

1 **Soil environmental heterogeneity allows spatial co-**  
2 **occurrence of competitor earthworm species in a gallery**  
3 **forest of the Colombian “Llanos”**

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16 **Abstract**

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

37 **Key words:** soil ecology; null models; biotic interactions; co-occurrence; niche  
38 overlap; community; soil fauna.

39

## 40 **Introduction**

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

53 The spatial patterning of soil organisms is shown to be generally clumped, with  
54 alternation of high- and low-density population patches ranging from small to larger  
55 scales, i.e. several cm to tens of metres (Albrecht and Gotelli 2001; Jiménez et al.  
56 2001; Ettema and Yeates 2003; Rossi and Nuutinen 2004), although regular pattern at  
57 short distances have also been described (Thomas et al. 2008). The factors that cause  
58 and control these discrete patches and their spatial segregation are difficult to identify  
59 and interpret and include heterogeneity of both environmental (biotic and abiotic)  
60 factors and internal population processes (fecundity and dispersal ability) (Ettema et  
61 al. 2000; Decaëns and Rossi 2001; Barot et al. 2007).

62 Co-occurrence of competing species takes place if the environment is spatially  
63 heterogeneous (from scales of cm to km) leading to spatial segregation (Amarasekare

64 2003). For example, competing species within a community may exhibit  
65 checkerboard distribution leading to competitive exclusion process (Diamond 1975).  
66 Moreover, at small scales two competitors may co-occur if they are spatially excluded  
67 from the patch where one of them is present. As mentioned above, spatially structured  
68 communities and patches of specific assemblages can reflect a response to the spatial  
69 heterogeneity of soil resources resulting in spatial exclusion between species having  
70 different ecological requirements. On the contrary, species co-occur in a given patch  
71 in relation to ecological complementary, i.e. differences in spatial and trophic niche  
72 axes, and higher resource availability may result in assemblages of competing species  
73 within the same patch (Amarasekare 2003). Despite this knowledge, data on spatial  
74 competitive co-occurrence from empirical studies on soil communities are not  
75 abundant.

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

88 scales, as previously reported in the natural savannas of this region (Jiménez et al.  
89 2006; Decaëns et al. 2009).

## 90 **Materials and methods**

### 91 **Study site**

92 Fieldwork was carried out at the CORPOICA-CIAT Carimagua research station in the  
93 well-drained isohyperthermic savannas of the Eastern Plains (“Llanos”) of Colombia  
94 (4° 37’ N, 71°19’ W, 170 m a.s.l.) during the rainy season of 1999. The Colombian  
95 Llanos south of the Meta River is a young alluvial plain consisting of Pleistocene and  
96 Holocene sediments of Andean origin (Goosen 1971). Climate in the area is defined  
97 as sub-humid tropical, with unimodal regime. The site receives annually 2280 mm  
98 precipitation and yearly mean temperature is 26°C, with a marked dry season from  
99 December to March (CIAT data, 1972-1995). A dense drainage network of gallery  
100 forests dissects the “Llanos Orientales” and feeds into the Orinoco catchment. Soils  
101 have been described as Oxisols in the upland savannas and Ultisols in the lowland  
102 areas, respectively. They are acid (pH [H<sub>2</sub>O] = 4.5) with >90% of Al saturation, and  
103 low values of exchangeable nutrients for plants. Fragmented ironstones are normally  
104 observed when erosion has exposed the ferruginous material (laterite) layer  
105 (Blydenstein 1967).

106 Earthworms and soil were sampled in a nearby GF located in “La Reserva”  
107 bordering the Carimagua Lake. This is a secondary forest where the most abundant  
108 tree species were *Dendropanax arboreum* (L.) Decne. & Planch. (1854) (Araliaceae),  
109 *Enterolobium* spp. (Leguminosae), *Ficus* spp. (Moraceae), *Jacaranda copaia* (Aubl.)  
110 D.Don (Bignoniaceae), *Copernicia tectorum* (Kunth) Mart. and *Hymenaea courbaril*

111 L. (Caesalpinaceae), and *Cecropia* sp. (Cecropiaceae), and palms like *Mauritia*  
112 *flexuosa* L.f. 1782, *M. minor* Burret, *Mauritiella* sp., and *Attalea maripa* (Aubl.) Mart.  
113 (Palmaceae) are normally found near the shore of Carimagua Lake.

#### 114 **Earthworm assemblages and soil sampling**

115 Based on previous results from sampling campaigns in the savanna (Decaëns and  
116 Rossi 2001; Jiménez et al. 2001, 2006), soil pits of 25x25 cm<sup>2</sup> and 20 cm depth,  
117 distributed in the nodes of a 10x10 points regular grid with 5 m inter-sample distance,  
118 were dug out to retrieve earthworms. The number of individuals for each species was  
119 annotated and earthworms were released back in the soil. Earthworms were at their  
120 maximal activity period by the time where sampling was conducted, and density of  
121 the anecic *Martiodrilus* sp. was estimated by counting the number of fresh casts  
122 deposited in the soil surface which was shown to be a reliable procedure (Jiménez et  
123 al. 1998). Litter was hand sorted prior to pit excavation and conserved in plastic bags  
124 until drying at 105°C for 48 h to calculate litter biomass.

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

127 1. Bulk density was determined with the core method (soil dry mass per volume)  
128 using a 5x5 cm metal cylinder; soil water content (soil water per volume, and  
129 soil water per dry mass) were determined gravimetrically.

130 2. The second soil core (0-5 and 5-10 cm) was taken for soil organic C (SOC)  
131 determination with the colorimetric method after digestion in H<sub>2</sub>SO<sub>4</sub>. The  
132 Kjeldahl method was used for total N concentration. Before analyses soil was  
133 oven dried at 75 °C for 48 h and finely grounded. The C:N ratio was simply

134 calculated as the SOC concentration divided by the total N concentration  
135 obtained. Available P was determined with Bray-II extraction.

136 3. The third soil core (15 cm depth and 10 cm diam.) was taken for determination  
137 of aggregate size-class distribution. Approximately 100 g of air-dried soil was  
138 used for standard dry-sieving through a sieve column of 4.75, 2.0, 1.0, 0.5 and  
139 0.250 mm and shaking for 30 min.

140 4. The fourth soil core (15 cm depth and 10 cm diam.) was used for root length  
141 (root length estimator) and biomass determination. In the lab the soil was  
142 washed and sieved to separate fine (<2 mm) and coarse roots (>2 mm), and  
143 then oven-dried at 105 °C for 48 h.

