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1 **Bioturbation and soil resistance to wind erosion in Southern**
2 **Tunisia**

3

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23 **ABSTRACT**

24 Wind erosion is a major threat to the sustainability of arid and semi-arid ecosystems. In these
25 environments, biological soil crusts positively impact soil resistance to erosion. Less is
26 known, however, on the impact of soil bioturbation by animals. In Southern Tunisia,
27 bioturbation is mainly carried out by termites, ants and rodents which deposit mineral and
28 organic components on the soil surface in the form of soil sheetings for termites or as soil
29 heaps for ants and rodents. We here question the properties of these soils and measure their
30 resistance to wind erosion. We showed that soil sheetings are made of sand grains linked
31 together by bridges of organic matter, clay particles and other small size minerals such as
32 carbonates and gypsum. The stability of these aggregates is comparable to that of biological
33 soil crusts, despite their very different organizations. Conversely, the soil excavated by ants
34 and rodents mainly consists in individual sand grains, which are impoverished in organic
35 carbon and prone to wind erosion. In conclusion, this study highlights the importance of
36 termites, as key soil bioturbator, on the dynamics of soil aggregates in Southern Tunisia. It
37 also shows that they have an opposite effect than that of ants and rodents on the resistance of
38 soil to erosion.

39

40 **Keywords:** soil biological crusts, termites, sheetings, ants, rodents, aggregation, clay, organic
41 matter

42

43 **1. Introduction**

44 To ‘soil bioturbation’ corresponds the ecological processes associated to the production of
45 soil from saprolite, its movement from belowground to the ground and/or downslope, as well
46 as its mixing and modification of properties by soil fauna (Wilkinson et al., 2009). Therefore,
47 soil bioturbation can significantly impact numerous ecological functions and ecosystem
48 services such as those associated to the dynamics of nutrients, water or plant and animal
49 diversity, as well as the resistance of soil to physical degradation (e.g., compaction and
50 erosion) (Lavelle et al., 1997; Wilkinson et al., 2009).

51 Soil bioturbation can be performed by many digging animals and a gradient of soil
52 bioturbation has been proposed, from the ‘soil bioturbators *sensu stricto*’, ‘soil aggregate re-
53 organizers’ to the ‘soil weathering agents’ categories (Bottinelli et al., 2015). To the first
54 group corresponds animals that only translocate soil aggregates or particles without changing
55 their internal organization. This group typically includes ants, beetles and other arthropods
56 (Lobry and Conacher, 1990; Eldridge and Pickard, 1994), as well as mammals such as
57 rodents, moles and wild boars (Whitesides and Butler, 2016; Anzah and Butler, 2017; Clark et
58 al., 2018; Don et al., 2019; Eldridge and Koen, 2021). The second and third groups include
59 animals that, in addition to the translocation of soil, modify the internal organization of soil
60 aggregates and fasten the weathering of soil minerals. They mainly include earthworms and
61 termites. The impact of earthworms is important in temperate and tropical humid
62 environments where they produce galleries and organo-mineral aggregates called casts (Van
63 Groenigen et al., 2019). When the environment gets drier, this role is mainly restricted to
64 termites, which produce galleries as well as subterranean chambers and aboveground organo-
65 mineral structures, commonly named termitaria or mounds, with specific soil physical,
66 chemical and biological properties (Jouquet et al., 2011). Some species also produce
67 protective covers (i.e. sheetings or sheaths) made of soil aggregates glued the one the other on

68 the ground, mostly to cover the litter that they consume (Harit et al., 2017). The impact of
69 termites is the most significant in arid and semiarid environments where they are the main
70 decomposers. For instance, termites consume as much as 10-30% and sometimes 50% of the
71 net primary production in the Chihuahuan desert, and they are responsible for most of the
72 organic matter turnover and nutrient cycling in soil (e.g., Schaefer and Whitford, 1981;
73 Whitford, 1991; Zaady et al., 2003; da Costa et al., 2019). In the Sahel, their activity has
74 significant impacts on soil porosity and they significantly reduce water runoff while
75 increasing water infiltration (Mando et al., 1999; Leonard and Rajot, 2001). Their activity can
76 also be at the core of agricultural practices aiming at optimizing the nutrient and water
77 dynamics through the decomposition of litter and the production of tunnels that increase water
78 infiltration (e.g., Kaiser et al., 2017).

79 In South-Eastern Tunisia, soils are sandy with very limited clay and organic matter
80 contents. Precipitations are scarce and the vegetation sparse. These environmental conditions
81 provide, therefore, very harsh living conditions for soil fauna. Moreover, the mechanization of
82 agriculture with the tillage of soil using more destructive tools (such as the disc plough or the
83 tiller) than the traditional ones (e.g., mouldboard plough) has deleterious impacts on soil
84 biodiversity, soil structure and wind erosion (e.g., Akrimi et al., 1993 ; Labiadh et al., 2011,
85 2013). Indeed, wind erosion is known to be a major threat to soil conservation in Southern
86 Tunisia, which is also one of the main pathways for air masses coming from the Sahara to the
87 central Mediterranean basin (e.g., Bergametti et al., 1989; Guerzoni et al., 1997; Moulin et al.,
88 1998; Israelevitch et al., 2012). Information on soil fauna and soil bioturbation is very limited
89 in this region and how they influence soil resistance to wind erosion totally unknown.
90 However, the accumulation of soil on the ground by soil fauna can either positively or
91 negatively impact soil properties and therefore wind erosion, depending on the amount and
92 stability of soil deposited on the ground by soil fauna. Understanding the functional impacts

93 of soil organisms is, therefore, a real challenge for the definition of soil conservation practices
94 (Ortiz et al., 2021) and for the sustainability and adaptation of south Tunisian agriculture
95 dominated by olive orchards and cereal fields in particular (Labiadh et al., 2011). Therefore,
96 the objective of this study was to determine the diversity of bioturbation agents adapted to the
97 harsh environmental conditions of this region and to quantify their impacts on soil dynamics
98 and soil resistance to wind erosion.

99

100 **2. Materials and methods**

101 *2.1. Study site*

102 The study was carried out in the Dar Dhaoui Experimental Range (54 ha) (33°17'41"N,
103 10°46'57"E), in the arid coastal Jeffara plain belonging to the governorate of Medenine.
104 Annual precipitation is low ($\approx 200 \text{ mm y}^{-1}$) irregular in space with a very strong annual and
105 monthly variability, with most precipitation falling from September to May. This area is
106 protected from grazing and other disturbances since the late seventies, and the natural
107 vegetation is dominated by *Retama raetam*, *Rhanterium suaveolens*, *Artemisia campestris*,
108 and *Aristida pungens* (Akrimi et al., 1993). The surrounding fields are intensively cultivated
109 by olive tree orchards, with strong evidence of sand movements in small dunes over bare
110 surfaces regularly tilled. The major soil type in the Jeffara plain area is classified as Arenic
111 Calcisol in the IUSS WRB (2014) classification with the occurrence at a depth between 0.60
112 to 1.0m of a calcic horizon sometimes indurated in a discontinuous petrocalcic horizon. The
113 occurrence of the calcic layer is probably due to capillary rise from deeper calcaric or
114 limestone layers. The soil has a low soil organic matter (SOM) content ($< 0.3\%$ in the topsoil)
115 and it is dominated by aeolian quartz ($\sim 80\%$ of sand) (Labiadh et al., 2013). Over 50% of the
116 sandy fraction is ranging between 75 and 100 μm . The experiment was carried out during the
117 summer in June-July 2019, during which precipitation and wind erosion events are rare

118 (Labiadh et al., 2013). In this area, soil bioturbation is mainly realized by termites, ants and
119 rodents, although other animals (e.g., scorpions, beetles and lizards) can also locally impact
120 soil structure. Bioturbation by termites is easily identifiable on the ground by the production
121 of sheetings, which correspond to soil aggregates glued to each other and anchored to the soil,
122 while ants and rodent bioturbation consists in the production of soil heaps on the ground
123 (Figure 1). Only one termite species belonging to the Hodotermitidae family, most likely
124 *Microhodotermes maroccanus*, was found in the study field. Conversely, several ant species
125 were identified in the area but only the most dominant ant species *Monomorium* sp. was
126 considered in this study. Rodents were represented by species of the genus *Meriones*.

