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1 **Humus profiles under main vegetation types in a rock savanna (Nouragues inselberg,**
2 **French Guiana)**

3

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5

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8

9 **Abstract**

10

11 The aim of our study was to describe succession related changes in humus profiles on
12 moderate slopes of a tropical inselberg (Nouragues, French Guiana). Nine humus profiles
13 were collected in a stratified manner under two main communities on well-drained sites:
14 carpets of *Pitcairnia geyskesii* (Bromeliaceae) and shrub thickets of *Clusia minor*
15 (Clusiaceae), the latter including two stages of its dynamic development. The 53 sampled
16 layers were analysed by an optical method, the volume ratio of 109 classes of litter/humus
17 components being quantified by a count point method. Correspondence analysis (CA)
18 revealed marked differences among humus forms. *Pitcairnia* carpets were characterized by
19 the dominance of cyanobacteria which formed crusts with low faunal activity, except when
20 they were colonized by enchytraeid worms. With advancing succession, we observed that leaf
21 litter did not accumulate but rather was incorporated into organo-mineral excrements of
22 macro-invertebrates under *C. minor*. The late developmental stage of *Clusia* thickets,
23 characterised by the establishment of *Myrcia saxatilis* (Myrtaceae), showed a thick layer of
24 undecayed litter and near absence of organo-mineral aggregates. The humus form varied from

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1 mor in cyano-bacterial crusts to tropical moder (with a few mull features) in *Clusia* thickets,
2 but comparisons among humus profiles revealed more complex successional processes than
3 expected on the basis of the composition of plant and soil animal communities.

4

5 *Keywords:* Humus form; Micromorphology; Tropical soils; Rock savanna

6

7 **1. Introduction**

8

9 Despite the widely reported lack of organic matter and nutrients in tropical soils, due
10 to rapid mineralization of leaf and root litter and intense leaching (Lavelle, 1984; Lavelle et
11 al., 1993), huge accumulations of organic matter can be observed on rocky substrates and
12 nutrient-depleted sandy soils (Lips and Duivenvoorden, 1996; Loranger et al., 2003).

13

14 In French Guiana, inselbergs in the form of granite outcrops rise abruptly from the
15 surrounding rain forest (Bremer and Sander, 2000). They constitute isolated islands of a
16 special type of vegetation restricted to this peculiar substrate. Unique plant communities
17 occur on these inselbergs, including predominantly evergreen and sclerophyllous shrubs,
18 belonging to Clusiaceae, Myrtaceae and Bombacaceae (Sarhou and Villiers, 1998).

19

20 On the basis of earlier studies on vegetation types and soil communities (Sarhou and
21 Grimaldi, 1992; Sarhou and Villiers, 1998; Vaçulik et al., 2004; Kounda-Kiki et al., 2004),
22 we studied the variation in the composition of humus horizons along a succession sequence
23 on the Nouragues inselberg. Our aim was to describe in detail the composition of these
24 superficial organic soils (Hamblen, 1964; Sarhou and Grimaldi, 1992; Bremer and Sander,
25 2000) and to understand what happens during the development of cryptogamic then

1 phanerogamic vegetation. *Pitcairnia geyskesii* L.B. Smith (Bromeliaceae, herb) and *Clusia*
2 *minor* L. (Clusiaceae, shrub) communities represent two seral stages of a low vegetation
3 called rock savanna, which is established on moderate slopes (Sarhou, 1992). Within the
4 *Clusia* community, two sub-stages can be distinguished, the one represented by *C. minor*
5 only, the other by the late addition of *Myrcia saxatilis* (Amshoff) McVaugh (Myrtaceae) and
6 several other woody species.

7
8 The successional development of humus profiles was analysed by studying different
9 members of a successional sere. Results were statistically analysed by Correspondence
10 Analysis (Greenacre, 1984).

11

12 **2. Materials and methods**

13

14 *2.1. Study site*

15

16 The field work was carried out at the Nouragues inselberg in French Guiana (411 m
17 above sea level), which protrudes from a plateau in the Nouragues natural reservation (4°5'N
18 and 52°42'W). The inselberg is a tabular outcrop of Caribbean granite, of pinkish monzonitic-
19 type, containing on average 27% potassium-feldspar (orthoclase) and 37% plagioclase, along
20 with 33% quartz as coarse-grained crystals and 2% accessory minerals (pyroxene, corundum,
21 apatite) (Grimaldi and Riéra, 2001). Whole-rock chemical analysis (Sarhou, 1992) shows that
22 the granite is highly siliceous (76.4% SiO₂) and rich in alkalis (4.6% K₂O, 4.2% Na₂O). The
23 climate is tropical humid, with a dry season from July to November and a wet season from
24 December to June that is interrupted by a very short dry period in March. Mean annual
25 precipitation is 3000 mm. The daily temperature varies from 18 to 55°C and the daily air

1 humidity from 20 to 100% (Sarhou, 1992). The temperature of the bare rock surface may
2 reach 75°C in the dry season. Most of the surface of the granitic outcrop is covered by
3 cyanobacteria (Sarhou et al., 1995). The bromeliad *P. geyskesii* is the most typical plant of
4 the inselberg. This epilithic species (30-50cm tall) always forms dense carpets, covering low
5 to medium slopes as well as gullies and shallow depressions (Sarhou and Villiers, 1998). The
6 *C. minor* (Clusiaceae) community is also widespread (Sarhou, 2001; Sarhou et al., 2003). It
7 represents the shrub vegetation unit of the rock savanna, forming dense thickets of 2-8 m tall
8 shrubs. This woody vegetation occurs in depressions and slopes that have sandy and organic
9 soils, respectively. On moderate slopes a succession takes place, from an early stage
10 characterized by cyanobacterial crusts and herbaceous vegetation (*Pitcairnia*), to mid and late
11 stages which can be identified in shrub (*Clusia*) thickets (Sarhou, 2001). *C. minor* establishes
12 from seeds within carpets of *P. geyskesii* and subsequently spreads vegetatively, in the end
13 developing into pure *C. minor* thickets with an outer circle of herbaceous vegetation. Various
14 woody species, among which *M. saxatilis* (Myrtaceae) is the most important one,
15 progressively enrich *C. minor* thickets, without replacing it, forming the late stage of
16 development of shrub vegetation. Intense runoff and violent storms, combined with internal
17 destruction of shrub vegetation by xylophagous fungi and termites, cause a periodical return
18 to pioneer stages of the sequence (personal observations), but we are unable to indicate the
19 time required for reaching each stage of the vegetation succession.

20

21 The present study was undergone on moderate slopes (30-35%), where soils are poorly
22 differentiated. They are made of humified organic matter, which accumulate in cyanobacterial
23 crusts and in the dense root mats of vegetation patches (Sarhou and Grimaldi, 1992). These
24 organic soils are acidic ($\text{pH}_{\text{KCl}} \leq 4$) and poor in nitrogen ($\text{C/N} = 20-30$). They are poorly

1 anchored to the granite and are subject to intense erosion. During showers, water can be seen
2 to flow freely between the granite and the lower side of the organic mass.

