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Specific functional signature in soil macro-invertebrate biostructures

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Summary

1. The aim of this study was to search for specific signatures of biogenic structures (i.e. earthworm casts, termite sheathings and mound material, and ant deposits) made by 15 species of soil engineers in a Colombian savanna. We thus investigated the organic matter (OM) biochemical composition of biostructures using near infrared spectroscopy (NIRS) and its relationship with selected biological (respirometry) and chemical attributes.

2. We found significant differences in OM quality and potential respiration rate among biostructures. These results were attributed to production patterns of biostructures and invertebrate feeding behaviour. A multiple co-inertia analysis was performed with NIRS, respirometry and chemical results. It separated (i) carton termite mounds, (ii) earthworm casts and organo-mineral termite mounds and (iii) termite sheathings and ant deposits.

3. These results suggest that NIRS spectra might be used as ‘fingerprints’ to identify organisms responsible for soil aggregate production. Moreover, the ordination given by the co-inertia analysis is proposed as a basis for a functional classification of soil engineers, assuming that different biostructure properties imply different effects on soil functioning.

Key-words: Near infrared reflectance spectroscopy, physical ecosystem engineers, soil aggregates, soil organic matter

Introduction

The effect of invertebrate diversity on soil function has been addressed in a number of experiments and models. Most studies give foodweb complexity a central role in the top-down control of nutrient cycling (de Ruiter, Neutel & Moore 1998; Moore et al. 2003), with predation regulating primary decomposer abundance and activity and the rate of release of mineral N and P. However, these models tend to ignore the effect of physical processes, such as the combination of elementary particles in aggregates of different compositions and sizes, and the abundance and size distribution of pores that determine fluxes of oxygen and water and the access of organisms to feeding resources.

Earthworms, termites and ants are ‘physical ecosystem engineers’ (sensu Jones, Lawton & Shachak 1994) that significantly influence soil organic matter (OM) dynamics, hydraulic properties and ultimately pedogenetic processes by producing solid organo-mineral structures (Lavelle 1996; Lavelle & Spain 2001). These structures are highly diverse, and widely distributed above (e.g. mounds, nests, sheathings or casts) and below (e.g. galleries or chambers, earthworm and termite casts) ground. They are considered as microsites where macro-scale ecosystem processes are regulated (Anderson 1993; Lavelle et al. 2004a) and affect the diversity of other organisms, from microorganisms to macrofauna (Loranger et al. 1998; Decaëns, Mariani & Lavelle 1999; Diouf 2003; Mora et al. 2003). Declines in the abundance and diversity of invertebrate engineer communities induced by inadequate soil management may actually impair soil hydraulic function and severely decrease plant production (Chauvel et al. 1999). Hence, the diversity of biostructures produced by ecosystem engineers has been hypothesized to represent the major functional attribute whereby macro-invertebrate diversity influences soil functioning (Lavelle 1996).
Although a few studies have addressed the diversity of these structures (Schrader & Zhang 1997; Decaëns, Galvis & Amezquita 2001; Davidson et al. 2002), their recognition once incorporated in the soil matrix has so far been impossible, and this has impeded identification of relationships between changes in soil engineer diversity, the diversity of structures produced and relevant indicators of soil function. Identifying specific signatures of soil invertebrate engineers in a range of biostructures is therefore a highly challenging topic for soil ecology. This would allow determination of the exact origin of any aggregate in the soil, and open new perspectives for explanatory and predictive modelling of the mechanisms involved in the formation and dynamics of soil structure.

In the present study, we tested the ability of near infrared spectroscopy (NIRS) and a few other classical analytical techniques to discriminate biogenic structures produced by different species of soil macroinvertebrates. NIRS allows a rapid, sensitive, non-destructive and accurate qualitative analysis of the molecular composition of an organic sample. It is an increasingly accepted tool for academic research in many areas ranging from chemistry to agriculture and from life science to environmental assessments (Foley et al. 1998; Joffre et al. 2001; Siesler 2002; Shepherd & Walsh 2002; Demattê et al. 2004). The objectives of our work were (i) to identify specific signatures for the biostructures produced by 15 ecosystem engineers in a Colombian savanna based on NIRS spectra and (ii) to compare this ordination with similar classifications based on standard chemical and microbiological properties to establish a functional classification of these biostructures.

