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1 **Age matters: dynamics of earthworm casts and burrows produced by the anecic**
2 ***Amyntas khami* and their effects on soil water infiltration**

3

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27 **Abstract**

28 By creating vertical and continuous burrows, anecic earthworms accelerate the
29 transfer of water in soils. However, the degradation mechanisms and lifespan of
30 burrows and the consequence of changes in burrow characteristics for water
31 infiltration remain poorly known. In this study, the dynamics of the degradation and
32 hydraulic properties of burrows made by the anecic earthworm *Amyntas khami* in a
33 clayey soil were investigated in a meadow and in a woodland in North Vietnam. We
34 selected three categories of surface casts, namely, (i) fresh (a few days old), (ii) dry (>
35 1 month old) and (iii) degraded by rain (older than the dry casts), as proxies of the age
36 of burrows. The physical and chemical properties of casts were measured and
37 compared to the surrounding soil aggregates without visible earthworm activity
38 (control). Soil cores were sampled below casts and control and the 3D structure of
39 burrows was characterized using X-ray tomography. Then, water infiltration was
40 measured in the saturated soil cores. Fresh and degraded casts had a lower water
41 stability than control aggregates, whereas higher values were found in dry casts.
42 Water infiltration was twice higher in columns below fresh and dry casts than in the
43 control. However, below degraded casts, the positive effect on water infiltration was
44 reduced or disappeared in some cases. The degradation of burrows led to significant
45 increase in the specific surface area, decrease in their minimum diameter and increase
46 in the abundance of cracks connected to burrows. Our results indicate that anecic
47 burrows persist at least for months below degraded casts but that aging due mainly to
48 physical processes reduces water infiltration. This study highlights the importance of
49 taking into account the lifetime of burrows in the soil when assessing the effect of
50 earthworms on soil structure and water transfer.

51 **Key words:** macrofauna, biopores, bioturbation, hydraulic conductivity

52

53 **1. Introduction**

54 Earthworms belong to one of the most important groups of soil fauna worldwide and
55 are good examples of soil bioturbators due to their ability to modify their habitat
56 physically (Bottinelli et al., 2015). Among earthworms, anecic and epi-anecic species
57 *sensu* Bouché (1971) produce continuous and vertical burrows connected to the soil
58 surface where they eject their dejections, the so-called casts. The role of anecic
59 burrows in water infiltration in soil may become more important as the soil
60 approaches water-saturated conditions (Pitkänen and Nuutinen, 1998). The activities
61 of anecic species may therefore help to mitigate the deleterious effect of heavy rains
62 by increasing soil water infiltration (Andriuzzi et al., 2015) and reducing runoff
63 (Jouquet et al., 2008b) especially in tropical humid ecosystems, where the erosion of
64 soil is a major issue.

65 The morphological characteristics of burrows measured by X-ray computed
66 tomography and image analyses such as burrow continuity, connection to other
67 macropores, size and length are important determinants of water infiltration
68 (Bastardie et al., 2005; Bottinelli et al., 2017; Capowiez et al., 2015). Hence, any
69 changes in these properties may influence the ability of burrows to transfer water.
70 Several mechanisms influencing burrow degradation have been described: breakdown
71 by tillage (Pelosi et al., 2017), compaction by machinery or livestock (Jégou et al.,
72 2002; Ligthart and Peek, 1997), and infilling by earthworm casts (Capowiez et al.,
73 2014). Comparatively, there is dearth of information on the influence of water
74 seepage (Van Den Berg and Ullersma, 1991) and the formation of desiccation cracks
75 (Kretzschmar, 2004) on the degradation of burrows. However, degradation by these

76 two last mechanisms could have significant effects on the hydraulic functionality of
77 abandoned anecic burrows, especially in soils presenting a high shrinkage capacity.

78 In North Vietnam, the anecic earthworm *Amyntas khami* (Megascolecidae
79 family) produces large casts on the soil surface (Jouquet et al., 2008a). These casts are
80 water stable and may last for months to years under some conditions. Our first
81 observations revealed that casts stop growing after one month and no new cast is
82 produced at the base of the cast, which indicates that the burrow below is no more
83 used by the earthworm. Casts produced by *A. khami* therefore offer a unique
84 opportunity to study burrow dynamics during aging by using the degradation stage of
85 casts as a proxy of the age of burrows. This study aimed to evaluate the effect of
86 aging on the temporal dynamics of the morphology of earthworm burrows and their
87 ability to transport water. We hypothesized that aging leads to a decrease in soil water
88 infiltration and this decrease is more important in soil with a greater shrinkage
89 capacity.

