
Diptera adults $^{\text{n.s., **}}$	0.113 (±0.025)	0.302 (±0.091)	0.317 (±0.045)
Hymenoptera (Ants) $^{\text{n.s.,***}}$	0.525 (±0.094)	2.659 (±0.513)	1.991(±0.478)
Oligochetes (enchytraeids) $^{\text{n.s., n.s.}}$	0.0013 (±0.0006)	0.0013 (±0.0003)	0.004 (±0.0016)
Shannon: total $^{\text{n.s., n.s.}}$	0.72 (±0.055)	0.84 (±0.044)	0.80 (±0.038)
Simpson: total $^{\text{n.s., n.s.}}$	0.62 (±0.029)	0.56 (±0.024)	0.57 (±0.022)
Richness: total $^{\text{n.s., ***}}$	7.95 (±0.423)	11.91 (±0.349)	10.52 (±0.365)
Evenness: total $^{\text{n.s., n.s.}}$	0.59 (±0.026)	0.63 (±0.023)	0.63 (±0.022)
Shannon: Collembola $^{\text{n.s.,***}}$	0.77 (±0.075)	1.05 (±0.047)	0.98 (±0.049)
Simpson: Collembola $^{\text{n.s., **}}$	0.57 (±0.039)	0.45 (±0.024)	0.48 (±0.025)
Evenness: Collembola $^{\text{*,n.s.}}$	0.77 (±0.018)	0.73 (±0.020)	0.69 (±0.018)
Collembola (proportion) $^{\text{n.s., **}}$	0.22 (±0.027)	0.33 (±0.032)	0.28 (±0.026)
Mites (proportion) $^{\text{n.s., *}}$	0.71 (±0.030)	0.59 (±0.033)	0.64 (±0.029)
Collembola: mite $^{\text{n.s.,**}}$	0.23 (±0.029)	0.36 (±0.034)	0.31 (±0.029)

Significance level for each main effect: n.s., *, **, *** where n.s. $p>0.05$, *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$ determined by repeated measures analysis of covariance. Superscript positions: ecosystem, disturbance main effects.

and dipteran adults, and spiders were associated with undisturbed wetlands and high concentration of soil organic matter. Hypogastrurid collembolans, diplurans, proturans, and symphylans were most closely associated with forest soils, whereas ants and neanurine collembolans were associated with undisturbed wooded sites, i.e., undisturbed forests and undisturbed wetlands.

In litter, the measured characteristics were nearly orthogonal and, therefore, unrelated in undisturbed forest, disturbed forest, and undisturbed wetland litter (Fig. 2). Centroids for taxa that lie near the vector, and therefore are associated with, undisturbed forest are larval dipterans and isotomid, neanurid, onychiurid and hypogastrurid collembolans. Entomobryid and sminthurid collembolans, spiders, mites and symphylans were associated more closely with disturbed forest litter. Pseudoscorpions, dipteran adults, and coleopteran larvae were associated more closely with undisturbed wetland than with forest litter (Fig. 2).

Table 5 Mean (± standard error) Morisita and Jaccard similarity indices computed for soil communities among ecosystems ($n=36$) and between contrasting disturbance levels within each ecosystem ($n=15$)

Comparison	Ecosystem(s)	Morisita	Jaccard
Among ecosystems	Agriculture, Forest	0.93 (0.009)***	0.73 (0.013)
	Forest, Wetland	0.95 (0.007)	0.79 (0.015)
	Wetland, Agriculture	0.91 (0.012)**	0.77 (0.014)
Between disturbance levels	Agriculture	0.87 (0.020)	0.75 (0.023)
	Forest	0.95 (0.007)	0.81 (0.016)
	Wetland	0.94 (0.010)	0.80 (0.013)

**: p<0.01, ***: p<0.001, no superscript: $p>0.05$

Table 6 *F* statistics from repeated measures analysis of covariance among disturbance levels and correlation of covariates with measures of invertebrate abundance (number per kg dry soil) and diversity in forest soil across ecosystems and disturbance levels at study sites for April, May, July and September 1994 and 1995 in North Carolina