### Materials and methods

#### STUDY SITE

The study was carried out at the Carimagua Research Centre (CIAT-CORPOICA), Meta, Colombia (4°37' N, 71°19' W), which is located in the ‘Llanos Orientales’ (eastern plains) of the Orinoco basin. Climate is tropical subhumid with an average annual rainfall of 2300 mm, a dry season extending from November to March, and an annual average temperature of 26 °C. Sampling was done in a well-drained Oxisol covered by a grassy natural savanna dominated by *Trachypogon vestitus* Andres and *Paspalum pectinatum* Nees. Vegetation was protected from cattle grazing and burnt once a year during the dry season.

#### BIOSTRUCTURE SAMPLING

Engineer invertebrates and their fresh above-ground biostructures were collected in November 2001. Specimens were identified at the generic or specific level (see the list of taxa in Table 1). Depending on their availability, 3 to 13 samples of 5–20 g dry material were taken for each biostructure, giving a total of 134 samples (see details in Table 1). All samples were air-dried for 1 week, crushed and sieved at 2 mm. Four control soil samples were also collected in the savanna plot to a depth of 10 cm with a 5-cm diameter cylinder. Their location was chosen at random, at least 10 m apart from any biostructure present at the soil surface.

#### SPECTROSCOPIC MEASUREMENTS

The NIRS characterizes the molecular composition of OM in soil samples by analysing reflected spectra of

### Table 1. List and main characteristics of the soil engineers and their above-ground biostructures. Alimentary diet: A = anecic; G = geophagous; L = leaf-cutting; N = nectivorous; O = omnivorous; P = polyhumin endogenous (Decaëns et al. 2001)

| Species | Diet | Biostructures | Type | Aspect | Species code | Sample number |
|---------|------|---------------|------|--------|--------------|---------------|
| *Atta laevigata* | L | Mineral mound | Light rubble heap | A1 | 13 |
| *Camponotus* sp. | O | Mineral mound | Light rubble heap | A2 | 13 |
| *Crematogaster* sp. | N | Mineral mound | Light rubble heap | A3 | 10 |
| *Pheidole* sp. | O | Mineral mound | Light rubble heap | A4 | 10 |
| *Acromyrmex landolti* | L | Mineral mound | Light rubble heap | A5 | 3 |
| *Acromyrmex* sp. 2 | L | Mineral mound | Light rubble heap | A6 | 10 |
| *Trachymyrmex* sp. 3 | L | Mineral mound | Light rubble heap | A7 | 10 |
| *Termite* sp. | G | Carton mound | Carton material | T1 | 13 |
| *Microcerotermes* sp. | G | Organo-mineral mound | Cemented material | T2 | 13 |
| *Velocitermes* sp. | G | Organo-mineral mound | Cemented material | T3 | 10 |
| *Spinitermes* sp. | G | Sheathings | Cemented rubbles | T4 | 10 |
| *Ruptitermes* sp. | G | Carton mound | Carton material | T5 | 5 |
| *Earthworms* (Oligochaeta, Glossoscolecidae) |
| *Martiodrilus* sp. | A | Casts | Compact material | E1 | 5 |
| *Andiodrilus* sp. | P | Casts | Compact material | E2 | 5 |
material exposed to radiative energy in the infra-red region (Reeves, McCarty & Meisenger 1999; Gillon, Houssard & Joffre 1999; Joffre et al. 2001). Five grams of each sample were packed into a quartz-glass cell and scanned with a NIRSystems analyzer 6500 spectrophotometer (NIRSystems, Silverspring, USA). Two reflectance measurements of monochromatic light were made from 400 to 2500 nm to produce an average spectrum with 1050 data points at 2 nm intervals over this range with a 0.5 nm wavelength accuracy. The band-pass used is 10 nm (thus leading to 103 reflectance values). Reflectance (R) is converted to absorbance (A) using the following equation:

\[ A = \log(1/R) \]

Spectral data were processed with the ISI Software System (Shenk & Westerhaus 1991).

CHEMICAL AND BIOLOGICAL ANALYSES

Analyses of total nitrogen and other minerals were carried out for 11 of the 15 identified biostructures (those for which a sufficient amount of material was available; details in Tables 1 and 2) and on control soil according to methods recommended by the Tropical Soil Biology and Fertility program (Anderson & Ingram 1993).

Respiratory activity (CO₂ release) was measured in standard laboratory conditions to assess the decomposability of OM. Samples of the 15 biostructures were placed in 320-ml glass bottles, and sterile sand was added to achieve a total weight of 50 g; moisture was maintained at field capacity with sterile distilled water. Bottles were hermetically closed and placed in an incubator at 28 °C. CO₂ measurements were realized after 1, 5, 8, 12, 14, 16, 19 and 21 days of incubation, with a BERYL-100 NDIR Analyser, Cosma spectrophotometer (Cosma Environment, Igny, France). Organic carbon was also measured to express results in C-CO₂ g carbon⁻¹.

