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Stability of the spatio-temporal distribution and niche overlap in neotropical earthworm assemblages

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ABSTRACT

The spatial distribution of soil invertebrates is aggregated with high-density patches alternating with low-density zones. A high degree of spatio-temporal organization generally exists with identified patches of specific species assemblages, in which species coexist according to assembly rules related to competitive mechanisms for spatial and trophic resources occur. However, these issues have seldom been addressed. The spatio-temporal structure of a native earthworm community in a natural savanna and a grass–legume pasture in the Colombian "Llanos" was studied during a 2-year-period. A spatially explicit sampling design (regular grid) was used to discern the distribution pattern of species assemblages in both systems. Earthworms were collected from small soil pits at three different sampling dates. Data collected from 1 m^2 soil monoliths were also used in the present study. Data were analyzed with the partial triadic analysis (PTA) and correlograms, while niche overlap was computed with the Pianka index. The PTA and correlogram analysis revealed that earthworm communities displayed a similar stable spatial structure in both systems during the 2-year study period. An alternation of population patches where different species' assemblages dominated was common to all sampling dates. The medium-sized *Andiodrilus* sp. and *Glossodrilus* sp. exhibited a clear spatial opposition in natural savanna and the grass–legume pasture for the duration of the study. The Pianka index showed a high degree of niche overlapping in several dimensions (vertical distribution, seasonality of population density) between both species. The inclusion of space-time data analysis tools as the PTA and the use of classical ecological indices (Pianka) in soil ecology studies may improve our knowledge of earthworm assemblages' dynamics.

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1. Introduction

Soil biota have long been known to be spatially aggregated (Bigwood and Inouye, 1988; Poier and Richter, 1992; Stein et al., 1992; Fromm et al., 1993; Robertson, 1994; Wallace and Hawkins, 1994; Boag et al., 1994; Robertson and Freckman, 1995; Crist and Wiens, 1996; Delaville et al., 1996; Adams, 1998; Crist, 1998; Nuutinen et al., 1998; Rossi et al., 1996, 1997; Rossi 2003a,b,), but recent studies have more precisely noted the various scales of spatial patterning (Ettema et al., 1998, 2000; Albrecht and Gotelli, 2000; Decaëns and Rossi, 2001; Jiménez et al., 2001; Rossi, 2003c; Ettema and Yeates, 2003; Rossi and Nuutinen, 2004; Whalen, 2004). The factors that cause and control these patterns are largely unknown and difficult to identify as spatial distribution originates from both environmental (biotic and abiotic) and internal

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community or population factors (Robertson and Freckman, 1995; Rossi et al., 1997). For example, the spatial distribution of soil invertebrates is influenced by the plant cover and its composition, resulting in a horizontal mosaic of areas subjected to gradients of nutrient availability and microclimatic conditions. While land use management and agricultural practices determine plant community composition and soil nutrient status, i.e. soil resource patchiness (Miles, 1985; Robertson et al., 1993; Wardle and Lavelle, 1997), plant community composition and the distribution and diversity of soil living organisms may also be affected by changes in soil heterogeneity (Tilman, 1988; Rossi et al., 2006), Furthermore, soil heterogeneity is also driven by the activities of soil invertebrates since they create trophic and spatial "hot spots" and modify their own and other organisms' resources (Jones et al., 1994; Anderson, 1995).

Communities of soil invertebrates show generally a high degree of spatio-temporal organization. Uneven distribution of resources may lead to spatial distribution of soil organisms in alternating high- and low-density patches. Patches are areas where specific species assemblages occur. Moreover, patches of different species also display different temporal distributions that are not linked to biotic resources but competition between species. The factors responsible for the composition of these discrete patches and their spatial segregation with regards to each other are still largely unresolved. Several hypotheses may explain the patterns observed, for example, species may coexist in a given patch thanks to ecological complementarity with regards to spatial and trophic resources. On the other hand, competitive interactions and environmental factors which act as filters for species may both determine species assemblage at different scale domains (Belyea and Lancaster, 1999). For instance, competing species may exhibit checkerboard distribution and mutually exclude themselves from the patches where they are present. On the opposite, spatial segregation between species may also reflect a response to resource spatial heterogeneity of species with different ecological requirements. While these issues are highly relevant in soil ecology studies, the joint analysis of niche overlap and spatio-temporal distribution of soil invertebrates has never been addressed in the scientific literature.

In this study, we assessed the spatio-temporal structure of earthworm assemblages by means of the partial triadic analysis (PTA) (Thioulouse and Chessel, 1987; Kroonenberg, 1989) in combination with a common tool in spatial statistics, the correlogram (Legendre and Fortin, 1989). The PTA is a principal component analysis (PCA) performed on three dimensional data matrices, and was developed by Escoufier (1973), although scarcely used in ecological studies, and afterwards it was called Structuration des Tableaux à Trois Indices de la Statistique ("STATIS") by L'Hermier des Plantes (1976). Examples in the field of soil ecology can be found in Decaëns and Rossi (2001); Rossi (2003c).

We used the Moran's I index (Moran, 1950) to test the statistical significance of the spatial autocorrelation common to all sampling occasions i.e. assess the significance of the spatial pattern of earthworm assemblages that is stable through time (at the scale of our study). The values of Moran's I index are plotted in a graph called the correlogram (Sokal and Oden, 1978; Legendre and Fortin, 1989). The correlogram shows the changes of autocorrelation coefficient with increasing distance classes (Sokal and Oden, 1978). Contrary to semi-variogram (a structure function used in Geostatistics), the correlogram allows testing for the presence of a significant spatial structure (Legendre and Fortin, 1989).

To test the degree of niche overlap between species that might also be linked to opposite spatial distribution of earthworms we used the O_{jk} index (Pianka, 1973, 1974). Pianka (1973) was one of the first authors who attempted to quantify the coexistence within communities by using an index based on the proportion of a given resource exploited by the entire community. Therefore, the degree of similarity or overlap between species could be measured. Niche overlap does not necessarily mean total competition between species; for example, when a given resource is abundant in the ecosystems then two competitive species shall share it without any harmful consequence for both species (Pianka, 1973).

The present work is part of a more detailed study of earthworm communities from the Colombian savanna soils, and was especially designed to address their spatio-temporal distribution at the community level. It aimed at determining both spatial and temporal scales of variability vs. stability in species assemblages and functional groups in the natural savanna and in a grass–legume pasture over a period of 2 years. A replicated spatial sampling in the same area for a given period of time allows for a better comprehension of population dynamics since it adds a significant temporal dimension to the spatial pattern of the communities of soil organisms. Some of the results have been obtained from a reanalysis of previously published data set (Jiménez et al., 2001). In this paper, however, all temporal data matrices were analyzed by means of the PTA together with the computing of the Pianka O_{jk} index. Several assumptions were made in this study:

- species assemblages in the earthworm community are in state of equilibrium throughout the 2-year study period;
- there are changes in the spatial distribution of species assemblages and their temporal stability linked to land use management;
- potentially competing species can coexist in a given habitat and avoid competitive exclusion by occupying spatially and/or temporally different areas.

