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Applied Soil Ecology 27 (2004) 143–151
Applied Soil Ecology
www.elsevier.com/locate/apsoil

Spatial and temporal distribution of earthworm patches in corn field, hayfield and forest systems of southwestern Quebec, Canada

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Received 18 September 2003; accepted 30 April 2004

Abstract

Earthworm populations exhibit an irregular and aggregated distribution that may be related to vegetation, soil characteristics and biotic interactions. Their contribution to processes such as decomposition, soil aggregation and plant production is presumably limited to patches where earthworms are active. The spatial distribution of earthworm populations and how that distribution changes through time in temperate regions is not well known. This study mapped the spatial distribution of earthworm populations in 25 subplots of 50 m × 50 m sampling grids established in: (1) a cultivated corn field; (2) a mowed hayfield and (3) a deciduous forest in Québec, Canada. Earthworms were collected three to four times a year using a combination of handsorting and formaldehyde extraction. Ten lumbricid species were found, the most common being *Aporrectodea rosea* Savigny. In 2001, we collected, on average, 46–177 earthworms m^{-2} in the corn field, from 138 to 224 earthworms m^{-2} in the hayfield and between 124 and 253 earthworms m^{-2} in the forest. Due to the spatial variation in earthworm distribution, at least 40 samples ha^{-1} are required to make an unbiased estimate of earthworm numbers and biomass. Five subplots (patches) from each site with the highest and lowest earthworm populations were re-sampled in 2002. Patches with high earthworm populations were generally distinguishable from those with low earthworm populations in the forest, but not in the agricultural sites; this may be due to greater heterogeneity in resource distribution in the forest than agricultural sites. Further work on earthworm spatial and temporal distribution is required to determine the scale at which earthworm induced changes in soil processes and plant production may be detected.

Keywords: Earthworm distribution; Spatial heterogeneity; Temporal variation; Patch dynamics; Sampling methods

1. Introduction

Spatial and temporal variation in earthworm populations can occur on the basis of both abiotic factors, such as resource availability, soils, temperature and moisture regimes, and biotic interactions at the population and community levels including synergism, competition, parasitism and predation (Edwards and Bohlen, 1996; Curry, 1998). In some forests and native grasslands, earthworm populations are associated with plant species that provide a favorable microhabitat through their architecture and degree of ground cover, or because of the amount and quality of above- or below-ground litter they produce (Zaller and Arnone, 1999; Campana et al., 2002; Nachtergale et al., 2002). Spatial variation in earthworm populations may be related to soil properties such as organic carbon content and soil hydrology (Hendrix et al., 1992; Poier and Richter, 1992; Cannavacciuolo

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doi:10.1016/j.apsoil.2004.04.004

et al., 1998; Nuutinen et al., 2001). Biotic interactions affecting earthworm spatial distribution are less well studied, although the spatial separation of some species may be due to competitive interactions for food and other resources (Nuutinen et al., 1998; Rossi et al., 1997). The aggregation of species that disperse slowly would probably also facilitate reproduction.

Earthworm communities have been found to be spatially structured at a scale of <100 m (Rossi et al., 1997; Nuutinen et al., 1998; Decaëns and Rossi, 2001; Whalen and Costa, 2003), but earthworms may be distributed with spatial structure (i.e., aggregation) and at multiple scales, depending on landscape and specific soil conditions. In calcareous soils of France, Margerie et al. (2001) found patches of variable sizes (15, 50 and 80 m) containing high or low numbers of earthworms. Earthworm patches in Colombian savannas were distributed horizontally at distances ranging from 27 to 57 m apart, but some species were aggregated in patches less than 10 m in diameter (Jiménez et al., 2001). These reports of spatial structure in earthworm communities indicate that a minimum number of samples should be taken to estimate earthworm populations accurately. Studies in experimental row-cropped agroecosystems and pastures have estimated earthworm populations by collecting 13–139 earthworm samples ha^{-1} from quadrats with a surface area between 0.125 and 0.144 m^2 to a depth of 15–20 cm (Whalen et al., 1998; Hubbard et al., 1999; Schmidt et al., 2003). In most forest systems, earthworm populations are estimated by sampling along transects (e.g., Dymond et al., 1997; Campana et al., 2002). The quantitative retrieval of earthworms is affected by the size and shape of the collection area, which may also influence the accuracy of earthworm population estimates (Dickey and Kladivko, 1989).

