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# Urbanization alters the functional composition, but not taxonomic diversity, of the soil nematode community

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**Abstract**

We evaluated the response of riparian forest soil nematode community structure to the physico-chemical environment associated with urban land use. Soils were sampled seasonally between December 2000 and October 2002 along an urban—rural transect in Asheville, North Carolina. We characterized the taxonomic (to genus) and functional composition (trophic groups) of the nematode community of forest soils, as well as several nematode ecological indicators (maturity index, channel index, weighted faunal index). The diversity of nematode genera was not affected by urban land use. However, there tended to be functional differences in the nematode communities along the land use gradient. The urban soils tended to have lower abundances of predatory and omnivorous nematodes. Differences in channel index scores indicated that there was less fungal dominance in the soil food webs of the urban soils. Our results indicate that the functional composition of the soil food web is an important component of soil biodiversity that can be affected by land use practices. This study was conducted in a relatively small city; hence the influence of pollutants on the soil environment was not as great as in larger cities. Correspondingly, the impact on the soil nematode community was not very severe. The utilization of the nematode community assemblage as an indicator of soil conditions should be further explored in urban places of differing magnitudes of environmental effects.
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*Keywords:* Maturity index; Urban soils; Food webs; Diversity; Disturbance; Nematoda; Faunal analysis

## 1. Introduction

The soil food web plays a primary role in the decomposition of organic detritus and the mineralization of nutrients. Soil microfauna, such as nematodes, regulate microbial populations, and hence nutrient cycling through controls on microbial activity and turnover (Griffiths, 1994). Microfauna–microbe interactions have been shown to influence plant productivity through regulation of nutrients (Setälä and Huhta, 1991; Alphei et al., 1996; Wardle, 1999). Because of their influence in soil food webs, and plant–soil interactions, the composition of the soil nematode community has been suggested to be a useful indicator of the status of soils subjected to anthropogenic disturbance and management (Bongers, 1990; Bongers and Ferris, 1999; Ferris et al., 2001). Nematodes have several characteristics that make them suitable for use in biotic indices. Such characteristics include the ability to live in many environmental conditions, that they are in intimate contact with their environment through living in soil water, identification can be determined visually without dissection (and without the need for biochemical techniques), and nematodes occupy several positions at several trophic

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levels in the soil food web (Bongers and Ferris, 1999). The composition of the nematode community thus provides information about nutrient status and soil ecosystem functioning.

Cities have been shown to impact on local and regional estimations of biodiversity (Savard et al., 2000; McKinney, 2002). As global trends move towards increasing degrees of urban land cover, it is becoming important to understand the biodiversity of urban places (Miller and Hobbs, 2002). Urbanization has been shown to drastically impact the physical and chemical properties of soils. Urban soils tend to be highly modified in comparison to their natural counterparts (Pickett et al., 2001) through environmental effects such as, the urban heat island effect (Oke, 1995) and pollution (Pouyat et al., 1995; Lovett et al., 2000). Urban soils can thus be structurally and functionally altered (Effland and Pouyat, 1997; Pickett et al., 2001).

While there is a growing understanding of the nature of urban soils, there is a dearth of information on the status of soil food webs and nematode communities in urbanized soils. There is a strong interest in the use of soil nematode community assemblages to indicate soil quality and ecosystem health (Porazinska et al., 1999; Yeates, 2003). Nematodes have been successfully used to assess soil responses to agricultural practices (Porazinska et al., 1999), forestry practices (Forge and Simard, 2001), and mining restoration (Hohberg, 2003). Previous studies looking at the nematode fauna in cities found mixed results. Pouyat et al. (1994) report lower densities of nematodes in urban soils than in rural soils. They concluded that observed changes in invertebrate densities were influenced by soil heavy metal concentrations, and may be related to decreases in fungal populations with urban land use. Ohtonen et al. (1992) did not find a correlation between nematode numbers along an urban sulfur pollution gradient. Several studies have investigated parasitic nematodes in urban soils, composts, and water sources. No studies have been conducted which investigate the diversity of free-living soil nematodes in an urban context. Nor have there been studies which apply nematode community indices to urban soil environments.

The objectives of this study are to: (1) characterize the nematode community of urban forest soils and (2) determine whether urban impacts on soil ecosystems are reflected in indices of the soil nematode community. We hypothesized that in response to urban land use, nematode abundance and diversity would decrease, and that the structure of the nematode community would shift, reflecting a loss of higher trophic groups (omnivores and predators).

## 2. Materials and methods

### 2.1. Site description

The study was conducted in and around Asheville, North Carolina, USA (35°35′N, 82°34′W). Field sites were selected along a 45 km transect running from Asheville to the Pisgah National Forest to the southwest. Four field sites were selected in each of three land use classes, urban, suburban, and rural (classes defined by political boundaries). Each field site was located in a riparian zone forest along streams in the French Broad River watershed. Sites were selected to minimize the natural environmental variation between sites, and have low elevations (660–760 m), similar soils (Hapludults, sandy loam), and are characterized as hardwood-conifer canopies. Physical, chemical, and biological properties of these field sites are given in Table 1; for methodological detail, see Pavao-Zuckerman and Coleman (in review).

### 2.2. Sampling and extraction

Soils were sampled once per season between December 2000 and October 2002. Samples were taken along a transect parallel to the stream at each site at intervals of 5 m.

At each field site, four soil samples were taken to a depth of 10 cm, and then divided into 0–5 and 5–10 cm depths. Soil cores included the organic layer, but not the litter layer. Each sample consisted of four adjacent bulked soil cores (each core was 5 cm × 5 cm).

