Spatio-temporal structure of earthworm community and soil heterogeneity in a tropical pasture

Thibaud Decaëns and Jean Pierre Rossi

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The spatio-temporal structure of an earthworm community was assessed in a tropical Colombian pasture and compared with the patterns of soil heterogeneity. Earthworms were sampled at six dates during a period of one year, while soil properties were assessed at a single date at the end of this period. Sample design was spatially explicit and consisted in a regular grid of 5 m mesh. At each date, 120 samples were taken for earthworm evaluations, while the single soil sampling consisted in 60 points. Multivariate and geostatistical analyses were performed to describe the spatial structure of collected data. Mantel and partial Mantel's tests were used to assess the links between the spatio-temporal patterns of earthworm distribution and soil heterogeneity.

The results clearly demonstrated the existence of structured spatial patterns in the earthworm community which were stable in time, at least at the temporal scale concerned by the study period. It mostly corresponded to an alternation of patches where particular species assemblages dominated. The ecological significance of these assemblages is discussed. Soil properties also displayed a significant spatial organisation. Only a small part of the spatio-temporal structures of earthworm distribution was correlated with soil properties. Small species were more abundant in patches where soil was more compact, while large species were associated with high root biomass and total C levels. The question whether earthworm spatio-temporal distribution induces similar patterns in soil properties or the contrary occurs is discussed. Our results suggest that earthworm community organisation mostly corresponds to a non-equilibrium system where mobile earthworm populations influence soil properties. The overall effect of earthworm community on soil is difficult to assess due to the predominance of factors that preferentially express themselves at large scales in the ecological hierarchy.

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Soil processes have a central regulatory function for most biogeochemical cycles in terrestrial ecosystems (Swift et al. 1979, Anderson and Flanagan 1989). The role played by large soil dwelling macroinvertebrates (e.g. earthworms, termites, ants) in these cycles has been widely recognised (Lavelle et al. 1993), and these organisms have been defined as ecosystem engineers (Jones et al. 1994). They produce physical structures (e.g., casts, mounds, galleries) that are specific sites of regulation for important macroscale soil processes (An-

derson 1995, Lavelle 1996) and that may influence the abundance and/or the community structure of other soil organisms. Jones et al. (1994, 1997) pointed out the need to assess the spatial patterns of engineer population in order to obtain a good understanding of their functional importance.

Earthworms are known to influence soil processes and properties at different scales of time and space (Syers and Springett 1984, Lavelle et al. 1992). Their casts are organo-mineral aggregates generally of higher

structural stability than soil aggregates (Lal and Akin-remi 1983, Lee and Foster 1991, Blanchart et al. 1997). Mineralisation of organic matter is enhanced in fresh casts, while depleted or even inhibited in dry casts (Martin 1991, Lavelle et al. 1998). It has been demonstrated that simplified species assemblages may have significant effects on soil properties and plant growth in microcosm conditions (Haimi and Huhta 1990, Bohlen and Edwards 1995, Derouard et al. 1997). On the other hand, there is a lack of information concerning possible in situ impacts of complex communities at larger spatio-temporal scales.

At the spatial scale of a few ten of metres, the distribution of soil fauna is often spatially aggregated (Webster and Boag 1992, Robertson and Freckman 1995, Rossi et al. 1995, 1997). Organisation patterns, even if they vary from one species to another, are mainly oppositions or alternations between patches of high density and others of lower density. The scale at which this heterogeneity occurs is generally < 100 m, ranging from 20 to 40 m for earthworms, but short-range structures may be present at scales of $2–10$ m (Rossi 1998). Factors inducing this relative ordering of spatial structures are largely unknown. They are likely to be complex, and may involve the influence of environmental heterogeneity and demographic parameters of populations per se (Rossi et al. 1997).

It has been recently demonstrated that spatial patterns of earthworm communities present a relative temporal stability, at least during a period of one or two years (Rossi 1998, Jiménez 1999). In some situations, spatio-temporal structures result in an alternation of areas where specific species assemblages or functional groups dominate. As a consequence, different patches may correspond to different effects on soil properties and plant growth (Rossi 1998). Therefore, the functional role of the spatio-temporal organisation of the community may play a regulatory role for some aspects of soil functioning at important spatio-temporal scales of observation (Rossi 1998).

The aim of this study was to assess the possible relationships between the spatio-temporal organisation of an earthworm community and the spatial heterogeneity of some soil properties in a tropical pasture. Numerous studies at this experimental site or elsewhere have demonstrated that some soil processes are regulated by earthworm activity at the observation scale of the bio-structure they produce (casts of a few cm) or in the nearby environment (a few ten cm). The goal of the present work was to verify whether the impacts of earthworm on soil may be observed at a larger scale (plot of a few ten metres). We tested the hypothesis that spatio-temporal structure of earthworm assemblages induces similar patterns of spatial soil heterogeneity (same size grain) rather than soil faunal assemblages are influenced by spatial heterogeneity.

