

Diversity and abundance of earthworms across an agricultural land-use intensity gradient

Richard G. Smith^{a,*}, Claire P. McSwiney^b, A. Stuart Grandy^c, Pongthep Suwanwaree^d, Renate M. Snider^e, G. Philip Robertson^c

^a W. K. Kellogg Biological Station and Department of Plant Biology, Michigan State University, Hickory Corners, MI 49060, USA

^b W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060, USA

^c W. K. Kellogg Biological Station and Department of Crop and Soil Science, Michigan State University, Hickory Corners, MI 49060, USA

^d School of Biology, Institute of Science, Suranaree University of Technology, Amphur Maung, Nakhonratchasima 30000, Thailand

^e Department of Zoology, Michigan State University, East Lansing, MI 48824, USA

ARTICLE INFO

Article history:

Received 27 October 2007

Received in revised form 6 March 2008

Accepted 21 April 2008

Keywords:

Management systems

No-till

Old-field

Organic

Soil biota

Succession

Tillage

ABSTRACT

Understanding how communities of important soil invertebrates vary with land use may lead to the development of more sustainable land-use strategies. We assessed the abundance and species composition of earthworm communities across six replicated long-term experimental ecosystems that span a gradient in agricultural land-use intensity. The experimental systems include a conventional row-crop agricultural system, two lower-intensity row-crop systems (no-till and tilled organic input), an early successional old-field system, a 40–60 years old coniferous forest plantation, and an old-growth deciduous forest system. Earthworm populations varied among systems; they were lowest in the most intensively managed row-crop system (107 m⁻²) and coniferous forest (160 m⁻²); intermediate in the old-field (273 m⁻²), no-till (328 m⁻²) and tilled organic (344 m⁻²) cropping systems; and highest in the old-growth deciduous forest system (701 m⁻²). Juvenile *Aporrectodea* species were the most common earthworms encountered in intensively managed systems; other species made up a larger proportion of the community in less intensively managed systems. Earthworm community biomass and species richness also varied and were lowest in the conventional row-crop system and greatest in the old-growth forest system. These results suggest that both land-use intensity and land-use type are strong drivers of the abundance and composition of earthworm communities in agricultural ecosystems.

Published by Elsevier B.V.

1. Introduction

Disturbance associated with agricultural intensification may influence the community of belowground invertebrates that inhabit soils and regulate ecosystem function (Fragoso et al., 1997). In particular, the suitability of soil for invertebrate colonization may be substantially affected by tillage, chemical applications, and litter inputs (Edwards et al., 1995; Clapperton, 1999; Callahan et al., 2003). These and other forms of disturbance affect the size and composition of the belowground invertebrate community by differentially affecting ecological groups that

exploit different soil niches and can vary with different agricultural practices (Lee, 1985; Edwards et al., 1995; Thomas et al., 2004).

Earthworms are an important component of the invertebrate community in most soils, both in terms of their contribution to overall belowground biomass and in terms of their effects on soil biogeochemical cycles (Lee, 1985; James, 1991; Bohlen et al., 1997). Soil structure, gas dynamics, water flow, and C and N turnover and stabilization may be altered by the presence and community structure of earthworms (VandenBygaert et al., 2000; Pouyat and Carreiro, 2003). Earthworms can be divided into several broad ecological groups based on their physiology and feeding and burrowing behavior (Bouché, 1977, reviewed in Lee, 1985; Hendrix and Bohlen, 2002): epigeic earthworm species inhabit and feed on the surface litter; anecic species produce deep vertical burrows in the mineral soil but browse on the soil surface and are important in the burial of surface litter; and endogeic species burrow horizontally and feed mainly in the rhizosphere and subsoil. These major ecological groups have different effects on

* Corresponding author at: US Department of Agriculture-ARS, Exotic and Invasive Weeds Research Unit, 800 Buchanan Street, Albany, CA 94710, USA. Tel.: +1 406 579 4667; fax: +1 510 559 5737.

E-mail address: richgsmith@gmail.com (R.G. Smith).

soils and their variable ecologies suggest that their responses to disturbance may differ greatly and may alter biogeochemical processes (Lee, 1985; Edwards et al., 1995; Bohlen et al., 1997; Hendrix and Bohlen, 2002; Hale et al., 2005). Further, their species-specific life-histories and exploitation of varying soil niches suggest that earthworm responses to soil disturbance may be difficult to predict and depend upon complex interactions between other aspects of agricultural land use and species traits (Hale et al., 2005).

