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Original article

Spatial dissociation between two endogeic earthworms in the Colombian “Llanos”

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Abstract

Although there has been a growing interest in the study of soil fauna spatial distribution during the past decade, the identification of the environmental driving factors behind the population patterning are difficult to highlight. Soil physico-chemical heterogeneity is partly responsible for structuring the population. However, the available statistical analyses show that the proportion of the population spatial variance that can be ascribed to soil habitat variability is modest. We studied the spatial distribution of two medium-sized endogeic earthworm species (*Andiodrilus* sp. and *Glossodrilus* sp.) and the spatial segregation between them. The survey was undertaken in a native savanna and a grass-legume pasture in the Colombian “Llanos”. The presence of spatial dependence in the data (i.e. earthworm counts) was tested using two different approaches: the Spatial Analysis using Distance IndicEs (SADIE) analyses and cross-coregionalization. The SADIE index allowed for testing the spatial association or dissociation between earthworm counts. The spatial organization of both species was well structured in the natural savanna while they were randomly distributed in the pasture in almost all sampling dates. When the spatial distribution was different from randomness it was always aggregated irrespective of the land-use system. There was no absolute stable spatial pattern in the natural savanna although a general pattern seemed to emerge. On the contrary, no pattern was observed in the pasture. Both species displayed opposite spatial distributions ($P < 0.05$) that were of different intensity depending on the sampling date. The presence of opposite patches and gaps suggests the presence of a competitive exclusion phenomenon (at least spatial) that deserves further investigations.

Keywords: Earthworms; Tropical savanna; Spatial ecology; SADIE analysis; Competition

1. Introduction

The assessment of the spatial distribution of soil organisms has become an important subject of study during the last years [1,8,12,19,21–23,25]. The spatial pattern of soil biota is controlled by biotic conditions and habitat distribution [2,16] but some species like ecosystem engineers [10] may in turn dramatically affect the physical structure of their habitat. In so doing, they potentially affect the distribution of other species [2,21]. Within a community, it is also possible that different species may have the same pattern due to similar ecological response to environmental constraints or positive interspecies relationships. Besides, two species may exhibit dissimilar distributions if they have different responses to environmental conditions or if they have negative interspecific relationships.

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Earthworm species often form complex communities comprising from 13 to 17 species [5]. There is a complex spatial vertical stratification of species depending on their adaptive strategies, feeding habits and the soil organic matter gradient [6,11]. Little is known however about the horizontal spatial distribution of species assemblages. The issue of the temporal stability of the assemblage structure has been examined in three studies [1,7,21] and opposite spatial patterns have been reported in [21] for two species.

This work aimed at examining the presence of non-random spatial distribution of two endogeic earthworms, i.e. *Andiodrilus* sp. and *Glossodrilus* sp. from the Colombian “Llanos”. We mainly focused in these two species only because they showed medium-term stable and opposite spatio-temporal distribution and a high degree of niche overlap [7]. Earthworms were sampled at three sampling occasions in order to assess the temporal variability of species spatial distribution. Emphasize was given to the spatial association/dissociation of species counts and to the fine description of the clusters of earthworm counts [19].

2. Materials and methods

2.1. Site description

The study was carried out at the CORPOICA-CIAT Carimagua research station, in the well-drained isohyperthermic savannas of the Eastem Plains of Colombia (4°37′N and 71°19′W, 175 m altitude). Climate is subhumid tropical with a 4-month dry period (December–March); average yearly rainfall and temperature is 2280 mm and 26 °C, respectively. Open herbaceous savannas with scattered trees and shrubs in the uplands (“altos”) and gallery forests and *Mauritia minor* and *M. flexuosa* palms (“morichales”) in the lowland savannas (“bajos”) are the dominant vegetation type. Soils are acidic (pH 4.5 in water) Oxisols (Tropeptic Haplustox Isohyperthermic) in the uplands and Ultisols (Ultic Aeric Plintaquox) in the lowlands (USDA).

In an upland area two plots were investigated: a native herbaceous savanna of *Andropogon bicornis*, *Gymnopogon* sp., *Panicum* spp., *Trachypogon* spp. and *Imperata* sp., and a 2 ha 17-year-old grass-legume pasture (*Brachiaria decumbens* and *Pueraria phaseoloides*). The pasture was fertilized and grazed at a rate of 1 AU ha^{-1} during the dry season and 2 AU ha^{-1} during the rainy season (AU = animal unit, 250 kg live weight).

