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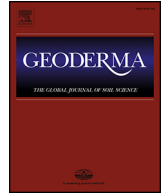


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Effects of endogeic earthworms on the soil organic matter dynamics and the soil structure in urban and alluvial soil materials



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ABSTRACT

Earthworms are considered as key actors of soil processes at different spatial and temporal scales and provide essential ecosystem services linked to climate regulation or primary production. However, little is known about their basic functional roles (e.g. organic matter decomposition, soil structuring processes) in perturbed systems such as urban or alluvial soils. Alluvial soils are characterized by regular physical perturbation through flooding and associated erosion/sedimentation processes which are rather similar to perturbations (e.g. temporal instability, spatial heterogeneity) affecting urban soils. Due to their close soil characteristics, we hypothesized that in both cases, soil functioning is similar with respect to soil fauna activity. Under controlled conditions, our objective was to investigate the effects of two endogeic earthworm species, *Allolobophora chlorotica* (pink morph) and *Aporrectodea rosea* (the two most abundant species found in the studied urban site), on soil organic matter (SOM) dynamics and soil structure (network of earthworm burrows) comparing an urban and an alluvial soil. We investigated the growth of individuals (weight gain and reproduction success) and assessed their effects on SOM decomposition (cumulative C–CO₂ emission, nitrogen and phosphorus mineralization) and soil structure (macroporosity, total length and connectivity of segments) after one and three months of incubation. Our results showed higher growth of *A. rosea* in the alluvial soil compared to the urban soil. However, the total length of burrows, carbon and nitrogen mineralization were often higher in the urban soil especially when the two species were combined. This trend can be mainly explained by lower organic matter content found in the urban soil which may influence positively the burrowing activity and negatively the growth of earthworms. Endogeic earthworms appear a key feature of the soil functioning in the urban context through their roles on organic matter transformation, the formation and maintenance of the soil structure.

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1. Introduction

Soil invertebrates such as earthworms are considered as key actors of soil processes at different spatial and temporal scales and provide essential ecosystem services (MEA, 2005; Blouin et al., 2013). As soil engineers (Jones et al., 1994; Lavelle et al., 2006), earthworms contribute significantly to the formation and the maintenance of the soil structure which positively influence physicochemical properties of soils (Jouquet et al., 2006; Lavelle et al., 2006; Blouin et al., 2013). In urban soils from temperate regions, endogeic earthworms (Bouché, 1977) are highly diverse (Schlaghamerský and Pižl, 2009; Glasstetter, 2012). Moreover, they are probably the most resistant earthworms recorded in disturbed soils (Lavelle and Spain, 2001; Jouquet et al., 2010). Despite the general recognition of the importance of earthworms in ecosystems, their

potential has not been explored much in urban soils. It is for example unclear if the effects of endogeic earthworms, whose roles in soil organic matter (SOM) transformation and soil structuration are well documented in natural and agricultural soils (Edwards and Bohlen, 1996; Lavelle and Spain, 2001; Edwards, 2004; Bernard et al., 2011; Capowiez et al., 2012), are similar in urban soils. Few studies reported the burrowing activity of earthworms under controlled conditions in different urban soils (Nahmani et al., 2005; Milleret et al., 2009; Pey et al., 2013) but no comparison exists between alluvial and urban soil materials.

In the urban context, the major constraints are the mixing of materials from several origins (e.g. bricks, glass, compost) as well as the compaction of soils (McKinney, 2002; Hazelton and Murphy, 2011). This can affect the soil structure, water infiltration and air circulation and limits living conditions for plants (e.g. root penetration) and for soil organisms (e.g. habitat reduction) (McKinney, 2008; Roithmeier and Pieper, 2009). Comparison of urban soils with natural ones is useful in order to assess if soil fauna has similar effects on soil processes in the urban context as in natural setting. Alluvial soils seem to be a good reference for urban soils

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in that they are both young soil systems which are constituted of materials that have been manipulated, disturbed or transported at different spatial and temporal scales (Amossé et al., 2014). In this context, the aim of this study was to compare the effects of two endogeic earthworm species, *Allolobophora chlorotica* (pink morph, Savigny, 1826) and *Aporrectodea rosea* (Savigny, 1825), on the SOM dynamics and the soil structure in urban and alluvial soil materials. We hypothesized that the growth and the effects of earthworms in urban soils are similar to alluvial soils due to their close characteristics. Under laboratory conditions (microcosms), we studied (1) the soil organic matter dynamics through C–CO₂, N–NH₄⁺, N–NO₃⁻ and available phosphorus measurements; (2) the characteristics of earthworm burrows (macroporosity, total length of burrows and number of nodes) using the X-ray computed tomography imaging method; and (3) assess the growth of earthworms (weight gain and reproduction rate) in urban and alluvial soil materials.

2. Material and methods

2.1. Soil properties and earthworm sampling

The physicochemical properties of the alluvial and the urban soil are shown in Table 1.