Nematodes were extracted from 5 g sub-samples of soil using Baermann funnels (72 h). Extracted nematodes were preserved using 5% formalin. All nematodes

Table 1
Means of soil physical, chemical, and biological properties (top 10 cm depth) by land use class along an urban to rural gradient in western North Carolina

| Soil properties | Means by land use type | | |
|---|---|---|---|
| | Rural | Suburban | Urban |
| Annual temperature (°C) | 11.9 | 12.6 | 13.0 |
| Soil moisture (g $H_2O$ g $soil^{-1}$) | 0.44 | 0.29 | 0.25 |
| Bulk density (g $cm^{-3}$) | 0.58 | 0.83 | 0.80 |
| Organic matter (%) | 13.1 | 11.9 | 9.5 |
| Soil C:N | 17.4 | 19.4 | 15.7 |
| Microbial biomass (μg C g $soil^{-1}$) | 574.7 | 346.1 | 443.7 |

Values are the mean of four rural, four suburban, and four urban sites from four seasonal sampling dates in 2002, except for soil temperature, which is from continuous data logger measurement (adapted from Pavao-Zuckerman and Coleman, 2005; Pavao-Zuckerman and Coleman, *in review*).

in each sample were counted, and the first 100 nematodes in each sample were identified to genus (nematodes of the family Rhabditidae were only identified to family) on an inverted microscope.

Soil from each sample was dried to constant weight at 105 °C to determine soil moisture to express nematode abundances on a dry weight basis.

### 2.3. Nematode calculations

Nematode genera were assigned to trophic groups (bacteriovores, fungivores, carnivore, omnivores, and plant feeders) according to Yeates et al. (1993). The ratio of fungivorous to bactiverous nematodes was calculated as:

$$\text{FF : BF} = 100 \times \text{fungivores}/(\text{fungivores} + \text{bacteriovores}).$$

The total number of genera in each sample was recorded (richness). The Shannon–Weaver index of diversity (Shannon and Weaver, 1949) was calculated as a measure of diversity of the nematode community. The reciprocal of the Simpson index (Simpson, 1949; Magurran, 1988) was calculated as a measure of dominance for the nematode community. These indices were calculated as:

$$H'(\text{Shannon} - \text{Weaver}) = -\sum p_i \ln p_i,$$

$$D(\text{Simpson}) = \frac{1}{\sum p_i^2}$$

where $p_i$ was the proportion of individuals in the $i$th genus.

Maturity indices (Bongers, 1990; Yeates, 1994) were calculated for the nematode community. The maturity index (MI) is a semi-quantitative index that uses life-history traits of nematode taxa to assess the condition of an ecosystem using the composition of the nematode community (Bongers, 1990). Nematode families are assigned a c-p value; from 1 to 5, based upon whether they are fast (colonizers, 'c') or slow (persisters, 'p') reproducers. Nematodes belonging to the plant-feeding trophic group are not included in the MI. The MI was calculated as:

$$\text{MI} = \sum v_i f_i$$

where $v_i$ was the c-p value of the $i$th taxa, and $f_i$ was the frequency of the $i$th taxa in the sample.

Bongers (1990) excluded plant-feeding nematodes from the MI, and suggests calculating a separate maturity index for plant parasites, the plant parasite index (PPI). However, Yeates (1994) argues that Bongers (1990) paper concerned mainly benthic samples, and that for terrestrial sites, this exclusion of plant feeders is unwarranted. Yeates (1994) therefore combines the MI and PPI into one index, the total maturity index (ΣMI). The ΣMI was calculated using the same formula as the MI, except that all trophic groups were included in the calculation.

Ferris et al. (2001) expand the maturity index concept to a weighted faunal analysis to allow enhanced assessment of the soil food web via analysis of the nematode community. Nematode taxa are assigned to functional guilds, where all nematodes in a functional guild have the same feeding habit (*sensu* Yeates et al. (1993)) and the same c-p value (i.e. the functional guild $Ba_2$ includes all bacteriovores with a c-p value of 2). These functional guilds are indicators of 'basal' (b), 'structured' (s), and 'enriched' (e) soil food web conditions. An enrichment index (EI) and structure index (SI) are calculated using an indicator weighting system based upon the importance of the functional guilds along hypothesized trajectories of enrichment and structure (Ferris et al., 2001). The EI and SI indicate the location of the soil food web along enrichment and structure trajectories, respectively, and were calculated as:

$$\text{EI} = 100\left(\frac{e}{e+b}\right), \qquad \text{SI} = 100\left(\frac{s}{s+b}\right)$$

where

$$e = \sum k_e n_e, \qquad s = \sum k_s n_s, \qquad b = \sum k_b n_b$$

and where, for example, $k_e$ are the weightings assigned to the guilds indicating enriched characteristics of the food web, and $n_e$ are the abundances of the nematodes in these guilds. The EI and SI are represented graphically for each land use type (see explanation in Fig. 3). Soils with high EI and SI tend to be from soils with low to moderate disturbance (e.g. physical disturbance, pollutants), soils with high EI and lower SI tend to have high levels of disturbance, soils with low EI and high SI tend to be from undisturbed soils, and soils with both low EI and SI tend to be from stressed systems (Ferris et al., 2001). Soils with high EI and low or high SI tend to be nutrient enriched, soils with low EI and high SI tend to have moderate levels of nutrient enrichment, while soils with low EI and low SI tend to be relatively depleted of nutrients. Additionally, following Ferris et al. (2001), the channel index (CI) was calculated as an indication of the nature of decomposition 'channels' in the soil

Table 2
One-way repeated measures analysis of variance of nematode data from the top 0–5 cm of soil along an urban to rural gradient in western NC

| Parameter | Land use ($df = 2$) | | Time ($df = 7$) | | Land use $x$ time ($df = 14$) | |
|---|---|---|---|---|---|---|
| | F | P | F | P | F | P |
| Richness | 0.97 | 0.414 | **3.76** | **0.002** | 1.12 | 0.361 |
| $H'$ | 1.177 | 0.225 | **7.29** | **<0.001** | 1.78 | 0.063 |
| $D$ | 1.76 | 0.226 | **36.86** | **<0.001** | 1.62 | 0.099 |
| Abundance | 0.99 | 0.408 | **9.75** | **<0.001** | 1.12 | 0.357 |
| Bacteriovores | 0.91 | 0.436 | **8.22** | **<0.001** | **1.96** | **0.037** |
| Fungivores | 0.45 | 0.648 | **15.35** | **<0.001** | 1.61 | 0.102 |
| Predators | **6.06** | **0.022** | **15.44** | **<0.001** | 1.36 | 0.204 |
| Omnivores | 1.02 | 0.398 | **3.60** | **0.003** | **2.96** | **0.002** |
| Plant feeders | 2.79 | 0.114 | **18.22** | **<0.001** | 1.44 | 0.163 |
| MI | 2.82 | 0.112 | **48.91** | **<0.001** | 0.67 | 0.790 |
| ΣMI | 0.49 | 0.629 | **112.75** | **<0.001** | **2.01** | **0.032** |
| FF:BF | 0.29 | 0.756 | **7.79** | **<0.001** | **1.93** | **0.040** |
| CI | **4.35** | **0.048** | 1.79 | 0.106 | 0.89 | 0.570 |

Only $P$-values <0.05 were considered statistically significant (indicated in bold font).