2.2. Earthworm sampling

In this study data were collected by applying a spatially explicit sampling strategy: soil monoliths (40 × 40 × 15 cm) were dug out in 64 sampling points (at the nodes of a 70 × 70 m grid). The soil was hand-sorted in the field on a plastic mantle and collected earthworms were identified, counted and released in the monolith emplacement. We surveyed the plots at three different dates: November 1993, November 1994 and May 1995, in the native savanna, and September 1993, October 1994 and June 1995 in the grass-legume pasture. To avoid sampling at the same points in the different dates samples were displaced along a spiral whose origin was represented by the point sampled at the first date. The difference of location (ca. 30 cm) was deemed negligible as compared to inter-sample distance and the sample position was therefore considered as identical from one date to another.

2.3. Earthworm species

Eight native species form the earthworm community of both the native herbaceous savanna and the grass-legume pasture. The main biology and ecology of each species is precisely described in [9]. This study mainly focused on the relationships between two endogeic species that dominate the community in terms of density, i.e. *Glossodrilus* sp. (width = 1.2–1.4 mm, length = 68.4 mm; weight = 0.08 g.f.w.) and *Andiodrilus* sp. (width 3.2 mm; = length = 70.6–75.1 mm; weight = 0.64 g.f.w.) has been considered to study the spatial autocorrelation between both. As stated in the introduction, we decided to perform such analysis on these two species because they showed a relative stable and opposite spatial distribution in the systems evaluated [7].

2.4. Data analysis

2.4.1. Cluster identification by Spatial Analysis using Distance IndicEs (SADIE) analysis

Earthworm counts were analyzed with the SADIE developed by Perry et al. [15]. Throughout this study we define the term “cluster” as a region of either relatively high density, i.e. a patch or relatively low mean density, i.e. a gap. The SADIE method was specifically developed to handle count data collected at spatially-referenced sampling units. It allows determining whether species display random, aggregated or regular spatial distribution using a global index of aggregation (I_a). For a random distribution its expected value is 1, while it is larger (lower) for aggregated (regular) patterns (see [15] for a complete description of the method). In addition, a local cluster index can be estimated for each sampling point (i.e. each count). It is positive (negative) for a sample that has more (less) individuals than expected under the null hypothesis of complete spatial randomness. Positive and negative index values are, respectively, referred to as vi and vj following Perry et al. [15]. The SADIE method allows testing these indices against the null hypothesis of complete spatial randomness by means of a random permutations procedure [15]. The positive (vi) and the negative (vj) index values permit a direct identification of samples that contribute to patches or gaps or that correspond to areas where the density displays no significant departure from its average value across the study plot. The individual significance of each sampling unit was assessed using the heuristic thresholds of 1.5 and –1.5 proposed by Perry et al. [15].

2.4.2. Patch and gap descriptions

Once the clusters were isolated and their type determined (patch, gap or non-significant values), they were described using various landscape metrics that are fully described in various references amongst which [4]. A patch (gap) consisted of at least one sample location where the vi (vj) index was significant. Adjacent sample locations having significant index values (either vi or vj) formed a single cluster (see [15] for details). The following indices were used: NC equals the number of clusters of a given type (i.e. patch, gap or random), PLAND equals the percentage the plot area comprised of the corresponding cluster type, LCI equals the percentage of the plot area comprised by the largest cluster of each type.

2.4.3. Species association–dissociation and date to date similarity

In order to determine whether the observed patterns were transitory or durable we used the association index developed with the SADIE system [14]. This index also allowed testing the spatial association or dissociation between earthworm counts [14]. The observed value of the index is tested against the null hypothesis of complete spatial independence of counts from each other. The test is based on random permutations [14]. Since two sets of counts are compared, it is possible to test the relationships between two species count data or to compare single species data at two different sampling occasions.

We additionally used cross-variograms to assess the relationships between species data [24]. It allows examining the joint variability of two variables. Cross-variograms between species density were estimated using the software VAR5 [28].

3. Results

The density of both species and fluctuated according to sampling date and differed markedly in relation to land-use type (Table 1). *Glossodrilus* sp. had higher density than *Andiodrilus* sp. The spatial variation was different from date to date and these two endogeic earthworm species displayed opposite spatial distributions (Fig. 1). For example in the savanna in 1995 (Fig. 1A,C), patches and gaps occupy different areas depending on the species. Moreover, when the observed cumulated spatial distribution is plotted (Fig. 1D,E), patches, gaps and random areas occupy different areas across the study plot (savanna).

