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Co-occurrence of earthworms in Lamto savanna: A null model analysis of community structure

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ABSTRACT

Diamonds assembly rules predict that competitive interaction leads to a non-random cooccurrence of patterns. Earthworms were sampled in three sites of vegetation of Lamto savanna to test the reducing level of co-occurrence of species among earthworm communities. Null model and spatial method were used as cokriging to generate patterns expected in the absence of species interactions. Three indices of null model showed that species co-occurrence in the three sites was less than expected by chance. Furthermore the cokriging revealed positive association between *Stuhlmannia porifera* and *Chuniodrilus zielae* and negative association between *Millsonia omodeoi* and the two other species. This study indicates that the non-random selection observed in the three sites of vegetation is due to an interaction between species close to the same ecological category.

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1. Introduction

The study of assembly rules that reflect species interactions is an active research area of community ecology [11,7,32]. Although assembly rules might imply the study of temporal changes in community composition [32], most investigators used assembly rules as descriptions of patterns at the community level [33]. Assembly rules can be defined as generalised restrictions on species presence or abundance that are based on the presence or abundance of one or several species or type of species [34]. Three decades ago, Diamond [12] described "checkerboard" distributions of avian species in the Bismarck Archipelago that never co-occurred, and predicted that competing species among assemblages should co-occur less than expected by chance. That study sparked a heated controversy in that the significance, or even the existence of assembly rules was questioned [15,1]. Connor and Simberloff [8] argued that assembly rules could not be inferred from observed patterns by comparing the patterns with those generated by Monte Carlo null model. Despite the controversy, species assembly rules based on the competition received with some further support from the study of Graves and Gotelli [16] in which they have reliably applied to Amazonian bird guilds. Later on, these rules were applied to other taxa, including plant, ants [17], ectoparasite [18] and recently to earthworms [31].

However, testing assembly rules remains tempting because of the lack of consensual methodology. Null models and cross-variogram have been chosen for such endeavour.

A null model is a statistical test (a pattern-generating model) that is based on the randomization of ecological data or random sampling from a known or imagined distribution [20]. Null models generate random community patterns that deliberately exclude a mechanism that is being tested. The comparison of random patterns with the observed patterns of natural communities provides an estimate of the effect of biotic interactions. Cross-variogram is a spatial analysis technique in which two variables are used with the aim of examining the spatial co-structure occurring between them.

In that study, we analyzed the co-occurrence patterns of earthworms in Lamto savanna. The study of earthworm communities has been carried out in various environments in western European forest [3], urban surroundings [31] and Grassland [5,13,22]. Most of those studies used diversity and association indices with the aim of comparing various ecosystems. However,

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deeper analysis of the structure of earthworm communities is rare [31]. Our study based on regular grid and extraction of earthworms by soil monolith will allow knowing the structure of earthworms. Lamto savanna is a mosaic of vegetation. Therefore earthworm populations are broken down in small communities that are often faced with unaccustomed competition. These communities actually represent excellent models that can be used for testing patterns of community assembly rules since earthworm community is recognized to be organized in well distinct soil strata that minimize the interspecific competition [4]: (1) the litter-dwelling or epigeic or detritivore earthworms live in the soil litter; (2) the anecic earthworms that spend most on their life within the soil and come out to feed on litter and (3) the soil-dwelling or endogeic polyhumic, endogeic mesohumic and endogeic oligohumic earthworms which live within the soil and feed on humic substances or dead roots.

The aim of this work is to use a Monte Carlo null models analysis [20] and cross-variogram to check for non-random patterns in co-occurrence of earthworms. The hypothesis is based on the prediction that species should co-occur less often than the expected by chance if there is a competition among a set of communities.

2. Materials and methods

2.1. Site description

The study site was located in the natural Reserve of Lamto (6°N, 5°2W) in Central Côte d'Ivoire. The reserve belongs to the transition zone between the semi-deciduous humid forest in the South and Soudanian savannas in the North. The 2700 ha of the reserve covered by a mosaic of forest and savanna is referred to Guinean savanna. The study plots are located in a grass savanna maintained by annual burning. Lamto is characterized by a bimodal rainfall indicating two wet seasons from April to July and from September to October. Mean annual temperature over 10 years (2000–2010) was 28.4 °C while rainfall is ranged between 8.4 mm in January and 189.7 mm in June with an annual sum of 1138.1 mm. Most soils lie on granitic bedrock are slightly acidic and classified as ferralsols (FAO classification) and constituted of 75% of sand.

2.2. Earthworms sampling

Earthworms sampling was carried out from July 2010 to September 2010 in rainy season on a 50 × 50 m plot obtained from grassy savanna, woody savanna and forest. Each plot was gridded at 5 m intervals to yield a block system of 10 "columns" and 10 "rows"; giving a total of 100 subplots of 25 m^2 each. A total of 100 monoliths of 50 cm side and 30 cm depth were systematically taken from the grid. Earthworms were extracted by direct hand sorting from the three successive strata of 10 cm depth [24]. However for this study all the strata were combined. Earthworms were all preserved in 4% formaldehyde. Individuals were identified in the laboratory to species level, counted and weighed. Species were determined using the taxonomic guides of Csuzdi and Tondoh [10].

