**The impact of red howler monkey latrines on the distribution of main nutrients
and topsoil components in tropical rain forests**

NADIA DOS SANTOS NEVES, FRANÇOIS FEER, SANDRINE SALMON,
CAROLE CHATEIL AND JEAN-FRANÇOIS PONGE*

*Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 avenue du Petit-Château,
91800 Brunoy, France*

Short running title: red howler latrines and topsoil components

* Correspondence: J.F. Ponge. Email: ponge@mnhn.fr

Abstract Scarcity of organic matter and nutrients in the topsoil is a typical feature of lowland primary tropical rain forests. However, clumped defecation by vertebrate herbivores and dung-beetle burying activity may contribute to locally improve soil biological activity and plant growth. We studied for the first time the impact of clumped defecation by the red howler monkey (*Alouatta seniculus*), a frugivorous primate, on the vertical distribution of topsoil (0-6 cm) main nutrients and microstructures in a tropical rainforest (French Guiana). Three roosts, where monkey troops regularly defecate, were sampled, together with adjoining controls for carbon, nitrogen, phosphorus and microscopic components. The vertical distribution of C and N was affected by clumped defecation: nutrients were mostly restricted to the top 2 cm in control areas while defecation areas exhibited homogeneously distributed C and N, resulting in higher C and N content below 2 cm. No marked effect of defecation was registered on Olsen P. A small although significant increase in pH (0.1-0.3 pH units) and a marked increase in soil respiration (x 1.5-2.5) were registered in defecation areas. Soil microstructures were studied by the small-volume method. Variation according to depth, site and clumped defecation was analysed by Redundancy Analysis. The three defecation areas were characterized by an increase in root-penetrated mineral-organic assemblages, mainly composed of recent and old earthworm faeces. The local stimulation of plant roots, microbial and earthworm activity was prominent, together with an increase in soil fertility.

Key words: tropical rainforests, latrines, soil biogenic structures, nutrient distribution.

INTRODUCTION

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37 In temperate and tropical grasslands clumped defecation by livestock leads to local
38 enrichment in main nutrients (Jewell *et al.* 2007) and small seeds (Pakeman *et al.* 2002).
39 Hot spots of microbial and animal biodiversity and activity develop within and below
40 dung pats (Lussenhop *et al.* 1980; Hay *et al.* 1998; Scown & Baker 2006), thereby
41 affecting the composition and structure of plant communities (Dai 2000). However,
42 much remains to be known about similar processes in the wild (James 1992; Bruun *et*
43 *al.* 2008). In non-fragmented primary tropical rain forests, which harbour the richest
44 herbivore faunas (Coley & Barone 1996; Parry *et al.* 2007), some species of vertebrates
45 are known for their recurrent use of definite sites for sleeping and reproduction,
46 resulting in clumped defecation in latrines (Théry & Larpin 1993; Julliot 1996a; Feeley
47 2005). In South America, dung deposition by troops of the frugivorous red howler
48 monkey (*Alouatta seniculus* L.), a widespread primary seed disperser (Julliot & Sabatier
49 1993; Julliot 1996a; Andresen 2002a), and subsequent dung burying and decomposition
50 by other organisms, have been shown to locally increase the soil seed bank (Pouvelle *et*
51 *al.* 2009) and to favour seedling establishment (Julliot 1997; Andresen & Levey 2004).
52 Besides seed concentration, the input of dung in repeatedly used latrines may have far-
53 reaching consequences on the availability and on the distribution of main nutrients. In
54 Venezuela it has been shown that places where howler monkey dung has been deposited
55 were enriched in nutrients compared to surrounding areas, the more so where defecation
56 occurred more frequently (Feeley 2005). Contrary to temperate ecosystems, where
57 earthworms (when present) are the main agents of vertebrate dung disappearance
58 (Hendriksen 1997; Svendsen *et al.* 2003), in neotropical rainforests dung beetles
59 excavate the topsoil and bury dung within a few hours after defecation (Gill 1991; Feer

1999; Andresen 2002b). The monkeys are at the origin of a unidirectional flow of dung resource processed by downstream specialized consumers. This ‘processing chain commensalism’ in the sense of Heard (1994) may be severely disturbed by habitat modification and fragmentation (Nichols *et al.* 2007) and by human impacts on mammal communities (Estrada *et al.* 1999; Vulinec 2000).

