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Topsoil as affected by dung deposition under resting places of red howler monkey (*Alouatta seniculus*)

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23

1 Running Title: TOPSOIL EFFECTS OF DUNG DEPOSITION

2

3 **Topsoil Effects of Dung Deposition under Red Howler Monkey (*Alouatta***
4 ***seniculus*) Resting Places**

5

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7

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10

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12

13 **ABSTRACT**

14

15 The short-term influence of dung deposition and its further redistribution by dung
16 beetles was studied under a resting place of the red howler monkey (*Alouatta seniculus*)
17 living in tropical rain forests of South America. Monkey dung was experimentally clumped
18 on the field in a place used by troops of howler monkeys for resting (Nouragues reserve
19 station, French Guiana). Dung-treated plots were sampled serially over three weeks and
20 compared with controls located in their immediate vicinity. The composition of the soil
21 matrix (top 10 cm) was studied in successive micro-layers by an optical method. Under the
22 influence of dung beetle activity the topsoil became more homogeneous, losing its litter, its
23 content in earthworm faeces increased in the course of time and surface mineral deposits

1 were penetrated by roots. The results were interpreted to the light of known effects of soil
2 animal activity on plant growth and seedling survival.

3

4 *Key Words:* dung beetle activity, earthworm faeces, roots, tropical rain forests

5

6 INTRODUCTION

7

8 In the French Guianan primary rain forest, fruit-eating monkeys, in particular the
9 most common red howler monkeys (*Alouatta seniculus* L.), defecate in places where troops
10 (ca. 7 individuals each) are resting for night or some time of the day (Julliot, 1996a; Julliot
11 *et al.*, 2001). Resting places are distributed over the whole territory of the troop and are
12 used regularly or occasionally according to seasons (Julliot, 1992). Dung ($\sim 1.5 \text{ kg}\cdot\text{day}^{-1}$ in
13 each troop) is incorporated in a few hours in the topsoil through the burying activity of
14 flying dung beetles which are olfactorily attracted to smears of fallen monkey faeces (Feer,
15 1999; Feer and Pincebourde, 2005). By this process the soil is locally enriched in fresh and
16 nutrient-rich organic matter (Feeley, 2005), a sparsely distributed component of the
17 tropical rain forest ecosystem (Cuevas and Medina, 1988; Burghouts *et al.*, 1998; Martius
18 *et al.*, 2004), and in seeds of a variety of trees and lianas with pulp fruits (Julliot and
19 Sabatier, 1993; Julliot, 1996b). As a result, a higher number of seeds and seedlings of
20 forest plant species have been shown to occur under resting places of the howler monkey,
21 thus pointing to the importance of this process for forest regeneration and richness in
22 species (Julliot, 1997; Julliot *et al.*, 2001). The impact of this processing chain (Heard,
23 1994) on the composition of the topsoil is still unknown. Short- and long-term effects are
24 expected, depending on the frequency with which resting sites are used by troops of howler
25 monkeys.

1

2 The present study, undergone in French Guiana, was focused on the composition of
3 the topsoil and the distribution of humus components (plant debris, roots, animal faeces)
4 following dung deposition by howler monkeys. We selected a place which was used
5 repetitively by the same troop of howler monkeys, a common pattern of their social
6 behaviour (Julliot and Sabatier, 1993). This is a preliminary assessment of the effects of a
7 processing chain involving plants (trees and lianas), vertebrates (monkeys) and
8 invertebrates (dung beetles, soil animals) on soils of the tropical rain forest.

9

10 We used an optical method, which has been designed for the quantitative analysis
11 of visually recognizable components of the topsoil in temperate (Bernier *et al.*, 1993;
12 Peltier *et al.*, 2001) and tropical (Loranger *et al.*, 2003; Kounda-Kiki *et al.*, 2006)
13 ecosystems.

14

15 MATERIALS AND METHODS

16

17 *Study site and sampling procedure*

18

19 The study site was a resting place used by a troop of howler monkeys, 100 m from
20 the ‘Nouragues’ research station (French Guiana, 100 km south of the Atlantic Coast),
21 which is located within a nature reservation from which human activities (hunting
22 comprised) are excluded, and without any human settlement for several centuries (Charles-
23 Dominique, 2001). The soil is a clayey Ferralsol, acid, yellowish, with a microaggregate
24 texture of biological origin, and a sparsely distributed litter cover on the ground floor
25 (Grimaldi and Riéra, 2001). The forest type is the equatorial rain forest, with canopy trees

1 as high as 50 m and a sparse understory (Poncy *et al.*, 2001). The annual rainfall averages
2 3000 mm, with a short dry season in September and October, and a mean annual
3 temperature of 26.3°C (Grimaldi and Riéra, 2001).

4

5 The site was used by monkeys on 17 April 2004. Excrements were immediately
6 collected then homogenized and grouped into clumps of near equal amount (~ 100g over 1
7 dm²) which were noted D1 to D4, their position being indicated in the field by a stamp, to
8 be retrieved later once dung has disappeared from the ground surface. The soil was
9 sampled at the same places at Day 12, 14, 21 and 23, respectively. Two control samples C1
10 and C2 were taken in the same site on Day 5 and 11, respectively, in places without any
11 sign of recent defecation.

12

13 At the centre of each sampling plot, a block of surface soil 25 cm² in area and 10
14 cm depth was cut with a sharp knife, with as little disturbance as possible, and litter and
15 soil underneath were carefully sampled. Each humus block was separated into individual
16 layers that could be identified macroscopically on the base of structure, composition and
17 other relevant properties (Kounda-Kiki *et al.*, 2006) or arbitrarily each cm when the soil
18 was visually homogeneous. The various layers were transferred into polypropylene jars
19 filled with 95% ethanol before transport to the laboratory. Care was taken that the jars were
20 completely filled with the sampled material in order to avoid changes in structure resulting
21 from shaking during transport to the laboratory.

22

23 *Microscopical analyses*

24

1 All 65 microlayers (~ 11 per soil block) were optically studied using the ‘small
2 volume’ micromorphological method developed by Bernier and Ponge (1994), to which
3 reference is made for details. Results from grid point counting (ca. 400 points) were
4 expressed as the percentage of a given class of litter/humus component. A total of 158
5 classes of litter/humus components were identified (Appendix). The use of an eye reticle
6 allowed to measure the size of organic or mineral particles or assemblages.