DATA ANALYSIS

A principal component analysis (PCA) of spectral data was computed to make an ordination of the biostructures (103 columns, i.e. number of variables = absorbance, and 134 rows, i.e. number of objects = samples). To facilitate the factorial interpretation, samples were grouped either according to engineer taxa or to five broad biostructure types, i.e. earthworm casts, organo-mineral or carton termite mounds (sensu Lavelle & Spain 2001), termite sheathings and ant nests. Group significance was tested by a permutation test (1000 permutations). Control soil samples were projected as additional rows in the analysis.

A multiple co-inertia analysis (ACOM) (Chessel & Hanafi 1996) was performed among NIRS, respirometry and chemical properties to highlight similar patterns among data sets. The ACOM analysis is a method of simultaneous ordination of K-tables (or matrices) that share the same variables or the same objects. A compromise factorial plan that maximizes the co-inertia between these K initial matrices is generated, and variables and objects of the initial K-matrices are projected on this plan in a simultaneous graphical representation. In the present case, the ACOM was applied to biostructures produced by 11 species for which complete data sets were available (Table 2). Matrices were constructed with the mean values of each parameter for each species. Hence, the three matrices contained 11 lines (i.e. the number of engineer species), and, respectively, 103, 11 and 8 columns for matrices made with NIRS, chemical and respirometry data, respectively. PCA, ACOM and related figures were created using the ADE-4 software (Thioulouse et al. 1997).

Comparisons of means were performed using Fisher PLSD test (P < 0.05). Prior to this, data normality was tested using a Kolmogorov–Smirnov test (Lilliefors 1967), using VerNorm 3-0 software.

Results

PRINCIPAL COMPONENT ANALYSIS OF NIRS SPECTRA

The first and second axes of the NIRS matrix PCA absorbed 64.1% and 12.8% of the total inertia, respectively (Fig. 1). Owing to the sharp decrease of eigenvalues, no other axes were retained for interpretation (Fig. 1a). Variables representing wavelengths were diversely correlated with the first two axes, although it was not possible to specify which chemical compound was represented by each wavelength intensity (Fig. 1b). Species ordination was significant at P < 0.001, and the first axis separated termite mounds and earthworm casts from ant structures and termite sheathings (Fig. 1d). The second axis mostly separated Microcerotermes sp. and Atta laevigata structures from Spinitermes sp. nests. Projections of the bulk soil samples on the first factorial plan were located in the neighbouring of organo-mineral earthworm casts and termite mounds on axis 1, and displayed very high positive values on axis 2.

CHEMICAL PROPERTIES

When compared with the bulk soil, earthworm casts and termite mounds presented higher OM and nutrient levels, and higher pH and lower aluminium levels (Table 2). Conversely, anthills and termite sheathings had lower OM content, pH, exchangeable aluminium and nutrient element concentrations than in the test soil.

SOIL RESPIROMETRY

Mineralization activity was higher in all the biostructures than in the bulk soil (Table 3). This was particularly obvious for earthworm casts and both types of
Table 2. Chemical properties of above-ground biostructures. Org C = organic carbon; $P_{\text{bray}}$ = assimilable phosphorus; $N_t$ = total nitrogen; $P_t$ = total phosphorus; $K_t$ = total potassium; Al sat = aluminium saturation; Al $e$ = exchangeable aluminium; Ca $e$ = exchangeable calcium; K $e$ = exchangeable potassium; Mg $e$ = exchangeable magnesium (all results except Org C after Decaëns et al. 2001). Samples codes refer to Table 1; SE in brackets; different letters indicate significant differences at $P < 0.05$.