A preliminary experiment in a latrine often used by red howler monkeys suggested that clumped defecation and subsequent burying of dung by Scarabaeidae increased topsoil content in earthworm faeces and roots within a few weeks (Pouvelle *et al.* 2008). In the present study we want to compare several latrines of the red howler monkey and to check (1) whether all of them display a similar shift in soil microstructures and roots and (2) whether this transformation of the topsoil is associated to changes in amount and distribution of main nutrients (C, N and P) and to increased microbial activity. The study took place in French Guiana, in a large rainforest nature reserve where monkey and dung beetle populations have been extensively studied (Julliot & Sabatier 1993; Julliot 1996a, b; Feer & Pincebourde 2005).

MATERIALS AND METHODS

Study site

The study was conducted at the Nouragues Research Station (French Guiana, South America), located 100 km south of Cayenne (4°5’N, 52°41’W, alt. 110 m). The station was established in 1986 in a 1000 km² wilderness reserve dominated by tropical

rainforest, from which human activities (hunting included) are prohibited, and without any human settlement for several centuries (Charles-Dominique, 2001). The climate is characterized by a long wet season lasting from December to August, generally interrupted by a short drier period around February or March. The average annual rainfall is 2990 mm and the mean temperature is 26.3°C (Grimaldi & Riéra 2001). Soils are acid ($\text{pH} < 5$) clay-sandy Ferralsols (FAO, 2006) with a micro-aggregate texture of biological origin and a sparsely distributed litter cover (Grimaldi & Riéra 2001). Scarcity of organic matter and phosphorus causes low soil fertility (Vitousek 1984), as is the case for most other tropical rainforest soils (except Amazonian Black Earths).

In the Nouragues area, the rainforest hosts a great diversity of trees, with an average height of 30-35, emergent trees reaching 50 m (Poncy *et al.* 2001). The red howler monkey is the dominant primate species near the research station. It lives in troops (6.3 individuals on average), preferentially feeding on ripe, fleshy fruits, but also on leaves and flowers in the tree canopy, depending on fruit availability (Julliot & Sabatier 1993; Simmen *et al.* 2001). Foraging monkeys travel up to several hundred metres per day within their home range (Julliot 1994, 1996b). They rest or sleep in tree crowns, which may be regularly used for several years, while others are used more erratically (Julliot 1996a). A troop defecates on average 1.5 kg dung per day, mostly after a resting period, scattering dung on the ground over about 10 m², enriching the micro-site with seeds which accumulate in the course of time (Julliot *et al.* 2001).

The local dung beetle community is rich in cohabiting species (79 species known to be attracted by howler monkey dung, F. Feer pers. obs.), which are

specialized according to activity rhythm and dung-processing behaviour (Feer & Pincebourde 2005). Within a few hours, dung beetles, especially tunneller species, bury dung to provision underground feeding and nesting chambers (Feer 1999). Intensive soil bioturbation results from the digging of galleries by large species.

Sampling design

We sampled the topsoil for micromorphological and nutrient analyses in March 2007. Three sleeping sites were selected, which were occupied by howler monkeys during the 2-week field session. The sites were at least 110 m and at most 270 m apart. The middle of each defecation area was visually determined, and was arbitrarily used as the centre from which we selected three sampling plots at each corner of a 3-m-side equilateral triangle, oriented with a corner in north direction. Control areas were arbitrarily selected 15 m east of sleeping sites, outside defecation areas but they were assumed to be under similar vegetation and soil conditions.

At each sampling plot, a block of topsoil (25 cm² surface area x 6 cm depth) was cut with a sharp knife then extracted with as little disturbance as possible. Each humus block was separated into layers (1 cm depth) which were immediately transferred into polypropylene containers filled with 95% ethanol before transport to the laboratory. Care was taken that sampled material completely filled the containers in order to avoid changes in structure resulting from shaking during transport.

A second soil sampling was conducted in June 2008 on the same defecation and control areas for the measurement of pH and respiratory activity. The topsoil (6 cm depth) was dug out with a spade at four randomly selected plots in each area, after litter had been discarded. The four soil samples were then pooled and homogenized in polythene bags (~1 kg) which were transported to the laboratory. Measurement took place in triplicate within three days, during which the soil was kept at ambient temperature.