2. Materials and methods

2.1. Study site

The study was carried out at the CIAT-CORPOICA Carimagua research station, in the well-drained isohyperthermic savannas of the Eastern Plains of Colombia (4°37′N and 71°19′W, 175 m altitude) between September 1993 and September 1995. Climate is subhumid tropical with a 4-month dry period from December to March and an average yearly rainfall and temperature of 2280 mm and 26 °C, respectively (1972–1995, CIAT data). Native vegetation is characterized by open herbaceous savannas with scattered trees and bushes in the

uplands ("altos") and gallery forests and palm trees ("morichales") in the low-lying savannas ("bajos"). Soils at the study site are well-drained silty clay Oxisols (Tropeptic Haplustox Isohyperthermic) in the uplands and Ultisols (Ultic Aeric Plintaquox) in the lowlands (USDA). They are characterized by their acidity (pH[H_2O] = 4.5), a high Al saturation (> 80%) and low values of exchangeable Ca, Mg and K.

Two plots in the upland Oxisol were investigated: a 17-year-old grazed grass–legume pasture and a native savanna. The grass–legume pasture plot was 2 ha and was sowed with the African grass *Brachiaria decumbens* Stapf. cv. Basilisk (Poaceae), and the tropical herbaceous legume *Pueraria phaseoloides* Benth. CIAT 9900 (Fabaceae). Cattle stocking rates were 1 animal unit (AU) ha^{-1} in the dry season and 2 AU ha^{-1} in the wet season (1 AU = 250 kg live weight). Fertilizer was applied at the following rates (kg ha^{-1}): 44 K, 14 Mg and 22 S at pasture establishment and 10 P, 9 K, 92.5 Ca, 9 Mg and 11.5 S every second year since 1987, for a total of four fertilizer applications before the study began (Lascano and Estrada, 1989). The native savanna was not managed (e.g. ungrazed and not burnt), and vegetation was dominated by *Andropogon bicornis* L., *Gymnopogon foliosus* (Wild.) Nees, *Panicum* spp., *Trachypogon* spp. and *Imperata brasiliensis* Trin.

2.2. Earthworm species

In the natural savannas of Carimagua the earthworm community comprised eight native species: *Andiodrilus* sp. (endogeic), *Andiorrhinus* sp.1 (endoanecic), *Andiorrhinus* sp. 2 (endoanecic?), *Aymara* sp. (epigeic), *Dichogaster* sp. (epigeic), *Glossodrilus* sp. (endogeic), *Martiodrilus* sp. (anecic) and *Ocnerodrilidae* sp. (endogeic). All these species were also present in the grass–legume pasture, where no alloctonous species were found (Jiménez et al., 1998b). The main biometric characteristics, adaptive strategies, reproduction biology and life cycle of the whole earthworm community are precisely described elsewhere (Jiménez et al., 1998b, 1999, 2000; Jiménez and Decaëns, 2000).

2.3. Earthworm sampling

Two sampling strategies were used in this study based on the data treatment.

2.3.1. Spatially explicit sampling
Earthworms were sampled from 40 × 40 × 15 cm soil pits taken in 64 sampling points distributed every 10 m in the intersections of a regular 70 × 70 m^2 grid. One soil pit was sampled at each point and the soil placed on a plastic bag to manually identify and count in situ all the earthworm species and cocoons. These were later returned together with the soil to the pit. Cocoons were not used in data analysis. Previous to the soil pit extraction, the large tower-like fresh casts deposited by the anecic worm *Martiodrilus* sp. in the soil surface were counted within a 1 m^2 metal frame. This allowed us to estimate the population density of this species using the direct positive relation (r = 0.907, P < 0.01) between the number of individuals and the number of fresh casts present at the soil surface (Jiménez et al., 1998a, 1998b).

This was done easily as *Martiodrilus* sp. casts are easily distinguished from other surface depositions.

Each plot was surveyed following this sampling strategy at three different dates when earthworms were active in the topsoil: September 1993, October 1994 and June 1995 in the grass–legume pasture, and November 1993, November 1994 and May 1995, in the native savanna. These sampling dates were selected a priori since no information on the biology and life cycle of the earthworm species was available at the beginning of our work. Soil monoliths at subsequent dates were taken in points separated about 50 cm along a spiral whose origin was represented by the sample of the first date. This displacement in space was, however, considered negligible at the scale of the plot, and sampling coordinates were taken as identical from one date to another. This enabled us to sample the same area during the 2 years of survey and to use spatial statistics for data analysis. A sample size of 64 values seems rather low but is within the range considered large enough to allow the use of spatial statistics (Legendre and Fortin, 1989).

2.3.2. Monthly sampling
It was designed to study in detail the population dynamics and life history of all earthworm species (not shown here). A stratified random sampling procedure was performed during 17 months (from April 1994 to September 1995) in both systems. In each plot 81 10 × 10 m^2 quadrates were grouped into five distinct areas. Every month earthworms were hand sorted from five 1 × 1 × 0.5 m^3 monoliths that were taken at the center of each quadrate (randomly selected a priori) in each area and in both plots. In some cases, sampling depth varied up to 80–90 cm depth to follow vertical seasonal variations of some species, i.e. *Martiodrilus* sp. (see Jiménez et al., 1998b; Jiménez and Decaëns, 2000, for details). Soil was dug out per stratum of 10 cm and earthworms were sampled and stored separately for each of them in order to describe population vertical distribution. Prior to monolith extraction the number of fresh surface casts deposited by *Martiodrilus* sp. were counted for the same reasons as those quoted for the spatially explicit sampling. Two 20 × 20 cm cores were sampled 1 m aside the 1 m^2 monolith for washing–sieving and sampling small species that were not efficiently sampled by hand sorting (after Lavelle, 1978; Jiménez et al., 2006, data not shown). Earthworms were fixed and stored in 4% formaldehyde solution, identified to species level and counted in the lab to calculate population density for each sampled soil stratum. Later, we measured length (mm), weight (g), preclitellar diameter of earthworms to obtain length/width and weight/width ratios.

2.4. The PTA as a tool to analyze multivariate spatio-temporal variability

The PTA is a multivariate method that analyzes matrices in a three dimensional data array (Thioulouse and Chessel, 1987; Kroonenberg, 1989; Rossi, 2003c). In this study we used three temporal matrices (three sampling dates) that described in observations (sampling points) for p variables (the species abundance). The objective of the PTA is to extract a multivariate structure that is expressed through the different

dates (Rossi, 2003c). The space-time data were analyzed following two steps. First, a PCA was performed in order to establish the ordination of the different dates (Rossi, 2003c). This analysis is called the interstructure analysis. It is intended to provide a global description of the sampling points as a function of the typology of the sampling dates, extracting the information common to all sampling dates. The objects of this analysis are the variables by samples (see Fig. 1 in Rossi, 2003c). The second step is the compromise analysis and involves a PCA of a fictitious data table constituted by the reorganization of the variable-sample scores (see Fig. 1 in Rossi, 2003c). This table is referred as to the compromise table (Rossi, 2003c). The compromise analysis allowed a multivariate synthesis of the information expressed through the first axis of the date ordination analysis. This step allows a description of sampling sites as a function of the typology of variables and the identification of the variables responsible for similar patterns at different

dates. Our approach therefore focused on the analysis of the species spatial pattern and their temporal variability/stability. All the computations involved in the PTA were directly processed with the module STATIS of the software ADE-4 (Thioulouse et al., 1997). Similarly, graphs were drawn using the various graphical modules of the ADE-4 software.

