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

3

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9

10 **Short running title:** red howler latrines and topsoil components

11

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

32

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

34

35 **INTRODUCTION**

36

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 al.*
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 al.*
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

60 1999; Andresen 2002b). The monkeys are at the origin of a unidirectional flow of dung
61 resource processed by downstream specialized consumers. This ‘processing chain
62 commensalism’ in the sense of Heard (1994) may be severely disturbed by habitat
63 modification and fragmentation (Nichols *et al.* 2007) and by human impacts on
64 mammal communities (Estrada *et al.* 1999; Vulinec 2000).

65

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

76

77 **MATERIALS AND METHODS**

78

79 **Study site**

80

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

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

93

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

105

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

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

112

113 **Sampling design**

114

115 We sampled the topsoil for micromorphological and nutrient analyses in March 2007.
116 Three sleeping sites were selected, which were occupied by howler monkeys during the
117 2-week field session. The sites were at least 110 m and at most 270 m apart. The middle
118 of each defecation area was visually determined, and was arbitrarily used as the centre
119 from which we selected three sampling plots at each corner of a 3-m-side equilateral
120 triangle, oriented with a corner in north direction. Control areas were arbitrarily selected
121 15 m east of sleeping sites, outside defecation areas but they were assumed to be under
122 similar vegetation and soil conditions.

123

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

130

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

138

139 **Micromorphological analysis**

140

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

147

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

153

154 **Soil respiration and nutrient content analysis**

155

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

163

164 The measurement of pH was done separately on the three aliquots which had
165 been used previously for respiratory activity. Each aliquot was oven-dried at 60°C
166 during 48h. The measurement of pH was done with a glass electrode according to ISO
167 10390:2005.

168

169 After micromorphological analysis, the alcohol-preserved material was
170 transferred into individual polypropylene jars to be evaporated at ambient temperature
171 during three weeks. Individual layers from the three sampling plots taken in the same
172 site (defecation or control area) were pooled at each depth level then they were sent in
173 dry condition to the National Laboratory of Soil Analysis (INRA, Arras, France).
174 Organic C and total N were determined according to ISO 10694:1995 and ISO
175 13878:1998, respectively. Available P (Olsen method) was determined according to
176 ISO 11263:1994.

177

178 **Data analysis**

179

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

186

187 The effects of defecation and depth (and their interaction), as well as site, on
188 topsoil nutrients and microstructures were tested by General Linear Mixed Models
189 (Clayton 1996) using depth (six levels) and defecation (two levels) as fixed factors
190 nested within site and site (three levels) as random factor. The effect of defecation and
191 site on soil pH and respiratory activity was tested by the same method, using defecation
192 as fixed factor (embedded within site) and site as random factor. These models were
193 separately applied to the following response variables: organic C, total N, C/N and
194 available P (first sampling, one replicate per depth per area per site), soil pH and
195 respiratory activity (second sampling, three measurement replicates per depth per area
196 per site). They were also applied to two bulk categories issued from
197 micromorphological analysis and selected for their high indicator value: the proportion
198 of root-penetrated mineral-organic assemblages, obtained by pooling categories 34, 36,
199 38, 40 and 42 in Table 1 and the proportion of earthworm faeces, obtained by pooling
200 categories 30, 33, 34, 44 and 45 in Table 1 (first sampling, three replicates per depth per
201 area per site). The Gaussian distribution of residuals was verified by Shapiro-Wilk's test
202 for normality (Shapiro and Wilk 1965) previous to analysis. A posteriori comparisons

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

206

207 **RESULTS**

208

209 Organic carbon was affected by depth, site and defecation and there was a highly
210 significant interaction between defecation and depth (Fig. 1a). In average there was
211 more carbon in the top 6 cm of control areas compared to defecation areas, but we
212 observed a negative exponential decrease with depth in control areas whereas organic
213 carbon was homogeneously distributed throughout the topsoil in defecation areas. In all
214 three sites there was more carbon in the top two centimetres of control areas compared
215 to defecation areas, while an inverse disposition was observed at deeper levels. A
216 similar interaction between defecation and depth was observed on total nitrogen (Fig.
217 1b) but the main effect of defecation was not significant. A weaker (while still
218 significant at 0.05 level) interaction effect was observed on the C/N ratio, which
219 decreased with depth in a more pronounced manner in control than in defecation areas
220 (Fig. 1c). The only significant effect of fixed factors (depth and defecation) and their
221 interaction, which could be observed on available phosphorus, was a decrease with
222 depth (Fig. 1d).