Materials and methods

Study site

The study was carried out at the CORPOICA-CIAT Research Station of Carimagua (4°37′N, 71°19′W) located in the phytogeographic unit of the well-drained isohyperthermic savannas of the Eastern Plains of Colombia. The climate is subhumid tropical with an annual mean temperature and rainfall of 26°C and 2300 mm respectively, and a pronounced dry season from November to March (unpubl. CIAT data). Native vegetation varies with topography: open savannas in the uplands ("altos"), and gallery forests or flooding savannas in the low-lying areas ("bajos"). Soils are Oxisols (Tropeptic Haplustox Isohyperthermic) in the uplands and Ultisols (Ultic Aeric Plintaquox) in the low-lying areas. Both are characterised by favourable physical properties (aggregation, porosity, water retention), high acidity (pH (H_2O) < 5) and very low chemical fertility (Al saturation $> 80\%$, CEC < 5 meq. 100 g dry soil^{-1}) (unpubl. CIAT data).

Samplings were carried out in a previously ploughed and sown 3-yr old pasture of *Brachiaria humidicola* (Rendle) (CIAT 679), *Arachis pintoi* Krap and Greg (CIAT 17434), *Stylosanthes capitata* Vog. (cv. Capica) and *Centrosema acutifolium* Benth. (cv. Vichada). This paddock was located on a well-drained upland and was freely grazed by cattle with an average stocking rate of 2.0 animal units ha^{-1}. Samples were taken on a 35 × 70-m plot that was situated in the middle of the pasture.

Earthworm sampling

The sampling dates were chosen in order to accurately cover a complete seasonal cycle. Earthworms were sampled from October 1995 to October 1996 at the dates: 1) October 1995, 2) every two months between February 1996 and October 1996.

Earthworms were sampled using a method adapted from the Tropical Soil Biology and Fertility Program (Anderson and Ingram 1993). A soil monolith of 25 × 25 × 30 cm was rapidly dug out with a spade. Soil was handsorted in the field on a plastic mantle and the collected earthworms were identified at species level (based on Jiménez 1999), counted and replaced in the monolith emplacement with the sorted soil.

Prior to the monolith extraction, the density of the large anecic species *Martiodrilus carimaguensis* Jiménez and Moreno was estimated by counting the fresh casts it produced at the surface of a 1 m^2 square that was centred on the monolith. Using the direct relation existing between the number of individuals and the number of fresh casts present at the soil surface was considered to be the more efficient method for assessing

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the populations of this species (Jiménez et al. 1998a). In fact, *M. carimaguensis* easily escapes into deep soil horizons when using classic hand-sorting method, due to its large size and the deep burrows it digs.

Samplings were regularly located each 5 m on the 35 × 70-m grid. By this, points were located in space by their x and y coordinates, allowing further spatially explicit statistical treatments. To avoid sampling two monoliths at exactly the same point, samples were displaced, from one date to another, along a spiral whose origin was represented by the point sampled at the first date. The difference of location (ca 30 cm) was considered as negligible when compared to the overall size of the studied plots, and sampling coordinates were considered as identical from one date to another. In total, 120 monoliths were sampled at each date. This was largely greater than the minimum sample number considered as necessary to achieve most of spatial analysis (Legendre and Fortin 1989, Rossi 1996).

Soil properties and root biomass

Soil was sampled once at the end of the period of earthworm sampling (September 1996). No attention was paid to the temporal dynamics of soil heterogeneity because it was assumed to be difficult to link up with contemporaneous dynamics of earthworm distribution. In fact, earthworms and soil are likely to influence each other with a certain temporal lag, which is the time necessary for structures to influence the neighbouring environment or for individuals to occupy suitable areas. As a consequence, these two compartments are not likely to display simultaneous spatio-temporal patterns in a given period. Hence, the sampling design of this study was assumed to produce two kinds of potential results corresponding to distinct types of interactions between the soil and its fauna. First, earthworm distribution is stable in time and strongly correlated with soil parameters, which means soil heterogeneity has a high temporal inertia and influenced organism distribution across all the sampling period (equilibrium assumption). Second, earthworm populations are mobile and their distribution is not correlated with soil or the correlation is slight, which means community and soil spatial patterns may influence each other in a non-equilibrated system.

Root biomass was also estimated at the same single date to check the impact of earthworms on plant growth. Aboveground biomass was not sampled because its instantaneous measurement was assumed to be influenced more by intensive cattle grazing than by earthworms or soil characteristics. Soil and roots were sampled in the 0–10 cm soil layer because most earthworms are active at this depth during the rainy season (Jiménez and Decaëns 2000).

Penetration resistance was measured at 4 depths (0, 2.5, 5 and 10 cm), using a DAIKI 5520 penetrometer (cone diameter of 1 cm, angle of 26°). Bulk density was assessed in the layers 0–5 and 5–10 cm by weighing a core of soil (5-cm diameter) previously dried at 75°C during one week. Total C was evaluated in the 0–10 cm layer with a standard acid digestion method followed by a colorimetric assessment on 2 g air dried samples of soil (Houba et al. 1988). Roots were collected by washing and sieving 10-cm diameter, 10 cm deep soil cores through a 0.053 mm sieve. Roots were dried at 75°C during 48 h and dry weights were recorded.

Sampling points were regularly located on the same grid than the one used for earthworm sampling. Only half of the 120 points were sampled, but the total number of 60 points remained higher than the one considered as sufficient for the spatial statistic analysis performed in this study (Legendre and Fortin 1989, Rossi 1996).

Statistical analysis

Partial triadic analysis

The partial triadic analysis (PTA) is a specific method of analysis for cubic data sets. It is useful when analysing a set of tables related to t sampling dates done at the same s location. At each date, p variables are assessed at each station and the PTA allows the extraction of the inertia structure that is common to the different dates. It involves three successive steps (Thioulouse and Chessel 1987, Centofanti et al. 1989) of which two were used in this study: 1) the interstructure analysis provides the description of the stations as a function of the date typology and extracts, for each of the p variables, the structure that is common to the different dates; 2) the compromise analysis enables the description of the stations as a function of the variable typology and the identification of the variables responsible for the structure that is common to the different dates.

