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Decreased burrowing activity of endogeic earthworms and effects on water infiltration in response to an increase in soil bulk density

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Abstract

Endogeic earthworms live and burrow in the soil to find their food. They burrow by pushing the soil aside or ingesting it and are thus sensitive to soil compaction. However there is a scarcity of data regarding the effects of soil bulk density on the burrowing behavior and activity of endogeic earthworms. We carried out laboratory experiments using repacked soil cores with various levels of bulk density (from 1.18 to 1.38 g cm^{-3}) in which individuals of *Aporrectodea caliginosa* or *Allolobophora chlorotica* were incubated for six weeks. The burrow systems inside the soil cores and the compaction around the burrows were then analyzed using X-ray tomography. Soil water infiltration measurements were also carried out. The increase in bulk density had a negative impact on all burrow system characteristics (length, volume, diameter, continuity, number of burrows). When bulk density increased from 1.18 to 1.38 g cm^{-3}, volume, diameter, continuity and the number of burrows decreased on average by 77%, 21%, 81% and 58%, respectively. The increase in density due to compaction around the burrows was similar whatever the species and the bulk density. Increasing soil bulk density from 1.18 to 1.38 g cm^{-3} also greatly decreased water infiltration (-89% for both species) and increased breakthrough time (10 and 25-fold for *A. chlorotica* and *A. caliginosa* respectively). However, compared to a control without earthworms, water infiltration in cores incubated with endogeic species was only increased significantly at 1.18 and 1.23 g cm^{-3}. This illustrates that burrows made by endogeic earthworms moderately increase water infiltration and only when the soil bulk density is low. Data provided in this study could be used to refine simulation models of earthworm burrowing behavior where burrowing is assumed to be mainly governed by soil water content, temperature and soil bulk density.

Keywords: compaction; burrow system; *Aporrectodea caliginosa; Allolobophora chlorotica*; behaviour

Abbreviations

BD: soil bulk density

Introduction

Compaction, partly due to an increase of engine loads, is a major threat to agricultural and forest soils and their resilience (Hansen 1996). Earthworms are particularly sensitive to soil compaction as they burrow their way in the soil either by pushing the soil aside or ingesting it (Beylich et al., 2010; Keller et al., 2017). Indeed, ingestion is the only possible way of moving in highly compacted soils (Dexter, 1978) and often results in higher quantities of excreted surface casts (Joschko et al., 1989). A high BD also means that more energy is spent burrowing (Ruiz et al., 2010). Although earthworms generally avoid highly compacted zones (Stovold et al., 1994), epi-anecic such as *Lumbricus terrestris*, earthworms have been observed to burrow in them under semi-field conditions in the presence of a plough pan (Capowiez et al., 2009). Epi-anecics and other species have also been found to burrow in compacted zones below wheels tracks under field conditions (Capowiez et al., 2012).

Thus bulk density (BD) is one important factor indirectly governing earthworm abundance in croplands (Chan and Barchia, 2007; Ouellet et al., 2008; Capowiez et al., 2009), forests (Jordan et al., 1999; Bottinelli et al., 2014), tallgrass prairies (Althoff et al., 2009) and urban soils (Smetak et al., 2007). Among earthworms, anecic and epi-anecic earthworms (*sensu* Bouché, 1972) are thought to be more powerful axially (Keudel and Schrader, 1999) and thus less sensitive to compaction (Beylich et al., 2010). Paradoxically, much more information has been reported on the effects of soil compaction on anecic or epi-anecic earthworm behavior than on other ecological categories. Rushton (1986) and Joschko et al. (1989) demonstrated that burrow length was decreased when *L. terrestris* was challenged with increased BD. Stovold et al. (1994) made a similar observation for *Aporrectodea nocturna* in a choice experiment. Kretzschmar (1991) estimated that *Aporrectodea* *longa* burrowing activity, as assessed by surface cast production, decreased for higher BD. This bias towards the anecic or epi-anecic species is explained by the fact that these species have a greater influence on water infiltration since their burrows are more vertical, more continuous (because less refilled) and have surface openings (Capowiez et al., 2015). In fact, compaction impacts not only burrow numbers but also burrow continuity (Schäffer et al., 2007; Capowiez et al., 2012) and this in turn can drastically reduce water infiltration (Kim et al., 2010). In comparison, information regarding the effects of compaction on endogeic earthworms is scarce. Langmaack et al (1999) studied *A. caliginosa* burrowing behavior in compacted vs non-compacted soils and concluded that in response to compaction this species increased burrow continuity but no clear trend was observed for burrow length. Dexter (1978) also found that high BD did not have a negative impact on *A. caliginosa* burrowing. In contrast, Söchtig and Larink (1992) determined that *A. caliginosa* burrow length decreased linearly when pore volume decreased (and thus BD increased).

In most of these studies, the effects of high BD on earthworms were measured indirectly, i.e. either by assessing surface cast production (assuming most of the casts were produced at the soil surface) or the burrows on the outer borders of soil cores (assuming these burrows were representative of burrows in the cores). This latter case is due to the absence of non-invasive techniques for estimating burrows in soil cores in past decades. Nevertheless the first application of X-ray tomography to analyze earthworm systems was in the early 90s (Joschko et al., 1991) and medical scanners are now readily available to solve this problem. Microtomography with an higher resolution can now also be used (Balseiro-Romano et al., 2020). Another point that sometimes limits the relevance of past studies is the fact that they were observed using choice experiments: earthworms were placed in mesocosms containing soils with different BD and their burrowing activity was estimated in the different situations (Stovold et al., 1994; Söchtig and Larink, 1992). This kind of study provides information on earthworm preferences but not really on their ability to burrow and live in compacted soils. Furthermore, in most studies only two to three BD were tested (Joschko et al., 1989; Joschko et al., 1993; Langmaack et al., 1999; Stovold et al., 1994; Jégou et al., 2002; Capowiez et al., 2012) whereas recent studies suggested that depending on the soil texture, earthworm responses in terms of burrowing are not always monotonic (see Figure 5 in Pöhlitz et al., 2020).