Field manipulation experiments that lead to increased or decreased earthworm populations show corresponding changes in soil structural aggregation, porosity, nutrient runoff and leaching, decomposition and microbial activity (Bohlen et al., 1997; Ketterings et al., 1997; Bohlen et al., 2002; Shuster et al., 2002). If natural earthworm populations are stable spatially, inhabiting a clearly delimited area or patch during some period of time, then it may be possible to predict how they affect ecosystem-level processes such as organic matter dynamics, nutrient cycling and plant production. Although the earthworm populations in tropical pastures exhibited stable spatial patterns during a 1-year period (Decaëns and Rossi, 2001), it is unclear whether these patterns persist for longer periods of time. In addition, the size and temporal variation of earthworm patches in temperate regions is not well known.

The objectives of this study were: (1) to characterize the spatial variation of lumbricid earthworm populations in temperate agricultural and forest systems and (2) to assess the temporal variation of patches in temperate agricultural and forest systems that were densely or sparsely populated with lumbricid earthworms.

2. Materials and methods

2.1. Site description

The research was conducted at the Macdonald Research Farm (corn field and hayfield) and Morgan Arboretum (mixed deciduous forest) in Ste-Anne-de-Bellevue, Québec, 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 of 940 mm (Environment Canada Atmospheric Environmental Branch, unpublished data). The corn (*Zea mays* L.) field was converted over from alfalfa (*Medicago sativa* L.) in May 2000. Grain corn was removed at harvest, and residues left on the field were incorporated with a moldboard plough in the fall. The site was disced in the spring before seeding and fertilized with inorganic fertilizers (urea, triple superphosphate and potash) at rates of 170 kg N ha^{-1}, 45 kg P_2O_5 ha^{-1} and 120 kg K_2O ha^{-1}. The grass-dominated hayfield contained about 80% grass and 20% legumes (surface area) and was generally mowed twice a year, in early August and in mid-September. The mixed deciduous forest was dominated by beech (*Fagus grandifolia* Ehrh.) and red maple (*Acer rubrum* L.). The study sites were located within a 2 km radius. Soils at the sites were loamy, mixed, frigid Typic Humaquepts (Humic Gleysols) with textures ranging from silt-loam to loam. General soil characteristics are provided in Table 1, while rainfall and temperature conditions during this study are given in Table 2.

Table 1
Selected properties of soils collected from the study sites in 2001 ($n = 75$ for each site)

Site	Texture	Sand[a] (kg 100 kg^{-1})	Clay[a] (kg 100 kg^{-1})	pH[b]	Total C[c] (g kg^{-1})	Total N[c] (g kg^{-1})
Corn	Loam	45	13	5.9	15.4	1.24
Hayfield	Silt-loam	35	8	6.5	22.7	1.93
Forest	Silt-loam	38	8	6.2	31.9	2.71

[a] Particle size analysis by the hydrometer method.
[b] Soil pH in 1:2 soil:water slurries.
[c] Carlo Erba Flash EA NC Soils Analyzer (Milan, Italy).

2.2. Earthworm sampling

In 2001, a sampling grid (50 m × 50 m) was established at each site (corn field, hayfield and forest) containing 25 units of 10 m × 10 m, which were further divided into subunits of 1 m^2. At each site, a 1 m^2 subunit was selected randomly from within each of the 25 units (subunits were chosen with a random number generator, no subunit was sampled twice) in May, July and September, 2001. In total, 225 subunits were sampled (25 subunits × 3 sites × 3 sampling dates). Soil blocks (38 cm × 38 cm) were removed (15 cm depth) from each subunit and handsorted to collect surface-dwelling earthworms. A dilute formaldehyde solution (7 mL of 37% formaldehyde mixed with 1 L of water) was poured into the bottom of each hole to collect earthworms living deeper than 15 cm such as *Lumbricus terrestris* L. and *Aporrectodea longa* (Ude). All earthworms were preserved in 5% formaldehyde solution upon collection.

Preserved earthworms were separated into age classes on the basis of clitellum development, and further 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 species using the Schwert key (Dindal, 1990). Preserved earthworms were then oven-dried (60 °C for 48 h) and ashed at 500 °C for 4 h to determine ash-free dry weight (AFDW).

We determined the sampling units (10 m × 10 m) at each site that contained, on an average, the greatest number of earthworms ($n = 5$) and the fewest earthworms ($n = 5$) during 2001. These units are referred to as high density patches and low density patches, respectively. Within each patch, earthworms were collected from a randomly selected subunit (no subunit was sampled twice during the study period) in May, June, July and October, 2002 using the procedure outlined above. In total, 120 subunits were sampled [(5 high density patches + 5 low density patches) × 3 sites × 4 sampling dates].