In this study, the original data set represented 6 initial tables (corresponding to 6 sampling dates), each composed of 120 lines (stations = sampling points) and 5 columns (variables = earthworm species density). The sample factorial coordinates extracted from the interstrucure analysis were mapped to describe the spatio-temporal distribution patterns of each species. Likewise, mapping the factorial coordinates given by the compromise analysis revealed the spatial patterns of species assemblages that were common to the different dates. Analysis and corresponding figures were processed with the STATIS module and the associated graphical modules of the ADE-4 software (Thioulouse et al. 1997).

Principal component analysis

A principal component analysis (PCA) was carried out to analyse soil parameters and root biomass. The data

table comprised 60 lines (sampling points) and 8 columns (soil parameters and root biomass). As previously described for the PTA, maps of the factorial coordinates of the sampling points were drawn to identify the spatial variation patterns of both soil properties and root biomass. This analysis was done with the PCA module of the ADE-4 software (Thioulouse et al. 1997).

Estimation of lacking values by kriging

Factorial coordinates on the axis of the PCA were estimated for the 60 points where neither soil nor roots were sampled, in order to allow further comparisons between the different spatial patterns revealed by the two factorial analysis. This was done using interpolation by punctual kriging (Burgess and Webster 1980, Yost et al. 1982) that takes into account the values of the variable at the nearby points and its autocorrelation as described by its semi-variogram (i.e. the representation of its semi-variance in function of the distance between pair of points). Both semi-variograms and kriged values were processed with the VAR5 software developed by the Hawaii Univ. (Yost et al. 1989).

Moran's autocorrelograms

The spatio-temporal structures extracted from multivariate analysis were tested and described by processing Moran's autocorrelograms (Moran 1950). Moran's index was calculated for the factorial coordinates of the sampling points on the first two axes of both the compromise analysis and the PCA. Data were allocated to 14 distance classes (see Table 1 for the limits and the number of pairs of points of each class). Each coefficient was tested at the statistical level $p = 0.05$. The whole correlogram was considered statistically significant when at least one coefficient was significant at the Bonferroni corrected level of probability: $0.003 = 0.05/14$ (14 = number of distance classes) (Cooper 1968). Prior to the computation of indices, the normality of the data frequency distribution was tested by means of the Kolmogorov-Smirnov statistic. When necessary, the Box-Cox transformation was used to reduce the asymmetry of the frequency distribution (Sokal and Rohlf 1995). All these steps were performed using different modules of the "R Package" (Legendre and Vaudor 1991).

Mantel's test

The simple Mantel's statistic r (Mantel 1967) was used to underscore common patterns between the spatiotemporal distribution of earthworms and the spatial structure of soil properties and root biomass. It consists in estimating and testing the correlation between two distance matrices that reflect the spatial structure of two given variables (Legendre and Troussellier 1988, Legendre and Fortin 1989). Here, four matrices were created, i.e. EAW1 and EAW2 with the factorial coordinates of samples on the first two axes of the compromise analysis, and SOIL1 and SOIL2 with the factorial coordinates of samples on the first two axes of the PCA (obtained after kriging). Mantel's test was thus performed between each EAW and SOIL matrices.

A significant Mantel's statistic may be the result of an unexpected factor that has similar and simultaneous effects on both studied variables (Legendre and Fortin 1989). Hence, the partial Mantel's statistic (Smouse et al. 1986) was further used to test this eventuality and underscore true correlations between EAW and SOIL matrices. It consisted in testing each EAW against each SOIL matrices conditionally to a SPACE distance matrix that was constituted from the sample geographical coordinates. The SPACE matrix was thus assumed to represent the spatial patterns common to all variables (Legendre and Troussellier 1988).

Both simple and partial Mantel's tests were processed with the "Mantel 3.0" module of the "R Package" of Legendre and Vaudor (1991). Their statistical significance was tested with a permutation test (1000 permutations) at $p = 0.05$ (Legendre and Fortin 1989).

Table 1. Inferior and superior limits and number of point pairs for each of the 14 distance classes used for correlogram computations.

Distance class	Inferior limit (m)	Superior limit (m)	Number of point pairs
1	0.0	5.6	217
2	5.6	11.2	740
3	11.2	16.8	635
4	16.8	22.4	1044
5	22.4	28.0	753
6	28.0	33.5	988
7	33.5	39.1	715
8	39.1	44.7	554
9	44.7	50.3	558
10	50.3	55.9	390
11	55.9	61.5	240
12	61.5	67.1	196
13	67.1	72.7	86
14	72.7	78.3	24

Results

Spatio-temporal structure of earthworm community

Earthworm community was mostly constituted by geophagous species (endogeic, sensu Bouché 1977) with a polyhumic (sensu Lavelle 1979) that ingests organic-rich soil (Ocnerodrilidae sp.), a mesohumic (sensu Lavelle 1979) that ingests soil with lower organic contents (*Andiodrilus* sp.), and an intermediate species (*Glossodrilus* sp.). Anecic species (sensu Bouché 1977) that ingests both fresh litter and soil and dig subvertical burrows were represented by the large *M. carimaguensis*, while a single species, *Aymara* sp., was identified as a litter dwelling (epigeic, sensu Bouché 1977) (Jiménez et al. 1998b).