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

## 148 **Data analysis**

### 149 Relationship between earthworm assemblages and environmental heterogeneity

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

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



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

191 For the computation of the correlogram data were allocated to 11 distance classes  
192 for convenience and a minimum of 50 pairs of points were used for each distance  
193 class. The overall statistical significance of the correlogram was performed with a  
194 Bonferroni corrected probability procedure. The corrected  $p^*$  was  $\alpha' = \alpha/k$ , with  $k$  the  
195 number of distance classes and  $\alpha < 0.05$  the global significance level (Oden 1984).  
196 The correlogram is statistically significant when at least one coefficient is significant  
197 at the corrected  $p^*$  of  $0.05/11 = 0.0045$  (Cooper 1968). The Kolmogorov-Smirnov  
198 test was used to test the normality of data frequency distribution. The asymmetry of  
199 the frequency distribution was reduced with a Box-Cox transformation when  
200 normality assumption was not achieved (Sokal and Rohlf 1995). All analyses were  
201 performed with the statistical package R 2.12.0 (R Development Core Team 2010),  
202 unless otherwise stated.

203 Null-model analysis of species co-occurrence patterns

204 Data of earthworm abundance was converted into a presence-absence matrix, which is  
205 the fundamental unit of analysis in community ecology. The advent of co-occurrence  
206 analysis and other statistical techniques have provided ecologists with more and more  
207 precise tools to explore non-random patterns in natural communities. In a given  
208 community not all species combinations are likely to occur, and some species pairs  
209 are forbidden or less probable because competing species are likely to exclude each  
210 other (Diamond 1975). Compared to randomly assembled, those competitively  
211 structured communities should contain fewer species combinations, more  
212 checkerboard pairs and higher C-score than expected by chance (EBC) (Gotelli and  
213 McCabe 2002). In our study, we tested if the relative spatial arrangement of species  
214 during the period of maximal earthworm activity presented less species co-occurrence  
215 than EBC (Gotelli 2000). The C-score index (Stone and Roberts 1990) was computed  
216 to analyze earthworm co-occurrence pattern in a presence/absence data matrix and  
217 also by using the row scores of the first axis extracted in the CA, explaining the  
218 maximal variance, that were later converted in a presence/absence data matrix. The C-  
219 score index is based on the average co-occurrence of all species pairs, and measures  
220 the checkerboard pattern of species' and/or species assemblages' mutual exclusion. It  
221 was used because of its statistical power and non-proclivity to Type I error (Gotelli  
222 2000).

223 A Monte Carlo null model simulation was used to randomize the species matrix  
224 with the swapping algorithm, i.e., the original matrix was shuffled repeatedly with  
225 random submatrices (Stone and Roberts 1990; Manly 1995). The observed index  
226 value was calculated and compared to 10,000 null communities that were randomly  
227 assembled. Because the co-occurrence tests are very sensitive to variation in species  
228 occurrence frequencies, row totals should be preserved as a constraint in the null

229 model (Gotelli 2000). We selected three algorithms to compute the C-score for the  
230 tests that were related to the questions asked:

231 (a) Fixed-equiprobable, where species occurrence totals are fixed (rows) and all sites  
232 (columns) are equiprobable, recommended for analysing ‘sample lists’ (Gotelli 2000).

233 b) Fixed-fixed, where both species occurrence totals and sites’ species numbers are  
234 maintained, so the random community contains the same number of species as the  
235 original community and each species occurs in the same frequency (Connor and  
236 Simberloff 1979). This model has more statistical power than the equiprobable model  
237 (Ulrich and Gotelli 2007).

238 c) Fixed-proportional, where species occurrence totals (rows) are fixed and sites differ  
239 in suitability. This algorithm is a hybrid between the first two, and it may cause the  
240 null hypothesis to be incorrectly rejected when using the C-score (Gotelli 2000).

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

246 Finally, the standardized effect size (SES) was calculated to quantify the direction  
247 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  
248 the 100 index values from the simulated matrices and compare to the observed index.  
249 SES values above -2.0 and below 2.0 indicate approximate statistical significance at  
250 the 5% error level (two-tailed test).

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

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

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

268 (a) Niche partitioning for trophic resources: we used individual matrices in which  
269 rows represented individual species or species assemblages and columns represented  
270 the range of soil nutrient-related variables like C, N and P concentrations, fine and  
271 coarse root length and biomass and the quality of soil organic matter ingested (C:N),  
272 thereafter. Each entry indicated the number of individuals collected in each sample for  
273 a given range in the variable.

274 (b) Niche partitioning for spatial resources: similar to trophic resources, space can  
275 be considered a resource in which species are able to compete (Chesson 2000b).

276 Individual matrices were used in which rows represented species or species  
277 assemblages (positive and negative row scores of the first three axes of the CA),  
278 columns represented the range of soil physical-related variables, i.e., bulk density,  
279 aggregation, compaction, penetration resistance and thereafter. Similarly to trophic  
280 resources, each entry indicated the number of individuals collected in each sample for  
281 a given range in the variable.

282 (c) Within a community, similar morphology between ecologically similar species  
283 results in non co-existence because of excessive overlapping in resource use  
284 (Hutchinson 1959). Consequently, morphological traits have been considered to  
285 assess the influence of competition in shaping community assembly (Dayan and  
286 Simberloff 2005). We calculated morphological niche overlap in matrices where rows  
287 represented species, columns represented biometric traits, and where entries consisted  
288 of average trait values measured for the collected individuals. Five biometric traits  
289 were used: body length (mm), weight (g), preclitellar diameter (mm), length/width  
290 and weight/width ratios, which have been reported to reliably describe earthworm  
291 external morphology (Jiménez et al. 2001). Before analysis data were normalised to  
292 reduce the effect of biometric data measured in the index calculation by dividing each  
293 entered value by the standard deviation of the corresponding column (variable) in the  
294 matrix.

295 Finally, average niche overlap was calculated for multidimensional trophic and  
296 spatial niche overlap index by averaging the single  $O_{jk}$  values for each resource  
297 exploited in the trophic and spatial dimensions by the community and selected  
298 assemblages and compared with a null model (10,000 simulations). This procedure  
299 over-estimates the actual value of the niche overlap index in opposition to the product

300 which underestimates the total  $O_{jk}$  index (Pianka 1973, 1974). In a community shaped  
301 by competition, niche overlap in a given assemblage should be lower than EBC for  
302 the considered niche dimension. We used a randomization algorithm that retains the  
303 niche breadth of each species, but randomizes which particular resource states are  
304 utilized (RA3 in Albrecht and Gotelli 2001). It corresponds to a simple reshuffling of  
305 each row of the matrix that assumes all the different resource states to be equally  
306 abundant (or usable) by all species.

307 We tested if species of the community showed patterns limiting biometric  
308 similarity for the five morphological traits that were used in the niche overlap  
309 analysis. For each trait the minimum segment length (MSL) and its variance ( $\sigma^2_{sl}$ )  
310 were calculated. The MSL measures the smallest difference in size found in all  
311 available species pairs, while the  $\sigma^2_{sl}$  for an entire assemblage is an index of the  
312 constancy of size ratios between species ordered by body size (Poole & Rathcke,  
313 1979). In a competitively structured community MSL and  $\sigma^2_{sl}$  should be higher and  
314 lower than EBC, respectively (Gotelli and Ellison 2002). If competition affects body-  
315 size ratios, the observed  $\sigma^2_{sl}$  should be smaller than EBC because the body-size ratios  
316 of adjacent species will be very similar to one another.  $\sigma^2_{sl}$  equals zero when body  
317 size of adjacent species is constant. We compared the observed  $\sigma^2_{sl}$  in each  
318 assemblage with the variance of 1000 randomly constructed assemblages consisting  
319 of the same number of species drawn from the local species pool. The minimum and  
320 maximum boundaries for the simulation were fixed by the smallest and largest values  
321 in species size used by the null model algorithm (Gotelli and Ellison 2002).