Table 3
One-way repeated measures analysis of variance of nematode data from the bottom 5–10 cm of soil along an urban to rural gradient in western NC

| Parameter | Land use ($df = 2$) | | Time ($df = 7$) | | Land use $x$ time ($df = 14$) | |
|---|---|---|---|---|---|---|
| | F | P | F | P | F | P |
| Richness | **6.99** | **0.015** | **4.41** | **<0.001** | 1.60 | 0.104 |
| H′ | 2.25 | 0.162 | **8.84** | **<0.001** | 2.09 | 0.025 |
| D | **4.96** | **0.035** | **28.52** | **<0.001** | 0.98 | 0.480 |
| Abundance | 0.11 | 0.895 | **32.4** | **<0.001** | **3.04** | **0.001** |
| Bacteriovores | 0.47 | 0.637 | **17.31** | **<0.001** | **2.40** | **0.010** |
| Fungivores | 0.17 | 0.850 | **13.78** | **<0.001** | **2.12** | **0.023** |
| Predators | **7.29** | **0.013** | **11.14** | **<0.001** | **1.94** | **0.040** |
| Omnivores | 1.54 | 0.267 | 1.89 | 0.086 | **2.71** | **0.004** |
| Plant feeders | 0.07 | 0.937 | **8.11** | **<0.001** | **2.31** | **0.013** |
| MI | **4.41** | **0.046** | **47.09** | **<0.001** | 0.44 | 0.954 |
| ΣMI | 1.85 | 0.212 | **58.86** | **<0.001** | 1.19 | 0.308 |
| FF:BF | **9.84** | **0.005** | **2.22** | **0.045** | 0.96 | 0.499 |
| CI | **5.08** | **0.033** | 1.12 | 0.361 | 1.01 | 0.460 |

Only $P$-values <0.05 were considered statistically significant (indicated in bold font).

food web. The CI was calculated as:

$$\mathrm{CI} = 100\frac{k_e\ \mathrm{Fu}_2}{(k_e\ \mathrm{Ba}_1) + (k_e\ \mathrm{Fu}_2)}$$

where $Fu_2$ represents the proportions of nematodes in the fungivore functional guild with a c-p of 2, and $Ba_1$ represents the proportions of nematodes in the bacteria ore functional guild with a c-p of 1. The CI is in essence a weighted ratio of fungal-feeding nematodes to bacterial-feeding nematodes.

### 2.4. Statistical analysis

All nematode data were log transformed to meet assumptions of normality. A repeated measures ANOVA was used to analyze the nematode data using the MIXED procedure in SAS. "Toeplitz" was selected as the covariance structure according to Littell et al. (1998). The models generated least squares means which were analyzed using the pdiff option of the MIXED procedure. The least square means were used to determine the lease significant difference at the $P < 0.05$ level. Results of statistical tests are provided in Tables 2 and 3.

## 3. Results

### 3.1. Diversity

Nematode richness ranged from 11 to 18 genera. A total of 60 genera were identified. Bacteriovorous taxa included, *Bunonema*, *Panagrolaimus*, *Rhabditidae*,

