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RELATIONSHIPS BETWEEN SPATIAL PATTERN OF THE ENDOGEIC EARTHWORM *POLYPHERETIMA ELONGATA* AND SOIL HETEROGENEITY

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Summary—Spatial distribution of the endogeic earthworm *Polypheretima elongata*, soil texture, carbon and nitrogen contents were investigated in a 10-y-old pasture established on a vertisol, by measuring each variable at 57 points randomly located in a 25 × 60 m plot. Soil variables were measured at three depths: 0–10, 10–20 and 20–30 cm. Principal component analysis (PCA) of the data set showed the absence of relationships between density of *P. elongata* and environmental variables. The first principal component expressed a marked gradient of soil texture and soil organic matter (SOM). Sampling point coordinates on the first principal component axis were used as a composite variable assumed to account for the major source of soil heterogeneity at this site. The spatial pattern of this variable and three age classes of *P. elongata* were investigated using geostatistics. There was no evidence of any relationship between soil heterogeneity and earthworm distribution. Population of *P. elongata* exhibited a marked patchy distribution with opposite patterns between adults and other age classes (juveniles and cocoons). These results suggest that at the study site processes responsible for the spatial distribution of *P. elongata* population are of demographic rather than environmental origin. © 1997 Elsevier Science Ltd

INTRODUCTION

Patterns of the horizontal distribution of earthworm populations and communities have rarely been assessed. Satchell (1955), Phillipson *et al.* (1976), Lavelle (1978), and Fragoso and Lavelle (1987) have described heterogeneous distributions in a temperate pasture, a beech wood (*Fagus sylvatica*), an African savanna and a tropical rainforest, respectively. Phillipson *et al.* (1976) found some correlations between species distribution and such soil characters as depth, bulk density, water content and litter standing crop. In the savanna, Lavelle (*loc. cit.*) devised the importance of the microrelief influencing drainage as a factor controlling earthworm distribution. In agroecosystems of Germany, Poier and Richter (1992) found relationships between soil organic carbon and both the density and biomass of *Lumbricus terrestris* in an arable loess soil and a correlation of aggregate density in the A1 horizon with *L. terrestris* (positive) and *Allolobophora* species (negative).

It is likely, however, that the spatial distribution of earthworms is also determined by biotic constraints. S. Martin (unpub. Ph.D. thesis, University of Paris VI 1991) running the simulation model DRILOTROP for 50 successive years formulated

the hypothesis that intrinsic properties of earthworm population dynamics might result in a patchy distribution, irrespective of the heterogeneity of the soil environment.

Our study was designed to test the latter hypothesis by investigating the spatial distribution of the tropical earthworm *Polypheretima elongata* and associated soil factors. The study site was a pasture located in south Martinique (FWI) in an area where only *P. elongata* is present and reaches biomass of ca. 3t ha⁻¹ at the rainy season (Barois *et al.*, 1988).

MATERIALS AND METHODS

Research was conducted at the S.E.C.I. (Station d'Essais en Culture Irriguées, Ste. Anne, Martinique). In a 10-y-old pasture established on a vertisol and regularly planted with the tropical grass *Digitaria decumbens*, 57 points randomly distributed across a 60 × 25 m² plot were sampled for earthworm population and soil variables in June 1992. Earthworms were handsorted out of 25 × 25 × 30 cm³ monoliths and allocated to three broad age classes, i.e. adults + sub-adults, juveniles and cocoons. Soil parameters were, respectively, measured at 0–10, 10–20 and 20–30 cm depth. Organic carbon and nitrogen contents were measured by a dry method using a Nitrogen

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Carbon Sulfur Analyser NA 1500 (Carbo Erba Instruments). The soil texture was determined by laser granulometry (Mastersizer E, Malvern). Soil depth down to the bedrock was measured.

Soil variables, i.e. clay, fine silt, coarse silt, fine sand and coarse sand contents (%), total carbon and nitrogen (%), carbon-to-nitrogen ratio in each of the three layers and depth (cm) down to the bedrock were processed using a standardized Principal Component Analysis (Webster and Oliver, 1990) with the software MacMul (Thioulouse, 1989, 1990). Biological variables (i.e. adult + sub-adults, juvenile and cocoon density (ind m⁻²) were standardized and projected onto the plane defined by the first two principal components obtained by PCA to examine relationships between earthworm densities and environmental variables.

