Humus components and biogenic structures under tropical slash-and-burn agriculture

S. TOPOLIANZ^a, J.-F. PONGE^a & P. LAVELLE^b

^a*Muséum National d'Histoire Naturelle, CNRS UMR 5176, 4 avenue du Petit-Château, 91800 Brunoy, and* ^b*Institut pour la Recherche et le Développement, UMR 137 BioSol, 32 avenue Henri-Varagnat, 93143 Bondy Cedex, France*

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Correspondence: J.-F. Ponge. E-mail: jean-francois.ponge@wanadoo.fr

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Summary

Slash-and-burn cultivation in the humid tropics can cause changes in the composition of topsoil, depending on the duration of the fallow. We studied differences between practices, using the small-volume micromorphological method, to quantify the distribution of solid components in the topsoil, concentrating on plant organs and biogenic structures created by soil animals. We compared samples of topsoil from five plots, two at Maripasoula, an Aluku village along the river Maroni (French Guiana), with short fallow (≤ 8 years), and the other three at Elahe, a Wayana village along the same river, with long fallow

(≥ 25 years). At both sites structures created by arthropods other than ants gave way to ones formed by ants and annelids under the influence of fire and cultivation. This change was more abrupt under long fallow, because of the time needed to restore the arthropod community. Charcoal and charred plant material were incorporated by earthworms into the mineral soil, forming dark grey to black aggregates. Charcoal became mixed with the mineral soil faster at Elahe than at Maripasoula, where it accumulated in the topsoil. The reason seems to be an imbalance between charcoal inputs (from repeated fires) and the capacity of burrowing animals (earthworms, ants) to mix it with the mineral soil.

Introduction

Traditional shifting agriculture in the tropics balanced food production and nature conservation. In French Guiana, this long-lasting equilibrium is threatened by increasing demographic pressure and settling of cultivators for social welfare, schools, medical care and administration. In Maripasoula (population 1200), a settlement along the Maroni river (bordering French Guiana and Suriname) of mostly Aluku people (of African lineage), the duration of fallow in the slash-and-burn system has decreased from 15 to 7-8 years in the last thirty years. It is much shorter than the 15 to more than 100 years in the traditional shifting cultivation still practised by Wayana Amerindians as in the village of Elahe (Fleury, 1998).

Under traditional shifting cultivation (alternating short periods of cropping with long fallows), burning of woody vegetation before cultivation fertilizes the soil with ashes. During the fallow, the nutrient status of the soil, impoverished by crops, regenerates after several years from the organic matter added by the regrowth of vegetation, and we know from many accounts how important soil organic matter is for the maintenance of soil fertility in the tropics. The stabilization of soil organic matter within biogenic structures such as earthworm faeces help to preserve a reservoir of water, nutrients and space in which plant roots, animals and microbes can grow. Among other approaches, the fate of charcoal, from incomplete combustion of wood, has been considered of potential use for alternative systems of tropical agriculture (Glaser *et al.*, 2002; Lehmann *et al.*, 2003; Glaser & Woods, 2004). Glaser *et al.* (2001) found that charcoal is a source of stable and fertile humus in Amazonian Terra Preta. Our own experiments showed that the combined use of charcoal and manioc peel could sustain legume production on rather infertile tropical soils (Topoliantz *et al.*, 2005).

The present study was done in southern French Guiana. Its aim was to compare the impact of slash-and-burn cultivation on humus components and biogenic structures in the soil of two agricultural systems, differing in the duration of the fallow (8 years in Maripasoula and >100 years in Elahe) and that of continuous cultivation (1 year in Maripasoula, 3 years in Elahe). Manioc (*Manihot esculenta* Cranz) was the major crop in both villages. These sites were chosen as typical examples of (i) traditional shifting agriculture, and (ii) change to permanent agriculture, on the basis of preliminary investigations on

the impact of agricultural practices on soil fertility along the Maroni river (Grandisson, 1997). The crop (manioc) was the same and the soils (Oxisols) are similar. The two sites differ only in the way they are managed.