Average earthworm density ranged from 4.8 to 95.4 ind. m^{-2} during February and June, respectively. Number of individuals was dominated by endogeics: Ocnerodrilidae sp. ($\approx$ 35% of the total earthworm density), *Andiodrilus* sp. ($\approx$ 35%) and *Glossodrilus* sp. ($\approx$ 20%). *Martiodrilus carimaguensis* only represented ca 2% of the total earthworm density, but dominated the community in terms of biomass, due to its very large size compared with other species.

Interstructure analysis
The eigenvalue of the first axis clearly stood out against the following, while the overall decrease was smooth (Fig. 1a). This suggested that only the first axis may be chosen for the compromise analysis.

The first axis (20.2% of the overall inertia) clearly corresponded to an inter-table "size effect" (all the variables presented the same sign on the axis) (Fig. 1b). This means that the inter-table correlations were all positive. In other words, there was no structure inversion from one date to another and the observed patterns of earthworm spatial distributions were, at least partially, common to all the sampling dates. The remaining data variability was not affected by stable spatio-temporal structures, reflecting the high overall spatio-temporal variability of species assemblages.

Mappings of the axial coordinates of the sampling points (Fig. 1c) revealed the existence of aggregated patterns that were stable in time, at least at the temporal scale taken into account in this study. Aggregated structure was particularly clear for the spatio-temporal distribution of *Glossodrilus* sp., which showed a well-delimited patch of high density in the south-western part of the grid. Inversely, *Andiodrilus* sp. presented high densities in the eastern part of the plot, while low densities were observed in the western half. Spatial structures were not so clear in the case of *M. carimaguensis*; however, a more populated zone was observed in the western half of the sampled zone. The observed patches of high density for the two species
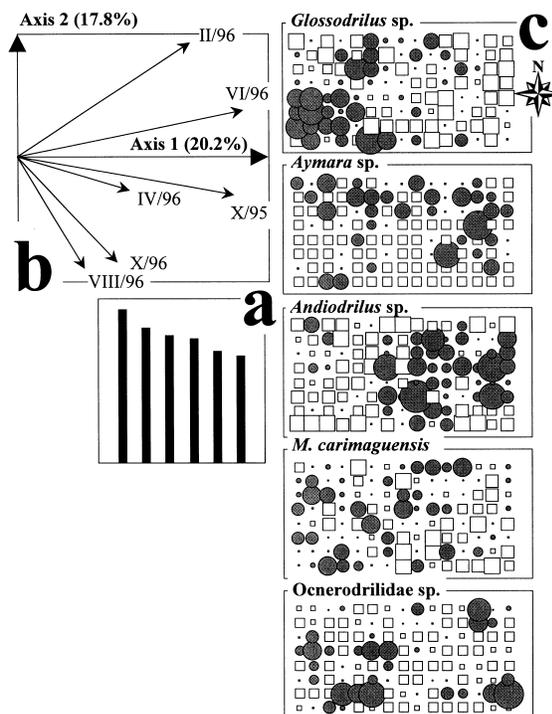

Fig. 1. Results of the interstructure table analysis: a) eigenvalue diagram; b) correlation circle showing the sampling dates on the factorial plan defined by the first two axes of the PCA of interstructure matrix; c) maps of the factorial coordinates of the 120 sampling points on the first component of the analysis for each of the five earthworm species (circles and squares respectively represent positive and negative coordinates, the symbol surface is proportional to the corresponding unsigned score value).

Glossodrilus sp. and *M. carimaguensis* were partly superimposable, and were clearly opposed to the high density plot of *Andiodrilus* sp. Small patches were observed for the other species, scattered across the whole plot or grouped in the northern part, respectively for the Ocnerodrilidae sp. and *Aymara* sp.

First compromise analysis
The decrease of axis-associated eigenvalues was sharp and justified the choice of only the first two axes for interpretation (Fig. 2a). This compromise analysis was performed with the first axis of the interstructure analysis, that only concerned 20.2% of the total inertia of the data matrix.

The first axis (34.2% of the total inertia) was mostly characterised by an opposition between two species assemblages: on the one hand *Andiodrilus* sp. and *Aymara* sp., on the other hand *Glossodrilus* sp. together with Ocnerodrilidae sp. and *M. carimaguensis* (Fig. 2b). The map of the sampling point coordinates on the first axis revealed the presence of two segregated zones: the first one in the southwestern part of the pasture, dominated by the assemblage *Glossodrilus* sp./Ocnerodrilidae

sp./*M. carimaguensis*; the second one in the northeastern part, mostly inhabited by *Andiodrilus* sp. and *Aymara* sp. (Fig. 2c). Moran's correlogram calculated on the point factorial coordinates was globally significant ($p < 0.001$, Fig. 3), while individual values were positive for the first 4 distance classes and negative from the 6th class and awards. This indicates that the described species assemblages were located in aggregated patches of ca 20 m in size.

