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Soil environmental heterogeneity allows spatial co-occurrence of competitor earthworm species in a gallery forest of the Colombian 'Llanos'

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Disentangling how communities of soil organisms are deterministically structured by abiotic and biotic factors is of utmost relevance, and few data sets on co-occurrence patterns exist in soil ecology compared to other disciplines. In this study, we assessed species spatial co-occurrence and niche overlap together with the heterogeneity of selected soil properties in a gallery forest (GF) of the Colombian Llanos. We used null-model analysis to test for non-random patterns of species co-occurrence and body size in assemblages of earthworms and whether the pattern observed was the result of environmental heterogeneity or biotic processes structuring the community at small scales by means of co-inertia analysis (CoIA). The results showed that earthworm species co-occurred more frequently than expected by chance at short distances, and CoIA highlighted a significant specific relationship between earthworm species and soil variables. The effect of soil environmental heterogeneity on one litter-feeding species but also the impact of soil-feeding species on soil physical properties was revealed. Correlogram analysis on the first axis extracted in the CoIA showed the scale of the common structure shared by the fauna and soil variable tables. The earthworm community was not deterministically structured by competition and co-occurrence of competing species was facilitated by soil environmental heterogeneity at small scales in the GF. Our results agreed with the coexistence aggregation model which suggests that spatial aggregation of competitors at patchily distributed resources (environment) can facilitate species coexistence.

Whether the spatial distribution of soil organisms is the result of abiotic or biotic processes or both is a key topic in soil ecology studies. Community assembly rules (Diamond 1975) rely on species interactions, mainly competition, and habitat constraints as factors generating predictable community patterns, and imply that a series of abiotic and biotic filters select species out of a regional pool (Weiher and Keddy 1999). Besides, species traits determine the response to environmental constraints as these act as filters and determine species assemblages' at different scales (Dunson and Travis 1991, Belyea and Lancaster 1999). Consequently, non-random spatial organization of species' assemblage involves the existence of at least one structuring factor, e.g. inter-specific competition and/or habitat constraints, while random species patterns could be interpreted as the joint action of contrasting factors, or stochasticity.

The spatial patterning of soil organisms is shown to be generally clumped, with alternation of high- and low-density population patches ranging from small to larger scales, i.e. several cm to tens of metres (Albrecht and Gotelli 2001, Jiménez et al. 2001, Ettema and Yeates 2003, Rossi and Nuutinen 2004), although regular pattern at short distances have also been described (Thomas et al. 2008). The factors that cause and control these discrete patches and their spatial segregation are difficult to identify and interpret and include heterogeneity of both environmental (biotic and abiotic) factors and internal population processes (fecundity and dispersal ability) (Ettema et al. 2000, Decaëns and Rossi 2001, Barot et al. 2007).

Co-occurrence of competing species takes place if the environment is spatially heterogeneous (from scales of cm to km) leading to spatial segregation (Amarasekare 2003). For example, competing species within a community may exhibit checkerboard distribution leading to competitive exclusion process (Diamond 1975). Moreover, at small scales two competitors may co-occur if they are spatially excluded from the patch where one of them is present. As mentioned above, spatially structured communities and patches of specific assemblages can reflect a response to the spatial heterogeneity of soil resources resulting in spatial exclusion between species having different ecological requirements. On the contrary, species co-occur in a given patch in relation to ecological complementary, i.e. differences in spatial and trophic niche axes, and higher resource availability may result in assemblages of competing species within the same patch (Amarasekare 2003). Despite this knowledge, data on spatial competitive co-occurrence from empirical studies on soil communities are not abundant.

Understanding the effects of local interactions is important in the study of inter-specific competition (Chesson 2000a). The influence of soil spatial variability in shaping species assemblages' of soil animal communities is poorly understood as there are few studies on the subject (Decaëns and Rossi 2001, Ellwood et al. 2009). New data are thus needed on co-occurrence patterns to explore the links between the degree of co-occurrence in earthworms and the spatial distribution of soil environmental resources exploited by the community. Amongst the current tools that specifically recognize non-random patterns in organisms, null-model analysis has frequently been used (Gotelli 2001). In the present study, we used null-model analysis in combination with niche overlap and multivariate ordination techniques to test whether the earthworm community of a gallery forest of the Eastern Plains of Colombia (hereafter referred to as GF) was structured by competition at short spatial scales, as previously reported in the natural savannas of this region (Jiménez et al. 2006, Decaëns et al. 2009).

Material and methods

Study site

Fieldwork was carried out at the CORPOICA-CIAT Carimagua research station in the well-drained isohyperthermic savannas of the Eastern Plains ('Llanos') of Colombia (4°37′N, 71°19′W, 170 m a.s.l.) during the rainy season of 1999. The Colombian Llanos south of the Meta River is a young alluvial plain consisting of Pleistocene and Holocene sediments of Andean origin (Goosen 1971). Climate in the area is defined as subhumid tropical, with unimodal regime. The site receives annually 2280 mm precipitation and yearly mean temperature is 26°C, with a marked dry season from December to March (CIAT data, 1972–1995). A dense drainage network of gallery forests dissects the 'Llanos Orientales' and feeds into the Orinoco catchment. Soils have been described as Oxisols in the upland savannas and Ultisols in the lowland areas, respectively. They are acid (pH $[H_2O] = 4.5$) with $> 90\%$ of Al saturation, and low values of exchangeable nutrients for plants. Fragmented ironstones are normally observed when erosion has exposed the ferruginous material (laterite) layer (Blydenstein 1967).

Earthworms and soil were sampled in a nearby GF located in 'La Reserva' bordering the Carimagua Lake. This is a secondary forest where the most abundant tree species were *Dendropanax arboreum* (Araliaceae), *Enterolobium* spp. (Leguminosae), *Ficus* spp. (Moraceae), *Jacaranda copaia* (Bignoniaceae), *Copernicia tectorum* and *Hymenaea courbaril* (Caesalpiniaceae), and *Cecropia* sp. (Cecropiaceae), and palms like *Mauritia flexuosa*, *M. minor*, *Mauritiella* sp. and *Attalea maripa* (Palmaceae) are normally found near the shore of Carimagua Lake.