Materials and methods

Study sites

The first site, typical of traditional slash-and-burn shifting agriculture, is upstream of the Amerindian Wayana village of Elahe, on the Tampock river, a subsidiary of Maroni (N 3°26'; W 53°59'). Three years ago a family had cut and burned contiguous fields (abattis) within a secondary forest. This forest seemed, from a census of woody species typical of mature forests such as *Astrocaryum sciophilum* (Miquel) Pulle and *Dicorynia guianensis* Amsh. (Poncy *et al.*, 2001), to have been let untouched for at least 100 years. We sampled an abattis which had been under cultivation for 3 years (EA), and the nearby untouched old secondary forest (EF) in July 1999, approximately 100 m from EA. The plot in the secondary forest was resampled in May 2000 after it was burnt in December 1999 for cultivation (EFB).

The second site is by the Maroni river (N 3°39'; W 54°2') near Maripasoula, 25 km downstream of the first site. It is in a large village inhabited mostly by Aluku people (black people of African lineage, descended from slaves who escaped at the end of the 18th century). During the last thirty years the increase of the population decreased the surface of cultivable land per family

and the duration of the fallow (Fleury, 1998). We sampled a one-year-old abattis at the end of the crop period, opened by an Aluku family by burning an 8-year-old woody fallow (MA), and the nearby unburnt fallow (MF), approximately 100 m from MA. The latter plot was characterized by typical pioneer woody species such as *Cecropia latiloba* Miq. and *Inga capitata* Desv. Unlike the inhabitants of Elahe village, who can exploit the same abattis for two or three years because cultivation occurs after long fallow, cultivators living in Maripasoula do not crop the same field for more than one season, due to a rapid decrease of yield and the invasion of their fields by weeds and crop parasites (Fleury, 1998). As above we sampled both plots in July 1999. We intended to resample in 2000 the woody fallow plot (MF), which should have been burnt in December 1999 by the Aluku family, but as it was not burnt and so we could not resample it as for EFB.

The mean size of abattis is 2 ha at Maripasoula and 1 ha at Elahe. At both sites, manioc is the basic food crop, and is supplemented by fishing and hunting. Abattis are roughly circular, originating from cutting and burning the forest in places accessible by foot or by canoe. The people of both communities prefer soils that are sandy. The Wayanas also prefer dark soils. Both people avoid valleys. In each abattis all tree trunks and saplings are cut, except those kept as holy trees. The felled trees are allowed to dry. Some wood is taken for timber and cooking, and the rest is burned and its residues left on the field. Manioc cuttings, from previous crop, are planted after resprouting. The soil is not cultivated, but excavated locally to plant the cuttings and then refilled with a hoe. The aspect of the site is used to select places proper for burying manioc

cuttings. Hollows in the undulating terrain are often used for bananas or rice. The main differences between Aluku and Wayana practices lie in the duration of the crop. Each year Alukus cut and burn new abattis around the village, whereas the Wayanas use the same abattis for two or three years, the precise duration depending on the soil's fertility and the spontaneous establishment and resprouting of vegetation, then shift to another place. They weed only by hand during the first four months following manioc planting, and they do not use herbicides, pesticides or fertilizers.

The climate is warm (mean annual temperature 26°C) and rainy (2000 mm per year), with a main dry season from September to December and a shorter one from March to April. Table 1 lists the main physico-chemical properties of the topsoil (Oxisol) which was sampled in the study plots. At both sites the soil was sandy and acidic, although slightly less acidic in Maripasoula (pH~5.0) than at Elahe (pH~4.7). The soil was air-dried before transport to the laboratory for chemical analyses. Soil pH was measured electrometrically on a 1:2.5 soil:water mixture. Total C and N were measured by the dry combustion method after hydrochloric dissolution of carbonates according to ISO 10694 and ISO 13878, respectively (Anonymous, 1999).

Soil micromorphology: the small-volume method

We studied the distribution of humus components and biogenic structures in topsoil by small-volume micromorphology *sensu* Bernier & Ponge (1994), further refined for biogenic structures by Peltier *et al.* (2001) and adapted by us

to agricultural soils (Topoliantz *et al.*, 2000). This optical method allows one to identify and estimate the proportion of solid components in successive layers of a given soil profile. Combined with multivariate methods, it can be used to compare soil profiles along gradients (Peltier *et al.*, 2001; Frak & Ponge, 2002; Sadaka & Ponge, 2003) and in vegetation patchworks (Patzel & Ponge, 2001).

Five samples for micromorphological analyses and five samples for physico-chemical analyses were taken in each of the five study plots. They were regularly spaced along a 30-m transect crossing the centre of each plot. This allowed us to embrace within-plot variation while avoiding edge effects.