Additional information was obtained by geostatistical analysis of the respective distribution of adult, juvenile, cocoon and total hatched population densities. Spatial structures were searched for using semi-variance analysis, and block kriging interpolation procedure (block size = 2 × 2 m²) allowed us to estimate variables at unsampled locations (Webster, 1985). Because of the large range in the earthworm densities, nonstationarity of the data seemed possible. Therefore, prior to estimate semi-variograms, two-dimensional polynomials of first and second degrees were fitted to original data. In spite of significant polynomial trends in the data

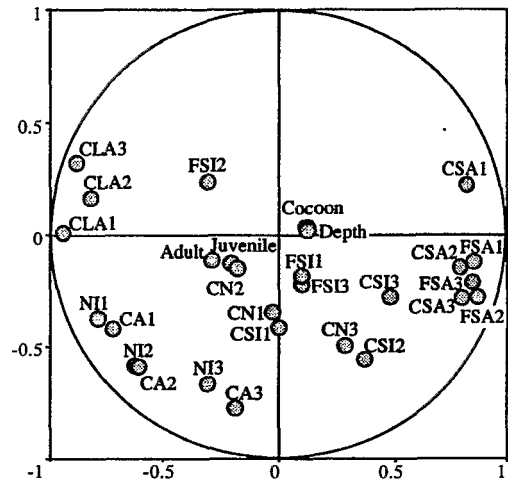


Fig. 1. Projection of variables on the plane determined by principal components 1 (horizontal) and 2 (vertical) extracted from PC analysis of soil data. CLA: Clay content; FSI: fine silt; CSI: coarse silt; FSA: fine sand; CSA: coarse sand; CA: carbon; NI: nitrogen; CN: C-to-N ratio; 1: 0–10 cm depth layer; 2: 10–20 cm; 3: 20–30 cm.

sets, semi-variograms were very similar to the originals and further analysis were thus performed on original data.

The first principal component (PC1), which accounted for a large part of the total variance of

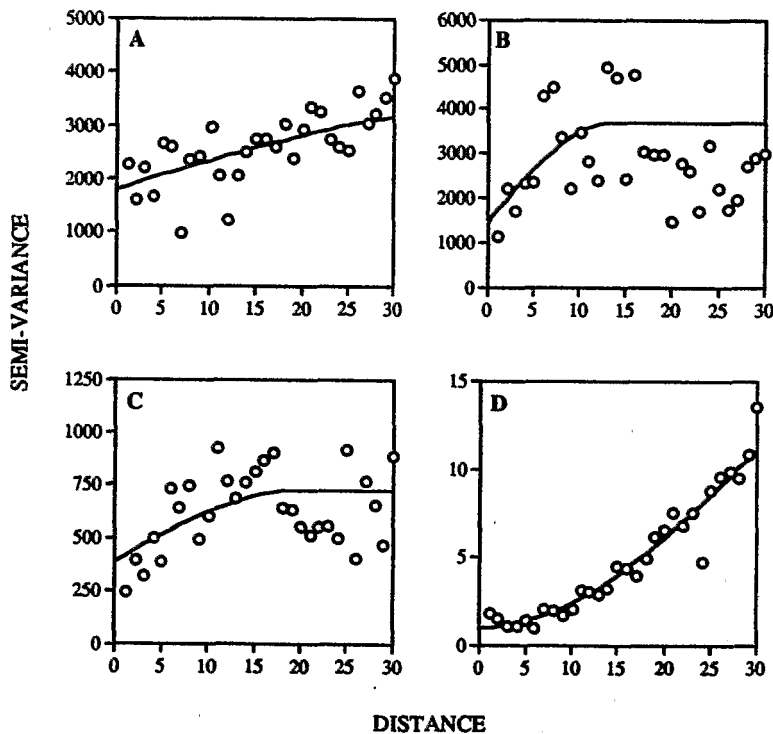


Fig. 2. Semivariograms calculated for (A): adults + sub-adults; (B): juveniles; (C): cocoons, and (D): environmental gradient (PC1). Distances are expressed in metres.