2.3. Null model analysis

The data of each grid were organized as a presence–absence matrix, where each row and column represents a different species and monoliths ($n = 100$), respectively. In such a matrix, the entries represent the absence (0) or presence (1) of a particular earthworm species in a particular monolith. The indices obtained from each matrix were compared with those derived from 5000 randomly assembled matrices (null matrices). The choice of null model algorithms was made according to Gotelli [20] who demonstrated the sensitivity of co-occurrence test reliability to variation in species occurrence frequencies, and recommended that the row totals (i.e. species occurrence totals) were fixed by using suitable algorithms not prone to type I error (false rejection of the null hypothesis). He also found that the results were insensitive to variation in column totals (i.e. species number per site), and he suggested adjusting this constraint according to sampling methods and data set type. Two null algorithms were used in that study:

(a) The fixed–fixed algorithm in which both species occurrence frequencies and site species numbers are maintained. This impedes analyzing matrices with empty columns (sites with no species), which was not the case in our study. That algorithm maintains differences between sites, and is well adapted to analyzing 'island lists' [20], i.e. nearly exhaustive species lists from islands or well-defined habitat patches. We considered that algorithm as relevant for analyzing the total matrix which corresponded to a community survey in a landscape context (fragmented habitats of specific characteristics).

(b) The fixed–equiprobable algorithm in which row sums are fixed while columns are treated as equiprobable. Each species occurrence is thus randomly re-shuffled within each row of the matrix and all sites are treated as equally suitable. This algorithm is recommended for analyzing 'sample lists' [20], i.e lists of species taken from standardized samples within areas of relatively homogeneous habitat. It was therefore assumed to be particularly relevant for the study of the grass savanna, wooded savanna and forest matrices.

Conceptually, both algorithms are satisfactory because they correspond to a colonisation model in which species colonise an archipelago of islands randomly with respect to one another [20]. Combining these two is also assumed to provide a high reliability in the results of the tests.

Co-occurrence patterns were analyzed by computing the number of species combinations (Combo) [28], the number of species pairs that present perfect checkerboard distributions (checker) [12], and the related *C*-score index [31].

2.3.1. The *C*-score

Stone and Robberts [30] introduced the *C*-score as an index. This index quantifies the number of checkerboard that can be found for each species pair. The number of checkerboard units (CU) for any species pair can be calculated as:

$$\mathrm{CU} = (R_i - S)(R_j - S)$$

where R_i and R_j are the row totals, respectively, for species i and species j and S is the number of sites occupied by both species. The *C*-score is the average CU calculated for all unique pairs of species. The *C*-score measures the degree to which species pairs segregates across a set of samples, but it does not require complete segregation.

The larger the *C*-score, the less the average pairwise species co-occurrence. For an assemblage that is competitively structured, the *C*-score should be significantly greater than the expected by chance [20].

2.3.2. The number of checkerboard species pairs

Diamond [12] introduced the idea of "checkerboard distributions" of species pairs that never co-occur because of competitive interactions. We counted the number of such unique checkerboard pairs in each matrix. In a competitively structured community, there should be more such checkerboard pairs than expected by chance [12,21].

2.3.3. The number of species combinations (combo)

In a community of n species, there are 2^n possible species combinations, including the combination in which none of the species are present. We counted the number of species combinations by scanning the columns of each matrix for distinct arrangements. In a competitively structured community, not all species combinations will be represented [12], although differences in sites quality will also cause some combinations to be missing [26]. If there are “assembly rules”, i.e. species interaction (competition), H_0 should be rejected for each index ($P < 0.05$).

The standardized effect size (SES) was calculated for each index to allow cross-comparisons with other studies. SES scales the results in units of standard deviations, which allows for meaningful comparisons among different tests [19]. The null hypothesis is that the average SES measured for the entire data set is 0. The SES measures the number of standard deviations that each of the observed indices is above or below the mean index of the simulated null assemblages. It is calculated as:

$$(I_{\text{obs}} - I_{\text{sim}})/S_{\text{sim}}$$

where I_{obs} corresponds to the index for the observed assemblage, I_{sim} corresponds to the index for the null assemblages, and S_{sim} is the standard deviation of the null assemblages. Assuming a normal distribution, 95% of the SES values should fall between −2.0 and 2.0. Values larger than 2.0 indicate non-random species segregation and values lower than −2.0 indicate non-random species aggregation.

All these analyses were computing using the ‘EcoSim’ software 7.2 [19].

