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Short-range structures in earthworm spatial distribution

Jean-Pierre Rossi

UMR 137 Biodiversité et Fonctionnement des Sols, IRD/Université Pierre et Marie Curie, 32 Avenue Varagnat, 93143 Bondy, France

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Summary

Populations of soil organisms and especially earthworms are spatially dependent at various scales. The present study was designed to assess the short-range spatial variability of different tropical earthworm populations in a savanna protected from fire for 15 years in the station d'Écologie Tropicale of Lamto (Côte d'Ivoire). Earthworms were sampled in 1995 and 1996 using 75 and 98 $25 \times 25 \times 10$ cm soil monoliths respectively. Sampling points were distributed along a transect with minimum inter-sample distance of 50 cm. The earthworms displayed clear spatial structures either when density or biomass were analysed. Some variograms displayed two plateaux thus indicating the presence of two distinct scales of spatial autocorrelation. However small the minimum sample spacing, the nugget variance remained high, which indicated the high value of residual, small-scale variability. SADIE analyses were used to test for statistical significance of the spatial aggregation and clusters description.

Key words: Earthworm, spatial distribution, short-scale, patch, gap

Introduction

The factors that govern the spatial patterning of earthworm populations are multiple and may be different according to the scale considered. Recent studies showed the complexity of soil biota spatial distribution and the potential consequences upon soil functioning (Ettema & Wardle 2002). Various studies illustrated the complexity of earthworm patterns (Phillipson et al. 1976; Poier & Richter 1992; Rossi et al. 1997; Nuutinen et al. 1998; Decaëns & Rossi 2001) and reported patches of several tens of metres. However, there is no data on the short-range spatial distribution of earthworms i.e. at the scale of 1–10 m. Exploring this scale can provide information on the within cluster distribution. Moreover this information may be useful to identify the factors responsible for the population spatial pattern and to design efficient sampling programmes. In addition short-range spatial variability may be favourably included in simulation models of earthworm population dynamics.

Materials and Methods

This survey was undertaken in a savanna protected from fire for 15 years in the station d'Écologie Tropicale of Lamto (Côte d'Ivoire). Earthworms were sampled in 1995 and 1996 using 75 and 98 $25 \times 25 \times 10$ cm soil monoliths respectively. Sampling points were distributed along a transect with minimum inter-sample

*E-mail: Jean-Pierre.Rossi@bondy.ird.fr

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distance of 50 cm. This short inter-sample distance lag was intended to provide information on the local earthworm distributions. The species density was recorded in both sampling campaigns whereas biomass was measured in 1996 only. In 1995 the sampling units were distributed on 2 aligned transects separated by 9 m.

Density and biomass data were analysed using geostatistics (variogram) in order to describe the spatial autocorrelation. Further statistical analyses were performed on the count data using the SADIE system (Perry et al. 1999). The SADIE analyses (Spatial Analysis using Distance IndicE) leads to a global index of spatial aggregation (I_a) and its associated randomisation statistical test. Further analyses using a second index (v_{ij}) allow to examine the presence of patches and gaps in the spatial distribution of the counts (Perry et al. 1999).

Results

The collected earthworms mainly belonged to 3 species all being members of the Eudrilidae family. *Hyperiodrilus africanus* Beddard, a medium sized epi-endogeic species (Tondoh 1998) and 2 small filiform endogeic species *Chuniodrilus ziaele* Omodeo and *Stuhlmannia porifera* Omodeo and Vaillaud were recorded. Given that distinguishing *C. ziaele* and *S. porifera* is not easy in the field and requires adult individuals they were grouped into a single category named “filiform Eudrilids”.

Descriptive statistics

In 1995 the density of *H. africanus* was 122 ind.m^{-2} with a standard deviation of 60 ind.m^{-2} and the density of the filiform Eudrilids was 154 ind.m^{-2} with a standard deviation of 157.6 ind.m^{-2}. For 1996 results about the filiform Eudrilids group density and biomass are reported. The density was 68.7 ind.m^{-2} (standard deviation = 48.8 ind.m^{-2}) with a total biomass of 2.1 g.m^{-2} (standard deviation = 1.67 g.m^{-2}). In addition the mean individual body mass of the filiform Eudrilids was estimated using the intact specimen (occasionally certain individuals are damaged during hand sorting and were therefore excluded from individual biomass estimation). It was 0.031 g per individual with a standard deviation of 0.021.