The alluvial soil material was sampled from a Fluvic Cambisol (Calcaric Siltic) (IUSS Working Group, 2007)/FLUVIOSOL TYPIQUE carbonaté, pierrique et polyphasé (Baize and Girard, 2009) in the natural floodplain of the Allondon river (Switzerland, canton of Geneva, 46°12'10" N, 5°59'57" E). The urban soil material was collected from a Terric Anthrosol (Siltic) (IUSS Working Group, 2007)/ANTHROPOSOL RECONSTITUÉ carbonaté, nivelé, polyphasé à matériau terreux et à artefacts (Baize and Girard, 2009) in a stone quarry restored in 1995 (Switzerland, canton of Neuchâtel, 47°0'20"N, 6°54'46"E). The alluvial and urban soil profiles were both constituted on a sequence of three soil horizons, respectively Aca/JpcaMca/IIDcaMca and LtpAzca/ILLtpAzcaSzca/IIIDca (Baize and Girard, 2009) as described by Amossé et al. (2014).

The alluvial and urban soil materials were collected from the first soil horizon (organomineral soil), air-dried and then sieved at 2 mm in order to remove stones. After a previous identification of earthworm species in the two sites, *A. chlorotica* (pink morph) and *A. rosea* – the dominant species in terms of abundance – were collected in the urban site with the digging method (Glasstetter, 2012). Adults were kept and transferred to the laboratory one week before the experiment for their acclimation to new environmental conditions.

2.2. Experimental design

Microcosms were filled up with 942 cm³ of urban (U) and alluvial (A) soil materials (PVC pipe, 12 cm in height × 10 cm in internal diameter;

Binet et al., 2006), that is equivalent to 1150 g (1.22 g·cm⁻³) of urban and 950 g (1.01 g·cm⁻³) of alluvial soil materials, respectively. Before the experiment, soils were moistened with tap water until the water hold capacity, respectively 0.29 and 0.33 g·g⁻¹ for urban and alluvial soil materials. Microcosms with and without earthworm were set-up (5 replicates) in order to assess the effects of earthworms on soils. Three adults of *A. chlorotica* (C, pink form) (mean weight 0.22 g ind⁻¹ ± 0.08 g ind⁻¹) or *A. rosea* (R) (0.20 g ind⁻¹ ± 0.04 g ind⁻¹) were relieved of their gut contents before the inoculation. A combination of two adults of each species (RC) was also tested in order to assess species interactions in urban and alluvial soil materials. Microcosms were closed air tight and incubated in an acclimatized chamber at 15 °C with a day/night cycle of 14 h light and 10 h dark per day. The study was carried out over one and three months of incubation in order to assess the growth of earthworms and the effects of each species over time. Soil respiration was monitored twice a week on the first month and once a week during the last two months of incubation when respiration measurements were more stable. At the end of each incubation period, microcosms were analyzed by X-ray CT imaging method (Capowiez et al., 1998; Nahmani et al., 2005) as described in Section 2.4. A metal core (5 cm in height × 2.5 cm in internal diameter) was thereafter introduced into the upper 5 soil centimeters of each microcosm in order to measure the soil bulk density. Finally, earthworms were hand-collected, counted and weighted and a mix of the upper 5 soil centimeters was air-dried and sieved before chemical analyses.

2.3. Soil respiration and chemical analyses

Respiration was assessed through the measurement of C–CO₂ in microcosms after an incubation period of 24 h. For this purpose, a beaker with 30 ml of NaOH (0.5 M) was laid in each microcosm to trap CO₂ from the soil. The sodium hydroxide coming from the beaker was then mixed with barium chloride in excess (20%) and titration (877 Titrino plus, Methrom) was made with hydrochloric acid (0.5 M) until the stoichiometric point (pH 8.6) to measure soil respiration (Binet et al., 2006). The amount of ammoniac N–NH₄⁺ and nitrates N–NO₃⁻ were respectively measured after extraction with H₂SO₄ (0.5 M) and KCl (0.5 M) by spectroscopy at 636 nm and 410 nm, respectively (Scheiner, 2005). Organic carbon C_{org} and total nitrogen N_{tot} were measured according to the CHN method after acid fumigation of soils in order to remove carbonates prior to analyses (Harris et al., 2001). Available forms of phosphorus (P_{available}) were quantified according to the Olsen method and total phosphorus (P_{tot}) was measured following mineralisation and spectroscopy at 720 nm (Carter and Gregorich, 2007).

2.4. Earthworm burrow network

Non-destructive X-ray computed tomography (X-ray CT), was used to analyze the burrow system (volume, total length of burrow segments, number of nodes, number and mean length of burrow segments). Microcosms were scanned with a LightSpeed VCT (GE Healthcare) scanner, which contains a 64-channel detector having an axial pitch of 0.625 mm. The X-rays emitted with a maximum energy of 120 keV (average energy spectrum of 70 keV) with a 640 mA tube current and focalized on 1.2 mm spot size. Particular attention was paid to the voxel size in order to undertake quantitative image analysis. One image slice was reconstructed with 512 × 512 pixels of size 0.215 × 0.215 mm. Although the detector resolution in the axial direction was 0.625 mm, the distance between slices was 0.312 mm due to an overlay of the scanned slices. Hence, the voxel size was 0.215 × 0.215 × 0.312 mm. To avoid artifacts of microcosm border, the image analysis was limited in each microcosm to a standardized cylindrical volume of 10.2 cm in height × 9.75 cm in diameter centered on the vertical axis of the microcosm.