For micromorphological investigations we took soil blocks 7 cm x 7 cm x 6 cm (length x width x height) which we shaped with a sharp knife without disturbing litter nor soil structure. Then we separated the top 5 cm by hand in successive layers 0.5 to 3 cm thick according to their appearance, which we considered homogeneous. Each layer was immediately fixed in 95% ethyl alcohol then transported to the laboratory for further analysis. In the immediate vicinity of each sampling plot another sample (10 cm deep) was taken, air-dried as soon as possible before transport to the laboratory for physico-chemical analyses. A total of 251 layers (for micromorphological analyses) and 25 topsoil profiles (for physico-chemical analyses) were sampled.

The material from each layer was gently spread in a Petri dish (150 mm diameter), with as little disturbance of the aggregates as possible, and then covered with alcohol. Ethyl alcohol precipitates colloids, thereby helping to

preserve aggregates, provided they are not crushed by forcing them with an instrument. We observed each layer under a dissecting microscope after covering the layer of solid matter with a transparent 600-pt grid, which we had previously prepared by piercing a transparency film at nodes of a 5-mm grid. Following dot lines under the dissecting microscope and changing the focusing plane every time a dot was encountered, each element which was located just below a node of the grid was identified then counted. This method allowed us to estimate the relative volume of components of the soil matrix, including plant organs at varying stages of development (for subterranean organs) or decomposition, mineral particles of varying size and nature, aggregates of varying colour, size and shape. The Munsell® code for soil colours was used to classify colours of aggregates into five broad classes (light, light brown, brown, light grey, grey, black).

Data analysis

Micromorphological data were analysed by correspondence analysis, CA (Greenacre, 1984). The matrix analysed crossed 81 layers (as columns) and 82 classes (as rows). Additional (passive) variables were added as rows, in order (i) to facilitate the interpretation of the factor axes, and (ii) to discern mean trends in the vertical distribution of humus components in the five plots studied. They comprised the five plots (MA, MF, EA, EF, EFB) and, for each plot, five depth levels (0-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm).

Results

Table 2 lists the 82 classes that were identified under the dissecting microscope. The projection of classes (topsoil components) in the plane of the first two factor axes of the CA (11% and 8% of total variance, respectively) displayed three branches (Figure 1). The percentages of variance extracted by axes 1 and 2 (19%) far exceeded the confidence interval given by random permutation of rows and columns (Lebart *et al.*, 1979), thus giving us confidence in the significance of these two axes. Axis 1 separated classes typical of woody sites (EF and MF, with positive values) from those typical of clearings (EA, EFB and MA, with negative values). Axis 2 separated EA (with positive values) from MA (with negative values), EFB being intermediate. The woody sites (EF and MF) were characterized by moss, leaf and wood litter at varying stages of decomposition, as well as a variety of holorganic (purely organic) faeces of arthropod origin (caterpillars, millipedes, springtails, mites, miscellaneous). Abattis (EA, EFB, MA) were characterized by annelid (earthworm, enchytraeid) faeces and ant pellets with varying carbon contents, charcoal (free or incorporated to faeces), roots and mineral particles. Within this group, the Elahe abattis (EA) was distinguished by the part played by dark (black, dark brown, dark grey) hemorganic material, and charred roots.

Changes in the vertical distribution of topsoil components were shown by the projection of depth indicators in the plane of Axes 1 and 2 of CA (Figure 2). At some depth (varying from 2 cm in MA to 3 or 4 cm in other plots) all sampled layers exhibited similar features, factor coordinates being negative both for axes

1 and 2. Prominent differences between plots were exhibited mostly in the top 1 cm of the soil. The composition of the top centimetre in MA did not differ to a great extent from that of forest soils (MF and EF), both showing positive values along axis 1, although differences between surface and deeper soil were much less pronounced in MA, because there was less litter (Figure 2). In contrast, at Elahe the top 2 cm of the soil was strongly affected by the shift to agriculture (EA, EFB to a lesser extent), exhibiting positive and slightly negative values along axis 2, respectively.

Mean values for the top 5 cm of the soil can be calculated for each class and each profile and averaged over the five profiles taken at each plot, giving mean values for the five plots (Table 2). The correspondence analysis displayed some trends common to gross classes (leaf material, charred material, charcoal, black and dark humus). These were compared between the five plots (Table 3). It appears that leaf material was at least 4 times more abundant in woody sites (MF and EF) than in abattis (MA, EA, EFB), each of these groups being fairly homogeneous. In particular, the topsoil of older abattis (EA, MA) had the same leaf litter content than the recently burnt forest (EFB).