Overall, there is an increasing demand for accurate estimates of the effects of BD on earthworm burrowing (Roeben et al., 2020) since this kind of information is required, for example, to simulate earthworm behavior and better assess their real exposure to pesticides. However, there is a scarcity of useable data in the literature, especially for endogeic species.

Thus, in the present study, we carried out a lab experiment with soil cores compacted at five different BD currently observed in orchard soils close to Avignon, France. We then studied the resulting effects on the burrow system characteristics of two very common endogeic species (*Aporrectodea caliginosa* and *Allolobophora chlorotica*). We also determined how BD and earthworm species modified water infiltration. Furthermore, it is known that earthworms can compact the soil when they burrow (Rogasik et al., 2014; Capowiez et al., 2011; Milleret et al., 2009) and thus we assessed whether the lateral compaction around the burrows was influenced by soil BD for these species.

Material and Methods

Soil and earthworms

Soil (0-20 cm depth) and earthworms were sampled in an orchard abandoned since at least ten years in Avignon, in the south east of France. The soil has the following characteristics: pH = 8.2, clay = 19.7%, silt = 50.8%, sand = 29.5%, OM = 3.4%, CEC = 8.48 cmol C kg^{-1}. The soil was sieved at 3 mm and kept at constant humidity (20% on a mass basis, i.e. about 80% of its water holding capacity). In this orchard, we found high densities of earthworms (> 300 individuals m^{-2}) and the most dominant species were two endogeic species: *Allolobophora chlorotica* (leucotypic form according to Bouché (1972) but often called pink morph) and *Aporrectodea caliginosa*. However, these two species presumably do not occupy exactly the same niche as these species were indeed described as an ‘intermediate‘ and ‘endogeic’ species by Bouché (1972), respectively. Recently, Bottinelli et al. (2020) demonstrated that each lumbricid earthworm species can be categorized by three percentages into the three main ecological categories defined by Bouché (1977). According to that study, *A. chlorotica* (leucotypic form) is 97% endogeic and 3% anecic, whereas *A. caliginosa* is 80% endogeic, 16% epigeic and 4% anecic.

Mesocosms and experimental design

Mesocosms were PVC cores (height: 30 cm, diameter:16 cm) filled with sieved soil. For each soil layer (600 g of soil at 80% WHC), the soil was pressed to the desired bulk density using a hydraulic press with increasing pressures. For this experiment, 50 cores were prepared with ten cores for each soil bulk density (BD): four with *A. caliginosa*, four with *A. chlorotica* and two control cores without earthworms. The five levels of BD were 1.18, 1.23, 1.29, 1.34 and 1.38 g cm^{-3}. This range was chosen to encompass the BD observed in orchards, from tilled zones under the row to compacted zones below wheel tracks (personal observation). In each core, we introduced three individuals of either *A. caliginosa* or *A. chlorotica* (thus a density of 150 individuals m^{-2}) or no earthworms. These endogeic densities can be found in most agricultural soils (excepted vineyards). Only adults were used in the experiment and the mean (+/- SD) biomass for each species was 0.57 (+/- 0.04) and 0.44 (+/- 0.04) g for *A. caliginosa* and *A. chlorotica,* respectively. At the end of the experiment (5 weeks), 5 ml of chloroform was poured into each core to kill earthworms and prevent further burrowing. In each core, surface casts were sampled, dried for 48 h at 110°C and weighed.

X-ray computed tomography and burrow system characterization

Macroporosity within the soil cores was analyzed by X-ray computed tomography using a medical scanner (BrightSpeed Exel 4, General Electric) in the INRA Nancy research centre. The scanner settings were 130 kV and 50 mA. DICOM images were transformed into 8-bit images using the following parameters WL = -1000 and WW = 2000 HU. The greylevel histograms of the images showed two well separated peaks, one for the soil matrix and one for the porosity. We decided to choose a binary threshold value set at 1/3 of the distance between the two peaks. Since the peak value is dependent on the density of the soil matrix, this ensures that differences in density between BD treatments did not influence the total macroporosity volume. Images were filtered using a mean filter of radius 2 to remove some noise. Burrow system 3D reconstructions and skeletonizations were obtained using Avizo software (ThermoScientific). Other computations were carried out using ImageJ (Schindelin et al., 2012) and the 'SoilJ' and 'BoneJ' plugins. We thus estimated burrow system volume. Mean burrow diameter was estimated by selecting the most circular pores ('circularity' > 0.8 in ImageJ) on 2D images, assessing their area and computing an equivalent diameter. To assess burrow system continuity, as no standardized measure exists, we compute the number of burrows whose vertical extension was larger than 30% of the core length (i.e. 9 cm) was counted. We also computed the degree of anisotropy of the burrow system using BoneJ ; this algorithm assesses whether objects are oriented in the same direction (degree of anisotropy close to 0) or randomly in 3D (degree of anisotropy close to 1). To assess whether the endogeic species compacted the soil around their respective burrows, we selected the 8 mm spatial zones around the burrows (as assessed visually on the images) and simply computed the mean greylevel in these zones. For cores without earthworms, we randomly selected zones of similar size in the images to compute the mean greylevel value.

Water infiltration

To study the effects of the presence of an earthworm burrow system and its characteristics on water infiltration, we used the same protocols in Capowiez et al. (2015). Soil cores were placed on a funnel to be able to observe water drainage below the cores. In brief, 150 ml of water was poured onto a soil core, the time was recorded until the water was completely absorbed and then a new volume was added. We also noted the time at which water began to drain (‘breakthrough time’). This procedure was repeated until a linear trend was observed (i.e. same time intervals between applied water volumes), which was typically after around eight volumes. This single-ring protocol allowed the steady-state infiltration rate to be estimated by linear regression for each core. The first data points of the relationship between time and the number of water volumes poured were removed.