7

8 Plant debris were classified into leaves, cuticle/epidermis, petioles/nerves,
9 stem/wood, bark, seeds, seed coats and according to the size of fragments. Roots and
10 mycorrhizae were separated by colour and diameter in section. Animal faeces were
11 classified by the size, the shape, the degree of mixing of mineral matter with organic
12 matter and their state of transformation and assigned to animal groups using Bal (1982),
13 Ponge (1991) and Topoliantz *et al.* (2000).

14

15 *Data analyses*

16

17 Percentages of occurrence of classes of litter/humus components in the 65 micro-
18 layers investigated were subjected to a correspondence analysis or CA (Greenacre, 1984).
19 The different classes of litter/humus components were the active (main) variables, coded
20 by their percentage of occurrence by volume. These components were classified into 61
21 gross categories, which were included as passive variables in the analysis.

22

23 All variables were transformed into $X=(x-m)/s+20$, where x is the original value, m
24 is the mean of a given variable, and s is its standard deviation (Sadaka and Ponge, 2003).
25 The addition to each standardized variable of a constant factor of 20 allows all values to be

1 positive, CA dealing only with positive numbers. Factorial coordinates of weighted
2 variables (with constant mean and variance) can be interpreted directly in terms of their
3 contribution to the factorial axes, contrary to raw data (Greenacre, 1984).

4

5 The volume percent of a given class (or gross category) of litter/humus components
6 can be averaged over the whole profile (0-10 cm), taking into account the different micro-
7 layers, each individual value being weighted by the thickness of the corresponding micro-
8 layer. This allowed to calculate the mean percent volume of the different classes of
9 litter/humus components and of the gross categories in each humus profile (Appendix).

10

11 RESULTS

12

13 When bulked over the 10 top cm, and when all components were pooled into 11
14 main gross categories, the composition of the six investigated humus profiles did not vary
15 to a great extent (Fig. 1). In all six sample profiles, the topsoil was mainly made of
16 earthworm mineral faeces, i.e. faeces with a poor content of organic matter given their
17 light colour (Schulze *et al.*, 1993). However, the percentage of earthworm faeces in the top
18 10 cm (20 to 40%) increased steadily with time from the start of sampling (linear
19 regression, $R^2 = 0.99$, $t = 14.1$, $P = 0.005$), beginning at a level lower than that of control
20 samples. The second most abundant component was roots (20 to 30%), which did not
21 increase with time but was higher in dung-treated samples than in controls (Mann-
22 Whitney, $U = 4.7$, $P < 0.0001$). Earthworm hemorganic faeces were the second most
23 abundant faecal component (7 to 15%) and earthworm holorganic faeces were nearly
24 absent (<1%). Faeces of other animals (mainly enchytraeids, but also millipedes and
25 termites, see Appendix) amounted to less than 10% of total solids. Non-root plant material

1 was but poorly represented (5 to 10%). Aggregates which could not be attributed to recent
2 faecal deposition amounted to 10 to 30% of total solids. Over the six studied humus
3 profiles, the distribution of mineral, hemorganic and holorganic categories was similar in
4 aggregates and earthworm faeces ($\chi^2 = 0.61$, $P = 0.74$).

5

6 Differences between dung-treated and control samples were much more
7 pronounced in the vertical distribution of topsoil components. The distribution of micro-
8 layers and categories of humus components in the plane of the first two axes of CA (Fig. 2)
9 showed that the composition of humus profiles varied according to depth, a complex of
10 factors which was represented by Axis 1 (Fig. 3a). As expected, control samples exhibited
11 a surface composition (see negative values of Axis 1) which contrasted greatly with that of
12 deeper layers (positive values), but this contrast was much less pronounced in dung-treated
13 samples. In control samples, the surface micro-layers were formed of plant material (roots
14 and litter debris) and holorganic faeces (gross categories 32 to 57, all with negative values
15 of Axis 1, with only a few exceptions) which were but badly represented at the surface of
16 dung-treated samples.

17

18 Visual examples of the distribution of gross categories of topsoil components are
19 given for root-permeated aggregates and faeces (Fig. 3b), earthworm mineral faeces (Fig.
20 3c) and root material (Fig. 3d). Root-permeated aggregates and faeces were present at the
21 soil surface in dung-treated places then increased steadily with depth while in control
22 samples they were absent in surface and present in a lesser amount underneath (Fig. 3b).
23 Earthworm mineral faeces increased steadily from surface to deeper layers but they
24 represented up to 30% of the soil matrix in the top 2 cm of dung-treated profiles while they
25 were near absent at the same depth level in control samples. Root material (free roots, not

1 included onto faeces or aggregates) was more abundant at the soil surface and remained
2 higher in content at depth in dung-treated samples than in control soil (Fig. 3d). An
3 increase from 0 to 3-4 cm followed by a decrease was observed in the vertical distribution
4 of root material in dung-treated samples, while this material decreased steadily in control
5 samples.

6

7 DISCUSSION AND CONCLUSIONS

8

9 The topsoil under resting places of howler monkeys is mainly made of earthworm
10 faeces of varying size and organic matter content, indicating a high level of biological
11 activity through the stimulation of microbial processes and nutrient cycles (Lavelle *et al.*,
12 1998; Ponge, 2003). This can be compared with the higher level of plant recruitment which
13 has been measured in these places (Julliot, 1997). Dung deposition (including seed of
14 fleshy fruits) is followed by a chain of soil biological processes which embraces the
15 burying action of dung beetles (Feer, 1999), the redistribution of organic and mineral
16 matter by soil animals (Anderson, 1995) and the development of the root system of plants
17 (Feeley, 2005).