2.3. Statistical analysis

Summary statistics and normality tests were calculated with the PROC UNIVARIATE function of SAS 6.12 for Windows (SAS Institute Inc., Cary, North Carolina, USA). Earthworm population and biomass data were transformed using a (log +1) transformation

Table 2
Monthly precipitation and temperature data during the study

Month	Monthly precipitation (mm)			Mean monthly air temperature (°C)		
	2001	2002	30 year average	2001	2002	30 year average
May	70.0	127.5	68.3	15.3	11.3	12.9
June	76.0	106.0	82.5	20.0	17.5	18.0
July	33.0	55.0	85.6	20.2	22.1	20.8
August	62.5	11.0	100.3	22.5	21.8	19.4
September	67.0	64.5	86.5	16.8	18.3	14.5
October	77.5	70.0	75.4	10.5	7.1	8.3
Total	386.0	434.0	498.6			

to equalize variance. We made pairwise comparisons of the number and biomass of earthworms in high and low density patches at each site with a one-way Student's *t*-test using the PROC MEANS function of SAS 6.12 for Windows.

The number of samples required to estimate earthworm populations was calculated by comparing the mean number and biomass from 25 sets of randomly selected samples ($n = 2$–15) from each grid to the mean from the entire grid ($n = 25$) using data from May 2001. Similar results were obtained in July 2001 and September 2001 (data not presented). The probability of obtaining an estimate within the 95% confidence interval of the measured mean was then calculated (Daniels et al., 2001; Sauer and Meek, 2003).

3. Results and discussion

Ten lumbricid earthworm species were found, the most common being *A. rosea* (Table 3). These species are among the fifteen exotic lumbricid species known to live in Southern Québec (Reynolds, 1976). There tended to be fewer earthworms in July than other sampling dates (Fig. 1), consistent with other studies from eastern Canada that report fewer earthworms were collected in the summer than in the spring or autumn (Tomlin et al., 1992). More earthworms were collected in 2002 than 2001, which could be related to the higher rainfall from May to October 2002 than from May to October 2001 (Table 2). While the seasonal fluctuations in soil moisture and temperature corresponding to rainfall events and temperature changes may affect the size of earthworm populations, such fluctuations probably affect the efficiency of earthworm collection methods as well. Yeates (1976) handsorted soil to a depth of 40 cm and found that virtually all earthworms in irrigated pastures were located in the top 10 cm when soil moisture was greater than 30% humidity, but that there was a downward migration of larger individuals when soil moisture declined. In addition, some earthworms enter quinescent states to avoid inclimate soil conditions (Edwards and Bohlen, 1996). This behavior, coupled with seasonal changes in soil moisture content and porosity, would make it more difficult to extract earthworms by the formaldehyde method at certain times of the year (e.g., during the summer).

The mean number of earthworms collected from May 2001 to October 2002 tended to be higher in the forest (124–480 m^{-2}) and the hayfield (138–322 m^{-2}) than the corn field (13–229 m^{-2}; Fig. 1). Mean earthworm biomass varied with sampling time but the range was similar among sites, with 2.0–14.1 g AFDW m^{-2} in the forest, 2.2–10.7 g AFDW m^{-2} in the hayfield, and between 1.1 and 12.7 g AFDW m^{-2} in the corn agroecosystem (Fig. 1). These results are consistent with other estimates of lumbricid earthworm populations in eastern Canada that contain from 5 to 435 individuals m^{-2} with biomasses from 0.5 to 27 g m^{-2} (Tomlin et al., 1992; Coderre et al., 1995; Estevez et al., 1996; Carter et al., 2002).

Between 70 and 95% of the individuals collected during the study were sexually immature (juveniles),

Table 3
Percentage of sexually mature earthworms of each species collected from the corn field, hayfield and forest sites in 2001 and 2002

Species	Percentage of sexually mature earthworms (%)		
	Corn field ($n = 110$)[a]	Hayfield ($n = 114$)	Forest ($n = 352$)
Allolobophora chlorotica (Savigny)	<1	0	<1
Aporrectodea longa (Ude)	11	0	<1
Aporrectodea rosea (Savigny)	35	80	71
Aporrectodea trapezoides (Duges)	5	0	0
Aporrectodea tuberculata (Eisen)	4	0	3
Aporrectodea turgida (Eisen)	25	5	21
Dendrobaena octaedra (Savigny)	6	0	0
Lumbricus castaneus (Savigny)	0	5	0
Lumbricus terrestris L.	14	10	3
Octolasion tyrtaeum (Savigny)	0	0	<1

[a] Total number of sexually mature earthworms (n) collected during the study.