Table 1
Initial physicochemical properties of alluvial and urban soil materials.

Texture (USDA, 1975 in Gobat et al., 2013)	Alluvial soil	Urban soil
	Loamy-clayed	Loamy
Clay (%)	33.0	20.7
Silt (%)	30.3	34.7
Sand (%)	36.7	44.6
pH _{H2O}	7.7	8.1
C _{org} (%)	4.0	2.2
N _{tot} (%)	0.28	0.17
N–NO ₃ ⁻ (mg·kg ⁻¹)	0.52	0.00
N–NH ₄ ⁺ (mg·kg ⁻¹)	19.67	10.30
C _{org} /N _{tot}	14.3	12.9
P _{tot} (mg·kg ⁻¹)	525.9	629.4
P _{available} (mg·kg ⁻¹)	12.2	33.2
CaCO ₃ (%)	22.7	19.6
CEC (cmolc·kg ⁻¹)	21.6	13.3
Water holding capacity (g·g ⁻¹)	0.33	0.29

2.5. X-ray CT image analysis

Three-dimensional computed tomography data were analyzed using the VSG AVIZO FIRE 7.0.1 software. An optimal threshold of intensity (gray values) was first visually determined on selected urban and alluvial microcosms, to best differentiate the void from the soil matrix. Due to the good contrast between the macro-voids and the soil matrix and to the similarity of the scanning parameters for all samples, this optimal threshold was systematically used to individualize (or segment) void volumes of all microcosms as shown in Fig. 1. The segmented voids were assimilated to the initial macroporosity of the microcosms (which appears negligible as shown in Fig. 1) and to the porosity created by earthworm burrows after one and three months of incubation. Macro-voids created by earthworms represent our feature of interest and its segmented volume was calculated for each soil sample. After a binarization of the images (macro-voids versus matrix), a linearization (skeletonization) of these essentially tubular voids was then computed with the Avizo XSkeleton pack. Skeletonization statistics, e.g. cumulated length of burrows, mean length of skeletonized segments, and number of vertices (or nodes). Finally, the verticality of burrows per microcosm was estimated from the calculation of the mean inclination of all skeletonized segments.

2.6. Statistical analysis

For all treatments and for each period of incubation, variables related to the growth of earthworms (weight gain and reproduction), SOM dynamics (cumulative C–CO₂ emission, N–NH₄⁺, N–NO₃⁻, C_{org} and P_{available} contents) and soil physical characteristics (soil bulk density, soil macroporosity, the total length of burrows and the number of nodes) were tested independently for homogeneity of variance using Levene's test (Levene, 1960). Variables were then analyzed using one or two way analyses of variance (ANOVA) in order to test for differences between treatments. All the experiments were done with n = 5 repetitions. The level of significance was fixed at p < 0.05. All statistical analyses were carried out with R (R Development Core Team, 2011).

3. Results

3.1. Earthworm growth and reproduction

After one and three months of incubation, the biomass of endogeic earthworm increased in both soils except for *A. rosea* in the urban soil (Table 2). Comparing earthworm species, *A. chlorotica* weight gain was higher than *A. rosea* in the alluvial and urban soils after one and three months of experiment and this difference was significant in the urban soil (p < 0.05). In the alluvial soil, the reproduction rate of *A. rosea* was the highest (mean value of 34 juveniles per replicate) after three months of incubation.

3.2. SOM mineralization and organic carbon in the soil

C–CO₂ emissions differed between urban and alluvial soil materials after one and three months of incubation (f_{1–40} = 190.2, p < 0.001 and f_{1–40} = 908.1, p < 0.001 respectively) and among earthworm treatments (f_{3–40} = 16.7, p < 0.001 and f_{3–40} = 21.5, p < 0.001 respectively). A synergic effect between soil materials and earthworms on soil respiration was also observed after both periods of incubation (f_{3–40} = 3.3, p < 0.05 and f_{3–40} = 5.2, p < 0.005 respectively) (Table 3).

In the controls, soil respiration was higher in the alluvial compared to the urban soil for both periods of experiment (Table 4). The effect of earthworm activity on soil respiration was the strongest in the urban soil and especially when the two species were combined after three months of incubation (p < 0.05). Compared to the control, an increase of 53% of C–CO₂ emission was observed in the urban soil with the combination of both species after three months while the increase was five times lower (9.6% of C–CO₂ emission compared to the control) in the alluvial soil.

After one and three months of incubation, soil respiration was similar in treatments inoculated with *A. chlorotica* or *A. rosea* in the urban soil. However, in the alluvial soil, the cumulative C–CO₂ emission was higher in the soil inoculated with *A. chlorotica* than in the soil inoculated with *A. rosea* after one month of experiment. No effect of earthworms on C_{org} content was observed in comparison to soil controls (Table 4).