18

19 When monkey dung is buried into the soil by dung beetles, deeper horizons (down
20 to 40 cm) are excavated and pushed up to the surface, where they form small aerated
21 mounds of yellow mineral soil resembling molehills (personal observations). We observed
22 that these mounds, which are not protected by any litter cover, are rapidly flattened by
23 canopy drip and disappear in a few days. Our study, done on the top 10 cm of soil, showed
24 that the excavated soil, although poor in organic matter (light colour), became extensively
25 colonized by earthworms and by roots within a few weeks (Fig. 1). Control samples did

1 not show any earthworm faecal material and any penetration of aggregates and faeces by
2 roots in surface layers, while it was the case after dung application (Fig. 3b). The
3 importance of earthworm faeces for the growth of the root system of plants has been
4 observed and experimentally established (Tomati *et al.*, 1988), as well as their favourable
5 role for soil structure (Blanchart, 1992) and water infiltration (Kladivko *et al.*, 1986). To
6 the light of existing literature, it can be suspected that any event which favours earthworm
7 activity will favour (i) the rapid development of the root system of trees and tree seedlings,
8 the latter being of paramount importance for forest regeneration (Julliot *et al.*, 2001), (ii)
9 the alleviation of ground floor toxicity following litter removal (Madge, 1965; Dalling and
10 Hubbell, 2002). It should be noted, too, that seeds of a variety of tree species with fleshy
11 fruits are concentrated in monkey dung (Julliot, 1996b) and that earthworms are known for
12 the vertical redistribution of seed (Willems and Huijsmans, 1994) and their selective action
13 on the soil seed bank (Thompson *et al.*, 1994; Decaëns *et al.*, 2003). All these aspects point
14 to a rapid, positive feed-back involving monkeys, dung beetles and earthworms, favourable
15 to the early and selective establishment of plant seedlings in a restricted array of favourable
16 micro-sites (Harper *et al.*, 1965; Grubb, 1986; Dalling and Hubbell, 2002).

17

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22

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7

1 **Figure captions**

2

3 **Fig. 1.** Composition in percent volume (gross categories) of the soil matrix in the top 10
4 cm of the six studied samples (D1 to D4 = dung-treated samples at Days 12, 14, 21
5 and 23; C1 and C2 = control samples)

6

7 **Fig. 2.** Projection of main categories (added as passive variables) and micro-layers of the
8 six studied samples in the plane of the first two axes of CA (correspondence
9 analysis). Codes of categories as in Appendix

10

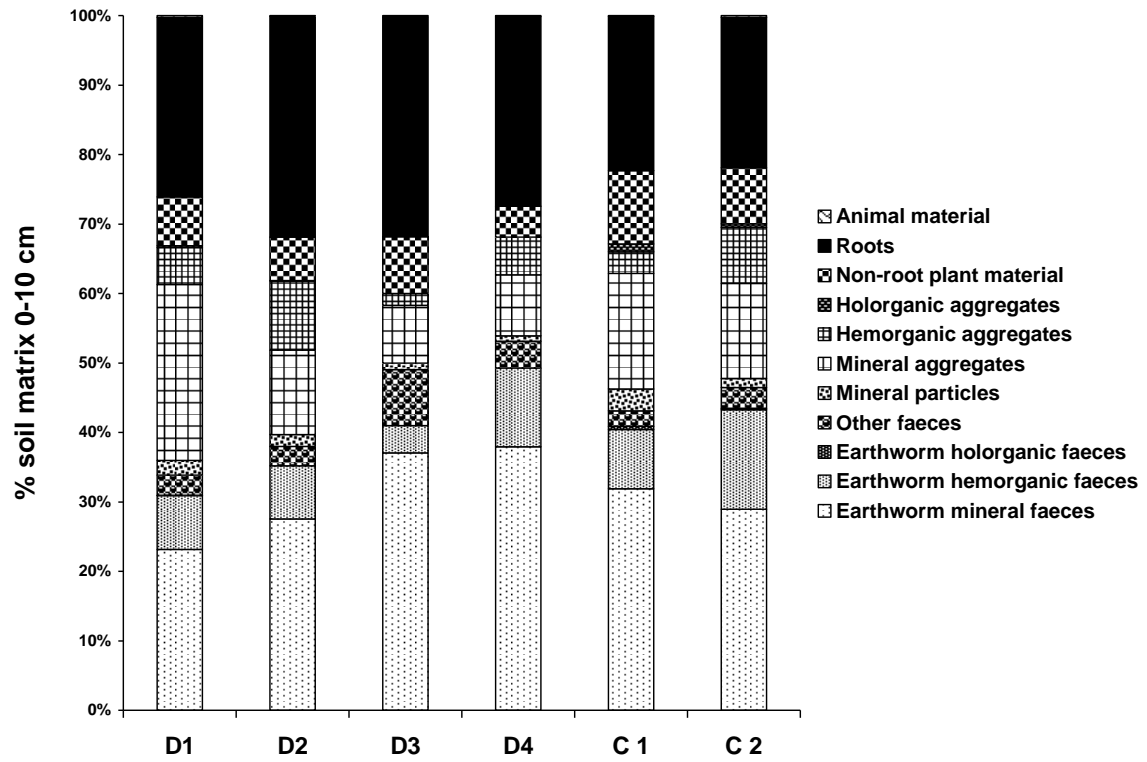
11 **Fig. 3.** (a) Vertical distribution of Axis 1 values (CA)

