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ScienceDirect
European Journal of Soil Biology 42 (2006) S284–S288
EUROPEAN JOURNAL OF SOIL BIOLOGY
http://france.elsevier.com/direct/ejsobi

Original article

Soil properties inside earthworm patches and gaps in a tropical grassland (la Mancha, Veracruz, Mexico)

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Available online 26 July 2006

Abstract

Earthworms often form spatially structured populations characterised by alternate clusters of either low or high density. This study compared various soil properties and herbaceous plant biomass between areas of high and low earthworm density (i.e. patches and gaps) in a tropical grassland (la Mancha, Veracruz, Mexico). We aimed at identifying those variables that might explain the observed spatial distribution or, conversely be explained by the community pattern. We examined the spatial aggregation by means of the Spatial Analysis by Distance IndicEs (SADIE) system and showed the presence of significant patches and gaps. Only a few variables significantly differed between patches and gaps. Areas corresponding to earthworm patches and gaps had more silt and clay, respectively, in the 10–30 cm soil layer. There was no difference in the C content in the different particle-size classes expressed in absolute values (mg C g^{-1} soil) but the proportion of C associated to > 200 μm particles was larger in the patches (0–10 cm layer) while there was more C associated to the fine particle (< 50 μm) in the gaps (10–30 cm soil layer). Patches and gaps did not differ significantly in terms of cation concentrations (K, Mg and Ca), pH, soil bulk density or herbaceous plant dry mass. The lack of clear relationships between earthworm distribution and soil parameters in this study suggest that earthworm populations and soil properties may occur at different spatial scales.

Keywords: Earthworm; Spatial pattern; Soil attributes; Soil organic matter; SADIE analysis

1. Introduction

Earthworm populations often exhibit non-random spatial structures [18,21] and the ecological factors that cause these patterns are poorly understood. Large scale variations of soil type and long-range trends in soil texture have been identified as important ecological factors affecting earthworm distribution [17]. Besides, it is likely that short-range variations of other ecological factors (e.g. micro-topography, soil water dynamics) may also play an important role in explaining local patterns (short-range variability) [20,23]. Furthermore soil carbon content and soil texture are good candidates to explain the level of earthworm abundance and its spatial variability [12,17]. The amount, availability and quality of organic matter are important parameters since endogeic earthworms often feed on fresh residues

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doi:10.1016/j.ejsobi.2006.07.024

(plant debris) although they are considered to be able to assimilate the organic matter from all the soil particle-size fractions [7,14]. However, earthworm activities in turn, affect soil in various ways. They alter soil organic matter turn-over [3,4] and strongly affect soil structure dynamics [1,9]. This study was designed to describe the spatial pattern of earthworm in terms of patches and gaps of abundance (formal definition below) in a tropical grassland (la Mancha, Veracruz, Mexico). We assessed various soil descriptors and soil vegetation biomass within areas corresponding to earthworm patches and gaps in order to determine which soil descriptor could be correlated to earthworm horizontal pattern of distribution.

2. Material and methods

2.1. Site, sampling and soil measurements

The survey was conducted in a grassland at the Centro de investigaciones costeras la Mancha (CICOLMA) (96°22′40″W 19°36′N), in the state of Veracruz, Mexico. Soils are regosols [11]. The climate is tropical subhumid with a rain season from June to September. The annual precipitations range between 1200 and 1500 mm and the average temperature is 24.5 C (maximum and minimum of 27 and 16 °C, respectively) [5].

2.2. Soil, vegetation and earthworm sampling

Earthworm community was assessed using 100 sampling points regularly distributed on the nodes of a 5 m grid within a 95 × 20 m plot. Earthworms were hand sorted from 25 × 25 × 30 cm monoliths, and preserved in 4% formaldehyde before identification and enumeration. From each monolith, sub-samples of soil were taken in two depth layers, 0–10 and 10–30 cm, respectively. Herbaceous plants were harvested, dried and weighed in order to measure their biomass following the recommendations by Anderson and Ingram [2]. All herbaceous vegetation was cut within the quadrats at 2 cm above the ground before the corresponding soil monolith was extracted for earthworm sampling. Plant material was dried at 65 °C during 48 hours. Sampling was done at the end of the rainy season when earthworm communities were presumed to be at peak of abundance and biomass [2].