2.5. Moran's autocorrelogram

We tested the spatial autocorrelation in species assemblages by analyzing the sample score of the first axis of the compromise analysis (Rossi, 2003c). The values of Moran's I index are plotted in a graph called the correlogram (Legendre and Fortin, 1989), the function on which the spatial pattern of the variable analyzed and the scale at which it expresses is represented (Sokal and Oden, 1978). The correlogram shows the changes of autocorrelation coefficients with increasing distance (Sokal and Oden, 1978). Data were allocated to nine
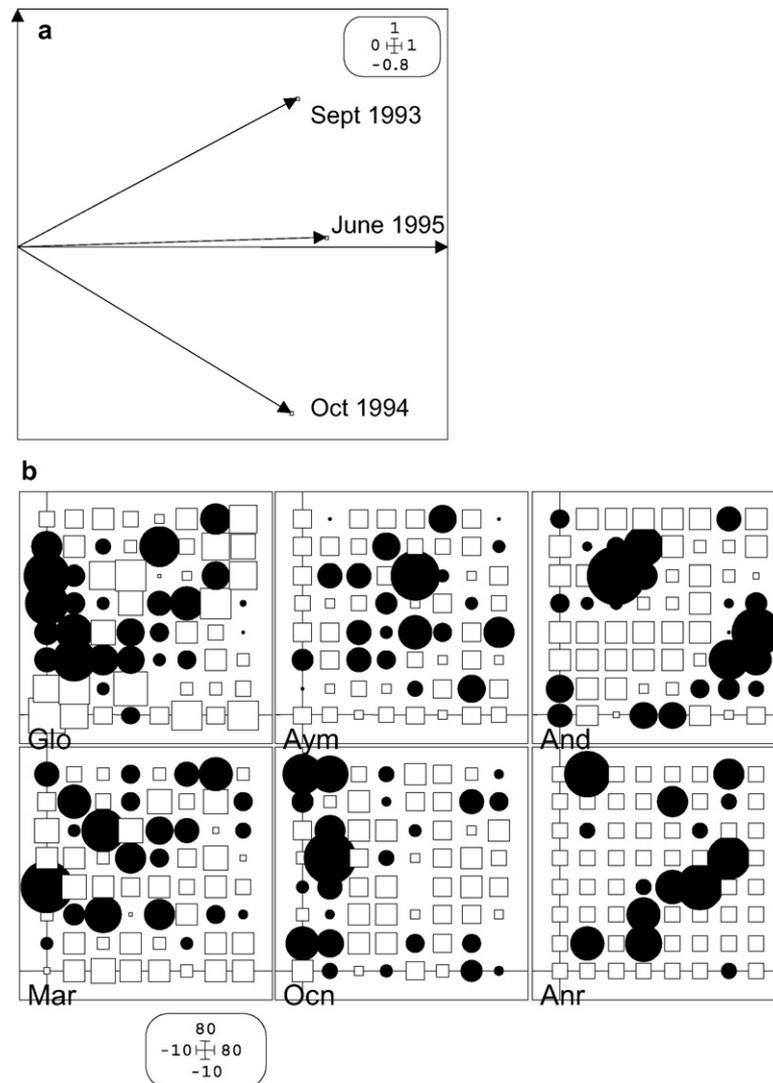

Fig. 1 – Results from the interstructure analysis; (a) ordination of sampling dates on the factorial plan defined by the first two axes of the PCA on the interstructure matrix (b) maps of the factorial coordinates of the 64 sampling points on the first axis of the interstructure analysis for each of the six species in the pasture. Glo: *Glossodrilus* sp.; Aym: *Aymara* sp.; And: *Andiodrilus* sp.; Mar: *Martiodrilus* sp.; Ocn: *Ocnerodrilidae* sp.; Anr: *Andiorrhinus* sp1. (circles and squares represent positive and negative scores and the surface is proportional to the corresponding value).

Table 1 – Lower and upper limits and number of pair points for each of the nine distance classes employed for computing the correlograms

Distance classes	Number of pair points	Inferior limit (m)	Upper limit (m)
1	112	0	11
2	194	11	22
3	460	22	33
4	346	33	44
5	380	44	55
6	276	55	66
7	178	66	77
8	60	77	88
9	10	88	99

Distance class is 11 m.

distance classes for convenience. The lower and superior limits (11 m apart) of each class, as well as the number of pairs of points are given in Table 1. The overall statistical significance of the correlograms was assessed using the Bonferroni corrected probability level (Oden, 1984). The corrected level of significance was $\alpha' = \alpha/k$, with k the number of distance classes and $\alpha = 5\%$ the global significance level (Oden, 1984). The whole correlogram was considered statistically significant when at least one coefficient was significant at the Bonferroni corrected level of probability: 0.005 = 0.05/9 (9 = number of distance classes) (Cooper, 1968).

Moran's index was calculated using the "Autocorrélation 3.03" module of the "R Package" of Legendre and Vaudor (1991), and the normality of the frequency distribution of the data were tested with a Kolmogorov–Smirnov test before the computation of Moran's index using the "VerNorm 3.0" module of the "R Package" (Legendre and Vaudor, 1991). When necessary, the Box–Cox transformation was used to reduce the asymmetry of the frequency distribution (Sokal and Rohlf, 1995).

2.6. Niche overlap (Pianka index)

The Pianka O_{jk} index ranges from 0 to 1 and the algorithm, a modification of the α competition coefficient (MacArthur and Levins, 1967) that can be estimated for two species is:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where p_{ij} and p_{ik} are the proportion of resource i used by species j and k, respectively.

In this study, a population dynamics niche overlap was calculated from the data obtained in the monthly sampling of 1 m^2 monoliths. We used the yearly average vertical stratification (cm) of population (percentage of individuals in each soil layer) and the seasonal variations in earthworm density (monthly number of individuals m^{-2} from July 1994 to June 1995) in both systems sampled. Another niche overlap index was computed using biometric attributes of species, i.e. average length, weight, diameter of earthworms and length/width and weight/width ratios. Both indices were multiplied to calculate the total spatio-temporal niche overlap. This procedure underestimates the actual value of the niche overlap index in opposition to the sum which over-estimates the total O_{jk} index (Pianka 1973, 1974).

The data collected from the 1 m^2 soil monoliths were used to compute the niche overlap among the following species: *Andiodrilus* sp., *Andiorrhinus* n.sp1., *Aymara* sp., *Glossodrilus* sp., *Martiodrilus* sp. and *Ocnerodrilidae* sp. (*Andiorrhinus* sp2. was only found in one sample during the 2-year study period).