3

4 2.2. *Sampling of humus profiles*

5

6 In each vegetation type three sites were sampled. Sampling took place in April 2002.
7 The low level of replication of our sampling procedure was due to remoteness of the sites and
8 lack of commodities for carrying samples to the French (metropolitan) laboratory. Three
9 humus profiles were sampled in the *Pitcairnia* community (cyanobacterial crusts) and three in
10 each of two dynamic stages of the *Clusia* community (*Clusia* and *Clusia-Myrcia*). The nine
11 vegetation patches were selected in the lower part of the inselberg, in an area with moderate
12 slope (30-35%) and South-facing aspect, locally called 'Les Terrasses'. Selection of sampling
13 points was done after a thorough examination of all vegetation patches which were present at
14 the study site (ca. 50), all of them being associated to a step of the plant succession according
15 to Sarthou (2001), on the base of their architecture and floristic composition. We arbitrarily
16 selected three patches in each of the three successional stages. At the centre of a vegetation
17 clump, a block of surface soil 25 cm² in area and 10 cm depth (except when the soil was
18 shallower) was arbitrarily selected, then cut with a sharp knife, with as little disturbance as
19 possible, and litter and soil underneath were carefully sampled. When a stone or a large root
20 was encountered in the top 10 cm, we discarded the sample then we arbitrarily selected
21 another location. It was decided to sample only the top 10 cm because most pronounced
22 stratification of the topsoil was seen to occur within this depth. In *Clusia-Myrcia*
23 communities, sampling was under the canopy of *M. saxatilis*. However, we could not exclude
24 the possible admixture of *C. minor* dead leaves and root systems from shrubs growing in the
25 immediate vicinity. In the field each humus block was separated into individual layers that

1 macroscopically could be identified on their structure, composition or other relevant
2 properties (Peltier et al., 2001). The various layers were transferred into polypropylene jars
3 filled with 95% ethanol before transport to the laboratory. Care was taken that the jars were
4 completely filled with the sampled material in order to avoid changes in structure resulting
5 from shaking during transport to the laboratory. Thicknesses of individual layers ranged from
6 0.5 to 3 cm. The layers were classified into OL (entire leaves), OF (fragmented leaves) and
7 OH (humified material) horizons, according to the classification of Brêthes et al., (1995),
8 other soil horizons being absent. When several layers were sampled in the same horizon (on
9 the basis of visible differences) sub-samples were numbered successively according to their
10 order from the top to the bottom of a given horizon, for example OL1, OL2, OF1, OF2, OH1,
11 OH2...

12
13 All 53 layers were microscopically studied using the 'small volume'
14 micromorphological method developed by Bernier and Ponge (1994), to which reference is
15 made for details. Results from grid point counting (429 points) were expressed as the
16 percentage of a given class of litter/humus component. 109 classes of litter/humus
17 components were identified (see Appendix).

18
19 The various kinds of plant debris were identified visually by comparison with a
20 collection of main plant species growing in the vicinity of the sampled humus profiles. Litter
21 leaves were classified according to plant species and decomposition stages on the basis of
22 morphological features. Dead and living roots were separated by colour and turgescence state,
23 helped when possible by the observation of root sections. Animal faeces were classified by
24 the size, the shape, the degree of mixing of mineral matter with organic matter and colour
25 according to animal groups when possible (Bal, 1982; Ponge, 1991; Topoliantz et al., 2000).

1 When necessary, the identification of litter/humus components was checked at higher
2 magnification. For that purpose, a small piece of a given litter/humus component was
3 mounted in a drop of chloral-lactophenol for examination in a phase contrast microscope at
4 400 X magnification.

5

6 After the quantification of litter/humus components was completed, each sample was
7 thoroughly inspected under the dissecting microscope, in order to establish all enchytraeids
8 that were present in the corresponding layer. This allowed us to add these terrestrial annelids,
9 which were poorly extracted by Berlese funnels (Kounda-Kiki et al., 2004) as an additional
10 item to the list of litter/humus components.

11

12 For bulk comparisons between the three main vegetation types the 109 classes of
13 humus components were pooled into 10 gross categories, taking into account the
14 decomposition stage of plant litter, its transformation into animal faeces and the degree of
15 incorporation of organic matter to mineral matter, without resorting to animal and plant
16 species (Table 1 and Appendix).

17

18 The material studied has been partly described in a previous paper dealing only with
19 cyanobacterial crusts (Vačulik et al., 2004). For the present study the corresponding micro-
20 layers have again been analysed by the same person (C. Kounda-Kiki).

21

22 *2.3. Data analysis*

23

24 Percentages of occurrence of classes of litter/humus components in the 53 micro-
25 layers investigated were subjected to a correspondence analysis or CA (Greenacre, 1984). The

1 different classes of litter/humus components were the active (main) variables, coded by their
2 percentage of occurrence by volume. Passive variables (OL, OF, OH horizons, vegetation
3 types, depth levels) were added in order to facilitate the interpretation of factorial axes
4 (Sadaka and Ponge, 2003).

5

6 All variables were transformed into $X=(x-m)/s+20$, where x is the original value, m is
7 the mean of a given variable, and s is its standard deviation (Sadaka and Ponge, 2003). The
8 addition to each standardized variable of a constant factor of 20 allows all values to be
9 positive, CA dealing only with positive numbers. Factorial coordinates of weighted variables
10 (constant mean and variance) can be interpreted directly in terms of their contribution to the
11 factorial axes (Greenacre, 1984).

12

13 The volume percent of a given class (or gross category) of litter/humus component can
14 be averaged over the whole profile, taking into account the different micro-layers, each
15 individual value being weighted by the thickness of the corresponding micro-layer. This
16 allowed to calculate the mean percent volume of the different classes of litter/humus
17 components and of the gross categories in each humus profile (Table 1 and Appendix).

18

19 **3. Results**

20

21 The results given below should be taken only as indicative of the variety of humus
22 profiles found under rock savanna vegetation, due to the low degree of replication used in our
23 study.

24

1 3.1. Micromorphological analyses

2

3 Most material present in the studied profiles was leaf and root material in varying
4 stages of decomposition (see Appendix). Table 1 shows the distribution of the 10 gross
5 categories of litter/humus components under the three vegetation types studied. Notice that
6 these gross categories were not mutually exclusive, thus their total was above 100%. For
7 instance, all components comprising fungal mycelia were included in the gross category
8 'Fungal mycelium', while some of them were also included in other gross categories.

9

10 Cyanobacteria were only found in *Pitcairnia* humus profiles (cyanobacterial crusts
11 bordering bromeliad carpets). There were but few organo-mineral faeces in *Clusia-Myrcia*
12 and none in *Pitcairnia* profiles (Table 1). Fungal mycelia were almost absent throughout
13 *Pitcairnia* profiles. The number of enchytraeids per cm of profile was at its highest in one
14 sample of the *Pitcairnia* stage (see Appendix). Charcoal was totally absent from our material.