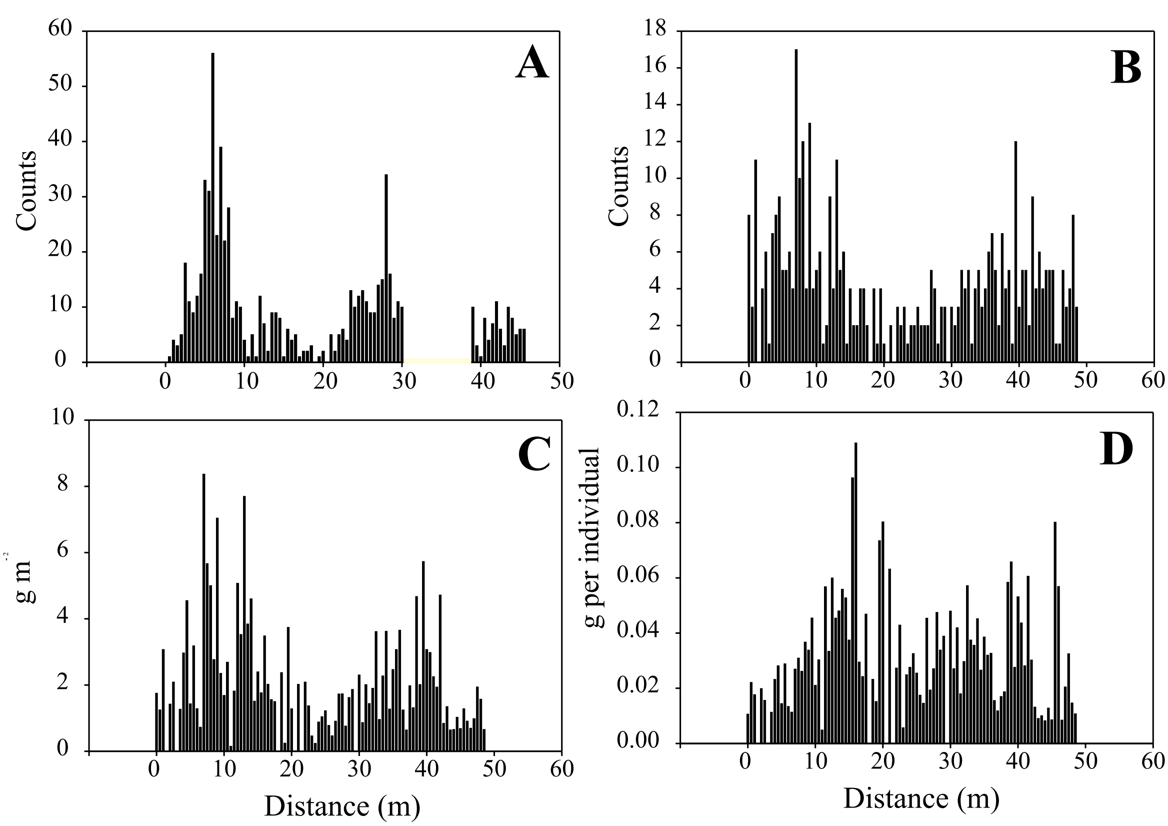

Fig. 1. Transect data for the filiform Eudrilidae (*Chuniodrilus ziaele* and *Stuhlmannia porifera*). A) counts in 1995 B) counts in 1996 C) total biomass in 1996 D) mean individual biomass in 1996. In 1995 no sample were collected between x = 30 and x = 39 m

Table 1. Variogram model parameters for the different variables under study log transformed data