Micromorphological analysis

All 108 micro-layers (6 per soil block) were optically studied using the ‘small volume’ micromorphological method formerly developed by Bernier & Ponge (1994) then simplified to be combined with multivariate analysis by Sadaka & Ponge (2003), to which reference is made for details. Results from grid-point counting (ca. 200 points) were expressed as the volume percentage of a given class of litter/humus/fauna component. A total of 64 classes of topsoil components were identified (Table 1).

Plant debris was classified into leaves, cuticle/epidermis, petioles/nerves, stem/wood, bark and seeds. Roots and mycorrhizae were separated by colour. Animal faeces and aggregates were classified using size, shape, degree of mixing of mineral and organic matter and state of penetration by roots and when possible they were assigned to animal groups using Bal (1982), Ponge (1991) and Topoliantz *et al.* (2000).

Soil respiration and nutrient content analysis

The measurement of soil respiration was done by infra-red CO₂ analysis (MGA 3000® multi-gas analyser, CEA Instruments Inc., Westwood, NJ) on three aliquots (~300 g) taken from composite samples collected during the second sampling campaign. Samples were put into 5-liter tight-air plastic jars. The jars were sealed then the atmosphere in the jar was pumped and an initial CO₂ concentration was measured immediately (beginning of the incubation). A second measurement was done after 4-hour incubation. Results were expressed as µg CO₂ per g soil per hour.

The measurement of pH was done separately on the three aliquots which had been used previously for respiratory activity. Each aliquot was oven-dried at 60°C during 48h. The measurement of pH was done with a glass electrode according to ISO 10390:2005.

After micromorphological analysis, the alcohol-preserved material was transferred into individual polypropylene jars to be evaporated at ambient temperature during three weeks. Individual layers from the three sampling plots taken in the same site (defecation or control area) were pooled at each depth level then they were sent in dry condition to the National Laboratory of Soil Analysis (INRA, Arras, France). Organic C and total N were determined according to ISO 10694:1995 and ISO 13878:1998, respectively. Available P (Olsen method) was determined according to ISO 11263:1994.

Data analysis

The volume percentages of 64 classes of litter/humus components in the 108 micro-layers investigated were subjected to Redundancy Analysis (Van den Wollenberg 1977) using the three sites, defecation vs. control areas, and the six depth levels as qualitative explanatory (independent) variables. Calculations were performed using XLSTAT® (AddinSoft SARL, Paris, France) under Excel® (Microsoft Corporation, Redmond, WA).

The effects of defecation and depth (and their interaction), as well as site, on topsoil nutrients and microstructures were tested by General Linear Mixed Models (Clayton 1996) using depth (six levels) and defecation (two levels) as fixed factors nested within site and site (three levels) as random factor. The effect of defecation and site on soil pH and respiratory activity was tested by the same method, using defecation as fixed factor (embedded within site) and site as random factor. These models were separately applied to the following response variables: organic C, total N, C/N and available P (first sampling, one replicate per depth per area per site), soil pH and respiratory activity (second sampling, three measurement replicates per depth per area per site). They were also applied to two bulk categories issued from micromorphological analysis and selected for their high indicator value: the proportion of root-penetrated mineral-organic assemblages, obtained by pooling categories 34, 36, 38, 40 and 42 in Table 1 and the proportion of earthworm faeces, obtained by pooling categories 30, 33, 34, 44 and 45 in Table 1 (first sampling, three replicates per depth per area per site). The Gaussian distribution of residuals was verified by Shapiro-Wilk's test for normality (Shapiro and Wilk 1965) previous to analysis. A posteriori comparisons

among means (post-hoc tests) were done by t-tests with Bonferroni correction for simultaneity. GLM calculations were performed using Minitab® 15 (Minitab Inc., State College, PA).

RESULTS

Organic carbon was affected by depth, site and defecation and there was a highly significant interaction between defecation and depth (Fig. 1a). In average there was more carbon in the top 6 cm of control areas compared to defecation areas, but we observed a negative exponential decrease with depth in control areas whereas organic carbon was homogeneously distributed throughout the topsoil in defecation areas. In all three sites there was more carbon in the top two centimetres of control areas compared to defecation areas, while an inverse disposition was observed at deeper levels. A similar interaction between defecation and depth was observed on total nitrogen (Fig. 1b) but the main effect of defecation was not significant. A weaker (while still significant at 0.05 level) interaction effect was observed on the C/N ratio, which decreased with depth in a more pronounced manner in control than in defecation areas (Fig. 1c). The only significant effect of fixed factors (depth and defecation) and their interaction, which could be observed on available phosphorus, was a decrease with depth (Fig. 1d).