127

128 2.2. Quantification of soil bioturbation and soil sampling

129 Soil bioturbation was measured in 10 randomly selected plots of 2 × 5 m. For each plot, the
130 surface and volume of soil mobilized by soil fauna were visually assessed according to the
131 field method proposed by Casenave and Valentin (1992) and in differentiating the soil
132 brought to the surface by rodents, ants and termites. A fourth unknown category included soil
133 for which the origin of the soil could not be visually determined.

134 Soil samples consisted in soil sheetings produced by termites, soil excavated on the
135 ground by rodents and ants (n = 4). Their properties were determined as explained below.
136 Since soil crust is the most dominant soil surface feature in this area, crusts (0-1 cm depth)
137 were sampled and considered as control (n = 4, Figure 1C).

138

139 2.3. Soil physical and chemical properties

140 Physical and chemical properties were measured from soil samples previously air-dried
141 during four days. The organic carbon concentrations (C_{org}) were measured with an elemental
142 analyser (Thermo Flash HT, Thermo Fisher Scientific Inc., Waltham, USA) and after

143 decarbonation using diluted HCl at 2%. Soils were sieved in water after SOM destruction with
144 H₂O₂. Complete dispersion was achieved with Na-hexametaphosphate (20 g L⁻¹) and
145 ultrasonication during 30 min. Five soil particle size classes were considered: clay (< 2 μm),
146 fine silt (2 - 20 μm), coarse silt (20 - 50 μm), fine sand (50 - 200 μm) and coarse sand
147 particles (200 - 2000 μm). Soil pH and electrical conductivity (EC) were determined in
148 soil/water suspension (soil:solution = 1:5).

149 Scanning electron microscope (SEM Zeiss EVO LS15) observations were performed
150 at 15 kV on gold or carbon coated soil samples. Since no difference in soil physical and
151 chemical properties could be measured between ants and rodent soils, only termite sheetings,
152 soil excavated by ants and the soil crust (composite samples) were considered. Identification
153 of particles was achieved from their elemental spectrum with an energy dispersive X-ray
154 microprobe (EDX, Oxford Instruments, INCA Energy 350) coupled to the microscope.

155

156 *2.4. Soil resistance to wind erosion*

157 As a proxy of soil resistance to wind erosion, soil structural stability was first measured by
158 dry sieving using a vibratory sieve shaker (Retsch AS 200). Samples (~10g, n = 10 per
159 treatment) were differentiated according to their sizes (> 2mm, 2-1mm, 1-0.5mm, 0.5-0.2mm,
160 0.2-0.1mm, 0.1-0.05mm and < 0.05mm) after 1 min of shaking with an amplitude of 50%.
161 The percentage of soil > 0.1 mm was used as a proxy of soil resistance to erosion since the
162 optimum grain size for wind erosion is measured at ≈ 80 μm (Bagnold, 1941; Chepil, 1951).

163 Soil resistance to wind velocity was also measured through a laboratory experiment.
164 Soil samples (~1g, n = 10 per treatment) were aspirated by a Dyson V11 vacuum placed at the
165 vertical of the samples. Three distances were recorded: (i) when particles started to set in
166 motion (h₀), (ii) when the smallest particles started to be aspirated into the vacuum (h₁), and (iii)
167 when the full sample was aspirated (h_f). The distance (mm) was thereafter converted in velocity

168 (m sec⁻¹) after calibration using an anemometer (Dorsmann TA 888 Hot Wire). Termite
169 sheetings are very fragile in the field and can rapidly be broken into smaller elementary
170 macro-aggregates ~2 mm in size. To test the impact of this fragmentation of sheetings into
171 smaller size aggregates, the simulation experiment was carried out from five soil aggregate
172 types: the control soil (i.e. the soil crust), intact termite sheetings, aggregates ~2mm in size
173 obtained by carefully fragmenting sheetings, and soil excavated by ants and rodents.

174

175 *2.5. Statistical analyses*

176 One-way analysis of variance (ANOVA) and least significant difference (LSD) tests were
177 performed to assess differences between means. Prior to the ANOVAs, data were log-
178 transformed (when required) to achieve homogeneity of variances and normality, which were
179 confirmed using Levene and Shapiro-Wilk tests. Pairwise comparisons were made with
180 Kruskal-Wallis tests with a false discovery rate correction when ANOVA assumptions were
181 not met. Principal component analysis (PCA) and Monte Carlo permutation tests (999
182 permutations) were also carried out from soil physical and chemical properties (i.e., electrical
183 conductivity, organic C content, particle size distribution and % of soil > 100 µm).
184 Differences among treatments were declared significant at the < 0.05 probability level. All
185 statistical calculations were carried out using R version 3.5.1 (<https://www.r-project.org/>) and
186 using “ade4”, “car”, “ggplot2” and “factoextra” packages.

187

188 **3. Results**

189 *3.1. Soil bioturbation and surface features*

190 In average, 9.75% of the soil surface was influenced by soil bioturbation (i.e., 975 cm² m⁻²,
191 Standard error SE: 329) and the quantity of bioturbated soil reached 1524 cm³ m⁻² (SE: 752).
192 Despite an apparent higher surface and volume of soil impacted by the activity of rodents, no

193 significant differences could be measured between rodents, ants and termites ($P > 0.05$
194 between treatments, surface = $325 \text{ cm}^2 \text{ m}^{-2}$ and volume = $504 \text{ cm}^3 \text{ m}^{-2}$ in average per
195 treatment), while the area and volume of soil impacted by the activity of unknown organisms
196 were significantly lower than for the other treatments (Kruskal-Wallis $\text{Chi}^2 = 9.18$ and 12.15 ,
197 P -values = 0.027 and 0.007 , for the area and volume, respectively) (Figure 2).

198

199 *3.2. Soil physical and chemical properties*

200 The PCA shown in Figure 3 differentiated three groups from their soil chemical and physical
201 properties (Monte Carlo permutation tests, P -value = 0.001). The overlap between ants and
202 rodents evidenced similar properties (see Appendix 1). Conversely, the soil crust and termite
203 sheetings were differentiated from their specific properties. Termite sheetings were
204 differentiated from the soil excavated by ants and rodents along the first and second axis,
205 which explained ~ 39 and 21% of the total variability, respectively. Termite sheetings had a
206 higher electrical conductivity, percentage of soil $> 100 \mu\text{m}$ (dry sieving), and higher clay (wet
207 sieving) and organic C contents than the soil excavated by ants and rodents ($P < 0.05$, see
208 Appendix 1). Termites sheetings were also differentiated from the soil crusts along the first
209 axis, mainly because of the higher electrical conductivity, clay and C contents of sheetings in
210 comparison with soil crusts. Finally, soil crusts had very similar properties than the soil
211 excavated by ants and rodents with the exception of the percentage of soil $> 100 \mu\text{m}$ which
212 was significantly higher in soil crusts.

213 SEM micrographs of the soil surface features are presented in Figures 4, 5 and 6. The
214 soil crust was characterized by sand grains embedded in a dense matrix of organic matter and
215 clay particles (Figures 4A and B). Bryophytes, plant residues and numerous filaments covered
216 by clay particles were observed and sealed the soil surface (Figure 4 B, C and D). Soil
217 excavated by ants (Figures 5) were made of individualized sand particles of varying sizes but

218 usually < 100 μm with coatings of clay minerals (Figure 5A). The few soil aggregates
219 observed were made of sand grains associated to each other by biotic filaments and clay
220 particles (Figures 5B, C and D). Smaller tubular pores surrounded by clay particles were also
221 observed. Finally, SEM micrographs of termite sheetings (Figures 6) displayed a very specific
222 organization with aggregates made of sand grains < 100 μm bounded together with clay
223 particles (Figure 6B). Filaments and small size minerals, displaying chemical composition of
224 carbonates and gypsum (See Appendix 2), were also observed associated with quartz grains.