2.3. Analytical methods

Soil samples were air-dried and sieved at 2 mm prior to fractionation and chemical analyses. The fractionation method developed by Feller [8] was applied to soil samples from the 0 to 10 and 10–30 cm. The carbon content of each particle-size class was determined by the Walkey and Black method. Soil texture of samples from the 0 to 10 and 10–30 cm was determined following [10]. Various exchangeable cations, calcium (Ca), magnesium (Mg) and potassium (K) were titrated with a flame spectrometer. Soil pH and soil bulk density were determined following Anderson and Ingram [2]. Given the large number of sampling locations we could not afford to do all the measurements on all the samples. A minimum of 70 measurements were done for each variable for each soil layer (0–10 and 10–30 cm). Samples used to make the measurements were randomly chosen. The exact number of measures available for comparison purpose within patches and gaps are indicated in the last columns of Table 1.

2.4. Data analysis

The earthworm data (in the form of counts) were analysed by means of the Spatial Analysis by Distance IndicEs (SADIE) method [15,16]. In that context the term “cluster” refers to a region of either relatively high density (i.e. a patch) or relatively low density (i.e. a gap). Readers can find a detailed description of the approach in [16] and examples of application in the context of earthworm ecology in [19]. Basically the analysis relies on the computation of a general aggregation index referred to as I_a and another aggregation index (v_{ij}) associated to each sampling unit. The former index indicates if the spatial pattern is globally non-random whereas the latter shows if a given sample (i.e. observed count) tends to contribute to a patch or a gap. Both indices are tested by means of a Monte Carlo procedure [16] based on 1560 randomisations. Following the original proposition by Perry et al. [16] we used heuristic thresholds of 1.5 and –1.5 for the v_{ij} index values, respectively: sampling units associated with index values > 1.5 indicated patches, whereas sampling units associated with index values < -1.5 revealed the presence of gaps. Isolating these points made it possible to identify clusters, determine their type (patches or gaps) and compute average values of soil descriptors within each type of cluster (see [16] for details). Soil descriptors were non-normally distributed with highly heterogeneous sample variances and some degree of autocorrelation. Therefore the classical mean comparison test (Student’s *t*-test) could not be used to assess possible differences between earthworm patches and gaps. We rather employed randomisation tests (1000 randomisations per test) proposed by Manly

Table 1
Mean and standard deviation of various soil descriptors and vegetation dry weight in a grassland at la Mancha, Mexico

Variable	Soil Depth (cm)	Unit	Mean (S.D.) Patches	Mean (S.D.) Gaps	Prob-ability	$\alpha = 0.05$		Number Patches	Number Gaps
pH	0–10		6.05 (0.34)	6.05 (0.3)	0.519	NS	–	37	28
pH	10–30		6.32 (0.24)	6.26 (0.32)	0.32	NS	–	35	28
Soil texture									
Clay	0–10	%	12.84 (2.77)	14.17 (3.11)	0.961	NS	–	35	27
Silt	0–10	%	9.3 (2.92)	7.85 (3.44)	0.038	NS	–	35	27
Sand	0–10	%	77.9 (3.05)	77.98 (3.74)	0.556	NS	–	35	27
Clay	10–30	%	13.04 (2.44)	15.47 (3.4)	0.999	**S**	*Gap > patch*	34	25
Silt	10–30	%	9.27 (2.71)	7.28 (3.01)	0.006	**S**	*Patch > gap*	34	25
Sand	10–30	%	77.69 (2.64)	77.25 (3.4)	0.286	NS	–	34	25
Soil organic carbon									
> 200 μm	0–10	mg C g^{-1} soil	2.09 (0.62)	1.92 (0.58)	0.212	NS	–	32	19
200–50 μm	0–10	mg C g^{-1} soil	6.43 (2.32)	7.51 (3.81)	0.902	NS	–	32	19
< 50 μm	0–10	mg C g^{-1} soil	6.66 (1.9)	8.11 (3.82)	0.960	NS	–	32	19
total	0–10	mg C g^{-1} soil	15.18 (3.96)	17.54 (7.57)	0.925	NS	–	32	19
> 200 μm	0–10	%	14.08 (4.27)	11.61 (3.15)	0.018	**S**	*Patch > gap*	32	19
200–50 μm	0–10	%	41.85 (6.26)	41.96 (7.5)	0.521	NS	–	32	19
< 50 μm	0–10	%	44.07 (7.97)	46.43 (8.35)	0.842	NS	–	32	19
> 200 μm	10–30	mg C g^{-1} soil	1.37 (0.62)	1.34 (0.47)	0.447	NS	–	28	19
200–50 μm	10–30	mg C g^{-1} soil	4.65 (1.62)	4.7 (1.39)	0.518	NS	–	28	19
< 50 μm	10–30	mg C g^{-1} soil	4.09 (2.28)	5.34 (2.08)	0.262	NS	–	28	19
Total	10–30	mg C g^{-1} soil	10.12 (3.59)	11.38 (2.71)	0.091	NS	–	28	19
> 200 μm	10–30	%	14.52 (5.77)	12.14 (3.87)	0.074	NS	–	28	19
200–50 μm	10–30	%	47.07 (8.79)	41.89 (10.21)	0.036	NS	–	28	19
< 50 μm	10–30	%	38.41 (9.42)	45.97 (11.54)	0.993	**S**	*Gap > patch*	28	19
Cations									
K	0–10	Cmol + kg^{-1} soil	0.52 (0.15)	0.45 (0.19)	0.283	NS	–	37	28
Mg	0–10	Cmol + kg^{-1} soil	3.12 (0.83)	2.92 (0.59)	0.148	NS	–	37	28
Ca	0–10	Cmol + kg^{-1} soil	8.50 (2.55)	9.32 (1.95)	0.920	NS	–	37	28
K	10–30	Cmol + k^{g-1} soil	0.34 (0.16)	0.32 (0.14)	0.421	NS	–	37	28
Mg	10–30	Cmol + kg^{-1} soil	1.98 (0.74)	2.04 (0.44)	0.640	NS	–	37	28
Ca	10–30	Cmol + kg^{-1} soil	8.13 (2.56)	7.56 (1.42)	0.148	NS	–	37	28
Soil bulk density	0–10	g cm^{-3}	1.50 (0.13)	1.52 (0.12)	0.558	NS	–	37	28
Soil bulk density	10–30	g cm^{-3}	1.50 (0.14)	1.54 (0.14)	0.628	NS	–	37	25
Vegetation (dry mass)		g m^{-2}	641 (302)	683 (273)	0.716	NS	–	37	28