90

91 **2. Materials and methods**

92 **2.2. Study site**

93 The field work took place at the 'M-Tropics' long-term observatory catchment
94 located in Dong Cao village in North Vietnam (20° 57'N, 105° 29'E). The climate is
95 subtropical humid with an annual mean temperature and rainfall of 20 °C and 1800
96 mm, respectively. The dominant soil is an Acrisol (WRB) (Podwojewski et al., 2008).
97 The catchment is covered by woodlands, secondary forests, meadows and fallows.
98 The experiment took place during the dry season in March 2017. We selected two
99 land uses, namely, one meadow and one woodland, presenting a large amount of
100 surface casts produced by *A. khami*. The mass of casts found in meadow compared to

101 those found in woodland was 2800 *versus* 4400 g (oven dry weight) per m² and the
102 number of fresh casts was 3 *versus* 2 per m², respectively. The soil (0-5-cm depth) in
103 the meadow compared to those in the woodland had an organic C content of 3.7
104 *versus* 2.5%, a pH (KCl) of 3.8 *versus* 3.9, a clay content of 58 *versus* 50%, a sand
105 content of 16 *versus* 17% and a coefficient of linear extensibility (COLE) of 0.07
106 *versus* 0.05. According to Grossman (1968), the COLE values indicated that the soil
107 in meadow and in woodland had a high and medium shrinkage capacity, respectively.

108

109 **Cast sampling and analyses**

110 As a proxy of the age of burrows, we selected three categories of surface casts
111 produced by *A. khami* based on visual inspection: 'A', fresh cast in production and
112 moist in appearance, assumed to be a few days old; 'B', dry cast and assumed to be
113 more than 1 month old; and 'C', dry cast with marked signs of degradation (greenish
114 color due to algae and with cracks at the surface) and assumed to be older than casts
115 'B' (Fig. 1). Both at the meadow and the woodland, the surface casts of each category
116 and their surrounding topsoil aggregates (0-5-cm depth) without visible earthworm
117 activity (control) were sampled in four 100-m² plots situated at 50 m distance from
118 each other. In total, 160 samples were collected: 2 land uses × 4 blocks × 4 (3 types of
119 casts + 1 control) × 5 replicates.

120 To test that the three categories of casts (fresh, dry and degraded) represented
121 an aging gradient, we measured their water stability, hydrophobicity and organic
122 carbon content assumed to change during the aging of casts (Decaëns, 2000; Decaëns
123 et al., 1999). To work on samples with similar physical properties, we broke the casts
124 and control aggregates into pieces to obtain aggregates between 10 and 13 mm. Water
125 stability of aggregates was measured after oven-drying samples at 40 °C for 2 days.

126 The mean weight diameter was calculated after immersion of 5 g of soil aggregates in
127 200 mL of distilled water (10 minutes), vertical sieving in the water through a column
128 of sieves (5, 3.15 and 0.2 mm) and oven-drying at 40 °C (Le Guillou et al., 2012).
129 Aggregate hydrophobicity was assessed by measuring the water drop penetration time
130 (WDPT) on 5 aggregates per plot. It corresponded to the time required for a 13- μ L
131 drop of deionized water to penetrate the aggregate that was previously oven-dried at
132 40 °C for 2 days (Chenu et al., 2000). The total soil organic carbon content was
133 determined by potassium dichromate oxidation titration for aggregates previously
134 crushed to a size of 2 mm.

135

136 **Burrow sampling and analyses**

137 Soil samples under ‘A’, ‘B’ and ‘C’ casts and in the surrounding soil without visible
138 of surface earthworm activity (control) were manually excavated with a sampler
139 device having cutting edges at its base. The device permits the introduction of one
140 PVC column (16 cm in height, 12.5 cm in diameter) in its inner space. The sampling
141 device was introduced vertically into the soil with a hammer. ‘A’ and ‘B’ casts were
142 always represented by a single type, while ‘C’ casts were either individual casts
143 (called ‘C1’) or composed of an accumulation of degraded casts (called ‘C2’). In the
144 woodland, ‘C1’ and ‘C2’ casts were found, whereas in the meadow, only ‘C2’ casts
145 were present. In total, 72 soil columns were sampled: 2 land uses x 4 blocks x (3 or 4
146 groups of casts + 1 control) x 2 pseudo-replicates.

