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### ► To cite this version:

Pascal Jouquet, Floriane Jamoteau, Sabyasachi Majumdar, Pascal Podwojewski, Prakash Nagabovanalli, et al.. The distribution of Silicon in soil is influenced by termite bioturbation in South Indian forest soils. *Geoderma*, 2020, 372, pp.114362. 10.1016/j.geoderma.2020.114362 . hal-02955560

**HAL Id: hal-02955560**

**<https://hal.science/hal-02955560v1>**

Submitted on 2 Oct 2020

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1 The distribution of Silicon in soil is influenced by termite bioturbation in South  
2 Indian forest soils

3

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20

21 **ABSTRACT**

22 Si is one of the most abundant element on earth and an abundant literature shows its beneficial  
23 effects on plant growth and resistance. We here question the influence of termites, as key soil  
24 bioturbators, on the distribution of Si in a tropical soil. The abundance and forms of Si in termite  
25 mounds build by *Odontotermes obesus* (TM) or in the soil eroded from TM but redistributed  
26 on the ground surface (EROD) were compared to those measured in the 0-5 (Ctrl<sub>0-5</sub>) and 70-  
27 120 cm soil layers (Ctrl<sub>70-120</sub>). Although termites use the soil from Ctrl<sub>70-120</sub> for building their  
28 mounds, we found that TM and EROD had intermediate soil physical, chemical and  
29 mineralogical properties between Ctrl<sub>0-5</sub> and Ctrl<sub>70-120</sub>. Clay content was not significantly  
30 different between soil materials. However, the lower variability measured in TM than in the  
31 soil suggested that termites used soil layers with higher amounts of clay fraction and with a  
32 preference especially for layers enriched in 2:1 clay minerals (smectite) most likely because  
33 they provide better physical properties in terms of plasticity and water retention than kaolinite.  
34 Finally, phytoliths and bioavailable Si (Si<sub>CC</sub>) contents were increased in TM in comparison with  
35 Ctrl<sub>70-120</sub>, suggesting an incorporation of phytoliths in termite construction through their saliva  
36 and/or an increasing availability of Si<sub>CC</sub> from the minerals. In conclusion, this study highlights  
37 how termites, through their feeding and building activities, impact Si distribution in tropical  
38 soils.

39

40

41 *Keywords:* Si, clay, mineralogy, phytoliths, bioturbation, soil profile

42 **1. Introduction**

43 Silicon (Si) is the second most abundant element in the earth's crust after oxygen, with  
44 approximately 28 and 47% of its mass, respectively (Singer and Munns, 1999). It is not included  
45 in the list of elements essential for plants but there is an abundant literature showing its  
46 beneficial effects on the resistance of plants to parasites and drought (Liang et al., 2015; Datnoff  
47 et al., 2001).

48 In soil Si is a major constituent of parent rock minerals (such as quartz, feldspars) and  
49 of secondary minerals originated from pedogenesis, such as clay minerals and amorphous silica.  
50 Biogenic amorphous silica particles can also be found in soil as plant and microorganism  
51 remains, i.e., phytoliths (Cornelis and Delvaux, 2016) and diatom frustules or thecamoebian  
52 tests (Sommer et al., 2006). These amorphous silica particles can play an important role in the  
53 cycling of Si because they constitute a pool of highly reactive silica (Frayse et al., 2009). Large  
54 fauna like grazers can also affect the cycling of Si through the accelerating transfer of plant Si  
55 to aquatic environments (Schoelynck et al., 2019) or through the increase production of  
56 biogenic silica (Melzer et al., 2010). The amount and quality of the different Si pools vary also  
57 with soil depth. Soil horizons are usually identified by different clay contents and minerals  
58 while phytoliths are usually concentrated in the topsoil and their content rapidly decreases with  
59 depth (Alexandre et al., 1997). The pool of Si extracted by 0.01 M CaCl<sub>2</sub> (Si<sub>CC</sub>) is used to  
60 estimate the Si immediately available for plants (Haysom and Chapman, 1975). The distribution  
61 of Si<sub>CC</sub> along soil profile may increase with depth and be associated with the clay fraction  
62 (Vandevenne et al., 2015). Another pool considered bioavailable for plant is the pool of Si  
63 adsorbed on the surface of minerals estimated by 0.05 M acetic acid extraction (Si<sub>AA</sub>) (Sauer et  
64 al., 2006). Si<sub>AA</sub> seems to be controlled by oxides and clay minerals and may also increase with  
65 depth (Cornelis et al., 2011 PLSO; Vandevenne et al., 2015). Surprisingly and despite their  
66 importance in the cycling of nutrients, the impact of soil macrofauna on Si dynamic has been  
67 poorly documented, with the exception of a recent article focusing on earthworms (Georgiadis

68 *et al.*, 2019), and there is a dearth of information on how soil macrofauna impacts clay  
69 mineralogy and the availability of Si for plants.

70 Amongst the soil macrofauna, organisms from the soil engineering group (*sensu* Lavelle  
71 *et al.*, 1997) impact soil functioning at different spatial and temporal scales (Bottinelli *et al.*,  
72 2015). This role is played by termites in tropical dryland ecosystems, and especially by termites  
73 from the fungus-growing functional group (Macrotermitinae subfamily) in Africa and Asia  
74 (Jouquet *et al.*, 2016). Termites are key decomposers of the litter in tropical environments  
75 (Amadou Issoufou *et al.*, 2019) and their building activity is associated to the redistribution of  
76 soil organic matter and elements in their biomass and organo-mineral constructions. Studies  
77 carried out in Africa and Asia showed that fungus-growing termites impact the distribution, the  
78 type of clay minerals (kaolinite vs. smectite) and the mineralogical properties of phyllosilicates  
79 (Jouquet *et al.*, 2002, 2007). Termites are also known to impact the dynamic of Si at the profile  
80 scale through the selective use of material coming from the deep soil layers within their nests,  
81 then resulting in the redistribution of clay minerals and elements (Holt and Lepage, 2000; Abe  
82 *et al.*, 2012; Mujinya *et al.*, 2010, 2011, 2013; Erens *et al.*, 2015). However, the depth at which  
83 termites fetch the clay particles remains mostly unknown and termite bioturbation and the  
84 upward translocation of soil from the deeper layers to the surface are likely to be associated  
85 with a redistribution of Si<sub>CC</sub> and Si<sub>AA</sub> pools in termite mounds and thereafter in the surrounding  
86 soil environment with the erosion of termite mounds.

87 In Southern India, the termite species *Odontotermes obesus* is known to play an  
88 important role in the decomposition of litter (Shanbhag and Sundararaj, 2013) and its mounds  
89 are conspicuous features of the landscapes (Shanbhag *et al.*, 2017). These mounds are especially  
90 abundant in protected areas such as in the deciduous forests of the Bandipur Tiger Reserve. In  
91 this environment termite mounds have specific soil physical and chemical properties (Jouquet  
92 *et al.*, 2017a) and a recent study showed that they are mainly made of soil collected between 70

93 to 120 cm depth (Jouquet et al., 2017b). The aim of this study was therefore to determine the  
94 impact of *O. obesus* bioturbation on the distribution of Si in soil. Our hypothesis was that  
95 termite feeding and building activities (i.e., the construction of mounds from material selected  
96 in the deep soil layers) participate in a selective redistribution of clay minerals, phytoliths and  
97 available Si ( $Si_{CC}$ ), which are thereafter redistributed to the soil surface.

98

## 99 **Material and Methods**

### 100 *Study site*

101 Soils were sampled in the Mule Hole experimental watershed (4.1 km<sup>2</sup>). This dry deciduous  
102 forest is located in the Bandipur Tiger reserve in Southern India at 11°44'N and 76°26'E  
103 (Chamarajanagar district, Karnataka state). The Mule Hole watershed is located in the sub-  
104 humid zone of the sharp climatic gradient induced by the Western Ghats. As a result of the  
105 short-term variability of the South-West Monsoon, the experimental watershed is characterized  
106 by rainfall ranging from 1000 to 1500 mm yr<sup>-1</sup>, usually concentrated during the monsoon from  
107 June to August and from October to November. The mean annual temperature is 27°C (Braun  
108 et al., 2009). The elevation of the watershed ranges from 820 to 910 m a.s.l. The relief is mostly  
109 undulating with gentle slopes. The soil cover of the watershed has been mapped by Barbiero et  
110 al. (2007) based on the FAO terminology (IUSS-Working-Group-WRB, 2015). Parent rocks  
111 consist of peninsular gneiss intermingled with much less abundant mafic to ultramafic rocks,  
112 mostly amphibolite. Soil depth is variable but ranging from 1 to 3 m in average (Barbiero et al.,  
113 2007; Braun et al., 2009). The main soil types are Ferralsols and Chromic Luvisols, with clay  
114 mineralogy dominated by kaolinite (1:1 clay) and characterized by an accumulation of iron and  
115 aluminum oxides. The soils have less than 20 g kg<sup>-1</sup> of C in the first soil layer and < 10 g kg<sup>-1</sup>  
116 below 20 cm depth. The clay content ranges from 30 to 40% and clays minerals are also  
117 dominated by 1:1 clays (kaolinite) (Jouquet et al., 2016b). The vegetation is a dry deciduous  
118 forest. In this environment, cathedral-shaped termite mounds are built by *O. obesus* (Chhotani

119 and Bose, 1979; Jouquet et al., 2016a,b, 2017a) (Figure 1). The soil of termite mounds has  
120 similar clay contents but it is impoverished in C (0.54-fold) in comparison with the surrounding  
121 topsoil (Jouquet et al., 2016, 2017a,b).