15

16 The 10 gross categories were used to build simplified profile diagrams, on the base of
17 data averaged for each vegetation type. Cyanobacteria were present only in the early stage of
18 vegetation succession, under *Pitcairnia* (Fig. 1a). Figure 1b shows that leaf material
19 decreased with depth, with a corresponding increase of roots (Fig. 1c). Decayed plant material
20 increased in volume under *Pitcairnia* down to 3 cm, indicating that it was overgrown by the
21 cyanobacterial crust, then decreased slowly (Fig. 1d). Under the other two vegetation types
22 decayed plant material decreased with depth. This was associated with a higher activity of
23 fungi under *Clusia* and *Clusia-Myrcia* (Fig. 1e). Fungi were visible under *Pitcairnia* in the
24 topmost cm, but disappeared beneath. An increase then a decrease in humified organic matter
25 was observed below 5 cm under *Clusia* and *Clusia-Myrcia* (Fig. 1f). Examination of the

1 faecal material showed that it began to accumulate in the first cm (Figs. 1g, 1h). Holorganic
2 faeces from millipedes, mites, enchytraeids, woodlice, earthworms, snails, insect larvae
3 (recognizable from their size and shape) and undetermined fauna increased with depth (Fig.
4 1g). Organo-mineral dominant animal faeces (millipedes and earthworms) were present in the
5 surface layer under *Clusia* vegetation, then disappeared from 2 to 4 cm, then increased
6 abruptly below 4 cm. There were but few organo-mineral faeces present under *Clusia-Myrcia*
7 and none under *Pitcairnia* (Fig. 1h). Despite their large content of organic matter, shown by
8 their black colour, organo-mineral faeces contain numerous mineral particles, visible under
9 the microscope. The percent volume of mineral particles increased from the top to the bottom
10 of humus profiles under *Clusia* and *Clusia-Myrcia*, under *Pitcairnia* mineral particles were
11 much more abundant: they increased down to 2 cm then decreased to 5 cm and increased
12 abruptly below 6 cm, at the contact with the granite (Fig. 1i).

13

14 3.2. *Synthesis by correspondence analysis (CA)*

15

16 The projection of active (main) and passive (additional) variables in the plane of the
17 first two factorial axes (8.9 and 7.7% of the total variance, respectively) showed a marked
18 heterogeneity among horizons (OL, OF, OH) and among humus profiles (Figs. 2, 3). Given
19 the number of rows (53) and columns (109) of our data matrix, the part of the total variance
20 extracted by each of the first two factorial axes was significantly different from random
21 (Lebart et al., 1979), and the distribution of active and passive variables in the plane of the
22 first two axes showed a meaningful structure. Mineral particles and cyanobacteria were
23 projected on the positive side of Axis 1, which separated *Pitcairnia* from other vegetation.
24 Axis 2 was correlated with depth (surface with positive values, depth with negative values).
25 Leaf material and decayed plant material were projected on the positive side of Axis 2, root

1 material being projected on the negative side of Axis 2. Excrements (holorganic and organo-
2 mineral faeces) were projected on the negative side of Axis 2.

3
4 Figure 3 expressed the changes occurring vertically along humus profiles (mean
5 trajectories for each vegetation type) and the distribution of horizons and vegetation types.
6 *Pitcairnia* was characterized by positive values of Axis 1 and was well separated from the
7 other two vegetation types. This means that humus profiles under *Pitcairnia* (cyanobacterial
8 crust) had a distinct composition. Along Axis 1, the sample Pit 3 was clearly separated from
9 Pit 1 and Pit 2, being farther from the origin: this profile exhibited a better differentiated
10 composition than the tow other profiles sampled under *Pitcairnia*. *Clusia* and *Clusia-Myrcia*
11 were characterized by negative values of Axis 1. Axis 2 displayed the vertical distribution of
12 OL, OF and OH horizons in the woody vegetation types. The OL horizon was restricted to the
13 surface of the profiles (positive values of Axis 2), the OF horizon was placed in an
14 intermediate position between OL and OH horizons (not far from the origin) and the OH
15 horizon underneath (negative values of Axis 2). Despite strong differences between the
16 humus profiles sampled under a given vegetation type, on average OL and OF horizons
17 characterized *Clusia-Myrcia* more than *Clusia*.

18
19 The projection of depth level indicators in the plane of the first two axes of CA
20 clarified vertical changes in the composition of humus profiles and revealed differences in the
21 rate of horizon differentiation between *Clusia* and *Clusia-Myrcia*. Linking successive depth
22 levels by straight lines displayed depth trajectories and revealed mean trends, helping us to
23 show changes in humus composition along topsoil profiles under the different vegetation
24 types (Fig. 3). The composition of the surface horizon was quite similar under *Clusia* and
25 *Clusia-Myrcia*, being typical of an OL horizon. However, at the bottom of humus profiles (10

1 cm), the composition of horizons was typical of an OH horizon under *Clusia*, being mainly
2 made of excrement and root material (Fig. 2), while it was still that of an OF horizon under
3 *Clusia-Myrcia*.

4

5 **4. Discussion**

6

7 *4.1. Pitcairnia stage*

8

9 The poor decay of the plant material observed under the bromeliad *Pitcairnia*, i.e.,
10 litter from neighbouring vegetation included into cyanobacterial crusts, could be explained by
11 a very low amount of fungal and macro-invertebrate activity, compared to further stages of
12 succession. The composition of the faecal material in *Pitcairnia* humus profiles revealed the
13 absence of soil macro-fauna under the cyanobacterial crust, which was confirmed by faunal
14 data (Kounda-Kiki et al., 2004; Vaçulik et al., 2004). Meso-fauna was also hardly active,
15 except in Pit 3 which contained a large volume of enchytraeid faeces (Appendix). Within our
16 limited sampling, Pit 3 depicted more soil development than the other two samples which
17 were done in cyanobacterial crusts. In the absence of earthworms enchytraeids play a leading
18 role in soil development (Didden, 1990). These animals were substituted by earthworms and
19 other macro-invertebrates under the two other vegetation types, as shown by faecal deposition
20 (the present study) and faunal extraction (Kounda-Kiki et al., 2004).

21

22 *4.2. Clusia and Clusia-Myrcia stages*

23

24 Decayed plant material decreased over a short distance in the humus profiles under
25 *Clusia* and *Clusia-Myrcia* stages with a greater activity of fungi and macro-invertebrates

1 (Kounda-Kiki et al., 2004), and litter was transformed into humus over a short distance under
2 *Clusia*. The presence of fungi and the intense earthworm activity observed under *Clusia* and
3 *Clusia-Myrcia* should be noted. They possibly indicate an increase in organic matter
4 decomposition accompanying the development of woody vegetation, despite an increase in
5 primary production when prostrated bromeliad carpets are locally replaced by dense shrub
6 thickets.