Slash-and-burn agriculture increased the content of the topsoil in black and dark hemorganic humus by a factor of 8 at Maripasoula. This class was 11 times more abundant at Elahe (EF) than at Maripasoula (MF) woody sites and remained 6 times more abundant at Elahe (EA) than in the abattis at Maripasoula (MA). Differences in the charcoal content of the topsoil were not so pronounced. Charcoal was less abundant in EF than in all other plots, the

highest value being observed in MA (almost 2 times the value observed in EA). Charred material was most abundant in the recently burnt forest (EFB), where it was 2.6 times more abundant than in the nearby untouched forest (EF). The least amount of charred material was in the Maripasoula woody fallow (MF).

The mean vertical distribution of these bulk classes is apparent in Figure 3. The leaf material, which was more abundant in woody sites (EF and MF) than in abattis, disappeared rapidly in the top 2 cm of the soil in all plots. The charred material, which was abundant at the soil surface in the two abattis at Elahe (EA, EFB), decreased with depth in these two plots. However, it disappeared much less rapidly than did the leaf material. In the other three plots, it increased progressively down to 1.5 to 2 cm, then decreased progressively. The vertical distribution of charcoal was similar to that of charred material in the recently burnt forest and in the cultivated abattis at Elahe, decreasing abruptly from 1.5 to 2.5 cm, then more progressively below this depth. In the Elahe forest (EF), there was a progressive increase in charcoal content from the surface to 2-3 cm, but the content remained very small. At Maripasoula (MA and MF), more charcoal had accumulated below 2.5 cm. In the abattis (MA), it reached on average 10% of the total solid matter at 2.5 cm, then decreased progressively. In the Maripasoula forest (MF) the charcoal content increased progressively, from 0 at the surface to a maximum of 6% from 3 to 5 cm. Over this depth range, there was no difference in charcoal content between the 8-year-old woody fallow and the abattis. Black and dark humus was much more abundant in Elahe abattis (EA, EFB) than in all other plots. It was already present as a large proportion of total soil volume near the soil surface, reaching 9% and 6%

of the total solid matter in EA and EFB, respectively. The proportion remained constant to 2 cm, then decreased progressively with increasing depth.

Discussion

Pronounced differences according to agricultural use of the rain forest were revealed by the biological material (leaf litter, charcoal and charred material, dark humus) which had accumulated in the topsoil. Biological activity in the soil was strongly affected by clearing of the forest. We registered a change from the activity of arthropods other than ants, as exemplified by the content in the topsoil of the faeces of caterpillars, millipedes, springtails and mites, to a community dominated by annelids and ants. The latter is characterized by (i) the incorporation of organic matter to mineral matter within earthworm and enchytraeid faeces and ant pellets, (ii) the building of an hemorganic humus profile (Figure 1). This pattern accords with the more even distribution of carbon in the topsoil after deforestation and cultivation observed in Amazonian soils by Nascimento *et al.* (1993). Our results point on the role of burrowing animals, namely earthworms, enchytraeids and ants, in this process. We did not record any faecal deposition by termites, although many termites are present in the soil. The incorporation of organic matter in mineral matter by tropical earthworms helps to stabilize organic matter, and associated water and nutrients (Lavelle *et al.*, 1998). Mutualistic interactions between earthworms and soil microbes (in particular the priming effect by intestinal mucus) were reasons to classify these animals as ecosystem engineers (Lavelle *et al.*, 1997). Earthworms, in association with additions of organic matter, have been used for

the bioremediation of tropical agricultural soils, increasing plant productivity and creating a stable soil structure (Pashanasi *et al.*, 1996; Brown *et al.*, 1999; Hallaire *et al.*, 2000). Ants, and moreover enchytraeids, are not widely recognized as promoting greater soil aggregation and stability, at least in the tropical world (Delabie & Fowler, 1995; Römbke & Meller, 1999). However, we found that earthworm faeces tunnelled by enchytraeids contributed noticeably to the total solid matter in the first 5 cm of the topsoil (Table 2).