122

### 123 *Soil sampling*

124 Termite mounds built by *O. obesus* vary considerably in size (Shanbhag et al., 2017) and only  
125 large mounds from 1.5 to 1.8 m high and  $> 0.5 \text{ m}^3$  were considered in this study. Samples were  
126 collected from the outer-wall of three termite mounds (TM) and from their periphery in a  
127 distance of about 15 cm (impacted by mound erosion, EROD). Soils were also sampled in the  
128 surrounding soil environment (control) in a distance  $> 5\text{--}10$  m ahead of the mounds in taking  
129 into account the gentle slope of the watershed (not impacted by mound erosion) at several soil  
130 depths down to 4.0 m in three different locations ( $n = 39$ ). Data were grouped according to  
131 their depths (Ctrl<sub>0-5</sub>: 0–5 cm, Ctrl<sub>70-120</sub>: 70-120 cm) with the assumption that termites collect the  
132 soil mainly from the 70-120 cm soil layer for building their mounds (Jouquet et al., 2017b).

133

### 134 *Analysis of soil properties*

135 The soil physical properties measured included the particle-size distribution, after destruction  
136 of organic matter and dispersion with sodium hexametaphosphate (AFNOR, NFX 31 107): clay  
137 ( $< 2 \mu\text{m}$ ) and silt (2–50  $\mu\text{m}$ ) were obtained by pipette method and sand (50–2000  $\mu\text{m}$ ) by  
138 sieving. To assess Soil Organic Matter (SOM) content, the C and N concentrations were  
139 measured using an elemental analyzer Flash 2000 HT. The cationic exchange capacity and the  
140 content of exchangeable cations (Ca, Mg, Na, K, Fe, Mn and Al) were determined at soil pH  
141 by exchange with cobaltihexamine (AFNOR, NF ISO 23470). The amount of  $\text{SiO}_2$ ,  $\text{Fe}_2\text{O}_3$  and  
142  $\text{Al}_2\text{O}_3$  were measured by ICP-OES after fusion with lithium metaborate  $\text{LiBO}_2$  and subsequent  
143 dissolution in a mixture of  $\text{HNO}_3$  (1 mol L<sup>-1</sup>),  $\text{H}_2\text{O}_2$  (0.5 % v/v) and glycerol (10 % v / v) at the

144 CNRS Service d'Analyse des Roches et des Minéraux (SARM) (Carignan et al., 2001). All  
145 these analyses were carried out on soil aggregates >2 mm that were ground before analyses to  
146 homogenize the material.

147

#### 148 *Si pools and phytoliths*

149 Plant available Si was measured in comparing the pools of readily soluble Si extracted by 0.01  
150 M CaCl<sub>2</sub> (Si<sub>CC</sub>, Haysom and Chapman, 1975) and the pool of adsorbed Si extracted by 0.5 M  
151 acetate-acetic acid (Si<sub>AA</sub>, Korndörfer and Lepsch, 2001; Narayanaswamy and Prakash, 2009,  
152 2010). Phytoliths were extracted using HCl (33%) to remove carbonates, 2/3 nitric plus 1/3  
153 perchloric acid to remove organic matter. Soil clays were removed by repeated decantations,  
154 and separation of biogenic silica particles from heavy minerals was achieved by densimetric  
155 separation using ZnBr<sub>2</sub> set at  $d = 2.3 \text{ g cm}^{-3}$ . The extracts were weighted and phytoliths were  
156 mounted on slides for observation under optical microscope. More than 250 phytoliths were  
157 counted per sample. Morphotypes with clear taxonomical identification were silica short cell  
158 phytoliths (rondel, bilobate, polylobate and cross) from Poaceae (grasses), spheroid psilate and  
159 decorated from woody dicotyledons (considered forest indicator phytoliths), and spheroid  
160 echinate from Arecaceae (palms). Other phytoliths included bulliform flabellate, acute bulbosus  
161 (silicified hair cells), and various elongate and blocky morphotypes which were mostly non-  
162 diagnostic (International Code for Phytolith Nomenclature, 2019). The ratio of spheroid  
163 decorated versus the sum of grass silica short cells (or D/P° index) increases with the increasing  
164 abundance of trees and shrubs versus grasses and is commonly used to trace the tropical  
165 forest/savanna boundary (Bremond et al. 2008). On the same slides, but in a separate counting  
166 session we measured the proportion of corroded vs. plain phytoliths to identify the origin of  
167 phytoliths with the assumption that phytoliths at depth likely underwent prolonged dissolution



168 than the more recent phytoliths located at the soil surface following Sommer et al. (2006).

169 Phytoliths relative abundance were calculated based on the total phytolith sums.

170

171 *Clay mineralogy*

172 Clay mineralogy from termite mound soil samples (TM and EROD) was compared to the  
173 mineralogy of the soil at 0-5 and 70-120 cm depths (Ctrl<sub>0-5</sub> and Ctrl<sub>70-120</sub>) (n = 3 per treatments).

174 Clay mineralogy was determined after extraction of the clay size fraction (particles < 2 µm)

175 from the bulk soil samples. The fractions < 50 µm were obtained by wet sieving and then

176 dispersed into 1 mol L<sup>-1</sup> NaCl (five saturations) and ultrasonication. The < 2 µm fractions were

177 obtained by sedimentation and were subsequently flocculated and saturated with 0.5 mol L<sup>-1</sup>

178 CaCl<sub>2</sub> (Caner et al., 2014). XRD patterns of oriented preparations were recorded in the air-dried

179 state (Ca-AD) and after saturation with ethylene glycol (Ca-EG) to identify the clay minerals

180 (Caner et al., 2014). Since no additional information was obtained from the saturation with

181 ethylene-glycol, only results from the Ca-AD preparation was shown. The X-Ray diffraction

182 patterns were decomposed into elementary peaks (Lanson, 1997) using Fityk software over the

183 3-14°2θ range. The procedure included removal of baseline and decomposition of the signal

184 into Gaussian elementary curves. The diffractograms were fitted with the minimum curves to

185 obtain a reliable fit of the experimental pattern. The parameters of the elementary curves

186 (position, full-width at half maximum – FWHM and maximum intensity, surface area) were

187 used to identify the soil clay mineral (kaolinite, illite, smectite, mixed layers illite/smectite)

188 species according to Righi et al. (1995) and Velde (2001). A semi-quantitative phase analysis

189 was performed using the relative surface peak area of each peak of clay minerals over the sum

190 of the peak surface areas. The relative surface peak area of each peak does not correspond to

191 the proportion of the respective mineral, however, the variations of relative surface areas

192 correspond to variations in mineral quantities if the samples comes from the same sequence

193 (Lanson 1997). Peaks at  $\sim 7.20$  and  $7.30\text{-}7.40$  Å were attributed to kaolinite (K). The peak of  
194 illite at  $\sim 10$  Å was decomposed into well crystallized illite (WCI) at  $10.0$  Å and poorly  
195 crystallized illite (PCI) at  $10.2\text{-}10.4$  Å. The peaks at  $\sim 15$  Å in AD state that displace to  $\sim 17$  Å  
196 were attributed to smectite (S) and the peaks between  $10$  and  $15$  Å in AD state that displaced  
197 between  $10$  and  $17$  Å in EG were attributed to mixed layers illite/smectite with variable  
198 proportion of the two components.

199

### 200 *Statistical analyses*

201 Residues were tested for normality of variance using the Shapiro–Wilk test and  $\log_{10}$ -  
202 transformed if required. Soil chemical and physical properties were analyzed by analysis of  
203 variance (ANOVA) with treatments as independent variables. LSD tests were then performed  
204 to assess differences between means. Post-hoc planned pairwise comparisons were performed  
205 by Wilcoxon–Mann–Whitney U tests when parametric ANOVA were impossible to use, even  
206 after data transformation. Impact of the treatments on soil variables and soil mineralogy were  
207 analyzed using a principal component analysis (PCA). Correlations between variables and the  
208 amount in  $\text{Si}_{\text{CC}}$ ,  $\text{Si}_{\text{AA}}$  and phytoliths were carried out using the spearman test. 95% confidence  
209 intervals associated to the percentages in phytoliths and 99% confidence intervals associated  
210 with the  $\text{D}/\text{P}^{\circ}$  ratios were calculated following Suchéras-Marx et al. (2019). All statistical  
211 parameters were calculated using R studio and R version 3.2.1 with ade4, factoextra,  
212 factoMineR and corrplot packages. Differences among treatments were declared significant at  
213 the 0.05 probability level.