A highly significant effect of defecation on pH and soil respiration was observed in the three investigated sites (Figs. 2a, b): both parameters were higher in defecation than in control areas and in average the soil respiration of defecation areas was twice

that of adjoining controls. Although not statistically testable because of a different sampling procedure (C content was measured on 2008 samples while respiration was measured on 2007 samples), a still higher increase (x 3) was observed in defecation areas when the respired CO₂ was calculated per unit of soil carbon (carbon mineralisation rate).

Among the 64 categories used to classify topsoil components, mineral assemblages of unknown origin, with (47) or without (46) roots inside, dominated in both defecation and control areas (Table 1), however variations in the distribution of topsoil components according to site, depth and defecation were revealed by Redundancy Analysis (RDA). Monte-Carlo simulation (500 random permutations of data) showed that the site-depth-defecation matrix explained a highly significant part of this distribution (pseudo-F = 2.03, $P < 0.0001$). Partial RDAs, discarding the effect of site, depth, defecation and their combinations, showed that each of these factors, alone or in combination, had a highly significant explanatory power. Upon lecture of scree plots, only the first three eigen values (4.54, 3.56 and 2.80, respectively), representing 80% of the constrained variation, were kept for bi-plot representation.

The projection of explained and explanatory variables in the space of the first two canonical axes displayed a depth gradient along Axis 1 (Fig. 3a). There was a decreasing rate of change as depth increased, most prominent changes in the distribution of topsoil components occurring from 0-1 to 1-2 cm. Near the surface (positive side of Axis 1) the topsoil was characterized by intact (2, 3, 4, 5) and skeletonised leaves (6), epidermis/cuticles (7) and petioles (8) while quartz particles (52) as well as mineral

aggregates, with (47) and without roots (46), black roots (21) and mineral-organic aggregates with roots (38) predominated at deeper levels (negative side of Axis 1). Axis 2 indicated the discrepancy between sites 1 and 3, site 2 being intermediate. Variations between sites concerned mainly differences in tree species composition which were expressed by the colour of roots, such as orange/red and brown roots (19, 20) in site 3 versus black roots (21) in site 1. Contrary to depth and site effects, expressed by the widely spread distribution of their modalities along Axes 1 and 3, respectively, the defecation effect (Defecation versus Control) did not exhibit any pronounced contribution to the first two canonical axes.

The second bi-plot showed that the defecation effect was better displayed along Axis 3 than along the first two canonical axes (Fig. 3b). Many more categories were projected on the negative (defecation) side of Axis 3 than on its positive (control) side. In particular root nodules (63), brown (20) and black roots (21), enchytraeid faeces (32) and root-penetrated mineral-organic assemblages of all kinds (34, 36, 38, and 42) were better represented in defecation areas (see also Table 1 for a global comparison).

The effect of depth, defecation and their interaction was tested on a gross category (categories 34, 36, 38, 40, 42) summing all assemblages which resulted from the mixing of mineral with organic matter and which were penetrated by roots (Fig. 4a). A defecation effect was prominent, without any significant interaction: in all three sites and at all depth levels, this gross category was better represented in defecation than in control areas. However, the effect was much more pronounced in site 1 than in the other two sites. An increase in the amount of earthworm faeces was observed in defecation

areas, without any interaction with depth. However, this effect was only observed in sites 1 and 3, since earthworm faeces were poorly represented in site 2 (Fig. 4b).

Unprocessed monkey dung (25), dung-beetle balls (26) and dung-beetle faeces (27) were retrieved in one sample taken in the defecation area of site 2 (0-1 cm, rapidly declining with depth). They were absent from all other samples.

