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Linking spatio-temporal dynamics of earthworm populations to nutrient cycling in temperate agricultural and forest ecosystems

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Summary

Numerous laboratory and small plot-scale studies have highlighted the importance of earthworm populations in decomposition and nutrient cycling. However, the simple scaling up of such results to explain conditions on a large field scale, across agricultural landscapes under varied management scenarios, or across landscapes made up of different types of ecosystems (agricultural, grassland, forest), is very much constrained by a lack of information about the spatiotemporal distribution of earthworm populations. This study documents the spatiotemporal variation in earthworm populations in temperate ecosystems. A mixed deciduous forest, grass-dominated hayfield and corn agroecosystem were each fitted with a single 50 m × 50 m sampling grid, consisting of twenty-five 10 m × 10 m cells. Earthworms were collected at distinct single georeferenced locations in each of the 25 cells. Locations varied according to the sampling date (May, July or September). The earthworms collected by hand-sorting and formalin extraction, were first separated by species, then counted and weighed. The soil characteristics (temperature and moisture content, extractable nutrients, organic matter, pH) were also assessed for each time and location. Geostatistical and correlation analyses served to generate spatial maps of earthworm populations and to assess which soil factors most closely paralleled the numerical distribution of earthworms. This provided some insight into small-scale heterogeneity in earthworm populations, possibly allowing for the future extrapolation of laboratory and controlled field study results to larger scales, and in turn a more accurate estimation of the role of earthworms in nutrient cycling at the ecosystem and landscape levels.

Key words: Earthworms, spatial heterogeneity, temporal variation, soil properties, geostatistics

Introduction

Earthworms, widely distributed in a number of terrestrial ecosystems, are considered "keystone organisms" capable of affecting nutrient dynamics by altering soil physical, chemical and biological properties (Parmelee et al. 1998). Indeed, laboratory, greenhouse and small field-plot studies have shown that earthworms play a

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key role in (a) nutrient cycling, particularly with respect to rates and spatial variability of plant litter decomposition, (b) plant production, (c) modifying soil porosity and aggregate structure, and (d) regulating other soil biota, particularly the composition, biomass and activity of soil microbial communities (Brown et al. 2000; Edwards & Bohlen 1996). Scaling up results from microcosm and plot studies to the ecosystem or landscape levels has been identified as a critical research area (Blair et al. 1995; Parmelee et al. 1998). Yet, the lack of information about the spatial distribution of earthworm populations, essential to an accurate extrapolation of small-scale results from the laboratory to the larger scales at which nutrient dynamics and plant production are generally studied (e.g., hectares), has resulted in little actual research being conducted.

Earthworm populations show considerable variation in time and space, with mean densities ranging from less than 10 to over 1000 individuals m^{-2} (Edwards & Bohlen 1996), according to external physico-chemical factors (climate, soil properties, vegetation and food resources) and biotic interactions within soil faunal communities (competition, predation, parasitism and disease) (Curry 1998; Edwards & Bohlen 1996). Seasonal fluctuations in earthworm populations related to soil temperature and moisture have been well documented. Earthworms are thought to inhabit discrete patches in soil, but the size of patches occupied by earthworms varies between species (Poier & Richter 1992). Spatial variation of some temperate earthworm species has been correlated to soil properties and vegetation (Nuutinen et al. 1998; Poier & Richter 1992), whereas demographic processes (immigration/emigration) appear to have a greater influence on spatial distribution of some tropical species (Rossi et al. 1997; Rossi & Lavelle 1998).

The purpose of this study was to 1) map the spatial distribution of earthworms in temperate ecosystems, including a corn agroecosystem, grass-dominated hayfield and mixed deciduous forest, 2) determine whether earthworm spatial distribution changed through time, and 3) determine the relationship between soil characteristics and earthworm population dynamics.

Materials and Methods

Study site

The research was conducted at the Macdonald Research Farm (corn and hayfield sites) and Morgan Arboretum (mixed deciduous forest) in Ste-Anne-de-Bellevue, Quebec, Canada (45 °3 'N 74 °11 'W). Mean monthly temperature ranges from –10.3 °C in January to 18.0 °C in July, with a mean annual precipitation level of 940-mm. The grain corn (*Zea mays* L.) agroecosystem was converted over from alfalfa (*Medicago sativa* L.) in May 2000. The corn field was conventionally tilled and received urea and triple superphosphate fertilizers at rates of 170 kg N ha^{-1} and 45 kg P ha^{-1}. Corn residues left on the field after harvest were moldboard ploughed in the fall and disced in the spring. The grass-dominated hay field contained about 80 % grass and 20 % legumes (visual estimation) and was generally mowed twice a year, in early August and mid-September. The mixed deciduous forest was dominated by beech (*Fagus grandifolia* Ehrh.) and red maple (*Acer rubrum* L.). The soils at the study sites were loamy, mixed, frigid Typic Humaquepts (Humic Gleysols) with textures ranging from silt-loam to loam. Some general soil characteristics are provided in Table 1. The sampling grid at each site (50 m × 50 m) contained 25 units of 10 m × 10 m, which were further divided into subunits of 1 m^2. Earthworms were collected from randomly selected subunits (chosen with a random number generator, no subunit was sampled twice) by first handsorting 38 cm × 38 cm quadrats to a depth of 15 cm. Dilute formalin (0.25 %) was then poured onto the bottom of each soil pit to collect the deeper-dwelling *Lumbricus terrestris* and *Aporrectodea longa*. All earthworms were preserved in 5 % formaldehyde. About 300 g of soil (0 to 15 cm depth) from each pit was retained and analyzed for gravimetric soil moisture content, texture, pH, organic matter, and extractable nutrient concentration (NH_4-N, NO_3-N, P, K, Ca and Mg).