214

## 215 **Results**

### 216 *Difference in soil chemical and physical properties*

217 The chemical properties of the 4 soil materials are shown in Table 1 and a PCA-projection of  
218 the samples from significant variables is shown in Figure 1. Soil materials were mainly

219 differentiated along the first axis while the variability within the samples was evidenced on the  
220 second axis, which explained 63.0 and 18.5% of the total variability, respectively. Samples  
221 varied from the soil surface (Ctrl<sub>0-5</sub>) to TM, EROD and finally Ctrl<sub>70-120</sub>. No significant  
222 difference in soil particle size fractions, in pH and in exchangeable Mg<sup>2+</sup> and K<sup>+</sup> contents could  
223 be measured between the four soil materials ( $P > 0.05$  in all cases) (Table 1). Ctrl<sub>0-5</sub> was  
224 enriched in C and N and characterized by a greater CEC and exchangeable Ca<sup>2+</sup> content but  
225 lower exchangeable Al<sup>3+</sup> content in comparison with the other treatments. Conversely, Ctrl<sub>70-</sub>  
226 <sub>120</sub> were impoverished in C and N but enriched in exchangeable Na<sup>+</sup>, Al<sub>2</sub>O<sub>3</sub> and Fe<sub>2</sub>O<sub>3</sub> in  
227 comparison with the other soil materials. In general, TM and EROD had intermediate properties  
228 in comparison with the Ctrl<sub>0-5</sub> and Ctrl<sub>70-120</sub> (Figure 1) and no significant difference occurred  
229 between them, with the exception of the concentration in exchangeable Mn<sup>2+</sup> that was similar  
230 in TM and Ctrl<sub>70-120</sub> but higher than in EROD and Ctrl<sub>0-5</sub> ( $P > 0.05$  between them, Table 1).  
231 Figure 2 shows the evolution of clay content in TM and EROD and at different soil depths. The  
232 amount of clay was highly variable (e.g. from < 10 to > 50% at 150 cm depth), especially in  
233 comparison with the clay content in TM and EROD. Despite this high variability, an increase  
234 in clay content was measured at about 50-150 cm depth.

235

### 236 *Si pools and phytoliths*

237 Figure 3 shows that the proportion of SiO<sub>2</sub> and the amount of Si<sub>CC</sub> were the lowest in Ctrl<sub>70-120</sub>,  
238 without any significant difference between the other treatments ( $P > 0.05$ ). Conversely Si<sub>AA</sub>  
239 content was the highest in Ctrl<sub>70-120</sub> and the lowest in Ctrl<sub>0-5</sub> while TM and EROD had  
240 intermediate positions. The proportion of phytoliths was low with percentages < 1%. The  
241 highest value was measured in Ctrl<sub>0-5</sub> in comparison with Ctrl<sub>70-120</sub> and TM ( $P < 0.05$  in both  
242 cases). Conversely, the lowest value was measured in Ctrl<sub>70-120</sub> in comparison with Ctrl<sub>0-5</sub> and  
243 EROD ( $P < 0.05$  in both cases). TM and EROD had a similar percentage of phytoliths with

244 intermediate values in comparison with the two control soils.  $Si_{CC}$  was not correlated with the  
245 soil physical and chemical properties, with the exception of a positive correlation with  
246 phytoliths ( $P = 0.028$ ) and  $Mg^{2+}$  ( $P = 0.017$ ). Conversely,  $Si_{AA}$  was negatively correlated with  
247 the amounts in C, N, the CEC and Si:Al ratio ( $P = 0.048, 0.048, 0.049$  and  $0.013$ , respectively)  
248 but positively correlated with the total amount in  $Al_2O_3$  ( $P = 0.013$ ). Moreover, the amount in  
249 phytoliths was positively correlated with the CEC and the amounts in C, N,  $Ca^{2+}$ ,  $Mg^{2+}$  and  
250  $Si_{CC}$  ( $P = 0.001, 0.008, 0.008, 0.001, 0.001$  and  $0.028$ , respectively) but negatively correlated  
251 to the amount in  $Fe^{3+}$  and  $Al^{3+}$  ( $P = 0.018$  and  $0.011$ , respectively).

252 Identification of the phytoliths shows that most of them came from grasses and woody  
253 dicotyledons (trees and shrubs), with little differences in the phytolith-inferred vegetation signal  
254 between  $Ctrl_{0-5}$  and  $Ctrl_{70-120}$ , but strong difference with TM. In TM, phytolith pool was  
255 essentially coming from grasses (phytolith ratio Dicotyledons:Poaceae,  $D:P^\circ < 0.7$ ), while it  
256 was coming from woody plants in the Ctrl samples ( $D:P^\circ > 2$ ) (Figure 4 and see appendix A  
257 for the detailed phytolith counts). A gradient of corrosion was observed from the top-soil to the  
258 deeper soil layers with a dominance of non-corroded phytoliths in  $Ctrl_{0-5}$ , a dominance of  
259 corroded phytoliths in the 90-100 cm soil layer and intermediate values in the 20-40 cm soil  
260 layer (Figure 5). In TM, phytoliths had intermediate proportion of corroded phytoliths than  
261 between the 0-5 and 20-40 cm soil layers (Figures 5 and 6).

262

### 263 *Variation in clay abundance and mineralogy with soil depth*

264 Differences in clay mineralogy between soil samples are shown in Figure 7. Soil materials were  
265 mainly differentiated by the second axis, which explained 30% of the total variability. Samples  
266 from the topsoil were enriched in smectite (S) and poorly crystallized illite (PCI) in comparison  
267 with soil sampled below 70 cm depth that were rich in kaolinite (K). TM and EROD had the

268 same signatures and intermediate properties between those of the soils sampled in Ctrl<sub>0-5</sub> and  
269 Ctrl<sub>70-120</sub>.

270

## 271 **Discussion**

### 272 *Bioturbation and translocation of clay*

273 Bioturbation and the edification of termite mounds by fungus-growing termites is associated  
274 with a translocation of soil material from the deeper soil layers to the surface. Usually evidenced  
275 by an enrichment in clay particles or the presence of minerals that are less abundant than in the  
276 topsoil, this process of translocation as well as the depth at which termites collect the soil remain  
277 poorly quantified. In a recent study, we showed that the soil from the outer-wall of *O. obesus*  
278 mounds mainly comes from the ~ 70 to 120 cm soil layer (Jouquet et al., 2017b). Here, measure  
279 of the percentage of clay fraction in soil did not evidence a significant difference between soil  
280 materials, mainly because of the high variability in clay content along the soil profile. This  
281 variability in clay content was reduced in termite mound soils, showing a possible regulation  
282 of the amount of clay fraction in soil by termites for strengthening cohesion between aggregate  
283 and ensuring the resistance of TM, as evidenced in laboratory conditions (Jouquet et al., 2002,  
284 Oberst et al., 2016) and for a better control of their habitat and resistance to predators (Jouquet  
285 et al., 2006).

286

### 287 *Si available pools*

288 The 0-5 cm soil layer was enriched in SiO<sub>2</sub> in comparison with the 70-120 cm soil layer, which  
289 was enriched in Al<sub>2</sub>O<sub>3</sub> content (see the [supplementary file 1](#) showing the higher concentration  
290 in Al<sub>2</sub>O<sub>3</sub> at this soil depth). Phytoliths in the 70-120 cm soil layer were also less abundant and  
291 more corroded than in the topsoil in a good agreement with previous observations (Alexandre  
292 et al., 1997; Sommer et al., 2006). Indeed, the dynamic of phytoliths in soil results from burial,  
293 illuviation and bioturbation processes and phytoliths from deeper horizons are usually less

294 abundant, older and more corroded than in the surface (Sommer et al. 2006; White et al., 2012).  
295 A similar amount of phytoliths was measured in TM and in the topsoil while EROD had  
296 intermediate phytolith contents between TM and Ctrl<sub>70-120</sub>. Difference in D:P<sup>o</sup> ratio between  
297 TM and Ctrl soils also shows that TM contained more phytoliths from grasses than control soil  
298 samples. Although this study does not allow to reject the assumption that phytoliths from deeper  
299 soil layers were selectively incorporated into TM, we consider this hypothesis unlikely since  
300 this would have resulted in higher representation of forest indicator phytoliths, as forest is the  
301 dominant vegetation at Mule Hole (Riotte et al., 2018). Moreover, phytolith morphotypes vary  
302 in size but grass silica short cell phytoliths and the forest indicator spheroids are in the same  
303 size range (8-30 microns). It is therefore unlikely that grass phytoliths were incorporated in TM  
304 because they were smaller and because they were differently associated to clay particles.  
305 Despite the fact that *O. obesus* can feed on a variety of litter components (e.g. elephant dung,  
306 wood and leaves) (Cheik et al., 2018, 2019; Shanbhag et al., 2019), grasses are mostly  
307 consumed by herbivores in Mule Hole catchment. The presence of grass phytoliths in TM  
308 therefore suggests that termites act as primary decomposers of herbivore dungs in the studied  
309 area. This hypothesis is in line with recent studies carried out in southern India which showed  
310 that elephant dung material is very attractive to termites which prefer this material over carton,  
311 wood or leaves (Cheik et al., 2018, 2019; Shanbhag et al., 2019). Indeed, despite inhabiting  
312 forested environments in Karnataka and the Nilgiri Region, elephants preferentially feed on  
313 Panicoideae grasses which constitute more than 84% of their annual bulk diet (Baskaran et al.  
314 2010). A large amount of these grasses is only partially decomposed, making this material very  
315 attractive to termites. Therefore, if the consumption of grasses is associated with a partial  
316 digestion of organic matter by termites for building their biomass and ensuring their activity,  
317 the Si contained in the phytoliths is not used by termites. From these findings we suggest that  
318 termites incorporate phytoliths in their constructions most likely when they moisten the soil

319 aggregate pellets with saliva and potentially faeces. This hypothesis is consistent with the  
320 presence of monosaccharides from plant origin in the epigeous nest of fungus-growing termites  
321 (Sall et al., 2002) and the higher C content measured in TM in comparison with Ctrl<sub>70-120</sub> and  
322 the positive correlation between phytoliths and the C content. Moreover, since phytoliths were  
323 mainly non-corroded phytoliths in TM, we even suggest that phytoliths resist to termite and  
324 microbial (including *Termitomyces* sp.) metabolisms.