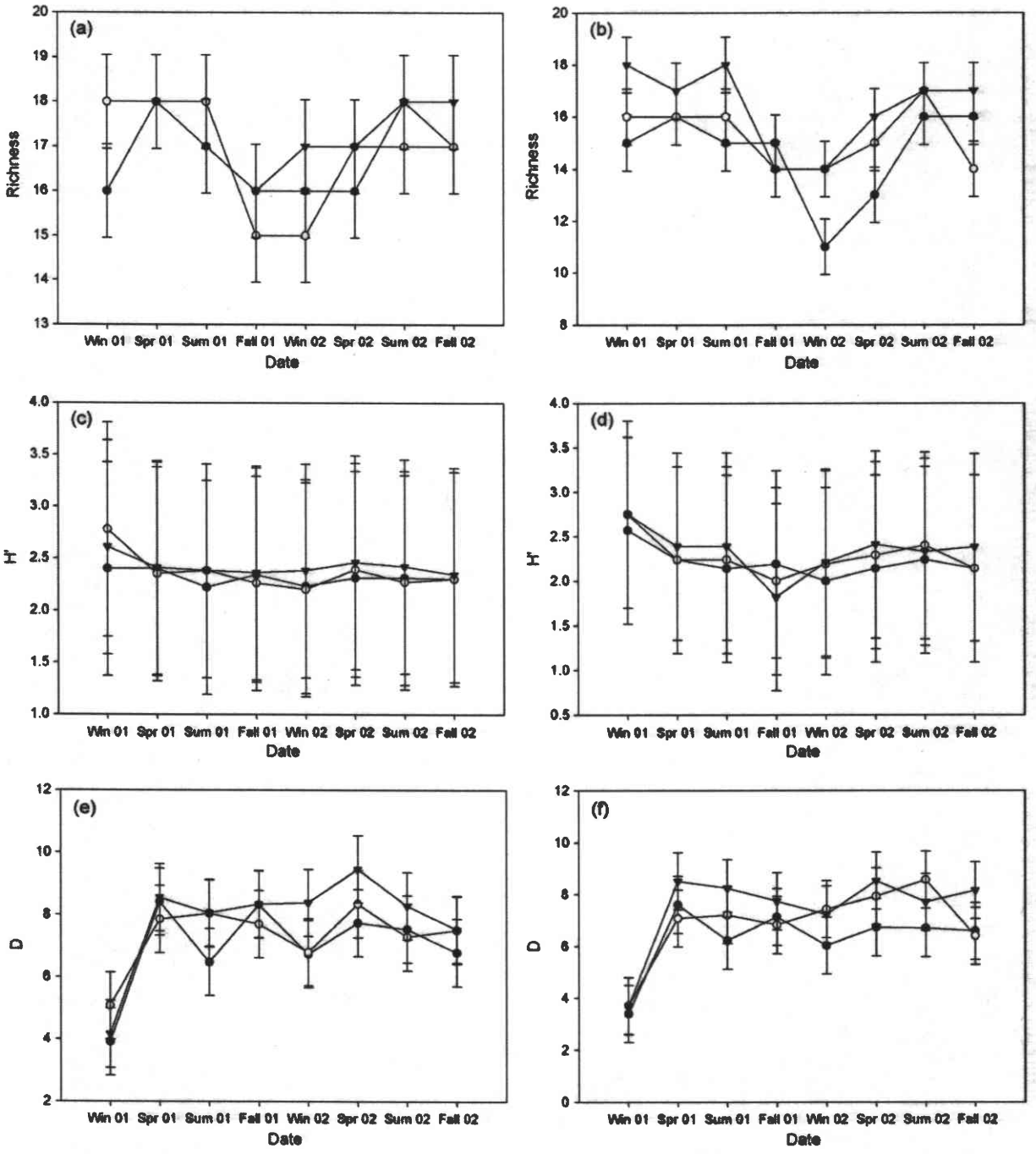


Fig. 1. Nematode genus level richness and diversity in response to land use class by season: effects of land use on: (a) genera richness in the top 0–5 cm of soil, (b) genera richness in the bottom 5–10 cm of soil, (c) genera diversity ($H'$) in the top 0–5 cm of soil, (d) genera diversity ($H'$) in the bottom 5–10 cm soil, (e) Simpson's evenness ($D$) in the top 0–5 cm of soil, and (f) Simpson's evenness ($D$) in the bottom 5–10 cm of soil. Closed circles are rural soils, open circles are suburban soils, and closed triangles are urban soils. Least square mean values +/−1 SE are presented.

*Pristionchus, Acrobeles, Acrobeloides, Cephalobus, Cervidellus, Chilopactus, Heterocephalobus, Zeldia, Eumonhystera, Geomonhystera, Plectus, Tylocephalus, Wilsonema, Metateratocephalus, Prodesmora, Bastiana, Dintheria, Prismatolaimus, Teratocephalus*, and *Alaimus*. Fungivorous genera included, *Aphelenchoides, Aphelenchus, Diphtherophora, Tylolaimophorus, Dorylaimoides, Tylencholaimus*, and *Tylencholaimellus*. Predatory genera included, *Tripyla, Clarkus, Mononchus, Prionchulus, Paractinolaimus, Aporcelai-*