7
8 Results on soil arthropod communities showed that species diversity and abundance
9 were highest at the *Clusia-Myrcia* stage (Kounda-Kiki et al., 2004). We cannot rule out a
10 possible higher foliage and root litter input at the *Clusia-Myrcia* stage, which could be in
11 excess of soil community requirements (Garay and Hafidi, 1990). The accumulation of
12 surface organic matter (undecayed litter) could also be due to terpene production by
13 Myrtaceae (Boland and Brophy, 1993). To the light of our results (Kounda-Kiki et al., 2004;
14 the present study) the recalcitrant nature of *Clusia-Myrcia* litter seems to offer better
15 conditions for macro-fauna than *Clusia*-only litter. The situation can be described as a balance
16 between positive (shelter) and negative (recalcitrance) effects, that results in an overall
17 positive effect for the animal community. A similar trade-off has been hypothesized in semi-
18 arid ecosystems (Peltier et al., 2001).

19

20 4.3. *The sequence of soil development on the Nouragues inselberg*

21

22 On the basis of their horizons the humus forms we described under rock savanna
23 belong to a group of tropical humus forms on nutrient-depleted or rocky substrates, which are
24 characterized by the accumulation of faunal excrements within a dense root mat, without or
25 with a poor incorporation of organic matter to the mineral soil (Lips and Duivenvoorden,

1 1996; Loranger et al., 2003). They share common features with moder which has been
2 described in temperate regions (Green et al., 1993). However, two samples taken under
3 *Pitcairnia* (Pit 1 and Pit 2) did not display such accumulation of faeces. They exhibited a
4 single horizon, made of accumulated cyanobacteria, quite similar to surface vegetation. These
5 features are typical of mor, if we consider cyanobacterial remains as plant remains. On the
6 other hand, the presence of earthworm and millipede organo-mineral faeces under *Clusia*
7 indicate the (limited) formation of hemorganic assemblages typical of temperate mull
8 (Brêthes et al., 1995).

9

10 Recent observations on the Nouragues inselberg point on the importance of erosive
11 processes in the establishment of *Myrcia saxatilis* and other Myrtaceae within thickets of
12 *Clusia minor*. The destruction of stems and branches of *C. minor* by wood-feeding termites
13 and wood fungi creates gaps which allow the establishment by seed of more woody species.
14 Partial or near total erosion of the organic soil which forms during the development of *C.*
15 *minor* occurs when the soil remains unprotected (Sarhou et al., *in prep.*). This erosive process
16 allows the rock savanna to rejuvenate periodically, at least on slopes. Awaiting further
17 development of our study, the successional sequence here described should be considered as a
18 combination of a primary sequence, i.e. the passage from bare rock to *Pitcairnia* then to
19 *Clusia* profiles, and a secondary sequence from *Clusia* to *Clusia-Myrcia*, following partial
20 erosion of the organic soil.

21

22 **5. Conclusions**

23

24 Although limited by the low degree of replication and lack of chemical data, our study
25 described for the first time the composition of organic soils of tropical inselbergs. The

1 biological origin of most components can be traced, on the basis of recognizable features of
2 rootq and faeces and previous analyses of soil animal communities (Kounda-Kiki et al.,
3 2004). Strong variation occurs between vegetation types of the rock savanna, the successional
4 development of vegetation being accompanied by the appearance of soil structure: first a fine-
5 grained structure created by enchytraeid activity in the absence of macrofauna under
6 cyanobacterial crusts, then a coarse-grain structure created by earthworms and millipede
7 activity under woody leaf litter. The establishment of Myrtaceae within thickets of *C. minor*
8 (the dominant scrub vegetation of the rock savanna) seems to indicate a decrease in the
9 process of bioturbation, possibly due to erosive processes followed by the input of a more
10 recalcitrant litter.

11

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13

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17

18 **References**

19

20 Bal, L., 1982. Zoological Ripening of Soils. Pudoc, Wageningen.

21

22 Bernier, N. and Ponge, J. F., 1994. Humus form dynamics during the sylvogenetic cycle in a
23 mountain spruce forest. *Soil Biol. Biochem.*, 26: 183-220.

24

- 1 Boland, D. J., and Brophy, J. J., 1993. Essential oils of the eucalypts and related genera. ACS
2 Symp. Ser., 525: 72-87.
3
- 4 Bremer, H., and Sander, H., 2000. Inselbergs: geomorphology and geocology. In: S.
5 Porembski and W. Barthlott (Editors), Inselbergs. Biotic Diversity of Isolated Rock
6 Outcrops in Tropical and Temperate Regions Springer, Berlin, pp. 7-35.
7
- 8 Brêthes, A., Brun, J. J., Jabiol, B., Ponge, J. F. and Toutain, F., 1995. Classification of forest
9 humus forms: a French proposal. Ann. Sci. For., 52: 535-546.
10
- 11 Didden, W. A. M., 1990. Involvement of Enchytraeidae (Oligochaeta) in soil structure
12 evolution in agricultural fields. Biol. Fertil. Soils, 9: 152-158.
13
- 14 Garay, I. and Hafidi, N., 1990. Study of a mixed forest litter of hornbeam (*Carpinus betulus*
15 L.) and oak (*Quercus sessiliflora* Smith). III. Organization of the edaphic
16 macroarthropod community as a function of litter quality. Acta Oecol., 11: 43-60.
17
- 18 Green, R. N., Trowbridge, R. L. and Klinka, K., 1993. Towards a taxonomic classification of
19 humus forms. For. Sci. Monogr., 29: 1-49.
20
- 21 Greenacre, M. J., 1984. Theory and Applications of Correspondence Analysis. Academic
22 Press, London.
23

- 1 Grimaldi, M. and Riéra, B., 2001. Geography and climate. In: F. Bongers, P. Charles-
2 Dominique, P. M. Forget and M. Théry (Editors), Nouragues: Dynamics and Plant-
3 Animal Interactions in a Neotropical Rainforest. Kluwer, Dordrecht, pp. 9-18.
4
- 5 Hambler, D.J., 1964. The vegetation of granitic outcrops in western Nigeria. *J. Ecol.*, 52: 573-
6 594.
7
- 8 Kounda-Kiki, C., Vaçulik, A., Ponge, J. F. and Sarthou, C., 2004. Soil arthropods in a
9 developmental succession on the Nouragues inselberg (French Guiana). *Biol. Fertil.*
10 *Soils*, 40: 119-127.
11
- 12 Lavelle, P., 1984. The soil system in the humid tropics. *Biology International*, 9: 2-17.
13
- 14 Lavelle, P., Blanchart, E., Martin, A., Spain, A., Toutain, F., Barois, I. and Schaefer, R., 1993.
15 A hierarchical model for decomposition in terrestrial ecosystems: applications to soils
16 of the humid tropics. *Biotropica*, 25: 130-150.
17
- 18 Lips, J.M. and Duivenvoorden, J.F., 1996. Fine litter input to terrestrial humus forms in
19 Colombian Amazonia. *Oecologia*, 108: 138-150.
20
- 21 Loranger, G., Ponge, J.F. and Lavelle, P., 2003. Humus forms in two secondary semi-
22 evergreen tropical forests. *Eur. J. Soil Sci.*, 54: 17-24.
23
- 24 Peltier, A., Ponge, J. F., Jordana, R. and Ariño, A., 2001. Humus forms in Mediterranean
25 scrublands with aleppo pine. *Soil Sci. Soc. Am. J.*, 65: 884-896.