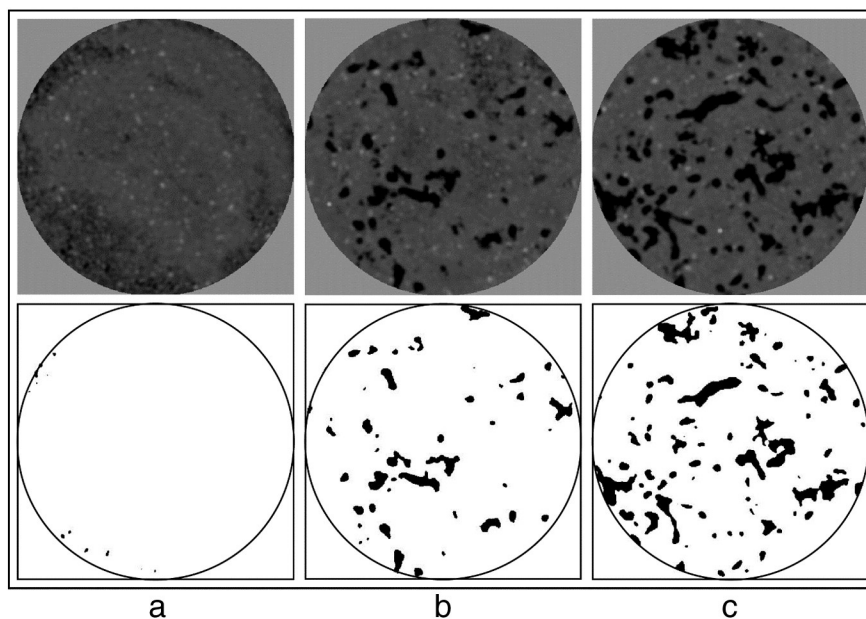


Fig. 1. Example of gray level images and porosity segmentation (voids in black and soil matrix in white) from one slice of urban soil material without (a) and with earthworms after one (b) and three months (c) of incubation.

Table 2

Weight gain per earthworm (%) ($R = A. rosea$; $C = A. chlorotica$) after one and three months of incubation and number of juveniles collected after three months in alluvial (A) and urban (U) soil materials (\pm standard deviation). For each column, different letters indicate significant differences (ANOVA, $p < 0.05$) between treatments ($n = 5$).

Treatment	Weight gain per earthworm after		Number of juveniles after three months
	one month (%)	three months (%)	
AR	10.4 \pm 2.2 ^{ab}	5.4 \pm 3.9 ^{ab}	34 \pm 8.4 ^a
AC	16.9 \pm 0.7 ^a	13.9 \pm 1.7 ^a	2.4 \pm 0.9 ^{bc}
ARC	9.0 \pm 0.8 ^{ab}	8.6 \pm 1.4 ^a	9 \pm 3.2 ^b
UR	-1.5 \pm 8.1 ^c	-17.4 \pm 20 ^b	3.6 \pm 1.8 ^{bc}
UC	13.4 \pm 0.7 ^{ab}	10.4 \pm 1.8 ^a	0.6 \pm 0.4 ^c
URC	4.3 \pm 2.3 ^{bc}	3.7 \pm 1.2 ^{ab}	2.4 \pm 0.9 ^c

Data with the same letter (“a”, “b”, or “c”) are not different at $p < 0.05$.

3.3. N mineralization study

The $N-NH_4^+$ content was significantly different between soil materials after one and three months of incubation ($f_{1-40} = 23.5$, $p < 0.001$ and $f_{1-40} = 550.9$, $p < 0.001$ respectively) (Table 5). After one month and three months of incubation, the $N-NH_4^+$ content in controls was significantly higher in the alluvial soil compared to the urban soil ($p < 0.001$). This trend was also observed for the $N-NO_3^-$ content after three months of incubation ($p < 0.001$) (Fig. 2).

Between earthworm treatments, the $N-NH_4^+$ content was significantly different after one month ($f_{3-40} = 8.4$, $p < 0.001$) (Table 5). This is explained by the decreased of $N-NH_4^+$ content with respect to earthworm activity except in the urban soil inoculated with *A. rosea* (Fig. 2). For the $N-NO_3^-$ content, difference between treatments was also observed after one and three months of experiment ($f_{3-40} = 6.3$, $p < 0.005$ and $f_{3-40} = 5.5$, $p < 0.005$ respectively) (Table 5). In the alluvial soil after one month, *A. chlorotica* and the two species combined increased significantly ($p < 0.001$) the $N-NO_3^-$ content. This trend was also observed in the urban soil inoculated with the combination of both species after one and three months of incubation (Fig. 2).

3.4. Available phosphorus

The available phosphorus content was different between soil materials after one and three months of incubation ($f_{1-40} = 313.0$, $p < 0.001$ and $f_{1-40} = 1534.6$, $p < 0.001$ respectively) and was higher in the alluvial soil material (Fig. 3). In the alluvial soil, endogeic earthworms increased significantly the $P_{available}$ content after both periods of incubation ($p < 0.05$) except for the treatment inoculated with *A. rosea* after one month of experiment. In the urban soil, a decrease of the $P_{available}$ content was observed after one month of incubation with respect to earthworm activity, while no difference was observed after three months (Fig. 3).