Earthworms were separated into age classes on the ba-

Table 1. Some chemical and physical properties of soils collected from the study sites in 2001. Values are the mean of 75 observations

Site	Texture	Sand[1] (kg 100 kg^{-1})	Clay[1] (kg 100 kg^{-1})	pH[2]	SOM[3] (kg 100 kg^{-1})	NH_4-N[4] (mg kg^{-1})	NO_3-N[4] (mg kg^{-1})
Forest	Silt-loam	38	8	6.2	8.4	0.5	4.0
Hayfield	Silt-loam	35	8	6.5	5.9	0.1	3.3
Corn	Loam	45	13	5.9	6.3	0.5	31.4

[1] Particle size analysis by the hydrometer method (Day 1965).
[2] Soil pH in 1 : 2 soil: water slurries.
[3] SOM = soil organic matter, loss on ignition (360 °C for 4 h).
[4] *2 M* KCl extracts (Maynard and Kalra 1993)

Table 2. Pearson's correlation coefficients of the relationships between selected soil characteristics and the number of earthworms m^{-2} at each site and sampling date. Values with an asterisk (*) indicate significant (*P<0.05*) correlations

Soil characteristics	Forest			Hayfield			Corn Agroecosystem		
	May	July	September	May	July	September	May	July	September
Soil moisture	0.58*	0.52*	0.44*	0.16	0.42*	0.16	0.34	0.41*	0.48*
NO_3-N	0.54*	0.36	0.21	-0.24	-0.05	0.21	-0.26	-0.16	-0.05
P	-0.67*	-0.38	-0.33	-0.17	-0.18	0.20	-0.06	-0.28	-0.20
Ca	0.53*	0.09	0.24	0.17	0.37	0.10	0.13	-0.10	0.23
Mg	0.70*	0.22	0.32	0.24	0.40*	0.08	0.19	0.24	0.32
pH	0.53*	0.08	0.57*	0.22	0.52*	0.03	0.35	0.19	0.37
Clay	-0.02	0.34	0.24	0.40*	-0.11	0.23	0.06	0.17	0.04
Soil organic matter	0.33	0.23	0.24	0.17	0.20	0.37	0.02	0.16	-0.05

sis of clitellum development and were categorized as fragments (incomplete earthworm fragments), juveniles, pre-clitellate adults (clitellum present but not fully developed) and clitellate adults (fully developed clitellum). Sexually mature specimens were identified to the species level using the Schwert key (Dindal 1990). Earthworms were oven-dried (60 °C for 48 h) and then ashed at 500 °C for 4 h to determine ash-free dry weight (AFDW).

Statistical analysis

Normality of the raw data was assessed using the Proc UNIVARIATE function of SAS 6.12 for Windows and descriptive statistics (mean, standard deviation and 95 % confidence intervals) were calculated. The relationships between soil characteristics and earthworm total number m^{-2} were assessed with Pearson's simple linear correlation coefficients. While the descriptive statistics and correlation analysis provided a summary of the data, they gave little insight into the spatial or temporal distribution of the collected variables. Thus, we used contour maps of the most distant sampling dates (May and September, 2001) to assess and contrast changes in the spatial pattern through time at each sites. Isotropic variograms, which decompose the spatial or temporal variability of observed variables among distance classes, were computed for earthworm populations at each site-sampling date (Legendre & Legendre 1998). Of the models fitted with GS+ software (version 5.0), the 'linear to sill' best described the relationship between semivariance and separation distance, as it produced with larger R^2 values and lower residual sum of squares values than other models. The 'linear to sill' isotropic model parameters were as follows:

$$g(h) = C0 + [h(C/A0)] \quad \text{for } h \leq A0 \qquad (1)$$

$$g(h) = C0 + C \quad \text{for } h > A0 \qquad (2)$$

where h = lag class interval (lag distance) the distance between two consecutive locations at which the data is collected or simply distance between two data points; C0 = nugget variance ≥0, 0, unexplained variance; C = structural variance ≥C0, and A0 = range parameter, distance where sill occurs.