322 Calculations and tests were done with the “Niche Overlap” and “Size Overlap”  
323 modules of Ecosim 7.0 (Gotelli and Entsminger 2009).

324 Adjustment of probability level

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

338 
$$P(i) \leq (\alpha/m)*i$$

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

342 
$$P_{\text{corr}} = (0.05*3)/1$$
, which is similar to a classical Bonferroni correction of the  
343 type  $0.05/3 = 0.0167$

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

## 347 **Results**

348 In the GF seven unclassified (Jiménez, unpublished) earthworm species were found  
349 (Table 1), with some of them being present in the natural savanna. A total number of  
350 688 earthworms were recorded and identified.

### 351 **Identification of species assemblages**

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

### 363 **Environmental heterogeneity as driving factor of species pattern**

364 Total inertia explained by the first two axes of PCA was 43.4% (not shown). The first  
365 two axes of the CoIA (Fig. 2a) explained 81.8% of the total variability ( $P < 0.0001$ ;  
366 Monte Carlo randomization test). Axis I (64.1% of total inertia) was referred to as the  
367 soil physical environment and separated sampling points where resistance to  
368 penetration, proneness to compaction, bulk density and very large aggregates (>10  
369 mm size) had high values, in opposition to sampling points with large proportion of



370 soil aggregates <5 mm. Axis II (17.7% of total inertia) basically indicated the  
371 concentration of C, N and P in the 0-5 cm soil layer, i.e., the soil organic matter in the  
372 topsoil. Coarse root length (CoRL) and fine root length (FiRL) were correlated with  
373 1-2 and 2-5 mm, and <1 mm aggregates, respectively (Fig. 2b). Species projection in  
374 the factorial plan formed by the first two axis of the CoIA clearly highlighted a strong  
375 correlation between the topsoil concentrations of C and N and to a lesser extent P and  
376 the presence of new genus 1, whereas *Andiodrilus* sp. was linked to those sampling  
377 points where soil bulk density (BD) and compaction were high (Fig. 2c). Summary  
378 statistics of soil variables analysed are listed in Table A1 (supplementary material  
379 Appendix 1).

#### 380 **Species spatial co-structure with soil variables**

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

#### 390 **Community assembly processes: null models and niche overlap**

391 Null-model analysis indicated that the observed C-score index was lower than the  
392 simulated matrices, except for the fixed-proportional model (Table 2). The observed  
393 V-ratios for initial data and factorial data were smaller than the simulated values in all

394 cases, indicating that earthworm species and assemblages were not competitively  
395 structured.

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

403 In general, the observed  $O_{jk}$  indexes for trophic and spatial resources of species  
404 assemblages identified in the three axes extracted from the CA were significantly  
405 higher than the simulated values for many variables related to trophic and spatial  
406 niche dimensions (supplementary material Appendix 1, Table A2), indicating that  
407 earthworm assemblages were not competitively structured. Non-significant values of  
408 the index were only found in assemblages CA1+, CA2- and CA3+ for some trophic-  
409 and spatial-related niche variables.

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

418 **Discussion**

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

431 **Spatial relationships between abiotic soil variables and species assemblages**

432 Species distribution can be partly explained by soil environmental heterogeneity  
433 (Philipson et al. 1976; Valckx et al. 2009), although earthworm activity also creates  
434 heterogeneity with lasting effects in the soil (Lavelle et al. 2007) influencing the  
435 spatial patterns of key soil ecosystem processes like litter decomposition and nutrient  
436 cycling (Ettema and Wardle 2002). Recent spatially explicit studies with earthworms  
437 have demonstrated preferences for particular microhabitats in the soil (Gutiérrez-  
438 López et al. 2010; Mathieu et al. 2010). In temperate environments, Valckx et al.  
439 (2009) found that the spatial variability of soil properties was not linked to the spatial  
440 distribution of several earthworm species, among which *Lumbricus terrestris* L.,  
441 *Aporrectodea caliginosa* (Savigny), *A. rosea* (Savigny), although a positive relation

442 was observed for *Aporrectodea longa* (Ude). Gutiérrez-López et al. (2010) showed  
443 relationship between soil abiotic factors and earthworms, although the spatial pattern  
444 was not significant as revealed by partial Mantel test, contrary to results obtained by  
445 Jiménez et al. (2011), where specific spatial relationship between earthworm species  
446 and selected soil properties was shown to be significant. Higher resource  
447 heterogeneity in the soil surface of the GF exists compared with the savanna, as the  
448 presence of litter, tree logs and other discrete large elements create specific “micro”  
449 sites where the local environment is different (Mathieu et al. 2009).

450 Our study showed that the co-structure between new genus 1 and C and N  
451 concentrations in the 0-5 cm soil layer (Figure 2), occupying the same space in the  
452 CoIA factorial axes plane, could indicate species preference to abiotic factors.  
453 Furthermore, environmental constraints and habitat preferences determine patches of  
454 distinct species assemblages which exploit areas with particular soil properties so  
455 competing species can co-occur in more heterogeneous environments. This was  
456 demonstrated by the positive species association SADIE index reported between  
457 *Andiodrilus* sp. and *Glossodrilus* sp. (Jiménez et al. 2011). The spatial co-occurrence  
458 of these competitive savanna endogeic species that display opposite spatial  
459 distributions by occupying different patches (Jiménez and Rossi 2006) is allowed in  
460 the GF. Our results agree with the “coexistence aggregation model” (Hanski, 1981;  
461 Inouye, 1999) which suggests that spatial aggregation of competitors at patchily  
462 distributed resources (environment) can facilitate coexistence without species having  
463 to avoid one another other by spatial segregation or reduced body-size overlap (Ives,  
464 1988). The tri-dimensional and compact nature of soil may allow the co-occurrence  
465 of a less competitive species in areas where a strong competitor is present, facilitating

466 physical isolation between individuals with only transitory co-occurrence of  
467 competing species.

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

#### 482 **Effect of biotic interactions on earthworm spatial pattern**

483 Null-model analyses have generally been used in soil invertebrate studies (Simberloff  
484 1983, Gotelli, 2000; Gotelli and Ellison 2002; Gotelli and McCabe 2002; Ulrich and  
485 Zalewski 2006; Ward and Beggs 2007; Azeria et al. 2009; Decaëns et al. 2008, 2009;  
486 2011; Ellwood et al. 2009; Birkhofer et al. 2010). Thus, the utilisation of null-model  
487 analysis from spatially explicit sampling protocols seems appropriate to unveil  
488 competitive interactions in soil communities at small scales. Birkhofer et al. (2010)  
489 used null-model based point-pattern statistics to study the impact of biotic interactions

490 under the assumption of environmentally heterogeneous or homogeneous conditions  
491 in litter arthropods predator-prey interactions. They found that biotic interactions were  
492 determinants in the spatial distribution of ground-active predators and their prey in  
493 forested ecosystem, and claimed for inclusion of environmental heterogeneity in  
494 spatial models, otherwise the driving factors structuring species assemblages would  
495 remain hidden.

