ELSEVIER

Applied Soil Ecology 7 (1998) 195–199

Applied Soil Ecology

Earthworm aggregation in the Savannas of Lamto (Côte d'Ivoire)

Jean Pierre Rossi *, Patrick Lavelle

Laboratoire d'Ecologie des Sols Tropicaux, ORSTOM / Université Paris 6, 32 Av. Varagnat, 93 143 Bondy Cedex, France

Received 25 July 1996; accepted 20 March 1997

Abstract

The spatial distribution of seven earthworm species from the Lamto savannas (Côte d'Ivoire) was investigated by Taylor's Power Law. The method yielded aggregation indices highly correlated with species demographic and morphological parameters. A Principal Component Analysis showed that the smaller an earthworm species was and the higher its annual fecundity, the more its spatial distribution was aggregated. Mapping of some species density showed the diversity of spatial patterns in the field. © 1998 Elsevier Science B.V.

Keywords: Earthworm; Spatial pattern; Taylor's Power Law; Savanna; Côte d'Ivoire

1. Introduction

Living organisms are generally distributed neither at random nor regularly. Many studies have demonstrated the clumped nature of organisms' spatial distribution irrespective of the kind of organism or the ecosystem considered. The spatial heterogeneity of populations and communities is an important issue in soil ecology. Basically three kinds of pattern may be distinguished: regular, random and clumped. Many organisms living in the soil display aggregated (clumped) distributions, e.g., earthworms (Poier and Richter, 1992; Rossi et al., 1997) and nematodes (Webster and Boag, 1992; Wallace and Hawkins, 1994; Robertson and Freckman, 1995; Rossi et al., 1996). Beyond the clumped nature of the distribution, assessment of pattern complexity requires mapping of the populations. The aim of this work was first to investigate the spatial distribution of the seven species forming the earthworm community in the savannas of Lamto (Côte d'Ivoire). In addition, several maps of the various species were established to describe the pattern at the field scale. Finally, the possible relationships between the aggregation index and the main biological parameters that determine ecological categories of earthworm species were assessed.

2. Materials and methods

2.1. Study site

This study was carried out at Lamto, Côte d'Ivoire (5°02′W, 6°13′N). The climate is characterized by a high mean annual temperature (28°C) and irregular rainfall (average 1300 mm year^{-1}) with a dry season

* Corresponding author. Tel.: +33-0-1-48-02-55-01; fax: +33-0-1-48-47-30-88; e-mail: rossijp@bondy.orstom.fr.

0929-1393/98/$19.00 © 1998 Elsevier Science B.V. All rights reserved.
PII S0929-1393(97)00033-4

from November to March and in August. Most soils lie on a granitic bedrock and are classified as Ferralsol (F.A.O. classification). The vegetation is a mosaic of grass and shrub savannas and forest patches. The savannas are maintained by annual burning. Three savanna types were investigated: a grass savanna, a shrub savanna and a savanna which had been protected from fire for 12 years.

In this paper we use data recorded in 1971 and 1972 by Lavelle (1978) to assess earthworm aggregation. Data collected by Rossi in 1994 and 1995 (Rossi, unpublished) were used to build earthworm maps and to illustrate their pattern at the field scale.

2.2. Sampling design

The Lavelle (1978) data were collected by sampling the three savanna types mentioned above each month from June 1971 to December 1972 by means of 12 monoliths ($100 \times 100 \times 60$ cm) randomly distributed in the different sites. The earthworms were handsorted (Lavelle, 1978).

Earthworm spatial pattern was investigated by analysing 100 sampling points regularly distributed on a square grid with 5 m sides. Earthworms were sampled in July 1994, and May and November 1995. A $25 \times 25 \times 10$ cm monolith was taken at each sampling point and the earthworms were handsorted.