12 (b) Vertical distribution of root-permeated faeces and aggregates

13 (c) Vertical distribution of earthworm mineral faeces

14 (d) Vertical distribution of roots

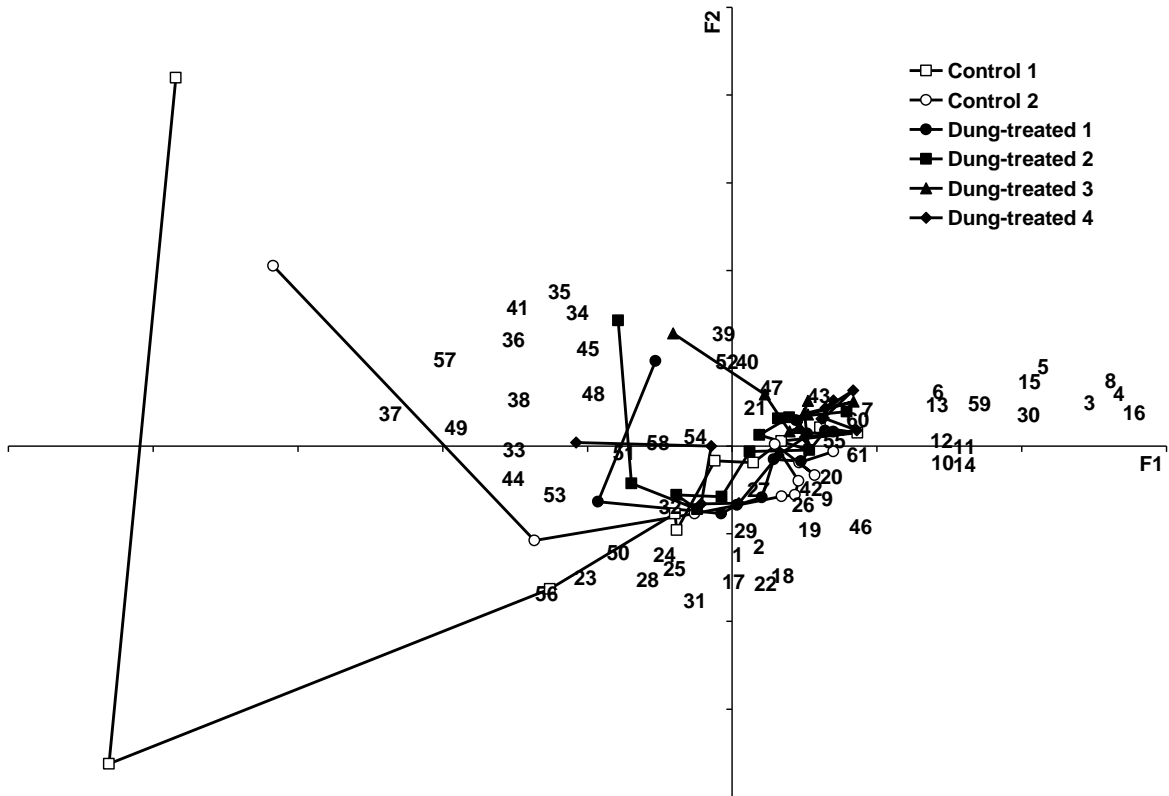
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2 Fig. 1

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2 Fig. 2

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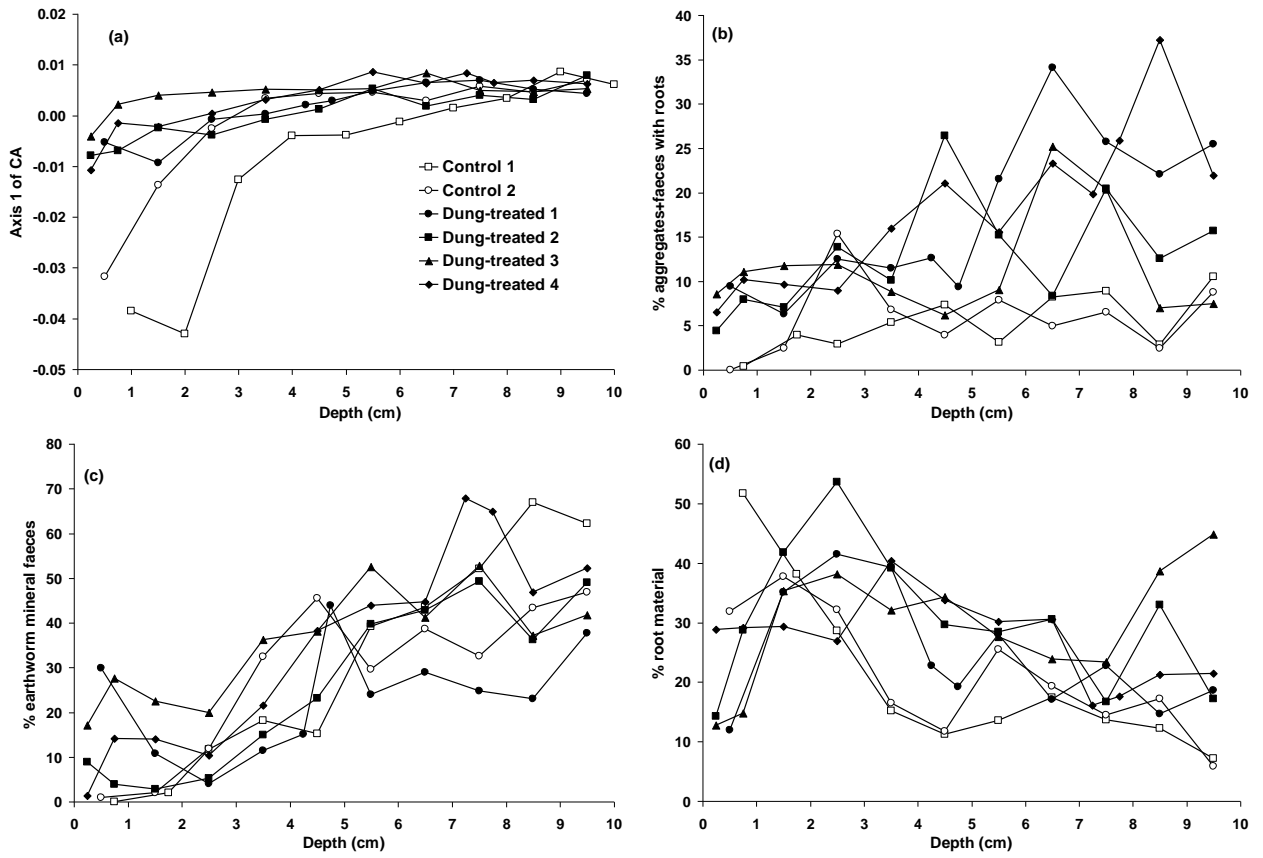


Fig. 3.