The second axis (23.0% of the total inertia) represented a segregation between small species (*Aymara* sp. and Ocnerodrilidae sp.) and species of larger size (*Glossodrilus* sp., *Andiodrilus* sp., *M. carimaguensis*) (Fig. 2b). Contrary to the pattern described for the first axis, the observation of the map of point coordinates on this axis did not reflect a clear spatial structure (Fig. 2c). However, small patches of positive or negative coordinates were observed, in the southeastern and the northeastern part of the pasture, and in the centre and the south-western part, respectively. The existence of these spatial structures was confirmed by Moran's correlogram ($p < 0.003$, Fig. 3), while positive autocorrelation only occurred for the second distance class. Hence, this

Fig. 3. Moran's correlogram processed from the factorial coordinates of the 120 sampling points on the first two axes of the PCA of compromise matrix ($\bullet$ = significant individual values at $p < 0.05$; $\bigcirc$ = no significant individual values; the p value stands for the global significant level of the correlogram).

axis reflected the opposition in space of morphologically different species that were located in small patches of ca 10 m in size.

Soil heterogeneity

Minimal and maximal values of soil properties and root biomass are given in Table 2. The decrease of the eigenvalues associated with the PCA axis was sharp, indicating that only the first two axes should be retained for interpretation (Fig. 4a).

The first axis (44.3% of the total inertia) was defined by an opposition between on the one hand total C and root biomass, and on the other hand variables that
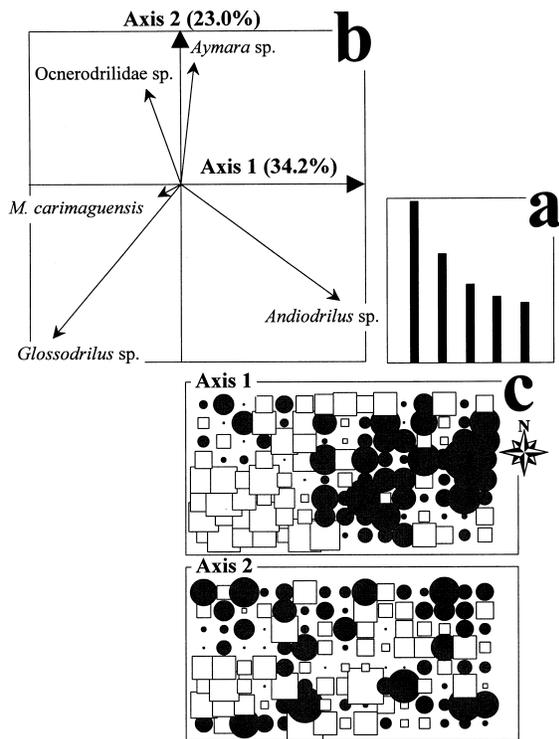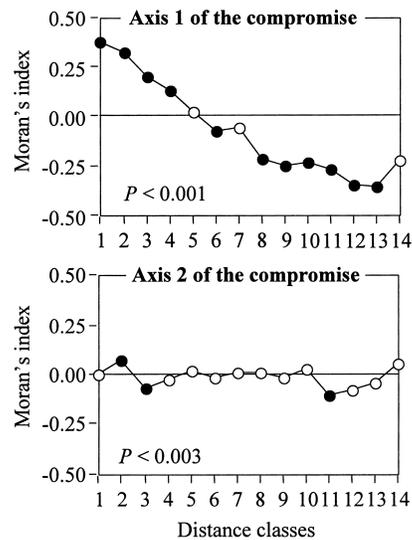

Fig. 2. Results of the compromise table analysis: a) eigenvalue diagram; b) correlation circle showing the variables (species) on the factorial plan defined by the first two axes of the PCA of the compromise matrix; c) maps of the factorial coordinates of the 120 sampling points on the first two components of the analysis (circles and squares respectively represent positive and negative coordinates, the symbol surface is proportional to the corresponding unsigned score value).

Table 2. Average soil properties and root biomass.

Properties	Soil layer (cm)	min	max
Total organic C (%)	0–10	2.2	3.6
Bulk density (g dry soil cm^{-3})	0–5	0.82	1.43
	5–10	1.07	1.77
Penetration resistance (kg cm^{-2})	0	0.0	4.3
	2.5	0.0	6.0
	6	0.7	8.3
	10	4.0	16.8
	20	8.8	17.8
	30	11.3	23.0
	40	15.2	25.0
	50	16.3	25.0
Root biomass (g dry roots m^{-2})	0–10	21.4	141.0

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Fig. 4. Results of the PCA on soil parameters and root biomass: a) eigenvalue diagram; b) correlation circle showing the variables on the factorial plan defined by the first two axes of the PCA (RB = root biomass; TC = total C; BD = Bulk density; PR = penetration resistance); c) maps of the factorial coordinates of the 60 sampling points on the first two components of the analysis (circles and squares respectively represent positive and negative coordinates, the symbol surface is proportional to the corresponding unsigned score value).
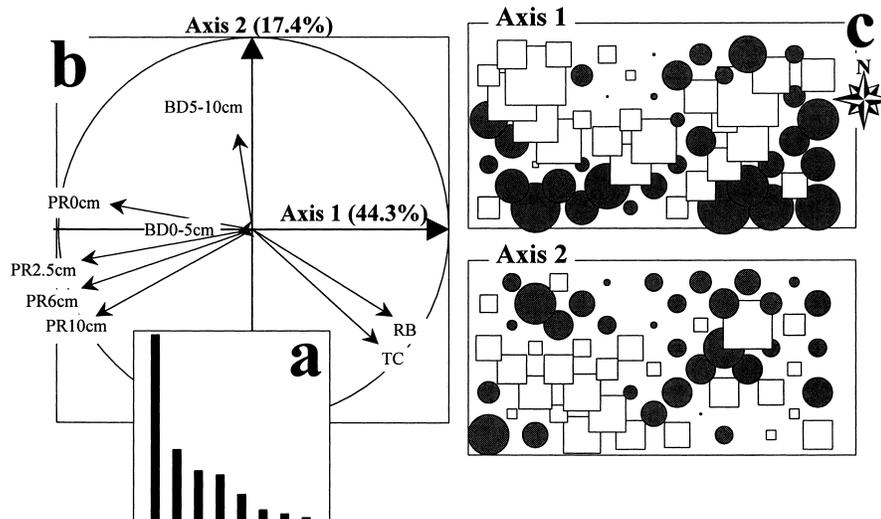
describe the compaction state of the soil (i.e. penetration resistance and bulk density) (Fig. 4b). The map of the factorial coordinates brought to the fore the presence of two zones easily identifiable in which coordinate values were positives (in the south-eastern and south-western of the grid) or negatives (in the centre of the plot) (Fig. 4c).

