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Nicodrilus nocturnus and *Allolobophora icterica* drill compacted soils but do not decrease their bulk density – A laboratory experiment using two contrasted soils at two different compaction levels

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ABSTRACT

Earthworms are known to play an important role in soil processes, especially in the regeneration of soil structure. However, quantitative studies about their role on soil physical properties are still scarce. In this study the effects of two earthworm species (*Nicodrilus nocturnus* as anecic, *Allolobophora icterica* as endogeic) following three treatments (*N. nocturnus only*, *A. icterica* only and both species with 80% weight of *N. nocturnus* and 20% of *A. icterica*) on soil specific volumes and pore properties are evaluated in mesocosms (30 cm height and 15 cm diameter) for a loamy Anthrosol and a silt loam Luvisol. The soils were repacked to bulk density observed in the field (1,15 and 1,25 g cm^{-3} respectively) and to compacted bulk density (1,4 and 1,5 g cm^{-3} respectively). Except earthworm-free controls, introduced earthworm biomass was close to 500 $g.m^{-2}$. The experiment lasted 23 weeks, under constant temperature and soil matrix potential, and earthworms were fed with hay. The impact of earthworms on soil porosities and specific volumes was assessed using (i) computed tomography on mesocosm and (ii) shrinkage analysis on undisturbed cubic samples (150 cm^3). Anecic surface cast bulk density was determined after wax coating.

At mesocosm scale, the specific volume of compacted soils increased significantly with the anecic and mixed earthworm treatments (+1.9% for the Anthrosol and +2.6% for the Luvisol), while no change was observed with endogeics regardless of the initial level of compaction or the soil type. After subtracting the burrow volumes, the remaining soil matrix specific volume showed significant decrease with earthworms in case of loose soils, particularly with endogeics with 5.6% decrease of the specific soil matrix volume, while the compacted soil matrix was not decompacted. At undisturbed cubic sample scale, shrinkage analysis confirmed these observations with earthworms decreasing the larger structural pores and promoting a more rigid plasma. Anecic surface casts showed intermediate bulk density (0.82 $cm^3\ g^{-1}$ for the Anthrosol and 0.73 $cm^3\ g^{-1}$ for the Luvisol) between compacted (0.73 $cm^3\ g^{-1}$ for the Anthrosol and 0.67 $cm^3\ g^{-1}$ for the Luvisol) and loose (0.88 $cm^3\ g^{-1}$ for the Anthrosol and 0.81 $cm^3\ g^{-1}$ for the Luvisol) soil matrices. We concluded that the decompaction effect of earthworms was due to the opening of burrows at mesocosm soil scale, while the matrix volume was i) either compacted in case of loose soil especially with endogeics at the expense of the >150 μm equivalent radius structural pores or ii) unchanged in case of compacted soil. Our results support the conclusion that earthworms alone cannot regenerate the matrix of compacted soils and even compact the soil matrix in case of loose soils.

1. Introduction

Earthworms are considered as "ecosystem engineers" (Lavelle, 1997) as they contribute to the interactions between physical, chemical and biological processes occurring within soils. In particular, their contribution to soil structure formation is well documented and studied (Edwards and Bohlen, 1996; Frazao et al., 2019; Lee and Foster, 1991; Pelosi et al., 2017; Schneider et al., 2018). Earthworm activity was

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found to increase the volume and continuity of larger pores and to improve water infiltration in the soil (Capowiez et al., 2015; Davidson and Grieve, 2006; Spurgeon et al., 2013), which was interpreted as a key factor for the recovery of damaged soil structures. Earthworms and roots are viewed as key factors and means for the restoration of soil structure and its corresponding functions after compaction (Drewry, 2006; Larink and Schrader, 2000; Radford et al., 2007). Capowiez et al. (2012) observed a recovery of soil macroporosity and water infiltration through earthworm burrowing 8 months after compaction in a shallow tillage cropping system. Hallaire et al. (2004) showed that bioturbation by earthworms creates packing voids, responsible for a friable structure over an entire horizon. Such a biological loosening may compensate for compaction due to the passage of machinery (Capowiez et al., 2012). However, after a compaction event, the mere presence of earthworm burrows does not mean that the whole soil structure was fully recovered, i.e., in a loosened state with full restoration of the associated soil functions. Furthermore, reported effects of earthworms on soil structure and their usefulness for regeneration of compacted soils are neither straightforward nor definitive and there are still contradicting results. In microcosms, Barré et al. (2009) showed that earthworms tend to densify loose soil and loosen dense soil towards a state of intermediate density. In their study, the bulk density of the casts produced by *L. terrestris*, *A. longa* and *Dendrobaena* sp. was independent of the initial bulk density of the ingested soil. The different ecological categories and species of earthworms (Bouché, 1972) have different effects on a compacted soil. Capowiez et al. (2009a) showed that the epi-anecic *L. terrestris* was able to break up a plough pan by deep burrowing activity, while the anecic *A. giardi*, and the endogeic *A. caliginosa* and *A. rosea* were able to create burrow networks below wheel tracks and compacted clods. In soil columns repacked to field bulk density, Milleret et al. (2009) showed that in the absence of plants the epi-endogeic *A. chlorotica* (green morph) was compacting the soil, in particular by decreasing the pore volume of all structural pore size classes (even for pores larger than 150 μm). For tropical soils, Blanchart et al. (2004) distinguished compacting and decompacting earthworm species. For example, *Pontoscolex corethrurus* and *Millsonia anomala*, both tropical endogeic earthworm species, excrete large compact castings, resulting in an increasing soil density and an increasing proportion of macro-aggregate formation, and thus promoting anaerobic conditions (Chauvel et al., 1999). Moreover, studies reporting the influence of earthworm activity on the soil structure are often limited to the observation of earthworm burrows and casts, and seldom address the whole soil physical properties. Kohler-Milleret et al. (2013) used shrinkage analysis to quantify the impact of earthworms on the physical properties of the soil at undisturbed soil core scale. This method allowed to collect a large range of physical information on pore types, pore sizes, water retention and hydro-structural stability and to study how they are affected by earthworm activities.

With a similar methodological approach, this study aims at characterizing the impact of different ecological types of earthworms on the soil structure and on soil physical properties (soil specific volumes and porosity characteristics) for different soil types and compaction levels, at mesocosm (soil core 15 cm diameter 30 cm length, i.e. 5300 cm^3), undisturbed cubic sample (150 cm^3), and surface cast (around 2 cm^3) scales.

2. Material and methods

2.1. Experimental setup

The two soils were an Anthrosol (IUSS Working Group WRB, 2006) already used by Milleret et al. (2009) with 27% clay content and 22 g kg^{-1} soil organic carbon content (SOC), and a Luvisol from the "La cage" long term experiment (Cosentino et al., 2006), which was used later by (Kohler-Milleret et al., 2013) and had 17% clay content and a low SOC (9 g kg^{-1}) (Table 1). The soils were sieved at 2 mm and repacked in PVC columns with 15 cm diameter filled with 30 cm of soil to bulk densities observed in the field and to compacted bulk densities, namely 1.15 and 1.4 g cm^{-3} for the Anthrosol, and 1.25 and 1.5 g cm^{-3} for the Luvisol.

Table 1
Main soil characteristics.

	pH (H_2O)	Sand % g g^{-1}	Loam	Clay	SOC g kg^{-1}
Anthrosol	7.8	45	28	27	22
Luvisol	7	27	56	17	9

The repacking was performed as such: the soil sieved to 2 mm size aggregates was equilibrated at approximately −7.5 kPa, and the mass of soil corresponding to the targeted bulk density was placed in successive layers of 1 cm gently pressed to the correct thickness. This procedure already used in Boivin et al. (2004), Kohler-Milleret et al. (2013) and Schaeffer et al. (2010) allowed to obtain a homogeneous bulk density while avoiding structure layering.

