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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 (Ctrl₀₋₅) and 70-
27 120 cm soil layers (Ctrl₇₀₋₁₂₀). Although termites use the soil from Ctrl₇₀₋₁₂₀ for building their
28 mounds, we found that TM and EROD had intermediate soil physical, chemical and
29 mineralogical properties between Ctrl₀₋₅ and Ctrl₇₀₋₁₂₀. 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_{CC}) contents were increased in TM in comparison with
35 Ctrl₇₀₋₁₂₀, suggesting an incorporation of phytoliths in termite construction through their saliva
36 and/or an increasing availability of Si_{CC} 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 CaCl₂ (Si_{CC}) is used to
60 estimate the Si immediately available for plants (Haysom and Chapman, 1975). The distribution
61 of Si_{CC} 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_{AA}) (Sauer et
64 al., 2006). Si_{AA} 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_{CC} and Si_{AA} 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 km²). 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⁻¹, 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⁻¹ of C in the first soil layer and < 10 g kg⁻¹
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 (Ctrl₀₋₅: 0–5 cm, Ctrl₇₀₋₁₂₀: 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 μm) were obtained by pipette method and sand (50–2000 μm) 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 SiO_2 , Fe_2O_3 and
142 Al_2O_3 were measured by ICP-OES after fusion with lithium metaborate LiBO_2 and subsequent
143 dissolution in a mixture of HNO_3 (1 mol L⁻¹), H_2O_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 CaCl₂ (Si_{CC}, Haysom and Chapman, 1975) and the pool of adsorbed Si extracted by 0.5 M
151 acetate-acetic acid (Si_{AA}, 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 ZnBr₂ 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 (Ctrl₀₋₅ and Ctrl₇₀₋₁₂₀) (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⁻¹ 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⁻¹

178 CaCl₂ (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 ~ 7.20 and $7.30\text{-}7.40$ Å were attributed to kaolinite (K). The peak of
194 illite at ~ 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 ~ 15 Å in AD state that displace to ~ 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 Si_{CC} , Si_{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 (Ctrl₀₋₅) to TM, EROD and finally Ctrl₇₀₋₁₂₀. No significant
222 difference in soil particle size fractions, in pH and in exchangeable Mg²⁺ and K⁺ contents could
223 be measured between the four soil materials ($P > 0.05$ in all cases) (Table 1). Ctrl₀₋₅ was
224 enriched in C and N and characterized by a greater CEC and exchangeable Ca²⁺ content but
225 lower exchangeable Al³⁺ content in comparison with the other treatments. Conversely, Ctrl₇₀₋
226 ₁₂₀ were impoverished in C and N but enriched in exchangeable Na⁺, Al₂O₃ and Fe₂O₃ in
227 comparison with the other soil materials. In general, TM and EROD had intermediate properties
228 in comparison with the Ctrl₀₋₅ and Ctrl₇₀₋₁₂₀ (Figure 1) and no significant difference occurred
229 between them, with the exception of the concentration in exchangeable Mn²⁺ that was similar
230 in TM and Ctrl₇₀₋₁₂₀ but higher than in EROD and Ctrl₀₋₅ ($P > 0.05$ 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 SiO₂ and the amount of Si_{CC} were the lowest in Ctrl₇₀₋₁₂₀,
238 without any significant difference between the other treatments ($P > 0.05$). Conversely Si_{AA}
239 content was the highest in Ctrl₇₀₋₁₂₀ and the lowest in Ctrl₀₋₅ while TM and EROD had
240 intermediate positions. The proportion of phytoliths was low with percentages < 1%. The
241 highest value was measured in Ctrl₀₋₅ in comparison with Ctrl₇₀₋₁₂₀ and TM ($P < 0.05$ in both
242 cases). Conversely, the lowest value was measured in Ctrl₇₀₋₁₂₀ in comparison with Ctrl₀₋₅ 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 Ctrl₀₋₅ and
269 Ctrl₇₀₋₁₂₀.

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 SiO₂ in comparison with the 70-120 cm soil layer, which
289 was enriched in Al₂O₃ content (see the [supplementary file 1](#) showing the higher concentration
290 in Al₂O₃ 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 Ctrl₇₀₋₁₂₀. Difference in D:P^o 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 Ctrl₇₀₋₁₂₀ 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_{CC} and Si_{AA} were respectively higher and lower in the topsoil layer in comparison with
326 Ctrl₇₀₋₁₂₀. 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 SiO₂, Si_{CC} and Si_{AA}. Although this study does not allow to disentangle the mechanisms
329 associated to this change in Si pools, the positive correlation between Si_{AA} and the amount of
330 Al₂O₃, but not the amount in clay, and the positive correlation between Si_{CC} 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_{AA} to Si_{CC}, (ii) a production of Si_{CC} from
333 phytolith dissolution, and/or (iii) a selection of particles from Ctrl₇₀₋₁₂₀ that were impoverished
334 in oxides (see supplementary file 2) but enriched in clay and Si_{CC}. Another explanation could
335 be that the dissolution of 2:1 clay minerals, mainly found on the topsoil and TM, increases the
336 Si_{CC} 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 Al₂O₃ 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⁻¹ 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_{CC} 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_{CC} 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

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407

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

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414

415

416

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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 SiO₂ and phytoliths (%), and the amounts in
614 Si_{CC} and Si_{AA} (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 (Ctrl₀₋₅ 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 (Ctrl₀₋₅) and 70-120 (Ctrl₇₀₋₁₂₀) 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 (Ctrl₀₋₅ and
629 Ctrl₇₀₋₁₂₀).