Measure	Disturbance *df*=1, 68	pH	EC dS m^{-1}	SOM %	Total *N* μg g^{-1}	Temperature	Moisture
Total community							
Total Arthropods	5.77*	0.12	10.36** pos	0.29	4.59* pos	17.99*** pos	3.98* pos
Shannon	1.5	0.36	0.24	0.89	0.31	12.55*** neg	7.37** neg
Simpson	18.20***	2.79	0.02	0.00	0.34	82.59*** pos	1.16
Richness	0.12	0.83	9.28** pos	0.22	3.07	0.07	1.09
Evenness	0.30	0.00	1.51	0.82	1.43	0.54	1.21
Collembola only							
Shannon	0.03	0.00	1.97	1.40	2.78	1.87	2.22
Simpson	4.04*	0.46	13.25*** neg	0.03	3.90	19.49*** pos	0.04
Evenness	0.06	0.25	2.88	0.53	0.00	0.18	0.00
Proportion of total							
Collembola	18.87***	0.77	4.21* neg	0.18	6.53* pos	39.04*** neg	0.36
Mites	14.86***	2.22	2.61	0.24	4.73* neg	46.13*** pos	1.56
Enchytraeids	0.78	0.19	0.18	3.56	1.39	11.37** neg	0.97
Collembola: Mite	21.02***	1.32	4.88* neg	0.24	5.40* pos	46.99*** neg	0.95

EC electrical conductivity, *SOM* soil organic matter, *Temp* cumulative temperature 7 days prior to sampling, *moist* cumulative rainfall 7 days prior to sampling. Where significant effects, *pos* positive association of covariate with the measure of abundance or diversity, *neg* negative association.

*significant at $P \leq 0.05$, ** significant at $P \leq 0.01$, *** significant at $P \leq 0.0001$, determined by repeated measures analysis of covariance

Discussion

Biological indicators

The most valuable indicators are those that are broadly applicable, i.e., they function across regions and secondarily perform well in more than one ecosystem or land use type. Even though we defined the relative level of disturbance of our sampled sites by how frequently or how recently the soil was disturbed physically, the communities that we assessed as indicators were influenced by and integrated physical and other kinds of disturbances of different magnitudes and frequencies. The overall goal of this study was to identify candidate bioindicators based on soil invertebrates that reflect relative levels of disturbance, as a proxy for soil condition, in large-scale environmental monitoring programs.

Abundance

Abundances of individual or groups of organisms are difficult to use as an indicator because of variability in response to different types of disturbance and differences in the ability of ecosystems to support populations. In this study, the abundances of several broad groups of microarthropods and enchytraeids were greater in relatively undisturbed than disturbed soils in all ecosystem types, whereas abundances of other groups showed the opposite response or were not detected in some ecosystems. There are multiple explanations for failure to detect an organism at a particular site. The organism may never have been there, sampling or extraction methods may have been inadequate to detect the organism's occurrence, or its numbers may have been reduced to undetectable levels by disturbance. Therefore, in our analyses, uncommon taxa, e.g., tomocerid collembolans and pseudoscorpions, were dropped from consideration and analysis because our goal was not to perform a complete census but to work within the limiting criteria established for large-scale monitoring programs.

Many studies suggest that soil mites are useful ecological indicators of various kinds of disturbance in agroecosystems (Koehler 1999; Ruf 1998), forests (Donegan et al. 2001; Vu and Nguyen 2000), and wetlands (Baur et al. 1996). In our study, mites comprised the most abundant and frequently detected