496 Diamond's seminal work (Diamond 1975) assumed a model where species  
497 interaction explained predictable community patterns. Competition is considered the  
498 main force of species interaction assembling natural communities (Weiher and Keddy  
499 1999; Gotelli and McCabe 2002), but also spatial patterns of species, either  
500 aggregated or regular, arise from habitat heterogeneity (Bell 2001). On the other  
501 hand, pure stochastic processes can also generate non-random patterns (Ulrich 2004;  
502 Bell 2005; Hubble 2005). Finally, stochastic and deterministic processes jointly  
503 influence the observed structure of soil communities (Ellwood et al. 2009). In our  
504 study, we were not able to conclude that the observed earthworm spatial co-  
505 occurrence is the result of stochastic process or species interaction where  
506 deterministic assembly rules operate.

507 In earthworm communities negative interactions prevail likely as a result of  
508 resource competition, which is related to the degree of niche overlap (Uvarov 2009).  
509 In our study, the results of niche partitioning and body size overlap indicated that the  
510 earthworm community was not shaped by competition in the GF, and that other  
511 factors influenced species co-occurrence at small scales, like differential resource use  
512 among species. Regular spacing of body size has been revealed for different groups  
513 of organisms like ground beetles (Brandl and Topp 1985), hoverflies (Gilbert et al.

514 1985), earthworms (Decaëns et al. 2009), although random patterns in body size  
515 overlap have been detected in invertebrate assemblages (Simberloff and Boecklen  
516 1981; Juliano and Lawton 1990). Although only a significant value was observed for  
517 earthworm diameter ( $MSL < EBC$ ) our findings showed that species size overlap in the  
518 GF tended to be under-dispersed while a consistent trend toward over- and even-  
519 spacing size overlap was reported for the savanna (Decaëns et al. 2009). This could  
520 be explained by higher availability of spatial and trophic resources in the GF  
521 compared with the savanna allowing coexistence of competing species in areas of  
522 high resource availability, although further research is needed.

523         Contrasting interactions have been reported between ecological categories with  
524 deep-burrowing species normally having positive effects on epigeics and endogeics,  
525 while competitive interactions seem to predominate in the latter groups (Uvarov  
526 2009). Spatial segregation of earthworms can be the result of species-specific  
527 differential preference for soil conditions rather than by interspecific competition  
528 process. Valckx et al. (2009) reported that patches occupied by endogeic species were  
529 not associated to clusters where anecic species were present, and Jiménez and Rossi  
530 (2006) found that the spatial segregation observed in patches of endogeic earthworms  
531 may result from interspecific competition. Our findings do not support the hypothesis  
532 of inter-specific competition in the earthworm community of the GF, unlike other  
533 studies in the area (Jiménez et al. 2006; Decaëns et al. 2009), and other deterministic  
534 processes (soil environmental heterogeneity) explained earthworm species co-  
535 occurrence. Earthworms are known to compete for trophic resources (Abbot 1980),  
536 and also for spatial resources by selecting areas with optimal soil conditions for their  
537 survival and reproductive strategies (Barot et al. 2007). Niche overlap in earthworms  
538 is reduced by differences in body size, temporal variation in yearly population

539 dynamics and average vertical distribution (Jiménez et al. 2006). No general rule  
540 seems to exist and the results obtained in the different studies to date are species-  
541 specific and site- and sampling-strategy dependant.

## 542 **Conclusions**

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

558       The use of factorial coordinates for community analysis has been successfully  
559 used by Rossi (2003), Jiménez et al. (2006), and Decaëns et al. (2009, 2011) to  
560 distinguish different species assemblages within the earthworm community. In the  
561 present study, species assemblages were defined by the row scores onto the three  
562 axes extracted from the CA that explained 34.2, 21.7 and 17.1% of total inertia,



563 respectively. Although the percentage of variability explained by the first axis of the  
564 CA was not high, the two species assemblages resulting from the first axis extracted  
565 in the CA showed a higher C-score than EBC at small scales. It could indicate the  
566 presence of biotic interaction (competition process) (Table 2).

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

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588 **References**

- 589 Abbott, I. 1980. Do earthworms compete for food? - *Soil Biol. Biochem.* 12: 523-530.
- 590 Albrecht, M. and Gotelli, N. J. 2001. Spatial and temporal niche partitioning in  
591 grassland ants. - *Oecologia* 126: 134-141.
- 592 Amarasekare, P. 2003. Competitive coexistence in spatially structured environments:  
593 a synthesis. - *Ecol. Lett.* 6: 1109-1122.
- 594 Azeria, E. T. et al. 2009. Using null model analysis of species co-occurrences to  
595 deconstruct biodiversity patterns and select indicator species. - *Divers. Distrib.*  
596 15: 958-971.
- 597 Barot, S. et al. 2007. Self-organization in a simple consumer-resource system, the  
598 example of earthworms. - *Soil Biol. Biochem.* 39: 2230-2240.
- 599 Belyea, L. R. and Lancaster, J. 1999. Assembly rules within a contingent ecology. -  
600 *Oikos* 86: 402-416.
- 601 Bell, G. 2001. Neutral macroecology. - *Science* 293: 2413-2418.
- 602 Bell, G. 2005. The co-distribution of species in relation to the neutral theory of  
603 community ecology. - *Ecology* 86: 1757-1770.
- 604 Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: A  
605 practical and powerful approach to multiple testing. - *J. R. Statist. Soc. B* 57:  
606 289-300.
- 607 Birkhofer, K. et al. 2010. Assessing the spatiotemporal predator-prey patterns in  
608 heterogeneous habitats. - *Basic Appl. Ecol.* 11: 486-494.
- 609 Blanchart, E. et al. 1997. Regulation of soil structure by geophagous earthworm  
610 activities in humid savannas of Cote d'Ivoire. - *Soil Biol. Biochem.* 29: 431-  
611 439.