147 Half of the soil columns sampled below ‘A’, ‘B’, ‘C1’ and ‘C2’ casts (N =
148 28) were scanned with a X-ray scanner (SIEMENS SOMATOM® Definition Flash)
149 at Bach Mai Hospital (Hanoi, Vietnam) using a voltage of 120 kV and a current of 93
150 mA. The acquired images were series of cross-sections in DICOM 16-bit grayscale

151 format (resolution of $330 \times 330 \mu\text{m}^2$, with an image acquired every $600 \mu\text{m}$). All
152 subsequent steps of image preparation and processing were carried out with ImageJ
153 and Avizo software. Images were (i) formatted in 8-bit TIFF format; (ii) rendered
154 isotropically (final resolution of $250 \times 250 \times 250 \mu\text{m}^3$); (iii) aligned on the Z axis and
155 (iv) filtered by Median-3D, with a radius of 2 pixels to decrease noise. We manually
156 selected the threshold for segmenting macropores at the $2/3$ distance between the peak
157 of the soil matrix and the peak of macroporosity (Capowiez et al., 1998). Then,
158 macropores $< 1 \text{ mm}^3$ in size were removed (Fig. 2a). We selected manually central
159 earthworm burrows defined here as round macropores in 2D images, presenting a
160 diameter superior to 3 mm and located below casts. First, central burrows (Fig. 2b and
161 2c) were selected on 2D images with the plugin “interactive geodesic reconstruction
162 3D” implemented in MorphoLibJ (Legland et al., 2016) for ImageJ software. Second,
163 on 3D images, pores connected to central burrows were isolated (Fig. 2d and 2e) with
164 the draw tool in the module “volume edit” in Avizo software. For ‘A’, ‘B’, and ‘C1’
165 columns only one central burrow was found (Fig. 2b). Conversely, ‘C2’ columns had
166 several central burrows with different ages (Fig. 2c). We therefore measured the
167 properties of all central burrows and averaged their properties. Macropore
168 quantification was performed with BoneJ (Doubé et al., 2010) in ImageJ software.
169 Central burrows were characterized by their volume and specific surface with the
170 plugin “particle analyzer” and their diameter with the plugin “thickness” (Table 1).

171 All soil columns ($N = 72$) were water-saturated for 4 days by gradually
172 raising the water level each day to avoid possible imprisonment of air bubbles as
173 much as possible. Water infiltration rate (L min^{-1}) was determined using a constant
174 head device with an apparatus similar to that reported by Bastardie et al. (2003). The
175 value of the hydraulic gradient (the difference between water levels imposed on the

176 inflow and outflow divided by the column length) was 4 and the outflow was recorded
177 during 3 min.

178

179 **Statistical analyses**

180 Prior to analysis, the data were tested for homogeneity of variance and normality and
181 log-transformed when required. For each land use, One-way ANOVAs for
182 randomized complete block design were performed to assess differences in soil
183 physico-chemical properties, macropore properties and water infiltration between the
184 different treatments. LSD post-hoc multiple comparison tests were performed to
185 assess the statistical significance of differences between means. Spearman
186 correlations were calculated to study the relationships between the aging of burrows
187 and water infiltration in 'A', 'B', 'C1' and 'C2' columns (N = 28). Differences were
188 considered significant only when P values were lower than 0.05. All statistical
189 analyses and plots were carried out with R software using "car", "agricolae" and
190 "ggplot2" packages.

191

192 **Results**

193 **Properties of earthworm casts as influenced by aging**

194 The properties of casts changed according to their degradation stage (Table 2). The
195 mean weight diameter of aggregates was lower in 'A' casts than in control (on
196 average 1.1-fold) but differences were only significant in the meadow. 'B' casts had
197 similar mean weigh diameter of aggregates than in control. From 'B' to 'C' casts, the
198 mean weight diameter of aggregates decreased (on average 1.5-fold) to reach values
199 lower than in control. Organic carbon content was higher in casts than in control (on
200 average 1.5-fold) without significant difference between types of casts. The water

201 drop penetration time of aggregates was higher in all the cast categories than in
202 control (on average 26-fold) and it increased from 'A' to 'C' casts (on average 3-
203 fold).