Means and standard deviation are estimated within areas corresponding to earthworm patches and gaps. Statistical significance is assessed by means of randomisation tests (10,000 randomisations for each test). Tests are two-sided. Number patches and number gaps indicate the number of measurements available within patches and gaps for each variable. S: Significant. NS: non-significant.

[13]. The null hypothesis was H0 "no difference between areas corresponding to earthworm patches and gaps" and the alternative hypothesis was H1 "there is a difference between areas corresponding to earthworm patches and gaps". Because we cannot make any assumption on the sign of the difference, we used a two-sided test [13]. As a consequence probabilities reported in Table 1 must be interpreted as follows: $P < 0.025$ indicated that the variable at hand has higher mean value within patches while a $P > 0.975$ denoted a higher variable mean value within patches (for a 5% level of significance).

3. Results

3.1. Earthworm community

The endogeic earthworm species *Polypheretima elongata* (Megascolecidae) represented 86% of the total earthworm biomass (66.6 g m^{-2}) and 31% of the total earthworm density (486.6 ind m^{-2}). Other endogeic species *Phoenicodrilus taste* (Ocnerodrilidae) and *Diplotrema murchiei* (Megascolecidae) corresponded to 11% of the earthworm density. Two epigeic species were encountered, *Dichogaster saliens* (Megascoleci-

dae) and *D. bolaui* and represented 35% of the total density. Unidentified endogeic juveniles amounted 23% of the total earthworm density.

3.2. Spatial aggregation

The global aggregation I_a was equal to 2.623 and found to be highly significant ($P < 10^{-3}$). Earthworm distribution exhibited both patches (mean $v_i = 2.653$; $P < 10^{-3}$) and gaps (mean $v_j = -2.313$; $P < 10^{-3}$). There were three gaps and five patches representing 28% and 37% of the plot area, respectively (Fig. 1).

3.3. Soil descriptors within patches and gaps

Table 1 shows the average values of the different soil descriptors measured in areas corresponding to earthworm patches and gaps. There was no difference of soil texture in the 0–10 cm soil layer whereas areas corresponding to earthworm patches and gaps had different amount of silt and clay when we considered the 10–30 cm soil layer (Table 1). Patches had more silt ($P = 0.006$) whereas gaps corresponded to areas with more clay ($P = 0.999$). If we considered the C content in the different particle-size classes expressed in absolute values (i.e. mg C g^{-1} soil) there was no significant differences between earthworm patches and gaps. We also report the results obtained when we expressed the C content in the soil fractions as the ratio to the total C content (reported as % in Table 1). Since the total C content was different in patches and gaps (gaps had a higher amount of C; Table 1) the ratios exhibited slightly different patterns. The proportion of C associated to > 200 μm particles was larger in the patches ($P = 0.018$; Table 1) in the 0–10 cm layer while there was more C associated to the fine particle (< 50 μm) in the gaps ($P = 0.993$; Table 1) in the 10–30 cm soil layer. Patches and gaps did not differ significantly in terms of cation concentrations, pH or soil bulk density (Table 1). The herbaceous plant dry mass was measured as 641 and 683 g m^{-2} in the areas corresponding to earthworm patches and gaps, respectively. These means were not statistically different ($P = 0.716$, Table 1).