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Appendix. List of categories identified in the soil matrix under the dissecting microscope, together with their mean percent volume and coordinates along Axis 1 of correspondence analysis

Code	Categories	D1	D2	D3	D4	C1	C2	Axis 1 (CA)
	Quartz particle 0-1 mm	1.08	0.50	0.49	0.74	2.79	0.87	-0.003
	Quartz particle 1-2 mm	0.61	0.50	0.42	0.05	0.14	0.19	0.011
	Quartz particle >2 mm	0.00	0.19	0.00	0.00	0.00	0.05	0.009
	Laterite particle	0.34	0.47	0.00	0.05	0.15	0.20	0.007
59	Enchytraeid faeces	2.73	2.69	7.51	4.20	2.15	2.16	0.017
	Earthworm mineral faeces <1 mm	3.95	4.13	3.56	4.60	6.95	5.33	0.018
	Earthworm mineral faeces 1-2 mm intact	2.11	1.94	1.87	2.05	2.74	2.94	0.017
	Earthworm mineral faeces 1-2 mm enchytraeid-tunnelled	2.36	5.05	5.01	4.36	2.18	1.54	0.022
	Earthworm mineral faeces 2-5 mm intact	0.86	0.62	1.50	1.13	1.70	2.58	0.015
	Earthworm mineral faeces 2-5 mm root-permeated	0.07	0.02	0.20	0.17	0.00	0.00	0.009
	Earthworm mineral faeces 2-5 mm enchytraeid-tunnelled	7.04	7.18	11.59	11.75	9.26	7.57	0.026
	Earthworm mineral faeces 2-5 mm root-permeated enchytraeid-tunnelled	1.59	1.59	1.42	2.17	0.43	0.19	0.018
	Earthworm mineral faeces 5-10 mm intact	0.00	0.07	0.17	0.00	0.23	0.45	0.006
	Earthworm mineral faeces 5-10 mm root-permeated	0.00	0.00	0.10	0.00	0.00	0.00	0.007
	Earthworm mineral faeces 5-10 mm enchytraeid-tunnelled	1.96	3.24	5.33	4.75	5.85	5.75	0.019
	Earthworm mineral faeces 5-10 mm root-permeated enchytraeid-tunnelled	1.67	2.16	3.51	3.50	1.04	0.63	0.019
	Earthworm mineral faeces 10-15 mm enchytraeid-tunnelled	0.10	0.00	0.43	0.87	0.18	1.36	0.011
	Earthworm mineral faeces 10-15 mm root-permeated enchytraeid-tunnelled	0.35	0.98	1.22	2.82	0.43	0.05	0.013
	Earthworm mineral faeces >15 mm intact	0.34	0.00	0.00	0.00	0.00	0.00	0.001
	Earthworm mineral faeces >15 mm enchytraeid-tunnelled	0.00	0.00	0.00	0.57	0.00	0.00	0.008
	Earthworm mineral faeces >15 mm root-permeated enchytraeid-tunnelled	0.00	0.00	0.55	2.51	0.00	0.00	0.010
	Mineral aggregate <1 mm	2.50	0.91	0.49	1.62	2.78	0.72	0.002
	Mineral aggregate 1-2 mm intact	0.22	0.00	0.00	0.17	0.88	0.14	-0.008
	Mineral aggregate 1-2 mm enchytraeid-tunnelled	1.67	1.06	1.14	0.75	0.47	0.29	0.012
	Mineral aggregate 2-5 mm intact	0.05	0.05	0.00	0.10	0.68	0.09	-0.011
	Mineral aggregate 2-5 mm root-permeated	0.00	0.00	0.00	0.00	0.10	0.00	0.002
	Mineral aggregate 2-5 mm enchytraeid-tunnelled	3.72	2.82	1.80	1.27	2.88	2.93	0.016
	Mineral aggregate 2-5 mm root-permeated enchytraeid-tunnelled	2.31	0.62	0.47	0.43	0.19	0.33	0.013
	Mineral aggregate 5-10 mm intact	0.05	0.00	0.00	0.00	0.22	0.00	-0.007
	Mineral aggregate 5-10 mm root-permeated	0.00	0.00	0.00	0.00	0.02	0.00	-0.013
	Mineral aggregate 5-10 mm enchytraeid-tunnelled	2.98	1.84	1.11	0.63	3.91	4.02	0.015
	Mineral aggregate 5-10 mm root-permeated enchytraeid-tunnelled	4.82	1.56	1.10	1.32	0.67	0.53	0.014
	Mineral aggregate 10-15 mm intact	0.00	0.00	0.00	0.00	0.30	0.00	-0.012
	Mineral aggregate 10-15 mm root-permeated	0.00	0.00	0.00	0.00	0.02	0.00	-0.013
	Mineral aggregate 10-15 mm enchytraeid-tunnelled	0.49	0.71	0.15	0.00	1.33	2.49	0.012
	Mineral aggregate 10-15 mm root-permeated enchytraeid-tunnelled	3.09	1.38	0.87	1.36	1.06	1.19	0.014
	Mineral aggregate >15 mm enchytraeid-tunnelled	0.49	0.00	0.00	0.20	0.38	0.67	0.012
	Mineral aggregate >15 mm root-permeated enchytraeid-tunnelled	2.09	0.97	1.11	1.69	0.29	0.00	0.012
	Earthworm hemorganic faeces <1 mm	0.85	0.45	0.31	0.26	0.68	1.31	-0.002
	Earthworm hemorganic faeces 1-2 mm intact	0.95	0.65	0.30	0.89	1.28	2.19	-0.002