The columns were then installed in a dark room at constant 13 °C temperature. A constant matric potential of −7.5 kPa was kept at the vertical centre of the soil column by placing the columns on a sand-bed with controlled suction to make sure that the soil remained in aerobic conditions during all the experiment. Those conditions were set both to provide good living conditions to earthworms (Perreault and Whalen, 2006) and to prevent shrink-swell cycles to occur in the soil during the experiment. We assumed, therefore, that no abiotic soil structuration process occurred during the experiment. The pH and redox potential were monitored using specific probes at the horizontal and vertical centre of the columns.

Two earthworm species were used in this experiment, namely the anecic *Nicodrilus nocturnus* (*Nn*), also known as *Aporrectodea nocturna* (according to Sims and Gerard (1999)) and the endogeic *Allolobophora icterica* (*Ai*) species, which are both commonly present in Swiss meadows. The earthworms were collected in different meadows using the mustard technique, rapidly rinsed in tap water (Lawrence and Bowers, 2002) and identified using the identification keys of Bouché (1972).

The following treatments were performed: 2 soils X 2 levels of compaction, with four earthworm treatment each, namely *Ai*, *Nn*, and *Ai* + *Nn* and the control without earthworm (*C*). Consequently, according to the presence or absence of earthworm (*Ai*, *Nn*, *Ai* + *Nn*, *C*), the two levels of compaction and the two types of soil, a total of 16 treatments were applied with 3 replications each (i.e. 48 mesocosms in total). The mesocosms were randomly distributed in the room.

All earthworm treatments received approximately 9 g of earthworms. The *Ai* + *Nn* treatment received 1.6 ± 0.1 g of *A. icterica* (4 individuals) and 7.2 ± 0.5 g of *N. nocturnus* (5 individuals), which corresponds to a biomass of 540 ± 30 $g.m^{-2}$. *Nn* treatment received 9.1 ± 1.9 g of *N. nocturnus* (6 individuals), corresponding to a biomass of 558 ± 116 $g.m^{-2}$. *Ai* treatment received 8.6 ± 0.7 g of *A. icterica* (18 individuals) corresponding to a biomass of 528 ± 43 $g.m^{-2}$. These values were within the range of earthworm biomass observed in meadows (Edwards and Bohlen, 1996).

The experiment lasted 5 months, during which fresh organic matter (hay) was regularly delivered at the top of the mesocosms (around 5 g every two week). Day and night cycles were simulated using indirect light.

2.2. Physical analysis

2.2.1. X-ray tomography

Physical measurements were performed at the end of the 5 months. The soil bulk volume (i.e. the inverse soil bulk density) in the whole mesocosms was measured by filling the top of the column with calibrated sand, and the soil bulk volume was then equalled to the column volume minus the sand volume added (Abedine el and Robinson, 1971; Favre et al., 1997). This allowed calculating the soil bulk density at

mesocosm scale since the dry mass of soil introduced in the columns was known.

The columns were then analyzed by X-ray computed tomography (CT), on a LightSpeed Ultra 8b-unit (General Electric Medical Systems, Milwaukee USA). The X-ray source was perpendicular to the mesocosms and set to 150 mA at 120 kV, which allowed characterizing 1.25 mm thick layers with a 0.625 mm over lapping. The image resolution was 0.4 mm per pixel. The images were processed with General Electric Advantage Windows Workstation 4.3 (General Electric Medical systems, Milwaukee USA) to get 3D. Images were transformed into 8-bit images by calibrating the greylevels between −100 and 200 Hounsfield Values. The images were then binarized by choosing a threshold value of 225 that clearly separated the two peaks (soil matrix and air-filled porosity) in the grey level histogram. Isolated pores with a volume <300 voxels (1 voxel = 0.4 × 0.4 × 0.625 mm^3) were discarded. We thus only retained pores that were large enough to be created by earthworms (Jégou et al., 2001). To characterize the earthworm burrow systems, we first computed the volume of macroporosity and the percentage of the burrow system in the upper and lower half of the core respectively. Then burrow diameters were assessed on the most circular pores in the 2D images (pores whose circularity was higher than 0.8) assuming that burrows are perfect cylinders. Finally, we also computed the skeleton of the burrow systems using the AnalyzeSkeleton plugin in ImageJ. This enabled assessment of burrow length and branching rate (number of branching pattern per m of burrow).

The specific volumes of the soil columns ($cm^3.g^{-1}$) (i.e, the inverse soil bulk density ($g.cm^{-3}$)) after subtraction of the burrow volumes were then calculated and refer to as soil matrix specific volume in the following.

2.2.2. Shrinkage analysis

After CT imaging, one undisturbed cubic sample of approximately 150 cm^3 was manually cut in the 20–25 cm depth layer of each mesocosm for shrinkage analysis (SA) while avoiding the few centimeters bordering the walls of the mesocosms.

The SA was performed according to the procedure described in Schäffer et al. (2008) enabling the quantification of the two soil pore systems, namely structural and plasma pores. The structural pores consist of biopores, cracks and packing voids (Brewer, 1964). The complementary volume is made of skeleton grains and plasma, defined as "material, mineral or organic, of colloidal size and relatively soluble material that is not contained in the skeleton grains" (Soil Science Society of America, 2017). Therefore, the plasma porosity is made of inter colloidal particle voids.

Briefly, the undisturbed cubic soil samples were equilibrated to −0.5 kPa matric potential before measurement of their volume with the plastic bag method (Boivin et al., 1990). Therefore, the undisturbed cubic sample was placed in a thin and flexible plastic bag. Moderate vacuum (-600 hPa) was applied to the plastic bag while the sample was immerged in an Erlenmeyer filled with water and placed on a electronic scale. After some seconds and with no contact between the Erlenmeyer and the bag, the measured weight was equal to the Archimedes pressure and, therefore, to the volume of the sample (Boivin et al., 2006). The samples were then placed to dry in the shrinkage apparatus, and a micro tensiometer was inserted at the center of the sample. The sample height, weight and matric potential change with time were recorded. The experiment lasted about 6 days before steady weight and height of the sample were observed. The air-dry volume was then measured with the plastic bag method before the samples were dried at 105 °C to measure the dry weight. The recorded weights were converted into gravimetric water content, and the recorded heights were converted into sample volume using:

$$V(t) = V_i \cdot \left(\frac{H(t)}{H_i}\right)^x$$

where $V(t)$ and $H(t)$ are the sample volume and height at time t, V_i and H_i are the initial volume and height of the sample, and x is the geometric factor calculated as:

$$x = \frac{Ln\left(\frac{V_f}{V_i}\right)}{Ln\left(\frac{H_f}{H_i}\right)}$$

where V_f and H_f are the final sample volume and height, respectively.

The experimental shrinkage curves (ShC) were then fitted with XP model (Braudeau et al., 1999) to determine the plasma and structural porosity of the samples at any water content (Schäffer et al., 2008). The recorded water retention curves (WRC) allowed calculating the equivalent pore size distribution in the tensiometric range using Jurin-Laplace's law. In the following, we mostly focused on soil volume at −1 kPa, structural and plasma porosity, and pores larger than 150 µm in equivalent radius, corresponding to the pores filled with air at −1 kPa.

2.2.3. Surface casts analysis

Earthworm casts were collected at the top of the columns of the *Nn* treatments and their dry bulk density was measured with Archimedes pressure using paraffin wax (Blake and Hartge, 1986; Jouquet et al., 2008) (Fig. 2).