| Ants | pH | Org C (%) | $P_{\text{bray}}$ (ppm) | $N_t$ (ppm) | $P_t$ (ppm) | $K_t$ (ppm) | Al $e$ (meq100 g soil$^{-1}$) | Ca $e$ (meq100 g soil$^{-1}$) | K $e$ (meq100 g soil$^{-1}$) | Mg $e$ (meq100 g soil$^{-1}$) | AL sat (%) |
|------|----|-----------|--------------------------|-------------|-------------|-------------|-------------------------|-------------------------|-------------------------|-------------------------|-----------|
| Atta laevigata | A1 | 4·0 (0·0) c | 5·6 (0·3) d | 0·5 (0·0) d | 721 (59) c | 192 (5) c | 1153 (61) c | 1·0 (0·1) c | 0·13 (0·06) c | 0·11 (0·05) c | 0·21 (0·02) f | 69·3 (2·7) b |
| Camponotus sp. | A2 | 4·5 (0·2) d | 6·1 (0·6) cd | 1·4 (0·2) d | 767 (57) c | 185 (4) c | 1067 (29) c | 1·0 (0·1) b | 0·14 (0·00) e | 0·16 (0·03) e | 0·32 (0·02) d | 62·8 (1·2) c |
| Crematogaster sp. | A3 | – | 5·7 (0·1-1) d | – | – | – | – | – | – | – | – | – |
| Pheidole sp. | A4 | 4·4 (0·1) d | 5·8 (0·2) d | 2·6 (0·1) d | 1011 (110) c | 206 (7) c | 837 (27) d | 1·7 (0·0) b | 0·26 (0·06) e | 0·22 (0·03) e | 0·14 (0·04) h | 73·6 (1·1) b |
| Acromyrmex landolit | A5 | 4·1 (0·1) d | 5·4 (0·2) d | 1·6 (0·2) d | 1005 (15) c | 202 (8) c | 941 (32) c | 1·8 (0·0) b | 0·17 (0·05) e | 0·17 (0·04) e | 0·13 (0·00) h | 79·5 (2·2) b |
| Acromyrmex sp. 2 | A6 | – | 6·6 (0·1) c | – | – | – | – | – | – | – | – | – |
| Acromyrmex sp. 3 | A7 | – | 5·6 (0·3) d | – | – | – | – | – | – | – | – | – |
| Trachymyrmex sp. | A8 | 4·4 (0·1) d | 6·3 (1·3) cd | 1·6 (0·5) d | 886 (119) c | 198 (5) c | 1052 (64) c | 1·0 (0·1) c | 0·28 (0·05) e | 0·29 (0·05) e | 0·26 (0·01) i | 54·6 (3·4) c |
| Termites | Microcerotermes sp. | T1 | 4·4 (0·1) d | 16·1 (0·7) a | 14·7 (0·7) a | 4578 (296) a | 3462 (142) a | 865 (27) d | 1·4 (0·0) c | 3·81 (0·05) a | 3·88 (0·08) a | 0·59 (0·02) a | 14·5 (1·3) f |
| Velocitermes sp. | T2 | 4·4 (0·0) d | 9·2 (0·8) b | 7·5 (0·2) b | 2463 (60) b | 255 (6) c | 867 (34) d | 1·6 (0·0) c | 1·63 (0·11) b | 1·21 (0·09) b | 0·43 (0·01) b | 32·8 (1·2) e |
| Spinitermes sp. | T3 | 4·7 (0·0) c | 8·5 (0·2) b | 16·1 (2·1) a | 2431 (119) b | 322 (5) c | 875 (57) d | 1·8 (0·1) b | 0·64 (0·05) d | 0·42 (0·05) d | 0·37 (0·01) c | 56·4 (1·5) c |
| Ruptitermes sp. | T4 | 4·0 (0·0) e | 6·5 (0·4) c | 1·9 (0·0) d | 987 (59) c | 184 (3) c | 818 (12) d | 1·4 (0·2) c | 0·20 (0·07) c | 0·17 (0·04) e | 0·08 (0·00) i | 74·5 (3·5) b |
| Termit sp. | T5 | – | 14·3 (1·1) a | – | – | – | – | – | – | – | – | – |
| Earthworms | Martiodrilus sp. | E1 | 5·2 (0·1) b | 8·4 (0·6) b | 4·2 (0·9) c | 2296 (61) b | 242 (6) c | 2156 (94) a | 1·4 (0·0) c | 0·94 (0·04) c | 0·66 (0·01) c | 0·19 (0·01) g | 3·9 (1·3) d |
| Andiodrilus sp. | E2 | 5·4 (0·0) a | 8·6 (0·6) b | 6·5 (0·5) b | 2042 (37) b | 577 (7) b | 1925 (34) b | 0·3 (0·1) d | 3·84 (0·25) a | 0·57 (0·01) c | 0·16 (0·01) h | 6·8 (2·2) g |
| Bulk soil | BS | 4·4 (0·1) d | 6·5 (0·6) cd | 1·6 (0·2) d | 2036 (872) b | 183 (7) c | 1017 (30) c | 2·9 (0·1) a | 0·23 (0·06) c | 0·14 (0·01) c | 0·14 (0·03) h | 85·2 (1·2) a |
termite mounds, in which production of CO$_2$ continuously increased with time, with highest values obtained after 21 days of incubation. By comparison, ant deposits and termite sheathings showed significantly lower mineralization rates ($P < 0.05$), close to those measured in the bulk soil.