The second axis (17.4% of the total inertia) opposed the bulk density (5–10 cm) to the root biomass and total C (Fig. 4b). The map of factorial coordinates showed the presence of mostly positive values in the northern half of the plot, and of mostly negative ones in the southern part (Fig. 4c).

Correlograms and semi-variograms calculated on the axial coordinates of the sampling points clearly demonstrated the presence of spatial autocorrelation for both axes (Fig. 5). Correlograms were globally significant ($p < 0.001$) and individual values were significant for the two first distance classes, revealing the presence of patches of ca 10 m characterised by specific soil properties. Theoretical models adjusted to the variograms were spherical in the two cases, with a range of 30 and 20 m, respectively for the first and the second axes. Hence, the analysis of the semi-variance (i.e. the shape of the model) also leads to the conclusion of aggregated soil properties, but seems to overestimate the size of the spatial structures (i.e. the distance at which the range is reached) when compared with the autocorrelation analysis. The mapped representation of factorial coordinates after the kriging procedure is shown in Fig. 6.

Correlations between earthworm community and soil heterogeneity

Only one significant correlation was found for Mantel's test performed between EAW2 and SOIL2 (Table 3).

This indicates that zones dominated by small earthworm species were also characterised by high bulk density in the 5–10 cm layer and by low total C contents and root biomass. Inversely, larger species dominated in patches where the soil presented lower bulk density in the 5–10 cm layer and higher total C contents and root biomass. However, this correlation only represented a rather small proportion of the total information contained in the initial data sets. In fact, it concerns the second axis of the first compromise of the PTA (23.0% of inertia), itself calculated from the first axis of the interstructure analysis (17.8% of the initial inertia), and the second PCA axis that only represented 17.4% of the soil and root parameter variance.

To discriminate between true and spurious correlation between EAW2 and SOIL2 we checked the significance of the Mantel statistic after having accounted for the effect of the SPACE matrix. The partial Mantel's test [EAW2.SOIL2].SPACE (partial test between EAW2 and SOIL2 conditionally to SPACE) was performed in order to verify the validity of the observed correlation. It gave a standardised r coefficient of 0.42 ($p = 0.039$). This signifies that the similarity observed between both spatial patterns of organisation corresponded to a true correlation.

Discussion

This study explicitly demonstrates the existence of structured assemblage in earthworm communities, at least at the temporal scale concerned with the sampling period. This mostly corresponds to an alternation of patches where particular species assemblages dominate. The overall pattern may be described at different levels of spatial organisation, which are nested at a given time
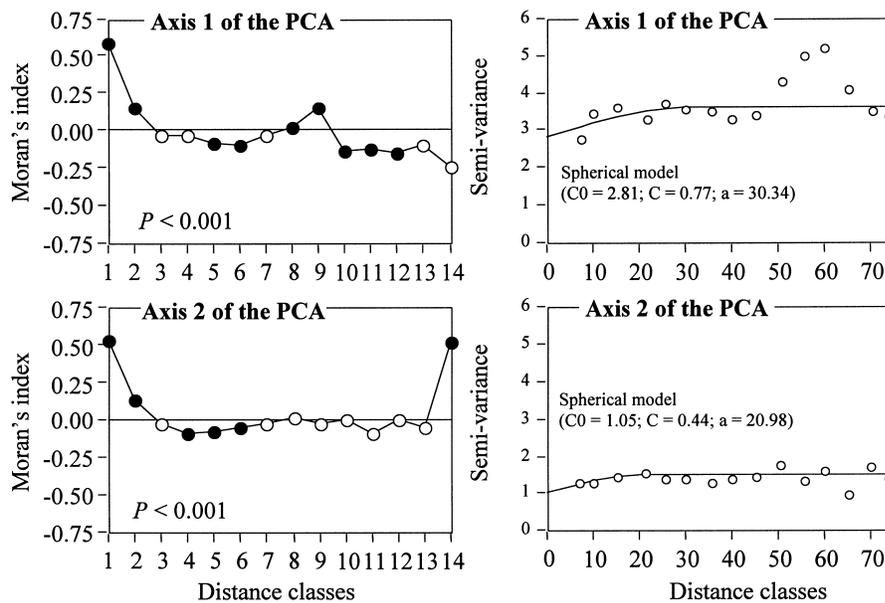
Fig. 5. Moran's correlograms and semi-variograms calculated from factorial coordinates of the 60 sampling points on the first two axes of the PCA.