- 1
- 2 Ponge, J. F., 1991. Food resources and diets of soil animals in a small area of Scots pine litter.
3 Geoderma, 49: 33-62.
- 4
- 5 Sadaka, N. and Ponge, J. F., 2003. Climatic effects on soil trophic networks and the resulting
6 humus profiles in holm oak (*Quercus rotundifolia*) forests in the high Atlas of
7 Morocco as revealed by correspondence analysis. Eur. J. Soil Sci., 54: 767-777.
- 8
- 9 Sarthou, C., 1992. Dynamique de la Végétation Pionnière sur un Inselberg en Guyane
10 Française. Doctorate thesis, Paris.
- 11
- 12 Sarthou, C., 2001. Plant communities on a granitic outcrop. In: F. Bongers, P. Charles-
13 Dominique, P.M. Forget and M. Théry (Editors), *Nouragues: Dynamics and Plant-
14 Animal Interactions in a Neotropical Rainforest*. Kluwer, Dordrecht, pp. 65-78.
- 15
- 16 Sarthou, C. and Grimaldi, C., 1992. Mécanismes de colonisation par la végétation d'un
17 inselberg granitique en Guyane Française. Rev. Ecol. Terre Vie, 47: 329-349.
- 18
- 19 Sarthou, C., Thérèzien, Y. and Couté, A., 1995. Cyanophycées de l'inselberg des Nouragues
20 (Guyane française). Nova Hedwigia, 61: 85-109.
- 21
- 22 Sarthou, C. and Villiers, J. F., 1998. Epilithic plant communities on inselbergs in French
23 Guiana. J. Veg. Sci., 9: 847-860.
- 24

- 1 Sarthou C., Villiers, J. F. and Ponge J. F., 2003. Shrub vegetation on tropical granitic
2 inselbergs (French Guiana). *J. Veg. Sci.*, 14: 645-652.
3
- 4 Topoliantz, S., Ponge J. F. and Viaux, P., 2000. Earthworm and enchytraeid activity under
5 different arable farming systems, as exemplified by biogenic structures. *Plant Soil*,
6 225: 39-51.
7
- 8 Vaçulik, A., Kounda-Kiki, C., Sarthou, C. and Ponge, J. F., 2004. Soil invertebrate activity in
9 biological crusts on tropical inselbergs. *Eur. J. Soil Sci.*, 55: 539-549.
10

1 **Figure captions**

2

3 **Fig. 1.** Distribution according to depth of cyanobacteria (a), leaf material (b), root material
4 (c), decayed plant material (d), fungal mycelia (e), humified organic matter (f),
5 holorganic faeces (g), organo-mineral faeces (h) and mineral particles (i) under the
6 three main vegetation types.

7

8 **Fig. 2.** Correspondence analysis of humus layers. Projection of active variables (categories of
9 litter/humus components) in the plane of the first two axes. Categories were coded as
10 in Table 1.

11

12 **Fig. 3.** Correspondence analysis of humus layers. Projection of passive variables (horizon
13 names, depth indicators and vegetation types) in the plane of the first two axes. Depth
14 levels (from cm to cm) are indicated by broken lines for each of the three sampled
15 successional stages, starting from 0-1 cm. Dotted line = *Pitcairnia* stage, hyphened
16 line = *Clusia* stage, full line = *Clusia-Myrcia* stage.

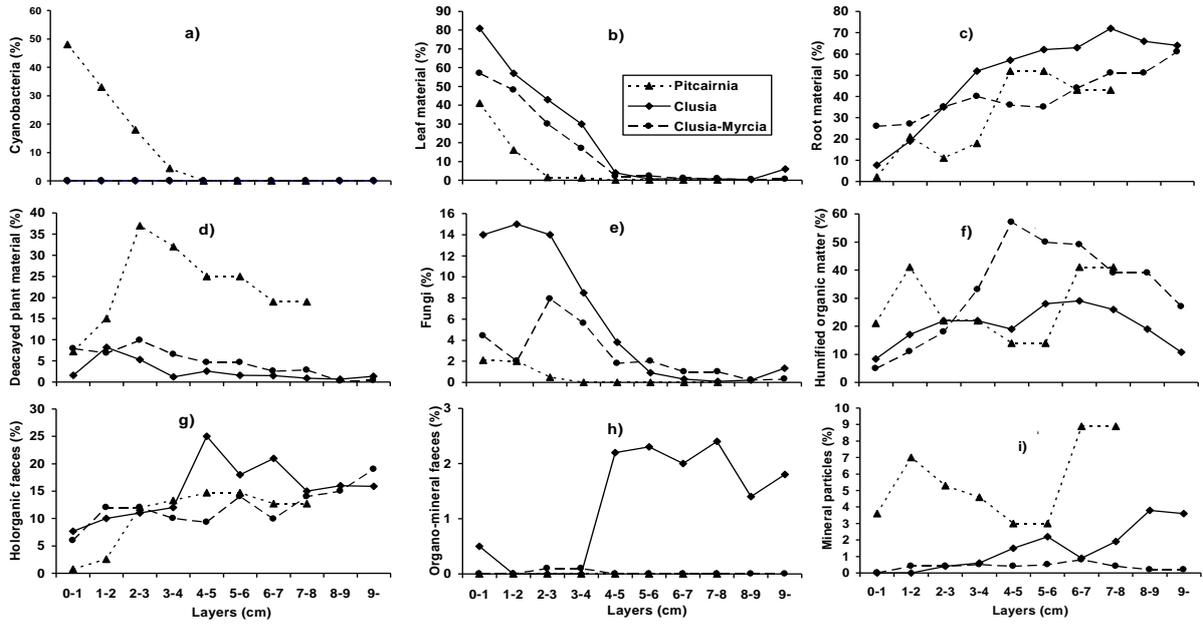
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Table 1. Mean volumes (in %±SE) of gross categories featuring litter/humus components in the three studied successional stages *Pitcairnia*, *Clusia* and *Clusia-Myrcia* (three replicates each).