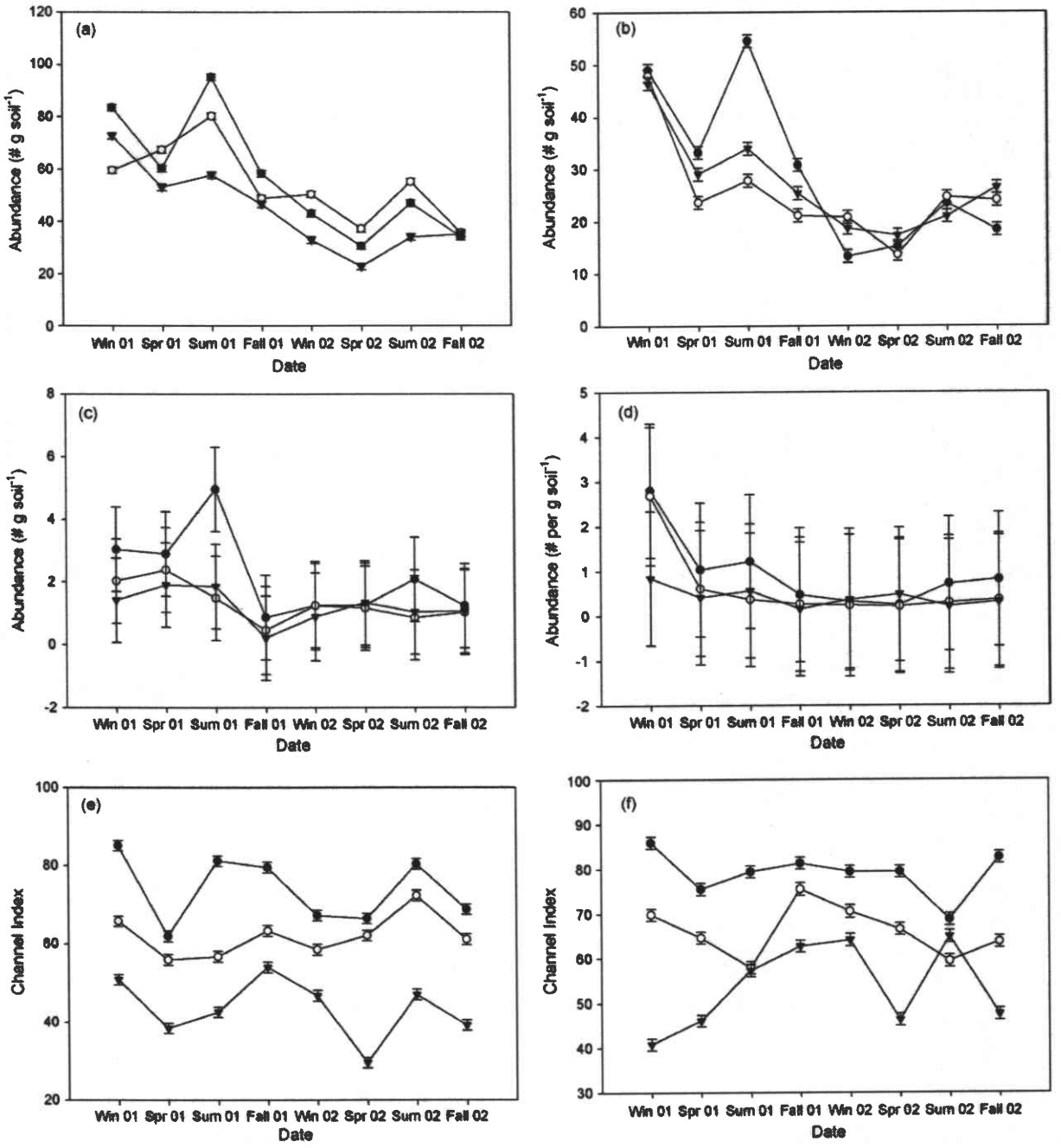


Fig. 2. Nematode abundance and trophic composition in response to land use class by season: effects of land use on: (a) total nematode abundance in the top 0–5 cm of soil, (b) total nematode abundance in the bottom 5–10 cm of soil, (c) predatory nematode abundance in the top 0–5 cm of soil, (d) predatory nematode abundance in the bottom 5–10 cm of soil, (e) channel index (a weighted fungal feeder to bacteria feeder ratio, see text and Ferris et al. (2001)) scores for the top 0–5 cm of soil, and (f) channel index scores for the bottom 5–10 cm of soil. Closed circles are rural soils, open circles are suburban soils, and closed triangles are urban soils. Least square mean values +/−1 SE are presented.

*mus*, and *Aporcelaimellus*. Omnivorous genera included, *Epidorylaimus, Eudorylaimus, Microdorylaimus, Thonus, Thornia, Dorylaimellus, Ecumenicus, Mesodorylaimus*, and *Prodorylaimus*. The plant-feeding taxa included *Filenchus, Malenchus, Tylenchus, Tylenchorhynchus, Helicotylenchus, Pararotylenchus, Rotylenchus, Pratylenchus, Heteroderidae, Criconematidae, Macroposthonia, Loofia, Paratylenchus, Longidorus*, and *Xiphinema*. Indices of nematode diversity did not significantly differ between land use classes in

the top 0–5 cm of soil (Fig. 1a). However, land use class did have a significant effect on richness and evenness in the bottom 5–10 cm of soil (Fig. 1b). The Shannon–Weaver index (Fig. 1c, d) did not differ between land use classes within sampling dates, except for in the 5–10 cm layer in the samples collected in Winter 2001. The Simpson index (Fig. 1e, f) also did not show any differences between land use classes within sampling dates.

### 3.2. Abundance and functional groups

Mean nematode abundance did not significantly differ between land use classes in the top 0–5 cm of soil (Fig. 2a), land use class did significantly affect abundance in the bottom 5–10 cm of soil (Fig. 2b). Nematode abundance ranged from 22.6 to 95.5 nematodes $g^{-1}$ dry soil in the top 0–5 cm of soil, and from 12.5 to 55.0 nematodes $g^{-1}$ dry soil in the bottom 5–10 cm of soil. There was a statistically insignificant trend towards lower nematode abundance in the urban soils in comparison with the rural soils within sampling dates.

Land use did not have a significant effect on the abundance of bacterial-feeding, fungal-feeding, or plant-feeding nematodes (Fig. 2). The number of predatory and omnivorous nematodes was significantly different between land use classes on some sampling dates (Fig. 2c, d). In general, the abundance of predatory and omnivorous nematodes decreased with increasing urban land use.

### 3.3. Maturity indices

The maturity indices provide information on the response of ecosystems to stress. The MI was not significantly different between land use classes in the top 0–5 cm of soil. The MI did tend to be lower in the urban soils than in the rural soils, although the differences were not very large (Tables 4 and 5). In the bottom 5–10 cm of soil, there was a significant decrease in MI with urban land use; however, there were no detectable differences in means (Table 5).

Inclusion of plant-feeding nematodes in the calculation of the maturity index (the ΣMI) tended to increase the maturity scores over those determined excluding plant-feeding nematodes (the MI, Table 5). This was due, in part, there being no plant-feeding nematode families ranked c-p 1 (Bongers, 1990), and also to the influence of c-p 2 taxa (e.g. Tylenchidae) and c-p 3 taxa (e.g. *Criconematidae, Heterderidae*) on the ΣMI index. Trends in ΣMI scores between land use classes were not discernable for the top 0–5 cm of soil, but tended to be lower in the urban soils than in the rural soils in the bottom 5–10 cm of soil.

Table 4
Nematode maturity indices in the top 0–5 cm of soil by land use class

| Index | Rural | Suburban | Urban |
|---|---|---|---|
| MI | | | |
| Winter 2001 | 2.42 | 2.58 | 2.45 |
| Spring 2001 | 1.93 | 1.74 | 1.72 |
| Summer 2001 | 2.68 | 2.54 | 2.46 |
| Fall 2001 | 2.50 | 2.43 | 2.42 |
| Winter 2002 | 1.53 | 1.32 | 1.39 |
| Spring 2002 | 2.75 | 2.60 | 2.79 |
| Summer 2002 | 1.95 | 1.65 | 1.68 |
| Fall 2002 | 1.93 | 1.86 | 1.80 |
| ΣMI | | | |
| Winter 2001 | 2.97 | 3.28 | 3.11 |
| Spring 2001 | 3.29 | 3.15 | 3.03 |
| Summer 2001 | 3.30 | 3.15 | 3.11 |
| Fall 2001 | 2.36 | 2.30 | 2.27 |
| Winter 2002 | 3.31 | 3.16 | 3.01 |
| Spring 2002 | 3.27 | 3.20 | 3.34 |
| Summer 2002 | 2.46a | 2.19b | 2.24a |
| Fall 2002 | 2.97 | 3.16 | 3.00 |

Least square means with different letters on the same date are significantly different at $P \leq 0.05$ (SAS pdiff option).