**Fig. 1.** PCA of the NIRS spectra of the 15 identified above-ground biostructures (codes refer to Table 1): (a) eigenvalue diagram; (b) correlation circle on F1–F2 plan; (c) ordination of biostructures on F1–F2 plan according to engineer taxa or (d) according to broad biostructure types; bulk soil was projected as additional columns. Species codes refer to Table 1.

**Table 3.** Accumulated CO$_2$ release (mg C-CO$_2$g carbon$^{-1}$, mean ± SD) in the above-ground biostructures after 1, 2 and 3 weeks of incubation in standard laboratory conditions. Different letters indicate significant differences at $P < 0.05$

|                     | $n$ | 1 week  | 2 weeks | 3 weeks |
|---------------------|-----|---------|---------|---------|
| Atta laevigata      | 10  | 3·36 (0·90) a | 3·74 (1·02) c | 4·11 (1·16) f |
| Camponotus sp.      | 10  | 8·46 (1·08) a | 11·08 (1·22) bc | 14·00 (1·67) cd |
| Crematogaster sp.   | 10  | 6·41 (0·42) a | 7·56 (0·50) bc | 8·76 (0·76) e |
| Pheidole sp.        | 10  | 7·87 (1·87) a | 9·37 (2·47) bc | 11·53 (3·70) de |
| Acromyrmex landolti | 3   | 6·47 (1·69) a | 8·07 (1·96) bc | 9·80 (2·20) de |
| Acromyrmex sp. 2    | 10  | 9·78 (4·60) a | 12·51 (4·58) bc | 15·70 (5·18) cd |
| Acromyrmex sp. 3    | 10  | 4·89 (1·26) a | 6·06 (1·69) bc | 7·55 (2·36) e |
| Trachymyrmex sp.    | 4   | 13·30 (4·16) a | 15·88 (4·54) abc | 18·61 (5·13) bcd |
| Microcerotermes sp. | 10  | 27·35 (18·89) a | 39·22 (25·77) a | 52·16 (31·55) a |
| Velocitermes sp.    | 10  | 18·32 (6·13) a | 24·91 (7·14) ab | 31·73 (8·80) ab |
| Spinitermes sp.     | 10  | 17·41 (4·43) a | 24·40 (5·59) ab | 31·37 (6·78) ab |
| Ropitermes sp.      | 10  | 10·77 (4·35) a | 14·20 (5·89) bc | 18·88 (8·00) cd |
| Termite sp.         | 5   | 13·48 (6·14) a | 19·80 (9·00) abc | 26·06 (10·85) bc |
| Martiodrilus sp.    | 5   | 12·43 (4·43) a | 17·01 (5·78) abc | 22·93 (7·68) bc |
| Andiodrilus sp.     | 5   | 12·30 (1·78) a | 16·75 (2·58) abc | 22·42 (3·75) bc |
| Bulk soil           | 5   | 4·53 (1·64) a | 5·55 (1·46) bc | 7·04 (2·00) ef |

**Multiple Co-Inertia Analysis**

The first axis of the ACOM absorbed 71% of the total covariance between the three matrices, and was the only one retained for interpretation owing to the rapid decline in eigenvalues (Fig. 2a). There were only
slight differences in the ordination of the 11 types of biostructures according to NIRS spectra, chemical and respirometric variables (Fig. 2). Ant deposits and termite sheathings with positive scores on the first axis, were characterized by high levels of aluminium saturation, low values for the other entire chemical parameters and low mineralization rates (Fig. 2a–c). The opposite pattern was found for the carton mounds of *Microcerotermes* sp., which had negative scores on axis 1, with high values for all the chemical parameters except for aluminium saturation and high mineralization rates. Earthworm casts and organo-mineral termite mounds presented intermediate scores.