4. Discussion

Our results showed that earthworm community displayed a structured horizontal distribution constituted by high and low density areas, namely the patches and the gaps. This result is not new and is largely in

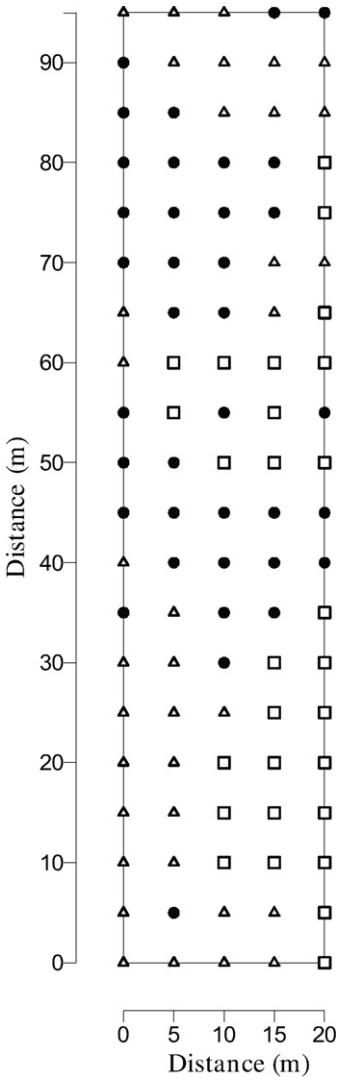

Fig. 1. Sampling units within the study plot. Black circles and open squares indicate sampling units contributing to patches and gaps, respectively. Open triangles represent sampling points associated to counts not significantly contributing to a spatial cluster.

accordance with other studies dealing with tropical [19,22] or temperate earthworm populations [18,24]. Patches of earthworm corresponded to areas with a higher proportion of carbon associated with coarse fractions (> 200 μm) in the 0–10 cm although the absolute values did not change significantly (2.09 and 1.92 mg C g^{-1} soil, respectively: Table 1). It has been shown that endogeic species are able to assimilate organic matter from all fractions [14] although fresh residues (large particle-size) constitute a more valuable trophic resource [7]. In the 10–30 cm soil layer we reported a higher proportion of C associated to fine fractions (< 50 μm) in areas corresponding to earth-

worm gaps. These results suggest that earthworm populations display higher abundance in patches of soil more favourable because there is more C in the coarse fraction. However, high population density would lead to high consumption rate and hence to a decrease of food resource (C content in coarse fractions). If patches were stable structures then we could expect the amount of C associated to coarse fractions to level off except if some external factor maintained it. However the pasture plot where this study was undertaken did not exhibit noticeable sources of habitat heterogeneity and neither vegetation biomass nor cation concentration was related to earthworm pattern. Therefore we failed to identify factors that could drive the earthworm community pattern.

The dynamics of earthworm community spatial structure has been relatively poorly documented. Available data show a relative stability [6,21] as well as a lack of stability [24]. In this study, we have no information on the dynamics of the earthworm spatial pattern or about carbon dynamics therefore the apparent relationship between soil carbon content and earthworm abundance remains to be supported by additional data. The lack of clear relationships between earthworm distribution and soil parameters in this study suggest that earthworm populations and soil properties may occur at different spatial scales [24]. This hypothesis requires a sizeable amount of additional data but constitutes a promising research avenue.

References

[1] P.O. Aina, Contribution of earthworms to porosity and water infiltration in a tropical soil under forest and long-term cultivation, Pedobiologia (Jena) 26 (1984) 131–136.

[2] J.M. Anderson, J.S.I. Ingram, Tropical Soil Biology and Fertility—A Handbook of Methods, second ed, CAB International, Oxford, 1993.

[3] P.J. Bohlen, R.W. Parmelee, D.A. McCartney, C.A. Edwards, Earthworm effects on carbon and nitrogen dynamics of surface litter in corn agroecosystems, Ecol. Appl. 7 (1997) 1341–1349.

