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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

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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 explanative 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; Dematté *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 = polyhumic endogenous (Decaëns *et al.* 2001)

Species	Diet	Biostructures			
		Type	Aspect	Species code	Sample number
Ants (Hymenoptera, Formicidae)					
<i>Atta laevigata</i>	L	Mineral mound	Light rubble heap	A1	13
<i>Camponotus</i> sp.	O	Mineral mound	Light rubble heap	A2	13
<i>Crematogaster</i> sp.	N	Mineral mound	Light rubble heap	A3	10
<i>Pheidole</i> sp.	O	Mineral mound	Light rubble heap	A4	10
<i>Acromyrmex landolti</i>	L	Mineral mound	Light rubble heap	A5	3
<i>Acromyrmex</i> sp. 2	L	Mineral mound	Light rubble heap	A6	10
<i>Acromyrmex</i> sp. 3	L	Mineral mound	Light rubble heap	A7	10
<i>Trachymyrmex</i> sp.	L	Mineral mound	Light rubble heap	A8	4
Termites (Isoptera, Termitidae)					
<i>Microcerotermes</i> sp.	G	Carton mound	Carton material	T1	13
<i>Velocitermes</i> sp.	G	Organo-mineral mound	Cemented material	T2	13
<i>Spinitermes</i> sp.	G	Organo-mineral mound	Cemented material	T3	10
<i>Ruptitermes</i> sp.	G	Sheathings	Cemented rubbles	T4	10
Termite sp.	G	Carton mound	Carton material	T5	5
Earthworms (Oligochaeta, Glossoscolecidae)					
<i>Martiodrilus</i> sp.	A	Casts	Compact material	E1	5
<i>Andiodrilus</i> 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 (CO_2 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. CO_2 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-CO_2 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 *Spini-termes* 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_{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 $P < 0.05$

		pH	Org C (%)	P _{bray} (ppm)	Total (ppm)			Exchangeable (meq100 g soil ⁻¹)				AL sat (%)
					N _t	P _t	K _t	Al _e	Ca _e	Mg _e	K _e	
Ants												
<i>Atta laevigata</i>	A1	4.0 (0.0) e	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) e	0.11 (0.05) e	0.21 (0.02) f	69.3 (2.7) b
<i>Camponotus</i> 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
<i>Crematogaster</i> sp.	A3	–	5.7 (0.1) d	–	–	–	–	–	–	–	–	–
<i>Pheidole</i> 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
<i>Acromyrmex landolti</i>	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
<i>Acromyrmex</i> sp. 2	A6	–	6.6 (0.1) c	–	–	–	–	–	–	–	–	–
<i>Acromyrmex</i> sp. 3	A7	–	5.6 (0.3) d	–	–	–	–	–	–	–	–	–
<i>Trachymyrmex</i> 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) e	54.6 (3.4) c
Termites												
<i>Microcerotermes</i> 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
<i>Velocitermes</i> 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
<i>Spinitermes</i> 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
<i>Ruptitermes</i> 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) e	0.17 (0.04) e	0.08 (0.00) i	74.5 (3.5) b
Termite sp.	T5	–	14.3 (1.1) a	–	–	–	–	–	–	–	–	–
Earthworms												
<i>Martiodrilus</i> 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
<i>Andiodrilus</i> 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) e	0.14 (0.01) e	0.14 (0.03) h	85.2 (1.2) a