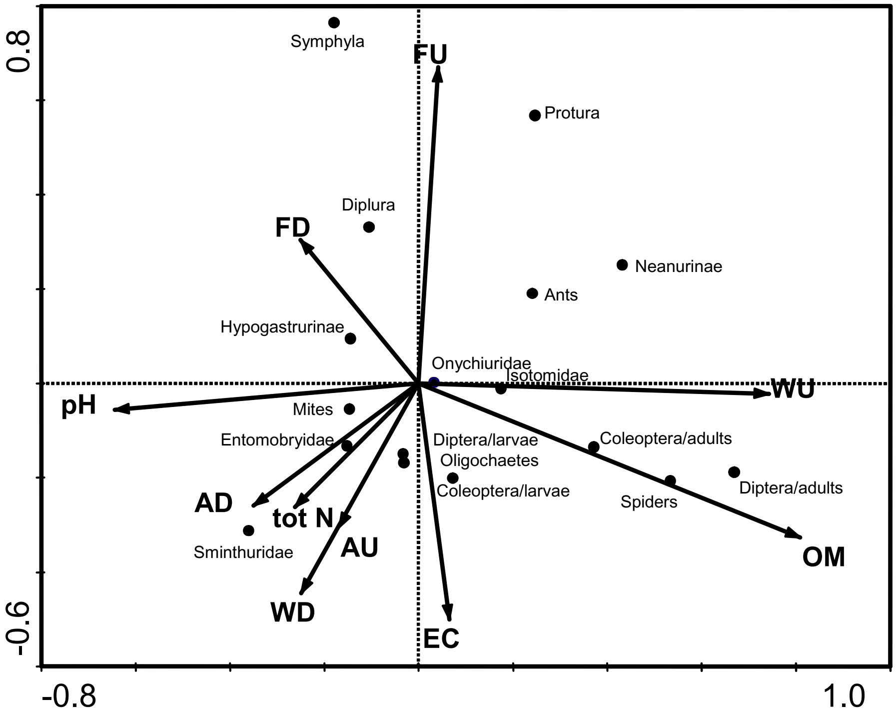

Fig. 1 Canonical correspondence analysis bi-plot of soil microarthropod families and environmental variables. Environmental variables including ecosystem-disturbance level (*FD* forest, disturbed; *FU* forest, undisturbed; *AD* agriculture, disturbed; *AU* agriculture, undisturbed; *WD* wetlands, disturbed; *WU* wetlands, undisturbed) and soil properties (pH; *ec* electrical conductivity; *om* % soil organic matter; *total N* total available nitrogen) are illustrated as vectors. Points represent numbers of microarthropods; abundances decrease with increasing distance from each point in a unimodal fashion (ter Braak and Smilauer 2002). Data represent two independent samples from all 18 sites sampled during April, May, July, and September of 1994 and 1995 combined (n=288). Eigenvalues (lambda) are 0.046 (p=0.0020), 0.031, 0.026, and 0.020 for first (horizontal), second (vertical), third and fourth axes, respectively. The first and second axes account for 32.7 and 23.5% of the variance in species-environment relationship, respectively

microarthropods and were associated positively with high SOM, as exemplified in undisturbed wetlands. In general, undisturbed soils harbor a greater species richness of mite fauna than agricultural soils (Lagerlöf and Andrén 1988). Numbers of mites in litter and soil in mature forests of Pacific Northwest were greater than in clearcut plots (Donegan et al. 2001).

Collembolan communities appear to be promising candidates for biological indicators of ecosystem condition because they are responsive to soil management practices and resulting soil conditions. In this study, collembolan abundance, diversity and proportion in the measured mesofauna were affected by both ecosystem type and disturbance level. In multivariate analysis, collembolan families were associated with ecosystem type, level of disturbance and soil characteristics. These results agree with the work of Fromm et al. (1993), who noted that field management had greater influence than soil type on numbers of collembolans. Miyazawa et al. (2002) observed that collembolan populations were larger in reduced than conventional tillage, smaller where synthetic pesticides were applied, and larger in fields with high organic matter.

In the wooded sites (undisturbed and disturbed forests, undisturbed wetlands) of this study, several indices based on collembolan families were useful. Other studies have shown that collembolan communities in forest soils show a high degree of evenness in young stands, whereas more established stands exhibit patterns of dominance by a few species (Donegan et al. 2001). This pattern suggests that in later successional stages a few species, better adapted to local resource supply, partition the resources in a strong hierarchical manner, and force other species into secondary roles in the community.

Separating groups of collembolans by habitat type may increase their utility as indicators. For example,