2.3. Statistical analysis

Aggregation of earthworm populations was quantified using Taylor's Power Law (Taylor, 1961; Taylor et al., 1978; Taylor, 1984). The method is based on an empirical relationship between the mean (m) and the variance (s^2) which appear to be related by a simple power law:

$$s^2 = am^b$$

The parameters a and b are population parameters. b is considered to be an intrinsic measure of population aggregation varying continuously from zero for regular distribution ($s^2 = a$ with $a < 1$) through 1 for random distribution ($s^2 = m$ with $a = 1$) to ∞ for highly clumped distribution (Taylor, 1961).

The parameter a is a scaling factor depending chiefly upon sample unit size (Taylor, 1961; Elliot, 1971). The exponent b is considered to be a true population statistic and is used as an aggregation index. The factors affecting the mean density are absorbed in a if they are proportional or in b if they are specific. Moreover, b is assumed to be independent of the mean and is thus a value measuring aggregation without being modified by mean density of the population under study (Taylor, 1971, 1984; Taylor et al., 1988).

The parameters a and b are determined by linear regression of sample means and variances after the data are log-transformed:

$$\log s^2 = \log a + b \log m$$

Taylor's power law was applied to the data from Lavelle (1978). For each earthworm species the data pairs used for regression analysis were the means and variance of 12 monoliths, independent of savanna type and sampling date.

Mesh maps of the earthworm density were generated from a data grid formed by values interpolated using the Weighted Moving Averages method (see e.g., Burrough, 1987, pp. 237–239). The weighted moving average is computed as:

$$\hat{Z}(x_0) = \sum_{1=1}^{n} w_i Z(x_i) / \sum_{i=1}^{n} w_i$$

where $\hat{Z}(x_0)$ is the estimate of the variable Z at point x_0, $Z(x_i)$ the sample value of the variable at point x_i, n the number of sample points used in the estimation procedure and w_i the weighting coefficients applied to the $Z(x_i)$ values. The weights are given by a function of the distance between x_0 and x_i. We used the inverse squared distance weighting:

$$\hat{Z}(x_j) = \sum_{i=1}^{n} \left[Z(x_i)/d_{ij}^2 \right] / \sum_{i=1}^{n} \left(1/d_{ij}^2 \right)$$

where the x_j are the points at which the variable is estimated and d_{ij} is the distance between x_i and x_j.

The relationships between the earthworms spatial dispersion and their morphological and life history traits were assessed by performing a standardized Principal Component Analysis (PCA) (Webster and Oliver, 1990) on the following parameters: annual fecundity, average fresh weight, average juvenile and adult length, growth period, life expectancy, vertical distribution and length to width ratio (data from Lavelle, 1973, 1979) and the index of aggregation. Table 1 lists the variables included in the standardized PCA and their abbreviations. In a standardized PCA, the data are normalized and thus the variances are equal to 1 while means are equal to zero for all variables. The eigenvalues are directly linked to the proportion of the total inertia that is accounted for by the factorial axes. Then, an eigenvalue greater than 1 corresponds to a factorial axis accounting for an amount of variability greater than any of the original variables do. A factorial axis is then taken as signifi-