### 3.4. Functional indices

The soils among the land use classes are plotted along their respective structure (SI) and enrichment (EI)

Table 5
Nematode maturity indices in the bottom 5–10 cm of soil by land use class

| Index | Rural | Suburban | Urban |
|---|---|---|---|
| MI | | | |
| Winter 2001 | 2.50 | 2.57 | 2.42 |
| Spring 2001 | 1.85 | 1.71 | 1.79 |
| Summer 2001 | 2.51 | 2.56 | 2.46 |
| Fall 2001 | 2.59 | 2.50 | 2.40 |
| Winter 2002 | 1.84 | 1.59 | 1.63 |
| Spring 2002 | 2.63 | 2.65 | 2.54 |
| Summer 2002 | 1.93 | 1.95 | 1.79 |
| Fall 2002 | 1.80 | 1.64 | 1.77 |
| ΣMI | | | |
| Winter 2001 | 3.08 | 3.17 | 3.11 |
| Spring 2001 | 3.33 | 3.22 | 3.06 |
| Summer 2001 | 3.23 | 3.32 | 3.13 |
| Fall 2001 | 2.45 | 2.32 | 2.33 |
| Winter 2002 | 3.53 | 3.15 | 3.22 |
| Spring 2002 | 3.22 | 3.39 | 3.26 |
| Summer 2002 | 2.57 | 2.63 | 2.44 |
| Fall 2002 | 3.25 | 3.32 | 2.90 |

Least square means with different letters on the same date are significantly different at $P \leq 0.05$ (SAS pdiff option).

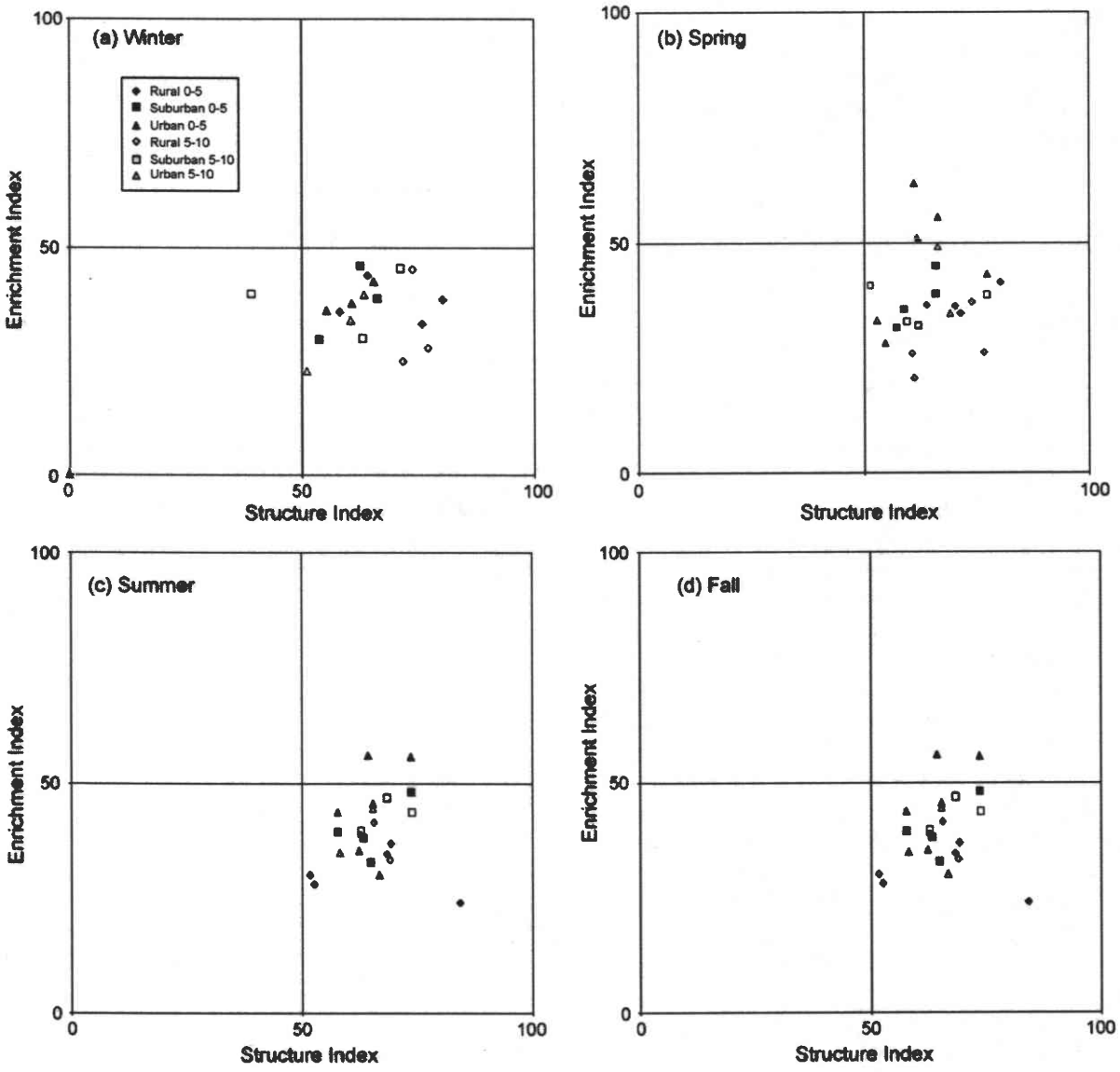


Fig. 3. Nematode weighted faunal analysis profiles (see text and Ferris et al. (2001)): (a–d) response by season of soil nematode community to land use in top 0–5 cm and bottom 5–10 cm of soil along axes of structure (SI) and enrichment (EI).

trajectories in Fig. 3. No discernible pattern between land use classes at either soil depth was found in the data. The nematode assemblages along the gradient did map into the quadrant associated with the nematode assemblages of forests (Ferris et al., 2001).

Ratios of fungal-feeding to bacterial-feeding nematodes provide information about the nature of detrital pathways in soils. While land use did not have a significant effect on the ratio of fungal-feeding to bacterial-feeding nematodes in the top 5 cm of soil, there was a significant interaction of land use and time in the top 5 cm of soil (Table 6, the Fall 2002 samples). There was a significant effect of land use on the ratio of fungal-feeding to bacterial-feeding nematodes in the bottom 5 cm of soil, with the urban soils tending to have a lower ratio than the rural soils (Table 7).

The CI was significantly different between land use classes in both the 0–5 and 5–10 cm of soil layers (Fig. 2e, f). The CI tended to decrease between land use classes within sampling dates; however, we were not able to detect any differences in these means (Fig. 2e, f).