225

226 3.3. Soil resistance to wind erosion

227 The dry sieving of soil evidenced large differences in term of soil aggregate fractions between
228 treatments (Figure 7). With the exception of the smallest particle size fraction (< 0.05 mm),
229 which constituted only ~5% of the soil, significant differences were measured for all the other
230 fractions (Table 1). Crusts were highly stable and dominated by large aggregates > 2 mm
231 (47% of the soil, in average), while the soil excavated by rodents and ants was mainly of
232 small size between 0.05-0.1 mm (60% of the soil). Termite sheetings had intermediate
233 properties between those of the crust and those of ants or rodents. While no difference was
234 measured between termites, ants and rodents for the 0.1-0.2 soil fraction (27% of the soil, $P >$
235 0.05 between treatments), termite sheetings were enriched in particles > 0.2 mm but
236 impoverished in particles < 0.1 mm in comparison with the soil excavated by ants and rodents
237 ($P < 0.05$ in all cases).

238 Figure 8 shows that the soil motion occurred only for broken sheetings, and soil
239 excavated by ants and rodents (i.e. no soil motion was evidenced for crusts and termite
240 sheetings). Soil motion (h_0) occurred at a lower wind velocity for ant and rodent soils, without
241 significant difference between them, in comparison with broken sheetings (1.5 vs. 2.2 m s^{-1} ,
242 for ants and rodents vs. broken sheetings, $P < 0.05$). The same trend was measured for h_1 with

243 first particles visually vacuumed for 1.9 m s^{-1} for ant and rodent soils ($P > 0.05$ between both)
244 while broken sheetings were vacuumed at 3.0 m s^{-1} ($P < 0.05$ between broken sheetings and
245 the other treatments). Finally, broken sheetings, and soil excavated by ants and rodents ($P >$
246 0.05 between them) were entirely vacuumed (h_f) at lower velocity than crusts and sheetings
247 with 6.3 against 25.7 m s^{-1} , respectively ($P > 0.05$ between crust soil and termite sheetings).

248

249 **4. Discussion**

250 *4.1. Bioturbation and soil translocation*

251 Because soil bioturbation is season-dependent, its snapshot quantification has to be
252 considered with cautious. In our study, soil bioturbation was measured before the summer
253 when temperature and soil moisture allowed soil fauna activity while the presence of plant
254 residues provided a substantial amount of resources for soil decomposers, amongst which
255 termites. As expected, soil bioturbation mainly resulted from the activity of rodents, termites
256 and ants while other organisms (e.g., scorpions, spiders, lizards) had only a limited impact.
257 Despite an apparent higher activity of rodents, the high variability measured between plots did
258 not allow measuring significant differences between bioturbation types in terms of surface
259 and volume of soil impacted by bioturbation.

260

261 *4.2. Bioturbation and soil properties*

262 The PCA carried out from the soil physical and chemical properties clearly differentiated the
263 soil excavated by ants and rodents from termite sheetings and to a lesser extent from the crust
264 soil. Soil structural and biological crusts constitute a key elements of arid and semi-arid
265 ecosystems and their dynamics and microstructure have been largely described (e.g., [Bresson](#)
266 [and Valentin, 1994](#); [Belnap and Lange, 2003](#); [Zhang et al., 2006](#); [Seppelt et al., 2016](#)).
267 Surprisingly, soil crusts had very similar properties as the soil excavated by ants and rodents
268 (i.e., no significant differences between variables, [Appendix 1](#)), with the exception of their

269 organization and stability. Indeed, SEM images showed that crusts consisted in sand grains
270 embedded in an organic matrix made of organic fragments and filaments, and most likely
271 polysaccharides excreted by filamentous cyanobacteria (Mazor et al., 1996; Lan et al., 2010)
272 or endolithic micro-organisms formed in saline conditions (Stivaletta and Barbieri, 2009) such
273 as in the close evaporitic Sebkhet el Melah depression, and transported by the wind.
274 Conversely, the soil exposed on the surface by ants and rodents mainly consisted in individual
275 sand grains. Only a few soil aggregates were observed with the SEM. The origin of these
276 aggregates is unknown but we assume that their presence could be explained by the
277 fragmentation of the surface crust and/or by the rise of belowground aggregates resulting from
278 the interaction between clay particles and roots and/or biotic filaments. Biological soil crusts
279 play a major role in the cycling of C through the fixation of CO₂ (Grote et al., 2010).
280 Consequently, higher organic C contents are usually measured in biological soil crusts in
281 comparison with the surrounding topsoils (Chamizo et al., 2012). In our study, no difference
282 in C content between crust soils and soils excavated by ants and rodents could be evidenced.
283 We assume that this lack of significant difference can be explained by our sampling design
284 and the fact that the majority of microbes and C peaks in biological soil crust are located in
285 the first mm (Garcia-Pichel and Belnap, 1996; Garcia-Pichel et al., 2003 ; Raanan et al., 2015;
286 Jung et al., 2018) while we sampled the soil crust plus the 0-1 cm soil layer below the crust.

287 As observed in West-Africa and Asia, termite sheetings were enriched in clay in
288 comparison with the other soil surface features (Appendix 1, Harit et al., 2017), then
289 confirming the importance of these minerals for termites as a construction element. The
290 selection of clay and its enrichment in termite constructions is usually explained by the higher
291 stability it confers to aggregates (Jouquet et al., 2002, 2004), as confirmed in our study with
292 the similar percentage of soil > 100 µm between termite sheetings and soil crusts. Termite
293 sheetings were also differentiated from the other soil surface features because of their higher

294 electrical conductivity. This higher electrical conductivity is controlled by the occurrence of
295 fine crystals of gypsum, slightly soluble in water ($\approx 2.5 \text{ g L}^{-1}$) with an electrical conductivity
296 close to 2 mS cm^{-1} at soil-water saturation with a 1/5 dilution. Therefore, since gypsum and
297 carbonates are concentrated in deeper layer, these findings suggest a translocation of soil from
298 the deep soil layers to the surface by termites. Images obtained from SEM showed that
299 bridges between sand particles were mainly made of clay (most likely illite or smectite),
300 carbonate and gypsum, then explaining the increase in electrical conductivity in termite
301 sheeting in comparison with the other treatments. Termites do not only select soil particles
302 and minerals for the construction of termite sheetings. It is likely that bridges between sand
303 particles can also be explained by the incorporation of organic matter, as evidenced by the
304 higher organic C content in termite sheetings than in the other treatments (almost two-fold
305 increase; see [Appendix 1](#)). Indeed, the production of stable soil aggregates involves the
306 transportation of soil and its humidification by saliva, which contains water and organic
307 molecules ([Contour-Ansel et al., 2000](#)). More research are clearly now needed to both
308 understand the mechanisms associated to the organization of soil aggregates and to determine
309 the fate of this organic matter exposed on the soil surface to the wind.

310

311 *4.3. Consequences in term of soil resistance to wind erosion*

312 In our study site, the wet and dry sieving of soil showed that it is dominated by fine sand
313 particles between 50 and 100 μm , which corresponds to the optimum grain size for wind
314 erosion (i.e., 80 μm) ([Bagnold, 1937](#); [Chepil, 1951](#)). This finding confirms the high
315 vulnerability of the soil in this area ([Labiadh et al., 2013](#)). In arid and semi-arid environments,
316 accelerating biological soil crust development provides a credible alternative for stabilizing
317 sand particles and reducing the susceptibility of soil to wind erosion ([Eldridge and Leys,](#)
318 [2003](#); [Fattahi et al., 2020](#); [Kheirfam and Asadzadeh, 2020](#)). Our study confirmed the high

319 stability of biological crusts in comparison with the other treatments. While no difference in
320 particle size fractions was measured between soil crusts and the soil excavated by ants and
321 rodents, the dry sieving of soil showed that most of the crust resisted to the dry sieving
322 procedure (> 50% of soil in the > 2 mm size fraction) while ant and rodent soils broke down
323 and were mainly found in the 50-100 μm size fraction against < 1% in the > 2 mm size
324 fraction. These results were confirmed by the wind erosion experiment which showed that soil
325 motion was rapidly detected for ant and rodent soils followed by their exportation while soil
326 crust remained stable until they are exported at a velocity higher than 20 m s^{-1} .