204

205 **3D properties of central earthworm burrows**

206 Three of the four replicates of the 'A', 'B', 'C1' and 'C2' central burrows are shown
207 in Fig. 3. 'A' burrows had similar diameters and none were degraded. 'B' burrows
208 showed more variability, some of which were not degraded, whereas others had
209 cracks connected to them. 'C1' burrows all showed marked signs of degradation,
210 characterized by cracks directly connected to burrows and other biopores connected to
211 cracks. 'C2' burrows were similar to 'C1' burrows except that several burrows were
212 present in each column. The quantification confirmed the visual impressions (Table
213 3). The 3D properties of the 'A' and 'B' central burrows were not significantly
214 different at the two land uses. The comparison of 'A' and 'C2' burrows revealed a
215 similar pattern of degradation with similar intensity. The degradation was
216 characterized by an increase in the specific surface area (on average 2.5-fold), an
217 increase in the volume of macropores connected to the central burrows (from 0 to
218 22458 mm³ in the meadow and from 2598 to 37886 mm³ in the woodland) and a
219 decrease in the minimum diameter (on average 2.5-fold). However, results were not
220 statistically significant in meadow for the minimum diameter. Comparison between
221 'C1' and 'C2' burrows in the woodland showed only a decrease in the volume
222 percentage of burrows (2-fold).

223

224 **Water infiltration**

225 'A' and 'B' columns had similar and higher water infiltration rate (on average 2-fold)

226 than control (Fig. 4). In the woodland, water infiltration rate decreased between 'B' to
227 'C1' columns (1.4-fold) to reach similar value than control. Between 'C1' to 'C2'
228 columns water infiltration rate increased to reach higher value than control. In the
229 meadow, water infiltration rate was always higher under casts than in control and it
230 decreased significantly from 'A' to 'C2' columns. Water infiltration rate in 'A', 'B',
231 'C1' and 'C2' columns was statistically significantly correlated ($P < 0.05$) with the
232 minimum diameter ($r = 0.47$) and the specific surface area ($r = -0.47$) of the burrows.

233

234 **Discussion**

235 **Water stability of earthworm casts as influenced by aging**

236 The water stability of earthworm casts has been widely documented, including the
237 stability of casts produced by *A. khami* (Jouquet et al., 2008a), but this study showed
238 that the water stability of casts is highly variable in the field depending on their age.
239 Fresh and degraded casts ('A' and 'C' casts) had lower water stability than control
240 aggregates, whereas higher values were found for dry casts ('B' casts). The decrease
241 in water stability of fresh casts can be attributed to the intense remolding that occurs
242 during the passage of soil through earthworms destroying the preexisting soil
243 microstructure (Marinissen and Dexter, 1990; Shipitalo and Protz, 1988), whereas the
244 increase in stability of dry casts results from hardening with age (Hindell et al., 1997),
245 the development of fungi or the production of polysaccharides of microbial origin
246 (Marinissen and Dexter, 1990; Shipitalo and Protz, 1989). The decrease in water
247 stability of degraded casts is consistent with Decaëns et al. (2000), who found that the
248 aging of casts produced by the anecic earthworm *Martiodrilus carimaguensis*
249 promoted the formation of cracks and colonization by soil macrofauna, resulting in a
250 decrease in bulk density and water stability. Finally, considerable changes in the

251 properties of casts (water stability and hydrophobicity) confirmed that the visual
252 appearance of casts can be used as a proxy of cast age.

253

254 **Morphology and hydraulic functionality of burrows as influenced by aging**

255 We observed that burrows of *A. khami*, once abandoned, persist at least several
256 months in clayey soils. This result is in line with the study of Potvin and Lilleskov
257 (2017), who found in a rhizotron facility that 67% of the burrows produced by the epi-
258 anecic earthworm *Lumbricus terrestris* persisted for more than 7 years in soils
259 dominated by sand. However, it seems unlikely that burrows made by *A. khami* would
260 last as long as those of *L. terrestris*. Indeed, *A. khami* individuals abandon their
261 burrow after one month once the cast connected to the entrance of the burrow become
262 dry and hard, which impeded the earthworm to burrow anymore. Conversely, *L.*
263 *terrestris* individuals are known to build permanent burrows associated with middens
264 (Butt et al., 2003). The midden is a collection of organic and inorganic materials plus
265 earthworm casting around the burrow entrance, which is regularly maintained by *L.*
266 *terrestris*. Also, the impact of the soil texture on the degradation dynamics of the
267 burrows is unknown. On one hand, the degradation might be faster in clayey soils
268 than in sandy soils since the former produce cracks when drying. On the other hand,
269 clayey soils are probably better able to withstand pressures exerted by the action of
270 infiltrating water during flooding events.