Statistical analysis

Our experimental design was balanced for comparing the responses of the two species (if we excluded cores without earthworms). For count data (burrow continuity), we used a GLM with a quasi-poisson family. For other burrow system characteristics and cast production, we used ANOVA since no large deviations from normality (Shapiro-Wilk test: all p-values > 0.061) or homoscedasticity (Levene test: all p-values > 0.047) were detected. In both cases, we first ran the analyses with two factors (BD and earthworm species) and then if the interaction was not significant (the most common case), we ran two tests (GLM or ANOVA) for each species separately. For infiltration data (infiltration rate and breakthrough time), we applied the same analysis but we also computed the infiltration gain, i.e. the difference between infiltration of each species compared to the cores at the same BD but without earthworms. These gains were also analyzed using a two-way ANOVA and then two one-way ANOVA. Linear regressions were carried out for burrow volume with the ‘lm’ function. All analyses were made in R (R core team, 2019).

Results

Effects of bulk density on the earthworm burrow system

Examples of the 3D burrow systems are shown in Figure 1. The two-way ANOVA indicated that BD had a highly significant effect on burrow volume whereas species and the interaction between BD and species were not significant (Table S1). One-way ANOVA for each species separately showed that burrow volumes were significantly larger at 1.18 g cm^{-3} than at other BD for both species (Fig. 2). At 1.38 g cm^{-3}, the burrow volume was significantly lower than at 1.18 and 1.23 g cm^{-3} for both species. The decrease in burrow volume between the minimal (1.18 g cm^{-3}) and maximal (1.38 g cm^{-3}) tested BD was high with -75% and -80% for *A. caliginosa* and *A. chlorotica,* respectively. The linear regressions between BD and burrow volume were significant ($p = 0.027$ and 0.0071) and the R^2 values were 0.79 and 0.91 and for *A. caliginosa* and *A. chlorotica* respectively, even if the linear trend was more obvious for the latter species. We observed very similar decreases and significant differences in burrow lengths (Table 1).

BD and species ($p < 0.001$) also had a significant influence on burrow diameter, but no interaction was observed between these factors ($p = 0.21$). For. *A. caliginosa*, burrow diameter was only significantly different at the lowest BD compared to the highest BD. For *A. chlorotica* diameter values at the two lowest BD were significantly different from those at the other BD (Table 1).

BD also has a significant effect on burrow continuity, assessed as the number of burrows with a vertical elongation larger than 9 cm (Table S1). At the lowest BD, a mean of 6 and 7 such burrows were observed for *A. caliginosa* and *A. chlorotica* respectively. At the highest BD, only one such burrow was observed on average for both species (Fig. 3). Thus, BD had a highly significant effect on burrow continuity ($p < 0.001$), whereas species and interaction did not ($p = 0.17$ and 0.16, respectively). For *A. caliginosa*, only the continuity for the lowest and the highest BD were different, whereas for *A. chlorotica*, continuity at the three highest BD was significantly different from that at the lowest BD.

The degree of anisotropy of the burrow systems increased with increasing BD whereas species and the interaction were not significant (Table S1 and Fig. 4). For both species, the degree of anisotropy for the two lowest BD was significantly lower than those observed at the highest BD which suggests that increased BD leads to less randomly orientated burrow systems. Finally BD or species (results not shown) did not affect burrow system verticality (mean deviation from the vertical of the segments of the skeleton).

Surface cast production was low (less than 10 g of dry soil) and not influenced by BD for *A. chlorotica* (Table 1). In contrast, for *A. caliginosa*, cast production was higher (15-32 g of dry soil; Table 1) and was the highest at a BD of 1.34 g cm^{-3} and significantly different from the amount produced at the two lowest tested BD.

Effects on water infiltration

BD ($p < 0.001$) had a significant impact on infiltration rates and breakthrough times, but the earthworm factor (with three modalities: *A. caliginosa*, *A. chlorotica* and no earthworm) and the interaction were not significant ($p = 0.36$ and 0.55 respectively for infiltration rate ; $p = 0.30$ and 0.21 respectively for breakthrough time). When BD increased, infiltration rates decreased and breakthrough times increased (Table 2).

When infiltration was expressed relative to the control without earthworms, BD has a significant impact ($p < 0.001$) but species (with two modalities: *A. caliginosa* and *A. chlorotica*) and the interaction were not significant ($p = 0.26$ and 0.17 respectively). Significant differences due to earthworm's presence were only observed at the lowest BD for *A. caliginosa* and at the two lowest BD for *A. chlorotica* (Fig. 5). No significant effect was observed for breakthrough times expressed relative to the control (data not shown).

Effects on soil bulk density around the burrows

The mean soil BD around the burrows increased when BD of the soil core increased (Fig. S2). Soil BD had a highly significant effect ($p < 0.001$) as did the presence of earthworms ($p < 0.001$), but there was no significant interaction between these two factors ($p = 0.83$). For each BD, the difference in BD around the burrows appeared to be similar (around five greylevels corresponding to 59 HU) in the presence or absence of earthworms.

Discussion

Effects of bulk density on earthworm burrowing and casting behavior

BD strongly and negatively influenced all the geometrical characteristics of the burrow systems of both endogeic species. First of all in terms of magnitude, the volumes (and lengths) of the burrow systems decreased almost linearly with increasing BD. Thus with our soil which lies between loam and silt loam soil, we did not observe a non-monotonic relationship between BD and soil macroporosity as reported by Pöhlitz et al. (2020) using the epi-anecic earthworm *L. terrestris*. This earthworm species has a mono-typical burrowing behavior with the creation of an often single vertical burrow, eventually with a few lateral branches close to the surface resulting in a Y-shaped burrow system (Shipitalo and Butt, 1999). These features make this species less prone to drastically decreasing burrow length since their burrow is also a vital shelter.

Burrow diameter gradually decreased when BD increased for both species, but this change was more marked for *A. chlorotica* for which we already observed a significant difference between 1.18 and 1.29 g cm^{-3}. As the earthworms were of similar weight at the beginning of the experiment, this suggests that they may have created thinner burrows in denser soil, probably to save energy.