223

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

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

232

233 Among the 64 categories used to classify topsoil components, mineral
234 assemblages of unknown origin, with (47) or without (46) roots inside, dominated in
235 both defecation and control areas (Table 1), however variations in the distribution of
236 topsoil components according to site, depth and defecation were revealed by
237 Redundancy Analysis (RDA). Monte-Carlo simulation (500 random permutations of
238 data) showed that the site-depth-defecation matrix explained a highly significant part of
239 this distribution (pseudo-F = 2.03, P < 0.0001). Partial RDAs, discarding the effect of
240 site, depth, defecation and their combinations, showed that each of these factors, alone
241 or in combination, had a highly significant explanatory power. Upon lecture of scree
242 plots, only the first three eigen values (4.54, 3.56 and 2.80, respectively), representing
243 80% of the constrained variation, were kept for bi-plot representation.

244

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

251 aggregates, with (47) and without roots (46), black roots (21) and mineral-organic
252 aggregates with roots (38) predominated at deeper levels (negative side of Axis 1). Axis
253 2 indicated the discrepancy between sites 1 and 3, site 2 being intermediate. Variations
254 between sites concerned mainly differences in tree species composition which were
255 expressed by the colour of roots, such as orange/red and brown roots (19, 20) in site 3
256 versus black roots (21) in site 1. Contrary to depth and site effects, expressed by the
257 widely spread distribution of their modalities along Axes 1 and 3, respectively, the
258 defecation effect (Defecation versus Control) did not exhibit any pronounced
259 contribution to the first two canonical axes.

260

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

267

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

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

277

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

281

282 **DISCUSSION**

283

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

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

309

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

320

321 Although we quantified only C; N and P, the increase in pH observed in red
322 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).

330

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.

344

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-

347 matter-rich micro-sites has been demonstrated in Amazonian rain forests (St. John *et al.*
348 1983). If we consider that most aggregates found in our soil profiles were old
349 earthworm faeces, which is quite probable for those in which organic matter seems
350 inextricably linked to mineral matter (Lee & Foster 1991), then it ensures that
351 neotropical earthworm faeces, or at least the nutrient-rich drilosphere resulting from
352 their activity, are favourable to root growth, as this has been demonstrated in European
353 lumbricids (Edwards & Lofty 1980; Tomati *et al.* 1988; Canellas *et al.* 2002). This self-
354 reinforcing underground process (Bengtsson *et al.* 1996; Wall & Moore 1999; Brown *et*
355 *al.* 2000) adds to the positive feedback between monkeys and plants, pointing to an
356 ecosystem-level bootstrapping into which soil organisms could be involved, too (Perry
357 *et al.* 1989; Ponge 2003; Wardle *et al.* 2004).