2.4. Spatial analysis

2.4.1. Variogram

In spatial statistics the theoretical variogram is a function describing the degree of spatial dependence of a spatial random field or stochastic process. It is defined as the variance of the difference between field values at two locations across realizations of the field [9]. It is estimated as:

$$2\gamma(h) = \frac{1}{n(h)} \sum_{i=1}^{n(h)} \left[z(x_i) - z(x_i + h)^2 \right]$$

where $n(h)$ is the number of sample pairs at each distance interval h and $z(x_i)$ and $z(x_i + h)$ are the values of the variable at any two places separated by a distance h. The lag h is a vector defined with both distance and direction.

The ‘2’ in front of the γ is there for mathematical convenience. The term $\gamma(h)$ is called the semi-variogram as the measure of the semivariance. The semivariance value when $\gamma(0) > 0$ is known as nugguet variance (C_0) and is caused both by sampling errors and by the spatial variability occurring within the minimum distance interval. The part of the variance attributed to spatial correlation is the spatial variance (C). The sill ($C_0 + C$) is the asymptote of the model and the range (a) represents the distance up to which two samples are correlated. The percentage of spatial dependence [$C/(C_0 + C)$] measures the proportion of the variance of a sample, which is explained by the spatial variance (C). If this proportion is close to 0, then the spatial dependence is low [9].

There are four common models used to fit semivariograms but in this study only three models were used: exponential, spherical, and gaussian. The exponential model is:

$$\gamma(h) = C_0 + C[1 - \exp(-|h|/a)]$$

where $C_0 + C$ is the sill, and a is the range. The spherical model is:

$$\begin{cases} \gamma(h) = C_0 + C\left[(3h/2a) - 0.5(h/a)^3\right], & 0 < h < a \\ C_0 + C, \quad h \le a \end{cases}$$

The Gaussian model is: $\gamma(h) = C_0 + C[1 - \exp(-h^2/a^2)]$ where terms are as defined above.

The relative variance is $C/(C + C_0)$ and the remaining variance is $C_0/(C + C_0)$.

2.4.2. Cross-variogram

Cross-variogram was used to assess the relationship between earthworm species (*Millsonia omodeoi*, *Chuniodrilus zielae* and *Stuhlmannia porifera*) in grass savanna. The Megascolecid *M. omodeoi* is a mesohumic endogeic (soil eater) earthworm that dominates the earthworm community in terms of biomass [24]. This species is classified as a compacting earthworm because it increases soil bulk density [6] whereas *C. zielae* (Omodeo) and *S. porifera* (Omodeo and Vaillaud) are endogeic species and belong to the functional decompacting species because they tend to decrease soil bulk density [6]. Furthermore the correlation matrix constructed with grassy savanna data (Table 1) showed a positive association between *C. zielae* and *S. porifera* and negative relation between *M. omodeoi* and the two others. Moreover *M. omodeoi* is endogeic mesohumic (soil eater) and *C. zielae* and *S. porifera* are endogeic polyhumic (soil eater).

It was performed using Gstat from “R package” [14]. Cross-variogram is a spatial analysis technique in which two variables are used with the aim of examining the spatial co-structure

Table 1
Correlation matrix.

Variables	Dis	omo	Sthp	Chuz	Chp	Agm	Dtn	Db	Da	Ago	Milsp1	Chsp1
Dis	1											
omo	0.01	1										
Sthp	0.02	-0.31^{**}	1									
Chz	−0.06	-0.24^{***}	0.39^{**}	1								
Chp	−0.07	−0.10	0.32	−0.01	1							
Agm	−0.08	0.01	0.09	0.06	0.03	1						
Dtn	−0.05	0.04	−0.08	0.03	−0.12	0.27	1					
Db	0.03	0.10	−0.10	−0.06	0.01	0.12	0.11	1				
Da	−0.08	0.08	−0.19	−0.16	−0.02	−0.06	−0.10	−0.11	1			
Ago	−0.03	−0.07	0.11	0.11	0.06	−0.05	−0.03	0.02	−0.04	1		
Milsp1	−0.03	−0.03	−0.11	−0.17	0.15	−0.13	0.03	0.07	−0.04	−0.05	1	
Chsp1	0.01	−0.30	0.17	−0.07	0.09	−0.16	−0.09	0.03	−0.13	−0.05	−0.01	1

Dis = *Dichogaster saliens*, omo = *Millsonia omodeoi*, Sthp = *Stuhlmannia porifera*, Chz = *Chuniodrilus zielae*, Agm = *Agastrodrilus multivesiculatus*; Dtn = *Dichogaster terrae-nigrae*; Da = *Dichogaster agilis*; Ago = *Agastrodrilus opysthogynus*; Milsp1 = *Millsonia* sp1; Chsp1 = *Chuniodrilus* sp1; ***Correlation is highly significant at 1% probability level, **Correlation is significant at 5% probability level.

Table 2
Density of earthworms (ind. m^{-2}) in the three stands of vegetation (mean ± SE, $n = 100$).