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 μ 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 Fe_2O_3 and Al_2O_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 Al_O) extracted by the DCB (Fe_{DCB} and Al_{DCB}) and oxalate methods (Fe_O and Al_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

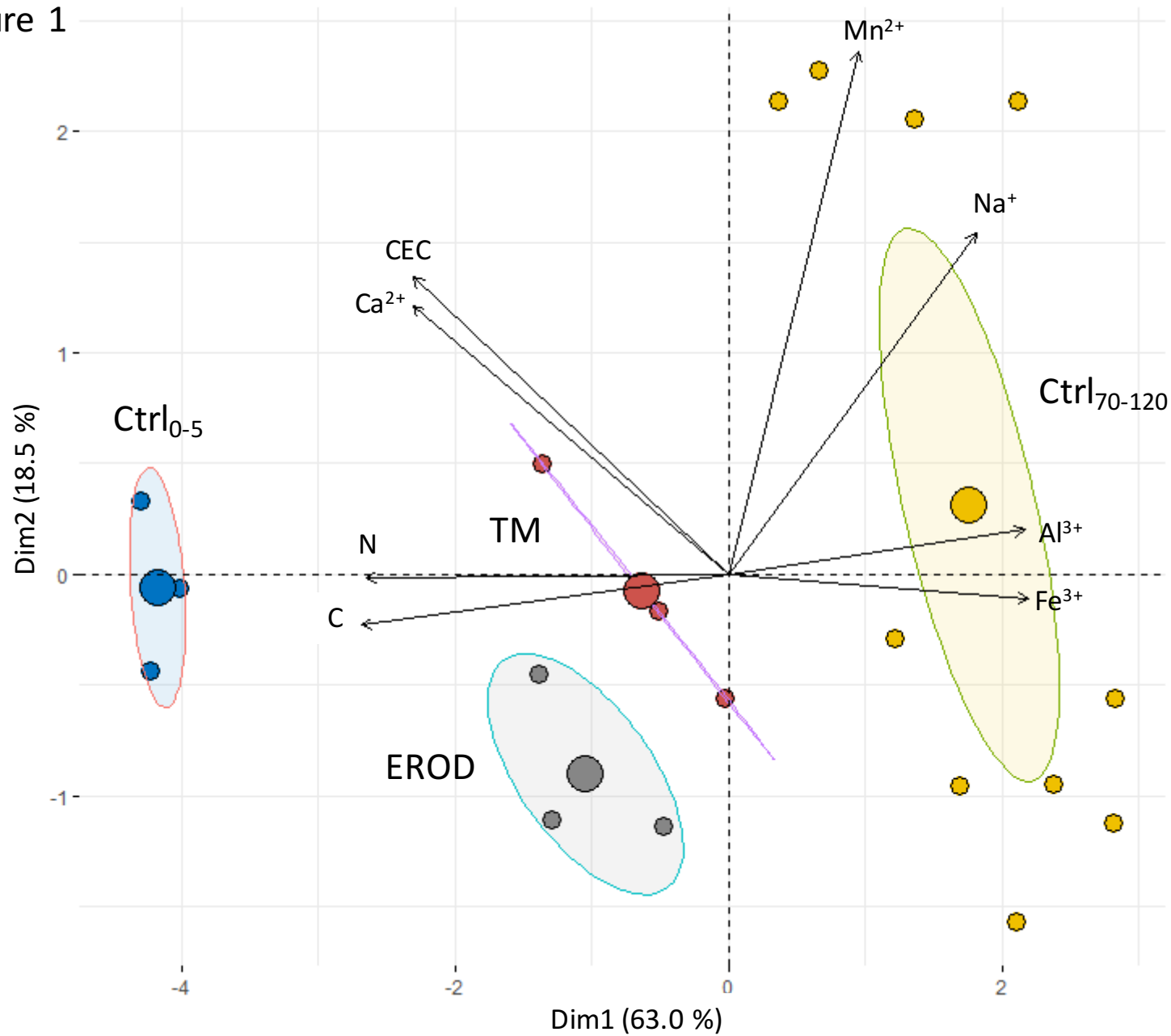


Figure 2

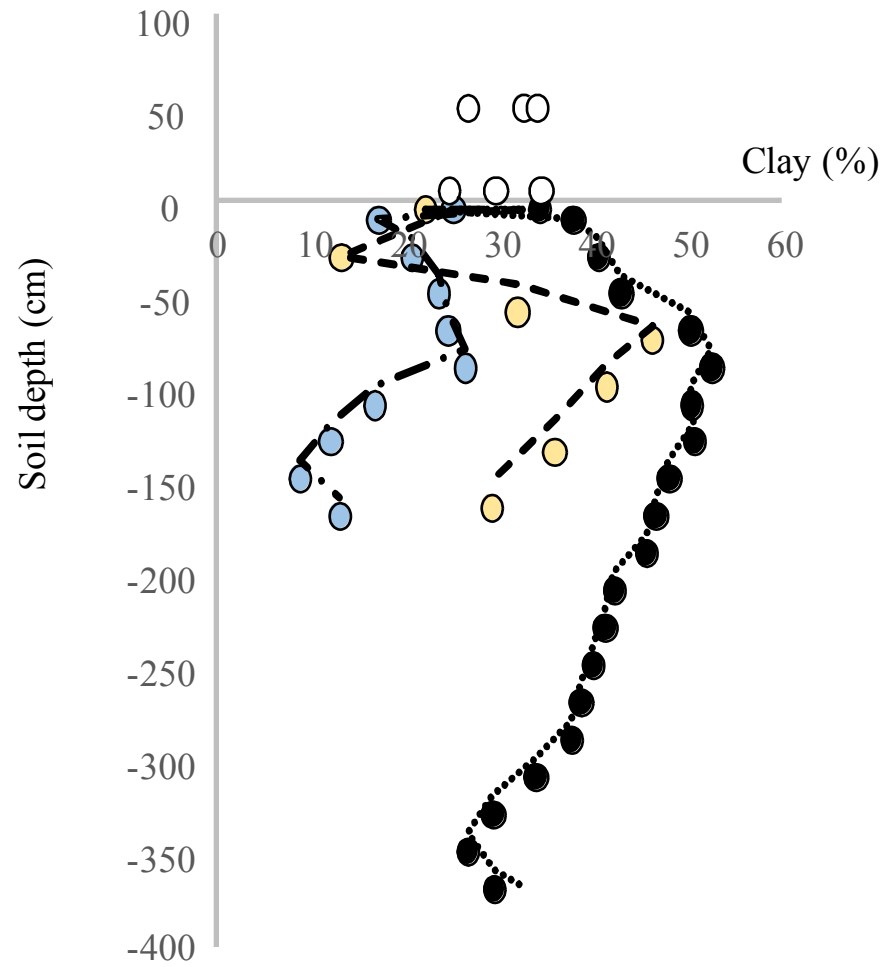


Figure 3