2.3. Statistical analysis

Statistical analyses were performed using the R software. First, homoscedasticity and normality were tested, and log-transformation was performed if needed. The effects of the treatments on the measured parameters were then compared by analysis of variance (ANOVA) with 3 factors: 'soil' (Luvisol, Anthrosol), 'level of compaction' (compacted, loose), 'earthworm' (anecic, endogeic, mixed, no earthworm). As the soil effect was systematically significant apart for branching rate (Table 2), two-way anova were then carried out separately for each soil to evaluate the mean effects of the factors 'earthworm' and 'level of compaction'. The R package multcomp (Hothorn et al., 2008) was used for pair-wise comparisons based on the Tukey test for each soil separately.

3. Results

3.1. Experimental conditions

The matric potential remained constant at −7.5 ± 0.2 kPa at the centre of the columns during the experiment. The pH (7.0 ± 0.2 for both soils) and Eh values remained in the goethite stability domain (0.32 ± 0.05 V for both soils), showing that no waterlogging occurred. The temperature varied slightly between 13 and 16 °C during the experiment, which is commonly reported as optimal temperature for both species (Lee, 1985). No significant change in soil pH and organic carbon content was observed between treatments. The gravimetric water content of the soil at the end of the experiment was 19.5 ± 0.1 and 23.0 ± 0.1 (%) for the Luvisol and Anthrosol soils, respectively.

3.2. Effects of compaction on earthworm burrow characteristics

Soil compaction had significant effects (Table 3) on the characteristics of the burrow systems (Fig. 1 and supplementary material Table S1) with similar trends for the two soils. Higher soil bulk density (i.e, level of compaction) resulted in decreased burrow volume (by 71% on average, $p < 0.05$), burrow length (by 69% on average, $p < 0.05$), and burrow diameter (by 8.8% for anecic and by 4.6% for endogeic on average) albeit only significant ($p < 0.05$) for the anecic and mixed treatment in the Anthrosol for this last parameter (Table 3 and Fig. 3 A-D). Moreover, it also resulted in an increase of the proportion of the

Table 2
Effect of earthworm, level of compaction and soil type on measured parameters with ANOVA 3 factors; Signification codes for the p-value: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1; p-values between brackets.

	Earthworm	Level of compaction	Soil	Interaction earthworm: level of compaction	Interaction earthworm:soil	Interaction level of compaction:soil	Interaction earthworm: level of compaction:soil
Burrow volume (cm^3)	*(0.031)	***($<2.10^{-16}$)	*(0.035)	*(0.014)	−(0.41)	*(0.017)	−(0.53)
Burrow length (m)	*** ($5.8.10^{-10}$)	***($<2.10^{-16}$)	**(0.0058)	***($4.06.10^{-8}$)	**(0.0094)	*(0.015)	−(0.65)
Percentage (volume) in the upper half	*** ($6.2.10^{-10}$)	***($3.2.10^{-6}$)	**(0.0015)	−(0.27)	**(0.0034)	−(0.69)	*(0.02133)
Diameter (mm)	*** ($4.9.10^{-16}$)	***($1.2.10^{-6}$)	**(0.0076)	.(0.054)	−(0.32)	*(0.013)	−(0.16)
Burrow branching rate (m^{-1})	*(0.011)	***($<2.10^{-16}$)	−(0.17)	***($7.0.10^{-6}$)	*(0.035)	*(0.030)	**(0.0018)
Specific Volume (SV)	*** ($1.1.10^{-8}$)	***($<2.10^{-16}$)	*** ($<2.10^{-16}$)	*(0.010)	−(0.12)	***($3.6.10^{-10}$)	*(0.035)
SV minus burrow volume (="matrix")	*** ($4.5.10^{-12}$)	***($<2.10^{-16}$)	*** ($<2.10^{-16}$)	***($3.2.10^{-9}$)	−(0.14)	***($2.7.10^{-7}$)	−(0.37)
SV of clods at −1 kPa	*** (0.00029)	***($3.5.10^{-12}$)	*** ($1.3.10^{-14}$)	*(0.045)	−(0.29)	−(0.26)	−(0.23)
Air volume at −1 kPa	**(0.0019)	***($1.7.10^{-10}$)	*** ($1.4.10^{-9}$)	*(0.044)	.(0.066)	−(0.24)	−(0.14)

Table 3
Effect of earthworm, level of compaction and interaction of both factors on measured parameters with ANOVA 2 factors ; Signification codes for the p-value: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1. p-values between brackets.

	Earthworm		Level of compaction		Interaction	
	Anthrosol	Luvisol	Anthrosol	Luvisol	Anthrosol	Luvisol
Burrow volume (cm^3) [a]	−(0.20)	.(0.0809)	***($2.6.10^{-9}$)	***($4.9.10^{-9}$)	−(0.19)	*(0.030)
Burrow length (m)	**(0.0017)	***($3.8.10^{-7}$)	***($7.7.10^{-10}$)	***($7.2.10^{-10}$)	**(0.0012)	***($2.4.10^{-5}$)
Percentage (volume) in the upper half	***($6.4.10^{-6}$)	***(0.00014)	*(0.0057)	***($7.5.10^{-5}$)	.(0.062)	−(0.24)
Diameter (mm)	***($1.6.10^{-9}$)	***($8.7.10^{-8}$)	***($1.6.10^{-6}$)	*(0.047)	**(0.004)	−(0.83)
Burrow branching rate (m^{-1})	**(0.0020)	−(0.89)	***($4.8.10^{-10}$)	***($3.9.10^{-8}$)	**(0.0037)	***(0.00025)
Specific Volume (SV)	***(0.00026)	***($4.0.10^{-5}$)	***($<2.10^{-16}$)	***($<2.10^{-16}$)	−(0.40)	**(0.0036)
SV minus burrow volume (="matrix")	***($2.2.10^{-6}$)	***($3.1.10^{-6}$)	***($<2.10^{-16}$)	***($<2.10^{-16}$)	***($2.1.10^{-5}$)	***(0.00014)
SV of clods at −1 kPa	**(0.0096)	*(0.015)	***($8.9.10^{-7}$)	***($3.4.10^{-6}$)	.(0.063)	−(0.27)
Air volume at −1 kPa	**(0.0067)	.(0.065)	***($6.0.10^{-6}$)	***($2.1.10^{-5}$)	.(0.078)	−(0.13)

[a] log transformation required for Luvisol.

burrows found in the upper half of the cores from 41.9% to 52.5% meaning that earthworms burrowed less deeply in the more compacted soils (Table 3 and Fig. 3C). Finally, compaction decreased significantly the branching rate of the burrow systems (Fig. 3E). Except for burrow diameter in the Anthrosol, burrow length and branching rate in both soils and burrow volume for Luvisol, the interaction between the two studied factors was not significant (Table 3).

The different earthworm treatments (excluding earthworm-free control) had no effect on burrow volume. In contrast, the burrow systems made by *A. icterica* were significantly different to *N. nocturnus* regarding the other characteristics with higher burrow length only in the loose soil, and lower burrow diameter and percentage in the upper part of the mesocosms except in the compacted Luvisol for this later parameter (Table 3 and Fig. 3 A-D).

The interaction between the two factors (earthworm and level of compaction) was highly significant for burrow length and branching rate with the same trends in both soils: burrow lengths were not significantly higher for *A. icterica* than for *N. nocturnus* in the compacted soils (Table 3).