[4] G.G. Brown, I. Barois, P. Lavelle, Regulation of soil organic matter dynamics and microbial activity in the drilosphere and the role of interactions with other edaphic functional domains, Eur. J. Soil Biol. 36 (2000) 177–198.

[5] Y. De la Cruz-Elizondo, Influencia de la humedad, el ganado y los arboles sobre la diversidad, actividad y abundancia de las lombrices de tierra en potreros de la Mancha, Veracruz. Tesis de licenciatura, Universidad Veracruzana, Xalapa, 1999.

[6] T. Decaëns, J.P. Rossi, Spatio-temporal structure of earthworm community and soil heterogeneity in a tropical pasture, Ecography 24 (2001) 671–682.

[7] T. Desjardins, F. Charpentier, B. Pashanasi, A. Pando-Bahuon, P. Lavelle, A. Mariotti, Effects of earthworm inoculation on soil organic matter dynamics of a cultivated ultisol, Pedobiologia (Jena) 47 (2003) 835–841.

[8] C. Feller, Une méthode de fractionnement granulométrique de la matière organique des sols. Application aux sols tropicaux, à texture grossière, très pauvres en humus, Cah. ORSTOM, Ser, Pédol. 17 (1979) 339–346.

[9] G.S. Francis, P.M. Fraser, The effects of three earthworm species on soil macroporosity and hydraulic conductivity, Appl. Soil Ecol. 10 (1998) 11–19.

[10] G.W. Gee, J.W. Bauder, Particle-size analysis, in: A. Klute (Ed.), Methods of Soil Analysis: Physical and Mineralogical, Methods, Soil Science Society of America, Madison, 1986, pp. 383–411.

[11] International Society of Soil Science (ISSS) Working Group R.B., World reference base for soil resources: introduction, in: J.A. Deckers, F.O. Nachtergaele, O.C. Spaargaren (Eds.), International Soil Reference and Information, Centre (ISRIC) and Food and Agriculture Organization of the United Nations (FAO), Acco. Leuven, 1998.

[12] K.E. Lee, Earthworms: Their Ecology and Relationships with Soils and Land Use, Academic Press, Sidney, 1985.

[13] B.F.J. Manly, Randomization and Monte Carlo Methods in Biology, Chapman and Hall, London, 1997.

[14] A. Martin, A. Mariotti, J. Balesdent, P. Lavelle, Estimate of soil organic matter assimilation of a geophagous tropical earthworm based on $\delta^{13}C$ measurements, Ecology 73 (1992) 118–128.

[15] J.N. Perry, Measures of spatial pattern for counts, Ecology 79 (1998) 1008–1017.

[16] J.N. Perry, L. Winder, J.M. Holland, R.D. Alston, Red-blue plots for detecting clusters in count data, Ecol. Lett. 2 (1999) 106–113.

[17] J. Phillipson, R. Abel, J. Steel, S.R.J. Woodell, Earthworms and the factors governing their distribution in an English beechwood, Pedobiologia (Jena) 16 (1976) 258–285.

[18] K.R. Poier, J. Richter, Spatial distribution of earthworms and soil properties in an arable loess soil, Soil Biol. Biochem. 24 (1992) 1601–1608.

[19] J.P. Rossi, Clusters in earthworm spatial distribution, Pedobiologia (Jena) 47 (2003) 490–496.

[20] J.P. Rossi, Short-range structures in earthworm spatial distribution, Pedobiologia (Jena) 47 (2003) 582–587.

[21] J.P. Rossi, The spatiotemporal pattern of a tropical earthworm species assemblage and its relationship with soil structure, Pedobiologia (Jena) 47 (2003) 497–503.

[22] J.P. Rossi, P. Lavelle, A. Albrecht, Relationships between spatial pattern of the endogeic earthworm *Polypheretima elongata* and soil heterogeneity, Soil Biol. Biochem. 29 (1997) 485–488.

[23] D.A. Wardle, P. Lavelle, Linkages between soil biota, plant litter quality and decomposition, in: G. Cadisch, K. Giller (Eds.), Driven by Nature: Plant Litter Quality and Decomposition, CAB-International, Wallingford, 1997, pp. 107–124.

[24] J.K. Whalen, C. Costa, Linking spatiotemporal dynamics of earthworm populations to nutrient cycling in temperate agricultural and forest ecosystems, Pedobiologia (Jena) 47 (2003) 801–806.