- 612 Blydenstein, J. 1967. Tropical savanna vegetation of the Llanos of Colombia. -  
613 Ecology 48: 1- 15.
- 614 Bouché, M. B. 1972. Lombriciens de France. Ecologie et systématique. - I.N.R.A.,  
615 Paris.
- 616 Bouché, M. B. 1977. Stratégies lombriciennes. - Ecol. Bull. (Stockholm) 25: 122-132.
- 617 Brandl, R. and Topp, W. 1985. Size structure of *Pterostichus* spp. (Carabidae):  
618 aspects of competition. - Oikos 44: 234-238.
- 619 Chesson, P. 2000a. General theory of competitive coexistence in spatially-varying  
620 environments. - Theor. Popul. Biol. 58: 211-237.
- 621 Chesson, P. 2000b. Mechanisms of maintenance of species diversity. - Annu. Rev.  
622 Ecol. Syst. 31: 343-366.
- 623 Connor, E. F. and Simberloff, D. 1979. The assembly of species communities: chance  
624 or competition?. - Ecology 60: 1132-1140.
- 625 Cooper, D. W. 1968. The significance level in multiple tests made simultaneously. -  
626 Heredity 23: 614-617.
- 627 Dayan, T. and Simberloff, D. 2005. Ecological and community-wide character  
628 displacement: The next generation. - Ecol. Lett. 8: 875-894.
- 629 Decaëns, T. and Rossi, J.-P. 2001. Spatio-temporal structure of earthworm community  
630 and soil heterogeneity in a tropical pasture. - Ecography 24: 671-682.
- 631 Decaëns, T. et al. 2009. A null-model analysis of the spatio-temporal distribution of  
632 earthworm species assemblages in Colombian grasslands. - J. Trop. Ecol. 25:  
633 415-427.
- 634 Decaëns, T. et al. 2008. Assembly rules within earthworm communities in North-  
635 Western France-A regional analysis. - Appl. Soil Ecol. 39: 321-335.

636 Decaëns, T. et al. 2011. Niche overlap and species assemblage dynamics in an ageing  
637 pasture gradient in north-western France. - *Acta Oecol.* 37: 212-219.

638 Diamond, J. M. 1975. Assembly of species communities. - In: Cody, M. L. and  
639 Diamond, J. M. (eds.), *Ecology and evolution of communities*. Harvard Univ.  
640 Press, pp. 342-444.

641 Dolédec, S. and Chessel, D. 1994. Co-Inertia analysis: an alternative method for  
642 studying species-environment relationships. - *Freshwater Biol.* 31: 277-294.

643 Dray, S. et al. 2003. Co-Inertia analysis and the linking of ecological data tables. -  
644 *Ecology* 84: 3078-3089.

645 Dunson, W. A. and Travis, J. 1991. The role of abiotic factors in community  
646 organization. - *Am. Nat.* 138: 1067-1091.

647 Ellwood, M. D. F. et al. 2009. Stochastic and deterministic processes jointly structure  
648 tropical arthropod communities. - *Ecol. Lett.* 12: 277-284.

649 Ettema, C. H. and Yeates, G. W. 2003. Nested spatial biodiversity patterns of  
650 nematode genera in a New Zealand forest and pasture soil. - *Soil Biol.*  
651 *Biochem.* 35: 339-342.

652 Ettema, C. H. and Wardle, D. A. 2002. Spatial soil ecology. – *Trends Ecol. Evol.* 17:  
653 177-183.

654 Ettema, C. H. et al. 2000. On spatiotemporal patchiness and the coexistence of five  
655 species of *Chronogaster* (Nematoda: Chronogasteridae) in a riparian wetland.  
656 - *Oecologia* 125: 444-452.

657 García, L. V. 2004. Escaping the Bonferroni iron claw in ecological studies. - *Oikos*  
658 105: 657-663.

659 Gilbert, F. S. et al. 1985. Morphological approaches to community structure in  
660 hoverflies (Diptera, Syrphidae). - *Proc. R. Soc. B.* 224: 115-130.

661 Goosen, D. 1971. Physiography and soils of the eastern Llanos, Colombia. Publ. no.  
662 20, Fys Geogr Bodemk. Lab. Univ. of Amsterdam. 198 p.

663 Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. - Ecology  
664 81: 2606-2621.

665 Gotelli, N. J. 2001. Research frontiers in null model analysis. - Global Ecol. Biogeogr.  
666 10: 337-343.

667 Gotelli, N. J. and Ellison, A. M. 2002. Assembly rules for New England ant  
668 assemblages. - Oikos 99: 591-599.

669 Gotelli, N. J. and Entsminger, G. L. 2009. EcoSim: Null models software for ecology.  
670 - Acquired Intelligence Inc. & Kesey-Bear.

671 Gotelli, N. J. and McCabe, D. J. 2002. Species co-occurrence: A meta-analysis of J.  
672 M. Diamond's assembly rules model. - Ecology 83: 2091-2096.

673 Gotelli, N. J. and Ulrich, W. 2010. The empirical Bayes approach as a tool to identify  
674 non-random species associations. - Oecologia 162: 463-477.

675 Gutiérrez-López, M. et al. 2010. Relationships among spatial distribution of soil  
676 microarthropods, earthworm species and soil properties. - Pedobiologia 53:  
677 381-389.

678 Hanski, I. 1981. Coexistence of competitors in a patchy environment without  
679 predation. - Oikos 37: 306-312.

680 Hubble, S. P. 2005. Neutral theory in community ecology and the hypothesis of  
681 functional equivalence. - Funct. Ecol. 19: 166-172.

682 Hutchinson, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of  
683 animals? - Am. Nat. 93: 145-159.

684 Inouye, B.D. 1999. Integrating nested spatial scales: implications for the coexistence  
685 of competitors on a patchy resource. - Journal of Animal Ecology 68: 150-162.

686 Ives, A.R. 1988. Aggregation and the coexistence of competitors. - *Ann. Zool. Fen.*  
687 25: 75-88.

688 Jiménez, J. J. and Decaëns, T. 2000. Vertical distribution of earthworms in grassland  
689 soils of the Colombian Llanos. - *Biol. Fert. Soils* 32: 463-473.

690 Jiménez, J. J. et al. 2006. Stability of the spatio-temporal distribution and niche  
691 overlap in neotropical earthworm assemblages. - *Acta Oecol.* 30: 299-311.

692 Jiménez, J. J. et al. 2011. Short-range spatial variability of soil physico-chemical  
693 variables related to earthworm clustering in a Neotropical gallery forest. - *Soil*  
694 *Biol. Biochem.* 43: 1071-1080.

695 Jiménez, J. J. et al. 1998. Earthworm communities in native savannas and man-made  
696 pastures of the Eastern Plains of Colombia. - *Biol. Fert. Soils* 28: 101-110.

697 Jiménez, J. J. and Rossi, J. P. 2006. Spatial dissociation between two endogeic  
698 earthworms in the Colombian "Llanos". - *Eur. J. Soil Biol.* 42: S218-S224.

699 Jiménez, J. J. et al. 2001. Spatial distribution of earthworms in acid-soil savannas of  
700 the eastern plains of Colombia. - *Appl. Soil Ecol.* 17: 267-278.

701 Juliano, S. A. and Lawton, J. H. 1990. The relationship between competition and  
702 morphology. I. Morphological patterns among co-occurring dytiscid beetles. -  
703 *J. Anim. Ecol.* 59: 403-419.