**Discussion**

**Organic signature of biogenic structures**

NIRS spectra may be considered as fingerprints of the OM composition (Gillon, Joffre & Ibrahima 1999; Joffre et al. 2001). In this study, we show for the first time that structures produced by different ecosystem engineers can be clearly separated according to this criterion in spite of the noise added to the signal by the mineral matrix. The use of multivariate analysis clearly underlined that the modifications of soil OM caused by ecosystem engineering result in species-specific organic fingerprints in their respective above-ground biostructures. These fingerprints and other properties of biostructures provide a method for novel functional classification of soil ecosystem engineers that can be derived from the ordination of a large set of similar data collected under a broad range of ecological conditions. Given the importance of aggregation in all soil processes, this finding may be considered a breakthrough in our quest to relate biodiversity in soil organisms, especially ecosystem engineers, and soil function (Hooper et al. 2000; Lavelle et al. 2004b).

Differences observed between biostructures result from the combination of three different factors. First, structures produced after gut transit (earthworm casts and mounds of humivorous termites) present higher OM contents than structures made by displacement of soil particles (ant deposits, termite sheathings). Second, the nature of the substrate(s) ingested by soil invertebrates and the addition of intestinal mucus or saliva during biostructure production are further reflected in NIRS signatures. Earthworm casts may contain at least some traces of intestinal mucus secreted during the digestion process and largely reabsorbed at the end of the gut (Martin et al. 1987). Termites use their saliva as an organic glue to assemble particles during the construction of the mounds and sheathings (see review by Brauman 2000). Contrary to earthworm casts and termite mounds, ant artefacts seem to be mainly constituted by separated soil particles (Elmes 1991). Finally, specific microbial activities in the gut of some engineer species and in their fresh biostructures probably affect the OM molecular composition via the production of specific mucigel and cellular compounds (Martin & Marinissen 1993; Harry et al. 2001; Lavelle et al. 2004c).

These three factors merely explain the variability in OM biochemical composition emphasized by the PCA. The first principal component was related to a gradient of OM concentration in the biostructures, which separated almost completely mineral ant artefacts from organic termite mounds, with intermediate positions for organo-mineral earthworm casts and termite mounds. This ordination clearly separated non-geophagous from geophagous species, with an increased microbial activity resulting from mutualistic digestion during earthworm and termite gut transit (Lavelle & Spain 2001).

Interestingly, control soil was closely associated with earthworm casts and termite mounds in factorial representations, suggesting a great participation of these organisms in soil aggregate formation. This hypothesis is largely supported by quantitative estimations, which have demonstrated that both earthworm and termite
organo-mineral constructions are the two dominant
above-ground biostructures in the Carimagua’s savannas
(Decaëns et al. 2002).

CARBON POTENTIAL MINERALIZATION

Results from the mineralization tests separated termite
mounds and earthworm casts with high mineralization
rates, from ant deposits and termite sheathings with
opposite characteristics. It must also be stressed that
significant differences may occur within each groups,
exemplified by the high values observed in Microcero-
terms sp. carton mounds as compared with other
termitex mound material.

In the field, structures with high potential mineral-
ization rates also had high structural stability. Diverse
experiments have shown that earthworm casts may
keep their physical integrity for periods of months to
several years depending on their clay contents and
their location in the soil profile (Blanchart et al. 1997;
Decaëns 2000). On the other hand, small ant deposits,
fresh earthworm casts or termite sheathings may be
destroyed by a single important rain event (Blanchart,
Bruand & Lavelle 1993; T. Decaëns & J. J. Jiménez,
personal observation). As a consequence, OM protected
inside biostructures only becomes available to micro-
orisms when biostructures are dispersed or crushed
(as done artificially in our laboratory test)(Martin 1991).

In our results, differences in potential OM mineraliza-
tion therefore reflect differences in OM chemical pro-
tection against microbial activity rather than physical
protection, i.e. differences in the concentration of easily
available C for microbial communities.

As previously discussed, earthworm casts and termite
mounds mostly differ from ant artefacts and termite
sheathings by the origin of their OM, and the gut
transit experienced before structure building (Brauman
et al. 2001; Kapler & Brune 2002). Thus, resource
quality for microorganisms in biostructures mostly
results from the combined effect of engineer foraging
specificity (Jiménez et al. 1998; Jiménez, Rossi &
Lavelle 2001; Mariani et al. 2001) and outputs of the
digestive mutualistic interactions (Lavelle & Gilot 1994;
Lavelle et al. 1995), both mechanisms leading to
differences in the OM humification rates.