Charcoal and charred material contributed substantially to the soil (Figure 3). This material accumulates in the topsoil, unlike leaf material (Figure 3). It is also incorporated into a variety of black and dark hemorganic faeces of earthworms, and into ant pellets (Table 2). In a previous paper (Topoliantz & Ponge, 2003), we showed experimentally that the peregrine earthworm *Pontoscolex corethrurus* could ingest small particles of charcoal and mix them with the mineral soil, then deposit dark excrement at varying depths. This activity is at the origin of a variety of dark colours of soil aggregates, which contain charcoal powdered by the earthworm gizzard then mixed in a liquid manner in the intestine (Barois *et al.*, 1993). We also observed that ants produced dark, even black, material (Table 2), but this material could come from ingested earthworm faeces of the same colour.

There was more black and dark humus and charred material and less charcoal in the 3-year-old abattis at Elahe than in the 1-year-old abattis at Maripasoula. These differences can be due (i) to a larger production of charcoal at Maripasoula where repeated burning (short fallow) leads to an accumulation

of charcoal in the course of the time (Van der Wal, 1999), and (ii) to a better incorporation of charcoal and charred material in the mineral soil at Elahe, as shown by our micromorphological data. Indeed, charred material and charcoal decreased from EFB (fire 6 months before) to EA (fire 3 years before) while black and dark humus increased during the same period. This suggests that both charcoal and charred material are sources of black and dark humus (Figure 3). At Maripasoula, the content of the black and dark humus in the topsoil was always small and charcoal accumulated, revealing the slow turnover of this type of carbon.

The origin of the fertile Terra Preta, or Amazonian Dark Earths, has been attributed to the incorporation of charcoal to the mineral soil, as a source of stable humus, once charcoal carbon becomes oxidized and chemically reorganized (Glaser *et al.*, 1998). Past bioturbation, in vanished civilizations of the Amazon Basin, has been postulated to explain the present-day enrichment of the soil in black carbon of charcoal origin at 30-40 cm depth (Glaser *et al.*, 2000; Glaser & Woods, 2004). We can now explain this phenomenon by the charcoal-feeding activity of earthworms such as *P. corethrurus*, which are abundant in Amazonian pastures and forest clearings (Römbke & Verhaag, 1992). The fact that black and dark hemorganic material was almost absent from the soil in the old forest, then increased in the recently burnt forest, then still further increased after 3 years of cultivation at Elahe (Figure 3), probably indicates that the process of incorporation is rapid, provided earthworms are sufficiently active, as observed in Elahe. In previous experiments we also showed that dark hemorganic humus (artificially made by mixing charcoal with

the mineral soil) was even ingested to a greater extent than pure charcoal, pointing on a positive feed-back (self-reinforcing) effect (Topoliantz & Ponge, 2005).

Our study shows that traditional shifting cultivation, as currently practised by Wayana Amerindians, causes charcoal and charred material to become well incorporated into the soil and to change gradually into stable humus. This probably occurred in the past to a much larger extent in the Amazonian basin (Glaser & Woods, 2004). Prior to burning the forest, Wayana cultivators select darker soils (personal communication with local agriculturists). The dark colour of the topsoil is probably caused by past fires that enriched the soil with stable carbon, through earthworm activity. This preference for soils containing incorporated charcoal reinforces the positive feed-back loop already mentioned. At Maripasoula, the accumulation of charcoal in depth and the quasi absence of black and dark humus in the 8-years-old forest (MF) suggest that more than 8 years are probably needed for complete incorporation of charcoal in dark humus. Frequent fires and short cultivation periods must not allow for a complete incorporation of charcoal by soil fauna, limiting to the short-term the fertilizing effect of burning the forest.

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511

512 **Figure headings**

513

514 **Figure 1.** Correspondence analysis (CA). Projection of active variables (humus
515 classes, see Table 2) and passive variables (plot indicators) in the plane
516 of the first two factorial axes. MA = Maripasoula Abattis, MF =
517 Maripasoula Fallow, EA = Elahe Abattis, EF = Elahe Forest, EFB = Elahe
518 Forest Burnt

519

520 **Figure 2.** Correspondence analysis (CA). Projection of depth indicators (for
521 each plot and each depth) in the plane of the first two factorial axes.
522 Successive sampling depths are shown at cm intervals. The top cm has
523 been labelled, the lower samples follow the lines. Abbreviations as for
524 Figure 1