3.1. Spatial aggregation

Using the SADIE index I_a led to contrasted results according to the land-use system considered (Table 2). The spatial distribution of both species was well structured in the natural savanna while spatial randomness prevailed in the pasture in all sampling occasions, except for *Glossodrilus* sp. in 1994 (I_a index, Table 2). Similarly, the cumulated counts (over all sampling occasions) were significantly aggregated (I_a index, Table 2). No regular spatial distribution was observed. Species aggregation generally corresponded to significant patches and gaps as indicated by the mean vi and mean vj values (Table 2).

Table 1
Descriptive statistics for earthworm's density in the savanna and pasture plots in the Colombian "Llanos". Density is number of individuals m^{-2}. Standard deviation is indicated between parentheses. $N = 64$ samples were collected at three sampling occasions

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)
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)

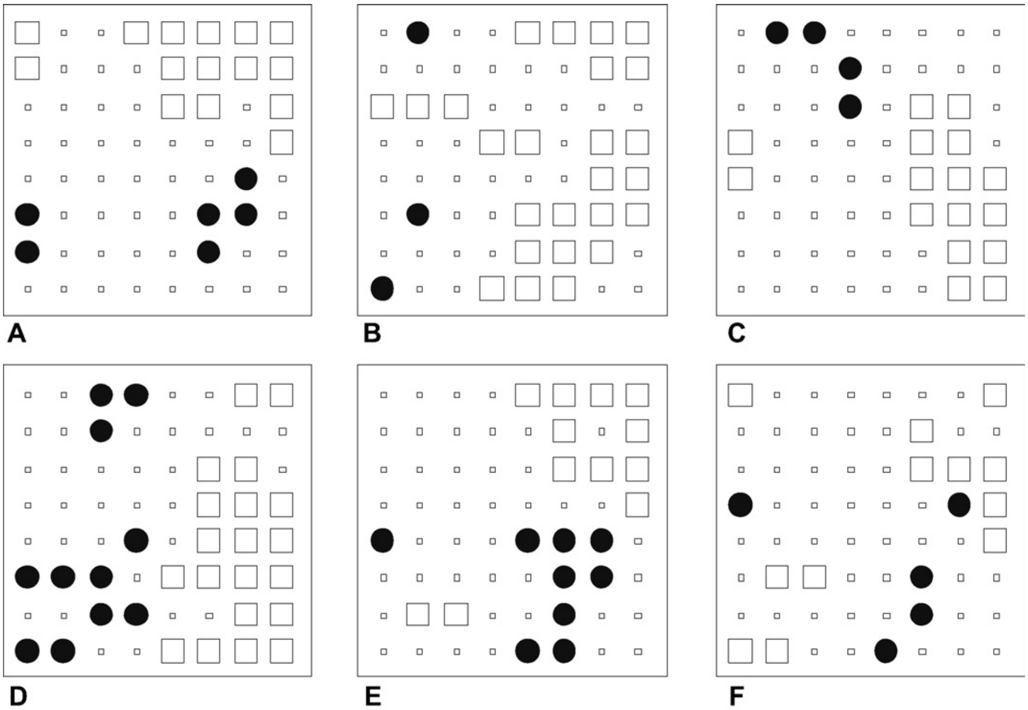

Fig. 1. Maps of the spatial aggregation index (SADIE) indicating the position of earthworm patches (circles), gaps (squares) in the savanna. Small squares indicate sampling units where earthworm counts did not significantly differ from the average count value across the study plot. A: *Glossodrilus* sp. (1995) B: *Andiodrilus* sp. (1993) C: *Andiodrilus* sp. (1995) D: *Andiodrilus* sp. (1993–1995 cumulated) E: *Glossodrilus* sp. (1993–1995 cumulated) F: *Glossodrilus* sp. (1993).

Table 2
SADIE aggregation indices and associated probability levels for *Glossodrilus* sp. and *Andiodrilus* sp. in a savanna and a pasture in the Colombian "Llanos"

System	Sampling Dates	I_a	Mean vj	Mean vi
Savanna				
Glossodrilus sp.	1993	1.298	–1.179	1.137
Glossodrilus sp.	1994	0.935	–0.899	1.019
Glossodrilus sp.	1995	1.464*	–1.515**	1.35*
Glossodrilus sp.	1993–1995[a]	1.479*	–1.408*	1.329*
Andiodrilus sp.	1993	1.584**	–1.586**	1.442**
Andiodrilus sp.	1994	1.262	–1.262	1.328*
Andiodrilus sp.	1995	1.516**	–1.516**	1.257
Andiodrilus sp.	1993–1995[a]	1.831***	–1.703**	1.653**
Pasture				
Glossodrilus sp.	1993	1.184	–1.258	1.265*
Glossodrilus sp.	1994	1.341*	–1.401*	1.245
Glossodrilus sp.	1995	1.072	–1.037	1.074
Glossodrilus sp.	1993–1995[a]	1.302	–1.341*	1.26
Andiodrilus sp.	1993	0.985	–0.983	0.959
Andiodrilus sp.	1994	0.9	–0.898	0.941
Andiodrilus sp.	1995	0.991	–0.995	1.003
Andiodrilus sp.	1993–1995[a]	1.073	–1.041	0.988