## 4. Discussion

The combined nematode community indices provide a complicated picture of the effects of urbanization in

Table 6
Nematode functional ratios in the top 0–5 cm of soil by land use class

| Index | Rural | Suburban | Urban |
|---|---|---|---|
| FF:BF | | | |
| Winter 2001 | 38.5 | 46.0 | 47.4 |
| Spring 2001 | 43.0 | 43.5 | 33.9 |
| Summer 2001 | 43.2 | 42.3 | 38.9 |
| Fall 2001 | 46.0 | 44.7 | 52.0 |
| Winter 2002 | 48.0 | 43.4 | 43.7 |
| Spring 2002 | 31.6 | 37.3 | 32.4 |
| Summer 2002 | 42.2 | 43.0 | 43.7 |
| Fall 2002 | 26.5a | 41.8b | 37.5b |
| Channel index | | | |
| Winter 2001 | 85.1 | 65.8 | 50.8 |
| Spring 2001 | 61.9 | 55.9 | 38.4 |
| Summer 2001 | 81.2 | 56.7 | 42.6 |
| Fall 2001 | 79.5 | 63.3 | 54.0 |
| Winter 2002 | 67.2 | 58.5 | 46.7 |
| Spring 2002 | 66.4 | 62.1 | 29.6 |
| Summer 2002 | 80.4 | 72.3 | 47.0 |
| Fall 2002 | 68.8 | 61.1 | 39.2 |

Least square means with different letters on the same date are significantly different at $P \leq 0.05$ (SAS pdiff option).

western North Carolina. The diversity of nematode genera was not affected by urban land use along the gradient. The urban soil environment, however, affected the composition of the nematode community assemblage. This suggests that nematode taxonomic diversity, *per se*, is not a useful indicator of the effects of urbanization on soils, as diversity indices mask effects on the trophic composition of the nematode community assemblage. Furthermore, these findings indicate that the functional composition of the soil food web is an important component of soil biodiversity. Comparison of functional group abundances indicates that urban soils tend to have lower abundances of higher trophic levels (predators and omnivores). These results hint at the complex nature of human influences on ecosystems and the response of ecosystems to patterns of global change. Our results suggest that the urban environment can modify the functional composition of the soil food web through alterations of abundances of functional groups. These shifts in the functional composition of the nematode community and soil food web have consequences at the ecosystem-level, in observed alterations to nutrient cycling rates (Pavao-Zuckerman and Coleman, 2005). In general, studies that investigate links between biodiversity and ecosystem functioning tend to follow the assumption that global change will affect biological communities through the elimination of individual taxa or whole trophic groups (Loreau et al., 2002). Our investigation of the nematode community in an urban environment suggests a more complex pattern of community change under anthropogenic influences.

Table 7
Nematode functional ratios in the bottom 5–10 cm of soil by land use class

| Index | Rural | Suburban | Urban |
|---|---|---|---|
| FF:BF | | | |
| Winter 2001 | 38.0 | 37.8 | 38.4 |
| Spring 2001 | 40.6 | 51.4 | 33.2 |
| Summer 2001 | 47.3 | 47.0 | 39.0 |
| Fall 2001 | 38.9 | 59.6 | 45.0 |
| Winter 2002 | 54.5 | 46.7 | 40.3 |
| Spring 2002 | 33.0 | 41.1 | 39.8 |
| Summer 2002 | 46.9 | 52.0 | 47.3 |
| Fall 2002 | 39.0 | 49.8 | 35.6 |
| Channel index | | | |
| Winter 2001 | 85.9 | 69.8 | 40.8 |
| Spring 2001 | 75.5 | 64.6 | 46.1 |
| Summer 2001 | 79.4 | 57.9 | 57.3 |
| Fall 2001 | 81.3 | 75.5 | 62.7 |
| Winter 2002 | 79.4 | 70.5 | 64.1 |
| Spring 2002 | 79.4 | 66.5 | 46.3 |
| Summer 2002 | 68.7 | 59.4 | 64.9 |
| Fall 2002 | 82.6 | 63.7 | 47.6 |

Least square means with different letters on the same date are significantly different at $P \leq 0.05$ (SAS pdiff option).

The CI tended to be greater in rural soils than in urban soils, suggesting that there is less fungal dominance in the soil food web in the urban soils. Pouyat and McDonnell (1991) and Pouyat et al. (1995) reported on heavy metal loading in urban soils, and found that this was linked to decreased densities of fungal populations in urban forest stands (Pouyat et al., 1994). We found the concentration of some heavy metals to be greater in urban soils (e.g. Mn 15 mg $kg^{-1}$ urban, 8 mg $kg^{-1}$ rural; and Zn 2.3 mg $kg^{-1}$ urban, 1.1 mg $kg^{-1}$ rural; see Pavao-Zuckerman and Coleman, in review); however, the degree of soil contamination in Asheville, NC is much less than that reported for New York City (Pouyat and McDonnell, 1991; Pouyat et al., 1995). Moreover, the heavy metal concentrations found in the Asheville urban to rural gradient fall well below critical values reported for soil invertebrates (Bengtsson and Tranvik, 1989).

Differences in the functional composition of the nematode community assemblage between urban and rural soils did not translate directly into the maturity indices calculated for the assemblages. There was some depression in MI and ΣMI scores in the urban soils when compared with the rural soils. This difference was not as great as reported in other studies, which made use of maturity indices as indicators of soil conditions (Bongers, 1990; Bakonyi et al., 2003; Hohberg, 2003), but was similar in magnitude to other reported values

(Forge and Simard, 2001). The concentration of pollutants in our study was not as great as reported in other studies, which used the maturity index. Bakonyi et al. (2003) applied the MI to soils treated with metal pollution (Cd, Cr, Se and Zn) at concentrations of 270 mg $kg^{-1}$, while we found soils in Asheville to have a maximum concentration of around 2.3 mg $kg^{-1}$ for Zn, and substantially lower concentrations for Cd (0.06 mg $kg^{-1}$), Cr (0.08 mg $kg^{-1}$) (Pavao-Zuckerman and Coleman, in review). The soils in this study tend to map into Quadrant C in the weighted faunal analysis (SI EI) (Fig. 3). This quadrant tends to be characterized by soils that have undisturbed, structured food web conditions, fungal dominant food web pathways, and moderate to high C/N ratios (Ferris et al., 2001). The weighted faunal analysis suggests that urban land use does not disturb the forest soils we studied enough to modify the structure index of the soil food web, despite decreases in the abundances of higher trophic groups of nematodes.