327 The higher clay and C contents and amount of gypsum (as evidenced by the measure
328 of the electrical conductivity) of soil sheetings in comparison with the other soil types and
329 their organization into small size macro-aggregates improved their resistance to wind erosion.
330 This was evidenced by both the dry sieving method and the soil erosion experiment, which
331 showed that intact soil sheetings had a resistance to wind almost equivalent to crust and
332 therefore significantly higher than the soil excavated by ants and rodents. The life-time of
333 sheetings is unknown in the field. If their specific organization can be observed when they are
334 recently built, sheetings are also very fragile in the field and they can be broken into smaller
335 size aggregates. The simulation experiment showed that once broken these aggregates become
336 more susceptible to erosion than intact sheetings although their stability, evidenced during the
337 dry sieving of soil aggregates, and large size and weight make them more resistant to wind
338 erosion than the soil excavated by ants and rodents.

339

340 **5. Conclusion**

341 Two types of soil bioturbation could be measured in this study. Termites, as soil aggregate
342 organizers (*sensu* Bottinelli et al., 2015), had a comparable effect to that of biological soil
343 crusts by their ability to form stable soil aggregates enriched in organic C and clay.
344 Conversely, rodents and ants only displaced soil, mainly sand grains, thus confirming their

345 role as bioturbators *sensu stricto*. Consequently, these two types of soil bioturbators have
346 opposite effects on the resistance of soil to wind erosion. Termites are comparable to
347 biological crusts and protect the soil against wind erosion through the production of stable
348 aggregates, while ant and rodent bioturbation leads to the deposition of sand grains on the
349 ground that can easily be transported by the wind. This information is especially important for
350 cultivated lands in the South of Tunisia where intense soil tillage hinders the activity of
351 termites but only slightly reduce those of rodents and ants.

352

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360

361

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- 521 Figure 1. Pictures showing the main soil surface features: termite sheetings (T), soil
522 excavated by ants (A) and rodents (R), and biological crusts (C).
- 523 Figure 2. Boxplots showing the area ($\text{cm}^2 \text{ m}^{-2}$) and volume of soil ($\text{cm}^3 \text{ m}^{-2}$) impacted by
524 soil bioturbation. Comparison is made between soil influenced by rodents, ants,
525 termites and unknown soil fauna. Boxes with similar letters have similar values at
526 $P > 0.05$.
- 527 Figure 3. Biplot showing the principal components analysis (PCA) from variables
528 describing the soil physical and chemical properties of the termite sheetings
529 (termites), soil excavated by ants, rodents and unknown fauna, and the
530 surrounding control soil. Variables are the organic C content (Corg), the clay, fine
531 and coarse silt and sand fractions obtained after dispersion by wet sieving,
532 electrical conductivity (EC), and proportion of soil $> 100 \mu\text{m}$ obtained by dry
533 sieving.
- 534 Figure 4. SEM micrographs of soil crust with quartz grains (q) embedded in a matrix of
535 clay (c), organic matter [A] made of filaments (f) and unidentified organic (org)
536 and plant debris (pl) [B, C]. Note the presence of bryophytes (b) associated to the
537 crust [D].
- 538 Figure 5. SEM micrographs of soil excavated by ants with well individualized quartz grains
539 (q) [A] and soil aggregates [B, C, D] with tubular pores (t) and filaments
540 associated to clay minerals (c).
- 541 Figure 6. SEM micrographs of termite sheetings with aggregates made of quartz grains (q)
542 associated the one to the others [A, C] and covered by clay minerals (c) [B].
543 Bridges between quartz grains made of a mixture of clay, carbonates (Ca), organic
544 filaments (f) and gypsum (gy) [B, D].
- 545 Figure 7. Barplots showing the proportion (in %) of soil obtained from the dry sieving of
546 soil crust, termite sheetings and soil excavated by ants and rodents. Soil size
547 fractions are > 2 , 2-1, 1-0.5, 0.5-0.2, 0.2-0.1, 0.1-0.05 and < 0.05 mm. For each
548 soil fraction, similar letters indicate similar values at $P > 0.05$.
- 549 Figure 8. Boxplots showing the velocity needed to produce soil motion (h_0), to vacuum the
550 first soil particles (h_1) and the entire soil samples (h_f). Similar letters indicate
551 similar values at $P = 0.05$.
- 552

Table 1. Results of the statistical analyses ($F_{3,20}$ and P -values) testing differences in soil aggregate size fractions obtained after dry sieving between termite sheetings, soil excavated by ants and rodents, and the surrounding crust soil (expressed in %).

Aggregate size fractions	$F_{3,20}$	P -values
>2 mm	68.69	< 0.001
2-1 mm	13.71	< 0.001
1-0.5 mm	29.29	< 0.001
0.5-0.2 mm	11.86	< 0.001
0.2-0.1 mm	20.22	< 0.001
0.1-0.05 mm	46.05	< 0.001
< 0.05 mm	1.63	0.213

Appendix 1. Soil physical and chemical properties (pH, electrical conductivity EC, clay, silt and sand contents, C content and % of soil > 100 μ m) of termite sheetings (termites), soil excavated by rodents and ants, and the surrounding soil crust. Results of the statistical analyses (ANOVA or Kruskal-Wallis rank sum test) are displayed. Values with similar letters are significantly similar at $P < 0.05$.

	pH	EC (μ S cm ⁻¹)	Clay (%)	Fine silt (%)	Coarse silt (%)	Fine sand (%)	Coarse sand (%)	C (%)	%>100 μ m
Crust	7.2 (0.2)	45.56 ^b (8.05)	7.88 ^b (0.24)	1.30 (0.24)	3.66 (0.94)	85.88 (1.64)	1.29 (0.20)	0.22 ^b (0.04)	69.94 ^a (4.73)
Rodents	7.6 (0.1)	34.99 ^b (2.67)	7.78 ^b (0.63)	1.62 (0.30)	5.90 (1.03)	82.49 (1.78)	2.22 (0.27)	0.24 ^b (0.03)	32.59 ^b (1.90)
Ants	8.0 (0.2)	30.27 ^b (0.55)	8.73 ^{ab} (0.35)	1.67 (0.30)	3.57 (0.29)	84.55 (0.55)	1.49 (0.11)	0.14 ^b (0.07)	38.73 ^b (1.26)
Termites	7.6 (0.2)	174.20 ^a (42.12)	12.31 ^a (2.24)	1.94 (0.17)	2.63 (0.79)	81.14 (2.29)	1.98 (0.68)	0.38 ^a (0.05)	58.71 ^a (4.55)
$F_{3,12}$	1.81	119.7		1.04	2.89	1.56		7.54	19.08
P -values	0.151	< 0.001		0.41	0.079	0.251		0.004	< 0.001
Chi ²			7.96				4.85		
P -values			0.047				0.183		

Appendix 2. Examples of energy dispersive X-ray results showing the presence of illite or smectite-type clay (a), clay and carbonate (b) and gypsum (c).