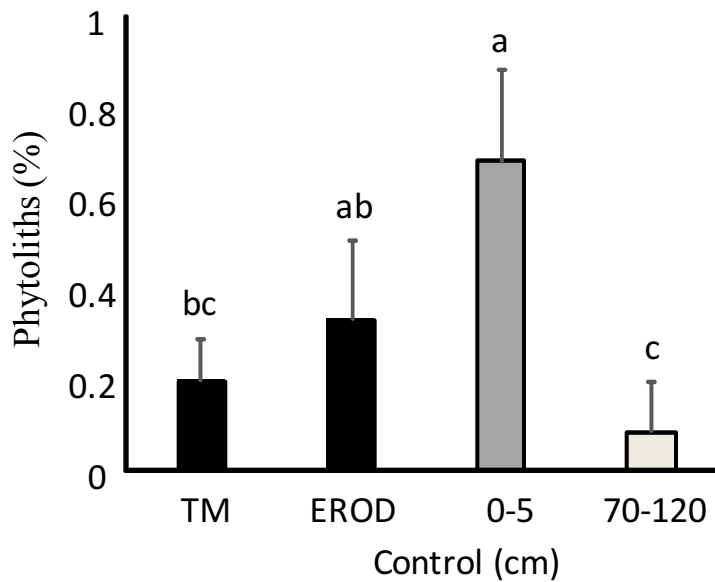
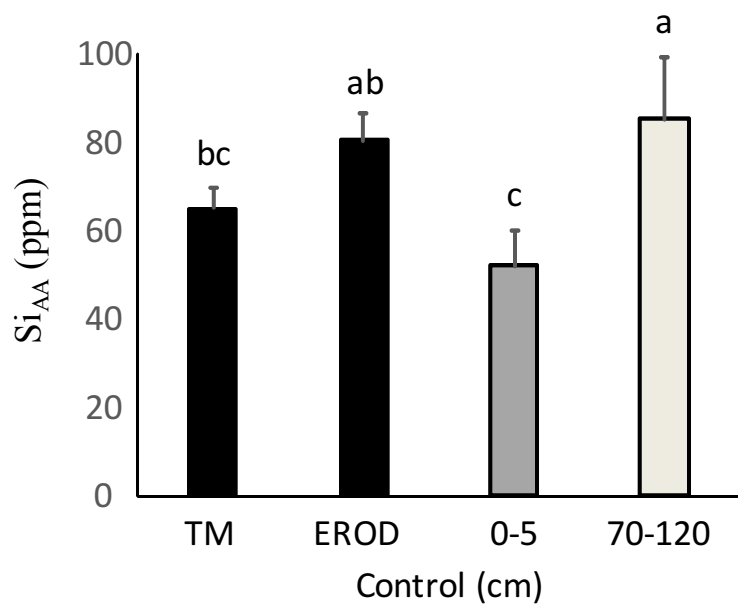
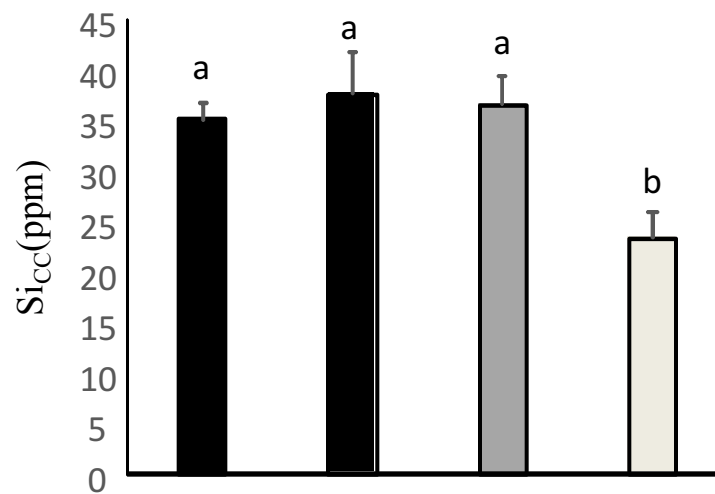
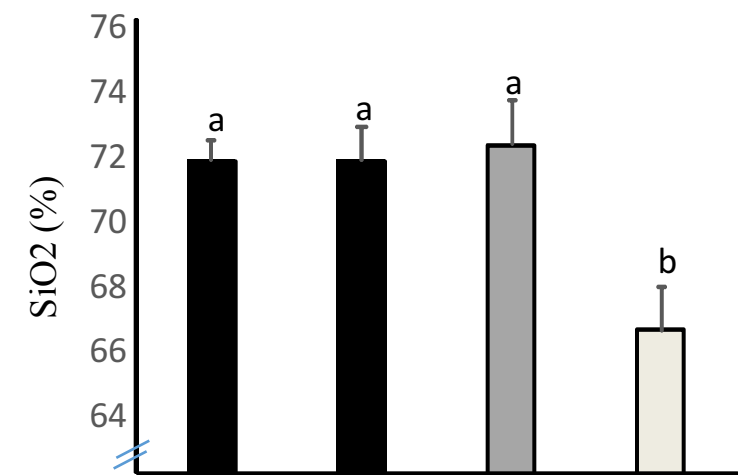
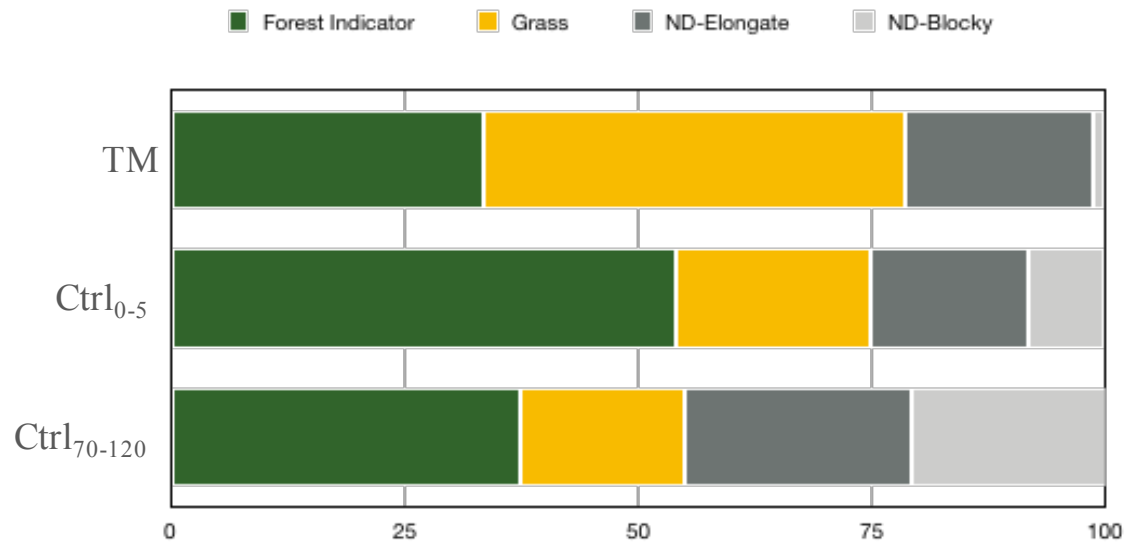