3. Results

3.1. PTA

3.1.1. Grass–legume pasture

The descriptive statistics of the three temporal matrices is shown in Table 2, and the interstructure analysis in Fig. 1. We only retained the first axis (44.9% of total variance) of the interstructure analysis since it was clearly higher than the subsequent values. The ordination of sampling dates within the plane formed by the axes of the PCA showed an "intertable size effect" (Fig. 1a). The structure extracted in the first axis indicates that a common spatial pattern across the different dates was detected during the 2-year period (Fig. 1b).

The pattern was more conspicuous for two species, i.e. *Glossodrilus* sp. and *Andiodrilus* sp. Populations of *Glossodrilus* sp. showed a well-delimited high-density U-shaped patch. *Andiodrilus* sp. had a patchy distribution within the plot with two high population density areas, one in the north-west corner and the other one at the south-east corner. These patches seemed to be in opposite areas to those occupied by *Glossodrilus* sp. Other patches were detected for *Ocnerodrilidae* sp., *Martiodrilus* sp. and *Aymara* sp., although these were small and scarcely distributed across the field. *Ocnerodrilidae* sp. was more abundant in the west zone of the field, while *Martiodrilus* sp. was present in the north half forming a

Table 2 – Descriptive statistics (number of individuals m^{-2} ± standard deviation) obtained for each earthworm species in the savanna and pasture (data from the explicit spatial sampling)

Species	Savanna			Pasture		
	November 1993	November 1994	May 1995	September 1993	October 1994	June 1995
Andiodrilus sp.	2.0 ± 4.4	2.8 ± 5.2	2.5 ± 4.4	3.5 ± 6.1	4.4 ± 8.7	6.2 ± 13.0
Andiorrhinus sp.	0	0	0.1 ± 0.8	1.4 ± 3.5	0.2 ± 1.1	0.4 ± 1.5
Aymara sp.	0	1.4 ± 3.6	7.8 ± 9.5	0	0.5 ± 1.6	13.5 ± 17.3
Glossodrilus sp.	46.3 ± 39.7	19.0 ± 19.7	30.5 ± 25.9	66.6 ± 55.5	36.9 ± 23.5	102.5 ± 68.4
Martiodrilus sp.	0	0.1 ± 0.8	0.7 ± 2.6	1.0 ± 2.5	1.9 ± 4.6	14.5 ± 14.9
Ocnerodrilidae sp.	2.0 ± 6.6	3.1 ± 3.2	7.0 ± 11.8	0	6.6 ± 10.6	18.8 ± 23.5

V-shape patch and a line that crossed the plot from west to east. *Andiorrhinus* sp. displayed a rather scattered distribution with a more conspicuous population density patch in the east zone of the field.

In the compromise analysis the main spatio-temporal patterns of earthworm species and relationships among variables (population density) were highlighted by extracting only the first two axes, i.e. 28.1% and 22.5% of total inertia, of the PCA performed on the compromise matrix. The first axis of the PCA revealed clearly an opposition between *Glossodrilus* sp. and *Andiodrilus* sp. (Fig. 2a). The mapping of the 64 sampling point coordinates onto the first axis showed the presence of an aggregated U-shaped zone of positive coordinate points, which corresponded to an area where *Glossodrilus* sp. (black circles) was present and where, on the contrary, the distribution of *Andiodrilus* sp. (white squares) was not consistent (Fig. 2b). A high population density patch of *Andiodrilus* sp. dominated the south-east area (squares, negative scores), and the north-west was occupied by *Glossodrilus* sp.

(circles, positive values). The second axis extracted from the compromise analysis was responsible for 22.5% of total inertia, and revealed a clear spatial opposition between two species assemblages: *Andiodrilus* sp./*Martiodrilus* sp./*Glossodrilus* sp. on one hand, and *Andiorrhinus* n. sp1. and *Ocnerodrilidae* sp. on the other hand. We observed no clear spatial pattern for the second axis. Axis II showed nearly the same structure to the one displayed in the first axis (since *Glossodrilus* sp. also had a strong positive correlation with this axis), and the distribution pattern of *Andiodrilus* sp. also contributed to this axis. In fact, the definition of axis II is given by the spatial pattern of these two species. *Martiodrilus* sp. and *Andiorrhinus* n. sp1. showed opposite patterns (they both participate in the definition of axis II but in opposite directions). Finally, *Aymara* sp. and *Ocnerodrilidae* sp. did not contribute in the definition of the axes. A detailed contour map showing the spatial distribution of *Glossodrilus* sp. in the grass–legume pasture at two sampling dates can be consulted in Jiménez et al. (2001).
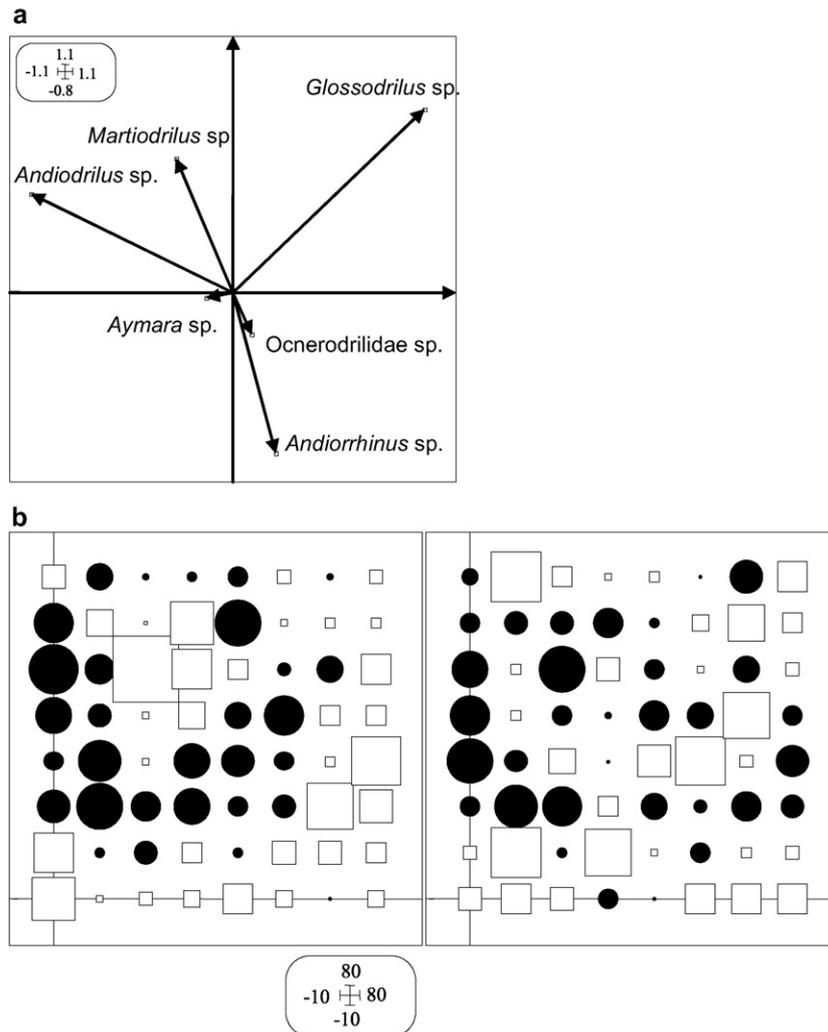

Fig. 2 – Results of the compromise analysis from the pasture; (a) correlation circle showing the ordination of variables (species) on the factorial plan defined by the first two axes of the PCA on the compromise matrix; (b) maps of the factorial coordinates of the 64 sampling points on the first two axes of the PCA on the compromise matrix (circles and squares represent positive and negative scores, respectively, and the surface is proportional to the corresponding value).