271 Even though burrows were found below degraded casts ('C1' and 'C2'), our
272 study revealed significant changes in their morphology characterized by an increase in
273 the specific surface area and the volume of macropores connected to them, and a
274 decrease in the minimum diameter compared to those of younger burrows. No
275 infilling by earthworm casts clogging the burrows was observed in the images, and no

276 compaction or tillage happened (as evidenced by the presence of surface casts).
277 Cracks but no biopores were found directly connected to burrows, indicating that the
278 formation of cracks after successive wetting/drying cycles had a strong influence on
279 the aging of burrows. Because the degradation of burrows was similar between the
280 two land uses, we suggest, contrary to our hypothesis that the difference in COLE
281 between the two soils (0.07 *versus* 0.05) was not sufficient to alter differently the
282 dynamics of burrows. Another mechanism that might explain the changes in the
283 morphology of burrows and the formation of cracks is the collapse of the burrow wall
284 due to the seepage force generated by the flow of water (Van Den Berg and Ullersma,
285 1991). This collapse could explain the significant changes in the specific surface area
286 and the minimum diameter.

287 One functional consequence of the aging of burrows was evidenced by the
288 change in water infiltration rate. Our study confirmed the findings of previous field
289 studies showing the efficiency of the burrows of anecic earthworms in transporting
290 water when the soil was saturated (Andriuzzi et al., 2015; Pitkänen and Nuutinen,
291 1998). However, this positive effect disappeared in degraded burrows ('C1') in
292 woodland and decreased significantly in the presence of multiple degraded burrows
293 ('C2') in meadow. The changes in water infiltration were partly explained by changes
294 in the morphology of the burrows, such as the increased specific surface area and the
295 decreased minimum diameter. These results confirmed our hypothesis that changes in
296 the 3D properties of burrows would have a large effect on the functionality of
297 burrows. Water infiltration rate of several degraded burrows in the woodland ('C2')
298 was similar than that in 'A' columns despite clear differences in the morphology of
299 the burrows between 'A' and 'C2' columns. This apparent contradiction could be
300 explained by the fact that water infiltration was measured for 72 columns, whereas

301 only half of the columns were analyzed by X-ray tomography. It also shows that the
302 presence of several central burrows, even degraded ones, can have a positive
303 influence on water infiltration.

304

305 **Conclusions**

306 Our results provide evidence that earthworm burrows produced by the anecic
307 earthworm *A. khami* can persist at least for months in clayey soils. However, the
308 morphology of burrows changed during aging, mainly due to physical processes, and
309 the positive influence of the burrows on water infiltration is reduced or even
310 disappeared in some cases. Further research is needed to assess the timescale of the
311 degradation dynamics of burrow systems of different earthworm species in a range of
312 pedo-climatic conditions.

313

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324

325

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452 **Figure captions**

453 **Figure 1:** Examples of earthworm casts used as proxies of the age of burrows: 'A'
454 fresh cast in production and humid in appearance, known to be a few days old; 'B'
455 dry cast assumed to be more than 1 month old; and 'C' dry cast with marked signs of
456 degradation (greenish color due to algae with cracks at the surface) and assumed to be
457 older than 'B' cast.

458 **Figure 2:** Illustration of the central earthworm burrows characterized in 3D in
459 columns under 'A', 'B', 'C1' and 'C2' casts. 'A', single burrow, known to be a few
460 days old; 'B', single burrow, assumed to be more than 1 month old; and 'C1' /'C2',
461 one/several burrows, assumed be older than 'B' burrow.

462 **Figure 3:** Three-dimensional visualization (using X-ray tomography) of central
463 earthworm burrows in 3 replicates of 1000 cm³ soil columns sampled along an
464 increasing aging gradient from 'A' to 'C2' in a meadow and a woodland: 'A', single
465 burrow, known to be a few days old; 'B', single burrow, assumed to be more than 1
466 month old; and 'C1'/'C2', one/several burrows, assumed be older than 'B' burrow.