Earthworm assemblages and soil sampling

Based on previous results from sampling campaigns in the savanna (Decaëns and Rossi 2001, Jiménez et al. 2001, 2006), soil pits of 25×25 cm^2 and 20 cm depth, distributed in the nods of a 10×10 points regular grid with 5 m inter-sample distance, were dug out to retrieve earthworms. The number of individuals for each species was annotated and earthworms were released back in the soil. Earthworms were at their maximal activity period by the time where sampling was conducted, and density of the anecic *Martiodrilus* sp. was estimated by counting the number of fresh casts deposited in the soil surface which was shown to be a reliable procedure (Jiménez et al. 1998). Litter was hand sorted prior to pit excavation and conserved in plastic bags until drying at 105°C for 48 h to calculate litter biomass.

In each of the 100 sampling points, four soil cores were taken at the four sides of the pit:

1. Bulk density was determined with the core method (soil dry mass per volume) using a 5×5 cm metal cylinder; soil water content (soil water per volume, and soil water per dry mass) were determined gravimetrically.
2. The second soil core (0–5 and 5–10 cm)was taken for soil organic C (SOC) determination with the colorimetric method after digestion in H_2SO_4. The Kjeldahl method was used for total N concentration. Before analyses soil was oven dried at 75°C for 48 h and finely grounded. The C:N ratio was simply calculated as the SOC concentration divided by the total N concentration obtained. Available P was determined with Bray-II extraction.
3. The third soil core (15 cm depth and 10 cm diam.) was taken for determination of aggregate size-class distribution. Approximately 100 g of air-dried soil was used for standard dry-sieving through a sieve column of 4.75, 2.0, 1.0, 0.5 and 0.250 mm and shaking for 30 min.
4. The fourth soil core (15 cm depth and 10 cm diam.) was used for root length (root length estimator) and biomass determination. In the lab the soil was washed and sieved to separate fine (< 2 mm) and coarse roots (> 2 mm), and then oven-dried at 105°C for 48 h.

Finally, soil structure was indirectly quantified by measuring the resistance of the soil to penetration (RP) with a penetrometer. Three readings were taken at each sampling point and graphed on recording cards. Soil penetration resistance was determined when the soil moisture content in the topsoil was ca 38% (pF = 2.8).

Data analysis

Relationship between earthworm assemblages and environmental heterogeneity

Correspondence analysis (CA) was performed on fauna data and principal component analysis (PCA) on soil environmental variables. Those species having less than 5% of frequency in total data were removed from the analysis. CA allowed the recognition of six species assemblages based on their positive or negative row scores onto the first three axes extracted in the analysis, e.g. A1+ (assemblage 1, positive coordinates onto the first axis), A1− (negative coordinates) and thereafter, A2+, A2−, A3+ and A3−.

Co-inertia analysis (CoIA), which is a generalization of the multivariate inter-battery methods developed by Tucker (1958), is an accepted flexible multivariate ordination method for examining the association between two data matrices (Dolédec and Chessel 1994, Dray et al. 2003) and to search for the relationships between species and environmental variables (Moretti and Legg 2009). CoIA aims at exploring the common structure of two tables that share the same rows, i.e. study objects, sampling points. One advantage of the CoIA is that it also enables the linkage between tables having quite different numbers of variables, species and/or samples. CoIA allows standard analysis like CA and PCA to be connected following any transformation of the data set (row weighted option is recommended) (Dolédec and Chessel 1994). The output of a CoIA from CA and PCA is very similar to canonical correspondence analysis (CCA) (ter Braak 1986) and the two approaches aim to find a site score that is a linear combination of environmental variables maximizing the variance of species centroid (i.e. separation of species niches). The CCA is sometimes recommended, although CoIA avoids the multicolinearity problem associated with CCA, in addition to its simplicity and robustness for matching two tables (Dolédec and Chessel 1994). When variables are correlated, i.e. concentrations of C, N and C:N ratio, CCA becomes unstable and CoIA is appropriate (Dray et al. 2003). Detrended correspondence analysis (DCA) has been suggested instead to remove the arch (horseshoe) effect; however, when CoIA is performed on faunistic and environmental data the arch effect is removed because the likely arch structure of the faunistic table has no equivalent to the structure of the environmental data (Dolédec and Chessel 1994). The statistical significance of the CoIA was assessed with a Monte Carlo permutation test (10 000 simulations).

Since the samples were taken in a spatially explicit sampling design with 100 points we consider the output of the CoIA as spatial co-structure. However, while the CoIA reveals patterns of co-variation between soil fauna and soil physico-chemical environment, it does not explicitly account or test for the presence of a spatial structure and its scale. We examined this feature by computing the Moran's autocorrelation index (Sokal and Oden 1978, Rossi 1997). Positive and negative sample scores of the first two axes extracted in the CoIA were used to describe common local structures of both data matrices (Thioulouse et al. 1995). This allowed us to assess the degree of autocorrelation of the co-structure between soil variables and fauna data.

For the computation of the correlogram data were allocated to 11 distance classes for convenience and a minimum of 50 pairs of points were used for each distance class. The overall statistical significance of the correlogram was performed with a Bonferroni corrected probability procedure. The corrected p* was $\alpha' = \alpha/k$, with k the number of distance classes and $\alpha < 0.05$ the global significance level (Oden 1984). The correlogram is statistically significant when at least one coefficient is significant at the corrected p* of $0.05/11 = 0.0045$ (Cooper 1968). The Kolmogorov–Smirnov test was used to test the normality of data frequency distribution. The asymmetry of the frequency distribution was reduced with a Box–Cox transformation when normality assumption was not achieved (Sokal and Rohlf 1995). All analyses were performed with the statistical package R 2.12.0 (R Development Core Team), unless otherwise stated.

Null-model analysis of species co-occurrence patterns

Data of earthworm abundance was converted into a presence–absence matrix, which is the fundamental unit of analysis in community ecology. The advent of co-occurrence analysis and other statistical techniques have provided ecologists with more and more precise tools to explore non-random patterns in natural communities. In a given community not all species combinations are likely to occur, and some species pairs are forbidden or less probable because competing species are likely to exclude each other (Diamond 1975). Compared to randomly assembled, those competitively structured communities should contain fewer species combinations, more checkerboard pairs and higher C-score than expected by chance (EBC) (Gotelli and McCabe 2002). In our study, we tested if the relative spatial arrangement of species during the period of maximal earthworm activity presented less species co-occurrence than EBC (Gotelli 2000). The C-score index (Stone and Roberts 1990) was computed to analyze earthworm co-occurrence pattern in a presence/absence data matrix and also by using the row scores of the first axis extracted in the CA, explaining the maximal variance, that were later converted in a presence/absence data matrix. The C-score index is based on the average co-occurrence of all species pairs, and measures the checkerboard pattern of species' and/or species assemblages' mutual exclusion. It was used because of its statistical power and non-proclivity to type I error (Gotelli 2000).