3.1.2. Natural savanna

The descriptive statistics of the three temporal data matrices is shown in Table 2 and the IA (Fig. 3). The first axis of the PCA was responsible for 38.4% of total data variability, and the inter-table size effect was also detected (Fig. 3a). Mapping of the axial coordinates of the 64 sampling points for each species is shown in Fig. 3b. Population of *Glossodrilus* sp. was placed in a diagonal from the north-west to the south-east corner, being more abundant in the former. We also observed two high population density patches in the south area of the field for *Andiodrilus* sp. The epigeic *Aymara* sp. revealed a high population patch in the south-east corner of the field. For the rest of earthworm species we were unable to detect any spatial pattern, either because of a low popula-

tion density or because of a weaker spatial autocorrelation level, except for *Martiodrilus* sp. in the south-west corner.

The first two "eigenvalues" of the compromise analysis explained 56.0% of total data inertia (33.1% and 22.9% for the first and second axis, respectively). Interestingly, the ordination of species in the plane defined by these two axes revealed the same general pattern that was observed in the introduced pasture, i.e. an opposite spatial pattern between population patches of *Glossodrilus* sp. and *Andiodrilus* sp. (Fig. 4a). *Martiodrilus* sp. was no longer associated with axis II because of its low and scattered population density in the native savanna (Jiménez et al. 1998a). Maps of the 64 sampling point coordinates onto the first two axes (Fig. 4b) showed the spatio-temporal structure displayed by *Glossodri-*
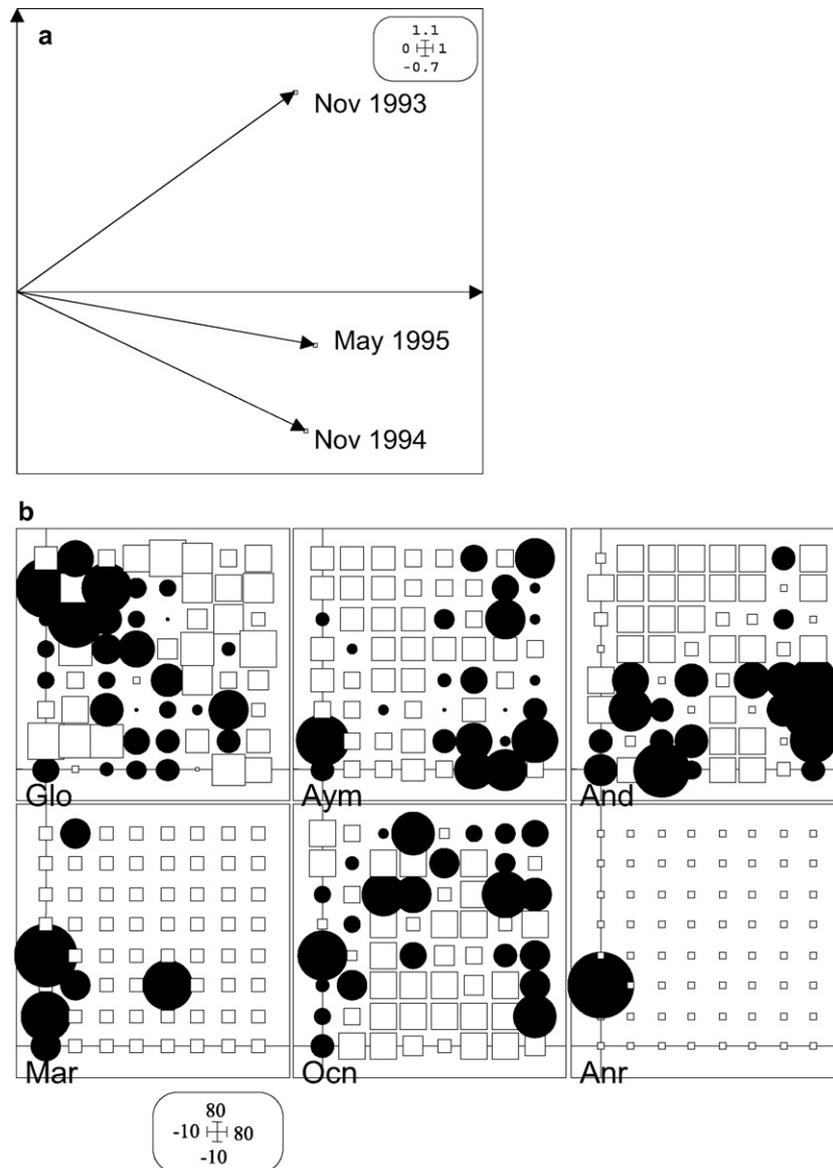