DISCUSSION

We showed that the organic matter content of the topsoil decreased abruptly with depth in control areas, while it remained nearly constant in defecation areas where monkey dung had been incorporated to the topsoil by dung-beetles and further processed by soil organisms. This redistribution of organic matter may have consequences for the maintenance of soil biological activity in warm, moist primary forest ecosystems where, to the exception of white sand podzols, the turnover of soil organic matter is very rapid (Stark 1971; Anderson & Swift 1983; Martius *et al.* 2004) and carbon is mainly stocked in the aboveground biomass (Brown & Lugo 1992; Vieira *et al.* 2005). Scarcity of soil fauna (in numbers although not in species) has been reported in tropical rainforests (Petersen & Luxton 1982), as a consequence of a shortage of organic matter rather than of nutrients (Burghouts *et al.* 1992; Tiunov & Scheu 2004). The organic matter which is incorporated by the action of dung-beetles underneath litter (Feer 1999; Andresen & Levey 2004), and is further redistributed by soil engineers such as earthworms, termites and ants (Nye 1955; Wood 1988; Lavelle *et al.* 1993), belongs probably to a labile pool of carbon (Duxbury *et al.* 1989), as ascertained by a C/N ratio remaining high

throughout latrine profiles (Fig. 1c). Thereby it is probable that the incorporated organic matter does not accumulate a long time and needs to be replenished by the recurrent use of the same trees as roosts by monkey troops (Julliot 1996a). This is shown by the higher soil respiration rate in latrines (x 2), still higher when expressed as carbon mineralisation rate (x 3): clearly this indicates a stimulatory effect of incorporated dung on topsoil microbial activity, despite a lower C content. Even though we sampled only the first top 6 cm of the soil we reject the alternative explanation that the observed decrease in the mean content of C and N in latrines was due to a deeper incorporation of dung by dung beetles: even though it is true that bigger species incorporate monkey dung at depths ranging

The evolution of phosphorus does not concur entirely with our first expectation that clumped defecation enriches latrines in nutrients of paramount importance for vegetation (Feeley 2005). We did not register any increase in available phosphorus in latrines compared to control areas, except in site 1 (Fig. 1d) which had been, from the experience of one of us (F. Feer), used frequently for several years by the same troop. We suspect that in tropical environments phosphorus, which is the main limiting factor to plant growth (Dabin 1980; Vitousek 1984), remains only a very short time in a form available to plants, being rapidly taken-up, and needs to be constantly replenished by fresh organic inputs in order to cope with plant requirements (Herrera *et al.* 1978; Adams *et al.* 1989; Tiessen *et al.* 1994).

Although we quantified only C; N and P, the increase in pH observed in red howler monkey latrines (Fig. 2a) suggests an improvement in soil fertility (Härdtle *et al.*

2004) due to nutrient-rich organic inputs when monkeys defecate after a fruit diet (Julliot & Sabatier 1993; Julliot 1996b). The combined effect of increased nutrient availability and abundant soil seed bank (Pouvelle *et al.* 2009) may explain that latrines of the howler monkey exhibit a particularly high seedling biodiversity, among which species with high nutrient requirements such as lianas and pioneer trees (Julliot 1997). A stimulatory effect of clumped defecation on soil microbial community can be also deduced from the observed increase in soil respiration (Martens 1987).

We observed a prominent increase in earthworm faeces in defecation areas of two sites (Fig. 4b). This confirms which had been observed to occur in the course of time when monkey dung was experimentally deposited on the ground then buried by dung-beetles (Pouvelle *et al.* 2008). This result points to the attractiveness of dung towards earthworms, well-known in temperate grasslands (James 1992; Scown & Baker 2006), but here described for the first time in tropical rainforests. Whether previous burial by dung-beetles is needed or not is out of scope of our study, but we may hypothesize that given the absence of anecic earthworms, which were not observed in our sites (J.F. Ponge, personal observation), dung deposited at the ground surface would be out of reach for soil-dwelling earthworms if no burying process existed. Using exclosures preventing the activity of dung beetles we observed that monkey dung remained intact on the soil surface and we noted no recent soil structures indicating an activity of soil fauna.

We also showed that root development within mineral-organic assemblages was favoured in monkey latrines (Fig. 4a). The increased branching of tree roots in organic-

matter-rich micro-sites has been demonstrated in Amazonian rain forests (St. John *et al.* 1983). If we consider that most aggregates found in our soil profiles were old earthworm faeces, which is quite probable for those in which organic matter seems inextricably linked to mineral matter (Lee & Foster 1991), then it ensures that neotropical earthworm faeces, or at least the nutrient-rich drilosphere resulting from their activity, are favourable to root growth, as this has been demonstrated in European lumbricids (Edwards & Lofty 1980; Tomati *et al.* 1988; Canellas *et al.* 2002). This self-reinforcing underground process (Bengtsson *et al.* 1996; Wall & Moore 1999; Brown *et al.* 2000) adds to the positive feedback between monkeys and plants, pointing to an ecosystem-level bootstrapping into which soil organisms could be involved, too (Perry *et al.* 1989; Ponge 2003; Wardle *et al.* 2004).