704 Lavelle, P. 1981. Stratégies de reproduction chez les vers de terre. - *Acta Oecol.* 2(2):  
705 117-133.

706 Lavelle, P. et al. 2007. Earthworms as key actors in self-organised soil systems. - In:  
707 Cuddington, K. M. D. et al. (eds.), *Ecosystem engineers: plants to protists.*  
708 *Concepts, theory, and applications in ecology.* Academic Press, pp. 77-106.

709 Manly, B. F. J. 1995. A note on the analysis of species co-occurrences. - *Ecology* 76:  
710 1109-1115.

711 Mathieu, J. et al. 2009. Spatial patterns of grasses influence soil macrofauna  
712 biodiversity in Amazonian pastures. - *Soil Biol. Biochem.* 41: 586-593.

713 Mathieu, J. et al. 2010. Habitat quality, conspecific density, and habitat pre-use affect  
714 the dispersal behaviour of two earthworm species, *Aporrectodea icterica* and  
715 *Dendrobaena veneta*, in a mesocosm experiment. - *Soil Biol. Biochem.* 42:  
716 203-209.

717 Moretti, M. and Legg, C. 2009. Combining plant and animal traits to assess  
718 community functional responses to disturbance. - *Ecography* 32: 299-309.

719 Oden, N.L. 1984. Assessing the significance of a spatial correlogram. - *Geogr. Anal.*  
720 16:1-16.

721 Phillipson, J. et al. 1976. Earthworms and the factors governing their distribution in  
722 an English beechwood. - *Pedobiologia* 16: 258-285.

723 Pianka, E. R. 1973. The structure of lizard communities. - *Annu. Rev. Ecol. Syst.* 4:  
724 53-74.

725 Pianka, E. R. 1974. Niche overlap and diffuse competition. – *Proc. Nat. Acad. Sci.*  
726 71(5): 2141-2145.

727 Poole, R.W. and Rathcke, B.J. 1979. Regularity, randomness, and aggregation in  
728 flowering phenologies. - *Science* 203: 470-471.

729 R Development Core Team. 2010. R: A language and environment for statistical  
730 computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-  
731 900051-07-0. URL <http://www.R-project.org>

732 Rossi, J.-P. 1997. Statistical tool for soil biology XI. Autocorrelogram and Mantel  
733 test. - *Eur. J. Soil Biol.* 32(4): 195-203.

734 Rossi, J. P. 2003. Short-range structures in earthworm spatial distribution. -  
735 *Pedobiologia* 47: 582-587.

736 Rossi, J. P. and Nuutinen, V. 2004. The effect of sampling unit size on the perception  
737 of the spatial pattern of earthworm (*Lumbricus terrestris* L.) middens. - Appl.  
738 Soil Ecol. 27: 189-196.

739 Simberloff, D. 1983. Sizes of coexisting species. - In: Futuyma, D. J. and Slatkin, M.  
740 (eds.), Coevolution. Sinauer Associates, pp. 404-430.

741 Simberloff, D. and Boecklen, W. 1981. Santa Rosalia reconsidered: size ratios and  
742 competition. - Evolution 35: 1206-1228.

743 Sokal, R. R. and Oden, N. L. 1978. Spatial autocorrelation in biology. 1.  
744 Methodology. - Biol. J. Linn. Soc. 10: 199-228.

745 Sokal, R. R. and Rohlf, F. J. 1995. Biometry: the principles and practice of statistics  
746 in biological research. - W. H. Freeman and Co.

747 Stone, L. and Roberts, A. 1990. The checkerboard score and species distribution. -  
748 Oecologia 85: 74-79.

749 ter Braak, C. J. F. 1986. Canonical correspondence analysis: a new eigenvector  
750 technique for multivariate direct gradient analysis. - Ecology 67:1167-1179.

751 Thioulouse, J. et al. 1995. Multivariate spatial analysis of spatial patterns: a unified  
752 approach to local and global structures. - Env. Ecol. Stat. 2: 1-14.

753 Thomas, F. et al. 2008. Comparative analysis of *Andiodrilus pachoensis* casts in  
754 forests and pastures of South-Eastern Amazon (Brazil). - Eur. J. Soil Biol. 44:  
755 545-553.

756 Tucker, L.R. 1958. An inter-battery method of factor analysis. - Psychometrika,  
757 23(2): 111-136.

758 Ulrich, W. 2004. Species co-occurrences and neutral models: reassessing J.M.  
759 Diamond's assembly rules. - Oikos 107: 603-609.



760 Ulrich, W. and Gotelli, N. J. 2007. Disentangling community patterns of nestedness  
761 and species co-occurrence. - *Oikos* 116: 2053-2061.

762 Ulrich, W. and Zalewski, M. 2006. Abundance and co-occurrence patterns of core and  
763 satellite species of ground beetles on small lake islands. - *Oikos* 114: 338-348.

764 Uvarov, A. V. 2009. Inter- and intraspecific interactions in lumbricid earthworms:  
765 their role for earthworm performance and ecosystem functioning. -  
766 *Pedobiologia* 53: 1-27.

767 Valckx, J. et al. 2009. Within-field spatial distribution of earthworm populations  
768 related to species interactions and soil apparent electrical conductivity. - *Appl.*  
769 *Soil Ecol.* 41: 315-328.

770 Verhoeven, K. J. F. et al. 2005. Implementing false discovery rate control: increasing  
771 your power. - *Oikos* 108: 643-647.

772 Ward, D. F. and Beggs, J. R. 2007. Coexistence, habitat patterns and the assembly of  
773 ant communities in the Yasawa islands, Fiji. - *Acta Oecol.* 32: 215-223.

774 Weiher, E. and Keddy, P. A. 1999. Assembly rules as general constraints on  
775 community composition. - In: Weiher, E. and Keddy, P. A. (eds.), *Ecological*  
776 *assembly rules. Perspectives, advances, retreats.* Cambridge University Press,  
777 pp. 251-271.

778

## List of tables

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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).

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.

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

Table 5. Local co-occurrence of an earthworm community species at small scales in two hypothetical soil environments with varying spatial patterns.

**Table 1**

Species	Family	Ecological category <sup>1</sup>	Pigmentation	Size <sup>3</sup> (mm)		Weight <sup>3</sup> (g.f.w.)	N	Mean density ± S.E.
				Length	Diam.			
<u>Andiodrilus</u> sp.	Glossoscolecidae	Endogeic	Unpigmented	109.0	4.4	1.38	22	3.1 ± 0.7
<u>Andiorrhinus</u> sp.	Glossoscolecidae	Endo-anecic <sup>2</sup>	Pink-coloured antero-dorsal	188.0	7.6	7.10	10	0.1 ± 0.1
<u>Aymara</u> sp.	Glossoscolecidae	Epigeic	Dark-red dorsal	58.1	1.5	0.06	15	6.5 ± 1.3
New genus 1	NC <sup>4</sup>	Epigeic	Dark-green dorsal	117.9	3.8	0.69	18	9.5 ± 5.1
<u>Glossodrilus</u> sp.	Glossoscolecidae	Endogeic	Unpigmented	83.9	1.5	0.10	13	8.5 ± 1.4
<u>Martiodrilus</u> 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

<sup>1</sup> 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, and Lavelle 1981).