3.3. Effects of soil compaction and earthworm treatments on soil specific volumes and porosity

3.3.1. At mesocosm scale

The specific volumes of the mesocosms as measured by filling the top of the columns with calibrated sand are presented in Fig. 3F and supplementary material Table S2. The changes in soil volume compared to the controls varied according to soil type, earthworm species and compaction level. In the compacted soils, both *Nn* and *Nn* + *Ai* treatments significantly increased the specific volume of the soil from 0.731 to 0.744 (*Nn*) and 0.745 $cm^3\ g^{-1}$ (*Nn* + *Ai*) and from 0.673 to 0.691 $cm^3\ g^{-1}$ (*Nn* and *Nn* + *Ai*) for the Anthrosol and Luvisol, respectively, while *Ai* alone did not change the volume. In the loose soils, no significant change was observed.

The specific volumes of the soil columns after subtraction of the burrow volumes, which we refer to as soil matrix specific volume in the following, are reported in Fig. 3G. The soil matrix specific volume was always lower with *Ai* than with *Nn* albeit non significantly with the loose Luvisol. The matrix specific volume of the earthworm-free controls was always equal to (compacted) or larger than (loose) the matrix specific volumes of the earthworm treatments. The matrix of the compacted soils was more compact after *Ai* treatment without significant volume decrease ($p > 0.05$). This shows that though the soil specific volume increased at mesocosm scale, the earthworms drilled the soil but did not de-compact the matrix in compacted soils or even compacted the matrix while creating large tubular (greater than 2 mm) pores in loose soils. In other words, earthworms burrowed at the expense of smaller pores.

3.3.2. At undisturbed cubic samples scale

At −1 kPa (swollen soil), the average specific volumes of the samples collected in the different treatments (Fig. 3H and supplementary material Table S2) show the same trends as the soil matrix at mesocosm scale, though less significantly due to larger variability within the samples. Compared to the control, *Ai* significantly decreased the specific volume of the loose soils, while these changes were not significant at the 0.05p level with *Nn* and *Nn* + *Ai* treatments, though showing the same trend.

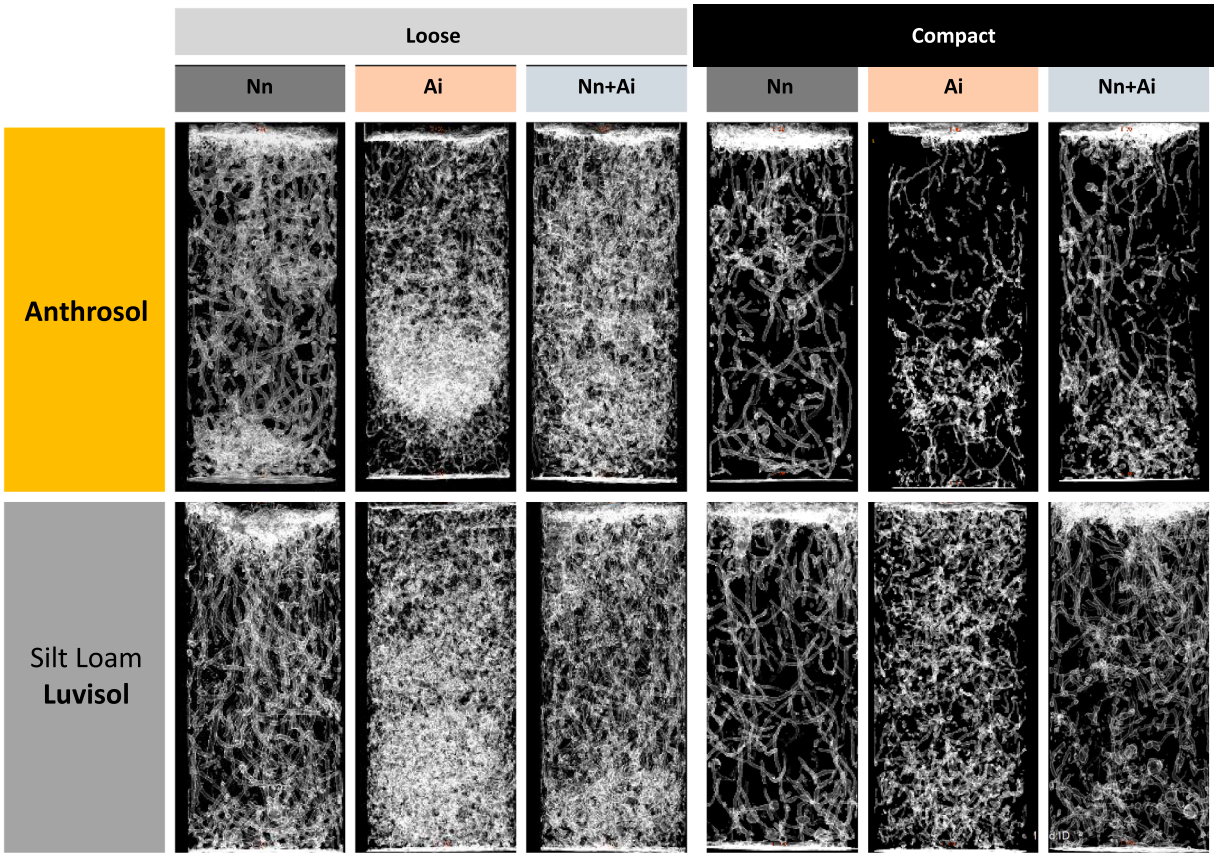

Fig. 1. Selected images of 3D reconstruction of earthworm burrow system in repacked soil cores (30 cm in height and 15 cm in diameter) after 5 months as assessed by computed tomography imaging.

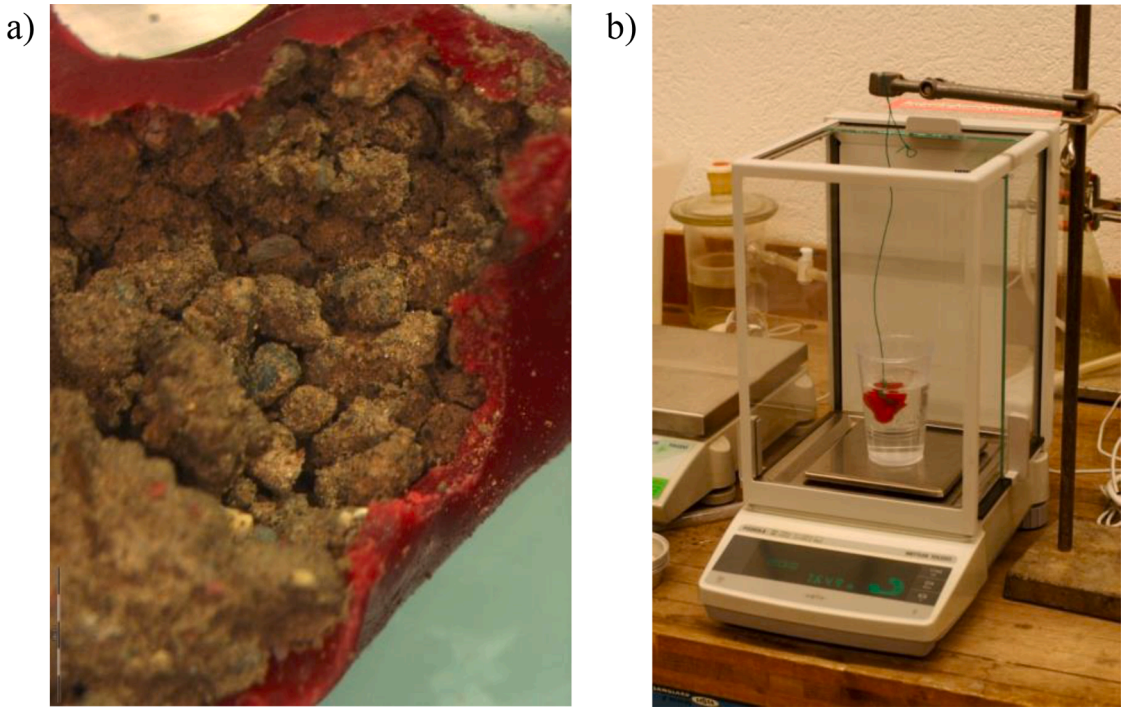

Fig. 2. a) Casts coated with paraffin wax b) Bulk volume measurement by immersion in water using Archimedes's law.