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Table 1. List of categories used in micromorphological analyses, with their code number and average percent volume in the topsoil (0-6 cm) of defecation and control sites. Values are means ($\pm$ SE) of three defecation or control sites

Code	Variables	Defecation	Control
1	Seedling	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01
2	Orange-yellow leaf	2.41 $\pm$ 0.99	5.57 $\pm$ 0.30
3	Bordeaux red leaf	1.06 $\pm$ 0.47	2.03 $\pm$ 0.69
4	Brown leaf	1.23 $\pm$ 0.51	3.93 $\pm$ 1.00
5	Black leaf	3.05 $\pm$ 1.39	0.97 $\pm$ 0.41
6	Skeletonized leaf	2.54 $\pm$ 0.72	4.15 $\pm$ 1.23
7	Epidermis/cuticle	0.12 $\pm$ 0.01	0.59 $\pm$ 0.13
8	Petiole	0.05 $\pm$ 0.03	0.17 $\pm$ 0.02
9	Wood/twig	3.66 $\pm$ 0.81	4.54 $\pm$ 1.53
10	Bark	1.45 $\pm$ 0.67	2.44 $\pm$ 1.24
11	Flower	0.01 $\pm$ 0.01	0.02 $\pm$ 0.017
12	Fruit/seed	1.84 $\pm$ 0.64	1.00 $\pm$ 0.39
13	Bud	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00
14	Moss	0.00 $\pm$ 0.00	0.03 $\pm$ 0.02
15	Unidentified plant material	1.80 $\pm$ 0.72	1.19 $\pm$ 0.74
16	Mycelial strand	0.06 $\pm$ 0.03	0.09 $\pm$ 0.06
17	White root	0.05 $\pm$ 0.04	0.01 $\pm$ 0.01
18	Yellow root	0.85 $\pm$ 0.20	1.52 $\pm$ 0.26
19	Bordeaux red/orange root	2.89 $\pm$ 2.05	7.41 $\pm$ 2.21
20	Brown root	4.24 $\pm$ 1.41	2.52 $\pm$ 0.58
21	Black root	12.16 $\pm$ 3.25	5.52 $\pm$ 0.56
22	Charred root	0.34 $\pm$ 0.27	0.35 $\pm$ 0.15
23	Root central cylinder	0.33 $\pm$ 0.21	0.06 $\pm$ 0.03
24	Absorbing hair	0.10 $\pm$ 0.04	0.01 $\pm$ 0.01
25	Unprocessed monkey dung	0.36 $\pm$ 0.29	0.00 $\pm$ 0.00
26	Dung-beetle dung ball	0.24 $\pm$ 0.19	0.00 $\pm$ 0.00
27	Dung-beetle faeces	0.14 $\pm$ 0.11	0.00 $\pm$ 0.00
28	Phytophagous insect faeces	0.02 $\pm$ 0.01	0.05 $\pm$ 0.04
29	Organic millipede faeces	0.06 $\pm$ 0.04	0.00 $\pm$ 0.00
30	Organic earthworm faeces	0.25 $\pm$ 0.20	0.00 $\pm$ 0.00
31	Unidentified organic faeces	0.02 $\pm$ 0.01	0.03 $\pm$ 0.02
32	Enchytraeid mineral-organic faeces	0.26 $\pm$ 0.11	0.01 $\pm$ 0.01
33	Mineral-organic earthworm faeces without roots	0.06 $\pm$ 0.03	0.18 $\pm$ 0.14
34	Mineral-organic earthworm faeces with roots	0.15 $\pm$ 0.13	0.03 $\pm$ 0.02
35	Unidentified mineral-organic faeces without roots	0.00 $\pm$ 0.00	0.01 $\pm$ 0.01
36	Unidentified mineral-organic faeces with roots	0.53 $\pm$ 0.43	0.00 $\pm$ 0.00
37	Mineral-organic aggregate without roots	3.28 $\pm$ 0.70	2.37 $\pm$ 1.13
38	Mineral-organic aggregate with roots	9.31 $\pm$ 4.74	2.52 $\pm$ 0.95
39	Charred mineral-organic aggregate without roots	0.04 $\pm$ 0.03	0.04 $\pm$ 0.01
40	Charred mineral-organic aggregate with roots	0.00 $\pm$ 0.00	0.02 $\pm$ 0.01
41	Mixed mineral-organic aggregate without roots	0.46 $\pm$ 0.37	0.15 $\pm$ 0.12
42	Mixed mineral-organic aggregate with roots	0.91 $\pm$ 0.73	0.40 $\pm$ 0.33
43	Mineral-organic aggregate with dung-beetle faeces	0.02 $\pm$ 0.01	0.00 $\pm$ 0.00
44	Mineral earthworm faeces without roots	0.31 $\pm$ 0.20	0.07 $\pm$ 0.05
45	Mineral earthworm faeces with roots	0.19 $\pm$ 0.13	0.01 $\pm$ 0.01
46	Mineral aggregate without roots	16.79 $\pm$ 4.38	24.26 $\pm$ 4.03
47	Mineral aggregate with roots	14.27 $\pm$ 1.43	17.99 $\pm$ 1.52
48	Mineral aggregate with dung-beetle faeces	0.33 $\pm$ 0.26	0.00 $\pm$ 0.00
49	Mineral aggregate with monkey dung	0.04 $\pm$ 0.03	0.00 $\pm$ 0.00
50	Charred mineral aggregate without roots	0.12 $\pm$ 0.10	0.31 $\pm$ 0.13
51	Charred mineral aggregate with roots	0.13 $\pm$ 0.11	0.22 $\pm$ 0.09
52	Quartz particle	6.23 $\pm$ 0.19	6.06 $\pm$ 0.31
53	Laterite particle	0.82 $\pm$ 0.52	0.17 $\pm$ 0.08
54	Other mineral particle	0.34 $\pm$ 0.27	0.01 $\pm$ 0.01
55	Centipede/Millipede	0.00 $\pm$ 0.00	0.03 $\pm$ 0.01
56	Termite	0.02 $\pm$ 0.01	0.00 $\pm$ 0.00
57	Unidentified arthropod	0.01 $\pm$ 0.01	0.02 $\pm$ 0.01
58	Arthropod cuticle	0.06 $\pm$ 0.03	0.04 $\pm$ 0.01
59	Insect wing	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00
60	Enchytraeid	0.15 $\pm$ 0.10	0.01 $\pm$ 0.01
61	Earthworm	0.06 $\pm$ 0.04	0.04 $\pm$ 0.02
62	Egg/cocoon/pupa	0.01 $\pm$ 0.01	0.01 $\pm$ 0.01
63	Root nodule	3.71 $\pm$ 2.04	0.78 $\pm$ 0.53
64	Miscellaneous	0.03 $\pm$ 0.02	0.06 $\pm$ 0.01

