



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

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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.

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 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

from November to March and in August. Most soils lie on a granitic bedrock and are classified as Ferral-sol (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 Data collected by Rossi in 1994 and 1995 (Rossi, unpublished) were used to build earthworm maps and to illustrate their pattern at the field scale.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 × 100 × 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 × 25 × 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:

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

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:

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

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-

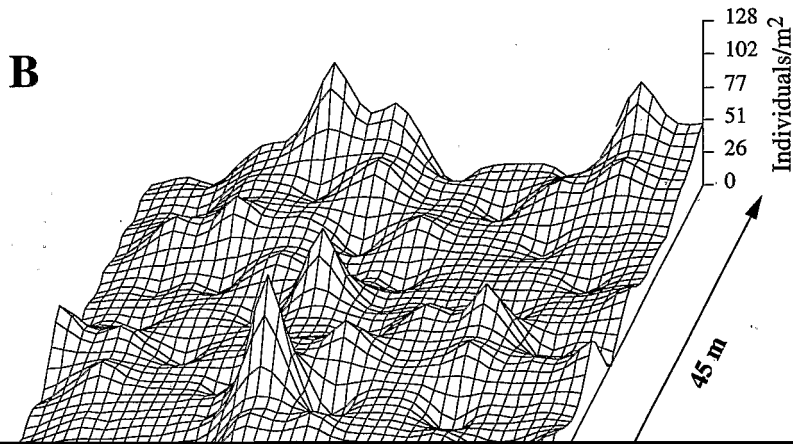
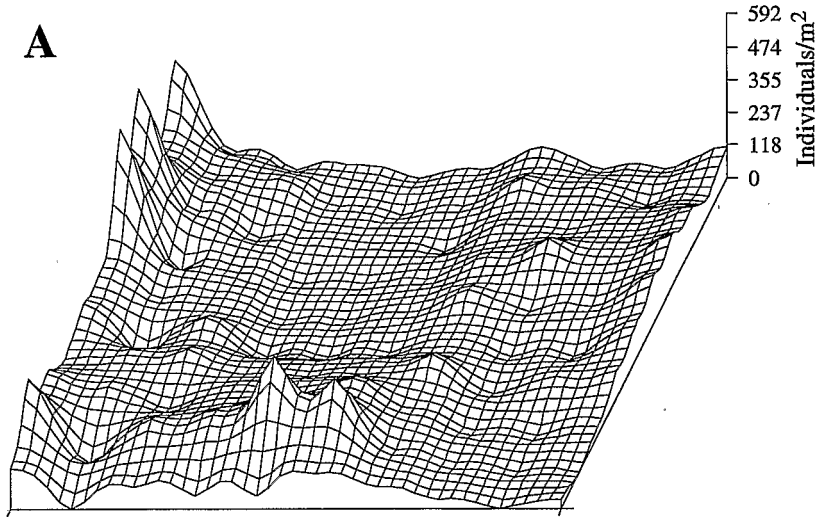


Table 1
Variables included in the standardized PCA and their abbreviations

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	<i>b</i> value
<i>Agastrodrilus opisthogynus</i> (Omodeo and Vaillaud)	1.140 (0.130)
<i>Dichogaster agilis</i> (Omodeo and Vaillaud)	1.324 (0.084)
<i>Dichogaster terrae nigrae</i>	1.121 (0.069)

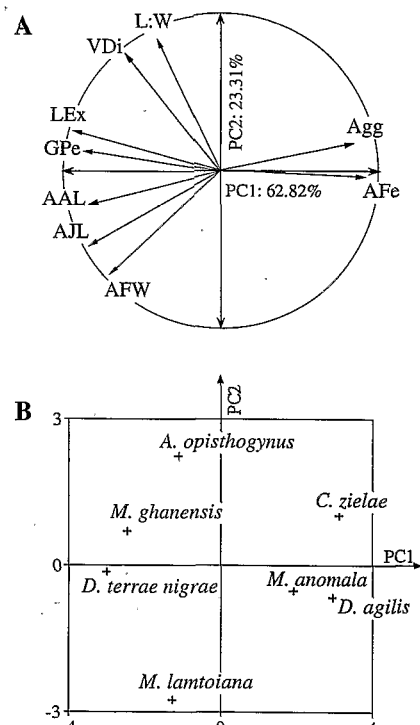
3.2. Earthworm maps

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).



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.

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