Earthworm species	Earthworm categories	Grassy savanna	Woody savanna	Forest
Agastrodrilus multivesiculatus	Endogeic oligohumic	1.64 ± 0.29	0.64 ± 0.15	6.44 ± 1.14
Agastrodrilus opisthogynus	Endogeic oligohumic	0.88 ± 0.4	0.76 ± 0.46	0.72 ± 0.34
Chuniodrilus palustris	Endogeic polyhumic	11.68 ± 1.79	1.44 ± 0.42	12.68 ± 1.95
Chuniodrilus sp1	Endogeic polyhumic	9.16 ± 2.15	4.44 ± 1.26	8.96 ± 1.56
Chuniodrilus sp2	Endogeic polyhumic	0	4.44 ± 1.26	2.76 ± 0.94
Chuniodrilus zielae	Endogeic polyhumic	21.96 ± 2.74	15.04 ± 2.07	13.36 ± 1.57
Dichogaster agilis	Epigeic detritivore	3.56 ± 0.65	11.44 ± 1.32	27.88 ± 2.19
Dichogaster baeri	Epigeic detritivore	0.92 ± 0.25	3.28 ± 0.78	3.4 ± 1
Dichogaster eburnea	Epigeic detritivore	0	1.04 ± 0.65	2.24 ± 2.1
Dichogaster saliens	Epigeic detritivore	0.24 ± 0.16	1.6 ± 0.59	0.24 ± 0.16
Dichogaster sp2	Epigeic detritivore	0	0.84 ± 0.37	0
Dichogaster sp3	Epigeic detritivore	0	0.52 ± 0.41	0.64 ± 0.52
Dichogaster terrae-nigrae	Endogeic oligohumic	0.72 ± 0.22	1.56 ± 0.3	0.96 ± 0.24
Hyperiodrilus africanus	Endogeic polyhumic	0	0.08 ± 0.56	0
Millsonia ghanensis	Endogeic oligohumic	0	0	0
Millsonia lamtoiana	Epigeic detritivore	0	0.88 ± 0.2	1.28 ± 0.27
Millsonia omodeoi	Endogeic mesohumic	21.68 ± 1.4	24.4 ± 1.6	7.72 ± 0.94
Millsonia sp1	Endogeic oligohumic	0.2 ± 0.08	0.32 ± 0.21	0.52 ± 0.15
Stuhlmannia porifera	Endogeic polyhumic	23.84 ± 2.47	7.08 ± 1.2	1.08 ± 0.65
Total		96.48 ± 12.6	75.36 ± 12.55	90.88 ± 15.72
Number of species		12	17	16

between them. Two variables are defined as cross correlated if the values of one at a given location depend (in a statistical sense) on the values of the others at nearby locations. Such variables are also named co-regionalized reference to the theory of Matheron [25]. Thus coregionalisation and cross-variogram are adequate tools to study interrelationships between different species density [27]. The spatial interdependence between v and w (two spatial variables) is expressed in the cross-variance estimated as:

$$\gamma_{vw}(h) = \frac{1}{2n(h)} \sum_{i=1}^{n(h)} [v(x_i) - v(x_i + h)][w(x_i) - w(x_i + h)]$$

where $n(h)$ is the number of all possible data pairs separated by a distance h. The cross-variogram is a plot of semi-variance against the distance h. The cross-variogram Graph of the three earthworms species was both drawn thanks to the package 'Gstat' from Ref. [25].

3. Results

3.1. Density of earthworm species

A total of 19 species of earthworms were recorded (Table 2). *M. omodeoi*, *C. zielae*, *Chuniodrilus palustris* and *S. porifera* were the most abundant in grassy savanna. *M. omodeoi* had the highest density in woody savanna, followed by *C. zielae* and *Dichogaster agilis*. *D. agilis* was the most abundant species in forest followed by *C. zielae* and *C. palustris*. The decreasing density order in the different sites was grassy savanna, forest and woody savanna. The student *t* test indicated that the highest density of earthworm was obtained in grassy savanna have followed by forest and wooded savanna ($P < 0.01$).

3.2. Variogram

The range of variogram model indicated that earthworms were spatially autocorrelated. Indeed three variograms models (Spherical, Gaussian and Exponential) were fitted to the estimated variogram for the three earthworms species. Table 3 summarizes the parameters of these models. The exponential model showed the best (Fig. 1) structure of the different earthworms species. Indeed the relative variance $[C/(C + C_0)]$ was high it varied from 70% to 90% for the three earthworms species. The variogram revealed the presence of a spatial autocorrelation up to 48.61 m. For *C. zielae*, nugget variance $(C_0) = 42$, structural variance $(C) = 379.8$ and range $(a) = 8.16$ m. The relative variance $[C/(C + C_0)]$ is high (90%). The relative nugget variance i.e. the remaining variance is 9%. The ratio C/C_0 (9.04) was large so the intensity of the spatial structure of earthworms was great.