and correspond to the different components of the compromise analysis. Such spatio-temporal structures have already been described for a few earthworm communities in savannas of Côte d'Ivoire (Rossi 1998, Tondoh 1998) and in Colombian pastures (Jiménez 1999). The spatial scale at which they are expressed (ca 20 m) agrees with that presented by other authors for earthworm spatial distribution in one date studies (Rossi et al. 1995, 1997, Nuutinen et al. 1998). It is important to point out that the described structures only represent a low proportion of the total variability of the matrix (57.0% of the 20.2% explained by the first interstructure axis). This means that species assemblages are rather mobile, while a relative spatial stability of assemblages occurs in some areas of the experimental plot. This lack of stability in earthworm spatio-temporal pattern may reflect a system characterised by a non-equilibrium state. Thus, oppositions between species assemblages may be due to competitive exclusion, or to spatial segregation in the case earthworm species respond to environmental factors that are not stables in time and space (i.e. if the factors are themselves characterised by a non-equilibrium state).

The first compromise axis mostly expressed a spatial segregation between *Andiodrilus* sp. and *Glossodrilus* sp. This result has been already observed in a native savanna and long-term legume based pasture of Carimagua (Jiménez 1999). Both species are endogeic, present rather similar biometrical characteristics and hence have a high index of niche overlapping (performed from biometrical and vertical distribution data, Jiménez 1999). Spatial opposition between these two species thus may be interpreted as the result of competitive exclusion. Hence, in patches where either one or the other dominates, the coexistence with other species should be the result of niche partitioning mechanisms. This seems to be a realistic hypothesis, considering that coexisting species are of different size, diet and/or adaptive strategies. However, more detailed ecological data are needed (e.g. diet) to 1) assess the degree of niche partitioning that really occurs within the community, and 2) identify what species compete, what kind of exclusion mechanisms occur, which is the best competitor, and what environmental factors allow the presence of the other species.
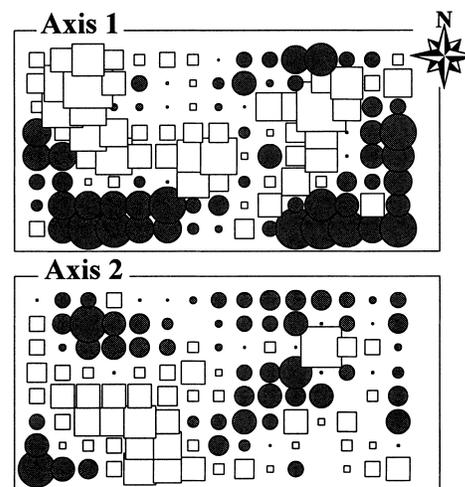

Fig. 6. Maps of the factorial coordinates of the 120 points on the first two axes of the PCA after punctual kriging intrapolation of the lacking values (circles and squares respectively represent positive and negative coordinates, the symbol surface is proportional to the corresponding unsigned score value).

Table 3. Standardised Mantel's r coefficients and associated probabilities (EAW1 and EAW2 = distance matrices for the factorial coordinates of the sampling points of the first and the second axes of the compromise analysis, respectively; SOIL1 and SOIL2 = distance matrices for the factorial coordinates of the sampling points of the first and the second axis of the PCA, respectively; * = significant at p < 0.05; NS = not significant).

	Standardised partial Mantel's r	Probability
EAW1.SOIL1	0.060	0.430 NS
EAW1.SOIL2	0.104	0.347 NS
EAW2.SOIL1	−0.123	0.406 NS
EAW2.SOIL2	0.412	0.044*

The second axis consisted in an opposition between relatively small species (i.e. Ocnerodrilidae sp. and *Aymara* sp.) and larger ones (i.e. *Glossodrilus* sp., *Andiodrilus* sp. and *M. carimaguensis*). Small and large species are supposed to have rather different habits and are not likely to compete. Thus, the alternation of patches described by this axis may be interpreted as the response of earthworm community to environmental heterogeneity (spatial segregation). Cattle dung, for example, may have positive effects on small species that preferentially ingest organic-rich substrate and may present opportunistic coprophagous habits, while larger species generally feed on leaf litter, dead roots and/or humified organic matter.

Patches dominated either by larger species or smaller ones corresponded to areas characterised by specific soil properties and root biomass levels. This, however, does not allow a definition of whether earthworm spatial distribution determines soil heterogeneity or the contrary occurs. Two main hypotheses may be postulated:

First, earthworms may influence soil properties so their spatio-temporal distribution induces similar patterns in soil heterogeneity. This hypothesis assumes that different species of earthworms produce casts of different size and properties, and have different effects on soil properties (Blanchart 1992, Derouard et al. 1997). At Carimagua, Ocnerodrilidae sp. produces small aggregates and is supposed to fragment larger casts produced by other species (Jiménez et al. 1998b), while *Aymara* sp. probably produces holorganic pellets with little effects on soil structure. Large-sized species produce organic-rich, compact and stable casts, which are degraded in a few months by other invertebrates that dig into and fragment them in smaller and less compact aggregates (Decaëns et al. 1999a, b, Decaëns 2000). An efficient regulation of soil structure may occur in patches dominated by larger species, leading to an increased macroaggregation that is likely to promote the accumulation of a C pool by physically shielding soil organic matter from mineralisation. Such impacts on soil organic matter and physical properties may logically bring effects on plant growth, as observed in terms of root biomass in this study. On the contrary, a dominance of small species that produce large amounts of small and slightly stable aggregates may lead to a weakened soil structure sensitive to animal trampling.