A better understanding of how earthworm communities vary with different types and intensities of agricultural land use may lead to more sustainable soil management strategies. However, there have been few studies of earthworm community response to management intensity that span a wide range of land uses, are not confounded by abiotic factors that can vary at larger spatial scales, such as soil type or climate, and are replicated. Here we report results of a study in which we measured the abundance and species composition of earthworm communities across six replicated long-term experimental ecosystems that ranged in land use and disturbance intensity from high input, intensively managed row-crop agriculture to old-field and old-growth forest ecosystems. The specific objective of the study was to determine how an important group of soil invertebrates vary across a broad range of agricultural land uses typical of the US Midwest.

2. Materials and methods

2.1. Study site

The study was conducted at the Long-Term Ecological Research (LTER) site at Michigan State University's W.K. Kellogg Biological Station in SW Michigan, USA (42°24'N, 85°24'W, elevation 288 m). Soils at the site developed from glacial outwash deposited 12,000 years ago, and are mainly in the Kalamazoo (fine-loamy, mixed, mesic Typic Hapludalfs) and Oshtemo (coarse-loamy, mixed, mesic Typic Hapludalfs) soil series (Robertson et al., 1997). Native vegetation in the area was beech-maple and oak-hickory forests interspersed with open oak savannas (Burbank et al., 1992). Most of the area was cleared for agriculture in the mid-1800s. Annual precipitation is 90 cm, about half of which is snow; mean annual temperature is 9.7 °C. Detailed site and soil descriptions are available at the W. K. Kellogg Biological Station LTER website (<http://lter.kbs.msu.edu>).

2.2. Land-use intensity gradient

Six replicated ecosystem types representing a gradient in land-use intensity were investigated. Three of the ecosystems were annual rotations of corn, soybean and winter wheat that differed in the type and intensity of agronomic management. These rotations were initiated in 1989. Management systems for the annual rotations were, in order of decreasing chemical input and soil disturbance, conventional tillage and inputs of fertilizer and herbicide (CON); no-till with conventional inputs of fertilizer and herbicide (NOT); and an organic system with tillage and leguminous cover crops (ORG). No manure or compost was applied to the ORG system. All three rotations were in winter wheat in 2001. In addition to the annual rotations, a successional old-field system (OLD) that was previously cropped but had been abandoned from agriculture when the LTER study was initiated in 1989 was also included. The least intensively managed systems at the site were two replicated forest systems: 40–60 years old conifer plantations, dominated by *Pinus resinosa*, *P. strobus*, and *Picea resinosa* (CF), and old-growth deciduous forests, dominated by *Acer saccharum*, *Prunus serotina*, and *Carya glabra* (DF). We

qualitatively ranked these six systems along a land-use intensity gradient of highest to lowest based on their history of disturbance and management: CON > NOT > ORG > OLD > CF > DF. Systems CON, NOT, ORG, and OLD were replicated six times in 1 ha plots, while the CF and DF systems, which are part of the larger KBS landscape, were replicated three times. All six ecosystems were underlain by the same soil type.

2.3. Earthworm sampling

Earthworms were sampled from all replicate plots from 19 June to 25 June 2001 using excavation and a non-toxic irritant. A template was used to define a 25 cm × 25 cm area in two randomly chosen locations in each replicate and samples were removed from the defined area in two depth increments (0–10 and 10–25 cm) using shovels. In the forested sites, the litter layer was removed prior to soil sampling and any worms found in the organic matter were collected. Soil samples were sorted by hand and earthworms removed and placed in plastic bags containing cool water, out of direct sunlight. Following excavation of the 10–25 cm section, 1 L of mustard solution (1 tablespoon of dry, ground mustard/1 L water) was poured into the hole and worms that emerged were collected for 20 min after mustard addition. The mustard solution served as a non-toxic irritant that drove deep burrowing earthworm species, such as *Lumbricus terrestris*, to the surface (Gunn, 1992; Lawrence and Bowers, 2002). Earthworms were held on ice until they were returned to the laboratory for preservation in 10% formalin solution.

2.4. Identification and determination of biomass and species richness

Earthworms were identified using the external morphology key of Reynolds (1977). Individuals were grouped into two classes, adults and juveniles, based on the presence or absence of the clitellum. Clitellate individuals were identified to species and pre-clitellate individuals were identified to genus only. Specimens that were damaged during the sampling process were identified to genus when head portions were present, and were included in abundance analyses. Specimens without heads were included in analyses of biomass only. Upon identification, each individual was patted dry with a paper towel to remove surface moisture and weighed to the nearest 0.01 g. The number of earthworm species per sample (species richness) was estimated by determining the number of distinct species per sample. Pre-clitellate individuals (identified to genus only) were included in the analysis of species richness only when clitellate individuals of the same genus were absent from the sample. Therefore, our estimates of species richness are somewhat conservative.