For *S. porifera*, the relative variance $[C/(C + C_0)]$ is high (63%) and the relative nugget variance, i.e. the remaining variance is 37%. The ratio C/C_0 (4.03) indicated a greatest intensity of the spatial structure of earthworms. The fitted variogram model (Exponential) revealed the presence of a spatial autocorrelation up to 48.61 (the range). For *M. omodeoi*, the relative variance $[C/(C + C_0)]$ is high (70%) and the relative nugget variance i.e the remaining variance

Table 3
Variogram model parameters for *Millsonia omodeoi*, *Chuniodrilus zielae* and *Stulhmannia porifera* in grassy savanna.

Variables	Model fitted	Ratio (C/C_0)	Relative structural variance	Remaining structural variance	Mean	Sill	Nugget (C_0)	Structure (C)	Range (a)
Millsonia omodeoi	Spherical	1.13	0.53	0.46	21.68	152.25	71.38	80.87	36.53
	Gaussian	0.36	0.27	0.73		129.50	94.57	34.93	17.95
	Exponential	2.41	0.70	0.29		214.46	62.84	151.62	24.82
Chuniodrilus zielae	Spherical	1.23	0.55	0.45	21.68	315.09	141.19	173.9	23.89
	Gaussian	0.27	0.21	0.78		258.14	202.27	55.87	12.44
	Exponential	9.04	0.90	0.09		421.80	42	379.8	8.16
Stuhlmannia porifera	Spherical	1.69	0.62	0.37	23.84	427.03	158.69	268.34	50.46
	Gaussian	0.59	0.37	0.63		328.75	206.49	122.26	20.40
	Exponential	4.03	0.80	0.20		743.70	147.87	595.87	48.61

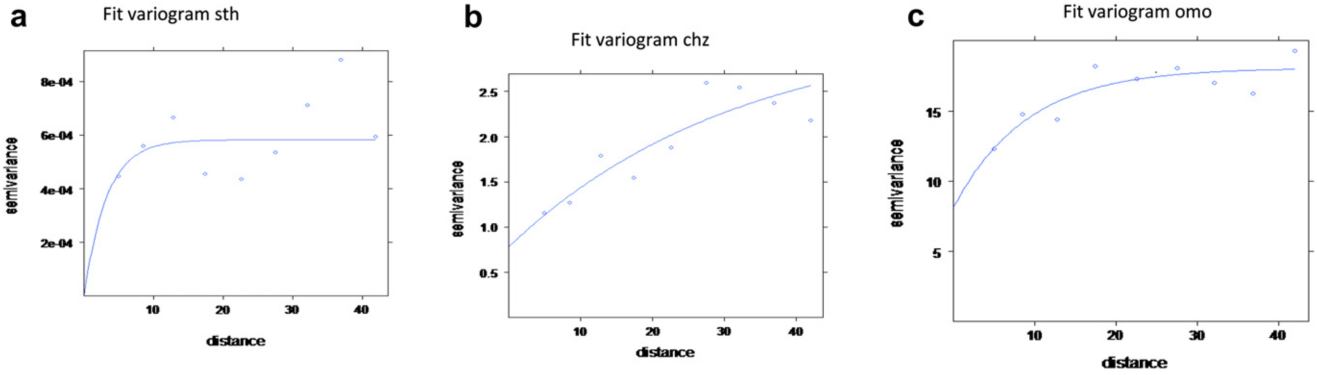

Fig. 1. Fit variogram model (exponential model) of *Stulhmannia porifera* (sth) (a), *Chunidrilus zielae* (chz) (b), *Millsonia omodeoi* (omo) (c).

was 30%. The ratio C/C_0 (2.41) indicated a lowest intensity of the spatial structure of earthworms. The fitted variogram model (Exponential) revealed the presence of a spatial autocorrelation up to 24.82 (the range).

3.3. *Cross-variogram*

The cross-variogram was made to establish relationships between the three populations of earthworms. The cross-variogram between *M. omodeoi* and the remaining species showed strong relationships that decreased with distance up to 15 m. The cross semi-variance was negative, which indicated that the three species counts varied in opposite ways at distances ranging from 5 to 15 m. On the contrary, the cross-semivariogram between *C. zielae* and *S. porifera* was positive. The cross-variogram graph (Fig. 2) indicated clearly the relationships between the three earthworms species. The survey related on the one hand a negative correlation between *M. omodeoi*, *C. zielae* and *S. porifera*, on the other hand a positive correlation between *C. zielae* and *S. porifera*.