Variables	Date	Model	Variance	Mean	Sill	Nugget C0	Structural C	Range (a)
Density (ind m^{-2})								
Filiform Eudrilidae	August 1996	Spherical #1	0.234	1.685	0.233	0.111	0.121	7.6
		Spherical #2	0.234	1.685	0.310	0.046	0.263	16.6
Filiform Eudrilidae	August 1995	Spherical	0.322	1.951	0.487	0.070	0.417	8.1
H. africanus	August 1995	Spherical	0.108	2.013	0.136	0.053	0.083	7.0
Mean individual biomass (g/individual)								
Filiform Eudrilidae	August 1996	Exponential	$7.8\ 10^{-5}$	$1.3\ 10^{-2}$	$7.5\ 10^{-5}$	$4.6\ 10^{-5}$	$2.8\ 10^{-5}$	2.3
		Spherical	$7.8\ 10^{-5}$	$1.3\ 10^{-2}$	$9.3\ 10^{-5}$	$3.2\ 10^{-5}$	$6.1\ 10^{-5}$	10.9
Total biomass (g m^{-2})								
Filiform Eudrilidae	August 1996	Spherical	0.048	0.433	0.058	0.034	0.024	13.8

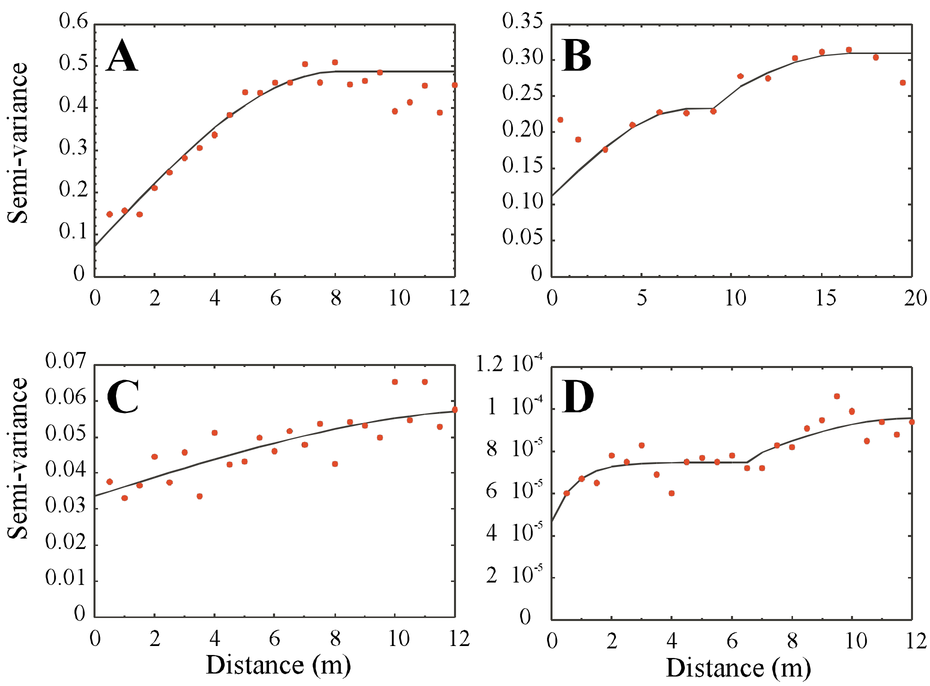

Fig. 2. Variograms of Log transformed data for the filiform Eudrilidae (*Chuniodrilus ziaele* and *Stuhlmannia porifera*). A) counts in 1995 B) counts in 1996 C) total biomass in 1996 D) mean individual biomass in 1996. Model parameters are given in Table 1

Geostatistics

The counts of species were spatially autocorrelated forming a succession of bumps for the filiform Eudrilids in 1995 and 1996 (Fig. 1) as well as for *H. africanus* in 1995 (not shown). Similar results were obtained for the total filiform Eudrilid biomass and mean individual biomass (Fig. 1).

All data sets were log transformed before analysis so as to improve data normality. Because some samples contained no individual the data were transformed as $x' = \log10(1+x)$. The variograms revealed the presence of a consistent spatial autocorrelation in all cases. The parameters of the theoretical models fitted to experimental variograms are given in Table 1. The variograms are shown in Fig. 2. The variograms for the filiform Eudrilids density (1996) and the mean individual biomass (1996) displayed a peculiar shape with two plateaux in the semi-variance (Fig. 2 and Table 1).

The variogram of the filiform Eudrilids and *H. africanus* density in 1995 were spherical with small ranges (Table 1). These results indicated that short-range spatial structures occurred which is not surprising given the clear pattern of raw data (Fig. 1).