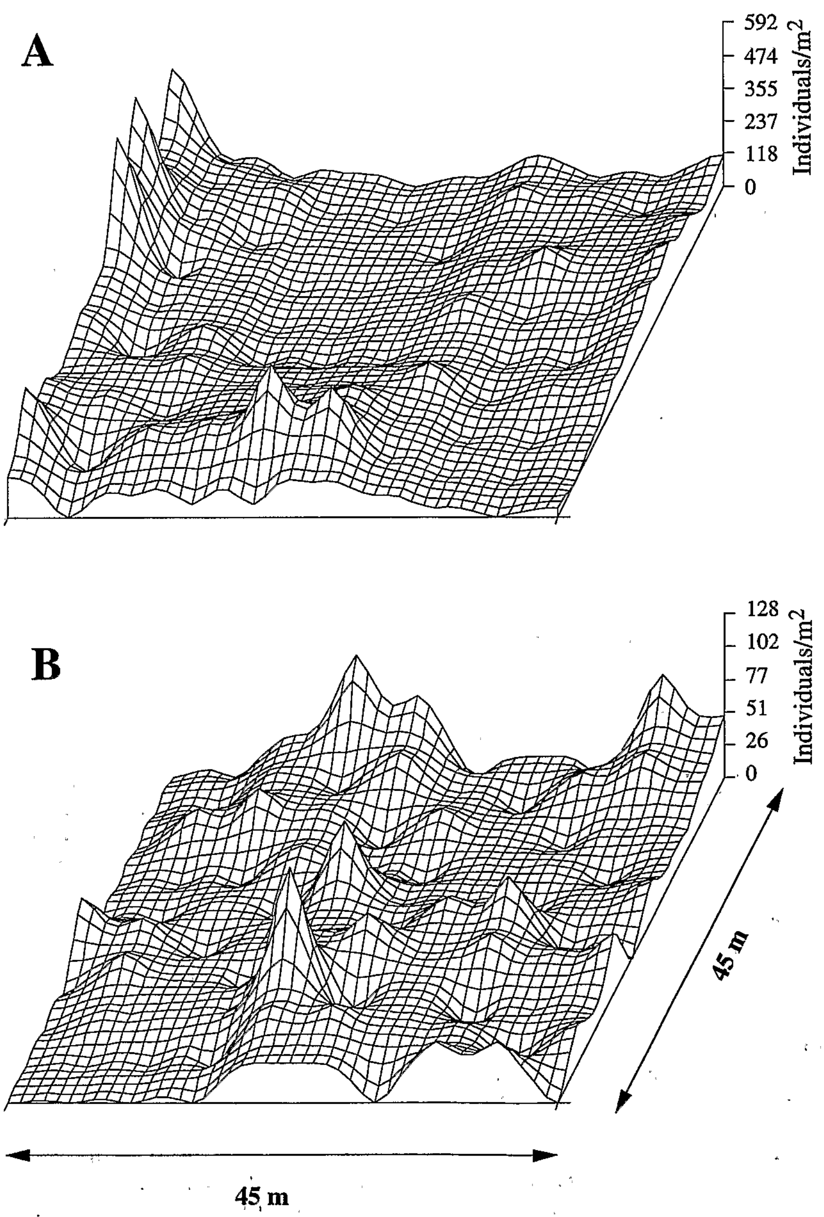

Fig. 1. (A) Map of the earthworm *Chuniodrilus zielae* density and (B) map of *Millsonia anomala* (juvenile) density in the grass savanna of Lamto.

Table 1
Variables included in the standardized PCA and their abbreviations

Variable	Abbreviation
Aggregation index	Agg
Annual fecundity	AFe
Average fresh weight	AFW
Average juvenile length	AJL
Average adult length	AAL
Growth period	GPE
Life expectancy	Lex
Vertical distribution in soil (average annual depth)	VDi
Length:Width ratio	L:W

cant provided its associated eigenvalue is greater than 1.

3. Results

3.1. Taylor's Power Law and aggregation

Seven earthworm species were investigated using the Taylor's Power Law. These comprised two epigeic species, (*Dichogaster agilis* (Omodeo and Vaillaud) and *Millsonia lamtoiana* (Omodeo and Vaillaud)), two polyhumic species (*Agastrodrilus opisthogynus* (Omodeo and Vaillaud) and *Chuniodrilus zielae* (Omodeo)), one mesohumic species (*Millsonia anomala* (Omodeo)) and two oligohumic species (*Dichogaster terrae nigrae* (Omodeo and Vaillaud), *Millsonia ghanensis* (Sims)). In each case, the slope of the log–log regression of the mean against the variance was highly significantly different from 0 ($P < 0.0001$). Table 2 gives the values of the index of aggregation.