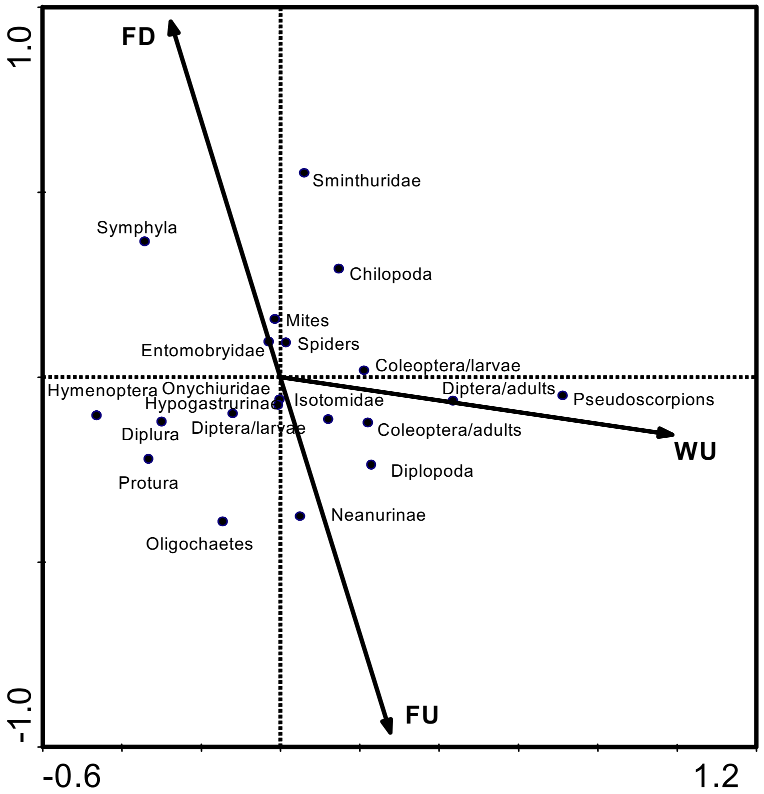

Fig. 2 Canonical correspondence analysis bi-plot of litter microarthropod families and environmental variables. Ecosystem-disturbance level (*FD* forest, disturbed; *FU* forest, undisturbed; *WU* wetlands, undisturbed) are illustrated as vectors. Disturbed wetlands are not illustrated because no litter layer existed. Points represent numbers of microarthropods; abundances decrease with increasing distance from each point in a unimodal fashion (ter Braak and Smilauer 2002). Data represent two independent samples from 9 sites with litter (undisturbed forest, disturbed forest, and undisturbed wetland ecosystems each in coastal plain, piedmont and mountain LRR) sampled during April, May, July and September of 1994 and 1995 combined (n=146). Eigenvalues (*lambda*) are 0.034 (p=0.0040), 0.027, 0.257, and 0.109 for first (*horizontal*), second (*vertical*), third and fourth axes, respectively. The first and second axes account for 55.4 and 44.6% of the variance in species-environment relationship, respectively

distribution of endogeic species is related to quality and quantity of organic matter content, including pH, C, N, and C/N ratio. However, epigeic species may be less useful as regional or national-scale indicators because they can be influenced more by geographical location than soil properties (Chagnon et al. 2000).

Although not an arthropod, enchytraeid worms were detected frequently in soil samples and were included in the analyses for this study. Enchytraeids (Cl. Oligochaeta) are distributed globally and play an important role in stabilizing structure and increasing porosity of soil (Briones et al. 1997; Didden et al. 1997; Topoliantz et al. 2000). van Vliet et al. (1995) hypothesized that enchytraeids have a greater influence on soil structure in agricultural fields than in forested areas, despite lower population densities. Our study agrees with observations that enchytraeids are detected in greatest abundance in acidic soils with high SOM content (Dash 1990; Nowak 2001; Schlaghamersky 2002).

In our study, ants responded negatively to disturbance and may be a potential candidate for use as a biological indicator. Ants are important in belowground processes through the alteration of the physical and chemical environment and through their effects on plants, microorganisms, and other soil organisms (Nkem et al. 2000). Ant species assemblages have been used as biological indicators of environmental condition in many different ecosystems (Hulugalle et al. 1997; Peck et al. 1998; Tshiguvho et al. 1999). In contrast to these reports, Whitford et al. (1999) concluded that ants cannot be used as indicators of ecosystem health or of rehabilitation success on rangeland ecosystems.

Diversity and similarity indices

Several of the diversity indices calculated with all groups differed between relatively disturbed and undisturbed soils within an ecosystem, but none were significant among all ecosystems. Although similarity indices distinguished relatively disturbed from undisturbed communities in some soils, they require identification of all taxa at fine resolution. In many instances, identification to fine resolution requires specialists and is labor-intensive. In addition, bivariate statistical procedures, showing only trends through time or in pair-wise comparisons, seem relatively uninformative relative to multivariate methods.

Community composition

Community composition can be more sensitive to disturbance than abundance or calculated diversity (Pietikainen et al. 2003). In our study, ordination provided results somewhat different from analysis using bivariate statistics. Based on ordination procedures, particular groups and measures derived from them warrant further investigation. In soil, mites, spiders, diplurans, proturans, symphylans, collembolans, coleopteran and dipteran adults and larvae, ants, and enchytraeids appeared promising for further investigation. In litter, response of spiders, mites, pseudoscorpions, symphylans, collembolans, dipteran adults, and coleopteran larvae to disturbance should be studied further.