A Monte Carlo null model simulation was used to randomize the species matrix with the swapping algorithm, i.e. the original matrix was shuffled repeatedly with random submatrices (Stone and Roberts 1990, Manly 1995). The observed index value was calculated and compared to 10 000 null communities that were randomly assembled. Because the co-occurrence tests are very sensitive to variation in species occurrence frequencies, row totals should be preserved as a constraint in the null model (Gotelli 2000). We selected three algorithms to compute the C-score for the tests that were related to the questions asked:

a) Fixed-equiprobable, where species occurrence totals are fixed (rows) and all sites (columns) are equiprobable, recommended for analysing 'sample lists' (Gotelli 2000).
b) Fixed-fixed, where both species occurrence totals and sites' species numbers are maintained, so the random community contains the same number of species as the original community and each species occurs in the same frequency (Connor and Simberloff 1979). This model has more statistical power than the equiprobable model (Ulrich and Gotelli 2007).
c) Fixed-proportional, where species occurrence totals (rows) are fixed and sites differ in suitability. This algorithm is a hybrid between the first two, and it may cause

the null hypothesis to be incorrectly rejected when using the C-score (Gotelli 2000).

The V-ratio index was also computed as a measure of the variability in the number of species present in each sampling point. The computation of the V-ratio with the first two algorithms is useful for determining if the number of co-occurring species is constrained by species interactions, and equals zero if there is the same number of species per site (Gotelli 2000).

Finally, the standardized effect size (SES) was calculated to quantify the direction and degree of deviation from the null model. This is a Z-transformed score ($Z = [x - \mu]/\sigma$), where $x =$ observed index value, $\mu =$ mean and $\sigma =$ the standard deviation of the 100 index values from the simu-lated matrices and compare to the observed index. SES values above -2.0 and below 2.0 indicate approximate statistical significance at the 5% error level (two-tailed test).

The C-score and V-ratio indices were computed with Ecosim simulation software ver. 7.72 (Gotelli and Entsminger 2009).

Pianka O_{jk} niche overlap index and species' size distribution analysis

Earthworm community species reduce their competition by feeding on organic resources of different type and quality and at varying soil depth (Bouché 1977, Jiménez and Decaëns 2000) and by body size differences (Jiménez et al. 2006). A community-level Pianka's O_{jk} niche overlap index (Pianka 1973) was calculated with the mean niche overlap of all possible species pairs. If the community is competitively structured mean niche overlap index should be less than EBC, whereas abiotic constraints on activity, like soil resources, should cause all species to have similar resource-use patterns, so that observed niche overlap would be greater than EBC (Albrecht and Gotelli 2001). The six species assemblages identified from the CA were further used to compute community structure indices, which were compared to the same indices calculated for the earthworm community. This was done to explore the main driving factors of community assembly at small scales in the GF. The following dimensions of resource utilization were used:

a) Niche partitioning for trophic resources: we used individual matrices in which rows represented individual species or species assemblages and columns represented the range of soil nutrient-related variables like C, N and P concentrations, fine and coarse root length and biomass and the quality of soil organic matter ingested (C:N), thereafter. Each entry indicated the number of individuals collected in each sample for a given range in the variable.
b) Niche partitioning for spatial resources: similar to trophic resources, space can be considered a resource in which species are able to compete (Chesson 2000b). Individual matrices were used in which rows represented species or species assemblages (positive and negative row scores of the first three axes of the CA), columns represented the range of soil physical-related variables, i.e. bulk density, aggregation, compaction, penetration resistance and thereafter. Similarly to trophic resources, each entry indicated the number of individuals collected in each sample for a given range in the variable.
c) Within a community, similar morphology between ecologically similar species results in non co-existence because of excessive overlapping in resource use (Hutchinson 1959). Consequently, morphological traits have been considered to assess the influence of competition in shaping community assembly (Dayan and Simberloff 2005). We calculated morphological niche overlap in matrices where rows represented species, columns represented biometric traits, and where entries consisted of average trait values measured for the collected individuals. Five biometric traits were used: body length (mm), weight (g), preclitellar diameter (mm), length/width and weight/width ratios, which have been reported to reliably describe earthworm external morphology (Jiménez et al. 2001). Before analysis data were normalised to reduce the effect of biometric data measured in the index calculation by dividing each entered value by the standard deviation of the corresponding column (variable) in the matrix.

Finally, average niche overlap was calculated for multidimensional trophic and spatial niche overlap index by averaging the single O_{jk} values for each resource exploited in the trophic and spatial dimensions by the community and selected assemblages and compared with a null model (10 000 simulations). This procedure over-estimates the actual value of the niche overlap index in opposition to the product which underestimates the total O_{jk} index (Pianka 1973, 1974). In a community shaped by competition, niche overlap in a given assemblage should be lower than EBC for the considered niche dimension. We used a randomization algorithm that retains the niche breadth of each species, but randomizes which particular resource states are utilized (RA3 in Albrecht and Gotelli 2001). It corresponds to a simple reshuffling of each row of the matrix that assumes all the different resource states to be equally abundant (or usable) by all species.

We tested if species of the community showed patterns limiting biometric similarity for the five morphological traits that were used in the niche overlap analysis. For each trait the minimum segment length (MSL) and its variance (σ^2_{sl}) were calculated. The MSL measures the smallest difference in size found in all available species pairs, while the σ^2_{sl} for an entire assemblage is an index of the constancy of size ratios between species ordered by body size (Poole and Rathcke, 1979). In a competitively structured community MSL and σ^2_{sl} should be higher and lower than EBC, respectively (Gotelli and Ellison 2002). If competition affects body-size ratios, the observed σ^2_{sl} should be smaller than EBC because the body-size ratios of adjacent species will be very similar to one another. σ^2_{sl} equals zero when body size of adjacent species is constant. We compared the observed σ^2_{sl} in each assemblage with the variance of 1000 randomly constructed assemblages consisting of the same number of species drawn from the local species pool. The minimum and maximum boundaries for the simulation were fixed by the smallest and largest values in species size used by the null model algorithm (Gotelli and Ellison 2002).

Calculations and tests were done with the 'Niche overlap' and 'Size overlap' modules of Ecosim 7.0 (Gotelli and Entsminger 2009).