358

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364

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647

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

649 **Figure legends**

650

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

656

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

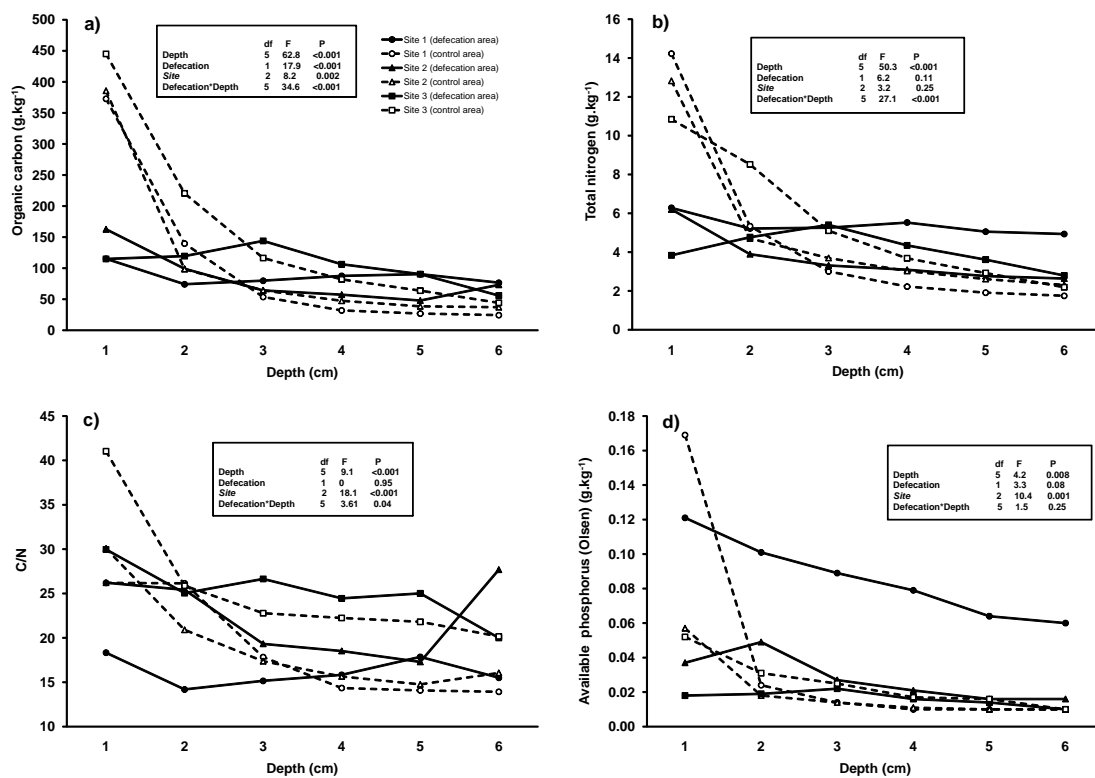
662

663 **Figure 3.** Redundancy Analysis (RDA) biplots of 64 micromorphological categories in
664 volume percent (dependent variables, indicated by their code number as in Table
665 1) and 11 independent qualitative variables (3 sites, 2 areas per site, 6 depth
666 levels) indicated by vectors. Projection in the space of Axes 1-2 (a) and Axes 1-
667 3 (b)

668

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

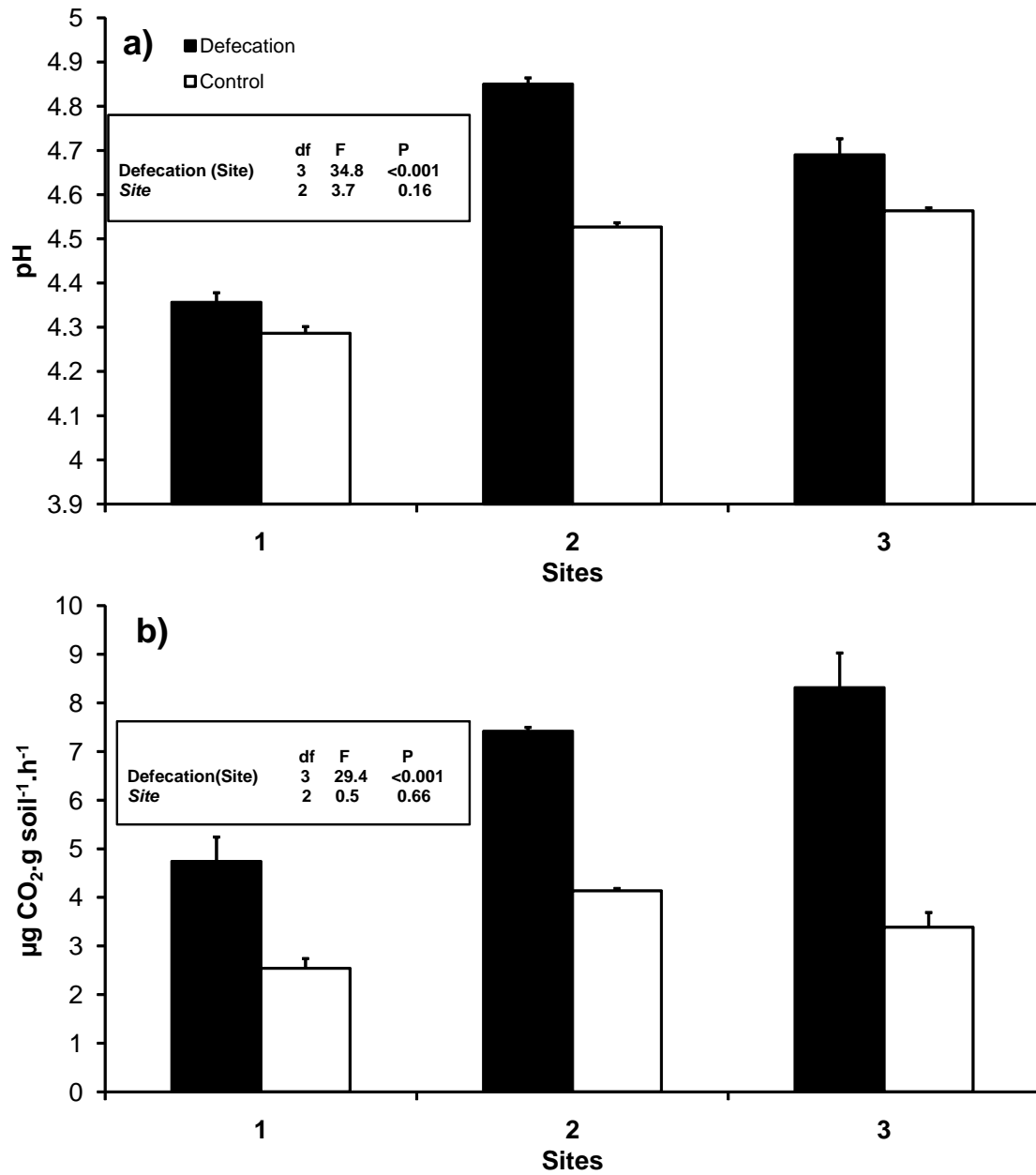
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675 Fig. 1