325 Si<sub>CC</sub> and Si<sub>AA</sub> were respectively higher and lower in the topsoil layer in comparison with  
326 Ctrl<sub>70-120</sub>. Interestingly, despite the fact that TM was mainly built from the soil at 70-120 cm  
327 depth, TM had a closer signature with the topsoil than with the deeper soil with similar amounts  
328 of SiO<sub>2</sub>, Si<sub>CC</sub> and Si<sub>AA</sub>. Although this study does not allow to disentangle the mechanisms  
329 associated to this change in Si pools, the positive correlation between Si<sub>AA</sub> and the amount of  
330 Al<sub>2</sub>O<sub>3</sub>, but not the amount in clay, and the positive correlation between Si<sub>CC</sub> and phytoliths  
331 suggest either (i) a total reorganization of the structure of soil pellets and a decrease in the  
332 interactions between Si and oxides and a shift from Si<sub>AA</sub> to Si<sub>CC</sub>, (ii) a production of Si<sub>CC</sub> from  
333 phytolith dissolution, and/or (iii) a selection of particles from Ctrl<sub>70-120</sub> that were impoverished  
334 in oxides (see supplementary file 2) but enriched in clay and Si<sub>CC</sub>. Another explanation could  
335 be that the dissolution of 2:1 clay minerals, mainly found on the topsoil and TM, increases the  
336 Si<sub>CC</sub> pool, even if this process is likely to be limited with a soil pH > 6. This explanation is in  
337 line with Violette et al. (2010) who found that the dissolution of smectite provides large amount  
338 of dissolved silica (i.e., 75% of the export of dissolved silica) in the study watershed.

339

#### 340 *Modification in clay mineralogy*

341 The 70-120 cm soil layer was characterized by a higher percentage of clay fraction and higher  
342 contents in kaolinite and Al<sub>2</sub>O<sub>3</sub> that are characteristics of kandic horizons (Brady and Weil,  
343 1999; Soil Survey Staff, 2014). The presence of the kandic horizon was confirmed with the X-

344 ray diffraction data that revealed the presence of smectites and poorly crystallized illite (i.e. 2:1  
345 phyllosilicates) in the topsoil and on the contrary a mineralogy dominated kaolinite (1:1  
346 phyllosilicate) in the kandic horizon. The presence of smectite on the topsoil was unexpected  
347 and suggests a high level bioturbation activity with the upward movement of soil and  
348 neoformation processes. The concentration of  $Mn^{2+}$  in soil solutions is largely controlled by  
349 oxidation and reduction reactions and the higher concentration of this cation in the kandic  
350 horizon also confirms a process of accumulation at this soil depth. Therefore, similar  
351 concentration in  $Mn^{2+}$  between the 70-120 cm soil layer and TM confirms the utilization of soil  
352 from the kandic horizon for building termite mounds. However, the lower concentration in  
353  $Mn^{2+}$  in EROD is likely to be explained by the high solubility of this cation in solution (Gilkes  
354 and McKenzie, 1988) and its rapid leaching from the soil eroded from the mound, despite the  
355 fact that this soil is poorly permeable in comparison with the surrounding topsoil (Traoré et al.,  
356 2019). Although TM were mainly made of soil coming from the kandic horizon, clay minerals  
357 in termite mounds had intermediate properties between those observed in the topsoil and those  
358 sampled in the deeper soil layers. Differences in clay minerals or in Si:Al ratio between TM  
359 and the surrounding topsoil have been evidenced in different environment (e.g., Wielemaker,  
360 1984; Abe et al., 2012). They are usually explained by the use of specific clay minerals and/or  
361 the ability of termites to modify the properties of clay minerals (Schaefer, 2001; Jouquet et al.,  
362 2011). Since the modification of clay minerals by termites is limited to the swelling ability of  
363 2:1 clay minerals (Jouquet et al., 2002; 2007), our results suggest that 2:1 clay minerals may be  
364 selected by *O. obesus* for building their nests than kaolinite, most likely because of their better  
365 physical properties in terms of plasticity and water retention (Andrade et al., 2011; Spagnoli et  
366 al., 2018). Another explanation could be 2:1 clay minerals found in TM could be produced from  
367 the dissolution of phytoliths and the interaction between  $Si_{iCC}$  and kaolinite (Sommer et al.,  
368 2006). In a highly weathered Oxisols in the Amazon forest, Lucas et al. (1993) showed that the



369 occurrence of kaolinite, instead of gibbsite, in the topsoil (or surface horizon) was attributed to  
370 the resilication of gibbsite by the soluble silica provided by phytolith dissolution. A similar  
371 process of resilication of kaolinite could be suggested for the formation of smectite in TM by  
372 the biological uplift of cations and highly reactive silica from the dissolution of phytoliths. Over  
373 longer period of time, the accumulation of 2:1 clay minerals in TM is likely to be important at  
374 the ecosystem scale. Indeed, *O. obesus* mound turnover rate has been estimated to reach a soil  
375 turnover of 3.1-31 mm ky<sup>-1</sup> in the same study site (Jouquet et al., 2017). Since clay minerals  
376 accumulated in termite mounds return to the surrounding soil environment after termite mound  
377 degradation, further research is needed to determine if the accumulation of this material  
378 contributes and/or explains the presence of 2:1 clay minerals in the topsoil.

379

### 380 *Conclusion*

381 Findings from this study show that *O. obesus* has a significant impact on the distribution of Si  
382 in soil. First, we explained the lower variability in clay content in comparison with the high  
383 variability measured along the soil profile by the need of termites to control the properties of  
384 their nests, i.e., the amount of clay fraction in TM, then highlighting the importance of this  
385 material for termites. The higher phytolith content in TM was unexpected but could be  
386 explained by termite foraging activity (i.e., the consumption of grasses) and the excretion of  
387 phytolith in termite saliva. Higher amount in Si<sub>CC</sub> was also surprising and raised the question  
388 of a possible impact of termites on the interaction between Si and minerals in soil. In  
389 perspective, we consider that more research is now needed to better understand the fate of the  
390 phytoliths in TM. Further studies are also needed to determine if the increase in Si<sub>CC</sub> content in  
391 TM contribute to explain the presence of 2:1 minerals in termite constructions (Jouquet et al.,  
392 2002) and the specific vegetation growing in the vicinity or on termite mounds in Africa (e.g.,

393 [Traoré et al., 2015](#)), as well as the utilization of TM soil as amendment for increasing soil  
394 fertility ([Loko et al., 2017](#)).

395

### 396 **Acknowledgements**

397 This project was supported by the French Institute for research for development (IRD) through  
398 “Allocations de recherche pour une thèse au Sud” (ARTS) grant and data from this study were  
399 partially obtained from the ALYSES facility (IRD-UPMC) which was supported by grants from  
400 Région Ile de France. The Mule Hole basin is part of the ORE-BVET project (Observatoire de  
401 Recherche en Environnement - Bassin Versant Expérimentaux Tropicaux, [http://bvet.omp.obs-  
403 mip.fr/](http://bvet.omp.obs-<br/>402 mip.fr/)) supported by the French Institute of Research for Development (IRD), CNRS and  
404 Toulouse University. The project also benefited from funding from the Indo-French Cell for  
405 Water Science (LMI CEFIRSE, <http://www.cefirse.ird.fr>) and the French National Program  
406 EC2CO-Biohefect “MACROFLUX”. Finally, we thank the Karnataka Forest Department and  
the staff of the Bandipur National Park for all the facilities and support they provided.

407

408 **Appendix A.** Supplementary data to this article can be found online at

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600 **Figures and table captions**

601

602 Figure 1. Biplot showing the principal components analysis (PCA) from variables describing  
603 soil physical and chemical properties showed in Table 1 and significantly influenced  
604 by the different treatments: control soil sampled at 0-5 and 70-120 cm depth in blue  
605 and yellow, respectively, and the termite mound soil (TM, in red) or the soil eroded  
606 from the mound (EROD, in grey).

607

608 Figure 2. Clay content along the soil profile, in the outer part of termite mound (TM, arbitrary  
609 displayed at + 50cm depth) and in the soil eroded from TM (EROD, arbitrary  
610 displayed at + 5 cm depth). The three different soil profiles are given in three different  
611 soil colors.

612

613 Figure 3. Histograms showing the percentages in SiO<sub>2</sub> and phytoliths (%), and the amounts in  
614 Si<sub>CC</sub> and Si<sub>AA</sub> (ppm) in the outer part of termite mound (TM), in the soil eroded from  
615 TM (EROD) and in the control soils at 0-5 and 70-120 cm depths (Ctrl<sub>0-5</sub> and Ctrl<sub>70-  
616 120</sub>, respectively). Bars represent standard errors and histograms with the same letters  
617 are not significantly different.

618

619 Figure 4. Abundance and diversity of phytoliths.

620 (a) Histograms showing the relative abundances of phytoliths in termite mound (TM)  
621 and control samples at 0-5 (Ctrl<sub>0-5</sub>) and 70-120 (Ctrl<sub>70-120</sub>) cm depths. The  
622 differentiation was made into forest indicators, grasses, ND-elongate and ND-blocky  
623 phytoliths.

624 (b) Ratio of spheroid decorated versus the sum of grass silica short cells (or D/P°  
625 index).

626

627 Figure 5. Proportion of corroded, non-corroded and undetermined phytoliths for termite  
628 mound (TM) and in the soil sampled at 0-5, 20-40 and 70-120 cm depths (Ctrl<sub>0-5</sub> and  
629 Ctrl<sub>70-120</sub>).