Other burrow system characteristics were also modified. The most drastic change was burrow system continuity. Its decrease with increasing BD was almost linear for *A. caliginosa,* but for *A. chlorotica* the most important changes occurred between 1.18 and 1.29 g cm^{-3} with a sharp decrease of -60%. This suggests that the burrows of this species were less vertically continuous as soon as the BD increases. Moreover, the degree of anisotropy of the burrow systems increased significantly with BD for both species. This showed that the burrows had no preferential orientation at low BD but then a trend for a non-preferential orientation appeared for higher BD. Taken together, these observations further suggests that *A. chlorotica* burrows less vertically in soil with intermediate to higher BD values, even if we did not observe significant differences for verticality.

Overall, we did not observe large differences between the responses of the two species to the increase in BD. However, for most of the burrow system characteristics (except the degree of anisotropy) the decreases observed at 1.34 compared to 1.18 g cm^{-3} were less marked for *A. caliginosa* than for *A. chlorotica*, even if the values observed for a BD of 1.38 g cm^{-3} were similar for both species. Thus although a BD of 1.38 g cm^{-3} was a strongly limiting factor for both species, *A.caliginosa* appeared to have a better resistance to lower but still high BD (1.34 g cm^{-3}).

Another striking difference between the two species was the production of casts at the surface with *A. chlorotica* producing very few casts regardless of the BD. In contrast, *A. caliginosa* produced more casts and showed a tendency to cast more at the soil surface when BD increased (except for the highest BD but in that case the burrow volume was very limited). This corroborates previous findings (Rushton, 1986; Kretzschmar, 1991) showing that when the soil is compacted the earthworms tend to produce more surface casts in order to increase the air-filled porosity and aeration within the soil. If we assume that the casts had the same BD than the soil from which they were created, we could compute the ratio of the volume of macroporosity (burrows) that was deposited at the soil surface as casts. In this case, the proportion of burrow volume increased with SBD for both species (Fig. S3) ; this increase was however higher for *A. caliginosa* with casts representing 100% of the burrow volume at the highest BD tested. The difference between the two species may partly be explained by the fact that *A. caliginosa* is epigeic at 16% (*A. chlorotica* at 0%) and thus is more prone to defecate at the soil surface.

Consequences for water infiltration

Breakthrough time characterizes the transient regime of infiltration while the infiltration rate is a measure of the stationary flow regime. In control samples without earthworms, infiltration rates decreased by a factor of 4.4 and and breakthrough time increased by a factor of 7.6 when BD increases from 1.18 to 1.38 g cm^{-3}. The occurence of macropores (earthworm burrows) in the homogeneous porous sample tended to mitigate the effect but only for the lowest BD. Infiltration rates and breakthrough times increased when BD increased. This finding was expected since an increased BD means lower macroporosity and generally a decreased continuity of such pores as illustrated in the present study with the decreased burrow continuity.

Endogeic burrows are often discontinuous, since they can be refilled by casts, and often less connected to the surface (Capowiez et al., 2014). Thus their involvement in increased water transfer efficiency is still open for debate. In the present study, we demonstrated that the effect of the activity of endogeic species on infiltration was only significant for low BD (1.18 g cm^{-3} for *A. caliginosa* and 1.18 and 1.23 g cm^{-3} for *A. chlorotica*). This may appear to be counterintuitive: when the soil is compacted the burrows could have been preferential pathways for air and water transfer (Mossadeghi-Björklund et al., 2016). However these pathways are less vertical and only partial since the burrow continuity rapidly decreased when BD increased. In addition, the burrow systems were less extensive at moderate and high BD and thus their functional role was limited.

We observed a small but significant increase in the soil matrix greylevels surrounding earthworm burrows (for both species). Thus, regardless of the initial BD, earthworm burrowing appears to cause a constant increase in the BD around the burrows. This also limit the roles of earthworm burrows in water transfer (Pelisek et al., 2018) since the two species produced discontinuous burrows and thus water would need to enter and go out of several burrows to reach the bottom of the cores. Rogasik et al. (2014) previously showed that *L. terrestris* burrowing caused a lateral compaction of the soil around the burrows. We further demonstrate that this is true for the two studied endogeic species. However, we were unable to detect an influence of BD on the intensity of this lateral compaction even though the burrow diameter significantly decreased at the highest tested BD.

Conclusions

We demonstrated that increasing BD impaired the burrowing behavior of two common endogeic species, and that total burrow volume and length decreased linearly with increasing BD. Although the earthworms promoted the soil infiltration capacity compared to control samples without earthworms, their effect was limited and only significant at low BD. These results were obtained using a single soil and only two species. The main findings could be compared with previous results obtained in other soils by computing an effective BD (Beylich et al., 2010) or by using a reference BD (Keller and Hakansson, 2010). Our results could be used in simulation models of earthworm behaviour, such as the model recently presented by Roeben et al. (2020). In this model, an energy budget is applied for each earthworm and our data could help parameterize the energy costs of burrowing as a function of bulk density.

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Figure legends:

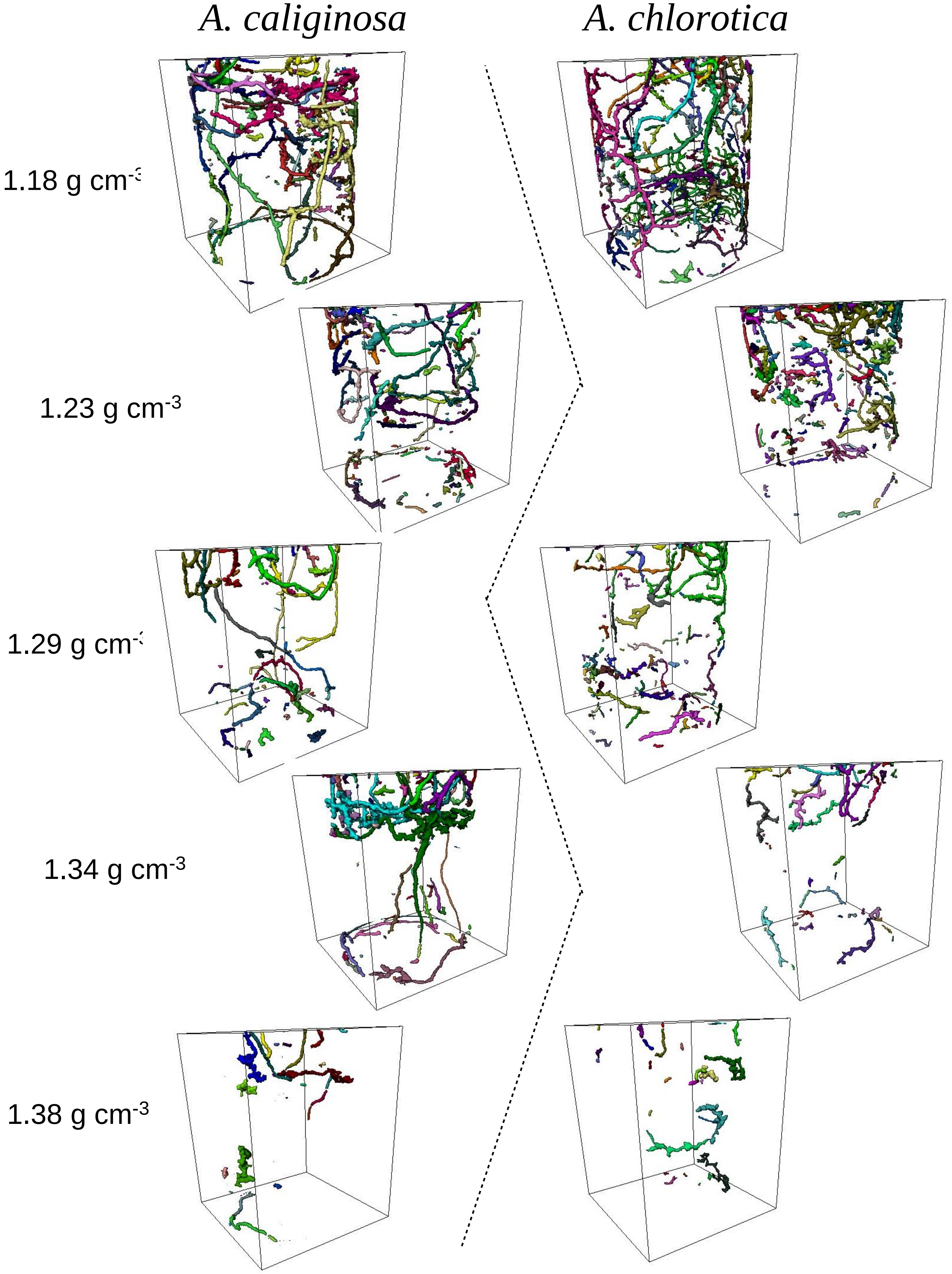
Fig. 1 Examples of 3D burrow systems made by three individuals of either *A. chlorotica* or *A. caliginosa* for 6 weeks in soil cores with increasing bulk densities.

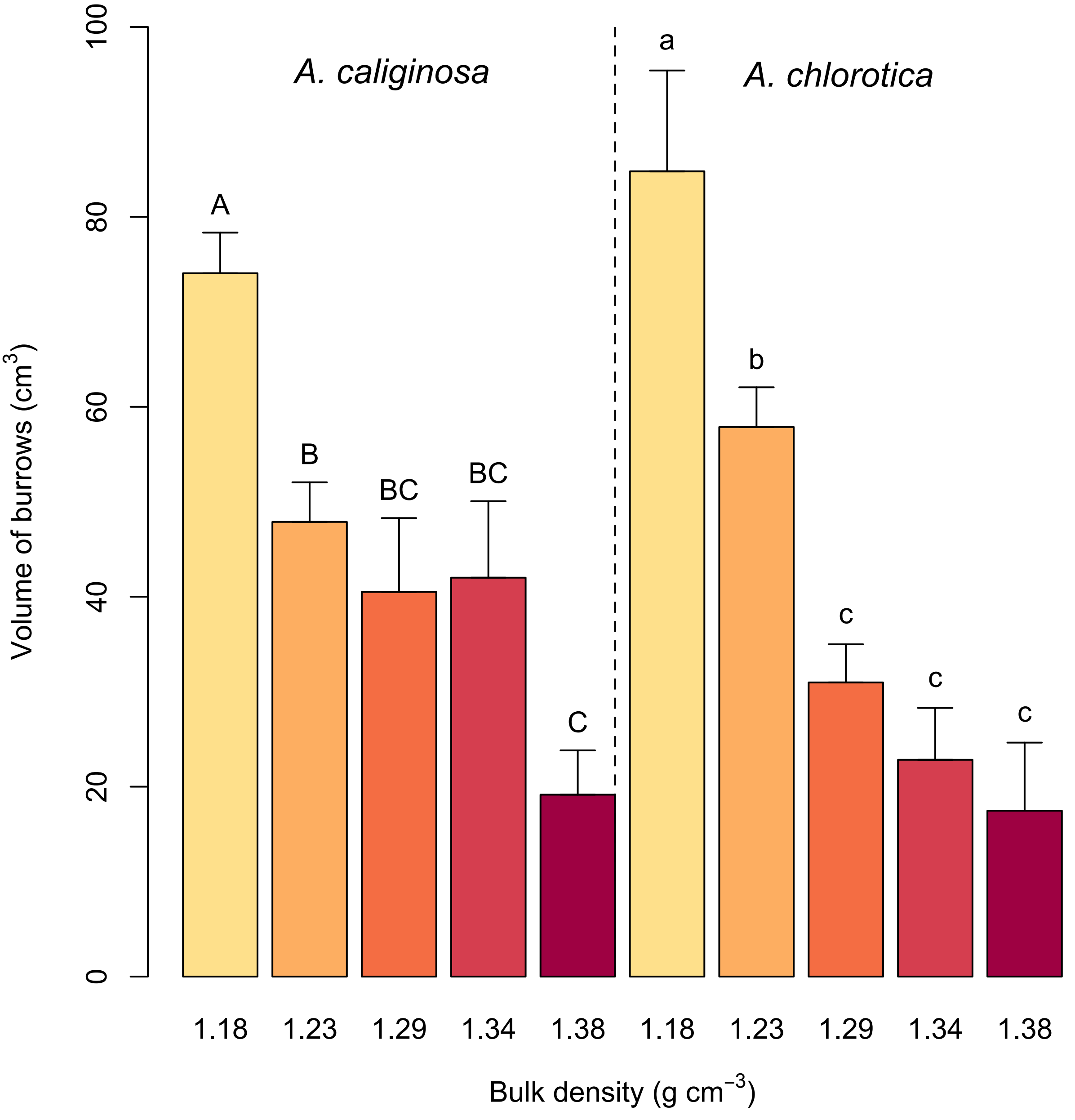
Fig. 2 Volume of burrows (means + SE) created by three individuals of either *A. chlorotica* or *A. caliginosa* for 6 weeks in soil cores with increasing bulk densities. Bars bearing different letters are significantly different (each species was tested separately).