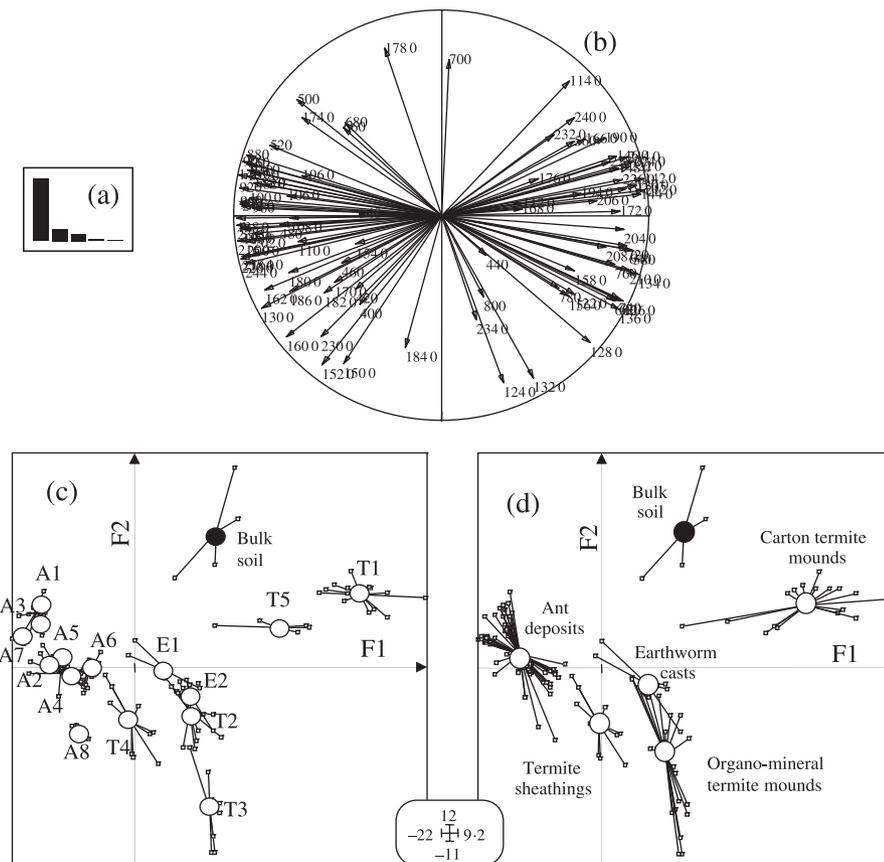


Fig. 1. PCA of the NIRS spectra of the 15 identified above-ground biostructures (codes refer to Table 1): (a) eigenvalue diagram; (b) correlation circle on F1–F2 plan; (c) ordination of biostructures on F1–F2 plan according to engineer taxa or (d) according to broad biostructure types; bulk soil was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

Table 3. Accumulated CO₂ release (mg C-CO₂g 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 $P < 0.05$

	<i>n</i>	1 week	2 weeks	3 weeks
<i>Atta laevigata</i>	10	3.36 (0.90) a	3.74 (1.02) c	4.11 (1.16) f
<i>Camponotus</i> sp.	10	8.46 (1.08) a	11.08 (1.22) bc	14.00 (1.67) cd
<i>Crematogaster</i> sp.	10	6.41 (0.42) a	7.56 (0.50) bc	8.76 (0.76) e
<i>Pheidole</i> sp.	10	7.87 (1.87) a	9.37 (2.47) bc	11.53 (3.70) de
<i>Acromyrmex landolti</i>	3	6.47 (1.69) a	8.07 (1.96) bc	9.80 (2.20) de
<i>Acromyrmex</i> sp. 2	10	9.78 (4.60) a	12.51 (4.58) bc	15.70 (5.18) cd
<i>Acromyrmex</i> sp. 3	10	4.89 (1.26) a	6.06 (1.69) bc	7.55 (2.36) e
<i>Trachymyrmex</i> sp.	4	13.30 (4.16) a	15.88 (4.54) abc	18.61 (5.13) bcd
<i>Microcerotermes</i> sp.	10	27.35 (18.89) a	39.22 (25.77) a	52.16 (31.55) a
<i>Velocitermes</i> sp.	10	18.32 (6.13) a	24.91 (7.14) ab	31.73 (8.80) ab
<i>Spinitermes</i> sp.	10	17.41 (4.43) a	24.40 (5.59) ab	31.37 (6.78) ab
<i>Ruptitermes</i> 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
<i>Martiodrilus</i> sp.	5	12.43 (4.43) a	17.01 (5.78) abc	22.93 (7.68) bc
<i>Andiodrilus</i> sp.	5	12.30 (1.78) a	16.75 (2.58) abc	22.42 (3.75) bc
Bulk soil	5	4.53 (1.16) a	5.55 (1.46) bc	7.04 (2.00) ef

termite mounds, in which production of CO₂ 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.