630

631 Figure 6. Examples of blocky and elongated non-corroded (a, b) and corroded phytoliths (c, d)  
632 obtained in the microscope. The scale is given with the horizontal bar which  
633 represents 40  $\mu$ m.

634

635 Figure 7. Biplot showing the principal components analysis (PCA) from variables describing  
636 clay mineralogy of the different soil materials. Treatments are the soil at 0-5 and 70-  
637 120 cm depth (in blue and yellow, respectively), the soil from termite mound (TM,  
638 in red) and the soil eroded from TM (EROD, in grey). Clays are kaolinite (K), well  
639 crystallized illite (WCI), poorly crystallised illite (PCI), inters-stratified (IS) and  
640 smectite (S).

641

642 Supplementary file 1. Percentage in  $\text{Fe}_2\text{O}_3$  and  $\text{Al}_2\text{O}_3$  along the soil profile, in the outer part of  
643 termite mound (TM, arbitrary displayed at + 50 cm depth) and in the soil eroded from  
644 TM (EROD, arbitrary displayed at + 5 cm depth).

645

646 Supplementary file 2. Percentage of well crystallized oxides in soil ( $\text{Fe}_{\text{DCB}} - \text{Fe}_\text{O}$  and  $\text{Al}_{\text{DCB}} -$   
647  $\text{Al}_\text{O}$ ) extracted by the DCB ( $\text{Fe}_{\text{DCB}}$  and  $\text{Al}_{\text{DCB}}$ ) and oxalate methods ( $\text{Fe}_\text{O}$  and  $\text{Al}_\text{O}$ )  
648 (Mehra and Jackson, 1960; Schwertmann, 1964) along the soil profile, in the outer  
649 part of termite mound (TM, arbitrary displayed at + 50 cm depth) and in the soil  
650 eroded from TM (EROD, arbitrary displayed at + 5 cm depth).