3.5. Burrow characteristics and soil bulk density

The results of the three-dimensional computed tomography and soil bulk density are presented in Tables 6 and 7. A selection of skeletonized

Table 3

Results of the soil respiration after one and three months of incubation. Treatments were alluvial or urban soil materials without or with earthworms (*A. rosea*, *A. chlorotica* or the combination of both species). *df* degrees of freedom, *MS* mean square, ANOVA ($n = 5$).

Variable	1 month			3 months	
	df	f-Value	p-Value	f-Value	p-Value
C-CO ₂					
Soils	1	190.2	<0.001	908.1	<0.001
Earthworms	3	16.7	<0.001	25.1	<0.001
Soils*earthworms	3	3.3	<0.05	5.2	<0.005
Residuals (MS)	32	245		454	

Table 4

Cumulative C-CO₂ emission ($\mu\text{g}\cdot\text{g}^{-1}$ soil) and organic carbon content (%) in soil materials after one and three months of incubation. For each column, different letters indicate significant differences (ANOVA, $p < 0.05$) between treatments ($n = 5$).

Treatment	Cumulative C-CO ₂ ($\mu\text{g}\cdot\text{g}^{-1}$ soil)		Organic carbon content (%)	
	1 month	3 months	1 month	3 months
A	163.6 \pm 12.0 ^b	455.6 \pm 12.7 ^c	3.93 \pm 0.05 ^{ab}	2.82 \pm 0.25 ^a
AR	177 \pm 11.2 ^b	468.6 \pm 6.0 ^{bc}	3.98 \pm 0.05 ^a	3.07 \pm 0.30 ^a
AC	225 \pm 5.5 ^a	485.8 \pm 13.1 ^{ab}	3.92 \pm 0.04 ^{ab}	3.2 \pm 0.13 ^a
ARC	205.8 \pm 3.2 ^a	499.4 \pm 13.2 ^a	3.82 \pm 0.04 ^b	2.84 \pm 0.29 ^a
U	104 \pm 2.9 ^d	221.4 \pm 5.2 ^f	2 \pm 0.06 ^c	1.5 \pm 0.05 ^b
UR	126.2 \pm 2.4 ^c	260.8 \pm 4.5 ^e	2.02 \pm 0.07 ^c	1.54 \pm 0.08 ^b
UC	132.2 \pm 2.8 ^c	276 \pm 6.2 ^e	2 \pm 0.06 ^c	1.71 \pm 0.22 ^b
URC	136.4 \pm 7.7 ^c	339.2 \pm 10.1 ^d	1.94 \pm 0.06 ^c	1.5 \pm 0.07 ^b

Data with the same letter (“a”, “b”, “c”, “d”, “e”, or “f”) are not different at $p < 0.05$.

images of earthworm burrows in the urban and the alluvial soil for both periods of incubation (single replicate) is shown in the Fig. 4.

For the soil porosity, difference between earthworm treatments was observed after one and three months of incubation ($f_{3-40} = 160$, $p < 0.001$ and $f_{3-40} = 92.2$, $p < 0.001$ respectively) (Table 7). Earthworms increased significantly soil macroporosity in the urban and the alluvial soil materials compared to the controls ($p < 0.05$) (Table 6). Comparing the burrowing activity of the two endogeic species, higher soil macroporosity ($p < 0.05$) was found after the inoculation of *A. chlorotica* in both soils and for both periods of incubation except in the urban soil after three months ($p > 0.05$).

Earthworms increased significantly the total length of segments in both soil materials ($p < 0.05$) (Table 6) and these differences were significant between earthworm treatments after both periods of incubation ($f_{3-40} = 150.2$, $p < 0.001$ and $f_{3-40} = 49.0$, $p < 0.001$ respectively) (Table 7). After one month of incubation, higher total length of segments observed in soils inoculated with *A. chlorotica* compared to *A. rosea*. This trend was no longer observed after three months of incubation in both soils. However, when the two species were combined, higher total length of segments was observed in the urban compared to the alluvial soil after one and three months of experiment.

For the number of nodes, significant difference between earthworm treatments was observed after both periods of incubation ($f_{3-40} = 44.7$, $p < 0.001$ and $f_{3-40} = 25.1$, $p < 0.001$ respectively) (Table 7). Except in the alluvial soil inoculated with *A. rosea* after one month of incubation, earthworms increased significantly the number of nodes in both soils after one and three months of incubation compared to the controls ($p < 0.05$) (Table 6). After one month of experiment, the alluvial soil with earthworms showed higher number of nodes than the urban soil except for the treatment with the combination of both species. This trend was no longer observed between soils after three months of experiment. Difference between species was observed after one month of incubation in both soils with higher number of nodes created by

Table 5

Results of $N-NH_4^+$ and $N-NO_3^-$ after one and three months of incubation. Treatments were alluvial or urban soil materials without or with earthworms (*A. rosea*, *A. chlorotica* or the combination of both species). *df* degrees of freedom, *MS* mean square, *NS* non-significant, ANOVA ($n = 5$).