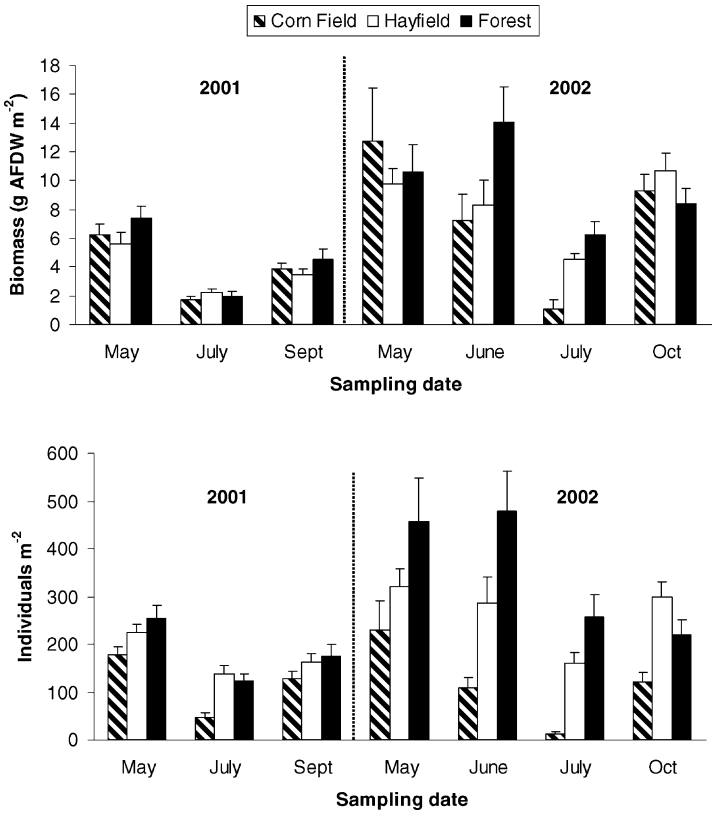

Fig. 1. Biomass and number of earthworms found in corn field, hayfield and forest sites during the study. Values are means and standard errors, $n = 25$ in 2001 and $n = 10$ in 2002.

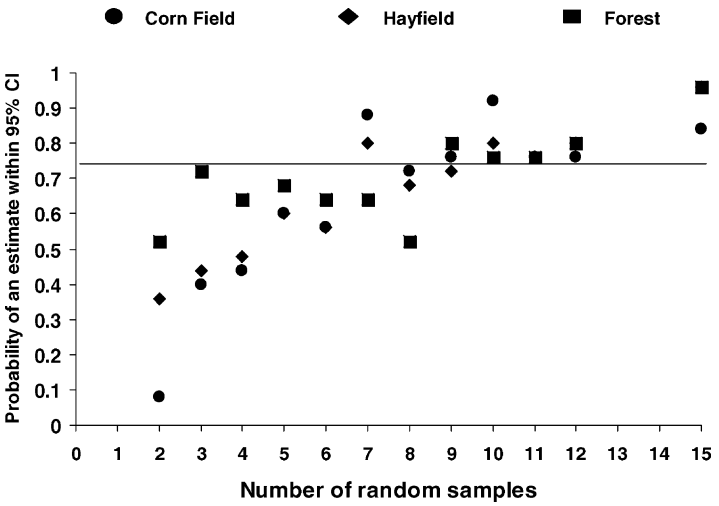

Fig. 2. Probability of obtaining an estimate of earthworms (individuals m^{-2}) with the 95% confidence interval of the measured mean ($n = 25$) in sampling grids of corn field, hayfield and forest sites using sets of randomly selected samples ($n = 2$–15) from each grid. The line represents a probability of 0.75.

which is consistent with other earthworm surveys in temperate regions. Using a similar collection method (handsorting and formaldehyde extraction), Whalen et al. (1998) found that earthworm populations contained 65–82% juveniles in corn agroecosystems of Ohio. Other studies in Québec found that the earthworm community contained 40–70% juveniles when earthworms were collected using the formaldehyde extraction method (Coderre et al., 1995; Estevez et al., 1996). It is difficult to compare the species composition and age structure of earthworm populations when different extraction methods are used; handsorting is an effective method for collecting juvenile earthworms and endogeic species, whereas formaldehyde extraction is more effective for extracting deeper-dwelling earthworms such as *L. terrestris* (Callaham and Hendrix, 1997; Schmidt, 2001).