2.5. Statistical analysis

Differences in earthworm density, biomass and species richness among ecosystem types and sampling depths were analyzed using a two factor (system, depth) ANOVA for a randomized complete block design, followed by Fisher's Protected LSD test at the $P = 0.05$ confidence level. Earthworm species richness estimates were square root transformed and density and biomass data were expressed on a m^{-2} basis and log transformed prior to analysis to meet the assumptions of ANOVA. Analysis of the age distribution of each sample (proportion juveniles) was conducted following arcsine transformation of the data. Untransformed data are presented in all tables and figures. All analyses were performed with SAS using the GLM procedure (SAS Version 8.02; SAS Institute, Cary, NC, USA).

3. Results

3.1. Earthworm populations and biomass

Earthworm populations varied across the six experimental ecosystems and with soil depth (ANOVA, system: $F_{5,67} = 8.86$, $P < 0.0001$; depth: $F_{2,67} = 117.74$, $P < 0.0001$; interaction: $P = 0.52$). Earthworm populations were lowest in CON and CF, intermediate in NOT, ORG, OLD, and highest in DF (LSD, $P < 0.05$, Fig. 1A). Across systems, more earthworms were recovered from the 0–10 cm soil depth increment than the 10–25 or >25 cm depths (LSD, $P < 0.05$; Fig. 2A). No earthworms were recovered from the >25 cm depth in CON (Table 1). Earthworm populations in the litter layer of CF and DF were relatively low compared to the subsoil (data not shown) and did not differ between the two systems ($P = 0.61$). Juveniles (pre-clitellate) made up the majority of individuals recovered from each sample (>88%) and their proportional abundance (relative to adults) was similar across systems and soil depths (ANOVA, system: $P = 0.35$; depth: $P = 0.73$; interaction: $P = 0.07$).

Earthworm community biomass (wet weight) varied among the six systems and with soil depth (ANOVA, system: $F_{5,67} = 7.50$, $P < 0.0001$; depth: $F_{2,67} = 25.12$, $P < 0.0001$; interaction: $P = 0.32$). The lowest biomass was in CON, where biomass was over two

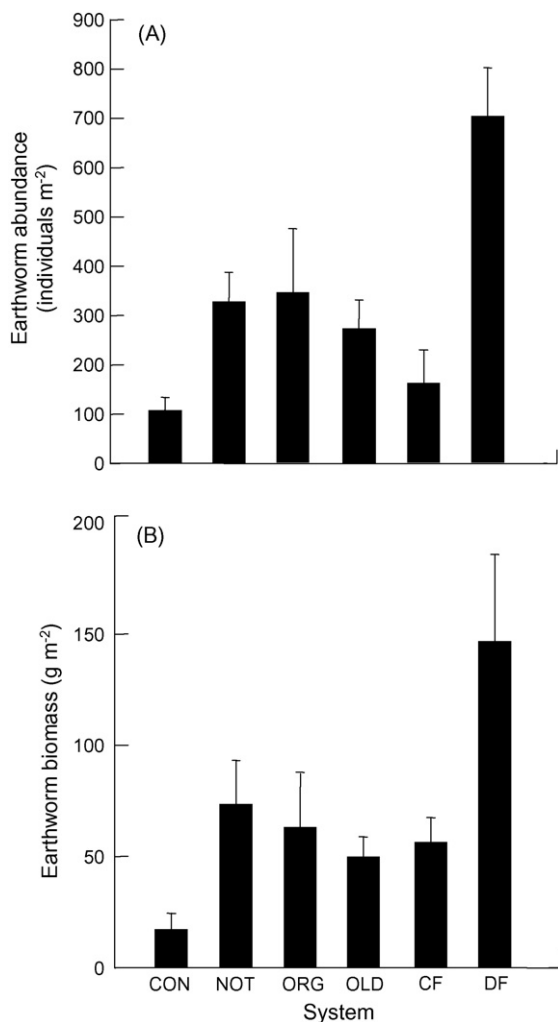


Fig. 1. Earthworm abundance (A) and biomass (B) across six ecosystems representing a land-use intensity gradient. For a description of the systems see Table 1. Values are means \pm S.E.; $n = 6$, CON, NOT, ORG, and OLD; $n = 3$, CF and DF.