Variable	1 month			3 months	
	df	f-Value	p-Value	f-Value	p-Value
$N-NH_4^+$					
Soils	1	23.5	<0.001	550.9	<0.001
Earthworms	3	8.4	<0.001	1.4	NS
Soils*earthworms	3	2.9	NS	0.0	NS
Residuals (MS)	32	0.4		0.0	
$N-NO_3^-$					
Soils	1	0.9	NS	0.1	NS
Earthworms	3	6.3	<0.005	5.5	<0.005
Soils*Earthworms	3	0.6	NS	1.6	NS
Residuals (MS)	32	0.3		2.0	

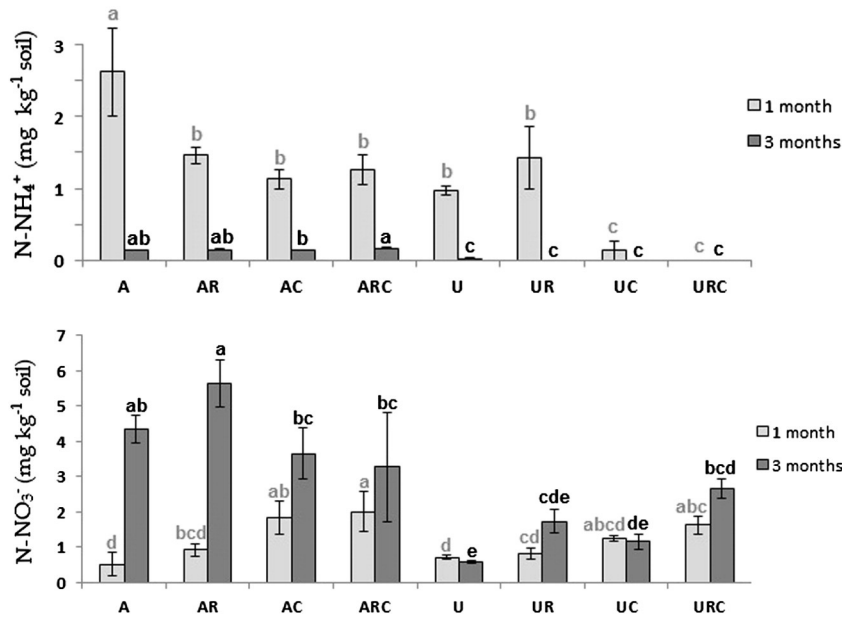


Fig. 2. N-NH₄⁺ and N-NO₃⁻ contents (mg·kg⁻¹ of soil) in the alluvial (A) and the urban (U) after one and three months of incubation. Histograms in pale gray (1 month) or gray (3 months) with the same letters are not statistically different (ANOVA, $p < 0.05$).

A. chlorotica compared to *A. rosea*. This trend was not observed after three months (Table 6).

Earthworm treatments on the soil bulk density were significantly different after one and three months of incubation ($f_{3-40} = 7.1$, $p < 0.001$ and $f_{3-40} = 18.2$, $p < 0.001$ respectively) (Table 7). Significant difference was observed between controls with higher soil bulk density found in the urban soil material ($p < 0.05$, Table 6). Earthworms decreased significantly the soil bulk density in both soils especially when the two species were combined ($p < 0.05$, Table 4). Differences between endogeic species were observed with lower soil bulk density in the treatment inoculated with *A. chlorotica* in the urban soil after one month (Table 6).

4. Discussion

4.1. Influence of soil properties on earthworm burrowing activity

As large inhabitants of soils, earthworms face major constraints including the need to live on relatively poor quality feeding resources (Satchell, 1980; Lavelle et al., 1983; Edwards, 2004). In urban soils, food shortage often occurs and can affect soil fauna activity (Bullock and Gregory, 1991). Before the experiment, organic carbon and mineral nitrogen (N-NH₄⁺ and N-NO₃⁻) contents were initially lower in the