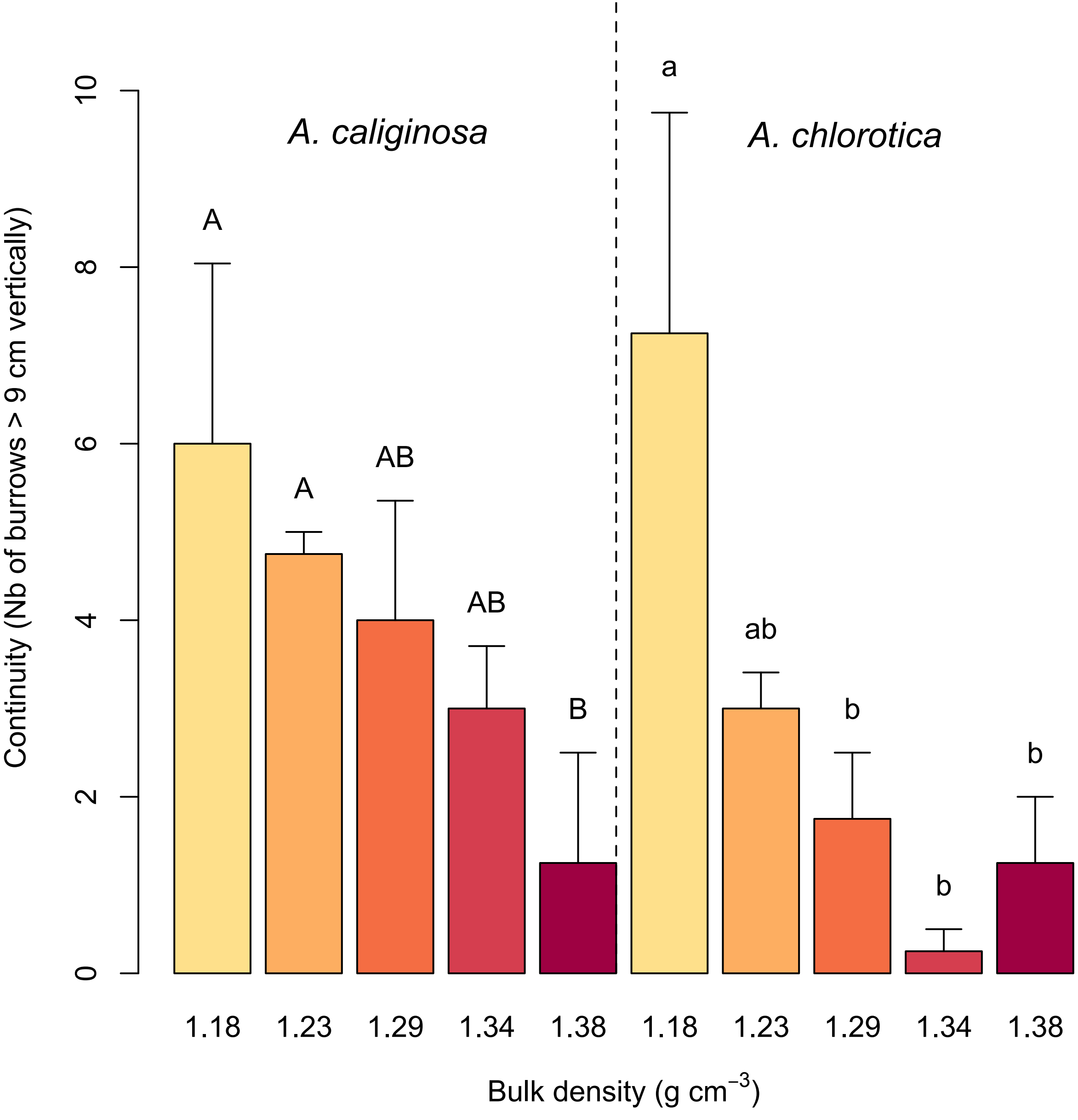
Fig. 3 Continuity of the burrow systems (means + SE) made by three individuals of either *A. chlorotica* or *A. caliginosa* for 6 weeks in soil cores with increasing bulk densities. Bars bearing different letters are significantly different (each species was tested separately).