Figure 4



D:P°

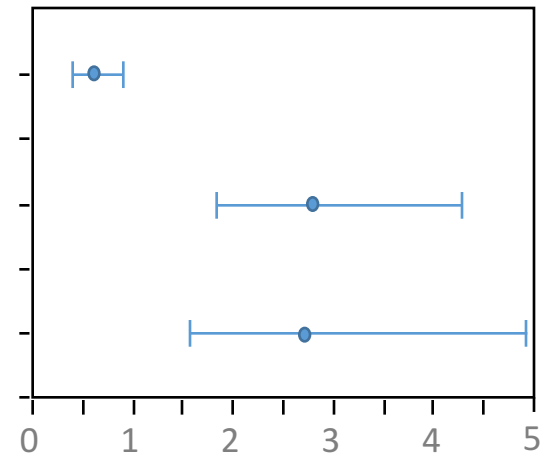


Figure 5

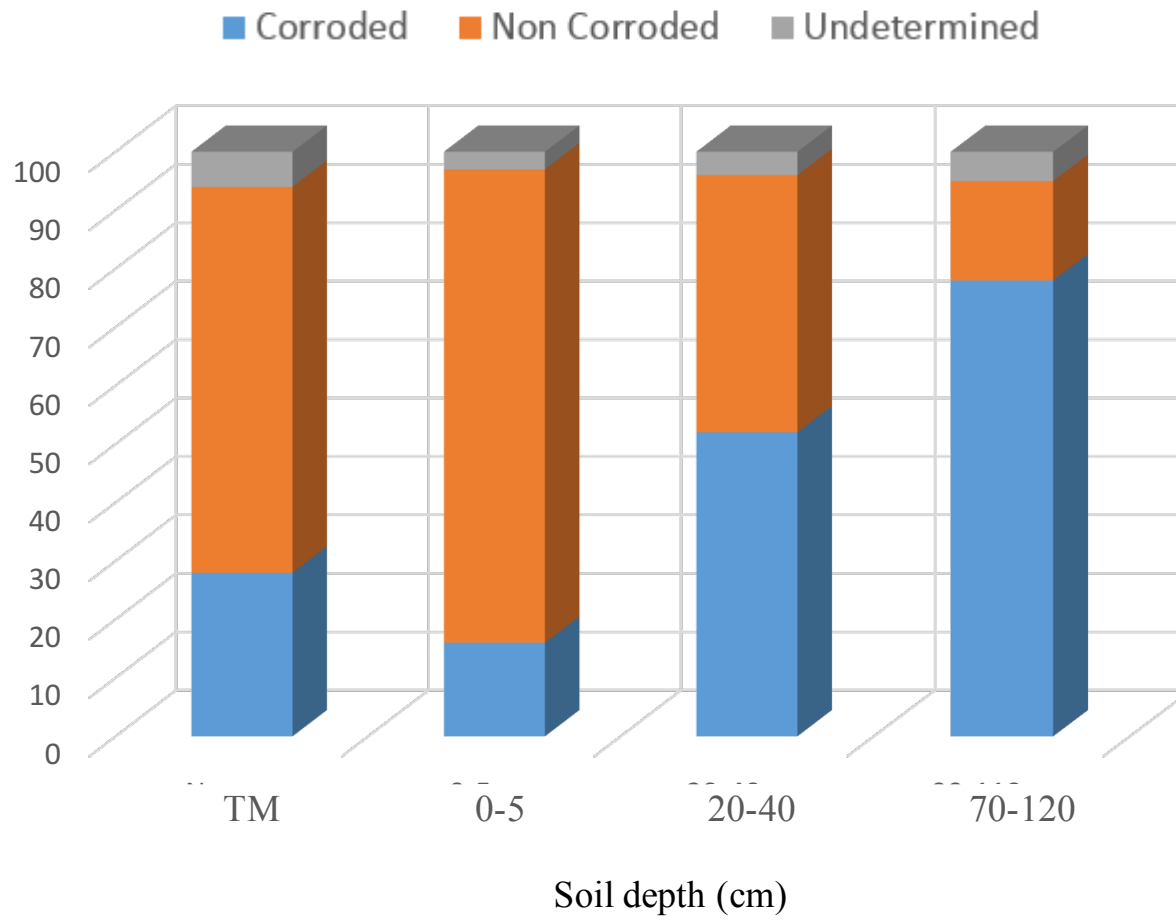
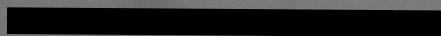
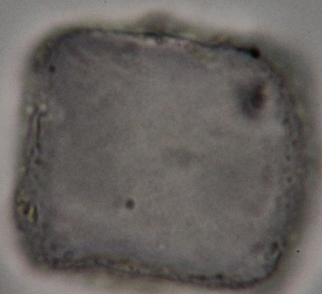
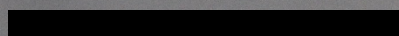
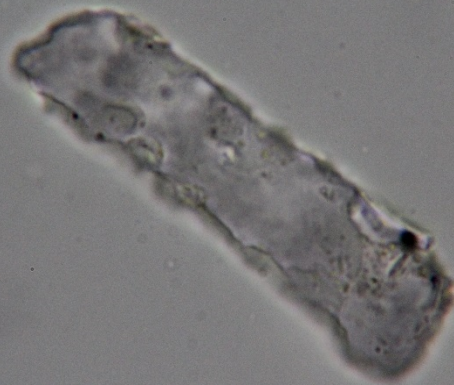