CLASSIFICATION OF THE BIOSTRUCTURES

In a pioneer study dedicated to the same set of species,
Decaëns et al. (2001) proposed a tentative classifica-
tion of biostructures based on physico-chemical
characteristics. Our findings support the results of this
preliminary study, and provide additional data to infer
the functional traits of soil engineers from the pro-
erties of their biostructures. Three broad functional
groups of engineers may thus be proposed:

1. Accumulators of protected OM. Carton termite
mounds are clearly the most different from the average
soil, and also differ from other types of structures
in most parameters. These holorganic structures present
a specific OM biochemical composition and high
potential mineralization rates. Although their life
span is not known with any certainty, they may
constitute a pool of protected OM, which may be
mineralized only if/when the mound is destroyed.

2. Soil compactors. Organo-mineral termite mounds
and earthworm casts are compact structures with
high structural stability and overall properties rela-
tively similar to the bulk soil. Their low mineraliza-
tion rates reflect a lower concentration of OM and a
more efficient chemical protection than carton
termite mounds. Therefore, whatever their life span,
their OM probably remains protected for a long
period of time after their disruption.

3. Soil decompactors. Ant mounds and termite sheath-
ings are characterized by a loose structure and low
organic contents and mineralization rates. The
impact of these structures on soil OM dynamics
is expected to be limited whereas they probably
influence soil physical properties by bringing to the
surface deep material with specific granulometric
characteristics. They participate in the disruption
of stable organo-mineral aggregates and have been
for this reason defined as decompacting species
(Blanchart et al. 1999).

Ecological functions of all soil macro-invertebrates
are not likely to fit into three categories only. We
propose to classify them in a continuous mode, according
to a set of relevant biological traits considered to be
predictors of their function in soil. Diaz et al. (1999)
proposed a distinction between ‘soft’ biological traits,
that are easily measurable, which in turn enable predic-
tion of ‘hard’ traits, i.e. characters that have direct
functional implications although they are very difficult
or impossible to measure. Biostructures can be defini-
tively considered as hard biological traits since their
nature, accumulation and distribution may clearly
affect critical soil processes (Lavelle 1996).

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References

Anderson, J.M. (1993) Soil organisms as engineers: microsite
modulation of macroscale process. Linking Species and
Ecosystems (eds C.G. Jones & J.H. Lawton), pp. 94–106.
Chapman & Hall, New York.
Anderson, J.M. & Ingram, J.S. (1993) Tropical Soil Biology
and Fertility: a Handbook of Methods, 2nd edn. CAB Inter-
national, Oxford.
Blanchart, E., Albrecht, A., Alegre, J., Duboiset, A., Gilot, C., Pashanasi, B., Lavelle, P. & Brussaard, L. (1999) Effects of earthworms on soil structure and physical properties. *Earthworm Management and Biochemistry 33*, 417–427.

Hooper, D.U., Bignell, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Lavelle, P., van der Putten, W.H., de Ruiter, P.C., Rusek, J., Silver, W., Tiedje, J.M. & Wolters, V. (2000) Interactions between above- and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. *BioScience 50*, 1049–1061.

Jiménez, J.J., Moreno, A.G., Lavelle, P. & Decaëns, T. (1998) Population dynamics and adaptative strategies of *Martioidrilus carimaguensis* (Oligochaeta, Glossoscolecidae), a native species from the well-drained savannas of Colombia. *Applied Soil Ecology 9*, 153–160.

Jiménez, J.J., Rossi, J.P. & Lavelle, P. (2001) Spatial distribution of earthworms in acid-soil savannas of the eastern plains of Colombia. *Applied Soil Ecology 17*, 267–278.

Jolliet, R., Agren, G.I., Gilion, D. & Bosatta, E. (2001) Organic matter quality in ecological studies: theories meets experiment. *Oikos 93*, 451–458.

Jones, C.G., Lawton, J.H. & Shackah, M. (1994) Organisms as ecosystem engineers. *Oikos 69*, 373–386.

Kapler, A. & Brune, A. (2002) Dynamics of redox potential and changes in redox state of iron and humic acids during gut passage in soil-feeding termites (*Cubitermes* spp). *Soil Biology and Biochemistry 34*, 221–227.

Lavelle, P. (1996) Diversity of soil fauna and ecosystem function. *Biologia International 33*, 3–16.

Lavelle, P., Bignell, D., Austen, M., Giller, P., Behan-Pelletier, V., Carey, V., Hawkings, P., Brown, G., St John, M., Hunt, W. & Paul, E. (2004a) Vulnerability of ecosystem services at different scales: role of biodiversity and implications for management. *Sustaining Biodiversity and Functioning in Soils and Sediments* (ed. D.H. Wall), pp. 213–224. Island Press, New York.