In the case of the filiform Eudrilids density in 1996, the experimental variogram exhibited an unusual

Table 2. SADIE aggregation indices for the Eudrilids and *H. africanus*. I_a is a global index of aggregation and P_a is the associated probability based on 1560 random permutations. Mean v_j and mean v_i respectively represent the mean of the negative and positive index values that indicate gaps or patches. The indices were tested for departure from randomness using 1560 permutations and probabilities are indicated by P(mean v_j) and P(mean v_i)

	H. africanus (1995)	*Filiform* **Eudrilidae** (1995)	*Filiform* **Eudrilidae** (1996)
I_a	2.493	1.91	2.042
P_a	0.0071	0.0391	0.0314
Mean v_j	−2.147	−1.875	−1.586
P(mean v_j)	0.0205	0.0474	0.1038
Mean v_i	1.91	1.918	1.768
P(mean v_i)	0.0506	0.0526	0.0673

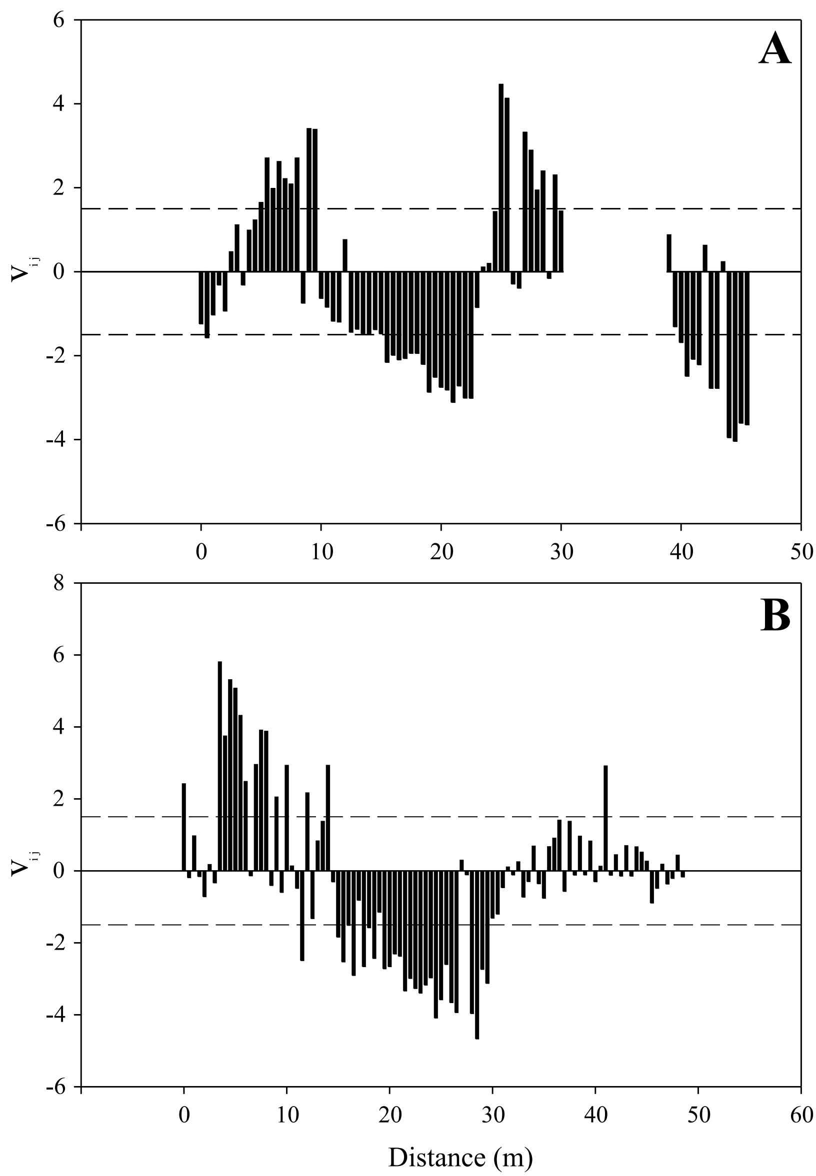

Fig. 3. Spatial variation of the SADIE cluster index (v_{ij}) for filiform Eudrilids in 1995 and 1996. Positive and negative values larger than 1.5 in absolute value respectively reflect the presence of patches and gaps in earthworm distribution. In 1995 no sample were collected between x = 30 and x = 39 m

shape. Two different sills emerged for ranges of 7.6 and 16.6 m. This is indicating two nested scales of variability. In addition the first 3 semi-variance values were higher than the following values. This pattern indicated that strong local discontinuities occurred at scales of 0.5 to 3 m.