Figure 1

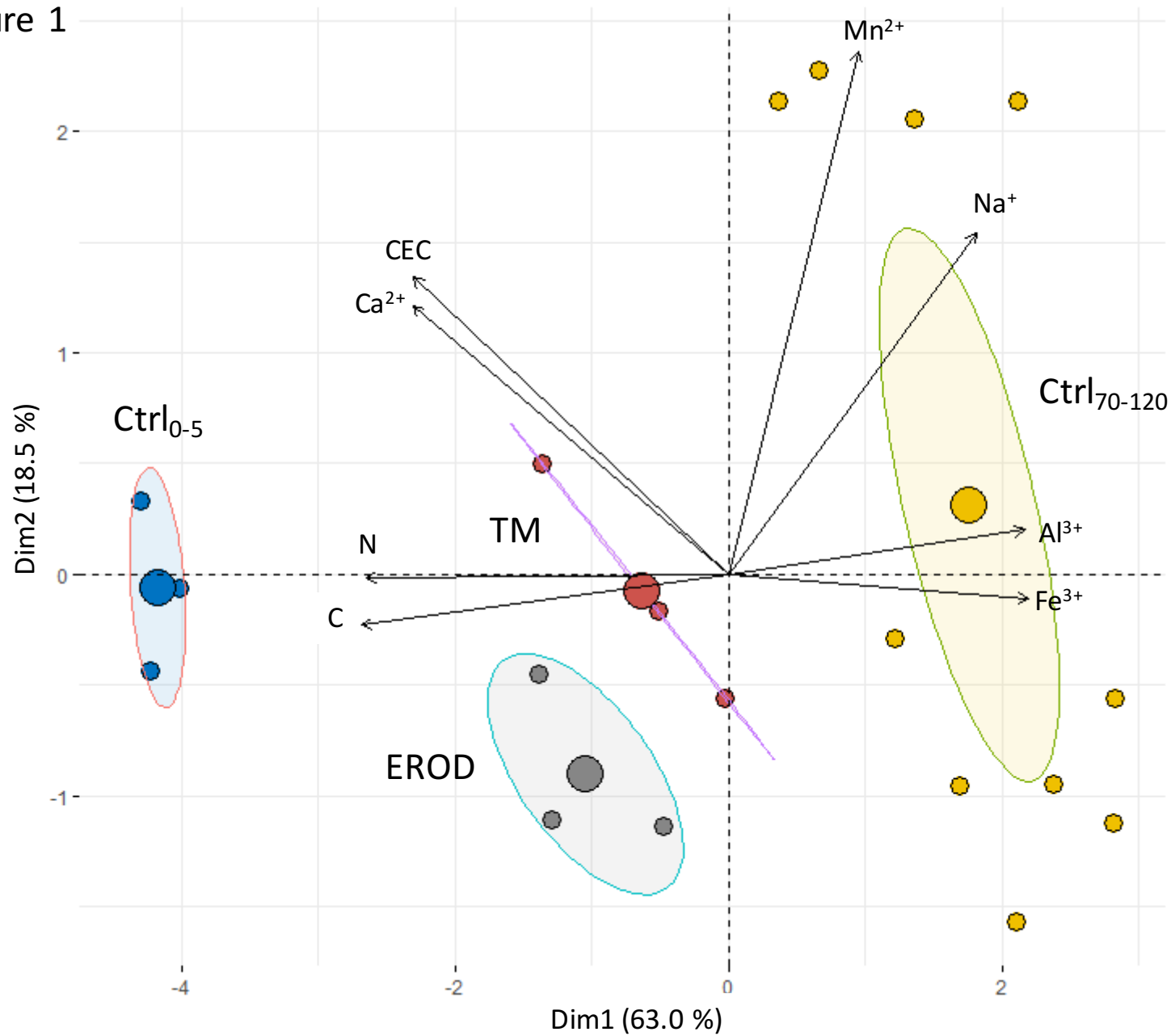


Figure 2

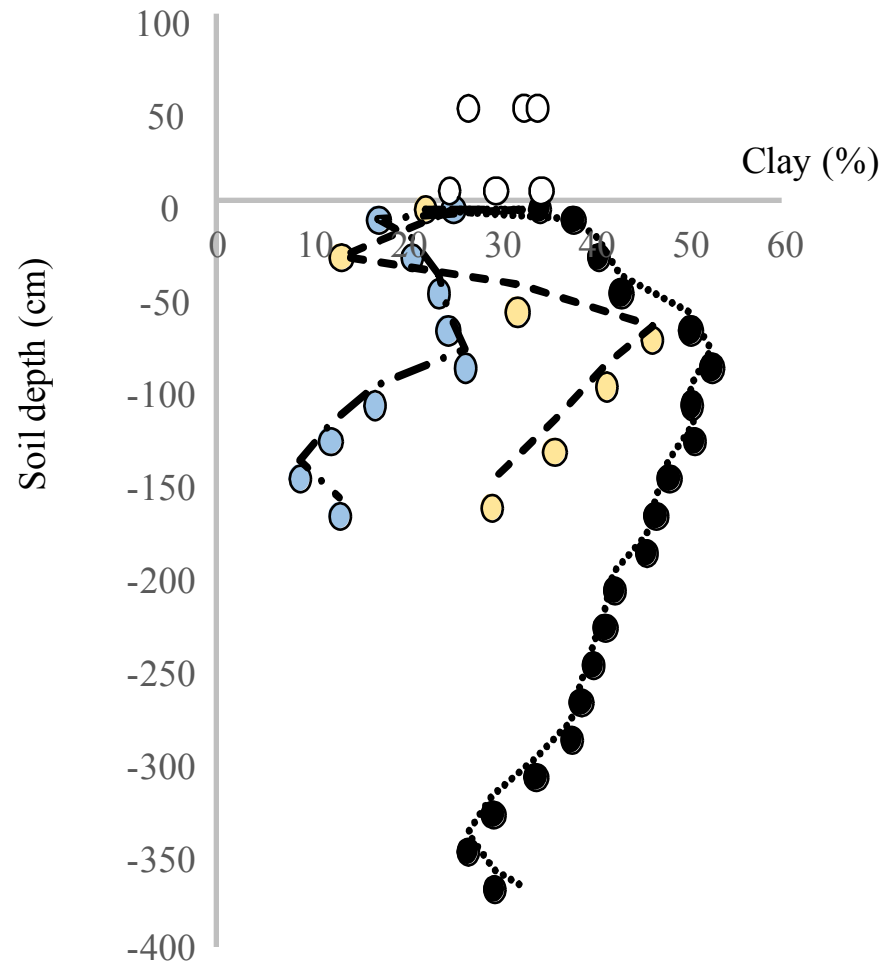


Figure 3

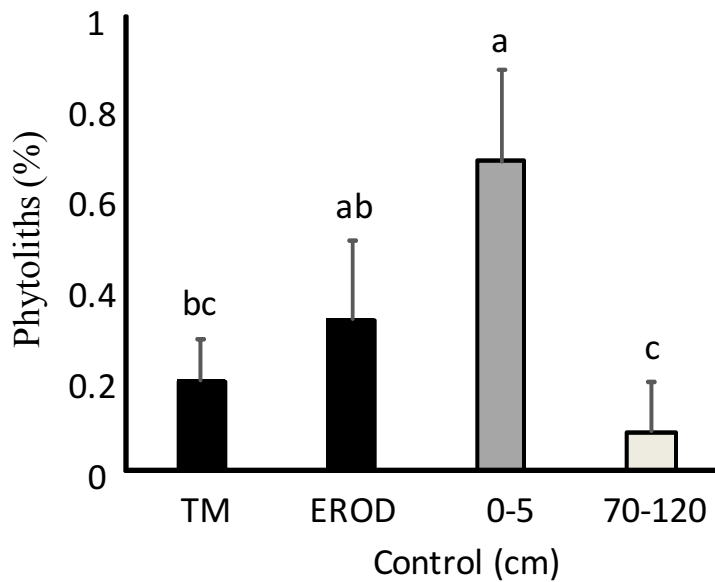
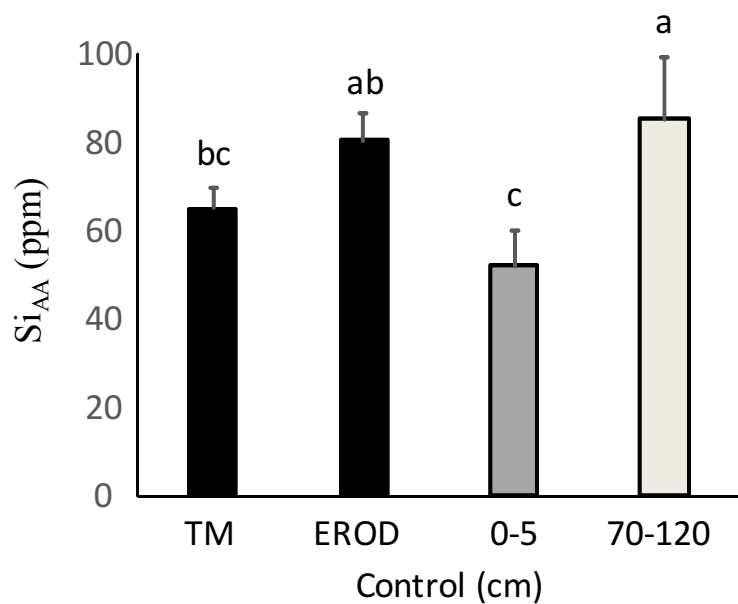
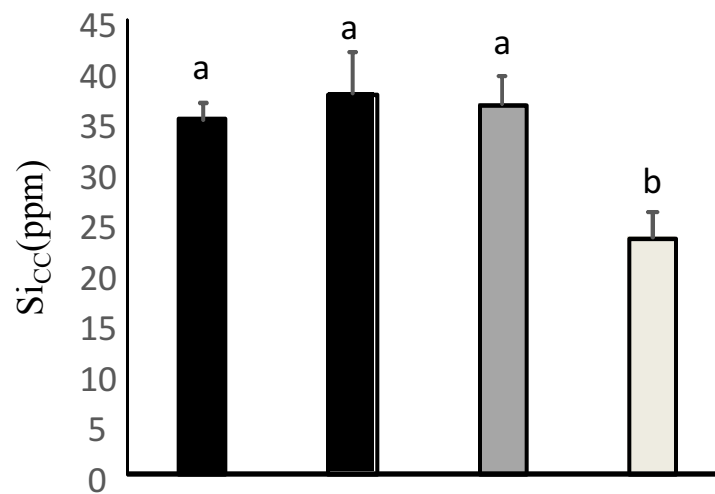
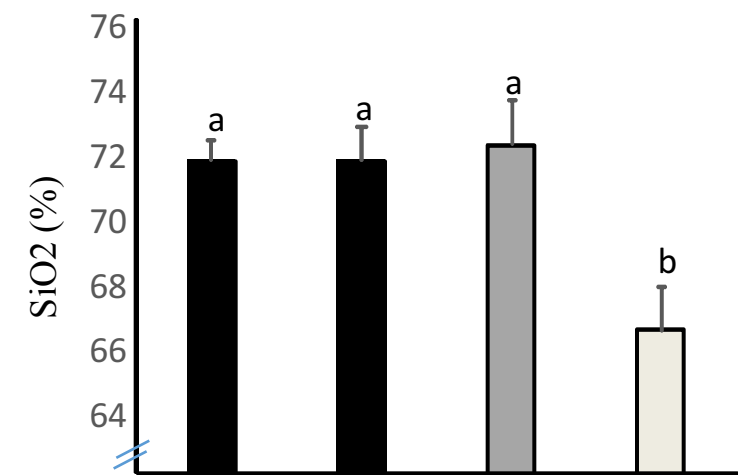
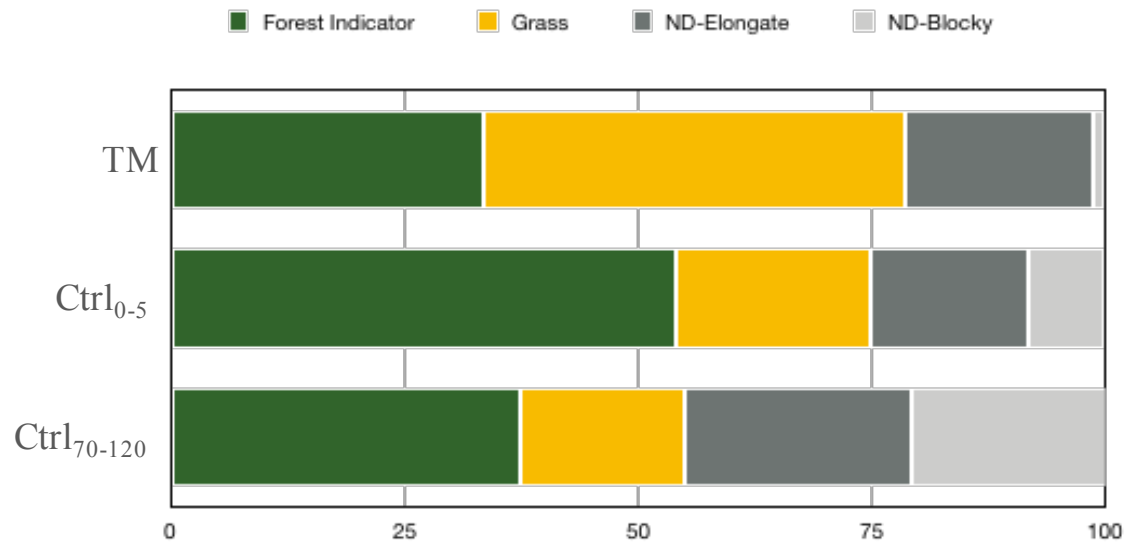


Figure 4



D:P°

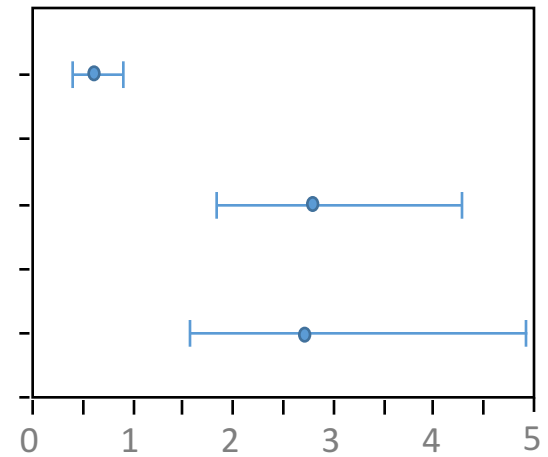




Figure 5

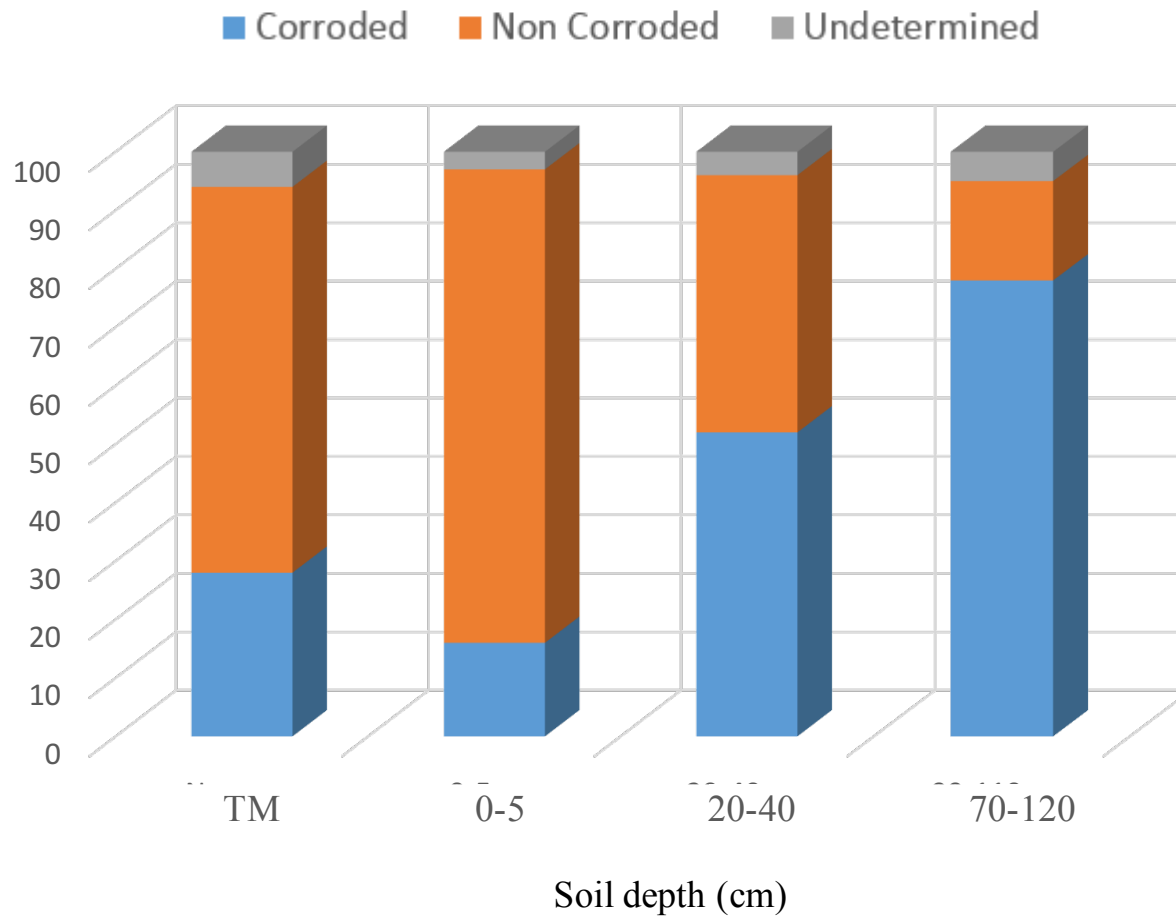
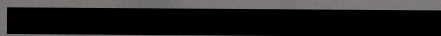
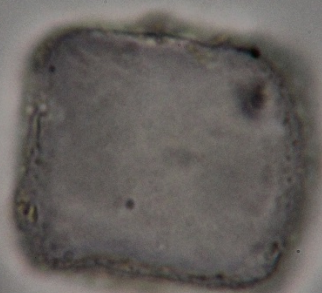
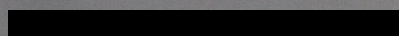
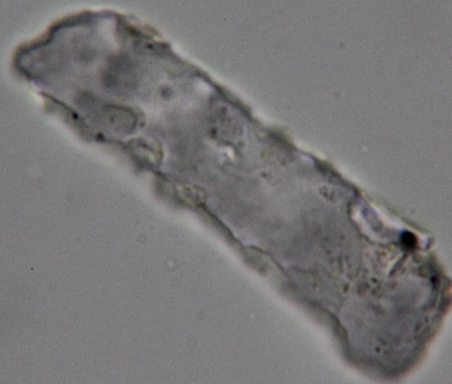