Adjustment of probability level

Corrections or adjustments to p-values are recommended for the analysis of species pairs where hundreds of comparisons are made (Gotelli and Ulrich 2010). The significant level $\alpha < 0.05$ was adjusted by using the false discovery rate (FDR) procedure for multiple comparisons (Benjamini and Hochberg 1995). The power of multiple tests is optimized while controlling for the proportion of significant results that could actually be type I errors (García 2004). The p-values from the individual tests are used to perform the corrections and search for significant differences at the corrected probability level (Benjamini and Hochberg 1995). In the co-occurrence analysis three tests were performed that corresponded to the three different null-models used. The comparison starts with the highest p-value obtained from the individual tests and then each value is checked until the first value that meets the requirement, i.e. the largest p-value that is smaller to the corrected p (see Verhoeven et al. 2005 for further details). In some cases the transformations are:

$$P(i) \leq (\alpha/m) \times i$$

where m is the number of tests (variables) and i is the test (variable) ranked in ascending order, i.e. $P(1) \leq \ldots\ldots \leq P(m)$, and $H(i)$ denotes the null hypothesis corresponding to $P(i)$. Final p-value corresponded to the following correction:

$P_{corr} = (0.05 \times 3)/1$, which is similar to a classical Bonferroni correction of the type $0.05/3 = 0.0167$

In the case of niche overlap calculations we used a precautionary approach and the final p-value calculated from 26 variables was fixed at the significant level $\alpha < 0.001$.

Results

In the GF seven unclassified (Jiménez unpubl.) earthworm species were found (Table 1), with some of them being present in the natural savanna. A total number of 688 earthworms were recorded and identified.

Identification of species assemblages

Eigenvalues (Fig. 1A) of the first three axes of the CA explained 73.0% of total inertia with 34.2, 21.7 and 17.1% for axis I, II and III, respectively. Six assemblages were identified. The first axis (Fig. 1B) separated new genus 1 (CA1+) from the rest of species (CA1−), while axis 2 separated endogeic species (*Andiodrilus*, *Glossodrilus* and new genus 2) on the positive side (CA2+) from epigeic (*Aymara*, new genus 1) and anecic species (*Martiodrilus*) on the negative side (CA2−). Axis 2 represented thus a transition from surface litter- to soil-feeding species in the negative and positive side of the CA plan, respectively. An increase in earthworm size was observed for soil-feeding species in axis 2. Lastly, axis 3 (Fig. 1C) separated *Martiodrilus*, new genus 2 and *Glossodrilus* (CA3+) from new genus 1, *Aymara* and *Andiodrilus* (CA3−).

Environmental heterogeneity as driving factor of species pattern

Total inertia explained by the first two axes of PCA was 43.4% (not shown). The first two axes of the CoIA (Fig. 2a) explained 81.8% of the total variability ($p < 0.0001$; Monte Carlo randomization test). Axis I (64.1% of total inertia) was referred to as the soil physical environment and separated sampling points where resistance to penetration, proneness to compaction, bulk density and very large aggregates (> 10 mm size) had high values, in opposition to sampling points with large proportion of soil aggregates < 5 mm. Axis II (17.7% of total inertia) basically indicated the concentration of C, N and P in the 0–5 cm soil layer, i.e. the soil organic matter in the topsoil. Coarse root length (CoRL) and fine root length (FiRL) were correlated with 1–2 and 2–5 mm, and < 1 mm aggregates, respectively (Fig. 2b). Species projection in the factorial plan formed by the first two axis of the CoIA clearly highlighted a strong correlation between the topsoil concentrations of C and N and to a lesser extent P and the presence of new genus 1, whereas *Andiodrilus* sp. was linked to those sampling points where soil bulk density (BD) and compaction were high (Fig. 2c). Summary statistics of soil variables analysed are listed in Table A1 (Supplementary material Appendix A1).

Table 1. Main characteristics and abundance ($N\ m^{-2} \pm SE$) of earthworm species studied in the gallery forest at Carimagua (Eastern Plains of Colombia).

Species	Family	Ecological category[1]	Pigmentation	Size[3] (mm) length	Size[3] (mm) diam	Weight[3] (g f.w.)	n	Mean density ± SE
Andiodrilus sp.	Glossoscolecidae	endogeic	unpigmented	109.0	4.4	1.38	22	3.1 ± 0.7
Andiorrhinus sp.	Glossoscolecidae	endo-anecic[2]	pink-coloured antero-dorsal	188.0	7.6	7.10	10	0.1 ± 0.1
Aymara sp.	Glossoscolecidae	epigeic	dark-red dorsal	58.1	1.5	0.06	15	6.5 ± 1.3
New genus 1	NC[4]	epigeic	dark-green dorsal	117.9	3.8	0.69	18	9.5 ± 5.1
Glossodrilus sp.	Glossoscolecidae	endogeic	unpigmented	83.9	1.5	0.10	13	8.5 ± 1.4
Martiodrilus sp	Glossoscolecidae	anecic	dark-grey antero dorsal	194.3	9.3	11.2	29	10.3 ± 1.4
New genus 2	Ocnerodrilidae	endogeic	unpigmented	22.8	0.7	0.006	157	24.0 ± 2.6

[1] epigeic: live and feed in the soil surface; endogeic: live and feed in the soil; anecic: live in the soil and dig vertical or semi-vertical burrows and feed in the soil surface (after Bouché 1972, Lavelle 1981).
[2] it refers to a worm with characteristics of anecic (antero-dorsal pigmentation) and endogeic (horizontal burrows digging).
[3] average biometric data for adults (fixed specimens in 4% formalin solution); g f.w. = gram fresh weight (gut content included).
[4] NC = not classified.