525

526 **Figure 3.** Mean vertical distribution of gross categories of humus components in
527 the five studied plots. Each point is the mean of five values from five
528 topsoil profiles. Abbreviations as for Figure 1

529

Table 1. Main physico-chemical features of the five study sites. Data are means of five topsoils followed by minimum and maximum values. Charcoal carbon was included in total C

	Maripasoula Abattis	Maripasoula Fallow	Elahe Abattis	Elahe Forest	Elahe Forest Burnt
	MA	MF	EA	EF	EFB
Clay/%	22.4 (20.4-25.3)	16.9 (13.7-20)	20 (6.6-31.3)	17.5 (15.5-19.1)	16.8 (14.9-18.3)
Silt/%	12.4 (9.5-17.4)	7.9 (7-9.2)	20.9 (13.2-32.8)	8.7 (7.1-9.6)	9.2 (7.6-10.3)
Sand/%	65.1 (58.8-69.7)	75.2 (72.3-78.7)	59.1 (35.9-80.2)	73.8 (71.4-76.7)	74 (72.1-76.4)
pH	5.13 (5.02-5.37)	5.01 (4.6-5.66)	4.74 (4.37-4.91)	4.83 (4.58-5)	4.30 (3.79-5.59)
Total C/g.kg ⁻¹	24.6 (16.9-39.8)	22.5 (18.6-28.4)	25.8 (16.3-36.3)	19.1 (14.7-25.3)	18.6 (17.9-19.7)
Total N/g.kg ⁻¹	1.65 (1.21-2.49)	1.48 (1.28-1.88)	1.78 (1.29-2.4)	1.39 (1.12-1.7)	1.35 (1.33-1.38)
C/N	14.7 (13.2-16)	15.2 (14.5-15.7)	14.6 (12.6-16.1)	13.7 (12.8-14.9)	13.7 (13.3-14.3)

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Table 2. List of classes identified under the dissecting microscope with code number and mean percent volume of the topsoil (0-5 cm) matrix in the five studied sites (5 profiles each). MA = Maripasoula Abattis, MF = Maripasoula Fallow, EA = Elahe Abattis, EF = Elahe Forest, EFB = Elahe Forest Burnt