	Earthworm hemorganic faeces 1-2 mm enchytraeid-tunnelled	0.68	0.84	0.35	0.43	0.24	0.92	0.005
	Earthworm hemorganic faeces 2-5 mm intact	0.73	0.43	0.57	0.38	0.63	1.76	0.000
	Earthworm hemorganic faeces 2-5 mm root-permeated	0.00	0.00	0.00	0.19	0.00	0.20	0.004
	Earthworm hemorganic faeces 2-5 mm enchytraeid-tunnelled	2.32	2.87	0.99	3.24	3.09	4.48	0.004
	Earthworm hemorganic faeces 2-5 mm root-permeated enchytraeid-tunnelled	0.29	0.29	0.05	1.05	0.14	0.10	0.007
	Earthworm hemorganic faeces 5-10 mm intact	0.05	0.00	0.20	0.14	0.09	0.10	0.007
	Earthworm hemorganic faeces 5-10 mm root-permeated	0.00	0.00	0.00	0.00	0.06	0.00	-0.011
	Earthworm hemorganic faeces 5-10 mm enchytraeid-tunnelled	0.89	0.83	0.59	3.28	1.67	2.08	0.006
	Earthworm hemorganic faeces 5-10 mm root-permeated enchytraeid-tunnelled	0.61	0.78	0.24	0.89	0.14	0.39	0.004
	Earthworm hemorganic faeces 10-15 mm intact	0.00	0.00	0.00	0.00	0.05	0.00	-0.013
	Earthworm hemorganic faeces 10-15 mm enchytraeid-tunnelled	0.00	0.10	0.00	0.59	0.19	0.24	0.003
	Earthworm hemorganic faeces 10-15 mm root-permeated enchytraeid-tunnelled	0.10	0.14	0.10	0.95	0.00	0.24	0.010
	Earthworm hemorganic faeces >15 mm root-permeated enchytraeid-tunnelled	0.00	0.12	0.19	0.00	0.00	0.00	0.002
	Hemorganic aggregate <1 mm	1.18	1.05	0.02	1.22	0.53	0.93	-0.005
	Hemorganic aggregate 1-2 mm intact	0.44	0.33	0.00	0.45	0.27	0.48	-0.015
	Hemorganic aggregate 1-2 mm enchytraeid-tunnelled	0.90	0.89	0.12	0.33	0.24	0.29	0.000
	Hemorganic aggregate 2-5 mm intact	0.05	0.14	0.00	0.21	0.27	0.20	-0.013
	Hemorganic aggregate 2-5 mm root-permeated	0.10	0.00	0.00	0.00	0.02	0.05	-0.008
	Hemorganic aggregate 2-5 mm enchytraeid-tunnelled	1.18	2.79	0.17	0.95	0.39	1.84	0.000
	Hemorganic aggregate 2-5 mm root-permeated enchytraeid-tunnelled	0.22	1.03	0.00	0.40	0.00	0.20	0.000
	Hemorganic aggregate 5-10 mm intact	0.00	0.00	0.00	0.00	0.20	0.00	-0.013
	Hemorganic aggregate 5-10 mm root-permeated	0.00	0.00	0.00	0.00	0.12	0.00	-0.013
	Hemorganic aggregate 5-10 mm enchytraeid-tunnelled	0.15	1.35	0.29	0.87	0.49	1.40	0.004
	Hemorganic aggregate 5-10 mm root-permeated enchytraeid-tunnelled	0.46	1.02	0.31	0.52	0.15	0.63	0.004
	Hemorganic aggregate 10-15 mm enchytraeid-tunnelled	0.25	0.12	0.42	0.14	0.00	0.71	0.007
	Hemorganic aggregate 10-15 mm root-permeated enchytraeid-tunnelled	0.20	0.58	0.33	0.80	0.29	0.54	0.004
	Hemorganic aggregate >15 mm root-permeated	0.00	0.00	0.00	0.00	0.00	0.54	0.004
	Hemorganic aggregate >15 mm enchytraeid-tunnelled	0.00	0.14	0.00	0.00	0.00	0.00	0.004
	Hemorganic aggregate >15 mm root-permeated enchytraeid-tunnelled	0.00	0.33	0.00	0.00	0.00	0.10	0.001
	Earthworm holorganic faeces <1 mm	0.00	0.00	0.00	0.00	0.05	0.05	0.001
	Earthworm holorganic faeces 1-2 mm	0.00	0.00	0.00	0.00	0.05	0.00	0.003
	Earthworm holorganic faeces 2-5 mm	0.00	0.00	0.00	0.00	0.24	0.09	-0.001
	Earthworm holorganic faeces 5-10 mm	0.05	0.00	0.00	0.00	0.10	0.05	-0.004
	Holorganic aggregate <1 mm	0.00	0.00	0.00	0.02	0.22	0.05	-0.006
	Holorganic aggregate 1-2 mm	0.10	0.00	0.00	0.00	0.17	0.00	-0.005
	Holorganic aggregate 2-5 mm	0.10	0.05	0.00	0.00	0.40	0.15	-0.016
	Holorganic aggregate 5-10 mm	0.05	0.00	0.00	0.00	0.29	0.20	-0.008
	Holorganic aggregate 10-15 mm	0.00	0.00	0.00	0.00	0.06	0.10	0.000
60	Millipede faeces	0.09	0.00	0.40	0.00	0.00	0.00	0.009
61	Termite faeces	0.00	0.00	0.00	0.00	0.00	0.77	0.009
	Leaf fragment <2 mm	0.05	0.10	0.14	0.35	0.06	0.13	-0.006
	Leaf fragment 2-5 mm	0.94	0.39	0.48	0.76	0.87	0.60	-0.015
	Leaf fragment 5-10 mm	0.89	0.34	0.47	0.49	1.48	0.82	-0.016