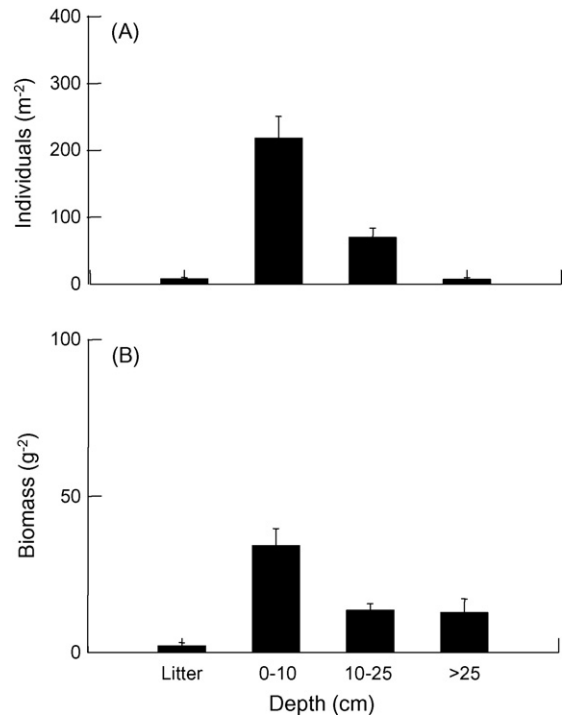


Fig. 2. Earthworm abundance (A) and biomass (B) by soil depth averaged across the six ecosystems representing a land-use intensity gradient. Values are means \pm S.E.; $n = 30$, 0–10, 10–25, >25 cm; $n = 6$, litter.

times lower than in the other two annual rotation systems, and nearly six times lower than in the DF system. Earthworm biomass in NOT, ORG, OLD and CF was not statistically different (LSD, $P > 0.05$; Fig. 1B). The pattern for earthworm biomass across the three sampling depths was similar to that of earthworm numbers (Fig. 2B). Earthworm biomass was highest in the 0–10 cm soil depth, intermediate at the 10–25 depth, and low at the >25 cm depth except in NOT, where a few large-bodied individuals recovered with mustard solution contributed disproportionately to biomass at the >25 cm depth (LSD, $P < 0.05$).

3.2. Earthworm species richness and community composition

The total number of earthworm species present in each system ranged from two in CON to six in DF and included the species *Aporrectodea tuberculata*, *Aporrectodea turgida*, *Aporrectodea limicola*, *L. terrestris*, *Lumbricus rubellus*, *Eisenia rosea*, and *Octolasion tyrtaeum*. Mean species richness per soil sample (no. species/0.0625 m²) varied among systems ($F_{5,19} = 16.54$, $P < 0.0001$), and was highest in DF (Fig. 3). The genus *Aporrectodea* was proportionately dominant across most systems (Fig. 4); however, absolute numbers of individuals varied among systems and with soil depth (ANOVA, system: $F_{5,67} = 5.72$, $P = 0.0002$; depth: $F_{5,67} = 157.85$, $P < 0.0001$; interaction: $P = 0.07$). Numbers of *L. terrestris* also varied among systems (system: $F_{5,67} = 14.56$, $P < 0.0001$; depth: $P = 0.85$; interaction: $P = 0.15$) and were relatively low in the annual rotations (CON, ORG, and NOT) and OLD compared to CF and DF (LSD, $P < 0.05$; Table 1). The mainly litter-dwelling species *L. rubellus* was found only in the two forest systems, and was most abundant in CF (LSD $P < 0.05$). Populations of the other species were too low to make valid statistical comparisons. Individuals of *E. rosea* were found only in OLD. Two species were found only in DF, *A. limicola* and *O. tyrtaeum*.

Table 1

Depth distribution of earthworm genera and species (m^{-2}) recovered from soil collected in six experimental systems representing a gradient in land-use intensity