	Gross category	Code	Pitcairnia	Clusia	Clusia-Myrcia
	Leaf material	LM	6.4±4.3	22±7.1	17±6.7
	Root material	RM	23±2.1	49±7.2	39±3.7
	Decayed plant material	DPM	11±7.1	2.6±0.9	5.0±1.9
	Miscellaneous plant	MP	1.7±1.3	1.1±0.2	1.2±0.2
	Cyanobacteria	C	46±20	0	0
	Fungal mycelium	F	0.8±0.1	6.1±3.5	3.1±1.5
	Humified organic matter	HOM	36±7.6	20±5.0	32±6.7
	Holorganic faeces	HF	10.4±6.4	16±0.5	13±2.3
	Organo-mineral faeces	OMF	0	1.3±1.1	0.01±0.01
1	Mineral particles	MP	4.4±0.9	1.5±0.9	0.36±0.22

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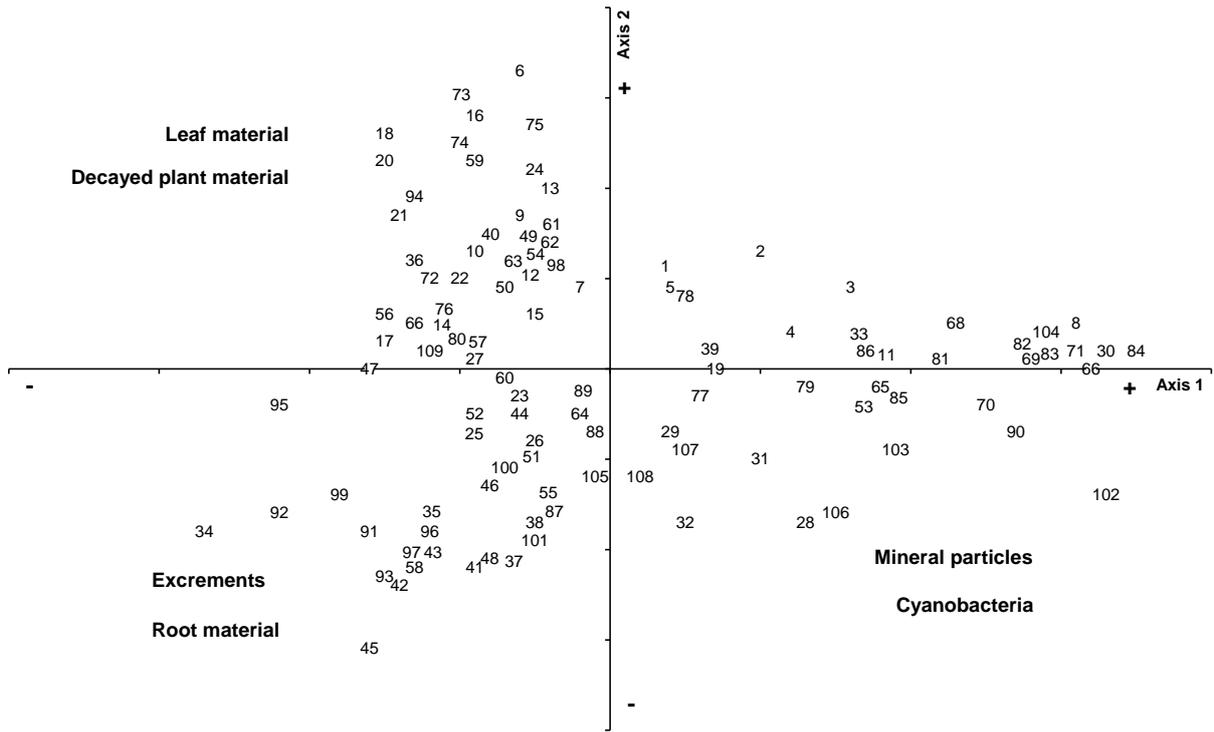


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4 **Fig. 1**

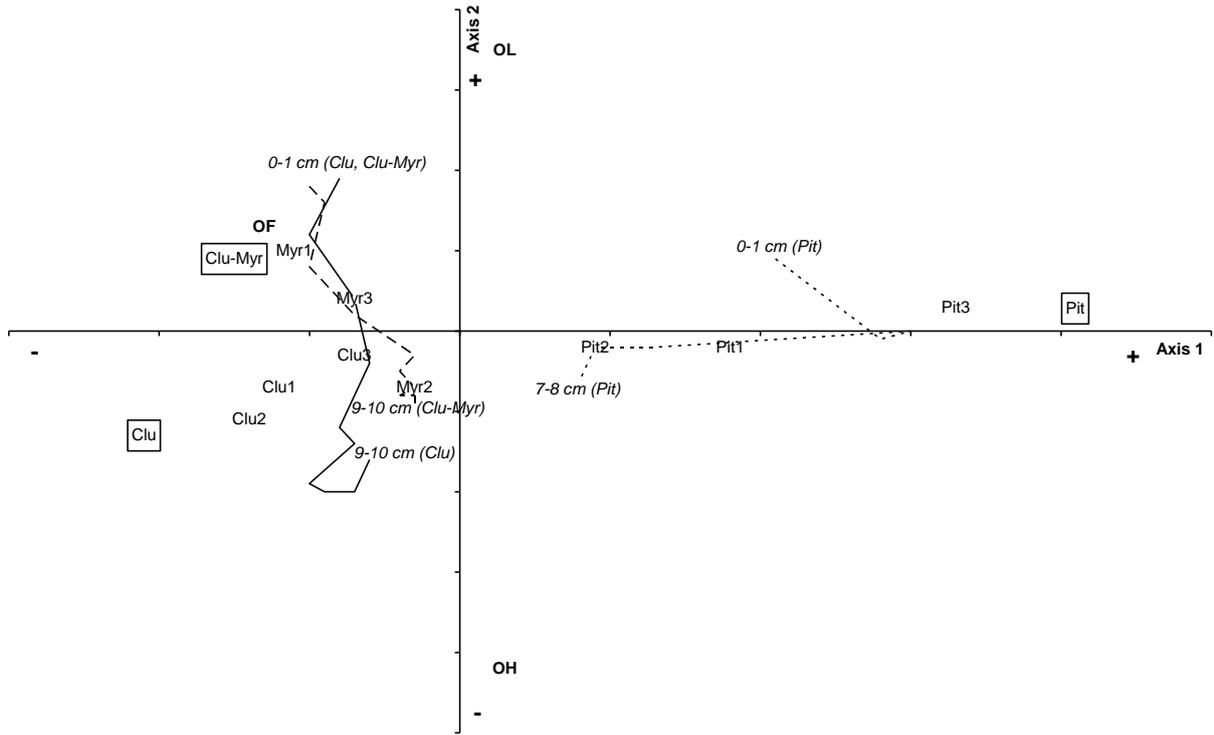
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2 **Fig. 2**

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2 **Fig. 3**

3

Appendix. Classes of litter/humus components and enchytraeids counted under the dissecting microscope with their code number and volume (in %) according to a count-point method in the nine profiles studied. Pitcairnia, Clusia and Clusia-Myrcia are three stages of a plant succession on the Nouragues Inselberg. C = cyanobacteria. DPM = decayed plant material. F = fungal mycelium. LM = leaf material. HF = holorganic faeces. HOM = humified organic matter. MP = mineral particles. MPM = miscellaneous plant material. OMF = organo-mineral faeces. RM = root material.