Effects of soil properties

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). Our results agree with previous studies that show that soil community composition in relatively disturbed and undisturbed agriculture, and disturbed wetlands converted to agricultural use was influenced by nutrient additions. This was reflected by relatively high pH and a positive association with EC and soil N in the disturbed agricultural sites. Bird et al. (2000) found that arthropod species richness, but not Shannon diversity, increased following N and P fertilization, indicating that the arthropod community responds to fertilization with a change in community composition rather than numbers of species. However, Lagerlöf and Andrén (1988) found few differences in species composition among four crops with different levels of soil physical and chemical disturbance.

Previously, we found that pH is a critical covariate to measure when examining the effect of disturbance on decomposition of lignin and cellulose (Neher et al. 2003). At the sites in our study, low pH was associated with slow decomposition rates. Van Straalen and Verhoef (1997) proposed an ‘arthropod acidity index’ which allows the median preferred pH of an arthropod community to be estimated from the indicator values, in conjunction with abundance scores in the field. The authors proposed that the pH-biological indicator system be used in monitoring programs for the analysis of ecological effects of long-term trends in soil acidity. Community composition of mites and collembolans, but not calculated diversity indices, were sensitive to changes in soil pH (Chagnon et al. 2000; Liiri et al. 2002).

Soil acidity can explain collembolan community composition along an altitudinal gradient, and density and diversity increase with increasing soil acidity (Loranger et al. 2001). The authors hypothesized that decomposition rates are slower in acid soils, leading to a buildup in SOM, a food source for collembolans. In our study, soil pH was associated positively with taxonomic richness, dipluran abundance, proportion of collembolans, and the Collembola:mite ratio. The positive association of SOM and wetlands is probably influenced by low pH. In the undisturbed wetland in the coastal plain, soil pH and percentage SOM were 3.3 and 41.6, respectively (Neher et al. 2003).

Measures that reflect soil fertility covaried similarly among the invertebrate groups in our study. EC, soil N, and disturbed agriculture were associated positively with each other. Previously, we found that EC was correlated positively with decomposition rates, with EC ranging from 0.05 to 0.28 $\mathrm{dSm^{-1}}$ (Neher et al. 2003). In general, EC values between 0 and 1.5 $\mathrm{dS\ m^{-1}}$ and pH values between 6 and 7.5 are acceptable for general plant growth and microbial activity. In our study, EC was associated positively with soil arthropod abundance and diversity but negatively with evenness. Available N was associated positively with arthropod abundance and diversity, but negatively with richness and evenness, suggesting the dominance of groups that thrive in or tolerate relatively high nutrient conditions. The negative association between total N, EC and undisturbed forest soils may be due to low fertility and the perennial, woody nature of the system in contrast to the fertilized, herbaceous, annual agricultural sites (Fig. 1).

The abundance and community composition of some surface-active and soil invertebrates can be determined more by soil microclimate than by disturbance or agricultural management practice or other soil characteristics (Rebek et al. 2002). Because of site limitations, we only measured soil temperature and moisture in wooded sites. The addition of soil climatic factors, e.g., temperature and moisture, affected the significance of some soil covariates (Tables 3 and 6). For example, the significant relationship between SOM and some wooded site invertebrate measures is lost when temperature and moisture are included in the analysis. This suggests that soil temperature, especially, was a significant environmental factor affecting communities in the wooded sites. This suggestion is supported by Lindberg et al. (2002), who found that drought decreased and irrigation increased the abundance and diversity of oribatid mites and collembolans, and changed their dominance structure. Hulugalle et al. (1997) found that the activity of Collembola was limited to periods when the soil moisture was adequate.

Conclusion

To be most useful in large-scale monitoring programs, indicators must respond more strongly to the factor or condition of interest and be less responsive to ecoregion or ecosystem. Based on the taxonomic resolutions used in this study, we did not identify a common biological indicator or index that could distinguish relative level of disturbance across all of the sampled ecosystems. To achieve the most effective method within the economic and technical constraints of a large-scale monitoring program, we will likely need to develop a greater understanding of the integration of responses by key taxa to various disturbances. We did identify groups and associated soil measures that did respond to disturbance in some of the ecosystem types that can be examined in more detail in future studies. Covariates that should be measured at a minimum are soil temperature, EC, and SOM. One approach to decreasing the numbers of potential indicators would be to determine sentinel taxa or groups that are abundant, sensitive or tolerant to stress or disturbance, and eliminate those with no discernable response (Fiscus and Neher 2002; Thompson 2006). Multivariate analysis can provide information on relationships of specific groups of fauna with system characteristics, and could help narrow down the pool of potential bioindicators.

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