Species/depth (cm)	Systems ^a					
	CON	NOT	ORG	OLD	CF	DF
<i>Aporrectodea</i> spp.						
Litter	ND	ND	ND	ND	2.7	0
0–10	60.0	217.3	200.0	149.3	42.7	402.7
10–25	21.3	52.0	96.0	61.3	5.3	29.3
>25	0	1.3	1.3	1.3	0	0
<i>A. turgida</i>						
Litter	ND	ND	ND	ND	0	0
0–10	6.7	0	8.0	14.7	5.3	13.3
10–25	5.3	0	4.0	4.0	0	2.7
>25	0	0	0	0	0	0
<i>A. tuberculata</i>						
Litter	ND	ND	ND	ND	0	2.7
0–10	1.3	1.3	0	6.7	5.3	29.3
10–25	0	0	2.7	1.3	0	2.7
>25	0	0	1.3	0	0	0
<i>A. limicola</i>						
Litter	ND	ND	ND	ND	0	0
0–10	0	0	0	0	0	40.0
10–25	0	0	0	0	0	10.7
>25	0	0	0	0	0	0
<i>Lumbricus</i> spp.						
Litter	ND	ND	ND	ND	0	0
0–10	0	0	0	0	0	0
10–25	0	1.3	0	1.3	0	5.3
>25	0	0	0	1.3	0	0
<i>L. terrestris</i>						
Litter	ND	ND	ND	ND	2.7	5.3
0–10	0	6.7	0	0	21.3	53.3
10–25	0	10.7	1.3	1.3	5.3	21.3
>25	0	16.0	4.0	0	2.7	8.0
<i>L. rubellus</i>						
Litter	ND	ND	ND	ND	2.7	0
0–10	0	0	0	0	40.0	16.0
10–25	0	0	0	0	10.7	2.7
>25	0	0	0	0	0	0
<i>Eisenia rosea</i>						
Litter	ND	ND	ND	ND	0	0
0–10	0	0	0	21.3	0	0
10–25	0	0	0	1.3	0	0
>25	0	0	0	0	0	0
<i>Octolasion tyrtaeum</i>						
Litter	ND	ND	ND	ND	0	0
0–10	0	0	0	0	0	10.7
10–25	0	0	0	0	0	0
>25	0	0	0	0	0	0

Values are means; $n=6$, CON, NOT, ORG, and OLD; $n=3$, CF and DF. ND: no determination.

^a Systems: CON, conventional agriculture with tillage, fertilizer, and herbicide; NOT, no-till agriculture with fertilizer and herbicide; ORG, organic input agriculture with leguminous cover crop and tillage, but no fertilizer and herbicide; OLD, old-field abandoned from agriculture in 1989; CF, coniferous forest plantation; DF, deciduous forest.

4. Discussion

Across the experimental ecosystems, variation in total earthworm abundance roughly corresponded to their qualitative ranking in land-use intensity, particularly at the extreme ends of the gradient (CON vs. DF). While the system approach employed in this study did not allow us to test hypotheses regarding the impact of specific management practices on earthworm communities it is possible to speculate on their relative importance within each system. For instance, in annual cropping systems tillage and

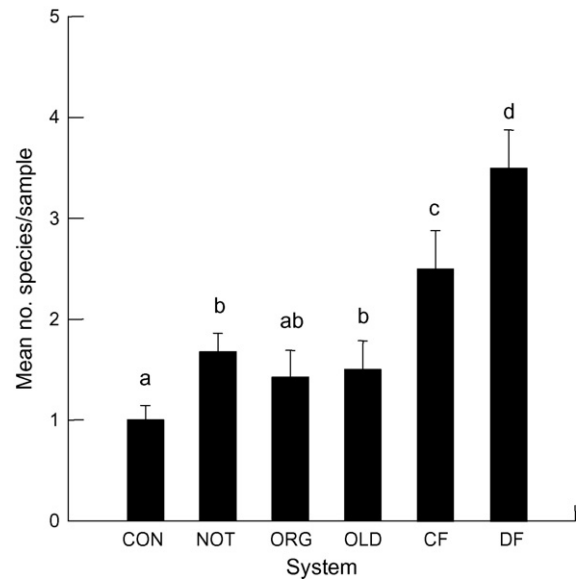


Fig. 3. Earthworm species richness across six ecosystems representing a land-use intensity gradient. For a description of the systems see Table 1. Values are means \pm S.E.; $n=6$, CON, NOT, ORG, and OLD; $n=3$, CF and DF. Bars sharing the same lower-case letter are not significantly different (LSD $P < 0.05$).

chemical inputs have been shown to affect earthworm populations; tillage by impacting soil organic matter and moisture and increasing exposure to predators and inclement weather conditions (Edwards et al., 1995; Clapperton et al., 1997; Curry, 1998), and long-term herbicide and chemical fertilizer use by decreasing soil surface residue, protective cover and soil organic matter and changing soil pH and Ca^{2+} (Lee, 1985; Paoletti, 1999). In some cases, tillage may reduce populations by 50% or more compared to no-till systems (Mele and Carter, 1999). Similarly, Schmidt et al. (2003) reported that earthworm populations increased from 211 to 572 individuals m^{-2} following conversion from conventional to no-till winter wheat intercropped with clover. Therefore, it is likely that all of these practices, tillage and herbicide and chemical fertilizer applications, contributed synergistically to the low abundance of earthworms in CON relative to NOT and ORG.