Code	Short description	MA	MF	EA	EF	EFB	Axis 1 of CA	Axis 2 of CA
1	Entire brown leaves	0.79	1.06	0.17	1.19	0.21	0.037	-0.002
2	Entire brown-orange leaves	0.59	5.03	0.05	3.58	0.18	0.037	-0.002
3	Entire red leaves	0.18	0.07	0.39	1.50	0.04	0.032	-0.003
4	Entire bleached leaves	0.12	3.77	0.24	2.70	0.12	0.038	-0.002
5	Entire blackened leaves	0.29	2.09	0.10	0.34	0.09	0.027	-0.003
6	Brown leaves nibbled by macrofauna	0.93	1.27	1.00	1.86	0.81	0.031	0.009
7	Brown-orange leaves nibbled by macrofauna	0.63	3.37	1.25	3.24	0.25	0.036	0.002
8	Red leaves nibbled by macrofauna	0.66	0.55	0.91	0.69	0.21	0.026	-0.004
9	Bleached leaves nibbled by macrofauna	0.11	1.62	0.08	1.36	0.37	0.033	-0.003
10	Blackened leaves nibbled by macrofauna	0.36	0.20	0.43	1.06	0.28	0.017	0.003
11	Skeletonized leaves	0.01	0.27	0.02	2.00	0.03	0.030	-0.003
12	Fungi	2.20	2.08	2.29	1.52	2.12	-0.017	-0.006
13	Moss	0.17	0.00	0.00	0.09	0.02	0.021	-0.003
14	Decaying stem/bark	2.53	1.71	1.10	1.85	2.16	0.016	0.000
15	Miscellaneous plant material	1.31	0.94	1.81	1.95	0.90	0.010	0.001
16	Miscellaneous charred material	1.46	0.51	1.73	2.54	6.14	-0.001	0.012
17	Free charcoal	4.94	2.35	1.88	1.05	3.90	-0.007	0.005
18	Living fine roots (< 2 mm)	10.06	17.84	13.15	13.14	13.62	-0.019	0.000
19	Living medium roots (2-4 mm)	1.44	2.36	1.01	2.69	2.06	-0.016	-0.010
20	Living large roots (> 4 mm)	1.74	1.70	0.63	1.92	1.36	-0.001	-0.011
21	Dead fine roots (< 2 mm)	2.05	0.81	2.93	2.46	2.54	-0.022	0.016
22	Dead medium roots (2-4 mm)	0.62	0.08	0.66	0.48	0.80	-0.017	0.005
23	Dead large roots (> 4 mm)	0.14	0.04	0.40	0.28	0.44	-0.007	-0.009
24	Charred fine roots (< 2 mm)	0.44	0.04	2.52	0.72	2.18	-0.009	0.015
25	Charred medium roots (2-4 mm)	0.06	0.00	1.85	0.29	0.80	-0.008	0.011
26	Charred large roots (> 4 mm)	0.00	0.00	1.28	0.05	0.27	-0.007	0.007
27	Type I holorganic macrofauna faeces	0.00	0.05	0.00	0.00	0.00	-0.003	-0.009
28	Holorganic caterpillar faeces	0.00	0.00	0.01	0.00	0.00	0.009	-0.002
29	Holorganic millipede faeces	0.02	0.01	0.00	0.04	0.06	0.010	-0.001
30	Holorganic earthworm faeces	0.13	0.00	1.04	0.24	0.52	-0.001	0.018
31	Holorganic enchytraeid faeces	0.05	0.06	2.48	0.47	0.08	0.004	0.012
32	Holorganic springtail faeces	0.01	0.00	0.05	0.04	0.02	0.019	0.007
33	Holorganic mite faeces	0.00	0.00	0.00	0.14	0.01	0.016	-0.005
34	Enchytraeid-crumbled holorganic earthworm faeces	0.00	0.00	1.39	0.00	0.00	-0.002	0.003
35	Miscellaneous holorganic faecal material	0.20	0.24	0.46	0.89	0.36	0.034	0.003
36	Light recent hemorganic earthworm faeces	7.89	2.52	7.86	0.22	1.35	-0.009	-0.015
37	Brown recent hemorganic earthworm faeces	6.71	7.77	10.19	0.75	2.51	-0.011	-0.009
38	Dark-brown recent hemorganic earthworm faeces	0.05	0.00	0.73	0.06	0.42	-0.009	0.020
39	Light-gray recent hemorganic earthworm faeces	1.46	6.98	0.65	0.04	0.11	0.001	-0.016
40	Dark-gray recent hemorganic earthworm faeces	0.08	0.03	0.65	0.14	0.15	-0.012	0.030
41	Light old hemorganic earthworm faeces	5.93	1.34	4.29	5.03	6.02	-0.016	-0.019
42	Brown old hemorganic earthworm faeces	7.65	4.69	4.00	6.84	9.26	-0.019	-0.019
43	Dark-brown old hemorganic earthworm faeces	0.21	0.00	0.18	0.34	0.32	-0.004	-0.007
44	Light-gray old hemorganic earthworm faeces	1.73	3.33	0.31	0.30	0.32	-0.004	-0.015
45	Dark-gray old hemorganic earthworm faeces	0.25	0.06	0.03	0.22	0.56	-0.007	-0.010
46	Black hemorganic earthworm faeces	0.22	0.01	1.47	0.19	1.58	-0.004	0.028
47	Light enchytraeid-crumbled hemorganic earthworm faeces	2.88	0.52	2.58	5.09	2.77	-0.018	-0.020