Component	Code	Gross category	Pitcairnia			Clusia			Clusia-Myrcia		
			Ph1	Ph2	Ph3	Clu1	Clu2	Clu3	Myr1	Myr2	Myr3
Leaf of <i>Pitcairnia</i>	1	LM	0	0	4.1	0	0	0	0.11	0	0
Leaf of <i>Pitcairnia</i> covered by humified organic matter	2	LM, HOM	0	0	0.51	0	0	0	0.17	0	0
Leaf of <i>Pitcairnia</i> covered by cyanobacterial crust	3	LM, C	0	0	0.06	0	0	0	0	0	0
Leaf of <i>Pitcairnia</i> covered by fungi	4	LM, F	0	0	0.17	0	0	0	0	0	0
Translucent leaf of <i>Pitcairnia</i> with tannin	5	LM	0	0	0.12	0	0	0	0	0	0
Leaf of <i>Clusia</i>	6	LM	0.68	0	7.2	5.1	20	13	11	0	0
Leaf of <i>Clusia</i> covered by humified organic matter	7	LM, HOM	0	0	1.4	2.3	0.05	2	0.3	0	0
Leaf of <i>Clusia</i> covered by cyanobacterial crust	8	LM, C	0.91	0	0.29	0	0	0	0	0	0
Leaf of <i>Clusia</i> covered by fungi	9	LM, F	0	0	0.7	1.08	10	1.3	0	0	0
Leaf of <i>Clusia</i> with tannin	10	LM	0	0	0	0.37	0	0	0	0	0
Leaf of <i>Clusia</i> covered by fungi and cyanobacterial crust	11	LM, F, C	0.23	0	0	0	0	0	0	0	0
Translucent leaf of <i>Clusia</i> covered by fungi	12	LM, F	0	0	0	0.08	1.2	0.04	0	0	0
Translucent leaf of <i>Clusia</i> with tannin	13	LM	0	0	0.02	0.05	0.23	0.15	0	0	0
Translucent leaf of <i>Clusia</i> covered by humified organic matter	14	LM, HOM	0	0	0	0.17	0	0.01	0	0	0
Translucent leaf of <i>Clusia</i> covered by fungi	15	LM, F	0	0	0	0.16	1	0	0	0	0
Translucent leaf of <i>Clusia</i>	16	LM	0	0	0.08	0.36	1.5	0.8	0.73	0	0
Leaf of <i>Clusia</i> covered by enchytraeid faeces	17	LM, HF	0	0	0	0.39	0.4	0.11	0.13	0	0
Leaf of <i>Myrcia</i>	18	LM	0	1.5	0	0.38	0	1.2	11	4.1	14
Leaf of <i>Myrcia</i> covered by cyanobacterial crust	19	LM, C	0	0.68	0	0	0	0	0	0	0
Translucent leaf of <i>Myrcia</i>	20	LM	0	0	0	0.11	0	0	1.9	0.33	1.7
Leaf of <i>Myrcia</i> covered by fungi	21	LM, F	0	0	0	0.18	0	0.04	1.7	0.22	1.28
Leaf of <i>Myrcia</i> with tannin	22	LM	0	0	0	0	0	0	0	0.45	0.81
Translucent leaf of <i>Myrcia</i> covered by fungi	23	LM, F	0	0	0	0	0	0	0.13	0.17	0
Petiole of <i>Clusia</i>	24	LM	0	0.11	0.39	0.69	0.81	0.37	0.74	0	0.02
Petiole of <i>Clusia</i> covered by humified organic matter	25	LM, HOM	0	0	0	0	0.1	0.17	0	0	0
Petiole of <i>Clusia</i> tunnelled by mites and filled with their excrements	26	LM, HF	0	0	0	0.11	0	0.03	0	0	0
Petiole of <i>Clusia</i> covered by fungi	27	LM, F	0	0	0	0	0.21	0.3	0	0	0
Living fine roots (0-3 mm)	28	RM	12	4.2	8.2	4.79	0	1.1	2.2	2.9	9.3
Living fine roots (0-3 mm) covered by humified organic matter	29	RM, HOM	3.5	11	0.21	1.5	0	1.9	0.62	0.66	0.68
Living fine roots (0-3 mm) covered by cyanobacterial crust	30	RM, C	0.11	0.11	0.06	0	0	0	0	0	0
Dead fine roots (0-3 mm)	31	RM	2	0.11	13	4.74	0	1.6	1.4	0.46	0.45
Dead fine roots (0-3 mm) covered by humified organic matter	32	RM, HOM	0.35	1.3	2	2.71	0	0	0.09	0.47	0.2
Dead fine roots (0-3 mm) covered by cyanobacterial crust	33	RM, C	0.46	0	0	0	0	0	0	0	0
Living medium roots (3-7 mm)	34	RM	0	0.44	0.51	26	12	15	15	9.3	12
Living medium roots (3-7 mm) covered by humified organic matter	35	RM, HOM	0	0	0	7.5	2.86	4.6	2.5	1.31	0.18
Living medium roots (3-7 mm) covered by fungi	36	RM, F	0	0	0	0.27	0.1	0	1.3	0.16	0.42
Dead medium roots (3-7 mm)	37	RM	5	0.88	1.6	3.65	2	4.7	7.2	10	3.4
Dead medium roots (3-7 mm) covered by humified organic matter	38	RM, HOM	0.12	1.1	0.74	0.09	1.32	1.6	1.4	3.32	0.67
Dead medium roots (3-7 mm) covered by cyanobacterial crust	39	RM, C	0	0.11	0	0	0	0	0	0	0
Dead medium roots (3-7 mm) covered by fungi	40	RM, F	0	0	0	0	0	0	0	0.04	0.09
Dead medium roots (3-7 mm) tunnelled by mites and filled with their excrements	41	RM, HF	0	0	0	2.6	0.34	0.73	0	0.49	0.12
Living large roots (>7 mm)	42	RM	0	0	0	3.37	9.9	6.9	0.11	1.3	1.6
Living large roots (>7 mm) covered by humified organic matter	43	RM, HOM	0	0	0	1.14	1.49	0.25	0.21	0.75	0.44
Living large roots (>7 mm) covered by fungi	44	RM, F	0	0	0	0.02	0	0.17	0	0	0
Dead large roots (>7 mm)	45	RM	0	0	0.65	4.56	10.7	2.5	3.9	3.5	4.3
Dead large roots (>7 mm) covered by humified organic matter	46	RM, HOM	0	0	0	1.38	0.12	0.6	0.04	0.31	0
Miscellaneous bark	47	MPM	0	0	0	0.15	0.07	0.13	0.13	0	0.04
Root bark	48	MPM, RM	0.12	0	0	0	0.14	0.07	0	0	0
Seed of <i>Clusia</i>	49	MPM	0	0	0	0.01	0	0	0	0	0
Unidentified seed	50	MPM	0.12	0	0.11	0	0	0.1	0.19	0.82	0.46
Unidentified seed tunnelled by mite and filled with their excrements	51	MPM, HF	0	0	0	0	0	0	0.08	0	0.02