Figure 6

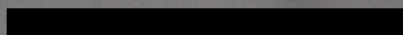
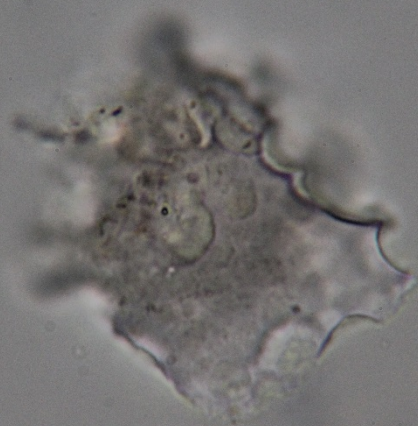
**a**



**b**



**c**



**d**

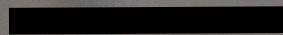
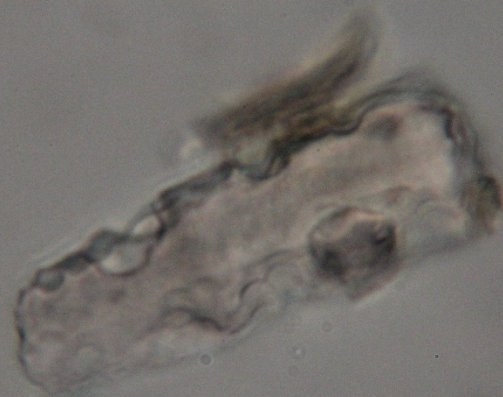
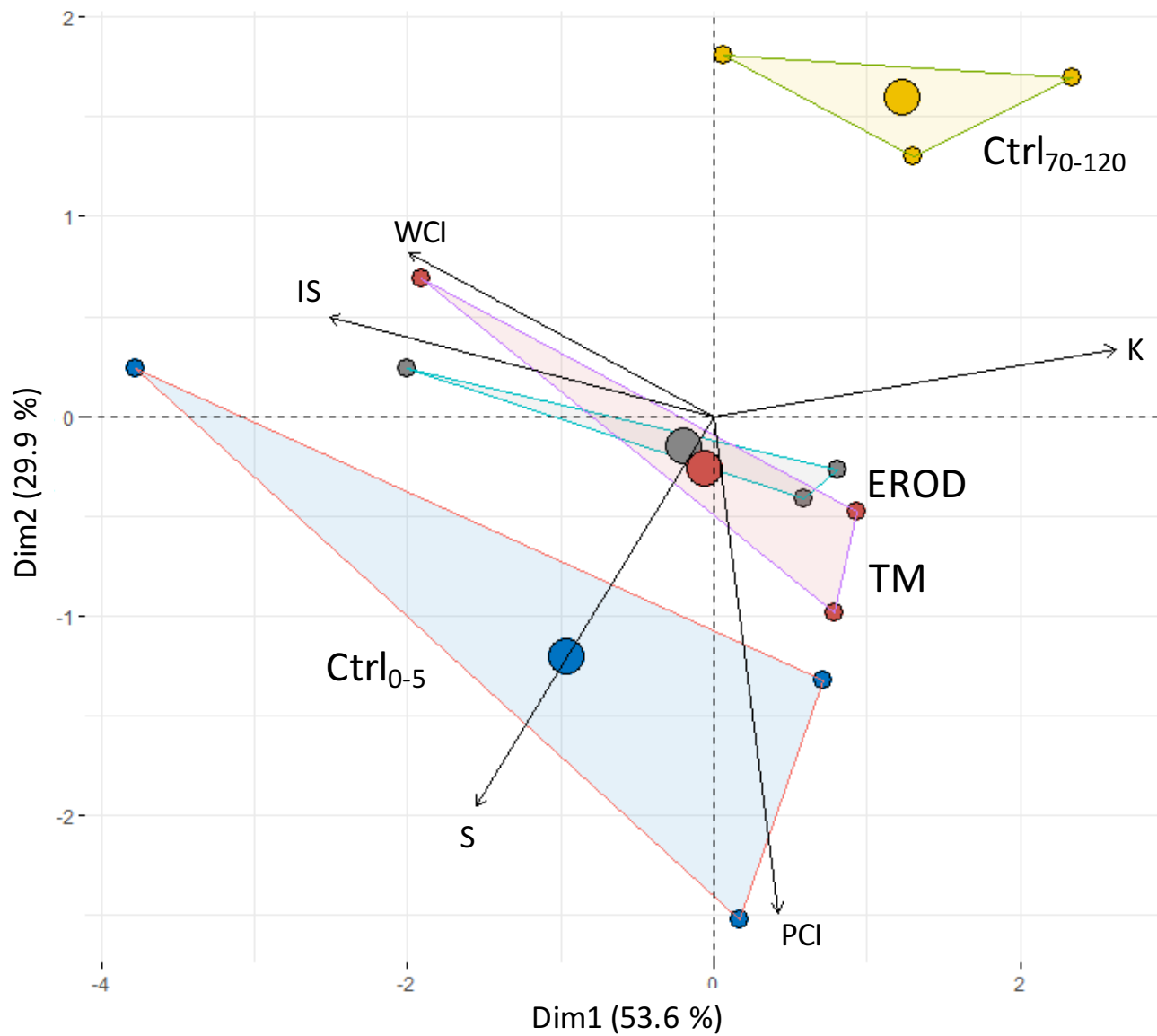
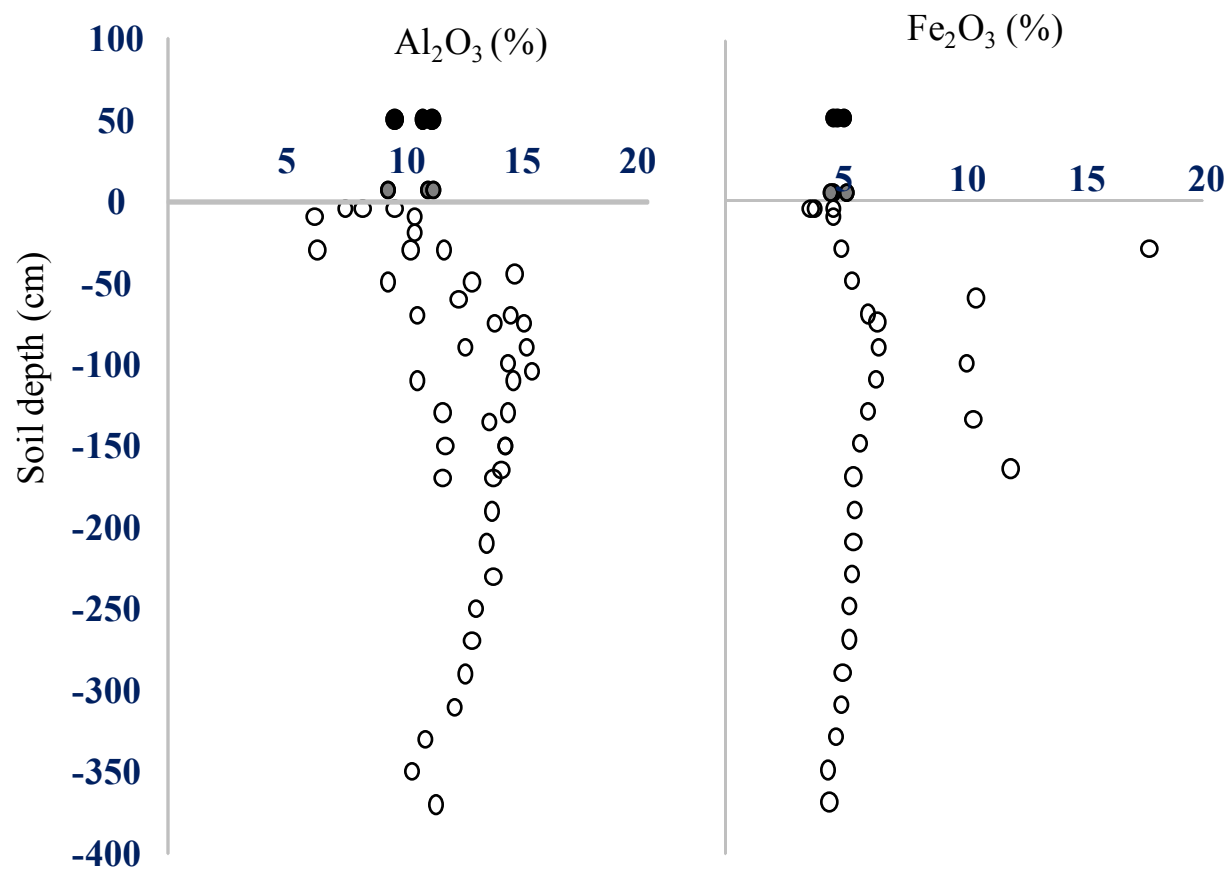