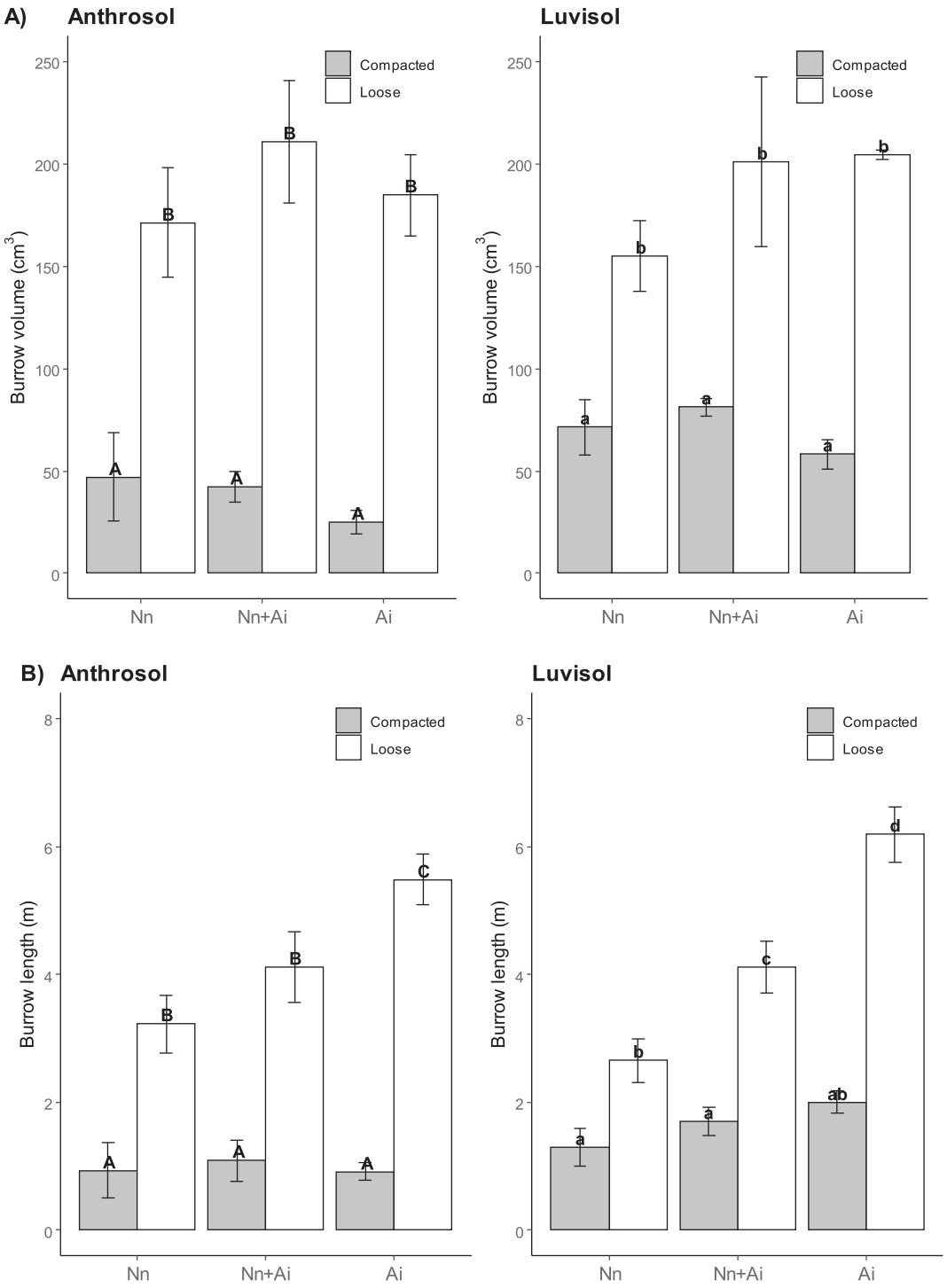

Fig. 3. Characteristics of the burrow systems in the mesocosms and soil physical properties at the end of the experiment. A) Burrow volume (cm^3) B) Burrow length (m) C) Percentage (volume) in the upper half D) Diameter (mm), E) Burrow branching rate (m^{-1}) F) Specific volume of the mesocosms (with burrow volume), in cm^3 g^{-1} G) Specific volume of the mesocosms without burrow volume (="matrix"), in cm^3 g^{-1}H) Specific volume of the clods at −1 kPa, in cm^3 g^{-1} I) Air volume of the clods at −1 kPa, in cm^3 g^{-1} according to soil type, level of compaction and earthworm species. Nn: *Nicodrilus nocturnus*. Ai: *Allolobophora icterica*. Values bearing different letters are different at the $p < 0.05$ threshold level (each soil was tested separately, capital letters were used for the Anthrosol).

The volume changes between loose and compacted undisturbed cubic samples were mostly due to the loss of air volume at −1 kPa (Fig. 3I). Air volume at −1 kPa corresponds to the pores with equivalent radii larger than 150 μm according to Jurin-Laplace's law. The decrease was observed with earthworms compared to controls in case of loose soils, but this effect was only significant for mixed and endogeic treatments in the case of the Anthrosol. The plasma porosity and plasma swelling remained unchanged in the case of the Luvisol, while the plasma volumes at air entry and shrinkage limit were significantly increased by *Ai* on the Anthrosol, thus revealing a more rigid plasma (not shown) as already reported by Milleret et al. (2009). The pore size distribution calculated using Jurin-Laplace law in the tensiometric