3.4. *Co-occurrence analysis*

3.4.1. *C-score index*

The *C*-score index calculated in forest and wooded savanna based on null model, fixed–fixed, was large ($P > 0.05$) (Table 4). Therefore the null hypothesis was accepted. The appearance of earthworm species was random in these sites of vegetation. Furthermore the *C*-score index of forest and wooded savanna with the fixed–equiprobable algorithm has larger values ($P > 0.05$) (Table 4) than expected by chance. The simultaneous occurrence of these organisms was random but in grassy savanna the null hypothesis was rejected ($P < 0.05$). The matrix of presence–absence constructed with functional groups showed a competition within the group of soil-dwelling earthworms in grassy savanna. The *C*-score index of grassy savanna calculated with the algorithm

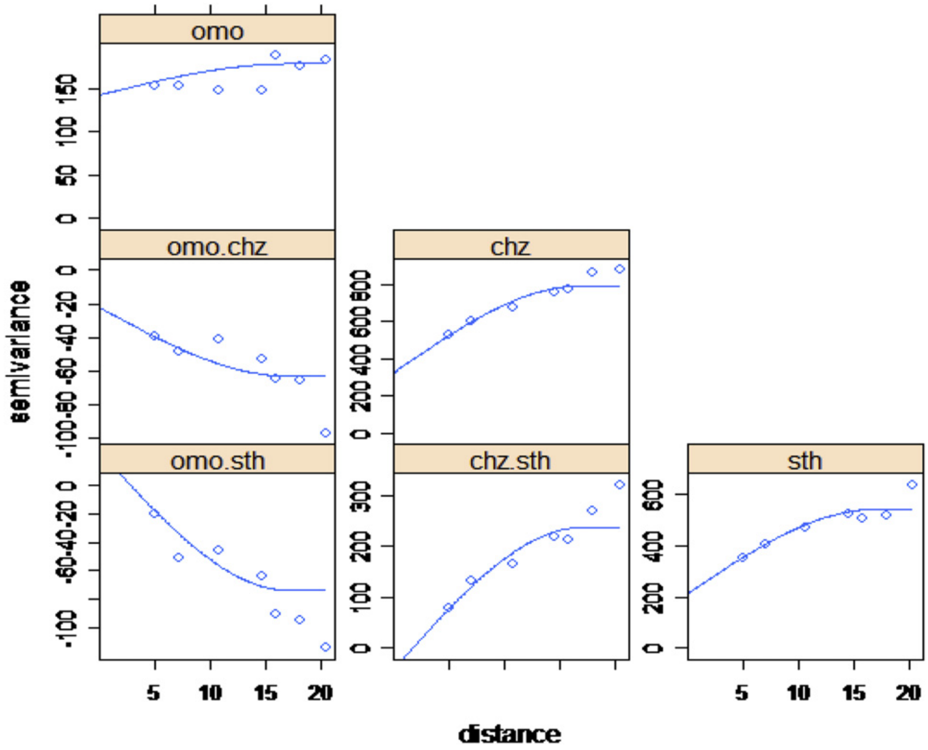

Fig. 2. Cross-variogram and variograms of density (ind. m^{-2}) of *Millsonia omodeoi* (omo), *Chuniodrilus zielae* (chz), *Stuhlmannia porifera* (sth) in the grass savanna.

Table 4
Null models (fixed–fixed and fixed–equiprobable) analysis of earthworms using *C*-score and Combo.

Null model	Observed indices	Mean of simulated indices	SES	Variance of simulated index	*P*
C-score					
Fixed–fixed					
F	181.16	178.22	1.46	2.77	NS
GS	139.67	138.52	0.71	2.63	0.008
WS	202.59	196.06	2.77	5.54	NS
Fixed–equiprobable					
F	181.16	197.93	−2.69	38.69	NS
GS	139.67	149.43	−1.91	25.96	0.02
WS	202.59	185.78	1.93	75.77	NS
Combo					
Fixed–fixed					
F	22	15.27	1.19	31.57	NS
GS	36	30.65	1.49	12.76	NS
WS	7	7.13	−0.07	2.99	NS
Fixed–equiprobable					NS
F	22	24.65	−0.92	8.27	NS
GS	36	31.17	1.38	3.49	NS
WS	7	7.37	−0.19	12.10	NS

P, tail probability that the observed index was greater than the expected by chance; SES, the standardized size effect, which is calculated as: (observed index − mean (simulated indices))/standard deviation (simulated indices). It scales the result in unit of standard deviations, which allows for meaningful comparisons among different tests; NS, Non-significant.
F = forest; WS = woody savanna; GS = grassy savanna.

fixed–equiprobale showed that the segregation of endogeics species was not random (SES > 2) (Table 5).

3.4.2. *Checkerboard index (checkerboard pattern)*

The results presented in Table 6 showed that earthworms appeared randomly in different sites of vegetations (forest, wooded savanna and grassy savanna). The checkerboard index calculated with fixed–fixed and fixed–equiprobable exhibited perfect checkerboard distribution of earthworms. This index did not show an interspecific competition between earthworms.

3.4.3. *Combo index (combination of species)*

The Combo index of grassy savanna, wooded savanna and forest calculated with the algorithm fixed–fixed and fixed–equiprobable showed that the null hypothesis was accepted (Table 4). Therefore these models showed that earthworms were not mutually exclusive. The algorithm fixed–fixed with the matrix of presence–absence showed that earthworm ecological categories appeared randomly in the different sites of vegetation (Table 7). The Combo SES with the two algorithms was less than 2 in all the sites.