467 **Figure 4:** Box plot of water infiltration rate (n = 4) measured in columns without
468 visible of surface earthworm activity (control) and under 'A', 'B', 'C1' and 'C2'
469 casts. 'A', single burrow, known to be a few days old; 'B', single burrow, assumed to
470 be more than 1 month old; and 'C1' /'C2', one/several burrows, assumed be older
471 than 'B' burrow. Values bearing different letters are statistically significantly
472 different. The number of stars for the significance level indicates the p-value range
473 (***) P <0.001)

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478 **Table 1:** Descriptions of quantified 3D properties measured on central earthworm

479 burrows.

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3D property	Definition
Volume percentage (%)	Ratio of the volume of the central burrows to the volume of soil
Specific surface area (mm^{-1})	Ratio of the central burrows surface area to the volume of soil
Mean diameter (mm)	Mean diameter of the central burrows
Minimum diameter (mm)	Minimum diameter of the central burrows
Volume connected (mm^3)	Volume of macropores connected to the central burrows

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499 **Table 2:** Average values (n = 4) of physical and chemical properties of the topsoil
500 aggregates without visible earthworm activity (control) and ‘A’, ‘B’ and ‘C’ casts in
501 the meadow and woodland. ‘A’, fresh cast in production and humid in appearance,
502 known to be a few days old; ‘B’, dry cast with a rounded shape, assumed to be more
503 than 1 month old; and ‘C’, dry cast with marked signs of degradation (greenish color
504 due to algae with cracks at the surface) and assumed to be older than ‘B’ cast. Water
505 stability of aggregates as quantified by the mean weight diameter (MWD), total
506 organic carbon (OC) and hydrophobicity represented by the water drop penetration
507 time (WDPT). Values bearing different letters are statistically significantly different
508 within each land use. The number of stars for the significance level indicates the p-
509 value range (*** P <0.001 and ** P <0.01).

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Land use	Aggregate	MWD (mm)	OC (%)	WDPT (s)
Meadow	Control	8.5 a	3.7 b	76 d
	A	7.7 b	4.5 a	2459 b
	B	8.6 a	4.8 a	436 c
	C	5.6 b	5.2 a	6098 a
	p-value	***	**	***
Woodland	Control	8.6 a	2.5 b	83 c
	A	7.8 a	3.6 a	745 b
	B	8.6 a	3.6 a	639 b
	C	5.8 b	3.8 a	2604 a
	p-value	***	***	***

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524 **Table 3:** Average values (n = 4) of morphological characteristics of the central
 525 burrows under ‘A’, ‘B’, ‘C1’ and ‘C2’ casts. ‘A’, single burrow, known to be a few
 526 days old; ‘B’, single burrow, assumed to be more than 1 month old; and ‘C1’ / ‘C2’,
 527 one/several burrows, assumed be older than ‘B’ burrow. Volume percentage (VP),
 528 specific surface area (SSA), mean diameter (MeD), minimum diameter (MiD) and
 529 volume of macropores connected to the central burrows (VC). Values bearing
 530 different letters are statistically significantly different within each land use. The
 531 number of stars for the significance level indicates the p-value range (*** P <0.001;
 532 ** P <0.01; * P <0.05 and ns for P >0.05).

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Land use	Column	VP (%)	SSA 10 ⁻³ (mm ⁻¹)	MeD (mm)	MiD (mm)	VC (mm ³)
Meadow	A	0.3 a	2.2 b	4.6 a	3.1 a	0 b
	B	0.2 a	1.9 b	4.4 a	3.7 a	14630 ab
	C2	0.3 a	5.6 a	4.0 a	1.8 a	22458 a
	P-value	ns	**	ns	ns	*
Woodland	A	0.2 b	1.8 b	4.3 a	3.8 a	2598 b
	B	0.3 b	2.1 b	4.6 a	3.1 a	2401 ab
	C1	0.4 a	4.2 a	3.7 a	1.5 b	39458 ab
	C2	0.2 b	4.2 a	3.9 a	1.4 b	37886 a
	P-value	**	***	ns	**	*