Figure 1

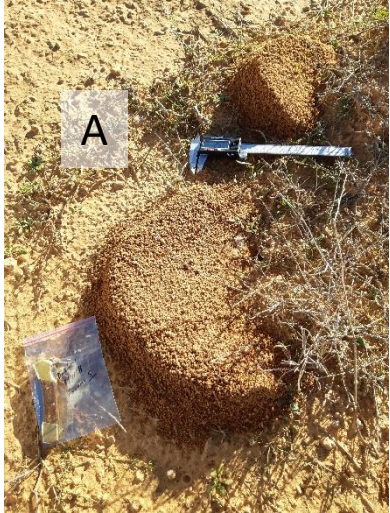


Figure 2

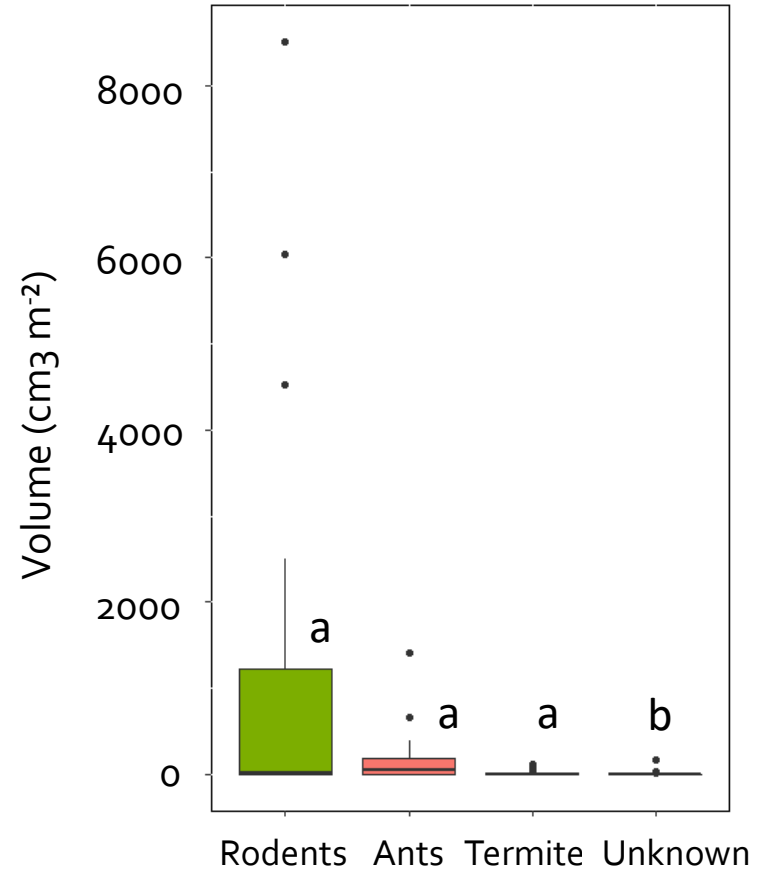
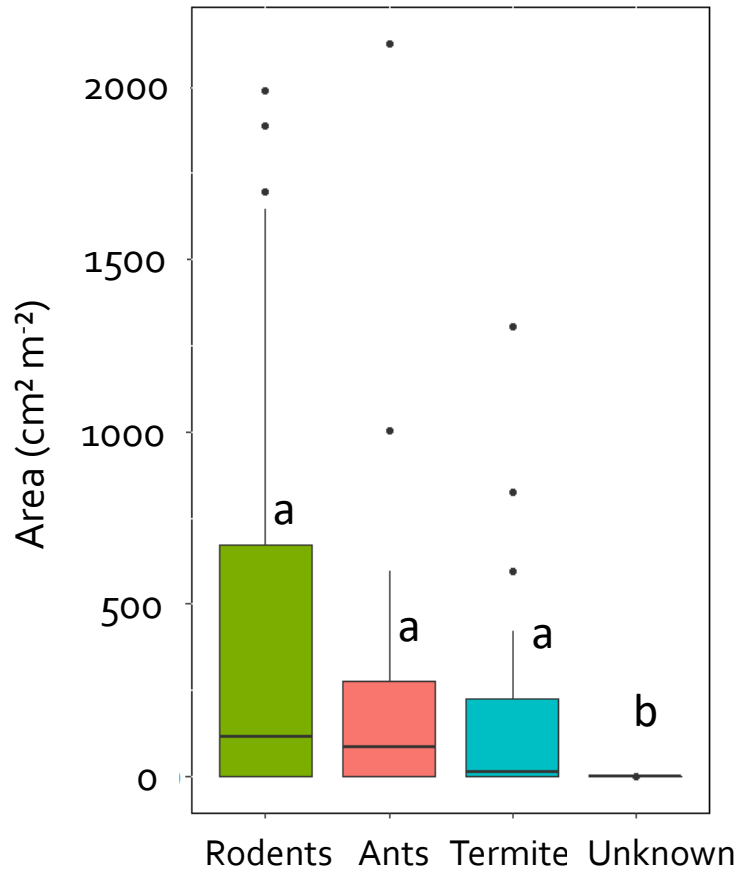