When most of the earthworms collected from the field are immature and cannot be identified to the species level, it becomes impossible to describe the spatial and temporal dynamics of each species present at the site. Two techniques that hold promise for resolving this problem are metabolic profiling and DNA sequencing. Bundy et al. (2002) demonstrated that three *Eisenia* species could be identified unequivocally when their coelomic fluid was scanned by high resolution nuclear magnetic resonance (NMR) spectroscopy. Molecular methods using 18S rDNA, 16S rDNA and cytochrome c oxidase have been used to distinguish lumbricid earthworm taxa (Pop et al., 2003). Such techniques could be used to verify the identification of adult earthworms as well, providing the cost of analysis was not too great.

The range in earthworm numbers and biomass within each 2500 m^2 area studied was considerable, indicating that earthworms were not distributed uniformly at this scale. Whalen and Costa (2003) found that the distance between patches containing similar numbers and biomass of earthworms at these sites was 16–21 m. This result suggests that collecting earthworms from fixed sampling points between 16 and 21 m apart (23–39 earthworm samples ha^{-1}) would not account for the spatial variation in these populations. The probability of obtaining an estimate of earthworm numbers (Fig. 2.) and earthworm biomass (data not shown) within the 95% confidence interval of the measured mean was >0.75 in all sampling grids if 10 or more subsamples were taken (Fig. 2.). If these findings can be extrapolated directly from 2500 m^2 sampling grids to larger scales, it suggests that collecting at least 40 earthworm samples ha^{-1} from 38 cm × 38 cm quadrats at these sites with a combination of handsorting and formaldehyde extraction would likely provide a reliable estimate of earthworm populations.

Further work is needed to confirm how many samples and what sampling frequency are needed to adequately explain the spatial and temporal distribution of earthworm populations. The number of samples required for a robust estimate of earthworm populations will likely be affected by the size and shape of the collection area (Dickey and Kladivko, 1989), as well as the collection method. If earthworm patches can exist concurrently at multiple scales, as suggested by results from Jiménez et al. (2001) and Margerie et al. (2001), grid sampling in cells with a uniform size (e.g., 10 m × 10 m) may not detect patterns of earthworm distribution occurring at smaller or larger scales. Most studies of earthworm population dynamics provide earthworm numbers and biomass on a monthly or bi-monthly basis, due to the time and effort required to sample earthworms. Since the cost and labor associated with more frequent random sampling of multiple grids could be considerable, it may be more feasible to sample earthworms from specific locations in the landscape based on factors such as slope position or vegetation. Yet, stratified sampling methods can only be successful if we have a priori knowledge of where earthworms are found in the landscape at different times of the year.

3.1. Stability of earthworm patches

No difference between 2001 high and low density patches in the corn field and hayfield could be detected in 2002, but in the forest, 2001 patches of high and low density were significantly ($P < 0.05$, *t*-test) different in May, July and October 2002 (Fig. 3). There was significantly ($P < 0.05$, *t*-test) more earthworm biomass in the high density than low density patches of the corn field in May and September 2001, but in the pasture, earthworm biomass was greater ($P < 0.05$, *t*-test) in the high density than low density patches in September 2001 only (Fig. 4). In the forest, the earthworm biomass was greater ($P < 0.05$, *t*-test) in high density than low density patches from May 2001 to May 2002, inclusive (Fig. 4). It was not possible to