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Fig. 1

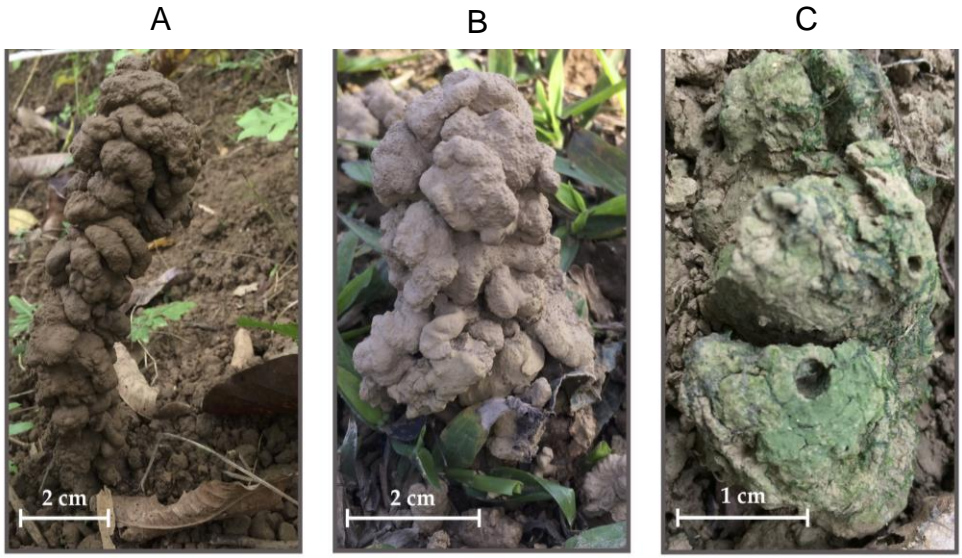


Fig. 2