Figure 3

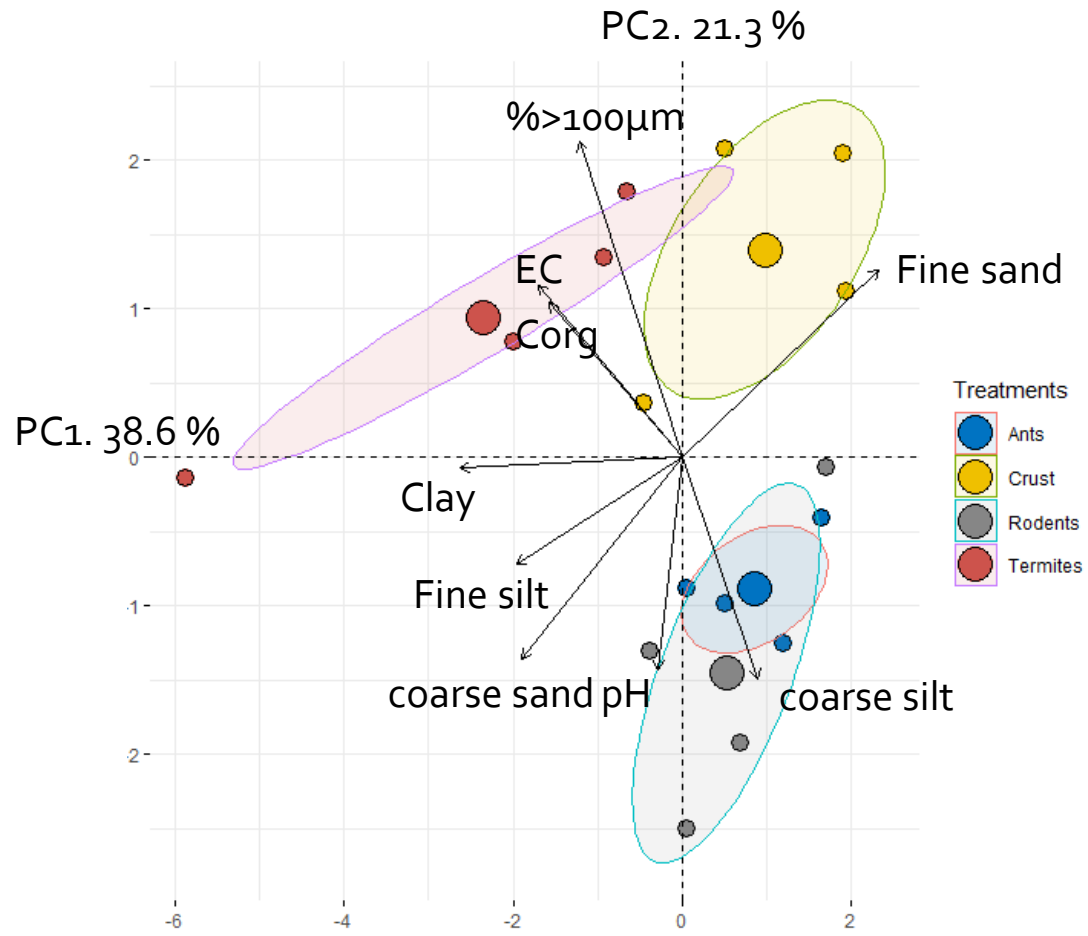


Figure 4

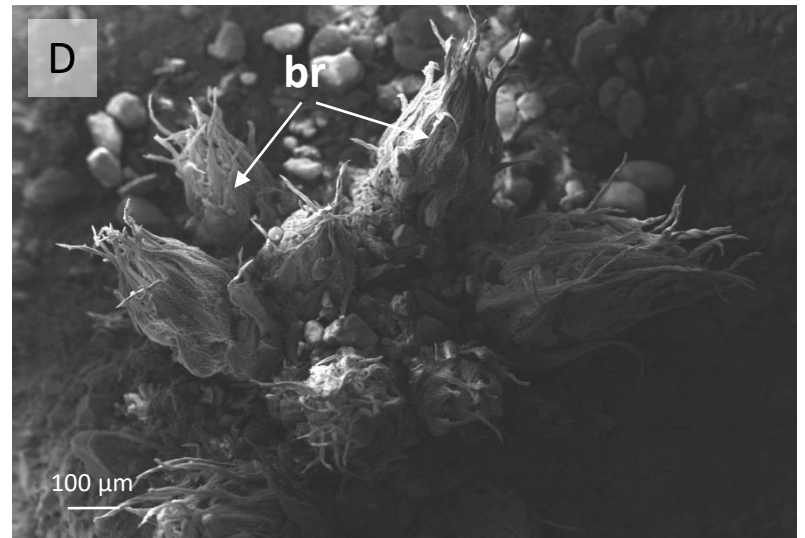
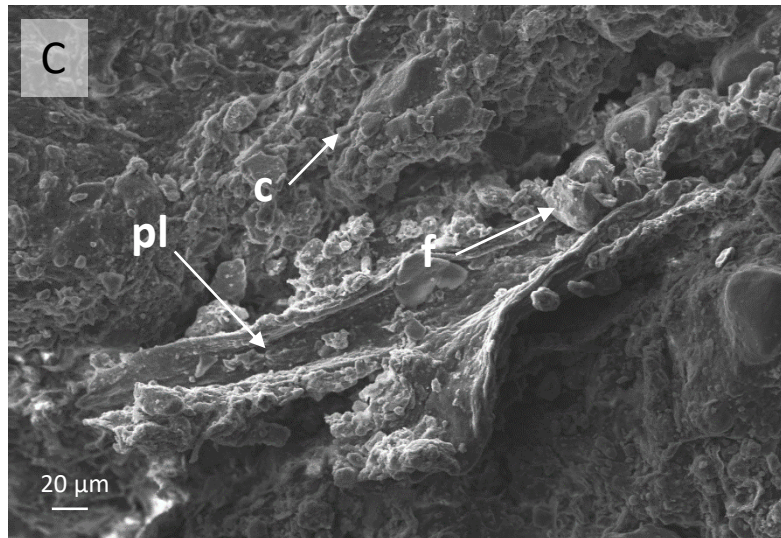
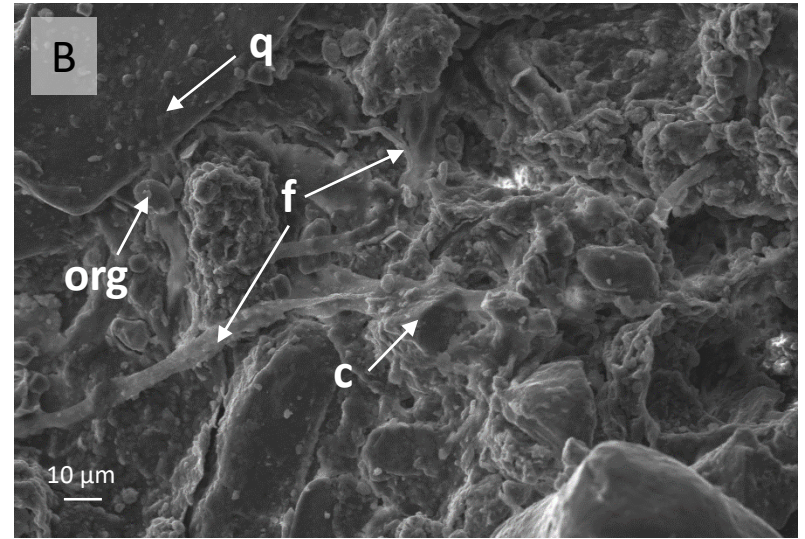
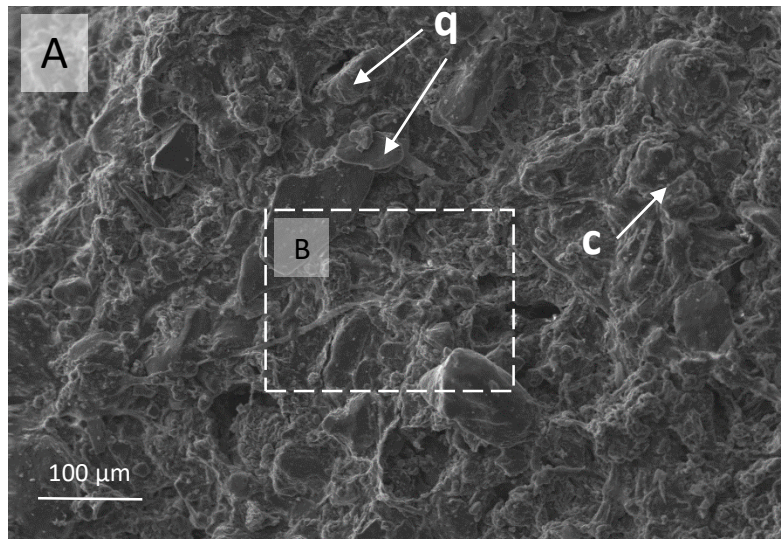