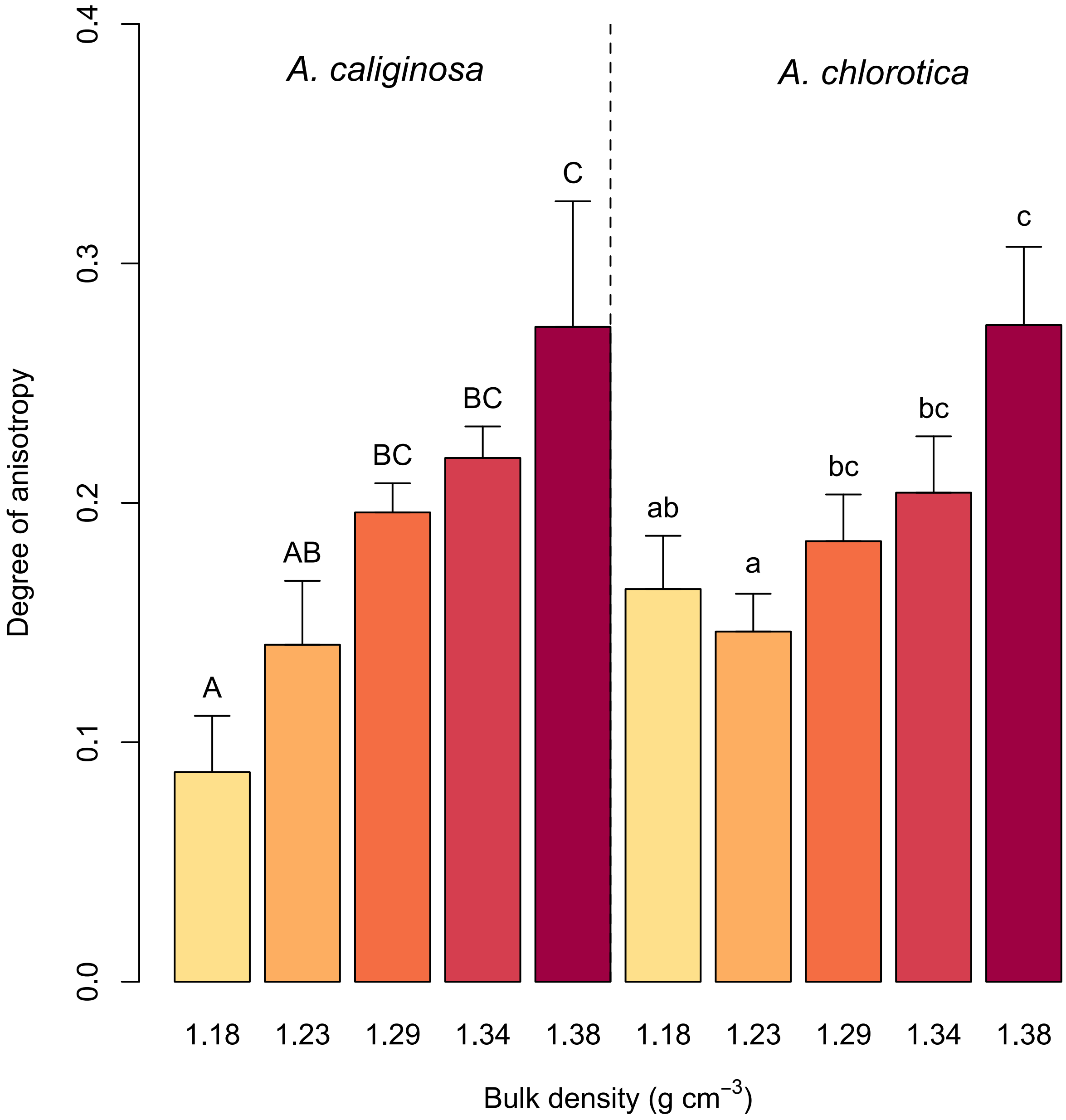
Fig. 4 Degree of anisotropy of the burrow systems (means + SE) made by three individuals of either *A. chlorotica* or *A. caliginosa* for 6 weeks in soil cores with increasing bulk densities. Bars bearing different letters are significantly different (each species was tested separately).

Fig. 5 Gain in water infiltration (means + SE) compared to control without earthworms, when three individuals of either *A. chlorotica* or *A. caliginosa* were incubated for 6 weeks in soil cores with increasing bulk densities. Stars indicate values significantly different from zero (each species was tested separately).


A. caliginosa
A. chlorotica
1.18 g cm-3
1.23 g cm-3
1.29 g cm-3
1.34 g cm-3
1.38 g cm-3


A. caliginosa
A. chlorotica
A
B
BC
BC
C
a
b
c
c
c
Volume of burrows (cm³)
0
20
40
60
80
100
1.18
1.23
1.29
1.34
1.38
1.18
1.23
1.29
1.34
1.38
Bulk density (g cm⁻³)


A. caliginosa
A. chlorotica
Continuity (Nb of burrows > 9 cm vertically)
0
2
4
6
8
10
A
A
AB
AB
B
a
ab
b
b
b
1.18
1.23
1.29
1.34
1.38
1.18
1.23
1.29
1.34
1.38
Bulk density (g cm^{-3})


A. caliginosa
A. chlorotica
Degree of anisotropy
0.0
0.1
0.2
0.3
0.4
A
AB
BC
BC
C
ab
a
bc
bc
c
1.18
1.23
1.29
1.34
1.38
1.18
1.23
1.29
1.34
1.38
Bulk density (g cm^{-3})