Fig. 3 – Results from the interstructure analysis; (a) ordination of sampling dates on the factorial plan defined by the first two axes of the PCA on the interstructure matrix (b) maps of the factorial coordinates of the 64 sampling points on the first axis of the interstructure analysis for each of the six species in the natural savanna. Glo: *Glossodrilus* sp.; Aym: *Aymara* sp.; And: *Andiodrilus* sp.; Mar: *Martiodrilus* sp.; Ocn: *Ocnerodrilidae* sp.; Anr: *Andiorrhinus* sp1. (circles and squares represent positive and negative scores, respectively, and the surface is proportional to the corresponding value).
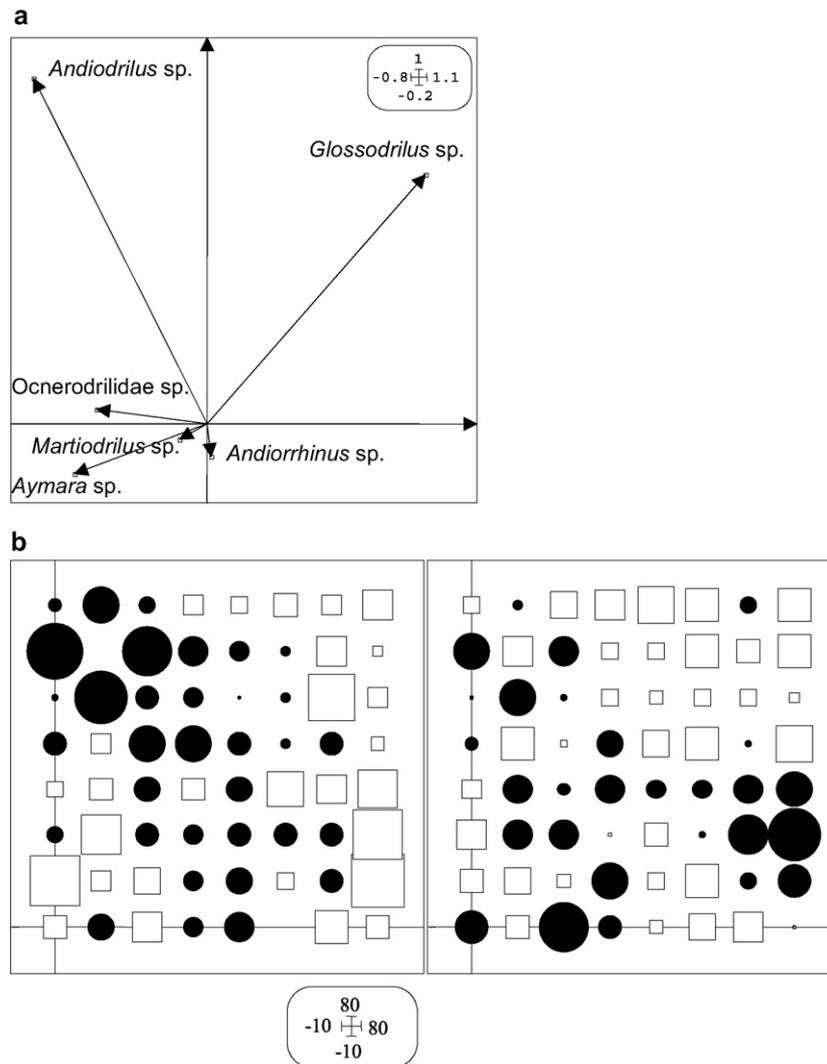
Fig. 4 – Results of the compromise analysis from the savanna; (a) correlation circle showing the ordination of variables (species) on the factorial plan defined by the first two axes of the compromise matrix, (b) maps of the factorial coordinates of the 64 sampling points on the first two axes of the PCA on the compromise matrix (circles and squares represent positive and negative scores, respectively, and the surface is proportional to the corresponding value).

lus sp. on the first axis (positive values, black circles) and *Andiodrilus* sp. (negative values, white squares). In other words, axis I showed the opposition between those areas occupied by *Glossodrilus* sp. compared with those areas where *Andiodrilus* sp. was dominant. An unclear and irregularly distributed pattern was observed for the second axis, although *Aymara* sp. and *Ocnerodrilidae* new genus sp. participated in the definition of this axis, whereas *Martiodrilus* sp. and *Andiorrhinus* sp. did not.

3.2. Correlograms

The correlograms computed with the sample scores upon the compromise PCA were significant at the Bonferroni corrected level for both the natural savanna and the grass–legume pasture ($P < 0.0055$). This means that spatial pattern of earthworm assemblage common to the sampling occasions was significantly autocorrelated. Correlograms of the

grass–legume pasture and the natural savanna displayed 3 and 1 significant Moran's I index values, respectively (Fig. 5a and 5b). Theses alternating values of the Moran's I index indicated the existence of two high-density patches of high population density of 20–30 m size, and a transition area between these two patches.

3.3. Niche overlap

Vertical niche separation among species was lower in the grass–legume pasture than in the natural savanna (Table 3a), although Pianka O_{jk} index for *Martiodrilus* sp. was very low in the savanna, due to the irregular density data obtained. The index ranged from 0.51 to 0.99 (mean = 0.77) in the pasture and from 0.10 to 0.98 (mean = 0.57) in the savanna.

Owing to the annual seasonal cycle of abundance the niche overlap index showed that populations of each species tended to be synchronized (Table 3b). In sites where a strong
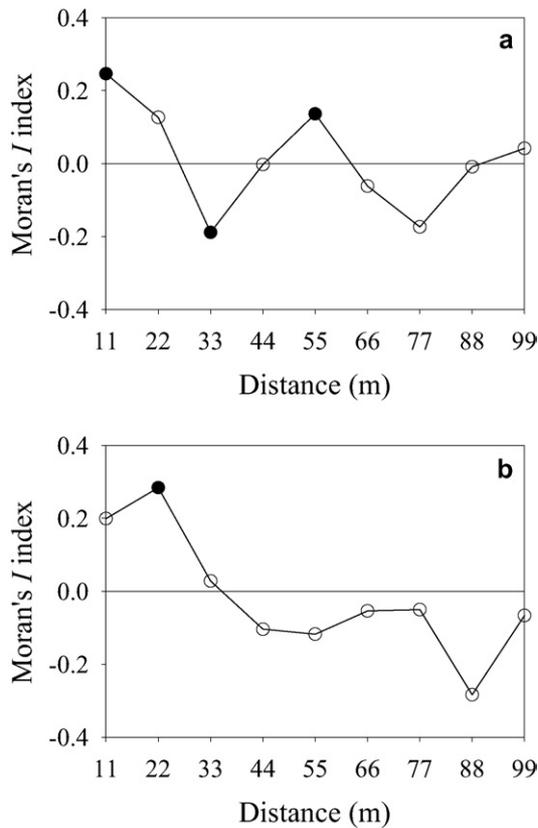
Fig. 5 – Moran's I index and correlograms computed from the factorial coordinates of the 64 sampling points on axis 1 of the PCA on the compromise-matrix in the pasture (a) and in the savanna (b) (○ = not significant; • = significant at the Bonferroni corrected probability level, P < 0.0055).

and rather long seasonality is present so varying soil moisture and organic matter content, as in Neotropical savannas, species are affected by the same environmental factors. The Pianka O_{jk} index ranged from 0.61 to 0.88 (mean = 0.74) and from 0.34 to 0.89 (mean = 0.66) in the grass–legume pasture and the natural savanna, respectively.

The biometric niche overlap index ranged from 0.25 to 0.99 (mean = 0.69) and from 0.43 to 0.95 (mean = 0.75) in the pasture and savanna, respectively (Table 3c). The lowest values were obtained between large species *Andiorrhinus* sp.

and *Martiodrilus* sp. and the smallest earthworm found *Ocnerodrilidae* sp. in both systems (biometric data of *Martiodrilus* sp. were not measured in the savanna due to the low-density).

The total spatio-temporal niche overlap (Table 4) was calculated as the product of each single O_{jk} index (vertical, population density and size). There was a greater spatio-temporal niche overlap in the pasture compared with the savanna. The O_{jk} index ranged from 0.13 to 0.73 (mean = 0.40) in the grass–legume pasture, whereas it ranged from 0.05 to 0.56 (mean = 0.32) in the natural savanna, respectively.