Figure 6

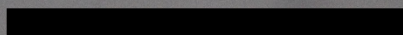
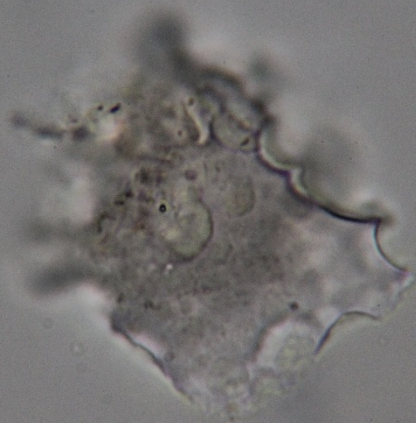
a



b



c



d

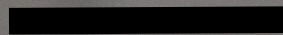
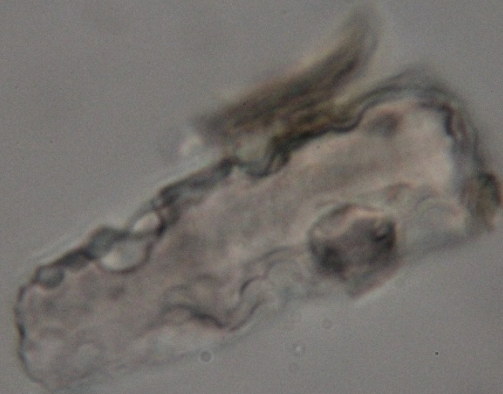
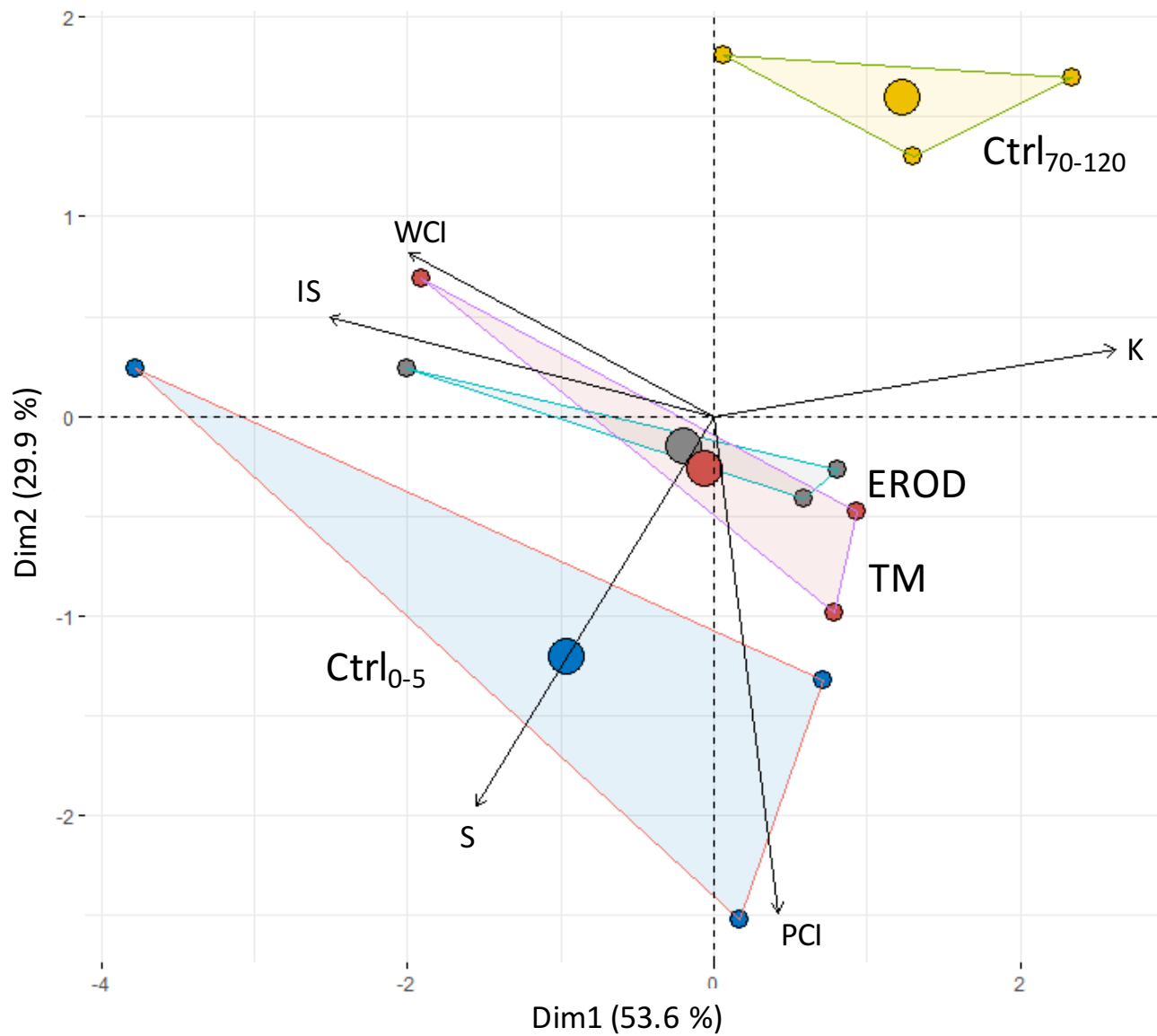
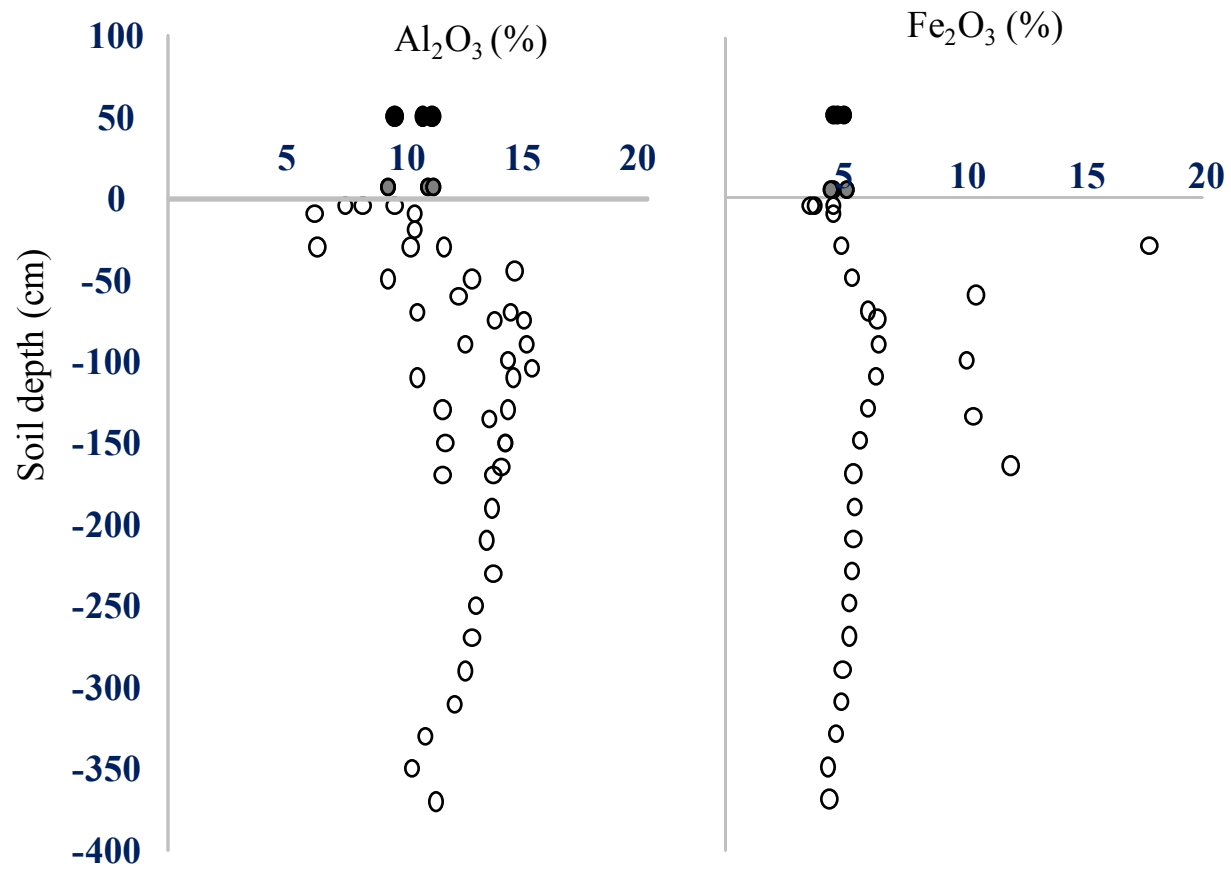