Figure 5

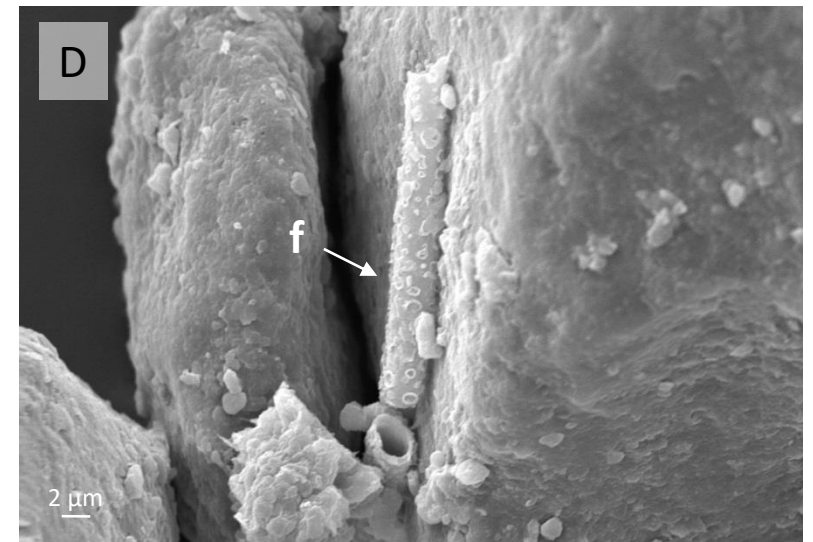
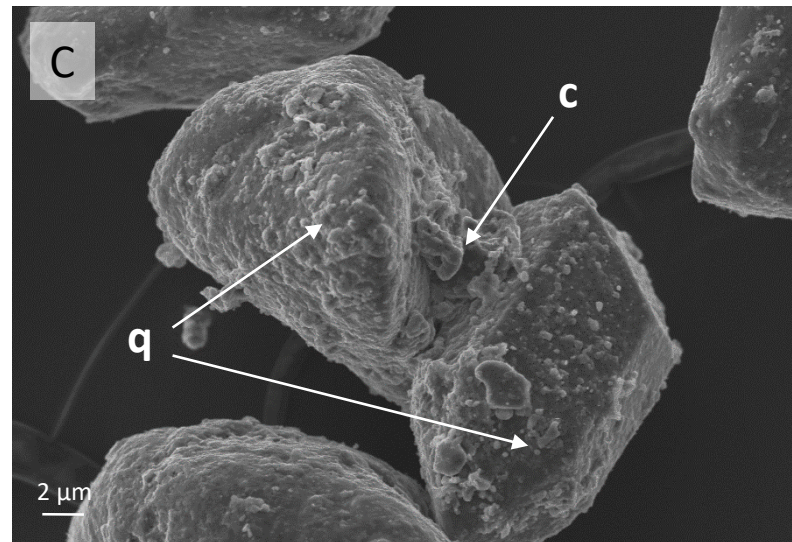
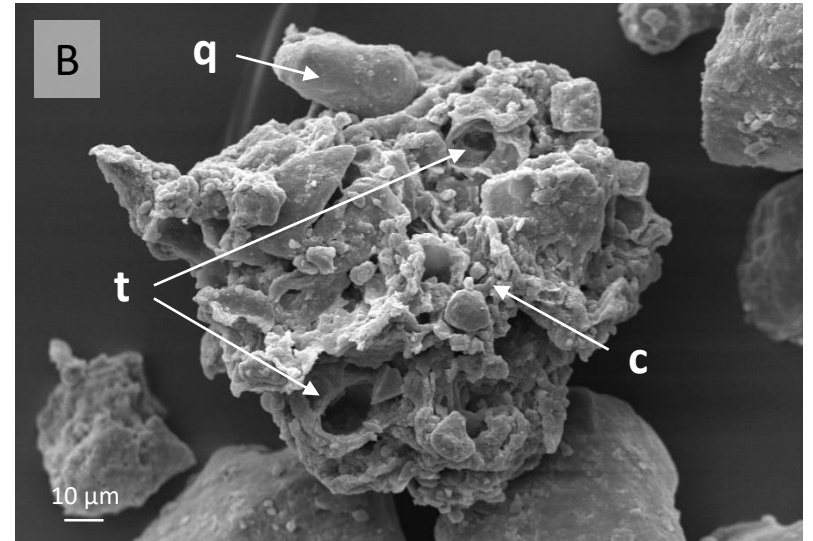
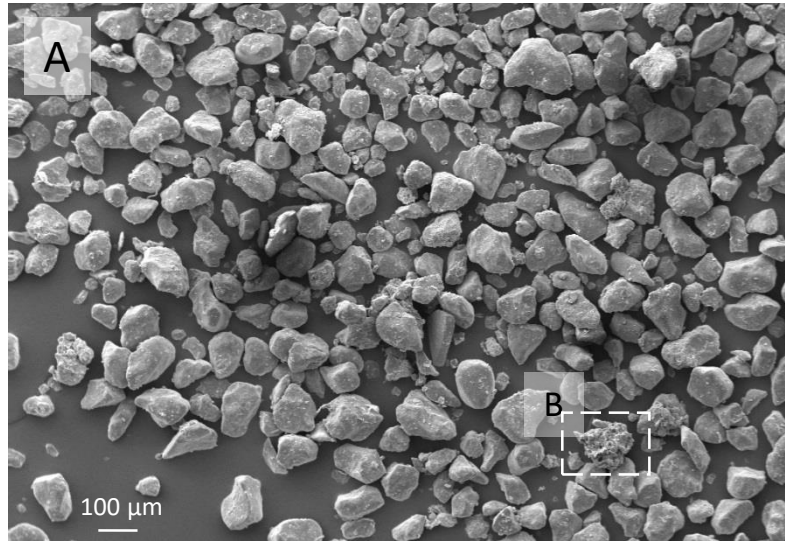


Figure 6

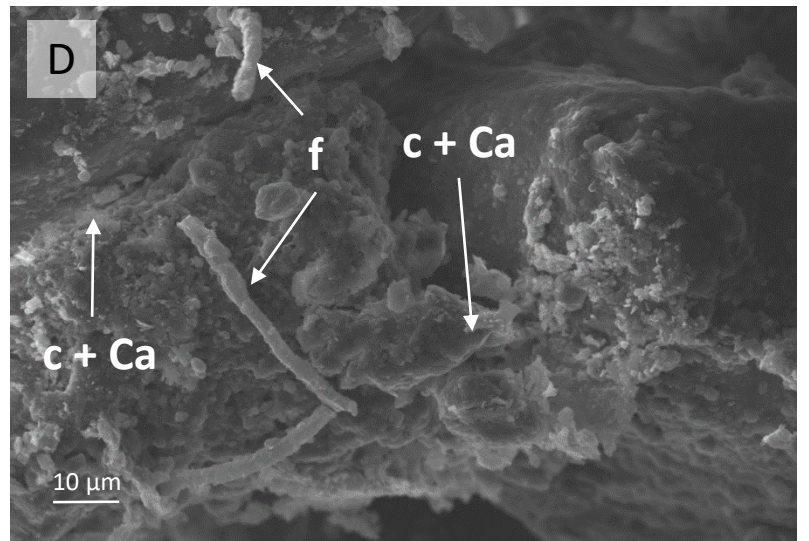
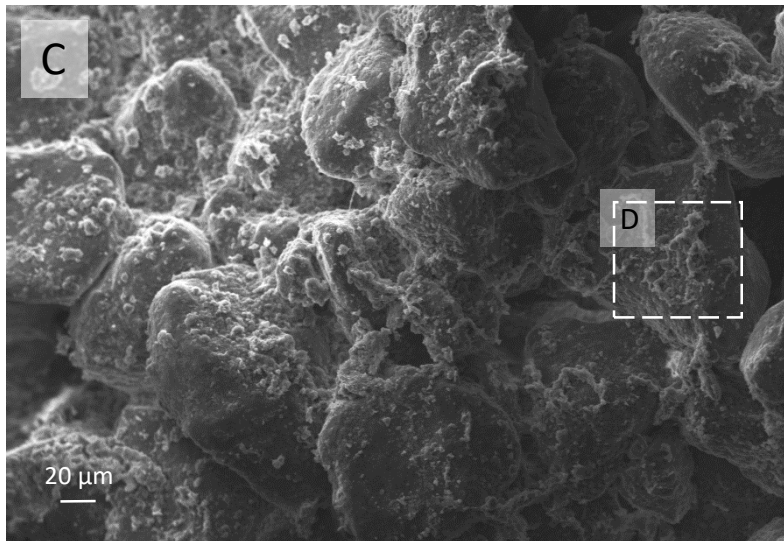
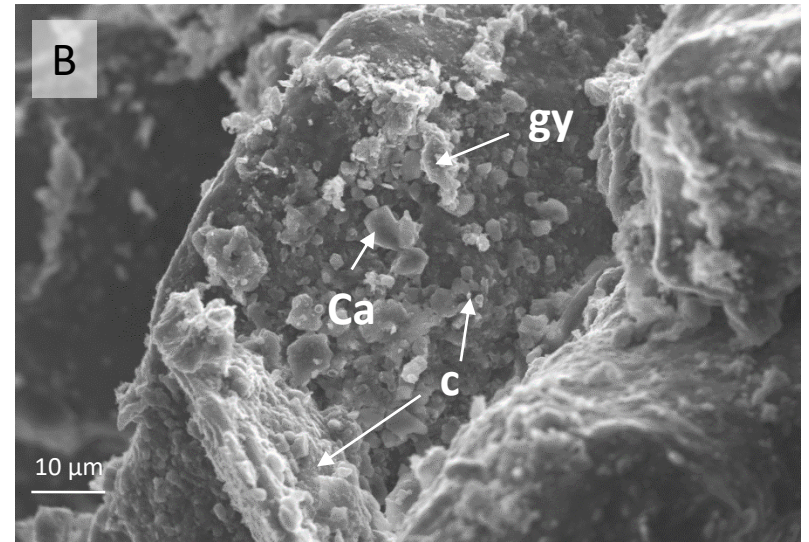
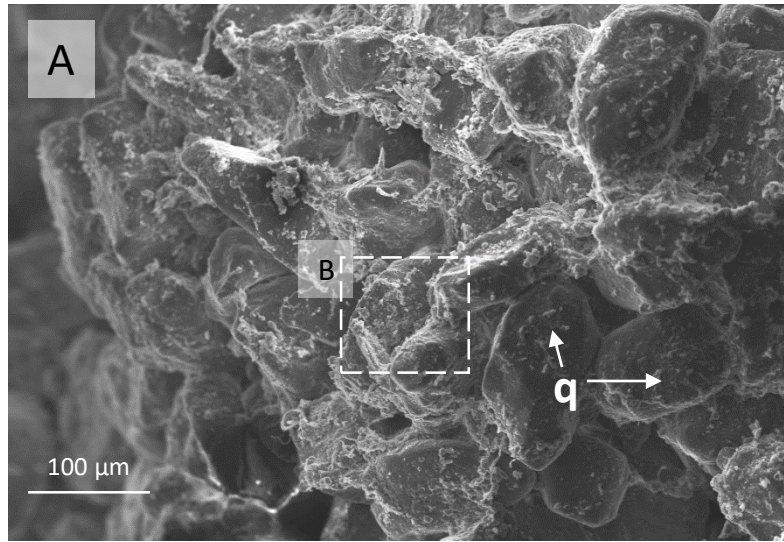