In contrast to the annual rotations, the low abundance of earthworms in the successional old-field (OLD) relative to CON was somewhat surprising, but not unprecedented (Lee, 1985; Paoletti, 1999; Didden, 2001). Other studies, have found variable soil macrofauna responses to old-field succession (Scheu, 1992; Lagerlöf et al., 2002; Thomas et al., 2004). In Sweden, Lagerlöf

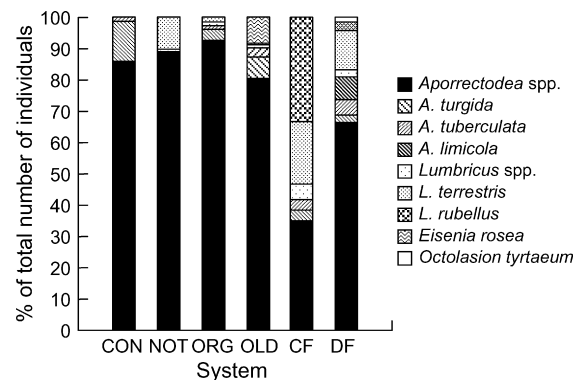


Fig. 4. Relative abundance of earthworm genera and species within communities sampled from six ecosystems representing a land-use intensity gradient. For a description of the systems see Table 1.

et al. (2002) found lower numbers of lumbricids in an uncultivated field boundary than in an adjacent intensively cultivated agricultural field, while Scheu (1992) found lower earthworm numbers and biomass in an 11-year old-field compared to a 2- and 50-year old-field. In contrast, Pizl (1992) found that earthworm populations rebounded following 2 years abandonment from agriculture and densities and biomass were similar in 4- and 10-year fallows. Some of the variation in earthworm response to early old-field succession may be related to changes in the quality and quantity of organic inputs available to earthworms as plant communities change (Bohlen et al., 1997; Hubbard et al., 1999), or to landscape or species-level factors controlling dispersal and colonization following reduction in disturbance (Decaëns and Jiménez, 2002; Thomas et al., 2004).

Changes in soil physical and chemical properties associated with conifer afforestation likely contributed to the low abundance of earthworms in CF relative to the other more intensively managed systems and DF. Conifer afforestation has been shown to result in reduced litter quality, decreased soil pH, and deterioration of soil structure, conditions which can reduce earthworm populations (Curry, 1998).

In contrast to earthworm abundance, species richness and community composition appeared to be more reflective of the qualitative differences in land-use intensity along the gradient. In the annual rotations high rates of disturbance and habitat simplification likely contributed to the low numbers of species and dominance by the genus *Aporrectodea*, which is relatively tolerant of agricultural activities such as disk tilling by being able to persist deeper in the subsoil than other endogeic species (Berry and Karlen, 1993; Sims and Gerard, 1999).

All species recovered in this study, with the exception of *E. rosea*, were observed in the DF system. Forest systems are often reported to have greater numbers of earthworm species compared to cultivated agricultural land because these systems tend to be more complex and have more niches which allow persistence of a greater number of species with variable ecologies (Lee, 1985; Edwards et al., 1995). Deciduous forests tend to be more species rich than conifer forests because soil conditions, including pH, are more favorable in these systems (Lee, 1985). Lee (1985) noted that earthworm communities in coniferous woodlands tend to be made up mainly of small litter-dwelling species. In accordance, we found that earthworm communities in CF contained a large number of the epigeic species *L. rubellus*, which has been noted to be tolerant of acidic soils (Ma et al., 1990; Sims and Gerard, 1999).