Table 2
Taylor's Power Law parameters for a range of African earthworm species (standard error in parentheses)

Species	b value
Agastrodrilus opisthogynus (Omodeo and Vaillaud)	1.140 (0.130)
Dichogaster agilis (Omodeo and Vaillaud)	1.324 (0.084)
Dichogaster terrae nigrae (Omodeo and Vaillaud)	1.121 (0.069)
Chuniodrilus zielae (Omodeo)	1.724 (0.169)
Millsonia anomala (Omodeo)	1.626 (0.221)
Millsonia ghanensis (Sims)	1.025 (0.076)
Millsonia lamtoiana (Omodeo and Vaillaud)	1.026 (0.007)

3.2. Earthworm maps

Only results obtained in the grass savanna are presented here. The map (Fig. 1A) of earthworm density shows the presence of large patches of ca. 20 m in diameter for *C. zielae*. The map for *M. anomala* (Fig. 1B) illustrates the alternating peaks and troughs often observed in earthworm spatial patterns (Rossi et al., 1997).

3.3. Principal component analysis

The analysis was performed with the software MacMul (Thioulouse, 1989, 1990). Only the first two axes accounted for a significant part of the total inertia (eigenvalues ≥ 1 respectively corresponding to 62.8% and 23.3% of the total inertia) (Fig. 2A).

PC1 shows the opposition between the variables fecundity and aggregation against life expectancy, growth period and species length (Fig. 2A).

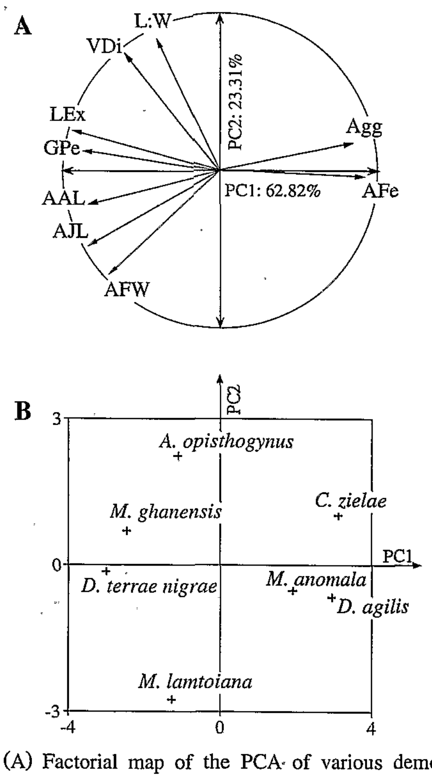

Fig. 2. (A) Factorial map of the PCA of various demographic morphological earthworm parameters and the Taylor's Power Law index of aggregation (see Table 1 for abbreviations) and (B) projection of the earthworm species onto the principal components PC1 and PC2.

Along PC2, the variables Length:Width ratio and vertical distribution are opposite to the average weight. PC2 shows the effect of the form and size of the earthworm species since L:W ratio and AFW are strongly correlated with that axis.

The ordination of the seven species on PC1 and PC2 shows a grouping of species with high aggregation index and fecundity on the right hand side in contrast to species with low aggregation, large size and long growth periods on the left side of PC1 (Fig. 2B).

PC2 segregates species in function of their shape (i.e., high L:W ratio: *A. opisthogynus* against low L:W ratio *M. lamtoiana*), separating smaller from larger species. The species spatial patterning has no effect on PC2 as the coordinates of the variable 'aggregation' along this axis are very low.

4. Discussion

The measurement of spatial distribution by the Taylor Power Law index provides values highly correlated with demographic and morphological variables and particularly with fecundity.

These results show that the smaller a species is and the higher its fecundity, the more it is aggregated. By contrast, large sized species that have a lower fecundity rate display spatial distribution close to random (i.e., b values close to 1).

These b values were estimated by computing the index from samples recorded in various savannas and at different dates, and hence may be taken as species specific (Taylor et al., 1988). The maps of earthworm density reveal the diversity of aggregated patterns and furnish complementary information. Our results indicate that the spatial dispersion of a given species is related to its life history and morphological traits and hence may be included in the definition of ecological categories.