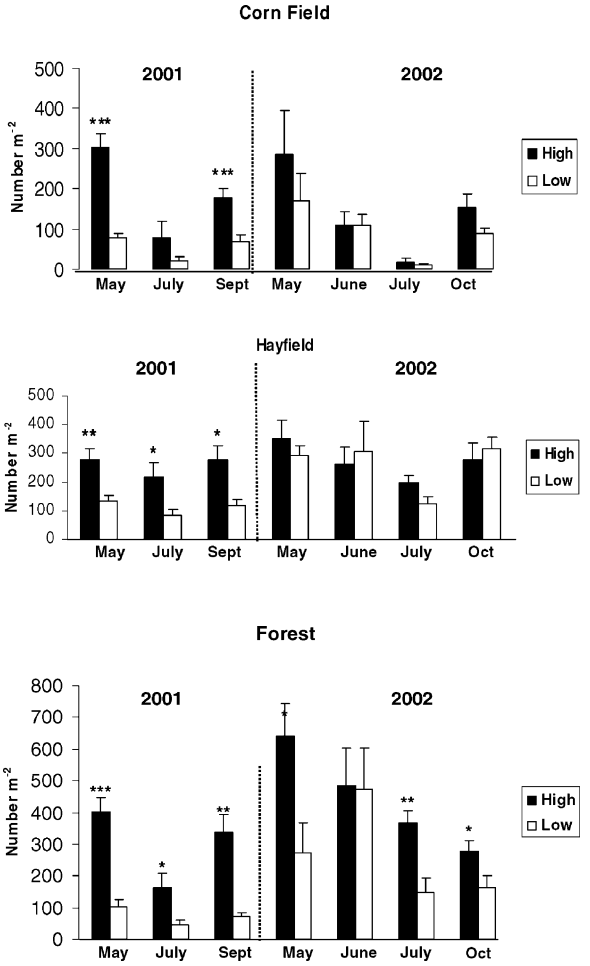

Fig. 3. Earthworms in patches containing high and low earthworm populations during 2001 and 2002. Values are means and standard errors ($n = 5$). Asterisks indicate significant differences (t-test) between high and low density patches at $^{*}P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

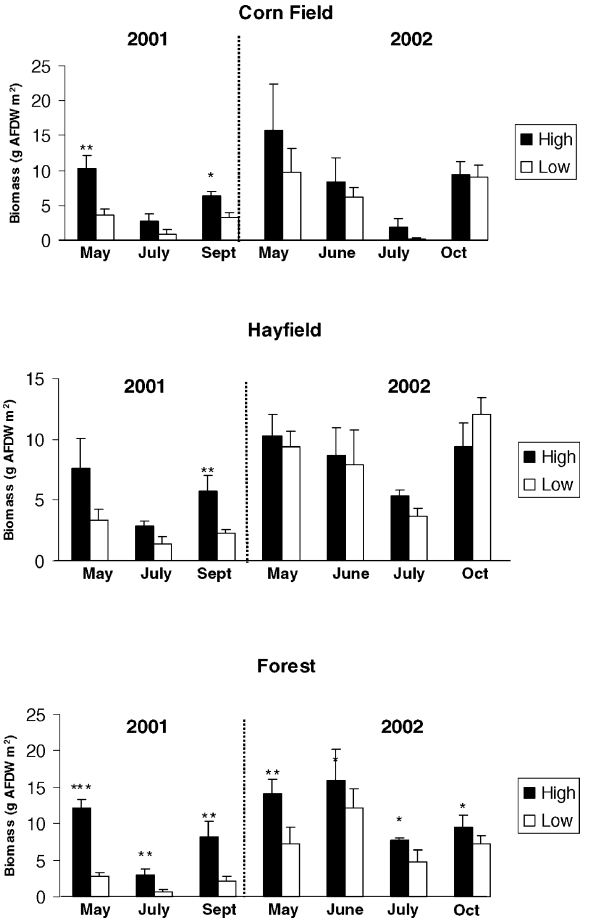

Fig. 4. Earthworm biomass in patches containing high and low earthworm populations during 2001 and 2002. Values are mean and standard error ($n = 5$). Asterisks indicate significant differences (t-test) between high and low density patches at $^{*}P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

determine whether there were differences in the type of species occupying high and low density patches because the majority of individuals collected in this study were immature and hence could not be identified to the species level.

These results indicate that earthworm populations in the forest were spatially more stable than those in the agroecosystems, but the reasons are not known. It is hypothesized that the patterns of earthworm spatial stability observed in this study occurred because of greater heterogeneity in soil conditions and food distribution in the forest than in the agroecosystems, but this remains to be tested. In the forest site, earthworm populations were positively correlated with soil moisture, but not with other soil parameters (Whalen and Costa, 2003). Variations in plant species and plant litter may influence earthworm spatial and temporal distribution in temperate regions, but this needs to be investigated.

Acknowledgements

This study was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC)

and Le Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT). The author would like to thank François Bernatchez, Camille Bourguignon, Matthias Brunner, Janna Carefoot, Pierre-Marc Gervais, Salka Hintikka, Quancai Hu, You Jiao, Sharada Keats, Elisabeth Lefrançois, Ameur Manceur, Tahir Waheed and Janet Whalen for assisting with earthworm sampling. Special thanks to Valérie Caron for helping with the earthworm identification and Luis Sampedro for a critical review of an earlier version of the manuscript.

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