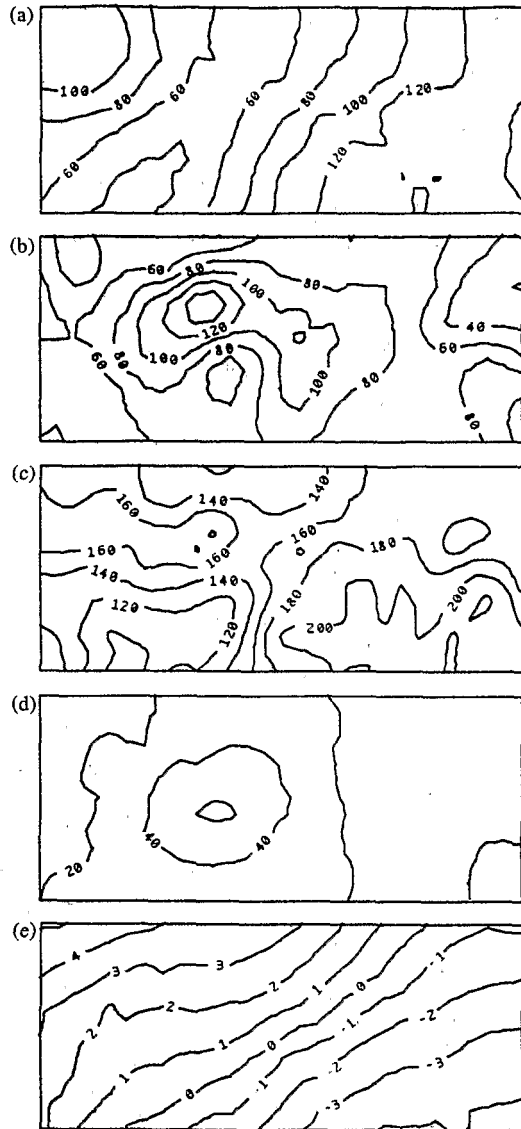


Fig. 3. Contour maps of horizontal distribution of (A): adults + sub-adults, (B): juveniles, (C): total hatched population, (D): cocoons, (E): environmental gradient (PC1). Earthworm densities are expressed in individuals per m^2 .

the environmental data, was also submitted to geostatistical treatments.

RESULTS

The first principal component (PC1) accounted for 36.5% of the total variance, while PC2 and PC3, respectively, accounted for 14.2 and 8.7%. PC1 essentially reflected a gradient of texture and SOM (Fig. 1) since it, respectively, opposed coarse silt and sand contents to clay contents in the three layers and carbon and nitrogen contents in layer 1 (0–10 cm depth) and 2 (10–20 cm depth).

Earthworm densities of all age classes are close to the origin of the axes on the plane defined by PC1 and PC2 (Fig. 1). This means that no peculiar association exists between earthworm density and soil heterogeneity described by PC1 and PC2.

Coordinates of the sampling points on PC1 were used as measures of a random variable and analysed with geostatistics, like earthworm density.

Semi-variograms were estimated using the programme VAR5 (Yost *et al.*, 1989), which is part of the statistical package developed by the University of Hawaii. Adult + sub-adult, juvenile, cocoon (Fig. 2) and total hatched population densities (not shown) of *P. elongata* yielded bounded sample semi-variograms that were adjusted to a spherical model using the modified least square fitting procedure (Cressie, 1985) of the programme VAR5 (Yost *et al.*, 1989) (Fig. 2). PC1 was spatially structured since the semi-variogram calculated with PC1 values at each sampling points exhibited a clear slope. A Gaussian model was fitted to the estimated semi-variogram and cross validation procedure was used to determine parameters of the model (Simard *et al.*, 1992).

A block kriging procedure was then used to estimate variables in $2 \times 2 m^2$ blocks. Data sets resulting from that operation were used to draw contour maps (Fig. 3). Adult *P. elongata* were concentrated in two large patches with very high density separated by an area with a much lower density (Fig. 3-A). The densities of juveniles and cocoons showed a different pattern (Fig. 3C, D) since a large patch with highest density was located approximately in the center of the area studied. Places where adult earthworms reach their maximum values correspond to areas of lower cocoon and juvenile density. The sum of all post cocoon stages reached its maximum density in two areas located in the right and top left parts of the field (Fig. 3B). The contour map of PC1 (Fig. 3E) reflects the gradient in soil texture and SOM due to slope effect. Negative values of PC1 correspond to high clay and SOM contents in the three layers, especially in the 0–20 cm depth layer, as opposed to positive values that indicate high sand contents.

DISCUSSION

P. elongata was clearly distributed in clumps of 20–30 m dia with different demographic structures. The occurrence of such patches has already been observed in a large variety of ecosystems such as temperate (Satchell, 1955) and tropical pastures (this study and Jimenez Jaen J.J., Rossi J.P., Moreno A. and P. Lavelle, unpub. data), temperate (Phillipson *et al.*, 1976) and tropical forests (Charpentier F., Granval A., Rossi J.P., Leroy-Guillaume C. and P. Lavelle, unpub. data), agroecosystems (Poier and Richter, 1992) and a tropical

savanna (Lavelle, *loc. cit.*). Adult stage of *P. elongata* was not spatially structured in relation to SOM and clay gradient. They were concentrated in two patches, one located in the upper left part of the plot where PC1 values are positive and maximum whilst the second was situated in the right part of the plot where PC1 reaches its minimum values corresponding to the largest clay and SOM contents. Distribution of juveniles and cocoons did not either relate with the clay and SOM gradient. On the contrary, a clear negative relationship exists between adult and juvenile or cocoon density. The map of the total hatched population reflects the superimposed patterns of adult and juvenile stages and again, there is no evidence for any relation with environmental gradient. Demographic processes such as intra-specific competition may lead to decreasing fecundity in places where adult density is high and thus decreasing juvenile and cocoon density. This might explain the lack of synchrony observed in population dynamics at the scale of 30–50 m dia. These patches are expected to move in time, and in the long-term, relationships between densities cumulated over time and soil variables might exist. Long-term observations of the spatial distribution of populations will allow this hypothesis to be tested.

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