We were able to distinguish two groups or species assemblages: *Andiodrilus/Andiorrhinus/Aymara/Glossodrilus*, and *Martiodrilus/Ocnerodrilidae* sp. In the grass–legume pasture, *Andiodrilus-Andiorrhinus* (0.73), *Aymara–Glossodrilus* (0.65) *Andiodrilus-Aymara* (0.51) and *Andiodrilus–Glossodrilus* (0.49) showed the highest values of total niche overlap. The O_{jk} index between *Martiodrilus* sp. and *Ocnerodrilidae* had the lower value (0.13), mainly due to differences in size and in the seasonal cycle of their population density. In the natural savanna the highest niche overlap within the first group was obtained for *Aymara-Glossodrilus* (0.56), *Aymara–Ocnerodrilidae* (0.54) and *Andiodrilus–Glossodrilus* (0.52). Except for the *Ocnerodrilidae* earthworm, these species are usually concentrated in the topsoil while they are active and increase their population density at the onset of the rainy season (Jiménez and Decaëns, 2000). Species within the second group showed a low niche overlap (0.27), although this value is probably underestimated due to the low-density of *Martiodrilus* sp. in the savanna.

4. Discussion

4.1. Spatio-temporal pattern of species

The spatio-temporal pattern of earthworm species expressed through the interstructure analysis revealed that populations were mostly distributed as an alternation of density patches and gaps at the scale of 20–40 m. These alternating patches corresponded presumably to species with a high degree of niche overlap. Two endogeic species like *Glossodrilus* sp. and *Andiodrilus* sp. presented a clearly clumped distribution that seemed to be highly stable across time. This pattern may be a consequence of both demographical and life history traits

Table 3 – Niche overlap index computed for the yearly average vertical distribution (left half), the seasonal cycle of abundance (center) and the biometric characteristics (right half) of the earthworm community in the grass–legume pasture (upper line) and in the savanna (lower line)

	Anr	Aym	Glo	Mar	Ocn	Anr	Aym	Glo	Mar	Ocn	Anr	Aym	Glo	Mar	Ocn
And	0.97	0.97	0.98	0.65	0.68	0.66	0.85	0.83	0.79	0.67	0.80	0.89	0.77	0.75	0.60
	–	0.90	0.98	0.10	0.64	–	0.81	0.82	0.51	0.76	–	0.63	0.65	–	0.43
Anr	–	0.99	0.99	0.65	0.56	–	0.65	0.83	0.67	0.81	–	0.60	0.60	0.95	0.41
	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aym	–	–	0.99	0.57	0.51	–	–	0.80	0.68	0.76	–	–	0.99	0.40	0.94
	–	–	0.80	0.16	0.71	–	–	0.74	0.34	0.83	–	–	0.95	–	0.91
Glo	–	–	–	0.60	0.55	–	–	–	0.66	0.88	–	–	–	0.40	0.94
	–	–	–	0.11	0.59	–	–	–	0.56	0.89	–	–	–	–	0.94
Mar	–	–	–	–	0.85	–	–	–	–	0.61	–	–	–	–	0.25
	–	–	–	–	0.72	–	–	–	–	0.38	–	–	–	–	–
	a)					b)					c)				

And: Andiodrilus sp.; Anr: Andiorrhinus sp.; Aym: Aymara sp.; Glo: Glossodrilus sp.; Mar: Martiodrilus sp.; Ocn: Ocnerodrilidae.

Table 4 – Total spatio–temporal niche overlap indices computed for the yearly average vertical distribution of the earthworm community in the grass–legume pasture (upper line) and the native savanna (lower line) together with some data regarding the life history traits of species: adult weight, demography strategy; adaptive strategy and yearly average vertical distribution in the soil (data from Jiménez and Decaëns, 2000; Jiménez et al., 1998a, 1998b, 2000)

Species	Life history	Abbreviation	Anr	Aym	Glo	Mar	Ocn
Andiodrilus sp.	1.30 g; r-strategy; no strategy; 8.3 cm	And	0.51	0.73	0.49	0.40	0.34
			–	0.46	0.52	0.05	0.21
Andiorrhinus sp.	7.1 g; K-strategy; no strategy; 12.1 cm	Anr	–	0.48	0.47	0.41	0.16
			–	–	–	–	–
Aymara sp.	0.07 g; r-strategy; paradiapause; 5.2 cm	Aym	–	–	0.65	0.15	0.39
			–	–	0.56	0.05	0.54
Glossodrilus sp.	0.09 g; r-strategy; paradiapause; 6.7 cm	Glo	–	–	–	0.18	0.45
			–	–	–	0.06	0.49
Martiodrilus sp.	11.2 g; K-strategy; diapause; 32.5 cm	Mar	–	–	–	–	0.13
			–	–	–	–	0.27
Ocnerodrilidae	0.006 g; r-strategy; paradiapause; 22.7 cm	Ocn	–	–	–	–	–
			–	–	–	–	–

of these species. Whereas their high demographic rates allow them to increase rapidly their densities (Jiménez, unpubl.), their endogeic behavior and their medium size imply a low displacement capacity. Hence both species are likely to display markedly aggregated distribution, which is corroborated by the Morisita's I_d and Taylor b indices employed in a previous analysis (Jiménez et al., 2001).

Very small species like Aymara sp. (epigeic) and the Ocnerodrilidae sp. (endogeic) also showed an aggregated spatial distribution. Both species are commonly found close to high rich-organic hotspots, such as fecal pellets, Coleopteran nests and cattle dung (Jiménez et al., 1998b; Decaëns, 2000). The epigeic Aymara sp. shows one of the highest values of Taylor b aggregation index in both systems studied (Jiménez et al., 2001). We hypothesize that their spatial distribution reflect local spots of trophic resources availability, although this needs to be further assessed since it has not been measured per se in this study. The dynamics of the tropical savannas is controlled by extremely marked seasonality and earthworms develop adaptive strategies to withstand these extreme conditions. This is costly in terms of energetic savings for these species which live in poor-resource acid-soils, either in terms of energetic trade-offs or in terms of compensatory changes in their biology. These are species with a high population growth rate (r strategists), increasing their population rapidly at the onset of the rainy season. The spatial pattern of both species was not easily detected because the density of both species decrease along the year and we collected samples for the assessment of the spatial distribution at the end of the rainy season in two out of three sampling dates.

Martiodrilus sp. (anecic) and Andiorrhinus sp1. (endo-anecic), although significantly contributing to the second axis of the compromise analysis in the pasture, display weak spatio-temporal patterns. This may be interpreted as the result of their low demographic dynamics. Martiodrilus sp. has for example been described as a K selected species regarding its adaptive strategies (Jiménez et al., 1998a), reproduction rates (Jiménez et al., 1999), and life history traits (this species takes 4 years to reach maturity, Jiménez, unpubl.). Additionally, both species are commonly observed at the soil surface after heavy rains that flood their vertical burrows (Jiménez and Decaëns, pers. obs.), a behavior that decreases markedly the temporal stability of population patchiness.

Aggregation measures like Taylor b and Morisita I_d aggregation indices obtained for this species are consequently the lowest obtained among the whole earthworm community (Jiménez et al., 2001). In the savanna the density of both species was so low that no interpretable pattern could be provided. Here we observed the effect of land use system on the spatial distribution of several species that did not reach important population densities in the savanna.

In the natural savanna, the absence of a clear spatial distribution for some earthworm species in the upper right area of the plot might be due to the presence of the grass I. brasiliensis (with more than 50% of the right side of the plot invaded only by this plant; quantitative data are not shown). This grass has large straight sharp-pointed roots that can damage seriously the earthworm body. Only the Ocnerodrilidae sp. seems not to be affected by this feature (Jiménez, pers. obs.)