Acknowledgements

We thank Raphaël Zouzou Bi Danko for field assistance in Lamto and two anonymous referees for detailed comments on an earlier draft.

References

Burrough, P.A., 1987. Spatial aspects of ecological data. In: Jongman, R.H., ter Braak, C.J.F., van Tongeren, O.F.R. (Eds.), Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen, pp. 213–251.

Elliot, J.M., 1971. Some Methods for Statistical Analysis of Samples of Benthic Invertebrates. Freshwater Biological Associates, The Ferry House, Ambleside, UK, 144 pp.

Lavelle, P., 1973. Peuplement et production des vers de terre dans les savanes de Lamto. Ann. Univer. Abidjan série E, Tome VI: 79–98.

Lavelle, P., 1978. Les Vers de Terre de la savane de Lamto (Côte d'Ivoire): peuplements, populations et fonctions dans l'écosystème. Publ. Lab. Zool., ENS, 12, 301 pp.

Lavelle, P., 1979. Relations entre types écologiques et profils démographiques chez les vers de terre de la savane de Lamto (Côte d'Ivoire). Rev. Ecol. Biol. Sol. 16, 85–101.

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

Robertson, G.P., Freckman, D., 1995. The spatial distribution of nematode trophic groups across a cultivated ecosystem. Ecology 76, 1425–1432.

Rossi, J.P., Delaville, L., Quénéhervé, P., 1996. Microspatial structure of a plant-parasitic nematode community in a sugarcane field in Martinique. Appl. Soil Ecol. 3, 17–26.

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

Taylor, L.R., 1961. Aggregation, variance and the mean. Nature 189, 732–735.

Taylor, L.R., 1971. Aggregation as a species characteristic. In: Patil, G.P., Pielou, E.C., Waters, W.E. (Eds.), Statistical Ecology Volume 1: Spatial Patterns and Statistical Distributions. Pennsylvania University Press, University Park, pp. 357–377.

Taylor, L.R., 1984. Assessing and interpreting the spatial distributions of insect populations. Ann. Rev. Entomol. 29, 321–357.

Taylor, L.R., Woiwod, I.P., Perry, J.N., 1978. The density-dependence of spatial behaviour and the rarity of randomness. J. Anim. Ecol. 47, 383–406.

Taylor, L.R., Perry, J.N., Woiwod, I.P., Taylor, R.A.J., 1988. Specificity of the spatial power-law exponent in ecology and agriculture. Nature 332, 721–722.

Thioulouse, J., 1989. Statistical analysis an graphical display of multivariate data on the Macintosh. CABIOS 5, 287–292.

Thioulouse, J., 1990. Macmul and Graphmu: two Macintosh programs for the display and analysis of multivariate data. Comp. Geosci. 16, 1235–1240.

Wallace, M.K., Hawkins, D.M., 1994. Applications of geostatistics in plant nematology. J. Nematol. 26, 626–634.

Webster, R., Boag, B., 1992. Geostatistical analysis of cyst nematodes in soil. J. Soil Sci. 43, 583–595.

Webster, R., Oliver, M.A., 1990. Statistical Methods in Soil and Land Resource Survey. Oxford Univ. Press, Oxford, 316 pp.

pour celui-là
rempli l'AMS
/1 LEST etc

Reprinted from

Applied Soil Ecology

A section of Agriculture, Ecosystems & Environment

Applied Soil Ecology 7 (1998) 195–199

Earthworm aggregation in the Savannas of Lamto (Côte d'Ivoire)

Jean Pierre Rossi *, Patrick Lavelle

Laboratoire d'Ecologie des Sols Tropicaux, ORSTOM / Université Paris 6, 32 Av. Varagnat, 93 143 Bondy Cedex, France

Received 25 July 1996; accepted 20 March 1997

Fonds Documentaire ORSTOM
010012717

ELSEVIER

Fonds Documentaire ORSTOM
Cote : B*12717 Ex : 1