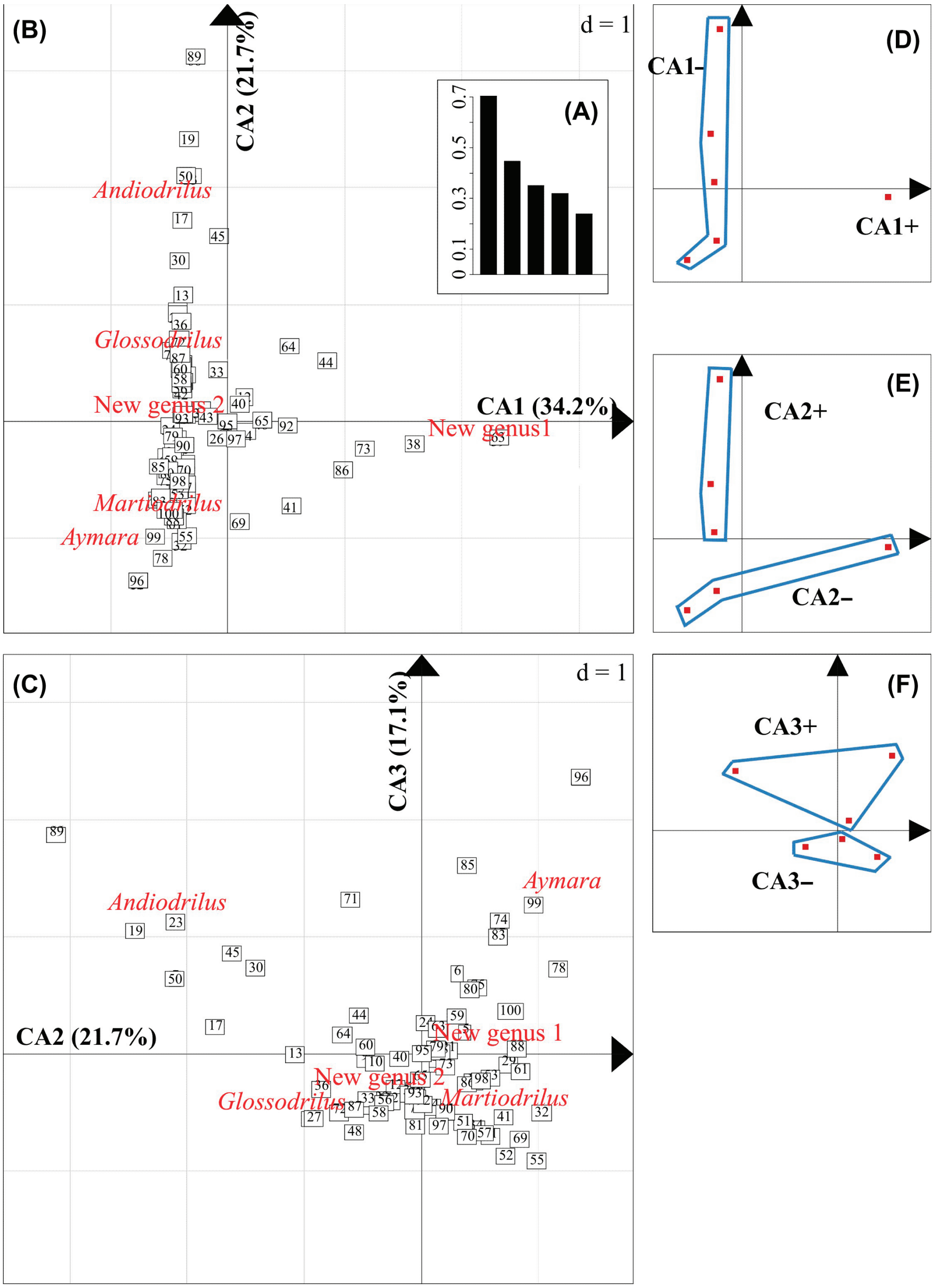

Figure 1. Correspondence analysis of earthworm species in the gallery forest with ordination of species and sampling sites in the factorial plan formed with axis 1 and 2 (A) and axis 2 and 3 (B) the 'eigenvalues' diagram, and the six species assemblages: CA1+, CA1− (C), CA2+, CA2− (D), and CA3+, CA3− (E).

Species spatial co-structure with soil variables

In the CoIA a cross matrix containing the maximal covariance between species abundance and environmental variables is computed. The correlograms computed with the row scores upon the first two axes of the CoIA were significant at various lag distances (Fig. 3a–b). Significant positive and negative autocorrelation was observed at short (between 7 and 16 m) and at higher (> 40 m) distances, respectively, for axis I. The computation of Moran's *I* index with the row scores of soil variable data matrix onto the CoIA axes highlighted the same spatial pattern of the co-structure. Significant spatial positive autocorrelation was detected up to 20 m of distance lag (Fig. 3a), while negative autocorrelation was observed at distances > 30 m (Fig. 3b).

Community assembly processes: null models and niche overlap

Null-model analysis indicated that the observed C-score index was lower than the simulated matrices, except for the fixed-proportional model (Table 2). The observed V-ratios

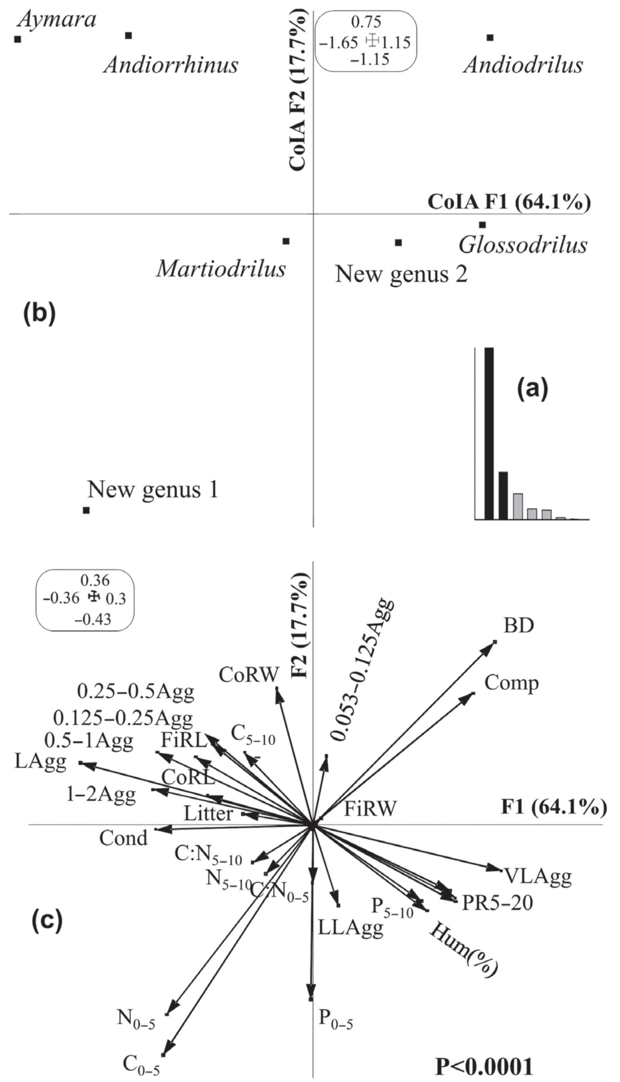

Figure 2. Co-inertia analysis (CoIA) indicating the 'eigenvalues' (A), the relationship between earthworm species (B) and soil variables (C) into the factorial plan of the new ordination CoIA axes. (P, phosphorous; C, carbon; N, nitrogen; FiRL, fine root length; CoRL, coarse root length; FiRW, fine root weight; CoRW, coarse root weight; PR, penetration resistance; 0.25−0.50, size-class aggregates 0.250−0.500 mm; LgAgg, large aggregates (2−5 mm); LLAgg, larger aggregates (5–10 mm); VLAgg, very large aggregates (> 10 mm); BD, bulk density; Comp, compaction; Cond, hydraulic conductivity. 0−5 and 5−10: 0–5 and 5−10 cm soil depth).

for initial data and factorial data were smaller than the simulated values in all cases, indicating that earthworm species and assemblages were not competitively structured.