Porazinska et al. (1999) assessed the utility of both diversity and ecological indices of the nematode community assemblage in a study of irrigation and mulching. Ecological indices, such as the maturity indices provided better insights into the response of the nematode community than the diversity indices. They highlight the inclusion of both quantitative and biological and ecological characteristics of the specific nematode taxa in generating a community level index response in the utility of the maturity indices over the diversity indices for assessing soil conditions (Porazinska et al., 1999).

## 5. Conclusions

Analysis of the soil nematode community assemblage as an indicator of soil conditions along a gradient of urban land use provided mixed results. While generic diversity was not affected by urban land use, the functional composition of the nematode community was slightly altered by urban land use. Such alterations of the nematode community can have implications for the functioning of forest soil ecosystems in cities. Asheville, NC, being a small city, tends to be less impacted by pollution than larger cities. Correspondingly, the impact on the soil nematode community was not very severe. It is likely that soils in larger and older cities will experience greater environmental stresses. The utilization of the nematode community assemblage as an indicator of soil conditions should be further explored in urban places of differing magnitudes of environmental effects.

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## References

Alphei, J., Bonkowski, M., Scheu, S., 1996. Protozoa, Nematoda, and Lumbricidae in the rhizosphere of *Hordelymus europaeus* (Poaceae): fuanal interactions, response of microorganisms and effects on plant growth. Oecologia 106, 111–126.

Bakonyi, G.P., Nagy, P., Kadar, I., 2003. Long-term effects of heavy metals and microelements on nematode assemblages. Toxicol. Lett. 140–141, 319–401.

Bengtsson, G., Tranvik, L., 1989. Critical metal concentrations for forest soil invertebrates. Water Air Soil Poll. 47, 381–417.

Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol. Evol. 14, 224–228.

Effland, W.R., Pouyat, R.V., 1997. The genesis, classification, and mapping of soils in urban areas. Urban Ecosyst. 1, 217–228.

Ferris, H., Bongers, T., de Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29.

Forge, T.A., Simard, S.W., 2001. Structure of nematode communities in forest soils of southern British Columbia: relationships to nitrogen mineralization and effects of clearcut harvesting and fertilization. Biol. Fert. Soils 34, 170–178.

Griffiths, B.S., 1994. Microbial-feeding nematodes and protozoa in soil: their effects on microbial activity and nitrogen mineralization in decomposition hotspots and the rhizosphere. Plant Soil 164, 25–33.

Hohberg, K., 2003. Soil nematode fauna of afforested mine sites: genera distribution, trophic structure, and functional guilds. Appl. Soil Ecol. 22, 113–126.

Littell, R.C., Henry, P.R., Ammerman, C.B., 1998. Statistical analysis of repeated measures data using SAS procedures. J. Anim. Sci. 76, 1216–1231.

Loreau, M., Naeem, S., Inchausti, P. (Eds.), 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford.

Lovett, G.M., Traynor, M.M., Pouyat, R.V., Carreiro, M.M., Zhu, W.X., Baxter, J.W., 2000. Atmospheric deposition to oak forests along an urban-rural gradient. Environ. Sci. Technol. 34, 4294–4300.

Magurran, A.E., 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton.

McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. BioScience 52, 883–890.

Miller, J.R., Hobbs, R.J., 2002. Conservation where people live and work. Conserv. Biol. 16, 330–337.

Ohtonen, R.A., Luotonen, H., Markkola, A.M., 1992. Enchytraeid and nematode numbers in urban, polluted Scots pine (*Pinus sylvestris*) stands in relation to other soil biological parameters. Biol. Fert. Soils 13, 50–54.

Oke, T.R., 1995. The heat island of the urban boundary layer: characteristics, causes, and effects. In: Cermak, J.E. (Ed.), Wind Climate in Cities. Kluwer Academic, Netherlands, pp. 81–107.

Pavao-Zuckerman, M.A., Coleman, D.C., 2005. Decomposition of chestnut oak (*Quercus prinus*) leaves and nitrogen mineralization in an urban environment. Biol. Fert. Soils 41, 343–349.

Pavao-Zuckerman, M.A, Coleman, D.C. (*in review*). Physical, chemical, and biological properties of urban soils in Asheville, NC. Urban Ecosystems.

Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.H., Pouyat, R.V., Zipperer, W.C., Costanza, R., 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annu. Rev. Ecol. Syst. 32, 127–157.

Porazinska, D.L., Duncan, L.W., McSorley, R., Graham, J.H., 1999. Nematode communities as indicators of status and processes of a soil ecosystem influenced by agricultural management practices. Appl. Soil Ecol. 13, 69–86.

Pouyat, R.V., McDonnell, M.J., 1991. Heavy metal accumulations in forest soils along an urban-rural gradient in southeastern New York, USA. Water Air Soil Pollut. 57/58, 797–807.

Pouyat, R.V., Parmelee, R.W., Carreiro, M.M., 1994. Environmental effects of forest soil-invertebrate and fungal densities in oak stands along and urban-rural land use gradient. Pedobiologia 38, 385–399.

Pouyat, R.V., McDonnell, M.J., Pickett, S.T.A., 1995. Soil characteristics of oak stands along an urban-rural land-use gradient. J. Environ. Qual. 24, 516–526.

Savard, J.L., Clergeau, P., Mennechez, G., 2000. Biodiversity concepts and urban ecosystems. Landscape Urban Plan. 48, 131–142.

Setälä, H., Huhta, V., 1991. Soil fauna increase *Betula pendula* growth: laboratory experiments with coniferous forest floor. Ecology 72, 665–671.

Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois, Urbana.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 668.

Wardle, D.A., 1999. How soil food webs make plants grow. Trends Ecol. Evol. 14, 418–420.

Yeates, G.W., 1994. Modification and qualification of the nematode maturity index. Pedobiologia 38, 97–101.

Yeates, G.W., 2003. Nematodes as soil indicators: functional and biodiversity aspects. Biol. Fert. Soils 37, 199–210.

Yeates, G.W., Bongers, T., de Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. J. Nematol. 25, 315–331.