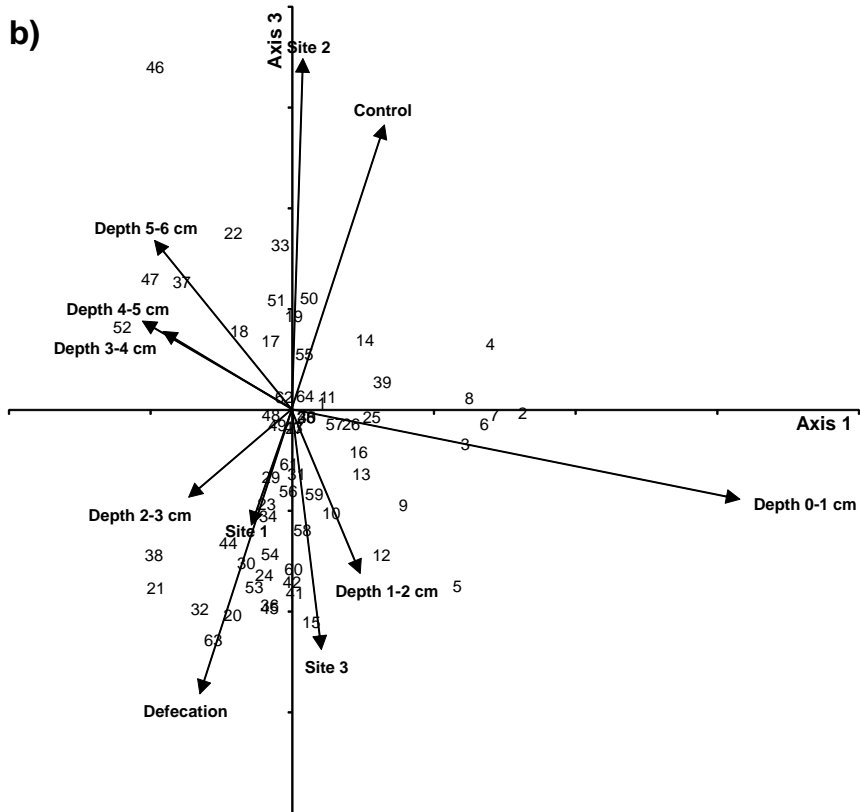
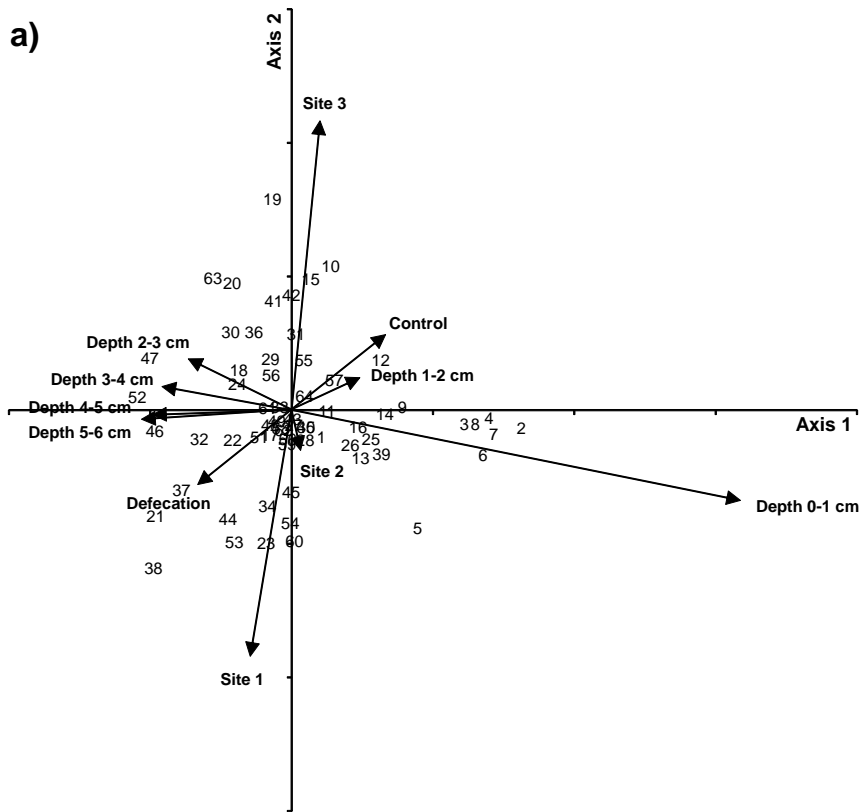
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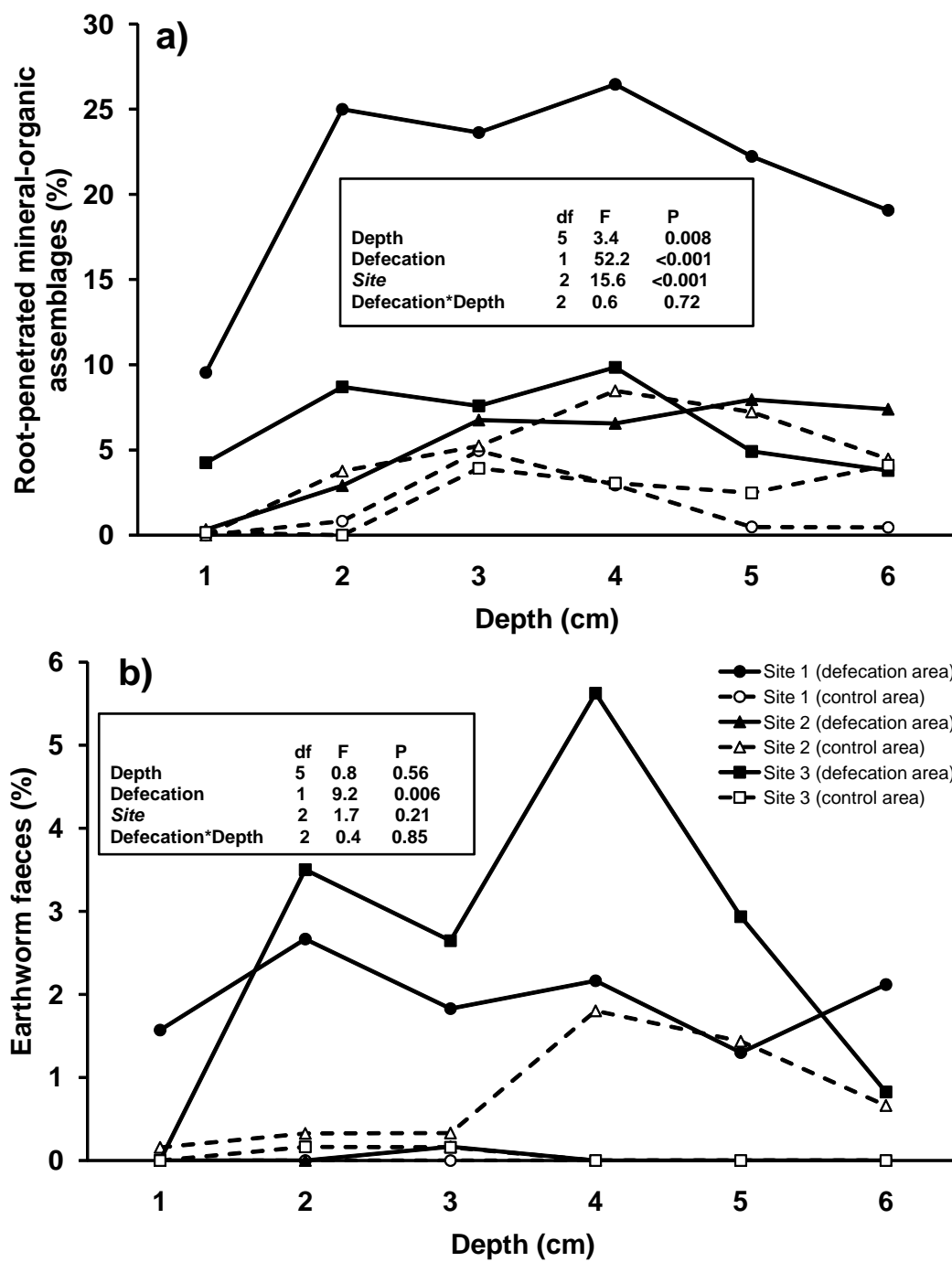
678 Fig. 2

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680

681 Fig. 3



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683 Fig. 4