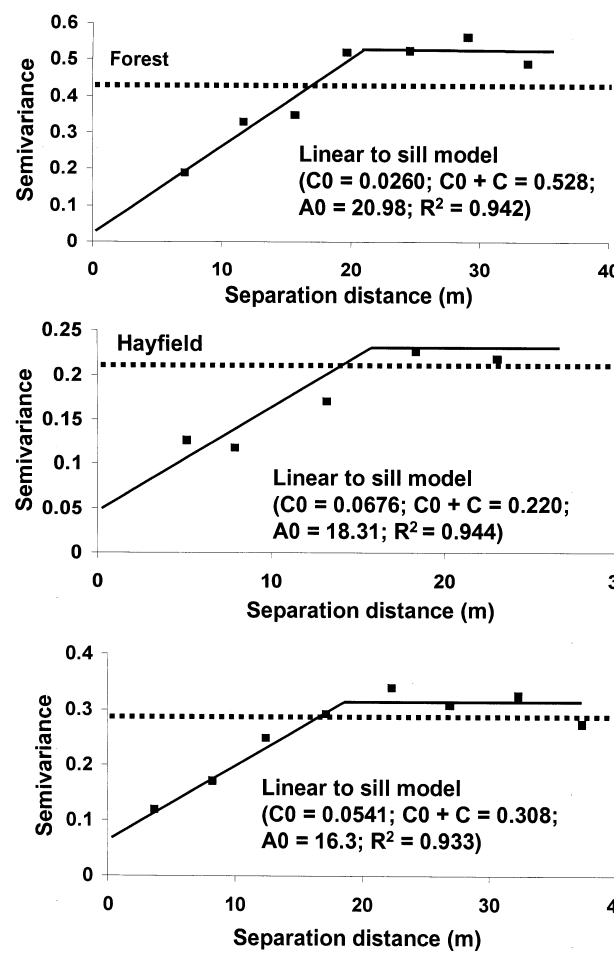

Fig. 1. Isotropic variograms of the earthworms m^2 collected from forest, hayfield and corn sites in May 2001