<sup>2</sup> It refers to a worm with characteristics of anecic (antero-dorsal pigmentation) and endogeic (horizontal burrows digging).

<sup>3</sup> Average biometric data for adults (fixed specimens in 4% formalin solution); g.f.w. = grams fresh weight (gut content included).

<sup>4</sup> NC = Not classified

**Table 2**

Null-model index	Data source	Model	Observed	Simulated	SES	Initial P	Corrected P <sup>†</sup>
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	<b>0.003</b>
	Assemblages (Axis I CA, 34.2%)	Fixed-equiprobable	1,280.00	217.45	10.237	<0.0001	<b>0.003</b>
		Fixed-fixed	1,280.00	1,280.00	0	1.000	1.000
		Fixed-proportional	1,280.00	178.34	11.547	<0.0001	<b>0.003</b>
V ratio	Species (presence/absence)	Fixed-equiprobable	0.884	1.001	-0.883	0.829	1.000
		Fixed-fixed <sup>‡</sup>	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

<sup>‡</sup> The V ratio is not computed with the fixed-fixed algorithm (see Gotelli 2000 for further details).

<sup>†</sup> \* p<0.05; \*\* p<0.01; \*\*\* p<0.001; NS = not significant.

**Table 3**

Niche dimension	Resource <sup>1</sup>	$O_{jk}$ overlap index		Average SES	Initial p	Corrected p
		Obs.	Sim.			
<u>Trophic</u>	SOC <sub>0-5</sub>	0.889	0.290	7.762	0.0001	0.0009 ***
	SOC <sub>5-10</sub>	0.917	0.240	8.177	0.0001	0.0009 ***
	N <sub>0-5</sub>	0.891	0.305	7.833	0.0001	0.0009 ***
	N <sub>5-10</sub>	0.912	0.309	6.944	0.0003	0.0027 **
	C:N <sub>0-5</sub>	0.771	0.393	5.856	0.0001	0.0009 ***
	C:N <sub>5-10</sub>	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 *
<u>Spatial</u>	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
<u>Biometric</u>	Morphological traits	0.794	0.592	5.109	0.0003	0.0027 **

<sup>1</sup> 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.

**Table 4**

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

<sup>†</sup> The p value indicates the probability that the standardized effect size (SES) differed from zero.

<sup>††</sup> \* p<0.05; \*\* p<0.01; \*\*\* p<0.001; NS = not significant.

## Figure captions

**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).

**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).

**Figure 3.** Correlogram computed with the factorial coordinates of axis 1 (□) and axis 2 (△) 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.