Figure legends

Figure 1. Vertical distribution of organic carbon (a), total nitrogen (b), C/N (c) and available (Olsen) phosphorus (d) in the topsoil (0-6 cm) of three defecation areas of the red howler monkey (full line) and their control areas (dotted lines). Results of GLMM analyses are indicated within windows. Fixed effects are printed in roman and random effects in italic type

Figure 2. Variation in pH (a) and soil respiratory activity (b) of the topsoil (0-6 cm) in three defecation areas of the red howler monkey (full bars) and nearby control areas (empty bars). Error bars indicate standard errors of means (3 replicate measures). Results of GLMM analyses are indicated within windows. Fixed effects are printed in roman and random effects in italic type

Figure 3. Redundancy Analysis (RDA) biplots of 64 micromorphological categories in volume percent (dependent variables, indicated by their code number as in Table 1) and 11 independent qualitative variables (3 sites, 2 areas per site, 6 depth levels) indicated by vectors. Projection in the space of Axes 1-2 (a) and Axes 1-3 (b)

Figure 4. Vertical distribution of root-penetrated mineral-organic assemblages (a) and earthworm faeces (b) in the topsoil of defecation and control areas of the three sites investigated. Results of GLMM analyses are indicated within windows. Fixed effects are printed in roman and random effects in italic type

Fig. 1

Fig. 2

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683 Fig. 4