4. Discussion

4.1. *Species co-occurrence patterns*

One of the fundamental questions in animal community ecology is whether communities are composed of species assembled randomly or if there are processes that influence the composition of species within communities [20]. The three indices of null model used in that study, namely the *C*-score, the checkerboard and the Combo showed that earthworms species are distributed randomly (non antagonism interaction) or non-randomly (antagonism interaction) according to vegetation sites of (forest, wooded savanna and grassy savanna). Our study showed that there is a competitive interaction between earthworms species. But among these three indices the checkerboard was a powerful tool in determining the community structure of earthworms. That index showed a perfect checkerboard pattern of the co-occurrence of earthworms. The particularity of that study lies on the fact that most studies concerning the co-occurrence of animal communities with the null model were made with large mammals, fish and birds [12]. However, recently some studies of soil organisms have been conducted including interspecific competition in the assembly of ants in England [2]. But the co-occurrence pattern of earthworms was conducted for the first time by Tiho and Josens [31] on Roosevelt Avenue, Brussels, Belgium. That study highlighted the interspecific competition between earthworm ecological categories. But the method of harvesting earthworms did not point up the community structure. Indeed, the study site (Roosevelt Avenue) failed to make monoliths. In our study the use of presence–absence matrices on a regular grid with the null models allowed us to highlight the relationship between the different categories of earthworms. That relationship of competition could be due to the

Table 5
Fixed–fixed and fixed–equiprobable null model analysis of earthworm ecological categories using *C*-score.

Null model	Ecological category	Observed indices	Mean of simulated indices	SES	Variance of simulated indices	*P*
Fixed–fixed						
F	Epigeic	443.8	438.85	1.38	14.14	NS
	Endogeic	182	175.95	1.60	14.20	NS
WS	Epigeic	346.5	354.21	−0.41	10.23	NS
	Endogeic	87.4	88.76	−0.39	12.08	NS
GS	Epigeic	186.16	159.07	3.28	68.13	NS
	Endogeic	271.8	272.19	−0.09	17.83	NS
Fixed–equiprobable						
F	Epigeic	443.8	434.94	0.26	1093.07	NS
	Endogeic	182	235.57	−2.89	341.74	0.002
WS	Epigeic	346.5	395.55	−1.16	1781.25	NS
	Endogeic	87.4	96.75	−0.82	130.03	NS
GS	Epigeic	271.8	271.63	0.006	736.23	NS
	Endogeic	44.66	57.62	−2.14	36.37	0.02

P, tail probability that the observed index was greater than the expected by chance; SES, the standardized size effect, which is calculated as: (observed index − mean (simulated indices))/standard deviation (simulated indices). It scales the result in unit of standard deviations, which allows for meaningful comparisons among different tests; NS, Non-significant.
F = forest; WS = woody savanna; GS = grassy savanna.

Table 6
Null models (fixed–fixed and fixed–equiprobable) analysis of earthworms using checkerboard.

Null model	Observed indices	Mean of simulated indices	SES	Variance of simulated index	*P*
Fixed–fixed					
F	82	87.07	−1.90	7.06	NS
GS	78	82.20	−1.59	6.97	NS
WS	58	64.20	−2.42	6.52	NS
Fixed–equiprobable					
F	82	88.59	−2.55	6.68	NS
GS	78	83.04	−1.84	7.45	NS
WS	58	65.008	−2.73	6.54	NS

P, tail probability that the observed index was greater than the expected by chance; SES, the standardized size effect, which is calculated as: (observed index − mean (simulated indices))/standard deviation (simulated indices). It scales the result in unit of standard deviations, which allows for meaningful comparisons among different tests; NS, Non-significant.
F = forest; WS = woody savanna; GS = grassy savanna.

Table 7
Fixed–fixed and fixed–equiprobable null model analysis of earthworm ecological categories using combo.

Null model	Ecological category	Observed indices	Mean of simulated indices	SES	Variance of simulated indices	*P*
Fixed–fixed						
F	Epigeic	26	25.17	0.58	1.95	NS
	Endogeic	26	24.25	1.16	2.24	NS
WS	Epigeic	13	14.56	−1.93	0.64	NS
	Endogeic	18	16.55	1.30	1.23	NS
GS	Epigeic	10	10.09	−0.10	0.80	NS
	Endogeic	19	18.39	0.53	1.25	NS
Fixed–equiprobable						
F	Epigeic	26	24.66	0.95	1.94	NS
	Endogeic	26	24.33	1.06	2.44	NS
WS	Epigeic	13	14.23	−1.34	0.84	NS
	Endogeic	18	16.14	1.31	1.98	NS
GS	Epigeic	10	10.43	−0.44	0.94	NS
	Endogeic	19	17.89	0.90	1.48	NS