48	Light-gray enchytraeid-crumbled hemorganic earthworm faeces	0.12	0.91	0.04	0.14	0.03	0.000	-0.014
49	Brown enchytraeid-crumbled hemorganic earthworm faeces	2.60	3.07	4.59	3.96	4.05	-0.020	-0.012
50	Dark-brown enchytraeid-crumbled hemorganic earthworm faeces	0.01	0.00	1.20	0.08	0.03	-0.001	0.007
51	Dark-gray enchytraeid-crumbled hemorganic earthworm faeces	0.00	0.00	0.02	0.02	0.04	-0.008	0.015
52	Black enchytraeid-crumbled hemorganic earthworm faeces	0.00	0.00	0.64	0.05	0.10	-0.004	0.031
53	Light hemorganic ant pellets	0.14	0.00	0.04	0.06	0.09	-0.009	-0.012
54	Brown hemorganic ant pellets	0.08	0.00	0.18	0.23	0.19	-0.012	0.001
55	Dark-brown hemorganic ant pellets	0.00	0.00	0.02	0.00	0.00	-0.005	-0.005
56	Light-gray hemorganic ant pellets	0.00	0.00	0.00	0.00	0.01	-0.001	-0.003
57	Dark-gray hemorganic ant pellets	0.00	0.00	0.00	0.02	0.00	0.001	-0.002
58	Black hemorganic ant pellets	0.00	0.00	0.17	0.02	0.02	-0.008	0.032
59	Hemorganic springtail faeces	0.00	0.00	0.00	0.06	0.01	0.009	-0.002
60	Light friable hemorganic material	1.13	0.56	2.16	2.46	1.04	-0.008	-0.019
61	Brown friable hemorganic material	0.87	1.98	2.53	0.87	0.89	-0.008	-0.019
62	Dark-brown friable hemorganic material	0.00	0.00	0.08	0.00	0.02	-0.011	0.029
63	Light-gray friable hemorganic material	0.05	0.72	0.08	0.04	0.05	0.010	-0.013
64	Dark-grey friable hemorganic material	0.03	0.00	0.17	0.03	0.00	-0.005	0.006
65	Black friable hemorganic material	0.00	0.00	0.15	0.01	0.40	-0.005	0.018
66	Light compacted hemorganic material	3.00	0.00	0.00	0.00	0.00	-0.003	-0.007
67	Brown compacted hemorganic material	0.92	0.00	0.51	0.00	0.00	-0.007	0.011
68	Dark-brown compacted hemorganic material	0.00	0.00	0.02	0.00	0.00	-0.008	0.032
69	Light-gray compacted hemorganic material	0.18	0.00	0.00	0.00	0.00	-0.003	-0.007
70	Dark-gray compacted hemorganic material	0.03	0.00	0.11	0.00	0.00	-0.009	0.029
71	Black compacted hemorganic material	0.00	0.00	0.06	0.00	0.00	-0.008	0.032
72	Charcoal embedded in faeces	2.46	1.28	1.20	0.38	0.93	-0.013	-0.002
73	Humified plant material embedded in faeces	0.52	0.47	0.70	0.38	0.35	-0.011	-0.021
74	Fine sand (0.02-0.2 mm)	3.60	3.45	3.83	4.64	5.59	-0.022	0.001
75	Coarse sand ((0.2-2 mm)	11.03	8.37	4.63	14.29	16.60	-0.028	-0.016
76	Gravel (2-20 mm)	1.08	1.29	0.41	0.50	1.15	-0.017	-0.015
77	Boulder (> 20 mm)	0.41	0.42	0.00	0.00	0.00	-0.004	-0.010
78	Iron nodules	1.71	0.01	0.00	0.00	0.00	-0.004	-0.010
79	Manganese nodules	0.20	0.00	0.03	0.00	0.03	-0.006	-0.013
80	Miscellaneous minerals	0.28	0.01	0.03	0.00	0.03	-0.005	-0.013
81	Living and dead fauna	0.24	0.08	0.14	0.17	0.01	0.001	-0.018
82	Unidentified	0.01	0.00	0.00	0.00	0.00	-0.002	-0.007

Table 3. Mean percent by volume of some main components of the topsoil (0-5 cm) matrix. Data are means of five profiles followed by minimum and maximum values. MA = Maripasoula Abattis, MF = Maripasoula Fallow, EA = Elahe Abattis, EF = Elahe Forest, EFB = Elahe Forest Burnt

	MA	MF	EA	EF	EFB
Leaf material	4.66 (1.48-9.94)	19.30 (10.7-27)	4.63 (0.8-11)	19.50 (16.3-22.8)	2.59 (0.17-6.58)
Charred material	1.96 (0.27-3.78)	0.55 (0.14-1.24)	7.39 (2.33-19.41)	3.60 (1.75-6.12)	9.39 (6.17-14.84)
Charcoal	7.40 (2.73-14.52)	3.63 (1.38-5.5)	3.08 (1.56-4.45)	1.43 (0.47-2.58)	4.83 (1.71-9.43)
Black and dark humus	0.89 (0.39-1.82)	0.11 (0-0.27)	5.71 (1.11-10.76)	1.19 (0.12-2.2)	3.65 (1.09-8.43)

533

534

Figure 1

538

539 **Figure 2**

540

Figure 3