Other factors also likely contributed to the abundance and composition of earthworm communities across the experimental gradient. Landscape structure and species-specific dispersal and colonization abilities may also have played a role in community differences among the systems (Decaëns and Jiménez, 2002; Thomas et al., 2004). As native habitat in the study area was originally deciduous woodland and oak savannah, we originally considered DF a baseline system from which to compare the effects of increased disturbance intensity and land use. However, care should probably be exercised with the interpretation of earthworm communities in DF as representing a pre-disturbance state. Earthworm abundance and species composition in the deciduous forests before the conversion to agricultural land (ca. 150 bp) are unknown (Snider, 1991) and were likely much different than at present due to Pleistocene glaciations (Hendrix and Bohlen, 2002). As all species recovered in this study were considered European in origin (Reynolds, 1977), and new earthworm species continue to be introduced to North America (Hendrix and Bohlen, 2002), it is possible that some species colonized the DF systems after the other systems were initially converted to agriculture. At least one of the two endogeic species unique to the deciduous forest, *A. limicola*, had

not previously been recorded in Michigan (Snider, 1991). Therefore, it is unlikely that the lack of *A. limicola* in the annual rotation or old-field systems was due to the influence of agricultural disturbance, other than to preclude their invasion at present. It is also unclear whether populations of species such as *A. limicola* or *O. tyraeum* were low in DF due to the fragmented nature of these systems (Kalisz and Wood, 1995), or due to recent invasion.

When possible, future studies that include undisturbed native habitat in which invasion histories are known, or where native earthworm species are present, may better help relate changes in earthworm community structure to long-term changes in land use and available species pools. Continued changes in land-use patterns and agricultural intensity in response to increasing human population pressures will necessitate a better understanding of the long-term effects of land use on organisms, such as earthworms, that control important ecosystem functions and services and are potential indicators of ecosystem health and sustainability (Hendrix, 1998; Kremen et al., 2002; Robertson and Swinton, 2005).

Acknowledgements

We would like to thank A. Corbin for technical assistance. T. Bergsma, C. Leroy, M. Plum, K. Quiñones-Gonzales, A. Smith, C.J. Wycoff, P. Wycoff, and B. Young assisted with field work. Financial support was provided by the US National Science Foundation (LTER Program) and the Michigan Agricultural Experiment Station. This is W. K. Kellogg Biological Station contribution 1401.

References

- Berry, E.C., Karlen, D.L., 1993. Comparison of alternative farming systems. II. Earthworm population density and species diversity. *Am. J. Altern. Agric.* 8, 21–26.
- Bohlen, P.J., Parmelee, R.W., McCartney, D.A., Edwards, C.A., 1997. Earthworm effects on carbon and nitrogen dynamics of surface litter in corn agroecosystems. *Ecol. Appl.* 7, 1341–1349.
- Bouché, M.B., 1977. Stratégies lombriciennes. In: Lohm, U., Persson, T. (Eds.), *Soil Organisms as Components of Ecosystems*. Biol. Bull., Stockholm, vol. 25, pp. 122–132.
- Burbank, D.H., Pregitzer, K.S., Gross, K.L., 1992. Vegetation of the W.K. Kellogg Biological Station, Kalamazoo County, Michigan. Michigan State University. Agricultural Experiment Station. Research Report 510.
- Callahan, M.A., Blair, J.M., Todd, T.C., Kitchen, D.J., Whiles, M.R., 2003. Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass. *Soil Biol. Biochem.* 35, 1079–1083.
- Clapperton, M.J., Miller, J.J., Larney, F.J., Lindwall, C.W., 1997. Earthworm populations as affected by long-term tillage practices in Southern Alberta. *Can. Soil Biol. Biochem.* 29, 631–633.
- Clapperton, M.J., 1999. Tillage practices, and temperature and moisture interactions affect earthworm populations and species composition. *Pedobiologia* 43, 658–665.
- Curry, J.P., 1998. Factors affecting earthworm abundance in soils. In: Edwards, C.A. (Ed.), *Earthworm Ecology*. St. Lucine Press, Boca Raton, FL, pp. 37–64.
- Decaëns, T., Jiménez, J.J., 2002. Earthworm communities under an agricultural intensification gradient in Colombia. *Plant Soil* 240, 133–143.
- Didden, W.A.M., 2001. Earthworm communities in grasslands and horticultural soils. *Biol. Fertil. Soils* 33, 111–117.
- Edwards, C.A., Bohlen, P.J., Linden, D.R., Subler, S., 1995. Earthworms in agroecosystems. In: Hendrix, P.F. (Ed.), *Earthworm Ecology and Biogeography in North America*. Lewis Publishers, Boca Raton, FL, pp. 185–213.
- Fragoso, C., Brown, G.G., Patrón, J.C., Blanchart, E., Lavelle, P., Pashanasi, B., Senapati, B., Kumar, T., 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of earthworms. *Appl. Soil Ecol.* 6, 17–35.
- Gunn, A., 1992. The use of mustard to estimate earthworm populations. *Pedobiologia* 36, 65–67.
- Hale, C.M., Frellich, L.E., Reich, P.B., Pastor, J., 2005. Effects of European earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, USA. *Ecosystems* 8, 911–927.
- Hendrix, P.F., 1998. Earthworms in agroecosystems: a summary of current research. In: Edwards, C.A. (Ed.), *Earthworm Ecology*. St. Lucine Press, Boca Raton, FL, pp. 259–266.
- Hendrix, P.F., Bohlen, P.J., 2002. Exotic earthworm invasions in North America: ecological and policy implications. *BioScience* 52, 801–811.
- Hubbard, V.C., Jordan, D., Stecker, J.A., 1999. Earthworm response to rotation and tillage in a Missouri claypan soil. *Biol. Fertil. Soils* 29, 343–347.