P, tail probability that the observed index was greater than the expected by chance; SES, the standardized size effect, which is calculated as: (observed index − mean (simulated indices))/standard deviation (simulated indices). It scales the result in unit of standard deviations, which allows for meaningful comparisons among different tests; NS, Non-significant.
F = forest; WS = woody savanna; GS = grassy savanna.

spatial occupation of earthworms. The *C*-score revealed some interactions between the soil-dwelling earthworms in grassy savanna and forest. The *C*-score index is related to the rules of assembly of species described by Diamond [12] but the demonstration of its non-random model does not constitute a proof for these rules. The factors that could influence the non-random process distribution include habitat heterogeneity and dispersal barriers [29,31]. In addition, stochastic processes can generate random patterns as detected by the null model. Our study showed that grassy savanna and forest soil-dwelling earthworms do not have a random structure. Thus, our findings are congruent with those of Tiho and Josens [31]. That could be due to the fluctuation of the season and soil heterogeneity, because of their seldom migration on soil surface. During sampling, we found that in both the rainy season and dry season these worms kept their soil-dwelling character. Often in the dry season it was noted that earthworms migrate further. Our study really shows that earthworms were not randomly distributed because of the diametrically opposition of two sites. Forests could be favourable for earthworms, because soil surface moisture is always maintained. The *C*-score algorithm fixed–fixed showed that the endogeic polyhumic earthworms parted to the other categories either in the forest as wooded savanna. But other groups had an aggregate distribution. The checkerboard index showed the same model of distribution. That model of earthworm distribution has been shown by Rossi [29]. That assemblage might be due to the factors such as soil temperature, moisture content, water content and the gradient of soil organic matter. It is observed in wooded savanna that patterns are random and this randomness may be due to a complex set of effect. Because the vegetation is a mixture of two types of vegetation litter (grass and wood). In this case 3 conditions can cause the random distribution of earthworms: (i) the competition is close and each species occupy an independent niche, (ii) there are sufficient resources for all the species, (iii) the presence of stochastic effect in the site therefore the competition is not possible.

The calculated SES was weak in our study. Its value was ranged from 0 to 3. Our present study really shows a strong influence of competition in structuring earthworm communities.

4.2. Spatial patterns

The absence of direct association between the cluster of *M. omodeoi* (endogeic) and *S. porifera* (endogeic polyhumic) could be due to a complete independence between the two different species of earthworm. That result also suggested that the both species do not share the similar niche. On the contrary, the structure of *C. zielae* and *S. porifera* evolved in the same way. That might be due to the fact that the two species belong to the same family and thus had the same structure and behaviour. Moreover they belong to the same functional group and shared the same niche. The negative correlation detected between *M. omodeoi* and *S. porifera* and *C. zielae* could be due to the fact the two functional groups of earthworm are not complementary. Our result could also be explained by a competitive interaction as interspecific competition between them due to an overlapping of niches. The competition could be linked to food resources or soil factor such as water content. Another explanation could be that *S. porifera* and *C. zielae* are endogeic polyhumic and sometimes feed on litter and soil whereas *M. omodeoi* which is an endogeic feeds on soil only. That survey presents a separated distribution pattern for pair of earthworm functional group and competitive exclusion process occurring beside. Our result was in agreement with those of Lavelle [23,24]. Our study pointed up the interaction between earthworm species, there was also an agreement between our results and those of Stone and Robberts [30] who studied earthworms aggregation in the Lamto savanna. They did not reveal the differentiation of earthworm niche because their study described the spatial distribution of earthworm in soil using geostatistic. The present study confirms the result of Blanchart et al. [6]. They found the opposite structure between the endogeic polyhumic (*C. zielae* and *S. porifera*) and the endogeic mesohumic (*M. omodeoi*).

It can be concluded that the null model indices (checkerboard and combo) used in this study showed that earthworms were randomly distributed in the forest and woody savanna at Lamto savanna. However, in grassy savanna, soil-dwelling earthworms were not randomly distributed. In addition the algorithm fixed–equiprobable *C*-score index showed that soil-dwelling organisms endogeic differed from the other categories neither in the forest nor in wooded savanna. The other categories (epigeic) of earthworms showed an aggregative nature. The actual study pointed up the inter-specific competition between earthworm species.

The semivariance performed in this survey showed that the structure of the different earthworm species was distinct. However each species was autocorrelated in this stand of vegetation. Moreover the spatial structure of endogeic mesohumic earthworm (*M. omodeoi*) and the endogeic polyhumic (*S. porifera* and *C. zielae*) were opposite.

Although our study showed the niche differentiation of the three earthworms we were unable to study the spatial process with several species at the same time. Our method allows us to study the spatial structure of two species only. We will recommend another spatial method which allows revealing niche partitioning of several species at the same time. Besides we recommend a future study to test earthworm niche partitioning by null model study for determining niche complementary according to soil strata. These studies will help to know how earthworms were spatially structuring according to soil strata.

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