Lavelle, P., Charpentier, F., Gilot, C., Rossi, J.P., Pashanasi, B., Derouard, L., André, J., Ponge, J.F. & Bernier, N. (2004b) Effects of earthworms on soil organic matter and nutrient dynamics at a landscape scale over decades. *Earthworm Ecology 2nd edn.* (ed. C.E. Edwards), pp. 145–160. CRC Press Boca, Raton.

Lavelle, P. & Gilot, C. (1994) Priming effects of macroorganisms on microflora: a key process of soil function? *Beyond the Biomass* (eds K. Ritz, J. Dighton & K.E. Giller), pp. 176–181. Wiley-Saye, Chichester.

Lavelle, P., Lattaud, C., Trigo, D. & Barois, I. (1995) Mutualism and biodiversity in soils. *The Significance and Regulation of Soil Biodiversity* (eds H.P. Collins, G.P. Robertson & M.J. Klug), pp. 23–33. Kluwer Academic Publishers, Dordrecht.

Lavelle, P., Rouland, C., Binet, F., Diouf, M. & Kersante, A. (2004c) *Regulation of Microbial Activities by Roots and Soil Invertebrates*. Springer Verlag, Berlin.

Lavelle, P. & Spain, A.V. (2001) *Soil Ecology*. Kluwer Scientific Publications, Amsterdam.

Lilledofs, H.W. (1967) The Kolmogorov-Smirnov-test for normality with mean and variance unknown. *Journal of American Statistical Association 62*, 399–402.

Loranger, G., Ponge, J.F., Blanchart, E. & Lavelle, P. (1998) Impact of earthworms on the diversity of microarthropods in a vertisol (Martineau). *Biologie and Fertility of Soils 27*, 21–26.

Mariani, L., Bernier, N., Jiménez, J.J. & Decaëns, T. (2001) Régime alimentaire d’un ver de terre anécique des savanes colombiennes: une remise en question des types écologiques. *Compte Rendus de l’Académie Des Sciences 324*, 733–742.

Martin, A. (1991) Short- and long-term effects of the endogeic earthworm *Millsonia ananula* (Omodeo) (*Megascolecidae,*
Oligochaeta) of tropical savannas, on soil organic matter. *Biology and Fertility of Soils* 11, 234–238.

Martin, A., Cortez, J., Barois, I. & Lavelle, P. (1987) Les mucus intestinaux de ver de terre moteur de leurs interactions avec la microflora. *Revue d’Ecologie et de Biologie Des Sol* 24 (4), 549–558.

Martin, A. & Marinissen, J.C.Y. (1993) Biological and physico-chemical processes in excrements of soil animals. *Geoderma* 56, 331–347.

Moore, J.C., McCann, K., Setälä, H. & de Ruiter, P.C. (2003) Top-down is bottom-up: does predation in the rhizo-sphere regulate aboveground dynamics? *Ecology* 84, 846–857.

Mora, P., Seugé, C., Chotte, J.L. & Rouland, C. (2003) Physico-chemical typology of the biogenic structures of termites and earthworms: a comparative analysis. *Biology and Fertility of Soils* 37, 245–249.

Reeves, J.B., McCarty, G.W. & Meisenger, J.J. (1999) Near infrared reflectance spectroscopy for the analysis of agricultural soils. *Near Infrared Spectroscopy* 7, 179–193.

de Ruiter, P.C., Neutel, A.-M. & Moore, J.C. (1998) Biodiversity in soil ecosystems: the role of energy flow and community stability. *Applied Soil Ecology* 10, 217–228.

Schrader, S. & Zhang, H. (1997) Earthworm casting: stabilization or destabilization of structure? *Soil Biology and Biochemistry* 29 (3/4), 469–475.

Shenk, J.S. & Westerhaus, M.O. (1991) ISIR NIRS-2: Software for near-infrared instrument. InfraSoft International, Silverspring, USA.

Shepherd, K.D. & Walsh, M.G. (2002) Development of reflectance spectral libraries for characterization of soil properties. *Soil Science Society of America Journal* 66, 988–998.

Siesler, H.W. (2002) Introduction. *Near-Infrared Spectroscopy. Principles, Instruments, Applications* (eds H.W. Siesler, Y. Ozaki, S. Kawata & H.M. Heise), pp. 1–10. Wiley, Weinheim.

Thioulouse, J., Chessel, D., Dolédec, S. & Olivier, J.-M. (1997) ADE-4: a multivariate analysis and graphical display software. *Statistic Computer* 7, 5–83.

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