Figure 7

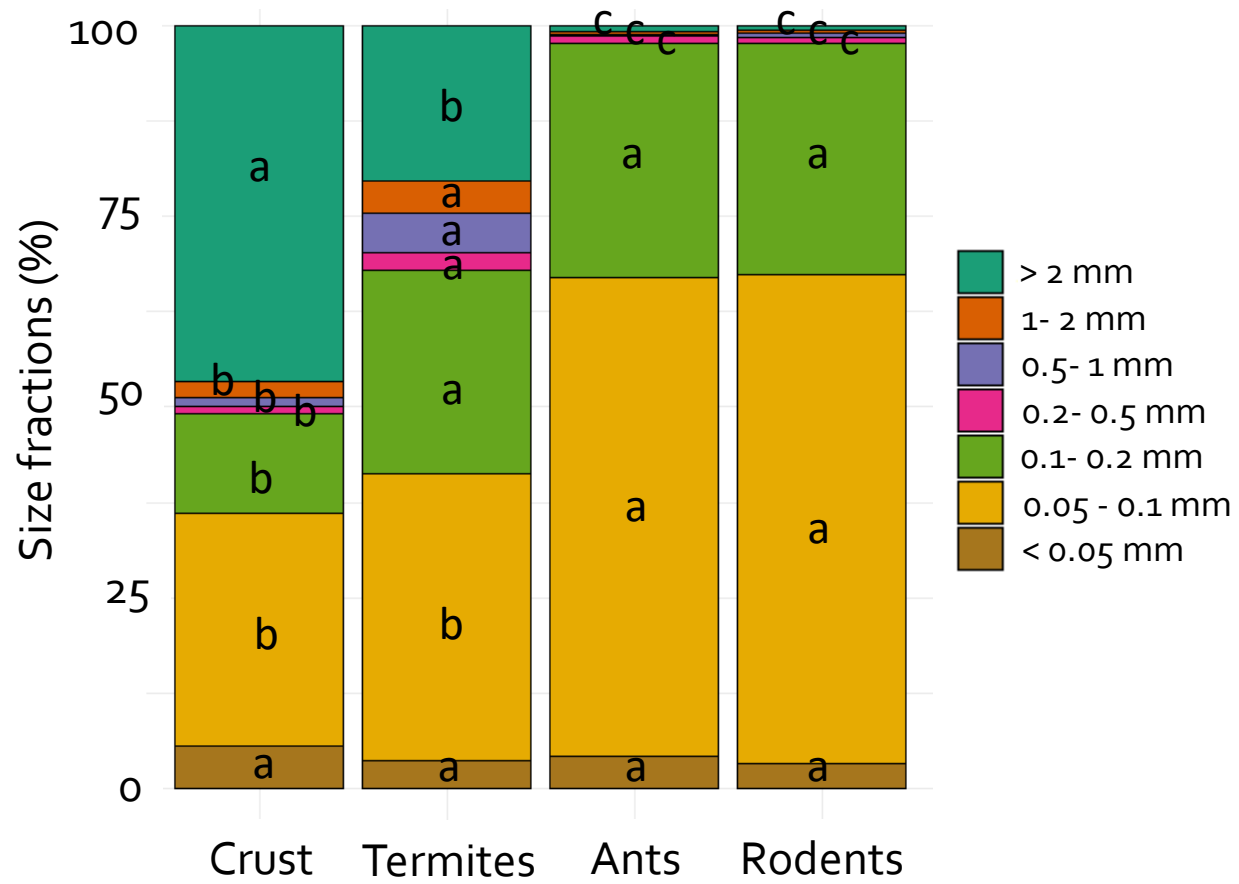
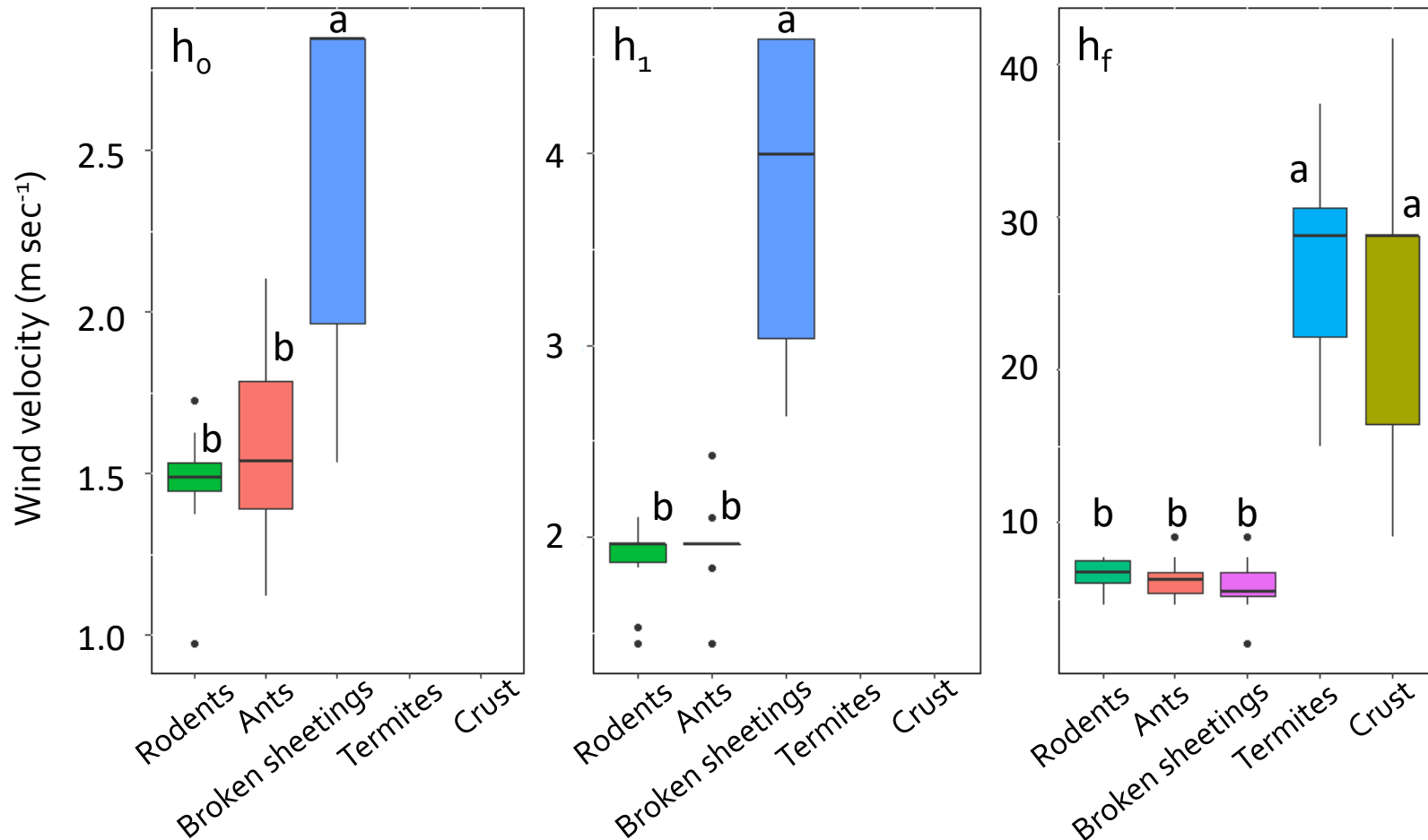


Figure 8



Appendix 2