Second, earthworm assemblages may be influenced by the spatial heterogeneity of soil environment. This hypothesis postulates that spatial segregation is the predominant mechanism leading to the observed species assemblage distribution. The large endogeic species (*Andiodrilus* sp. and *Glossodrilus* sp.) are located in zones where their trophic resource availability is greater, i.e. in zones with high soil C content. High levels of soil C are likely to be associated with high root biomass and soil aggregation (Fisher et al. 1994, Gijsman and Thomas 1995, Gijsman 1996, Rao 1998). In patches of lower organic contents soil will present a lower carrying capacity, leading to a decrease in large endogeic abundance and a proportional increase of the relative dominance of small species. Furthermore, the dominance of polyhumic species may be accentuated by their aptitude for living in compact soil. Such capacity has been demonstrated for small African Eudrilidae species (Blanchart et al. 1997, Rossi 1998), which have morphological and ecological similarities with Ocnerodrilidae sp.

To settle which hypothesis is close to reality, it is important to consider that the correlation only concerned a small part of the initial data variability. In fact, one could assume that the temporal variability of soil parameters is much less than the variability of the spatial distribution of earthworms. Then, if earthworm communities would respond to environmental heterogeneity (i.e. if species would locate in patches where optimal life conditions occur), a low temporal variability of their spatial patterns of organisation should be observed, as well as a high correlation with soil parameters. The observed low correlation rather indicates that earthworms influence soil, while effects are difficult to observe due to a high spatio-temporal variability of species assemblage. Thus, the correlation between the community and its environment is only perceptible where a relative temporal stability of assemblages occurs (i.e. the structures observed with the PTA).

The first hypothesis is also supported by other empirical and experimental studies dealing with the impact of *M. carimaguensis* on soil functioning. Even if this species does not participate significantly to the described distribution patterns, its effects on soil may be disproportionate in relation to its density due to its very high individual weight. The production of surface casts by this species is considered of local importance for soil structure, organic matter dynamics and nutrient release, and local peaks of root biomass were found in the soil located just beneath these bio-structures (Decaëns et al. 1999b, Decaëns 2000). In a recent work, Decaëns et al. (1999c) demonstrated that the disappearance of *M.*

carimaguensis leads to a rapid superficial compaction of the soil and a short-term decrease of soil C levels, root and shoot biomass. Such results are consistent with the idea that earthworms regulate soil structure, organic matter dynamics and plant growth at the scale of their casts and the nearby soil (Edwards and Lofty 1978, 1980, Martin 1991, Lavelle and Martin 1992, Lavelle et al. 1998). At the larger scale of the grassland plot, the impacts on soil structure of earthworm spatial distribution, when characterised by an opposition of patches dominated by species of different size, have been recently described in a grassland savanna of Côte d'Ivoire (Rossi 1998).

A striking feature of this study is that the larger part of the variability in soil properties and root biomass was not linked with earthworm spatio-temporal distribution. This means that other factors play a predominant role in the regulation of soil functioning, or earthworm impacts mostly express at a smaller spatio-temporal scale that was not taken into account by the mesh of the present sampling (e.g. the scale of the bio-structures they produce). Root biomass, for example, seems to have a predominant role. An additional partial Mantel's test where root biomass was tested against total C gives a correlation index $r = 0.62$ ($p < 0.001$). This result supports the conclusions of recent studies showing that high root biomass leads to C accumulation (Fisher et al. 1994, Rao 1998), and hence favours improved soil structure (Gijsman and Thomas 1995, Gijsman 1996) and maintains physical properties (Gijsman and Thomas 1996) in soils of Colombian savannas. Both roots and earthworms are considered as ecosystem engineers, and their role in soil seems to present some convergent characteristics at least for a few specific functions (e.g. C storage, soil aggregation, etc.). Further studies are needed to assess the functional role of a large range of soil organisms in order to define functional groups of soil ecological engineers.

Functional attributes of one species or functional group may be considered at different levels of observation within a hierarchy of interacting and nested systems. When ascending this hierarchy, the successive levels will describe the same processes, but with slower and slower dynamics and at larger and larger spatial scales (Allen and Starr 1982). A widely used means to identify earthworm functions is to describe the individual impacts of species. This is a necessary first step but implies some hazardous extrapolations when trying to extend the obtained results at the scale of the ecosystem (i.e. in a bottom-up approach, Anderson 1995). In this work, a top-down approach was used to deduce the functional attributes of individual species from a large-scale field study. Correlations were identified, but it was difficult to bring them to the fore. This is probably inevitable in such experimental design due to the predominant effects of environmental factors that may regulate both soil processes and communities at higher

levels in the hierarchical scale (Anderson 1995). However, top-down studies of the functional role of soil organisms are necessary to settle to what extent studies at the level of individuals may be extrapolated at larger spatio-temporal scales.

In conclusion, there were little indications to check whether earthworms influence soil properties or the contrary occurs. Some results, however, indicate that the system was at a non-equilibrium state, and that mobile earthworm populations influenced soil with an overall effect that was hard to detect. Testing this hypothesis will imply comparative studies of spatio-temporal dynamics of both earthworm assemblages and soil properties to identify time-lags and establish causal links between these two compartments.

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