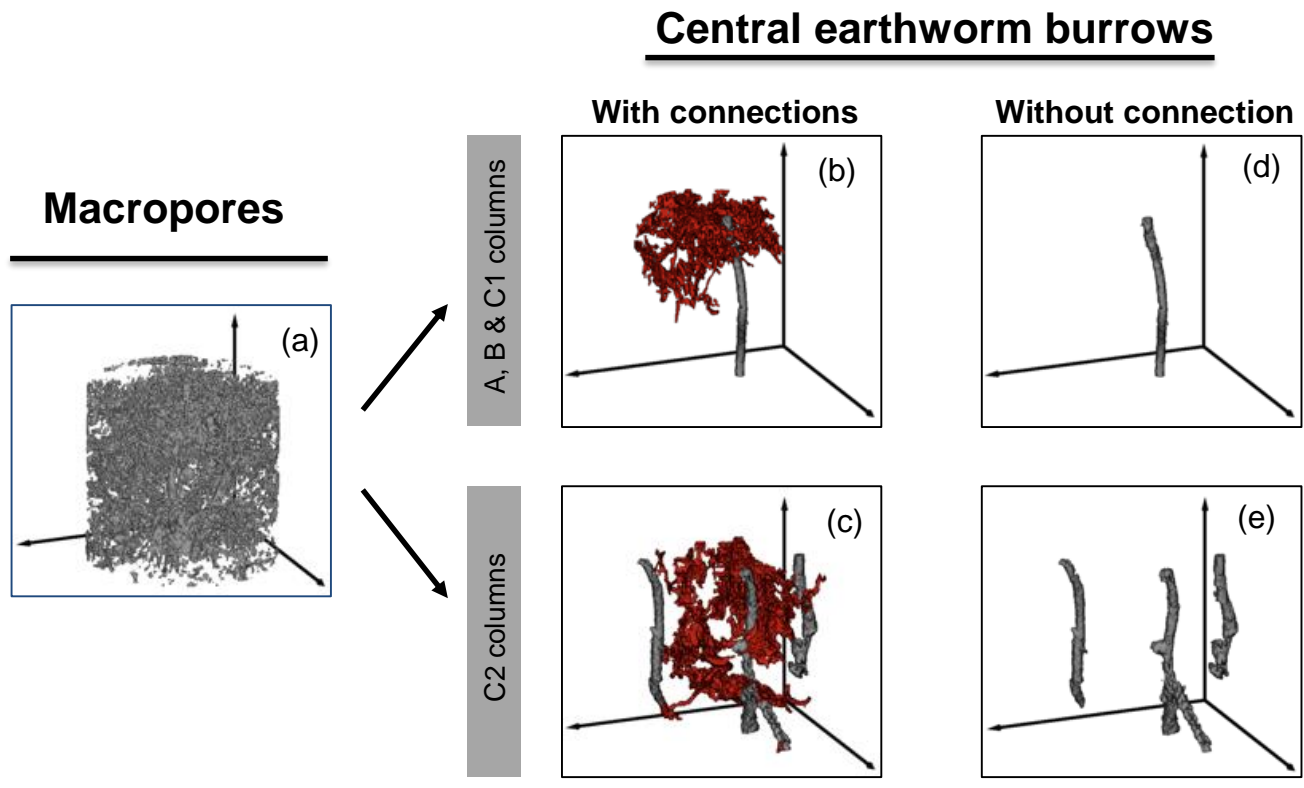


Figure 3

Meadow

Woodland

Aging of earthworm burrows

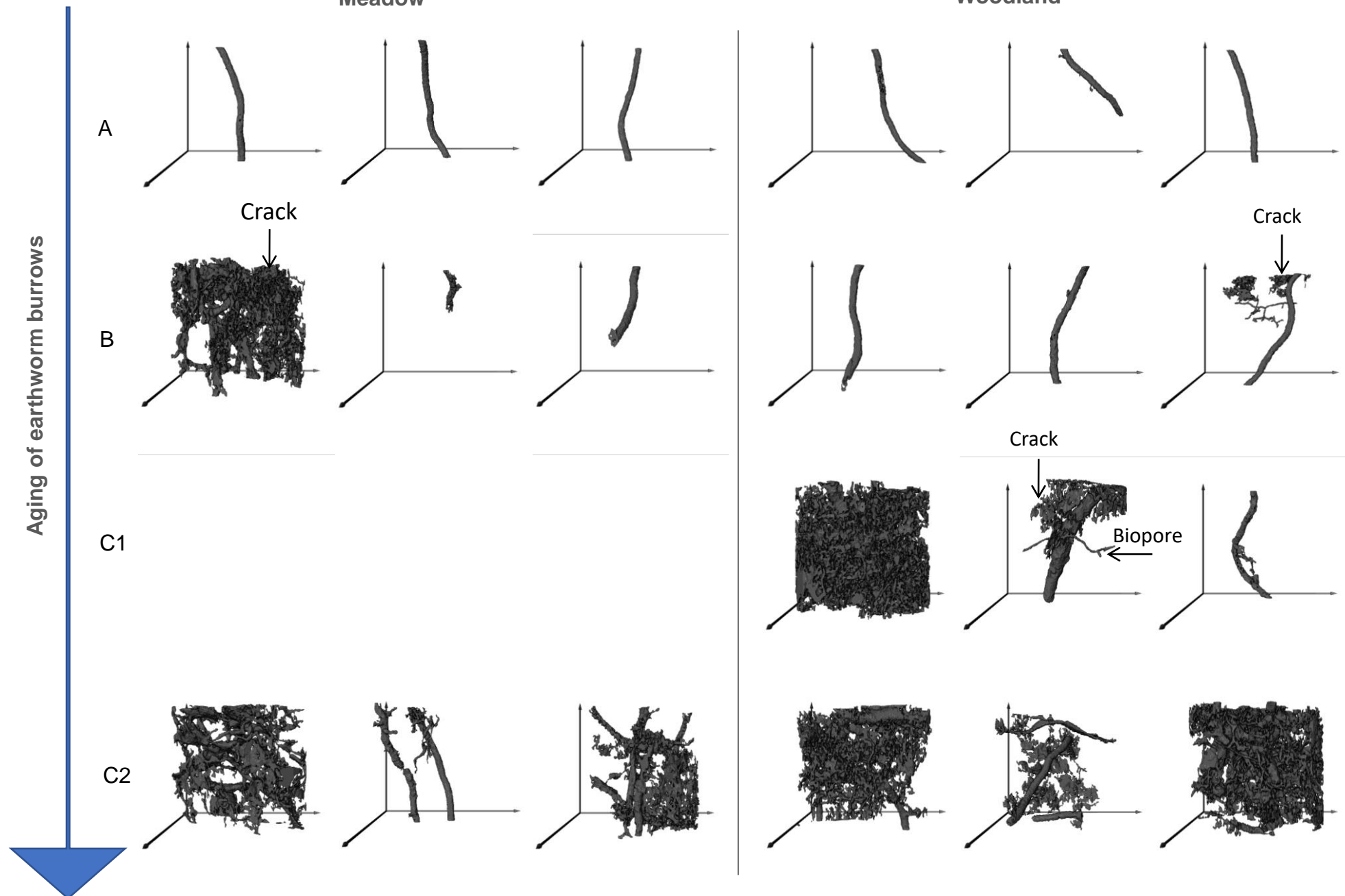


Fig. 4