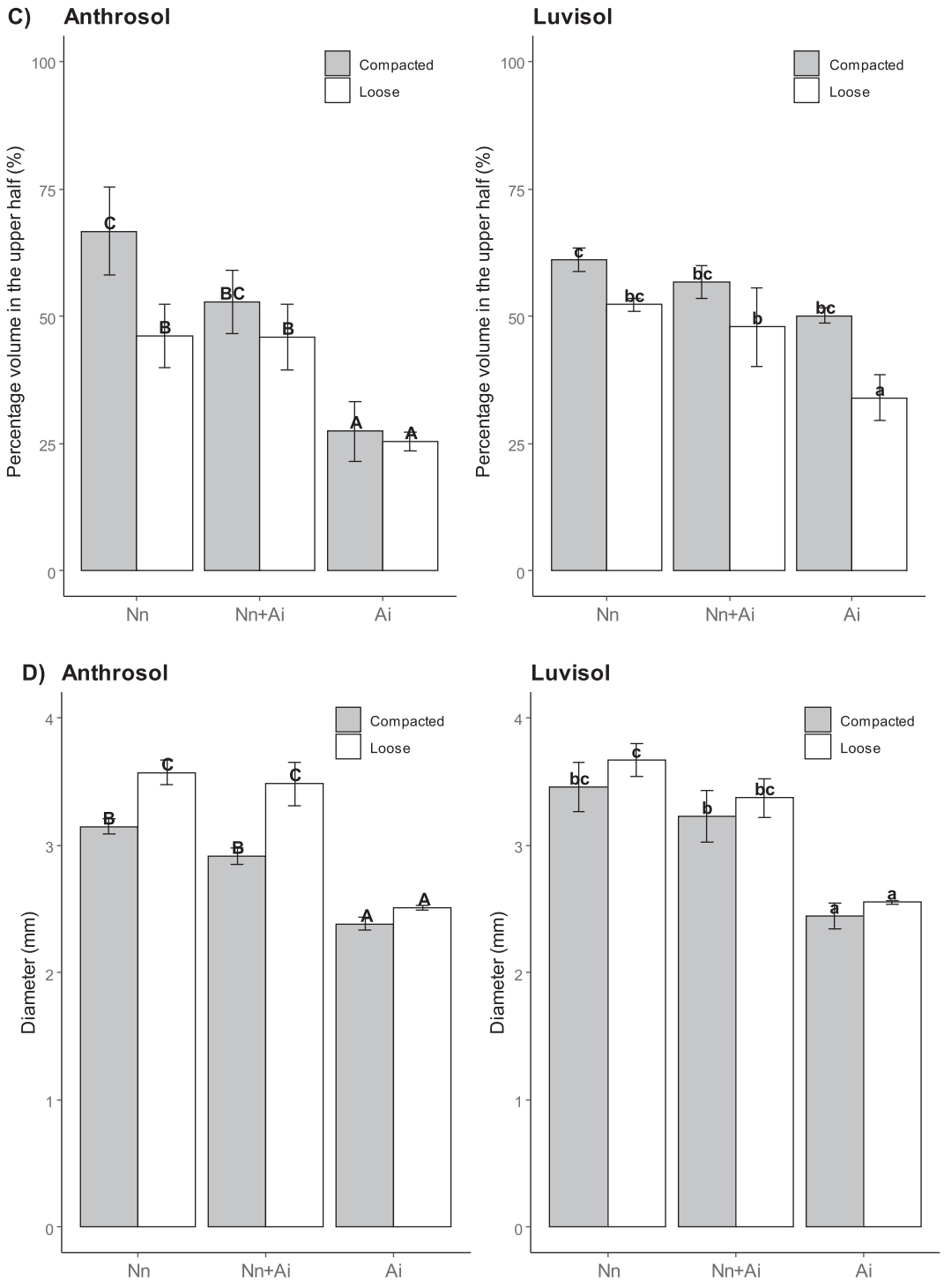

Fig. 3. (*continued*).

matric potential range revealed no significant changes in the 10–150 μm radius pore size range, though the endogeic species tended to induce a decrease of the volume of all these pore sizes. This confirms that earthworms mostly impacted the larger pores and the structural porosity in general.

3.3.3. *Anecic surface casts*

The specific volumes of the air-dried surface casts of the anecic earthworms were 0.82 ± 0.03 $cm^3\ g^{-1}$ for the Anthrosol and 0.73 ± 0.04 $cm^3\ g^{-1}$ for the Luvisol, without significant difference between the level of compaction of the soil. These values are lower than those observed in the loose soils' matrix after the different earthworm treatments (Fig. 3G), which is compacted with respect to the control. However, compared to the compacted soils' matrix (Fig. 3G), the casts have a higher specific volume that means a lower bulk density.

4. Discussion

The experimental setup worked properly with steady conditions favourable to earthworm life and activity, and little variability between soil mesocosms. Although the magnitude of the observed changes differed across the two soils, the effects of earthworms and compaction

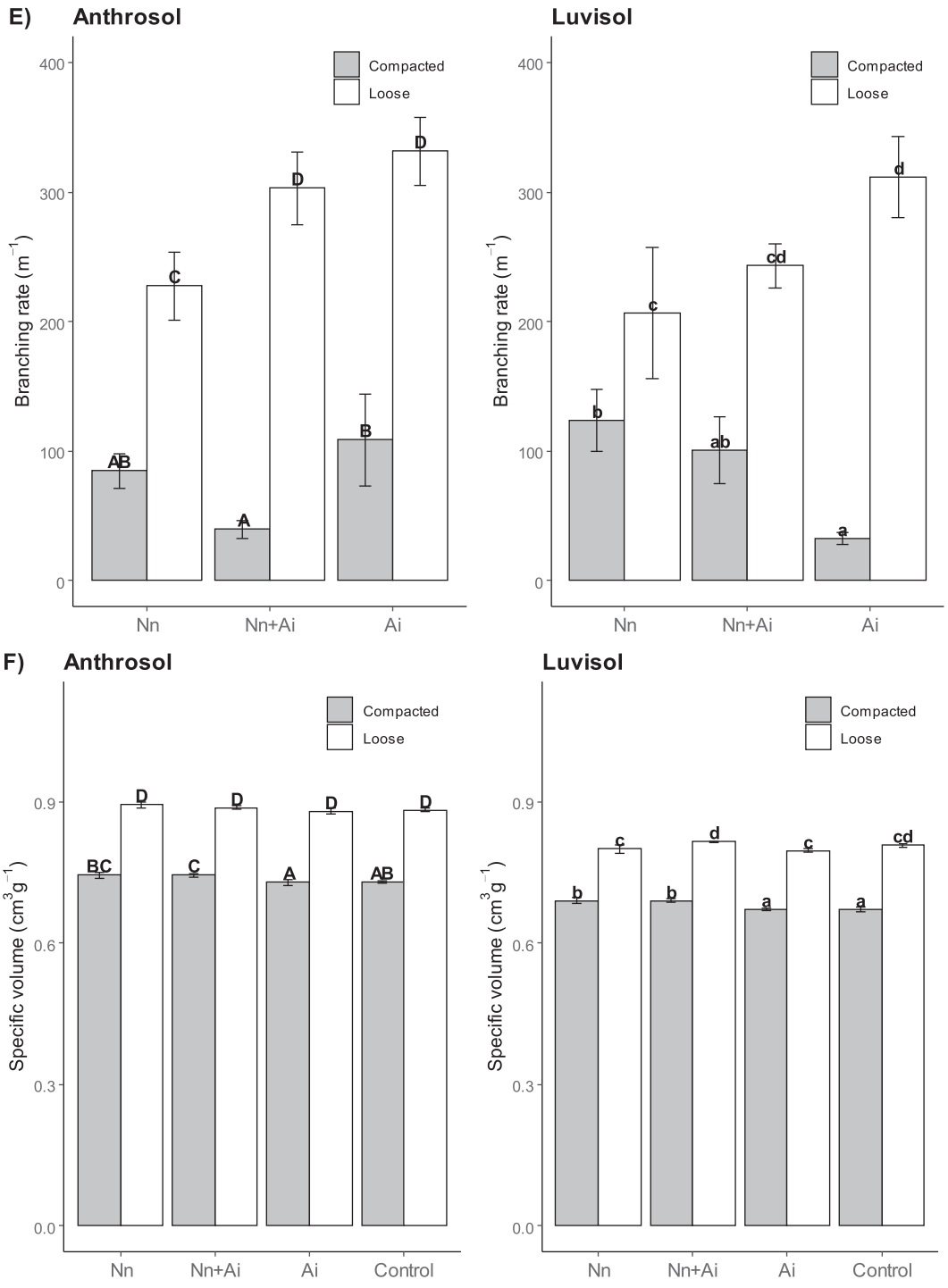

Fig. 3. (*continued*).

levels showed very similar trends.