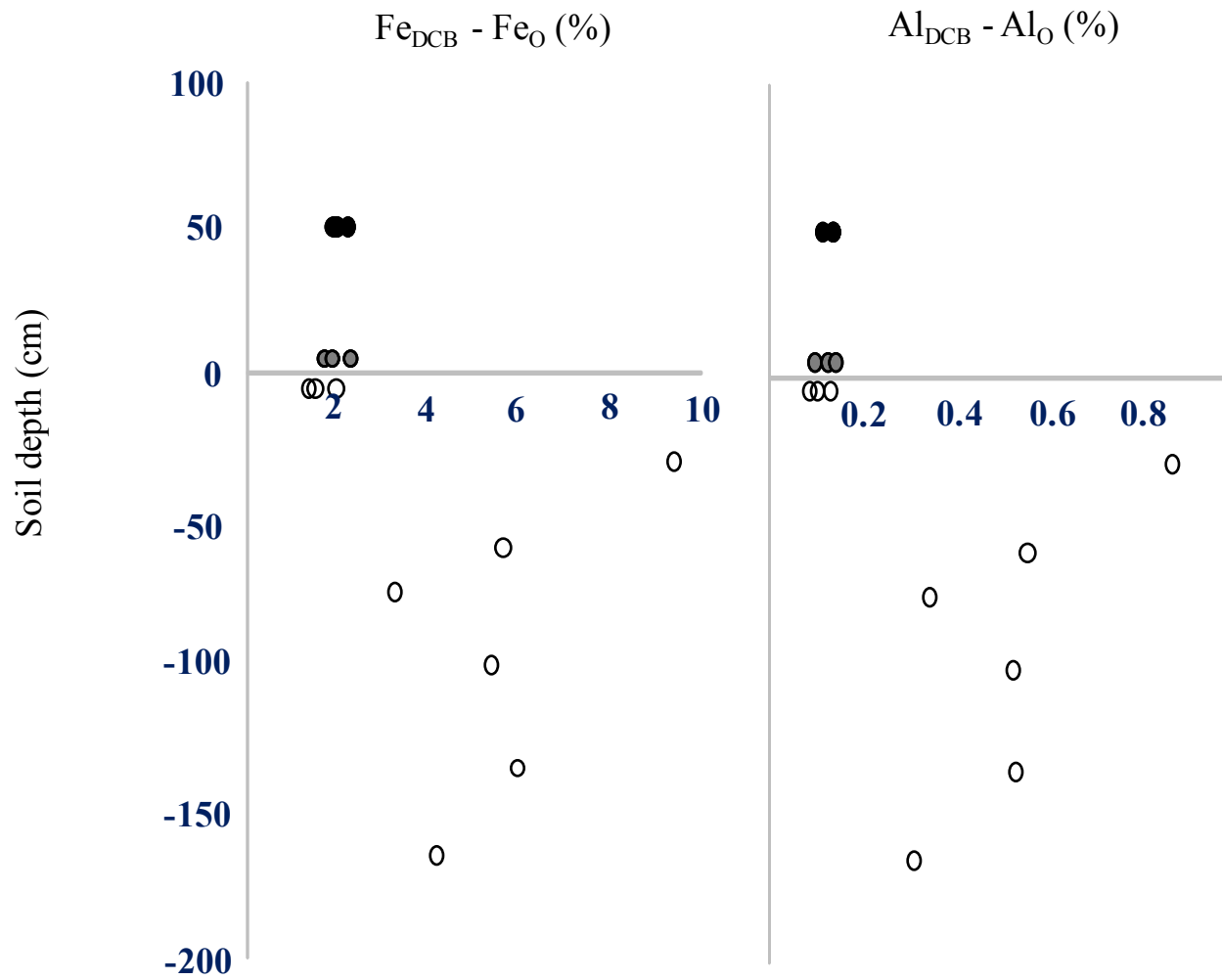
Figure 7



# Supplementary file 1



# Supplementary file 2



651 Table 1 Major physical (contents in clay, silt and sand, in %) and chemical properties (contents in C and N in %, CEC, Ca<sup>2+</sup>, Mg<sup>2+</sup>, Na<sup>+</sup>, K<sup>+</sup>,  
 652 Fe<sup>3+</sup>, Mn<sup>2+</sup> and Al<sup>3+</sup> in cmol<sup>(+)</sup> kg<sup>-1</sup>) in the control soils at 0-5 and 70-120 cm depth (Ctrl<sub>0-5</sub> and Ctrl<sub>70-120</sub>, respectively) and in termite  
 653 mound (TM) or the soil eroded from TM (EROD). Values in parentheses are standard errors, values with the same letter are similar at *P*  
 654 = 0.05. Results from the ANOVA (*F* and *P*-values) and Wilcoxon–Mann–Whitney U (*Chi*<sup>2</sup> and *P*-values) tests are also given.

655

656

	C	N	Clay (%)	Silt	Sand	CEC	Ca <sup>2+</sup>	Mg <sup>2+</sup>	Na <sup>+</sup> (cmol <sup>(+)</sup> kg <sup>-1</sup> )	K <sup>+</sup>	Fe <sup>3+</sup>	Mn <sup>2+</sup>	Al <sup>3+</sup>	pH
TM	1.75 <sup>b</sup>	0.13 <sup>b</sup>	31.2	18.1	50.7	13.30 <sup>b</sup>	9.25 <sup>b</sup>	2.96	0.043 <sup>b</sup>	0.27	0.016 <sup>ab</sup>	0.18 <sup>a</sup>	0.09 <sup>a</sup>	6.03
(n = 3)	(0.38)	(0.03)	(3.87)	(0.6)	(1.8)	(0.61)	(0.60)	(0.05)	(0.002)	(0.04)	(0.001)	(0.03)	(0.01)	(0.07)
EROD	1.95 <sup>b</sup>	0.14 <sup>b</sup>	29.7	18.9	51.4	13.80 <sup>b</sup>	9.68 <sup>b</sup>	3.22	0.039 <sup>b</sup>	0.40	0.016 <sup>ab</sup>	0.04 <sup>b</sup>	0.09 <sup>a</sup>	6.45
(n = 3)	(0.30)	(0.02)	(4.85)	(0.2)	(2.6)	(0.25)	(0.21)	(0.12)	(0.009)	(0.06)	(0.002)	(0.01)	(0.01)	(0.22)
Ctrl <sub>0-5</sub>	3.43 <sup>a</sup>	0.25 <sup>a</sup>	26.6	17.4	56.0	19.50 <sup>a</sup>	14.83 <sup>a</sup>	3.40	0.025 <sup>b</sup>	0.47	0.010 <sup>b</sup>	0.02 <sup>b</sup>	0.05 <sup>b</sup>	6.23
(n = 3)	(0.29)	(0.03)	(5.14)	(0.3)	(2.9)	(0.78)	(0.92)	(0.21)	(0.003)	(0.11)	(0.003)	(0.03)	(0.01)	(0.13)
Ctrl <sub>70-120</sub>	0.49 <sup>c</sup>	0.05 <sup>c</sup>	37.23	18.06	44.72	11.78 <sup>b</sup>	8.00 <sup>b</sup>	3.36	0.111 <sup>a</sup>	0.49	0.022 <sup>a</sup>	0.16 <sup>a</sup>	0.13 <sup>a</sup>	6.75
(n = 10)	(0.27)	(0.03)	(14.87)	(2.02)	(3.17)	(1.11)	(0.89)	(0.34)	(0.01)	(0.09)	(0.002)	(0.04)	(0.01)	(0.90)
<i>F</i> <sub>3,15</sub>	15.75	52.27	0.80	0.05	1.74	5.84	6.9		11.36	1.85	5.34	5.62	5.94	1.88
<i>P</i>	<0.001	<0.001	0.511	0.986	0.202	0.007	0.004		<0.001	0.182	0.010	0.008	0.007	0.222
	***	***				**	**		***		*	**	**	
<i>Chi</i> <sup>2</sup>								1.08						
<i>P</i>								0.781						

657