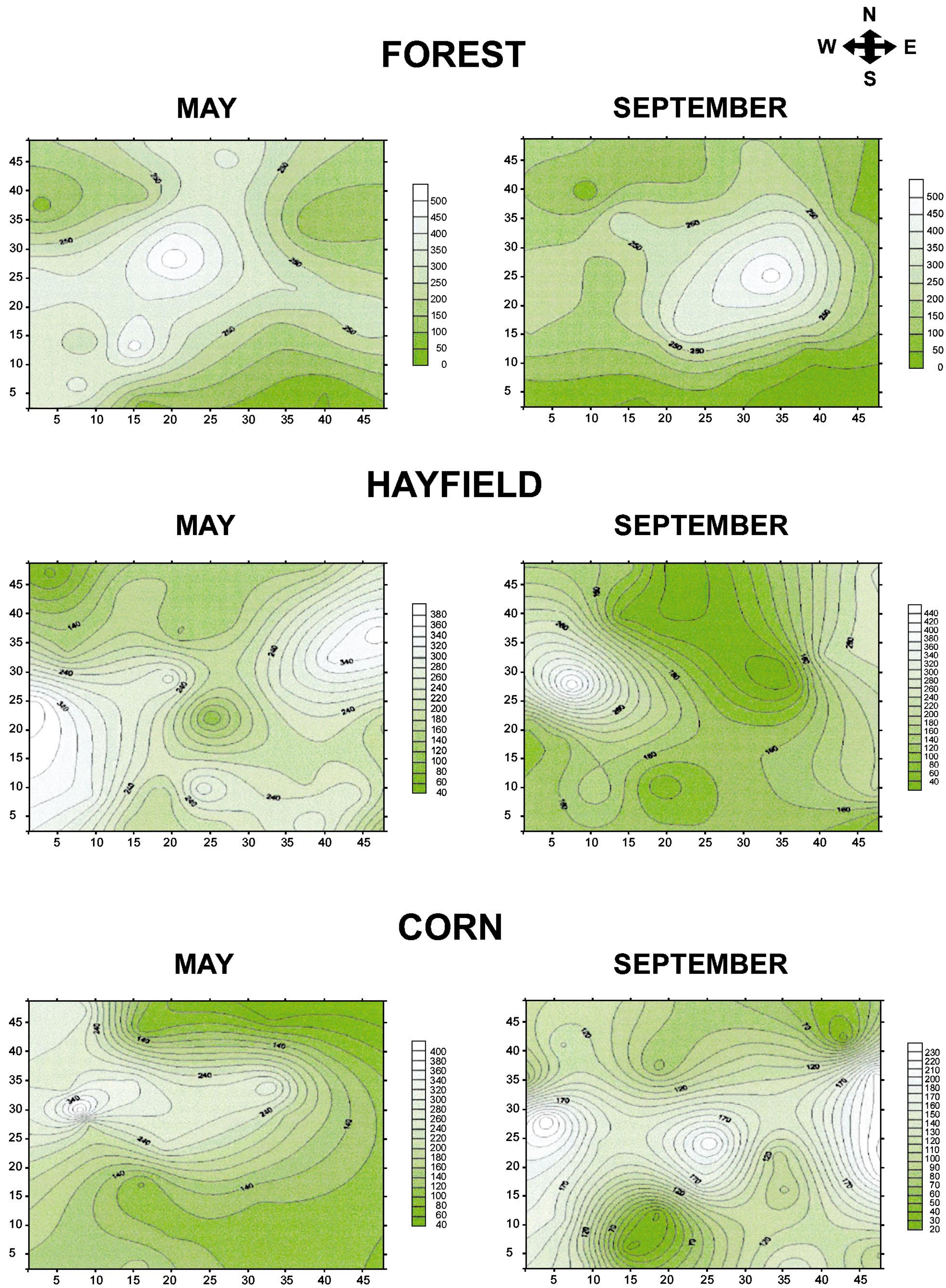

Fig. 2. Contour maps of the earthworms m2 collected from forest, hayfield and corn sites in May and September, 2001

Results and Discussion

The number of earthworms collected from May to September 2001 tended to be higher in the forest (118 to 234 m^{-2}) and the hayfield (121 to 220 m^{-2}) than the corn agroecosystem (41 to 169 m^{-2}). The mean biomass of earthworms varied with sampling time but the range was similar among sites, with 1.58 to 5.70 g AFDW m^{-2} in the forest, 1.64 to 4.74 g AFDW m^{-2} in the hayfield, and between 1.28 and 5.22 g AFDW m^{-2} in the corn agroecosystem. Although earthworms were more numerous in the forest site, they tended to be smaller than the earthworms collected from the corn agroecosystem. Most of the earthworms collected were juveniles; only 5 to 32 % of the individuals collected could be classified as pre-clitellate and clitellate adults. The six species of earthworms recovered were *Aporrectodea rosea* (Savigny), *Aporrectodea turgida* (Eisen), *Aporrectodea tuberculata* (Eisen), *Aporrectodea longa* (Ude), *Lumbricus terrestris* L. and *Lumbricus castaneus* (Savigny). One individual of *Allolobophora chlorotica* (Savigny) was found in the forest in July 2001, but at no other time.

The structural component of the variance (C/C0+C) describing the number of earthworms m^{-2} ranged from 0.70 to 0.95 (Fig. 1), indicating a high spatial dependence in earthworm populations that is consistent with other reports (Margerie et al. 2001; Nuutinen et al 1998; Rossi et al. 1997). The separation distance between patches of similar density was between 16 and 21 m, which is similar to the spatial aggregation of 20 to 40 m reported for earthworms in the literature (Decaëns & Rossi 2001; Nuutinen et al. 1998; Rossi et al. 1997). Although forest soils, which are undisturbed and support a variety of tree and understory plant species, are likely to be more heterogeneous than soils under grass-dominated hayfield or corn agroecosystems, land management did not much affect the spatial aggregation of earthworms. Jimenez et al. (2001) also found that the spatial patterns of neotropical earthworm populations were not affected by land use (native savanna and introduced pasture).

The number of earthworms m^{-2} collected from each site was not well correlated with most soil properties measured (Table 2). Similar, or weaker, correlations were observed between earthworm biomass (g ash-free dry weight m^{-2}) and soil properties (data not shown). In some studies, earthworm populations have been associated with soil extractable phosphate (Nuutinen et al. 1998), organic C (Poier & Richter 1992) and hydrology (Cannavacciuolo et al. 1998; Nuutinen et al. 2001), but other workers have found no clear relationship between earthworm distribution and soil properties (Rossi et al. 1997). The lack of consistent relationships between earthworms and soil parameters in this study suggests that variations in earthworm populations and soil properties occur at different spatio-temporal scales. When we compared maps of the earthworm distribution in May and September, 2001, it was apparent that earthworm patches were dynamic; the location of the patches with the highest and lowest numbers of earthworms changed within 4 months at all sites (Fig. 2). Generally, patches with the highest number of earthworms in September were displaced by several meters from patches that had the highest number of earthworms in May (Fig. 2). In contrast, the spatial structure of some tropical earthworm communities appears to be relatively stable through time (Decaëns & Rossi 2001; Jimenez et al. 2001). Further work is needed to describe the spatio-temporal structure of earthworm populations and to determine what factors influence the dynamics of earthworm patches.

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