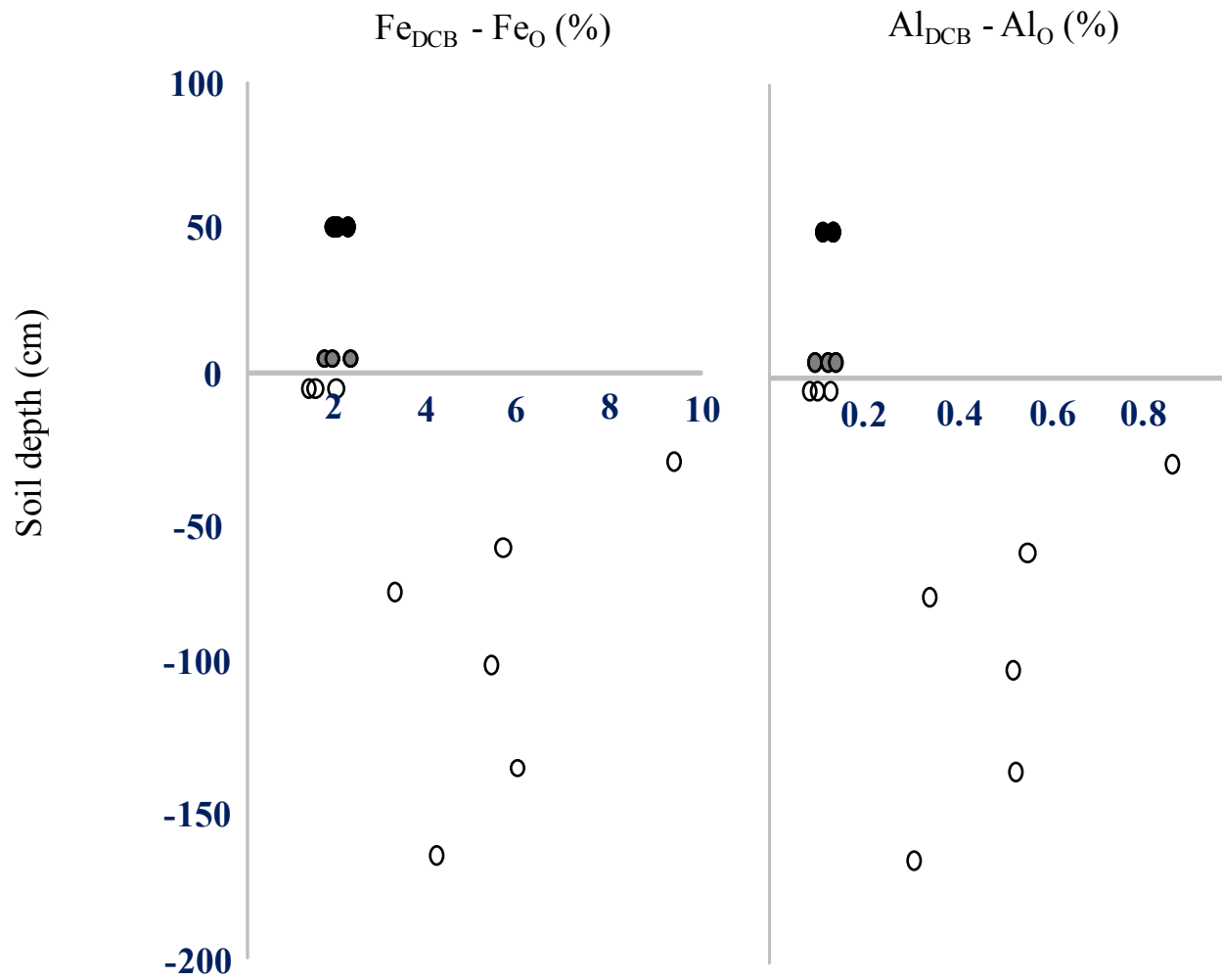
Figure 7



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, Ca²⁺, Mg²⁺, Na⁺, K⁺,
 652 Fe³⁺, Mn²⁺ and Al³⁺ in cmol⁽⁺⁾ kg⁻¹) in the control soils at 0-5 and 70-120 cm depth (Ctrl₀₋₅ and Ctrl₇₀₋₁₂₀, 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*² and *P*-values) tests are also given.

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	C	N	Clay (%)	Silt	Sand	CEC	Ca ²⁺	Mg ²⁺	Na ⁺ (cmol ⁽⁺⁾ kg ⁻¹)	K ⁺	Fe ³⁺	Mn ²⁺	Al ³⁺	pH
TM	1.75 ^b	0.13 ^b	31.2	18.1	50.7	13.30 ^b	9.25 ^b	2.96	0.043 ^b	0.27	0.016 ^{ab}	0.18 ^a	0.09 ^a	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 ^b	0.14 ^b	29.7	18.9	51.4	13.80 ^b	9.68 ^b	3.22	0.039 ^b	0.40	0.016 ^{ab}	0.04 ^b	0.09 ^a	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 ₀₋₅	3.43 ^a	0.25 ^a	26.6	17.4	56.0	19.50 ^a	14.83 ^a	3.40	0.025 ^b	0.47	0.010 ^b	0.02 ^b	0.05 ^b	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 ₇₀₋₁₂₀	0.49 ^c	0.05 ^c	37.23	18.06	44.72	11.78 ^b	8.00 ^b	3.36	0.111 ^a	0.49	0.022 ^a	0.16 ^a	0.13 ^a	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> _{3,15}	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> ²								1.08						
<i>P</i>								0.781						

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