- James, S.W., 1991. Soil, nitrogen, phosphorus, and organic matter processing by earthworms in tallgrass prairie. *Ecology* 72, 2101–2109.
- Kalisz, P.J., Wood, H.B., 1995. Native and exotic earthworms in wildland ecosystems. In: Hendrix, P.F. (Ed.), *Earthworm Ecology and Biogeography in North America*. Lewis Publishers, Boca Raton, FL, pp. 117–126.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. U.S.A.* 99, 16812–16816.
- Lagerlöf, J., Bénédicte, G., Vincent, C., 2002. The importance of field boundaries for earthworms (Lumbricidae) in the Swedish agricultural landscape. *Agric., Ecosyst. Environ.* 89, 91–103.
- Lawrence, A.P., Bowers, M.A., 2002. A test of the “hot” mustard extraction method of sampling earthworms. *Soil Biol. Biochem.* 34, 549–552.
- Lee, K.E., 1985. *Earthworms: Their Ecology and Relationships with Soils and Land use*. Academic Press, New York, 411 pp.
- Ma, W., Brussard, L., De Ridder, J.A., 1990. Long-term effects of nitrogenous fertilizers on grassland earthworms (Oligochaeta: Lumbricidae): their relation to soil acidification. *Agric. Ecosyst. Environ.* 30, 71–80.
- Mele, P.M., Carter, M.R., 1999. Impact of crop management factors in conservation tillage farming on earthworm density, age structure and species abundance in south-eastern Australia. *Soil Till. Res.* 50, 1–10.
- Paoletti, M.G., 1999. The role of earthworms for assessment of sustainability and as bioindicators. *Agric. Ecosyst. Environ.* 74, 137–155.
- Pizl, V., 1992. Succession of earthworm populations in abandoned fields. *Soil Biol. Biochem.* 24, 1623–1628.
- Pouyat, R.V., Carreiro, M.M., 2003. Controls on mass loss and nitrogen dynamics of oak leaf litter along an urban-rural land-use gradient. *Oecologia* 135, 288–298.
- Reynolds, J.W., 1977. *The Earthworms (Lumbricidae and Sparganophilidae) of Ontario*. The Royal Ontario Museum, Toronto, 141 pp.
- Robertson, G.P., Klingensmith, K.M., Klug, M.J., Paul, E.A., Crum, J.R., Ellis, B.G., 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. *Ecol. Appl.* 7, 158–170.
- Robertson, G.P., Swinton, S.M., 2005. Reconciling agricultural productivity and environmental integrity: a grand challenge for agriculture. *Front. Ecol. Environ.* 3, 38–46.
- Scheu, S., 1992. Changes in the Lumbricid coenosis during secondary succession from a wheat field to a beechwood on limestone. *Soil Biol. Biochem.* 24, 1641–1646.
- Schmidt, O., Clements, R.O., Donaldson, G., 2003. Why do cereal-legume intercrops support large earthworm populations? *Appl. Soil Ecol.* 22, 181–190.
- Sims, R.W., Gerard, B.W., 1999. *Synopses of the British Fauna (No. 31 Revised)—Earthworms*. FSC Publications, Shrewsbury, 169 pp.
- Snider, R.M., 1991. Checklist and distribution of Michigan earthworms. *Mich. Acad.* 24, 105–114.
- Thomas, F., Folgarait, P., Lavelle, P., Rossi, J.P., 2004. Soil macrofaunal communities along an abandoned rice field chronosequence in Northern Argentina. *Appl. Soil Ecol.* 27, 23–29.
- VandenBygaart, A.J., Fox, C.A., Fallow, D.J., Protz, R., 2000. Estimating earthworm-influenced soil structure by morphometric image analysis. *Soil Sci. Soc. Am. J.* 64, 982–988.