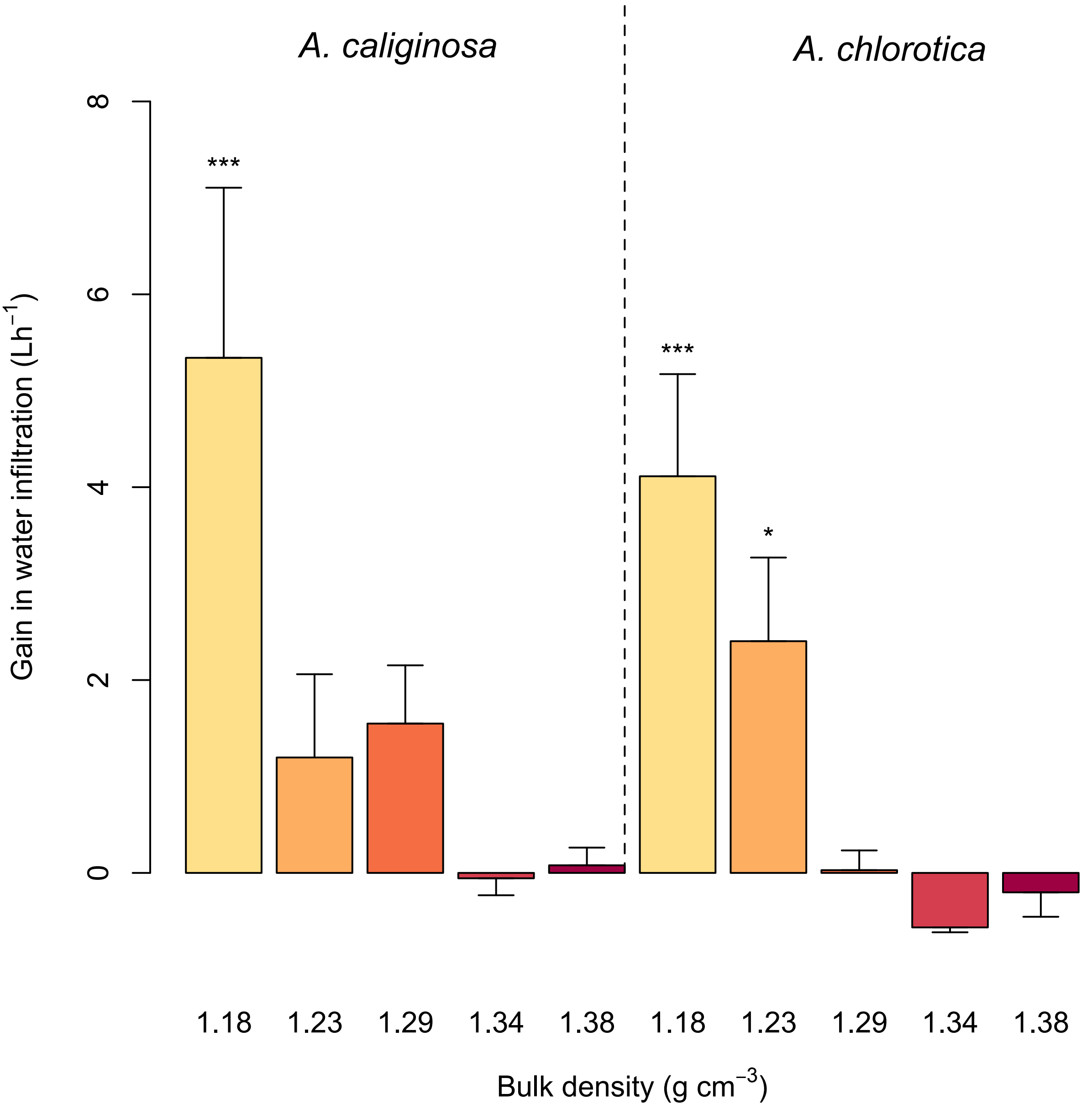

A. caliginosa
A. chlorotica
Gain in water infiltration (Lh^{-1})
8
6
4
2
0
***
***
*
1.18
1.23
1.29
1.34
1.38
1.18
1.23
1.29
1.34
1.38
Bulk density (g cm^{-3})

Table 1. Effects of an increase of soil bulk density on mean (SE) burrow diameter, total length and surface cast production in soil cores incubated with three individuals of either *Aporrectodea caliginosa* or *Allolobophora chlorotica.* ANOVA were carried out for each species separately. Values bearing different letters are different at the 5% significance threshold.

	Soil bulk density (g cm^{-3})				
	1.18	1.23	1.29	1.34	1.38
A. caliginosa					
Burrow diameter (mm)	2.97^{a} (0.06)	2.96^{ab} (0.07)	2.87^{ab} (0.07)	2.82^{ab} (0.06)	2.65^{b} (0.14)
Burrow length (cm)	58.82^{a} (5.66)	38.52^{ab} (3.52)	34.74^{b} (6.73)	35.02^{b} (5.93)	15.73^{c} (3.95)
Surface cast production (g)	17.17^{b} (3.65)	15.17^{b} (1.84)	24.36^{ab} (4.97)	32.11^{a} (5.43)	24.85^{ab} (6.33)
A. chlorotica					
Burrow diameter (mm)	2.71^{a} (0.09)	2.62^{a} (0.09)	2.36^{b} (0.06)	2.30^{b} (0.06)	2.59^{b} (0.14)
Burrow length (cm)	73.89^{a} (9.85)	50.00^{ab} (4.48)	30.05^{b} (4.08)	21.50^{b} (4.52)	15.02^{c} (6.02)
Surface cast production (g)	11.12 (2.13)	10.42 (0.78)	8.49 (0.25)	11.59 (2.44)	6.03 (1.88)

Table 2. Mean (SE) infiltration rates and breakthrough times in the soil cores incubated with three individuals of either *A. caliginosa* or *A. chlorotica* or no earthworm (control) for six weeks. Values bearing different letters are statistically different (each species tested separately).

	Soil bulk density (g cm^{-3})				
	1.18	1.23	1.29	1.34	1.38
Infiltration rate (L h^{-1})					
A. caliginosa	9.95^{a} (1.58)	3.70^{b} (0.96)	4.00^{b} (1.00)	1.66^{b} (0.64)	1.12^{b} (0.52)
A. chlorotica	8.72^{a} (1.48)	4.91^{ab} (1.11)	2.48^{b} (0.79)	1.15^{b} (0.54)	0.84^{b} (0.46)
Control	4.61 (1.07)	2.50 (0.79)	2.45 (0.78)	1.71 (0.65)	1.04 (0.51)
Breakthrough times (mn)					
A. caliginosa	0.55^{b} (0.27)	6.89^{a} (1.31)	6.73^{a} (1.29)	9.08^{a} (1.51)	14.28^{a} (1.89)
A. chlorotica	1.93^{b} (0.69)	2.58^{b} (0.80)	9.60^{ab} (1.55)	18.80^{a} (2.17)	12.63^{a} (1.78)
Control	2.23 (0.75)	6.93 (1.32)	11.35 (1.68)	15.72 (1.98)	16.96 (2.06)