urban compared to the alluvial soil material and probably influenced endogeic earthworm growth (weight gain and reproduction) and also their burrowing activity. After one and three months of incubation, weight loss and lower weight gain were found respectively for *A. rosea* and *A. chlorotica* in the urban compared to the alluvial soil material explaining the difference of burrow characteristics (soil macroporosity, total length of segments and number of nodes), and especially in treatments inoculated with both species. In the urban soil, earthworms probably spent more energy allocated for the research of food (MacArthur and Pianka, 1966; Edwards and Bohlen, 1996; Hirth, 1996) which reduced the weight and the reproduction of earthworms. This difference was particularly marked in soils inoculated with *A. rosea* in which juvenile densities were nearly ten times higher in the alluvial compared to the urban soil material after three months of incubation. A study from an English beech wood reported that *A. rosea* had low assimilation efficiency (Edwards and Bohlen, 1996) and this can explain the lower aptitude of this species to live in urban soils compared to *A. chlorotica*. In our study, *A. rosea* created less burrows than *A. chlorotica* in the urban soil material which were often longer and less branched (Bolton and Philipson, 1976; McKenzie and Dexter, 1993; Table 4 and Fig. 4). *A. rosea* is known to feed by a “grazing” procedure and preferentially lives in more organic soils (Nordström and Rundgren, 1974, in Bolton and Philipson, 1976). Endogeic earthworms have developed different ways to use soil organic matter (Bouché, 1977; Lavelle, 1981; Brown, 1995). *A. chlorotica* has probably a more geophagous regime (Zangerlé et al., 2011) and may thus increase soil macroporosity and connectivity through its numerous burrows (Bastardie et al., 2002; Capowiez et al., 2011, Table 4 and Fig. 4). As observed in the studied urban soil material, this species has a strong aptitude to live in disturbed soils (Lee, 1985, in Bolton and Philipson, 1976; Gerard, 1967, Satchell, 1967, Bouché, 1972; Bouché, 1977, in Le Bayon et al., 2013).

In our case, the urban soil functioning is intimately related to food resources, which can affect earthworm species growth and activity. However, feeding resources cannot explain all differences between species in urban and alluvial soil materials. Others measured variables such as soil bulk density or soil texture may influence earthworm growth and activity (Phillipson et al., 1976, in Bolton and Philipson, 1976; Lapied et al., 2009; Capowiez et al., 2012). For example, Nordström and Rundgren (1974) (in Edwards and Bohlen, 1996) reported that *A. rosea* abundance was strongly correlated to clay content in grasslands

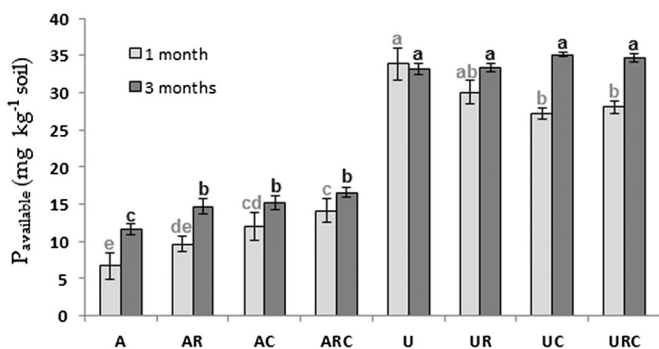


Fig. 3. Available phosphorus (mg·kg⁻¹ of soil) in the alluvial (A) and the urban (U) soil after one and three months of incubation. Histograms in pale gray (1 month) or gray (3 months) with the same letters are not statistically different (ANOVA, $p < 0.05$).

Table 6

3D tomography and soil bulk density results in alluvial (A) and urban (U) soil materials (\pm standard deviation) inoculated without or with earthworms in microcosms (R = *A. rosea*; C = *A. chlorotica*). For each row, different letters indicate significant differences (ANOVA, $p < 0.05$) between treatments ($n = 5$).