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

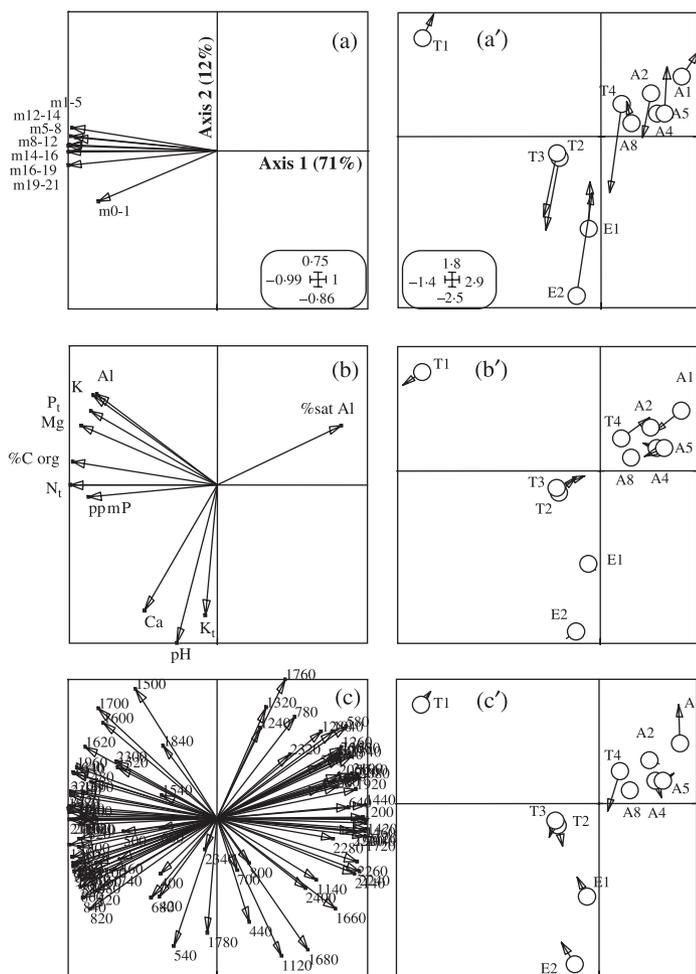


Fig. 2. ACOM performed on chemical properties, potential mineralization and NIRS spectra of 11 different above-ground biostructures: each initial set of variable is projected on the compromise plan: (a) potential mineralization at different time of incubation; (b) chemical properties and (c) NIRS wavelengths. For each data set, biostructure ordination is represented (arrow heads) together with their ordination on the compromise plan (circles) (a' to c'). Codes refer to Tables 1 and 2.

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 *Microcerotermes* sp. carton mounds as compared with other termite mound material.

In the field, structures with high potential mineralization 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 microorganisms when biostructures are dispersed or crushed (as done artificially in our laboratory test) (Martin 1991). In our results, differences in potential OM mineralization therefore reflect differences in OM chemical protection 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 classification 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 properties 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 relatively similar to the bulk soil. Their low mineralization 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 decompackers.** Ant mounds and termite sheathings 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 decompressing 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 prediction of 'hard' traits, i.e. characters that have direct functional implications although they are very difficult or impossible to measure. Biostructures can be definitively considered as hard biological traits since their nature, accumulation and distribution may clearly affect critical soil processes (Lavelle 1996).

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