Leaf fragment >10 mm	0.50	1.77	1.11	0.49	0.83	1.04	-0.005
Cuticle/epidermis fragment <2 mm	0.05	0.21	0.02	0.07	0.02	0.04	-0.007
Cuticle/epidermis fragment 2-5 mm	0.00	0.14	0.02	0.05	0.19	0.00	-0.008
Cuticle/epidermis fragment 5-10 mm	0.00	0.00	0.00	0.00	0.13	0.00	-0.011
Petiole/nerve fragment <2 mm	0.05	0.02	0.00	0.00	0.31	0.00	-0.020
Petiole/nerve fragment 2-5 mm	0.35	0.02	0.00	0.02	0.24	0.00	-0.004
Petiole/nerve fragment 5-10 mm	0.10	0.05	0.00	0.00	0.13	0.04	-0.010
Petiole/nerve fragment >10 mm	0.05	0.00	0.00	0.12	0.00	0.18	-0.008
Stem/wood fragment <2 mm	0.00	0.02	0.26	0.00	0.53	0.51	-0.018
Stem/wood fragment 2-5 mm	0.29	0.02	0.07	0.00	1.05	0.22	-0.021
Stem/wood fragment 5-10 mm	0.05	0.00	0.15	0.00	0.00	0.04	0.001
Stem/wood fragment >10 mm	0.00	0.15	0.00	0.28	0.06	0.10	-0.002
Bark fragment <2 mm	0.98	1.00	1.32	0.94	1.55	0.48	0.002
Bark fragment 2-5 mm	0.66	0.70	0.94	0.55	1.56	1.52	-0.016
Bark fragment 5-10 mm	0.05	0.19	0.38	0.26	0.58	0.88	-0.014
Bark fragment >10 mm	0.05	0.00	0.05	0.02	0.00	1.12	-0.008
Seed coat fragment <2 mm	0.00	0.00	0.00	0.00	0.06	0.00	-0.011
Seed coat fragment 2-5 mm	0.00	0.12	0.26	0.00	0.06	0.00	0.001
Seed coat fragment 5-10 mm	0.05	0.00	0.35	0.09	0.00	0.00	0.006
Seed coat fragment >10 mm	0.00	0.05	1.14	0.24	0.50	0.18	-0.001
Seed <2 mm	0.00	0.02	0.02	0.00	0.00	0.00	0.001
Seed 2-5 mm	0.10	0.00	0.00	0.00	0.00	0.00	0.002
Seed 5-10 mm	0.00	0.02	0.14	0.05	0.00	0.00	0.006
Seed >10 mm	1.59	0.71	0.70	0.00	0.00	0.00	0.001
Club moss (Selaginella)	0.00	0.00	0.00	0.02	0.13	0.04	-0.014
Mycelium	0.05	0.00	0.07	0.00	0.05	0.05	0.003
Black rhizomorph	0.07	0.02	0.02	0.05	0.17	0.05	-0.004
White rhizomorph	0.05	0.02	0.00	0.00	0.20	0.09	-0.019
Miscellaneous (humified or unidentified) plant material	2.07	0.80	0.26	0.72	0.55	0.99	-0.007
Charcoal	0.05	0.10	0.23	0.09	0.00	0.00	0.004
Fruit fragment	0.02	0.05	0.19	0.00	0.24	0.00	0.011
Bud	0.00	0.00	0.00	0.00	0.05	0.00	-0.001
Black root Ø <0.5 mm	0.05	0.07	0.23	0.00	0.05	0.09	0.005
Black root Ø 0.5-1 mm	0.15	0.19	0.57	0.07	0.20	0.76	0.004
Black root Ø 1-2 mm	0.05	0.17	0.57	0.00	0.00	0.86	0.006
Brown root Ø <0.5 mm	4.28	6.92	6.91	7.60	5.19	0.77	0.002
Brown root Ø 0.5-1 mm	7.22	6.97	4.93	8.10	3.02	2.35	0.002
Brown root Ø 1-2 mm	2.54	3.99	6.06	4.90	1.57	0.88	0.007
Brown root Ø >2 mm	1.31	3.59	10.37	3.02	0.29	0.63	0.010
Beaded root Ø <0.5 mm	0.02	0.16	0.00	0.00	0.57	0.00	-0.006
Beaded root Ø 0.5-1 mm	1.15	2.96	0.23	0.86	2.39	2.63	-0.016
Beaded root Ø 1-2 mm	1.07	1.46	0.14	0.45	0.72	3.09	-0.010
Beaded root Ø >2 mm	0.10	0.00	0.00	0.00	0.20	1.90	-0.005
Detached bead (from beaded root)	0.49	0.84	0.23	0.22	0.27	0.78	-0.002
Red root Ø <0.5 mm	0.02	0.05	0.00	0.00	0.25	0.05	-0.010
Red root Ø 0.5-1 mm	0.00	0.33	0.19	0.00	0.10	0.73	-0.006
Red root Ø 1-2 mm	0.00	0.19	0.00	0.00	0.05	0.27	-0.007
Light-brown root Ø <0.5 mm	3.06	1.35	0.05	0.96	0.33	1.50	0.011
Light-brown root Ø 0.5-1 mm	1.40	0.87	0.05	1.46	1.19	1.99	0.004
Light-brown root Ø 1-2 mm	0.50	0.05	0.00	0.10	0.33	0.58	0.009
Light-brown root Ø >2 mm	0.00	0.00	0.00	0.00	0.29	0.00	0.005
White root Ø <0.5 mm	0.86	0.17	0.24	0.89	0.66	0.39	0.000
White root Ø 0.5-1 mm	0.00	0.05	0.14	0.40	0.00	0.10	0.010
White root Ø 1-2 mm	0.05	0.00	0.00	0.00	0.00	0.00	0.007
White root with hairs Ø <0.5 mm	0.05	0.07	0.00	0.00	0.11	0.24	-0.002
White root with hairs Ø 0.5-1 mm	0.00	0.00	0.00	0.00	0.00	0.36	-0.009
White root with hairs Ø 1-2 mm	0.00	0.00	0.00	0.00	0.00	0.09	-0.009
White root with hairs Ø >2 mm	0.00	0.00	0.00	0.00	0.00	0.04	-0.009
Root with claret-coloured mycorrhizae Ø <0.5 mm	0.00	0.10	0.00	0.00	0.51	0.00	-0.011
Root with claret-coloured mycorrhizae Ø 0.5-1 mm	0.15	0.14	0.00	0.00	1.81	0.00	-0.016
Root with claret-coloured mycorrhizae Ø 1-2 mm	0.05	0.00	0.00	0.00	0.13	0.00	-0.011
Root with claret-coloured mycorrhizae Ø >2 mm	0.00	0.00	0.00	0.00	0.20	0.00	-0.010
Root with orange mycorrhizae Ø <0.5 mm	0.00	0.00	0.00	0.09	0.00	0.00	0.010
Root with orange mycorrhizae Ø 0.5-1 mm	0.00	0.00	0.00	0.34	0.22	0.00	-0.010
Root with orange mycorrhizae Ø 1-2 mm	0.00	0.00	0.00	0.14	0.00	0.00	0.010
Root fragment	0.42	0.45	0.26	0.05	0.91	0.14	-0.006
Voided root Ø <0.5 mm	0.10	0.14	0.05	0.02	0.27	0.09	-0.011
Voided root Ø 0.5-1 mm	0.59	0.57	0.10	0.00	0.89	0.49	-0.013
Voided root Ø 1-2 mm	0.07	0.00	0.19	0.02	0.15	0.15	0.005
Root fibers	0.27	0.33	0.47	0.41	0.19	0.05	0.009
Ant	0.00	0.00	0.00	0.05	0.00	0.00	0.007
Potworm (Enchytraeida)	0.00	0.00	0.09	0.14	0.00	0.00	0.004
Insect larva	0.00	0.00	0.00	0.00	0.00	0.04	-0.009
Arthropod cuticle	0.24	0.10	0.07	0.00	0.10	0.18	0.000
Arthropod	0.00	0.00	0.00	0.00	0.02	0.00	-0.013
1 Total quartz particles	1.69	1.20	0.91	0.79	2.93	1.11	0.000
2 Total mineral particles	2.04	1.67	0.91	0.84	3.08	1.31	0.002
3 Total earthworm mineral faeces 1-2 mm	4.47	6.98	6.88	6.41	4.92	4.48	0.025
4 Total earthworm mineral faeces 2-5 mm	9.56	9.41	14.71	15.20	11.39	10.35	0.027
5 Total earthworm mineral faeces 5-10 mm	3.63	5.47	9.11	8.25	7.12	6.82	0.021
6 Total earthworm mineral faeces 10-15 mm	0.44	0.98	1.66	3.69	0.61	1.41	0.014
7 Total earthworm mineral faeces >15 mm	0.34	0.00	0.55	3.07	0.00	0.00	0.009
8 Total earthworm mineral faeces	22.40	26.98	36.47	41.23	30.99	28.38	0.027
9 Total mineral aggregates 1-2 mm	1.89	1.06	1.14	0.92	1.35	0.43	0.007
10 Total mineral aggregates 2-5 mm	6.08	3.49	2.26	1.79	3.84	3.35	0.015
11 Total mineral aggregates 5-10 mm	7.85	3.40	2.20	1.95	4.82	4.55	0.016
12 Total mineral aggregates 10-15 mm	3.58	2.09	1.02	1.36	2.71	3.68	0.014
13 Total mineral aggregates >15 mm	2.59	0.97	1.11	1.89	0.66	0.67	0.014
14 Total mineral aggregates	24.49	11.93	8.22	9.53	16.16	13.40	0.016
15 Total mineral aggregates with roots	15.99	9.29	10.54	15.96	4.25	2.93	0.021
16 Total mineral material	51.65	43.27	53.11	55.80	52.39	45.26	0.028
17 Total earthworm hemorganic faeces 1-2 mm	1.64	1.49	0.66	1.32	1.52	3.11	0.000