Pollen grain	52	MPM	0	0	0.03	0.51	0	0.42	0.5	0.12	0
Spider web	53	MPM	0	0	4.2	0	0	0	0	0	0
Mite egg	54	MPM	0	0	0	0.04	0	0	0	0	0
Spider egg	55	MPM	0	0	0	0.17	0	0	0	0	0
Decayed piece of wood	56	MPM	0	0	0	0.08	0.07	0.21	0.06	0.03	0.37
Decayed piece of wood covered by fungi	57	MPM	0	0	0	0.06	0	0	0	0.02	0
Flower stem of <i>Clusia</i>	58	MPM	0	0	0	0.26	0.38	0.42	0	0	0
Flower stem of <i>Myrcia</i>	59	MPM	0	0	0	0	0	0	0.48	0.02	0
Gum	60	MPM	0	0	0	0.01	0	0.06	0	0	0
Seedling of <i>Clusia</i>	61	MPM	0	0	0	0	0	0	0.03	0	0
Seedling of <i>Myrcia</i>	62	MPM	0	0	0	0	0	0	0.03	0	0
Unidentified seedling	63	MPM	0	0	0	0	0	0	0.05	0	0
Unidentified fruit	64	MPM	0	0	0	0	0	0	0	0	0.05
Mass	65	MPM	0.46	0	0	0	0	0	0	0	0
Decayed plant material	66	DPM	0.92	0.66	5.1	0.17	0.02	0.77	0.07	0.01	0.02
Decayed plant material covered by fungi	67	DPM, F	0.34	0.22	0	0.22	0.12	0.76	1.6	0.13	0.81
Decayed plant material covered by cyanobacterial crust	68	DPM, C	1.9	0.11	1.2	0	0	0	0	0	0
Decayed plant material covered by humified organic matter	69	DPM, HOM	2.3	0.66	12	0.22	0.17	1.2	3	0.57	2.47
Decayed plant material covered by enchytraeid faeces	70	DPM, HF	0	0	5.6	0.35	0.05	0.81	0.25	0	0
Decayed plant material covered by mite faeces	71	DPM, HF	0	0	0.31	0	0	0	0.04	0	0
Translucent decayed plant material covered by fungi	72	DPM, F	0	0	0	0.35	0.12	0.18	0.97	0	0.09
Translucent decayed plant material	73	DPM	0.11	0	0.06	0	0.69	0.09	0.65	0.17	0.96
Translucent decayed plant material covered by mite faeces	74	DPM, HF	0	0	0.06	0	0.17	0	1.15	0.1	0
Translucent decayed plant material with tannin	75	DPM	0	0	0.14	0	0.4	0.01	0.18	0.06	0.33
Translucent decayed plant material covered by humified organic matter	76	DPM, HOM	0	0	0.02	0.23	0	0.41	0.23	0.44	0.48
Decayed plant material covered by cyanobacterial crust and fungi	77	DPM, C, F	0	0.33	0	0	0	0	0	0	0
Decayed plant material covered by humified organic matter and fungi	78	DPM, HOM, F	0	0	0.12	0	0	0.07	0.08	0	0
Decayed plant material covered by cyanobacterial crust and enchytraeid faeces	79	DPM, C, HF	0	0	0.66	0	0	0	0	0	0
Decayed plant material with tannin	80	DPM	0	0	0	0.08	0	0	0	0	0.09
Cyanobacterial crust	81	C	31	36	1.9	0	0	0	0	0	0
Cyanobacterial crust covered by fungi	82	C, F	0	0	0.06	0	0	0	0	0	0
Cyanobacterial crust covered by enchytraeid faeces	83	C, HF	0	0	0.22	0	0	0	0	0	0
Isolated cyanobacterial filaments	84	C	2.2	2.2	2.3	0	0	0	0	0	0
Aggregate of cyanobacteria and humified organic matter	85	C, HOM	27	31	0.06	0	0	0	0	0	0
Fungal fructification	86	F	0.23	0	0	0	0	0	0	0	0
Crust of humified organic matter	87	HOM	4	4.6	6.4	2.45	4.64	17	12	1.41	25
Grease-like humified organic matter	88	HOM	0	0	0	0	0	0	0	35	0
Hologanic mite faeces	89	HF	0	0	0.4	2.35	0	1.4	0.52	0.65	12
Hologanic enchytraeid faeces	90	HF	0	0	10	0.27	0.68	2.2	0.64	0.02	0
Heap of hologanic enchytraeid faeces	91	HF	0	0	0	2.27	1.27	3.7	1.1	0	0
Hologanic millipede faeces	92	HF	0	0	0.03	2	5.4	1.4	3.6	0.53	1.53
Heap of hologanic millipede faeces	93	HF	0	0	0	0.17	0.74	0.06	0.61	0	0.02
Hologanic woodlice faeces	94	HF	0	0	0	0.24	0.06	0.42	0.64	0.09	0.47
Hologanic earthworm faeces	95	HF	0	0	0	1.84	1.57	0.17	1.3	0.14	1.45
Enchytraeid-tunnelled hologanic earthworm faeces	96	HF	0	0	0	2.85	2.54	4.4	2	6.4	0
Snail faeces	97	HF	0	0	0	0.27	1.44	0.03	0.2	0.01	0.61
Hologanic faeces of insect larvae	98	HF	0	0	0	0.25	0	0	0	0	0
Hologanic unidentified faeces	99	HF	0	0	0	0.6	0.29	0.65	0.55	0.3	0.26
Organo-mineral millipede faeces	100	OMF	0	0	0	1.11	0.07	0.16	0	0	0
Organo-mineral earthworm faeces	101	OMF	0	0	0	2.4	0	0.28	0.04	0	0
Gravel particle (> 2 mm)	102	MP	2.8	1.4	1.6	0.74	0.22	0.46	0.05	0.62	0.07
Gravel particle (> 2 mm) covered by humified organic matter	103	MP, HOM	0.93	0.23	2.4	0.3	0	0.51	0	0.1	0.09
Gravel particle (> 2 mm) covered by humified organic matter and cyanobacteria crust	104	MP, HOM, C	0.34	0.22	1.1	0	0	0	0	0	0
Gravel particle (> 2 mm) covered by mite faeces	105	MP, HF	0	0	0	0.81	0	0	0	0	0
Coarse sand particle (0.2-2 mm)	106	MP	0.81	0.66	0.34	0.65	0.07	0.17	0	0.04	0.03
Coarse sand particle (0.2-2 mm) covered by humified organic matter	107	MP, HOM	0	0	0.25	0.23	0	0	0	0	0
Fine sand particle (0.05-0.2 mm)	108	MP	0	0.11	0.06	0.45	0	0	0.01	0.04	0.03
Fauna	109		0.11	0.77	0.09	0.14	0.47	0.72	1.7	0.06	0.28
Enchytraeids/cm			0	0	647	48	19	46	35	64	0.6