4.1. Effects of soil compaction and earthworm treatments on the characteristics of the burrow systems

4.1.1. Compaction effect

The increased soil bulk density (compacted soil) significantly influenced the burrowing behaviour of both earthworm species. The decrease in burrow length or volume with increasing soil bulk density was also reported by Capowiez et al. (2021), Pöhlitz et al. (2020), Capowiez et al. (2012), Langmaack et al. (2002), Joschko et al. (1993), and Rushton (1986). In the present experiment, we further observed that, for both species, the proportion of burrows closer to the surface tended to increase while the burrow diameter decreased with compaction with significant changes for anecic and mixed treatments in Anthrosol. This effect on burrow diameter was greater for anecics than for endogeics in the Anthrosol, leading to a significant interaction between the two studied factors (Table 3). The increased proportion of burrows closer to the surface and decreased burrow diameter could be due to the increased energy necessary to burrow in denser soils (Hansell, 1993; Ruiz et al., 2015).

The mixed treatment with both species showed intermediate burrow characteristics compared to the treatments with single species (except for the parameter burrow volume in the case of loose Anthrosol and

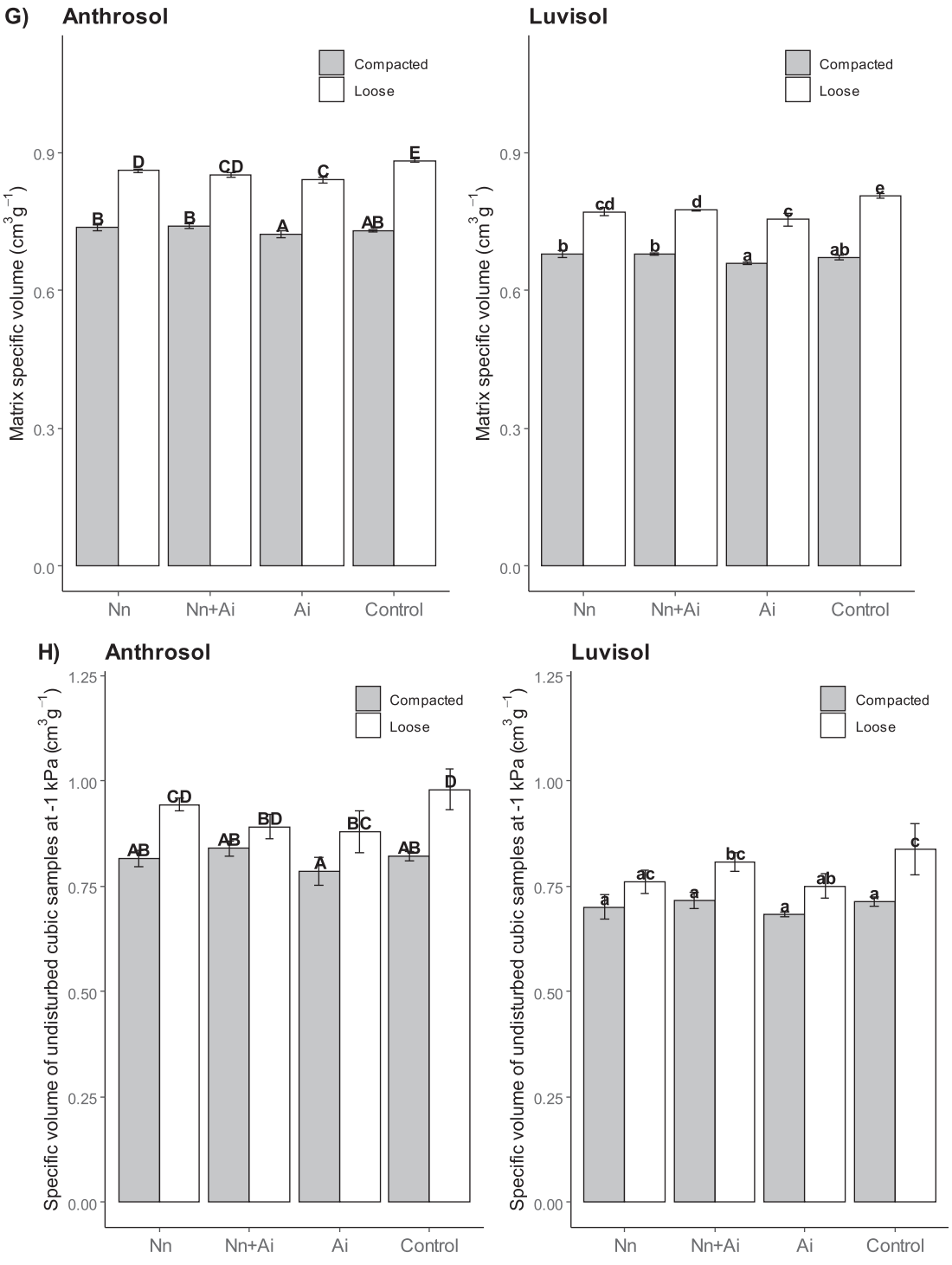

Fig. 3. (*continued*).

compacted Luvisol, and for parameters length and branching rate for compacted Anthrosol). For most parameters, the mixed treatment was however closer to the burrow system made by *N. nocturnus* from which it differed by one individual only (5 vs 6) whereas the number of endogeic was much lower (4 vs 18).

4.1.2. *Earthworm species effect*

The two species of earthworm belong to different ecological categories and created very different burrow systems as expected. Even if the burrow volumes were not different between earthworm treatments, we observed that the endogeic species produced larger burrow lengths especially in loose soils with a smaller diameter. The resulting burrow system showed a lower proportion of burrows in the upper half of the core except for compacted Luvisol. These differences are similar to those reported by Capowiez et al. (2015), Jégou et al. (1998) and Le Couteulx et al. (2015) and are in accordance with the expected behaviour of endogeic and anecic earthworms respectively, as postulated by Lee and Foster (1991). For instance, Le Couteulx et al. (2015) observed that the number of burrows produced by *A. icterica* increased with depth. *A. icterica* is indeed reported to be a typical endogeic earthworm

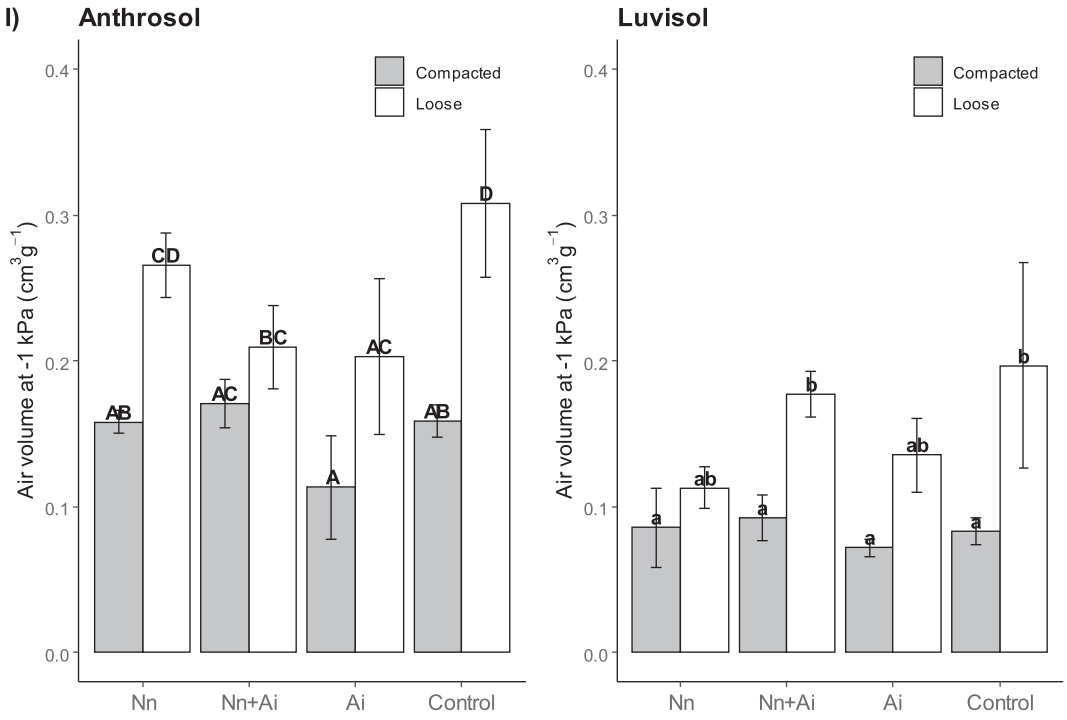

Fig. 3. (*continued*).