I_a is a global index of aggregation. Mean vj and mean vi represent mean negative and positive index values that indicates gaps or patches, respectively (see [14] for details). Indices were tested for departure from randomness using 1560 permutations. Probability levels are indicated as follows: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

[a] Data cumulated over the indicated period of time.

3.2. Cluster attributes

We only report here the results corresponding to the savanna plot because spatial aggregation was very weak in the pasture plot (Table 2). In the savanna, the number of clusters (i.e. patches or gaps) ranged from 2 to 5 for *Glossodrilus* sp. and 1 to 3 *Andiodrilus* sp. (Table 3). The percentage of the plot area covered by the patches or gaps was low for both species (Table 3). Similarly, the largest cluster index was low and varied substantially for both species and across sampling occasions (Table 3). Most of the plot surface corresponded to non-significant local cluster indices (vi or vj) referred to as random in Table 3. The values of the LCI for these zones were generally high indicating that a large proportion of the corresponding surface was constituted by one large cluster. On the contrary, the LCI for patches and gaps varied substantially for both species and across sampling occasions (Table 3).

3.3. Species spatial association

The coefficient of association indicated a tendency towards dissociation (i.e. negative index value) in the savanna and the pasture although it was only significant for two dates (Table 4). When analyzing the cumulated data over the whole sampling period in the savanna both species showed an aggregated pattern (Table 2, I_a values) comprising areas of patches and gaps (Table 2, mean vi and mean vj values). The association

Table 3
Descriptive statistics of the spatial clusters characteristics for *Glossodrilus* sp. and *Andiodrilus* sp. in a savanna in the Colombian "Llanos"

Species	Date	Type	NC	PLAND (%)	LCI (%)
Glossodrilus sp.	1993	Patch NS	3	7.81	4.69
	1993	Random	1	73.44	73.44
	1993	Gap NS	5	18.75	9.37
	1994	Patch NS	1	1.56	1.56
	1994	Random	1	92.18	92.18
	1994	Gap NS	2	6.25	4.68
	1995	Patch*	2	9.37	6.25
	1995	Random	1	67.19	67.19
	1995	Gap**	2	23.44	20.31
	1993–1995[a]	Patch*	2	14.06	12.50
	1993–1995[a]	Random	2	67.19	65.62
	1993–1995[a]	Gap*	2	18.75	15.62
Andiodrilus sp.	1993	Patch**	3	4.69	1.56
	1993	Random	2	56.25	51.56
	1993	Gap**	3	39.06	21.87
	1994	Patch*	3	9.37	4.68
	1994	Random	1	71.87	71.87
	1994	Gap NS	2	18.75	14.06
	1995	Patch NS	1	6.25	6.25
	1995	Random	1	68.75	68.75
	1995	Gap**	2	25.00	21.87
	1993–1995[a]	Patch**	2	17.19	12.50
	1993–1995[a]	Random	1	51.56	51.56
	1993–1995[a]	Gap**	2	31.25	28.12

NC: number of clusters of each type (patch, gap and random) type; PLAND and LCI: percentage the plot area corresponding to a given cluster type and to the largest cluster of each type, respectively. Cluster significance was tested for departure from randomness using 1560 permutations. Probability levels are indicated as follows: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$; NS non-significant.

[a] Data cumulated over the indicated period of time.

Table 4
SADIE association index for *Glossodrilus* sp. and *Andiodrilus* sp. in a savanna and a pasture in the Colombian "Llanos" and associated probability levels

System	Sampling Date	Association Index	P Level	
Savanna	1993–1995[a]	–0.1384	0.8502	
	1993	–0.2536	0.9603	
	1994	0.1884	0.077	
	1995	–0.3012	*0.987*	*Dissociation*
Pasture	1993–1995[a]	–0.0729	0.7094	
	1993	–0.0729	0.6997	
	1994	–0.2893	*0.977*	*Dissociation*
	1995	–0.1225	0.8213	

P-values less than 0.025 and larger than 0.975 indicate significant association and dissociation, respectively. The overall level of significance is 0.05.