With regards to trophic and spatial niche dimensions, the O_{jk} niche overlap index was higher than the simulated values in all cases (Table 3). The average community O_{jk} index for trophic and spatial resources was 0.800 and 0.698, respectively. The average SES was significantly higher than 2 except for litter, soil compaction, bulk density, aggregates < 0.25 mm, and aggregates ranging from 2 to 5 mm. Average niche overlap for biometric traits was also higher than EBC, and the average SES was also significantly higher than 2.

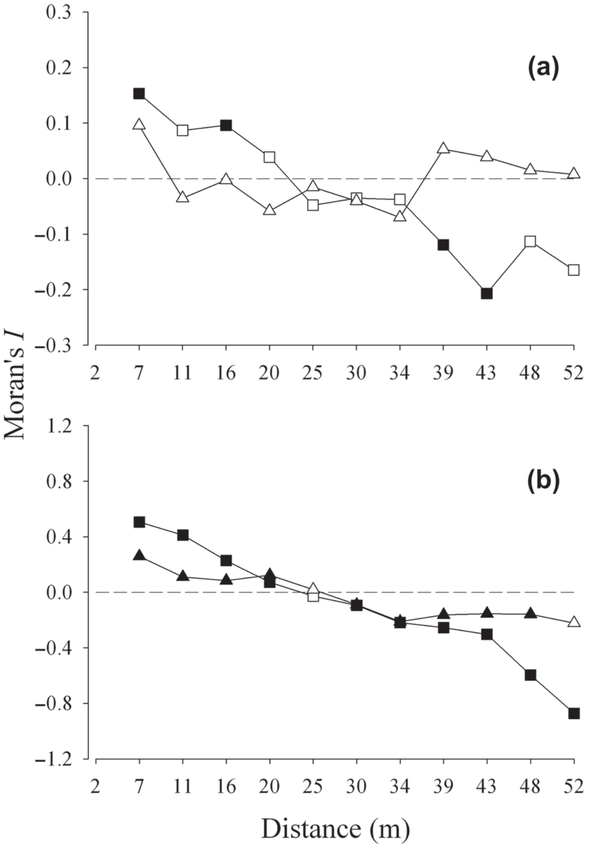

Figure 3. Correlogram computed with the factorial coordinates of axis 1 (□) and axis 2 (Δ) extracted in the CoIA depicting the co-structure of fauna data (matrix 1; A), and soil variable table (matrix 2; B). Lag distance at which the correlogram is significant at the Bonferroni corrected probability level is indicated with black symbols.

In general, the observed O_{jk} indexes for trophic and spatial resources of species assemblages identified in the three axes extracted from the CA were significantly higher than the simulated values for many variables related to trophic and spatial niche dimensions (Supplementary material Appendix A1 Table A2), indicating that earthworm assemblages were not competitively structured. Non-significant values of the index were only found in assemblages CA1+, CA2− and CA3+ for some trophic- and spatial-related niche variables.

Finally, a random pattern was detected in body size overlap. Body size distribution analysis indicated that the earthworm community of the GF tended to under-dispersed spacing in the biometric variables. Average MSL tended to be lower than EBC, except for body length where MSL was higher than EBC (Table 4). However, the corresponding average SES values were not significant. The observed value of MSL was lower than the simulated value only for body diameter and the corresponding average SES was significantly lower than zero. Average VarSL was higher than the simulated value for all five morphological traits.

Table 2. Results of the null model analysis performed on earthworm presence/absence data matrix and the assemblages identified (positive and negative row scores on axis I of the correspondence analysis). The C-score, V-ratio, standardised effect size (SES), and initial and corrected associated one-tailed probability ($p < 0.05$) are indicated after the false discovery rate (FDR) procedure (Benjamini and Yekutieli 2001).

Null-model index	Data source	Model	Observed	Simulated	SES	Initial p	Corrected p
C-score	species (presence/absence)	fixed-equiprobable	338.90	323.10	0.782	0.215	0.645
		fixed-fixed	338.90	339.81	−0.334	0.616	1.000
		fixed-proportional	338.90	259.20	3.794	< 0.001	**0.003**
	assemblages (axis I CA, 34.2%)	fixed-equiprobable	1280.00	217.45	10.237	< 0.0001	**0.003**
		fixed-fixed	1280.00	1280.00	0	1.000	1.000
		fixed-proportional	1280.00	178.34	11.547	< 0.0001	**0.003**
V ratio	species (presence/absence)	fixed-equiprobable	0.884	1.001	−0.883	0.829	1.000
		fixed-fixed¶	0.884	–	–	–	–
		fixed-proportional	0.884	1.437	−3.707	1.000	1.000
	assemblages (axis I CA)	fixed-equiprobable	0.130	0.999	−8.686	1.000	1.000
		fixed-fixed	0.130	–	–	–	–
		fixed-proportional	0.130	1.036	−9.691	1.000	1.000

¶the V ratio is not computed with the fixed-fixed algorithm (see Gotelli 2000 for further details).

Discussion

Species, populations and communities of soil organisms are spatially structured as a consequence of environmental heterogeneity and biotic interactions like predation and competition (Ettema and Wardle 2002, Birkhofer et al. 2010). The formation of patches through self-organization has also been explained without soil environmental variability or the result of species interactions as driving factors of spatial distribution in earthworms (Barot et al. 2007). Besides, earthworm dispersal behaviour remains little studied and complex feedbacks between habitat quality (environmental constraints), earthworm engineering (Lavelle et al. 2007) and dispersal have been argued as factors structuring patches of high density (Mathieu et al. 2010). These factors are not exclusive but complementary for community organization, and how and to which extent they influence the spatial distribution of species assemblages is a key research area in community ecology of soil organisms.