(Bastardie et al., 2005) generally living deeper in the soil (Bernier, 1998). *Soil effect*

The larger burrow volume in the loose Anthrosol (anecic and mixed treatments) compared to the loose Luvisol could be related to its lower bulk density. This soil probably requires less burrowing energy. Interestingly, the burrow length and volume of the compacted soil showed inverse results, with larger burrowing intensity in the Luvisol (though sharply decreased compared to the loose soil). This could be explained by the lower organic matter content of the Luvisol as in a compacted soil, the OM content may become an explanatory factor of burrowing intensity (the more OM, the less earthworms burrow). However, such effect of OM is still under discussion (Bottinelli et al., 2017).

4.2. *Effects of soil compaction and earthworm treatments on soil physical properties*

4.2.1. *Earthworms effects on soil porosities*

Overall, at mesocosm scale, the anecic and mixed treatments slightly increased the non-compacted soil volumes and strongly increased the compacted soil volumes while the endogeic treatment did not increase the bulk mesocosm volumes. CT imaging showed that the soils were intensely burrowed, with the presence of large tubular burrows in case of earthworm treatments compared to the earthworm-free controls. When removing the earthworm burrow volumes, however, we showed that the loose soil matrix was indeed compacted by the earthworms, and that the previously compacted soil was not really de-compacted. By drilling the soil, the earthworms decreased the soil matrix porosity (loose soil) or left it unchanged (previously compacted soil). The increase of the volume of the compacted soil at mesocosm scale is due to the upward transport of soil materials in the form of anecic casts, thus increasing the overall volume while the matrix was not de-compacted. Therefore, earthworms mostly create large pores eventually allowing for rapid transfers of air and solutes to occur, provided that these pores are connected to the surface (Bottinelli et al., 2017; Capowiez et al., 2015), but they do not perform a real de-compaction of the compacted soil matrix, and they even compact the matrix of a loose soil.

Observations at the scale of undisturbed cubic samples accorded with those obtained on the soil matrix at mesocosm scale and with previously reported results using another endogeic species and the same soils without pre-compaction (Kohler-Milleret et al., 2013; Milleret et al., 2009). All earthworm species tended to decrease the soil volume of the samples, particularly endogeic species in loose soil. The plasma volume was not impacted at −1 kPa and was more rigid for the Anthrosol with endogeic species as revealed by the increased air entry point plasma volume. Most of the pore volume decrease at this scale was accounted for by the decrease in air saturated pore volume at −1 kPa, which correspond to pores of more than 150 μm in equivalent radius including burrows. According to the equivalent pore size distribution calculated from water retention curves, the pores smaller than 150 μm in equivalent radius were not significantly impacted, meaning that only the larger structural pores were affected by earthworms drilling the soil. Shrink-swell processes did not occur because of the standardized matric potential, thus no cracking occurred. The structural pores were therefore only inter-aggregates packing voids produced when repacking the soils and burrows. The matrix compaction observed at mesocosm scale on the loose soil is probably due to the compression of these packing voids upon earthworm body pressure (Barré et al., 2009; Keudel and Schrader, 1999). This was limited or not observed on the compacted soils since these voids were already decreased or eliminated by compaction. Accordingly, the burrow diameter was narrower in the compacted soils especially for the endogeic treatment, which is in accordance with reported field observations (Capowiez et al., 2012).

4.2.2. *Influence of casts*

The specific volumes observed at undisturbed samples scale at the end of the experiment were close to those of earthworm casts, i.e. intermediate between compacted and loose controls. The casts contained no structural porosity (Jouquet et al., 2008; Lipiec et al., 2015), in particular no packing voids. More recently, Le Bayon et al. (2020) showed that earthworm aggregates may have a smaller volume and a greater volumetric mass than non-earthworm aggregates. This is in accordance with the observation of larger impact of endogeic earthworms, which are known to eject their casts in the soil unlike anecic species who tend to eject some of them at the topsoil (Capowiez et al.,

2012). The change in the plasma behaviour was also in agreement with the transformed structure of the soil plasma after ingestion by the earthworms. However, a limited plasma swelling limits soil cracking under more pronounced drying-wetting cycles, which is one of the main process of soil resilience (Kay, 1998).

4.3. Earthworms and soil structure regeneration

Earthworms as "ecosystem engineers" are commonly assumed to be able to improve soil structure through burrowing activities, and thereby to allow remediation of compacted soils. Our results depict a more complex soil-earthworm interaction. A general model of earthworm impact on soil structure can be proposed based on these results. Earthworms drill burrows even in compacted soils, which is good for percolation and aeration, particularly with anecic species. This may promote further drying/wetting cycles in depth and thus indirectly contribute to the future regeneration of the compacted soil. However, earthworms will not by themselves de-compact the soil matrix, which should be performed by other abiotic or biotic factors (Drewry, 2006). By compacting a loose soil with body pressure, by filling the burrows with casts (endogeic species), or by creating a cast layer at the soil surface or along the burrow walls (anecic species), earthworms alone would tend to produce a semi-compacted soil, with bulk density close to that of the casts. Regarding burrow walls, Capowiez et al. (2021) and Rogasik et al. (2014) observed indeed compaction around them during mesocosm experiments. However, no effect of soil bulk density on the magnitude of this burrow walls compaction was reported in Capowiez (2021).

5. Conclusions

It is often stated that earthworms can build, take care or restore soil structure. These experiments highlighted the limited potential of earthworms alone, at least for European lumbricidae, to remediate compacted soils. This could be limited to the opening of some large connected biopores allowing for rapid air and water flows. However, earthworms do not allow the regeneration of the fine structural porosity. In addition, burrows are generally less numerous in compacted zones (Capowiez et al., 2009b; Radford et al., 2007). Our results were obtained on two different soil types and show good accordance with reported literature. They could therefore apply in many situations. Furthermore, they may help simulating earthworm behaviour through models as suggested by Capowiez et al. (2021). But such experiments can be partially transferred to field situations as the effects of soil biota is much more complex. For example, our results may have been different if plants or mycorrhizae were included in our experimental design. Milleret et al. (2009) showed that while *Allobophora chlorotica* alone induced soil structural porosity compaction, it was not the case anymore when associated with leek roots and mycorrhizae. Earthworms generally do not act alone, except in case of ecological perturbation (Chauvel et al., 1999). They participate in many interactions, in particular with roots. Van Groenigen et al. (2019) have thus shown that Relative Cast Fertility was strongly dependent on the presence of plants or residues. Therefore, our results plea for an ecological vision of soil restoration involving earthworm contribution and other factors rather than thinking in an over-simplified way with earthworm as the single factor of soil restoration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2021.115164.

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