[a] Data cumulated over the indicated period of time.

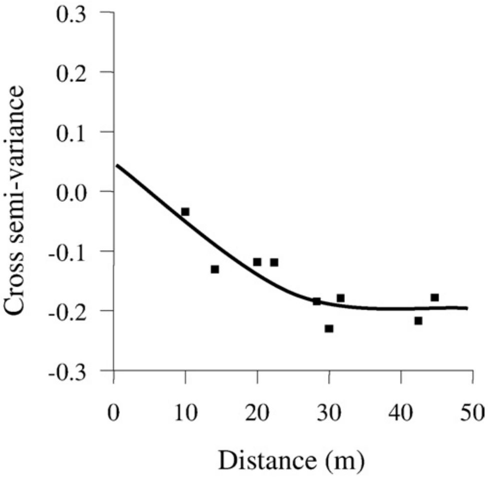

Fig. 2. Cross-variogram for *Glossodrilus* sp. and *Andiodrilus* sp. in the savanna (September 1993). The model parameters are: Nugget cross semi-variance $C_0 = 0.05$; spatial cross semi-variance $C = –0.257$; the sill $C + C_0 = –0.207$ and the range $a = 37.7$ m.

index was negative i.e. indicated a tendency towards dissociation but was non-significant. The cross-variograms revealed a clear relationship between earthworm species, but only in 1993 in the savanna (Fig. 2). The cross semi-variance was negative, which indicated that the two species counts varied in opposite ways at distances ranging from 8 to 45 m.

3.4. Date to date similarity

The date to date similarity in count distribution was only assessed in the natural savanna since the pasture showed very poor spatial clustering. There was no stable spatial pattern as date to date comparisons fell to give significant association index (results not shown).

4. Discussion

A more holistic understanding of the underlying processes determining the spatial distribution of soil organisms has been provided with the work of [1–3,19,20,23]. In this study, the use of spatial statistics allowed for the detection of different areas occupied by two endogeic species, and revealed the possible existence of spatial exclusion phenomena in a natural savanna. The scale of spatial patterns reported in this study (between 20 and 40 m) agrees with those reported by other authors [18,19]. In patches where either one or the other dominates, the coexistence with other species might be the result of niche partitioning mechanisms. Actually, both species show a high degree of niche overlap [7] as measured by the Pianka O_{jk} index [17]. However, a more detailed ecological study on feeding habits is necessary to assess the degree of niche partitioning and intensity of competition. The spatial segregation is probably the predominant mechanism that leads to the observed species distribution [1], although results must be cautiously interpreted since both SADIE analyses and cross-variograms only showed formal spatial dissociation at certain sampling occasions.

The present study focused on two species out of the community and revealed a lack of stability through time in the grass-legume pasture. Another study [7] showed that if we analyzed the earthworm community as such using adapted statistical tools, it was relatively stable through time. These results are only conflicting apparently because the tools involved as well as the aims of these studies are different. First the methods (SADIE indices and the cross-variogram) used in the present study directly analyzed the count data whereas the tool used in [7] (the Partial Triadic Analysis) extracted and only analyzed the information common to all dates [21]. By doing this, it allowed to remove random-like variability and focus on temporally stable spatial information. This is not the case when we analyzed the raw data and this may be the reason why we only clearly perceive the populations' aggregation at all dates. Besides this also explain why the opposition between species distributions are not significant at all dates.

There were some differences between the patterns observed in the natural savanna and the grass-legume pasture. The spatial aggregation and association of earthworm species was more clearly detected in the savanna than in the grass-legume pasture. One explanation could be the presence of a higher amount of random variability in the data collected in the pasture i.e. the patterns are not expressed as clearly as they are in the natural savanna. In that case, the PTA—which removes the random-like noise from the data—is more efficient in detecting the patterns than the SADIE analysis or the cross-variogram and it provides to similar community organization irrespective of the land-use [7]. In this study, however, we focused on the relationships between two species and the multivariate analyses like PTA are not applicable. We showed the cross-variograms to be a useful tool to preliminary highlight the co-variation between the spatial patterns of populations. However the structure functions used in geostatistics (e.g. variogram, cross-variogram) are not always appropriate when one is dealing with count data [13], and the SADIE method provides a very interesting alternative in that instance [14,15]. A combination of spatial techniques is recommended to better understand the underlying processes in the distribution of organisms in the soil [26,27].

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