18	Total earthworm hemorganic faeces 2-5 mm	3.34	3.60	1.61	4.86	3.87	6.53	0.003
19	Total earthworm hemorganic faeces 5-10 mm	1.55	1.62	1.02	4.31	1.97	2.57	0.005
20	Total earthworm hemorganic faeces 10-15 mm	0.10	0.24	0.10	1.55	0.24	0.48	0.006
21	Total earthworm hemorganic faeces >15 mm	0.00	0.12	0.19	0.00	0.00	0.00	0.002
22	Total earthworm hemorganic faeces	7.47	7.52	3.88	12.30	8.28	14.00	0.002
23	Total hemorganic aggregates 1-2 mm	1.34	1.22	0.12	0.78	0.51	0.77	-0.010
24	Total hemorganic aggregates 2-5 mm	1.54	3.96	0.17	1.56	0.68	2.28	-0.005
25	Total hemorganic aggregates 5-10 mm	0.61	2.38	0.60	1.39	0.96	2.02	-0.004
26	Total hemorganic aggregates 10-15 mm	0.45	0.70	0.75	0.95	0.29	1.25	0.005
27	Total hemorganic aggregates >15 mm	0.00	0.48	0.00	0.00	0.00	0.64	0.002
28	Total hemorganic aggregates	5.12	9.78	1.66	5.90	2.98	7.90	-0.006
29	Total hemorganic aggregates with roots	1.98	4.30	1.22	4.81	0.94	2.98	0.001
30	Total aggregates with roots	17.97	13.59	11.76	20.77	5.19	5.91	0.020
31	Total hemorganic material	12.59	17.30	5.54	18.20	11.26	21.90	-0.003
32	Total earthworm holorganic faeces	0.05	0.00	0.00	0.00	0.43	0.19	-0.004
33	Total holorganic aggregates	0.24	0.05	0.00	0.02	1.13	0.49	-0.015
34	Total leaf fragments	2.38	2.61	2.20	2.09	3.25	2.60	-0.011
35	Total cuticle/epidermis fragments	0.05	0.36	0.05	0.12	0.34	0.04	-0.012
36	Total petiole/nerve fragments	0.55	0.10	0.00	0.14	0.67	0.22	-0.015
37	Total stem/wood fragments	0.34	0.20	0.48	0.28	1.64	0.88	-0.024
38	Total bark fragments	1.73	1.90	2.68	1.78	3.70	4.00	-0.015
39	Total seed coat fragments	0.05	0.17	1.75	0.33	0.63	0.18	-0.001
40	Total seeds	1.69	0.76	0.86	0.05	0.00	0.00	0.001
41	Total non-root plant material	6.79	6.09	8.03	4.79	10.22	7.92	-0.015
42	Total black roots	0.25	0.43	1.37	0.07	0.24	1.71	0.005
43	Total brown roots	15.36	21.48	28.27	23.61	10.07	4.62	0.006
44	Total beaded roots	2.84	5.43	0.60	1.53	4.16	8.41	-0.015
45	Total red roots	0.02	0.57	0.19	0.00	0.39	1.05	-0.010
46	Total light-brown roots	4.95	2.27	0.10	2.52	2.14	4.08	0.009
47	Total white roots	0.91	0.21	0.38	1.30	0.66	0.49	0.003
48	Total white roots with hairs	0.05	0.07	0.00	0.00	0.11	0.74	-0.010
49	Total roots with claret-coloured mycorrhizae	0.20	0.24	0.00	0.00	2.64	0.00	-0.019
50	Total roots with orange mycorrhizae	0.00	0.00	0.00	0.57	0.22	0.00	-0.008
51	Total roots	25.00	31.15	31.18	29.65	21.56	21.23	-0.007
52	Total roots Ø <0.5 mm	8.35	8.89	7.44	9.54	7.68	3.04	0.000
53	Total roots Ø 0.5-1 mm	10.07	11.52	6.11	11.23	8.93	8.93	-0.012
54	Total roots Ø 1-2 mm	4.26	5.85	6.76	5.59	2.80	5.77	-0.003
55	Total roots Ø >2 mm	1.41	3.59	10.37	3.02	0.97	2.57	0.007
56	Total voided roots	0.76	0.71	0.33	0.05	1.30	0.73	-0.013
57	Total plant material	34.90	39.14	40.46	35.65	34.24	30.96	-0.020
58	Total animal material	0.24	0.10	0.16	0.19	0.12	0.23	-0.005