4.2. Spatial pattern of species assemblages

The significance of the spatial distribution of the earthworm community has been detected by the correlogram (Sokal and Oden, 1978). Following Legendre and Fortin (1989), the type of correlogram obtained in our study suggests that the spatial structure of earthworm assemblages was significant and characterized by the presence of several patches in the pasture whereas in the savanna only one patch was detected (Fig. 5a, b). The introduction of pasture has affected the size of the spatial structure but not the short-term temporal stability of the spatial distribution.

An alternation of patches (20–40 m) where particular species assemblages dominate was clearly observed, and the overall pattern may be described at different levels of spatial organization. These patterns have already been reported by Decaëns and Rossi (2001) in a grass–legume pasture (B. humidicola + several legume species) of the same study site, and by Rossi (2003c) in African savannas of Lamto (Côte d'Ivoire). It must be stated, however, that this spatio-temporal structure only represents a low proportion of the total variability of the initial data matrix (50.6% of the 44.9% explained by the first interstructure axis in the pasture, and 56% of 38.4% explained by the first interstructure axis in the savanna, respectively). This means that despite a high stability of the spatio-temporal distribution in earthworm assem-

blages, a large amount of variability remains unexplained. Sources of unexplained variability include among other factors short-range spatial patterns, i.e. below the scale of the minimum inter-sample distance (Rossi and Nuutinen, 2004), earthworm movements (Mather and Christensen, 1992) and sampling errors.

In both plots, a common spatial structure observed across sampling dates corresponds to a spatial opposition between the two medium-sized endogeic species *Glossodrilus* sp. and *Andiodrilus* sp., a pattern that was previously described by Decaëns and Rossi (2001). Both species display a high degree of niche overlap, which suggests a potential competition for resources. Two alternative interpretations may thus be proposed to explain this pattern. First, spatial segregation between both species may be the result of a mechanism of competitive exclusion. The presence of both species in the same plot would thus be attributed to co-occurrence mechanism within a community in a non-equilibrium stage (Tilman, 1982; Chesson, 1985; Ives, 1988; Huston and DeAngelis, 1994). This hypothesis, which has been proposed by Decaëns and Rossi (2001), implies a low temporal stability of the observed spatial opposition. Second, opposition may result from a response to soil heterogeneity with regard to earthworm resources or abiotic conditions. In this case species simultaneous presence would be related to true co-existence within a community at a stage of equilibrium (Chesson, 1985; Ives, 1988). This would thus imply a high correlation between earthworm an environmental heterogeneity, and a resulting high temporal stability of the spatial patterns. There is no evidence in our data to support one of these two hypotheses, and further investigations will be needed to clearly understand the factors responsible for the observed patterns.

4.3. Niche overlap and competition

Niche overlap refers to the utilization of some of the same resource types by two or more species. There are few studies on earthworm communities where the Pianka O_{jk} index has been computed. Lavelle (1983) reported average vertical niche overlap values in African savannas of Lamto (Cote d'Ivoire) to be 0.47. Similar values were cited by Nemeth (1981) in the neotropical rainforest of Venezuela, i.e. 0.50, and Fragoso (1993) also in a tropical rainforest in the Chajul and Los Txutlas region of Mexico, obtained values for this index that ranged from 0.48 to 0.75, respectively. The vertical niche overlap index obtained in our study was greater than in studies mentioned above. At Carimagua, earthworms were more abundant in the pasture topsoil than in the savanna. Litter quality material incorporated in the soil and/or root biomass which is greater in the grass–legume pasture than in the savanna (Rao, 1998; Thomas et al., 1995) may be responsible for the species aggregation observed, although this hypothesis should be further investigated.

Niche partitioning (Giller, 1984), niche overlap reduction (Pianka, 1973) and spatial partitioning, thanks to small scale environmental patchiness (Begon et al., 1996), have been proposed to explain co-existence mechanisms within soil communities (Atkinson and Sorrocks, 1981). As long as heterogeneity is becoming complex, the number of species within a

community increase, since the resource spectrum to be exploited is wider. Those species that overlap "too much" in any niche dimension cannot coexist in a given patch, and those that do coexist must differ in any resource use or niche dimension (e.g. body size or trophic morphology) that allows them to exploit different resources.

In our study, pairs of similar species were spatially segregated in different discrete patches. This was for example the case for the large pigmented *Andiorhinus* sp. and *Martiodrilus* sp. in the pasture, as well as for the small non-pigmented *Andiodrilus* sp. and *Glossodrilus* sp. in the pasture and in the savanna. Although these species may reduce their niche overlap through slight differences in their vertical distribution, annual density cycle and body size (Table 4), they seemingly present a too-high morphological similitude and a too-low total niche differentiation to co-exist at the patch scale. This suggests that competition acts as an important driving factor of community spatio-temporal patterns (non-equilibrium hypothesis).

Additionally, species simultaneously present in a given patch had different sizes, feeding regimes and adaptive strategies (Jiménez et al., 1998b; Jiménez and Decaëns, 2000; Mariani et al., 2001). The co-existence of potentially competing species within a patch may be interpreted as a consequence of ecological complementarity and of related deterministic assembly rules (Atkinson and Sorrocks, 1981). Species thus may avoid competition by occupying different microsites with specific soil properties (texture, organic matter content, root distribution), by being active in different soil layers or by ingesting size classes of soil particles. This, again, suggests that the studied earthworm communities are in a state of non-equilibrium in which competition represent the main type of interspecific interactions.

More ecological data are however needed to disentangle the different factors responsible for spatio-temporal patterns in earthworm communities. Especially a comprehensive study of the feeding regime of co-occurring species is necessary to:

- fully quantify the degree of niche partitioning;
- identify which species are competing, what kind of exclusion mechanisms occur;
- describe the assembly rules that allow co-existence in species assemblages;
- assess and quantify the availability of resources exploited by the species forming the earthworm community.

5. Conclusions

In our study we showed the existence of a clumped structured spatial distribution in the earthworm community of the natural savanna and the grass–legume pasture, within a significant temporal stability of 2 years. The range of factors that determine these spatial features are not yet clearly understood. Our results that population dynamics, environmental heterogeneity (also affected by changes in land use), and competitive interactions may act simultaneously at different scales to generate the observed patterns. Competition should be an important local factor, as suggested by the per-

sistence of separated distribution patterns for pair of morphologically related species, and by the limited niche overlap of species coexisting at the patch scale. Nonetheless, we do not conclude that a competitive exclusion process is occurring. Besides, this type of information is somehow rare and still absent in soil community ecology. The spatial ecology of soil organisms must be studied together with a complete and detailed assessment of the species ecology and biology when these are not known, the feeding regimes, adaptive strategies and population dynamics of earthworm communities. Future research should aim at disentangling the different driving factors of spatial en temporal dynamics in earthworm and other soil communities. This would also help to develop new insights in spatial soil ecology studies (Ettema and Wardle, 2002).

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