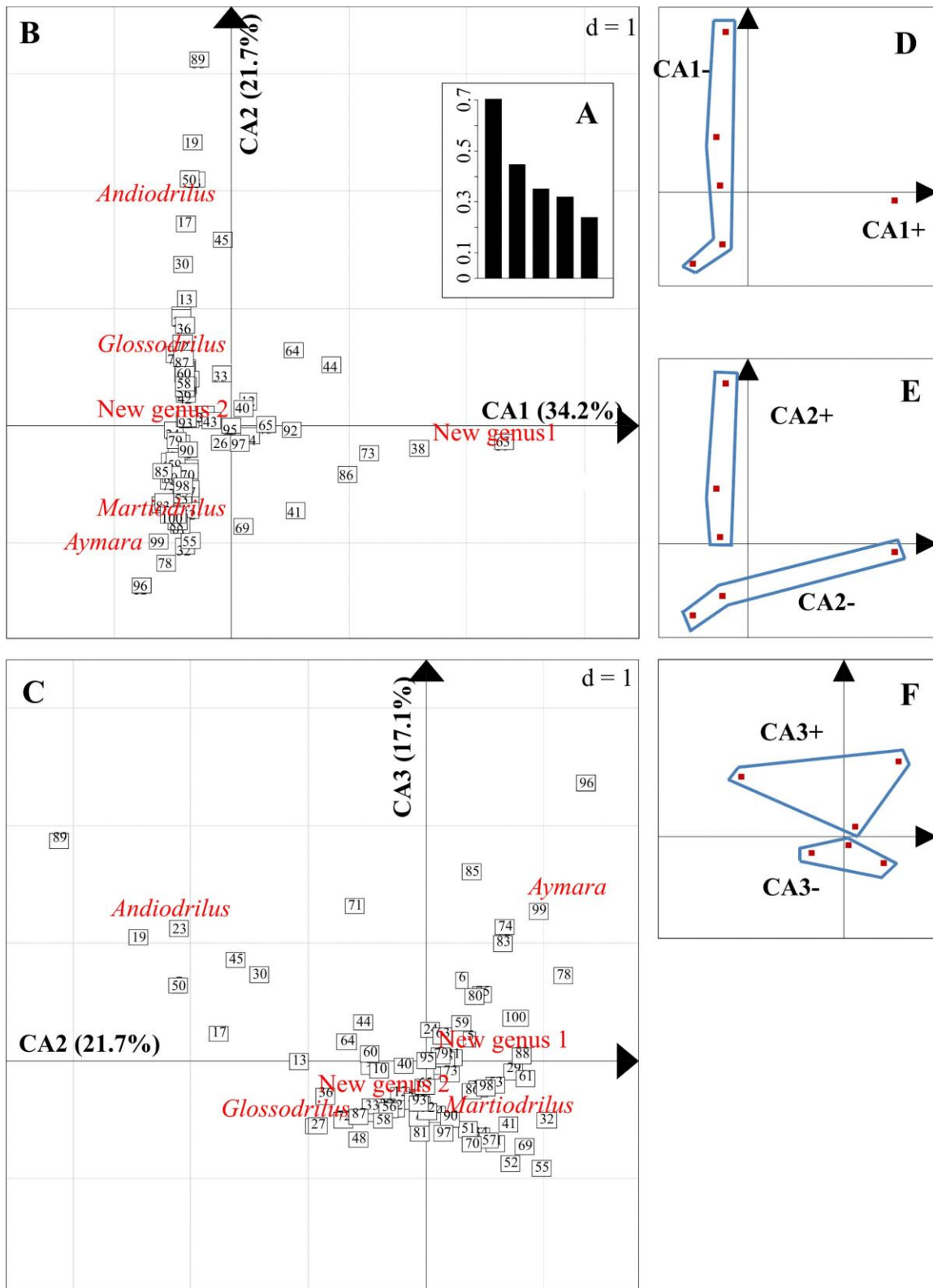


Figure 1



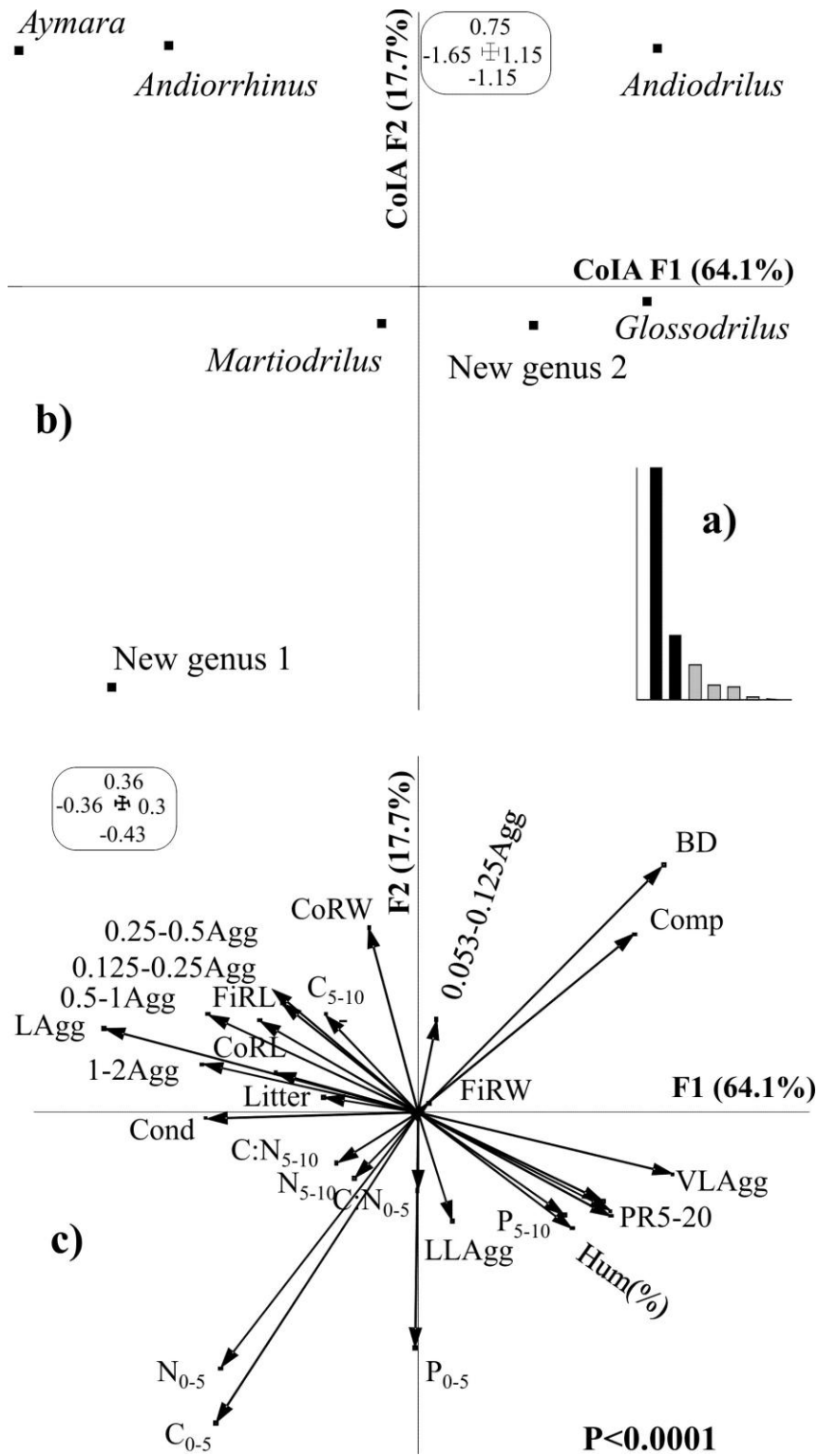


Figure 2

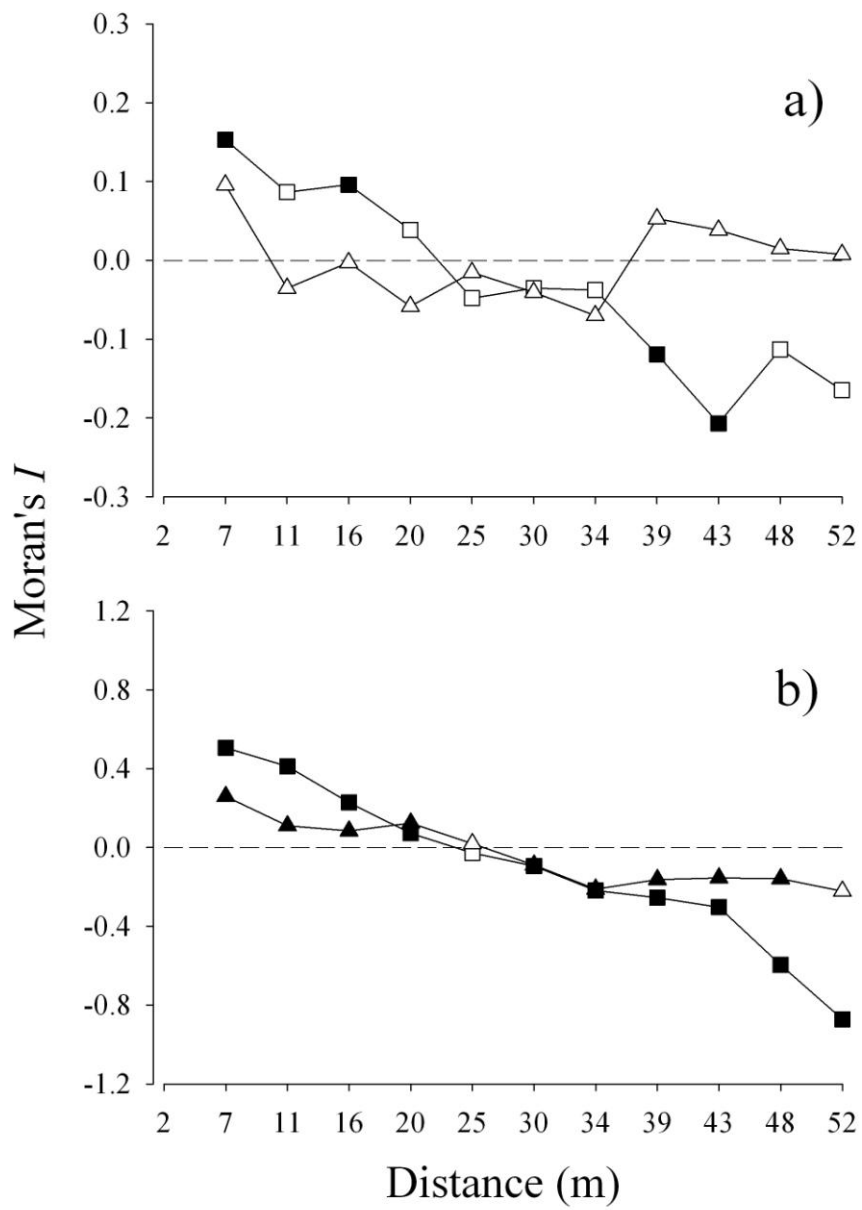


Figure 3