The same global trends applied for the mean individual biomass variogram (Fig. 2) with 2 distinct ranges: 2.6 and 10.9 m (Table 1).

SADIE analyses

The global aggregation index I_a was tested using 1560 random permutations and proved to be significant for the 3 variables (counts of the filiform Eudrilids in 1995 and 1996 and *H. africanus* in 1995: Table 2). The local cluster index v_{ij} was estimated at each sample location and the mean of the negative (v_j) and positive (v_i) values were tested using 1560 random permutations. The v_i and v_j mean values were significant for the filiform Eudrilids and *H. africanus* counts in 1995 but not for the counts of filiform Eudrilids in 1996 (Table 2). This indicated that the latter distribution, although significantly aggregated (I_a) only featured moderately marked patches and gaps. Fig. 3 presents the spatial distribution of the v_i and v_j values of the filiform Eudrilids in 1995 and 1996. The negative (v_j) and positive (v_i) index values respectively indicate gaps and patches. Values larger than 1.5 in absolute values were taken as significant (Perry et al. 1999). Index values larger than 1.5 are grouped along the transect and indicate clusters of very different sizes. A succession of patches and gaps was observed (Fig. 3).

Discussion

The presence of short-range structures in the form patches and gaps (Sadie analyses) indicated that earthworm populations were spatially autocorrelated within the range of spatial scales commonly reported in the literature which is several tens of meters (Poier & Richter 1992; Rossi et al. 1995, 1997; Jiménez et al. 2001). Typically these structures constitute one source of the nugget variance of the variograms (Robertson 1987). However, the variograms reported here featured a somewhat high ratio of nugget variance to sill (Table 1). This result showed that a reduced inter-sample distance allowed to pick up short-scale clusters although there was an important proportion of unexplained variance. This term is due to the remaining local discontinuities that are easily seen in Fig. 1.

Biomass analyses also showed spatial dependence. Again, scales are short (a few meters as indicated by the variograms range (Table 1)). Mean individual biomass analysis also revealed the presence of autocorrelation with patches containing heavier individuals. Such pattern may reflect non-random distribution of earthworm cohorts. In that case, the presence of an alternation of patches of different age-class structures could reflect the result of population processes. However, the filiform Eudrilids variable encompassed two species and although their have comparable size, single species based data are necessary to further discuss that aspect of the population spatial pattern.

Nested structures were observed for the filiform Eudrilid density (1996) and mean individual biomass (1996) (Fig. 2; Table 1). Geostatistics (variogram) are well adapted to the detection of multiple scaling of spatial variability. The presence of different sills and ranges in some variograms clearly revealed these nested structures (Robertson & Gross 1994). At shorter scales (ca. 2 to 8 m., Table 1) the filiform Eudrilids distribution may be influenced by local factors like plant characteristics (identity, size, minimum distance to its closest neighbour and root architecture), soil local conditions (moisture) and microtopography. These factors together with intrinsic population processes constitute proximate controlling factors of population structure. At larger scales i.e. several tens of meters other factors are acting such as gradients in soil organic matter (quantity and or quality), texture, vegetation cover structure (Ettema & Wardle 2002). Available information in the literature mainly concerns that scale with studies reporting earthworm populations displaying patches of ca 20–30 m (Poier & Richter 1992; Rossi et al. 1995, 1997; Nuutinen et al. 1998; Jiménenz et al. 2001).

This study showed that earthworm populations were highly structured including autocorrelation at scales < 5–10 m. The Sadie analyses allowed a description of the nature and properties of the clusters forming the population spatial pattern. Both patches and gaps were reported and clearly exhibited very variable size. In this one-dimensional study it was not possible to fully investigate the shape and spatial pattern of clusters themselves. Further, a two-dimensional survey with small inter-sample distance would certainly elucidate more completely the population structure within patches and gaps as well as the cluster distribution.

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