Spatial relationships between abiotic soil variables and species assemblages

Species distribution can be partly explained by soil environmental heterogeneity (Phillipson et al. 1976, Valckx et al. 2009), although earthworm activity also creates

Table 3. Community niche overlap analysis for selected trophic and spatial resources and biometric traits. The initial p value indicates the probability that the standardized effect size (SES) differed from zero. The corrected p* value indicates the probability at $p < 0.05$, after FDR procedure correction of $p = 0.0055$ (0.05/9) and $p = 0.0062$ (0.05/8) for trophic and spatial multidimensional niche overlap, respectively.

		O_{jk} overlap index				
Niche dimension	Resource[1]	obs.	sim.	Average SES	Initial p	Corrected p[2]
Trophic	SOC_{0-5}	0.889	0.290	7.762	0.0001	0.0009***
	SOC_{5-10}	0.917	0.240	8.177	0.0001	0.0009***
	N_{0-5}	0.891	0.305	7.833	0.0001	0.0009***
	N_{5-10}	0.912	0.309	6.944	0.0003	0.0027**
	$C{:}N_{0-5}$	0.771	0.393	5.856	0.0001	0.0009***
	$C{:}N_{5-10}$	0.831	0.461	5.524	0.0003	0.0027**
	Litter	0.618	0.504	2.190	0.0380	NS
	FiRL	0.700	0.373	4.935	0.0011	0.0099**
	FiRW	0.676	0.466	3.693	0.0049	0.0441*
Spatial	RP2.5	0.754	0.470	5.243	0.0008	0.0064**
	RP5	0.780	0.471	5.613	0.0004	0.0032**
	Comp	0.615	0.381	3.497	0.0063	NS
	BD	0.678	0.428	3.493	0.0079	NS
	Agg < 0.25	0.692	0.626	1.147	0.1236	NS
	< 1Agg > 0.25	0.715	0.411	4.841	0.0007	0.0056**
	< 2Agg > 1	0.761	0.435	5.363	0.0005	0.0040**
	< 5Agg > 2	0.586	0.534	1.109	0.1334	NS
Biometric	Morphological traits	0.794	0.592	5.109	0.0003	0.0027**

[1] SOC, soil organic carbon; N, nitrogen; FiRL, fine root length; CoRL, coarse root length; FiRW, fine root weight; CoRW, coarse root weight; PR, penetration resistance; < 0.250 Agg, aggregates < 0.250 mm; BD, bulk density; Comp, susceptibility to compaction; Cond, hydraulic conductivity.
0−5: soil depth 0−5 cm; 5−10: soil depth 5−10 cm; MPa: megaPascals.

[2] *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$; NS = not significant.

Table 4. Results of body-size structure analysis. For each biometric trait minimum segment length (MSL) and its variance (σ^2_{sl}) was analysed.

Biometric trait	Metric	Observed	EBC	Average SES	p†	Corrected p††
Length	MSL	0.099	0.075	0.383	0.710	NS
Length	σ^2_{sl}	0.134	0.176	−0.386	0.417	NS
Diameter	MSL	0.000	0.072	−1.181	<0.001	0.003**
Diameter	σ^2_{sl}	0.132	0.164	−0.309	0.463	NS
Weight	MSL	0.009	0.070	−1.018	0.105	NS
Weight	σ^2_{sl}	0.300	0.151	1.568	0.925	NS
L/D	MSL	0.020	0.082	−0.884	0.193	NS
L/D	σ^2_{sl}	0.261	0.211	0.368	0.733	NS
W/D	MSL	0.056	0.069	−0.228	0.513	NS
W/D	σ^2_{sl}	0.219	0.149	0.755	0.822	NS

†the p-value indicates the probability that the standardized effect size (SES) differed from zero.
††*$p<0.05$; **$p<0.01$; ***$p<0.001$; NS = not significant.

heterogeneity with lasting effects in the soil (Lavelle et al. 2007) influencing the spatial patterns of key soil ecosystem processes like litter decomposition and nutrient cycling (Ettema and Wardle 2002). Recent spatially explicit studies with earthworms have demonstrated preferences for particular microhabitats in the soil (Gutiérrez-López et al. 2010, Mathieu et al. 2010). In temperate environments, Valckx et al. (2009) found that the spatial variability of soil properties was not linked to the spatial distribution of several earthworm species, among which *Lumbricus terrestris*, *Aporrectodea caliginosa* and *A. rosea*, although a positive relation was observed for *Aporrectodea longa*. Gutiérrez-López et al. (2010) showed relationship between soil abiotic factors and earthworms, although the spatial pattern was not significant as revealed by partial Mantel-test, contrary to results obtained by Jiménez et al. (2011), where specific spatial relationship between earthworm species and selected soil properties was shown to be significant. Higher resource heterogeneity in the soil surface of the GF exists compared with the savanna, as the presence of litter, tree logs and other discrete large elements create specific ‘micro’ sites where the local environment is different (Mathieu et al. 2009).

Our study showed that the co-structure between new genus 1 and C and N concentrations in the 0–5 cm soil layer (Fig. 2), occupying the same space in the CoIA factorial axes plane, could indicate species preference to abiotic factors. Furthermore, environmental constraints and habitat preferences determine patches of distinct species assemblages which exploit areas with particular soil properties so competing species can co-occur in more heterogeneous environments. This was demonstrated by the positive species association SADIE index reported between *Andiodrilus* sp. and *Glossodrilus* sp. (Jiménez et al. 2011). The spatial co-occurrence of these competitive savanna endogeic species that display opposite spatial distributions by occupying different patches (Jiménez and Rossi 2006) is allowed in the GF. Our results agree with the ‘coexistence aggregation model’ (Hanski 1981, Inouye 1999) which suggests that spatial aggregation of competitors at patchily distributed resources (environment) can facilitate coexistence without species having to avoid one another other by spatial segregation or reduced body-size overlap (Ives 1988). The tri-dimensional and compact nature of soil may allow the co-occurrence of a less competitive species in areas where a strong competitor is present, facilitating physical isolation between individuals with only transitory co-occurrence of competing species.

In our study, the second axis of the CA clearly segregated soil-feeding from litter-feeding species along a gradient of earthworm size from new genus 2 to *Glossodrilus* sp. and *Andiodrilus* sp. This result clearly indicated the impact of earthworm size on soil aggregation by ingesting soil particles of larger size and egesting more compacted casts. The co-structure observed between *Andiodrilus* sp. and soil physical properties bulk density and higher susceptibility to soil compaction is probably the result of the engineering activities of endogeic earthworms through the formation of compact casts in the topsoil (Blanchart et al. 1997). The assemblage CA2- was characterized by litter-feeding species distributed along a gradient of soil organic matter quality, with species exploiting soil areas from rich to very high rich organic resources. Consequently, the relationship between the spatial distribution of earthworms and soil environmental heterogeneity is not unidirectional or straightforward and more studies are necessary to disentangle the spatial interactions between species and their environment.

Effect of biotic interactions on earthworm spatial pattern

Null-model analyses have generally been used in soil invertebrate studies (Simberloff 1983, Gotelli 2000, Gotelli and Ellison 2002, Gotelli and McCabe 2002, Ulrich and Zalewski 2006, Ward and Beggs 2007, Azeria et al. 2009, Decaëns et al. 2008, 2009, 2011, Ellwood et al. 2009, Birkhofer et al. 2010). Thus, the utilisation of null-model analysis from spatially explicit sampling protocols seems appropriate to unveil competitive interactions in soil communities at small scales. Birkhofer et al. (2010) used null-model based point-pattern statistics to study the impact of biotic interactions under the assumption of environmentally heterogeneous or homogeneous conditions in litter arthropods predator-prey interactions. They found that biotic interactions were determinants in the spatial distribution of ground-active predators and their prey in forested ecosystem, and claimed for inclusion of environmental heterogeneity in spatial models, otherwise the driving factors structuring species assemblages would remain hidden.

Diamond's seminal work (Diamond 1975) assumed a model where species interaction explained predictable community patterns. Competition is considered the main force of species interaction assembling natural communities (Weiher and Keddy 1999, Gotelli and McCabe 2002), but also spatial patterns of species, either aggregated or regular, arise from habitat heterogeneity (Bell 2001). On the other hand, pure stochastic processes can also generate non-random patterns (Ulrich 2004, Bell 2005, Hubble 2005). Finally, stochastic and deterministic processes jointly influence the observed structure of soil communities (Ellwood et al. 2009). In our study, we were not able to conclude that the observed earthworm spatial co-occurrence is the result of stochastic process or species interaction where deterministic assembly rules operate.

In earthworm communities negative interactions prevail likely as a result of resource competition, which is related to the degree of niche overlap (Uvarov 2009). In our study, the results of niche partitioning and body size overlap indicated that the earthworm community was not shaped by competition in the GF, and that other factors influenced species co-occurrence at small scales, like differential resource use among species. Regular spacing of body size has been revealed for different groups of organisms like ground beetles (Brandl and Topp 1985), hoverflies (Gilbert et al. 1985), earthworms (Decaëns et al. 2009), although random patterns in body size overlap have been detected in invertebrate assemblages (Simberloff and Boecklen 1981, Juliano and Lawton 1990). Although only a significant value was observed for earthworm diameter (MSL < EBC) our findings showed that species size overlap in the GF tended to be under-dispersed while a consistent trend toward over- and even-spacing size overlap was reported for the savanna (Decaëns et al. 2009). This could be explained by higher availability of spatial and trophic resources in the GF compared with the savanna allowing coexistence of competing species in areas of high resource availability, although further research is needed.

Contrasting interactions have been reported between ecological categories with deep-burrowing species normally having positive effects on epigeics and endogeics, while competitive interactions seem to predominate in the latter groups (Uvarov 2009). Spatial segregation of earthworms can be the result of species-specific differential preference for soil conditions rather than by interspecific competition process. Valckx et al. (2009) reported that patches occupied by endogeic species were not associated to clusters were anecic species were present, and Jiménez and Rossi (2006) found that the spatial segregation observed in patches of endogeic earthworms may result from interspecific competition. Our findings do not support the hypothesis of inter-specific competition in the earthworm community of the GF, unlike other studies in the area (Jiménez et al. 2006, Decaëns et al. 2009), and other deterministic processes (soil environmental heterogeneity) explained earthworm species co-occurrence. Earthworms are known to compete for trophic resources (Abbott 1980), and also for spatial resources by selecting areas with optimal soil conditions for their survival and reproductive strategies (Barot et al. 2007). Niche overlap in earthworms is reduced by differences in body size, temporal variation in yearly population dynamics and average vertical distribution (Jiménez et al. 2006). No general rule seems to exist and the results obtained in the different studies to date are species-specific and site- and sampling-strategy dependant.

Conclusions

In the earthworm community of the GF we observed that earthworm co-occurrence was shaped by soil environmental heterogeneity at small scales. However, our aim was to unveil the spatial co-structure between earthworm assemblages (group of species) and soil variability. Spatially explicit statistical tools in combination with null-model analysis of co-occurrence and the use of factorial axes extracted from CoIA highlighted that earthworm community presented a significant spatial pattern that was linked to environmental heterogeneity at scales ranging from 7–16 m (positive) and from 39–43 m (negative). Earthworm mobility and dispersal in combination with other factors like habitat constraints and demography influence the formation of high-density patches (Barot et al. 2007, Matthieu et al. 2010). We conclude that earthworms showed high capacities of habitat selection at small scales and they selected areas of trophic and spatial resource exploitation for their life cycle strategies. However, earthworm dispersal behaviour studies under field conditions are necessary to complement our findings on the scale at which earthworms respond to environmental heterogeneity.

The use of factorial coordinates for community analysis has been successfully used by Rossi (2003), Jiménez et al. (2006) and Decaëns et al. (2009, 2011) to distinguish different species assemblages within the earthworm community. In the present study, species assemblages were defined by the row scores onto the three axes extracted from the CA that explained 34.2, 21.7 and 17.1% of total inertia, respectively. Although the percentage of variability explained by the first axis of the CA was not high, the two species assemblages resulting from the first axis extracted in the CA showed a higher C-score than EBC at small scales. It could indicate the presence of biotic interaction (competition process) (Table 2).

The scale used to address earthworm co-occurrence could influence our insight of the spatial patterns and assembly structuring forces found in the community. Despite intensive sampling conducted in the habitat studied, a non-replicated, single snapshot in time might be insufficient to draw conclusions on the driving factors structuring the earthworm community at small scales. The necessity to adopt new approaches allowing multi-scale exploration of soil ecological data is essential. CoIA has been successfully used in soil invertebrate studies (Moretti and Legg 2009), emphasizing that soil ecologists are embracing the use of more efficient and sophisticated multivariate ordination methods for species traits and environment relationships. More empirical studies on spatial co-occurrence of soil communities are essential to identify patterns of co-occurrence of competing species at small scales. How species assemblages relate with soil abiotic factors and interact between them at small scales is a key topic for further research.

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Supplementary material (available online as Appendix O20428 at <www.oikosoffice.lu.se/appendix>). Appendix A1.