	A	AR	AC	ARC	U	UR	UC	URC
<i>1 month of experiment</i>								
Soil macroporosity (%)	0.49 \pm 0.06 ^e	5.14 \pm 0.46 ^{cd}	6.85 \pm 0.68 ^b	8.33 \pm 0.83 ^a	0.14 \pm 0.02 ^e	4.20 \pm 0.42 ^d	5.73 \pm 0.57 ^{bc}	8.93 \pm 0.89 ^a
Total length of segments (mm)	2766 \pm 341 ^e	8066 \pm 500 ^d	10545 \pm 458 ^{bc}	11721 \pm 631 ^b	821 \pm 99 ^f	7071 \pm 770 ^d	9641 \pm 514 ^c	13904 \pm 715 ^a
Number of nodes	1424 \pm 133 ^{cd}	1797 \pm 164 ^{bc}	2307 \pm 106 ^a	2324 \pm 151 ^a	623 \pm 62 ^e	1414 \pm 178 ^d	1910 \pm 110 ^b	2543 \pm 96 ^a
Soil bulk density (g·cm ⁻³)	0.59 \pm 0 ^d	0.57 \pm 0.01 ^{de}	0.57 \pm 0.01 ^{de}	0.54 \pm 0.02 ^e	0.74 \pm 0.01 ^a	0.71 \pm 0.02 ^{ab}	0.65 \pm 0.01 ^c	0.69 \pm 0.02 ^{bc}
Number of segments	942 \pm 113 ^f	1781 \pm 186 ^{de}	2482 \pm 163 ^{bc}	2632 \pm 207 ^{ab}	340 \pm 39 ^g	1403 \pm 208 ^e	2110 \pm 117 ^{cd}	2934 \pm 129 ^a
Mean length of segment (mm)	2.78 \pm 0.02 ^c	4.28 \pm 0.23 ^b	4.2 \pm 0.11 ^b	4.18 \pm 0.21 ^b	2.34 \pm 0.05 ^c	5 \pm 0.31 ^a	4.6 \pm 0.16 ^{ab}	4.87 \pm 0.24 ^a
Inclination (°)	17.6 \pm 0.4 ^d	27.2 \pm 0.8 ^c	28.0 \pm 0.4 ^{bc}	29.2 \pm 0.4 ^b	15.7 \pm 0.5 ^e	28.0 \pm 0.5 ^{bc}	28.9 \pm 0.5 ^{bc}	30.7 \pm 0.2 ^a
<i>3 months of experiment</i>								
Soil macroporosity (%)	0.49 \pm 0.06 ^d	6.67 \pm 0.62 ^c	9.45 \pm 0.68 ^{ab}	10.07 \pm 0.47 ^{ab}	0.20 \pm 0.02 ^e	8.46 \pm 1.53 ^{bc}	10.83 \pm 0.64 ^{ab}	12.58 \pm 0.61 ^a
Total length of segments (mm)	2823 \pm 361 ^c	15445 \pm 1504 ^b	14752 \pm 1363 ^b	15834 \pm 1598 ^b	1116 \pm 262 ^c	15384 \pm 2691 ^b	18463 \pm 1106 ^{ab}	21197 \pm 1810 ^a
Number of nodes	1416 \pm 149 ^b	3147 \pm 333 ^a	3124 \pm 270 ^a	3031 \pm 340 ^a	701 \pm 82 ^b	2879 \pm 488 ^a	3414 \pm 221 ^a	3757 \pm 388 ^a
Soil bulk density (g·cm ⁻³)	0.63 \pm 0 ^{cd}	0.60 \pm 0.02 ^{de}	0.57 \pm 0.02 ^{ef}	0.54 \pm 0.01 ^f	0.79 \pm 0.01 ^a	0.74 \pm 0.02 ^{ab}	0.73 \pm 0.02 ^b	0.65 \pm 0.02 ^c
Number of segments	972 \pm 133 ^c	3037 \pm 372 ^b	3425 \pm 320 ^b	3495 \pm 410 ^b	427 \pm 84 ^c	3205 \pm 650 ^b	4096 \pm 286 ^{ab}	4667 \pm 549 ^{ab}
Mean length of segment (mm)	2.75 \pm 0.01 ^c	4.99 \pm 0.26 ^a	4.06 \pm 0.06 ^b	4.83 \pm 0.34 ^a	2.40 \pm 0.08 ^c	4.72 \pm 0.19 ^a	4.67 \pm 0.20 ^a	4.61 \pm 0.19 ^{ab}
Inclination (°)	18.7 \pm 0.8 ^c	28.1 \pm 0.9 ^b	28.4 \pm 0.4 ^{ab}	29.4 \pm 0.2 ^{ab}	18.00 \pm 1.5 ^e	28.8 \pm 0.9 ^{ab}	29.5 \pm 0.4 ^{ab}	30.6 \pm 0.2 ^a

Data with the same letter (“a”, “b”, “c”, “d”, “e”, “f” or “g”) are not different at $p < 0.05$.

and forests in Sweden. Higher clay content was found in the alluvial soil (33%) compared to the urban soil (20.7% of clay content) and may explain the rapid development of *A. rosea* in the alluvial soil.

4.2. Endogeic earthworms as actors of the soil organic matter dynamics and the formation of soil structure in urban soils

In the Swiss law, the soil is deemed fertile if it is a “diverse and biologically active habitat, which entails a typical soil structure as well as undisturbed capacity to decompose organic matter” (Osol, 1998, in Havlicek, 2012). Earthworms are suitable actors of soil fertility in urban soils in that they are key regulators of soil structuring processes, organic matter transformation and its integration in the soil in many ecosystems (Fonte et al., 2009; Blouin et al., 2013). Through the comparison of SOM dynamics (soil respiration, nitrogen mineralization) and soil structuring processes (macroporosity, total length of segments and number of nodes) in urban and alluvial soil materials, endogeic earthworms showed strong ability to fulfill basic functions (e.g. organic matter transformation, soil structure formation) in urban soils. However, if carbon and nitrogen

Table 7

Results of burrow characteristics and soil bulk density after one and three months of incubation. Treatments were alluvial or urban soil materials without or with earthworms (*A. rosea*, *A. chlorotica* or the combination of both species). *df* degrees of freedom, *MS* mean square, *NS* non-significant, ANOVA ($n = 5$).

Variable	1 month			3 months	
	df	f-Value	p-Value	f-Value	p-Value
<i>Soil macroporosity</i>					
Soils	1	2.5	NS	7.3	<0.05
Earthworms	3	160.0	<0.001	92.2	<0.001
Soils*earthworms	3	1.9	NS	1.4	NS
Residuals (MS)	32	44,423,107		1.5235e08	
<i>Total length of segments</i>					
Soils	1	1.2	NS	2.9	NS
Earthworms	3	150.2	<0.001	49.0	<0.001
Soils*earthworms	3	5.5	<0.005	2.3	NS
Residuals (MS)	32	1,469,648		11,631,565	
<i>Number of nodes</i>					
Soils	1	13.7	<0.001	0.0	NS
Earthworms	3	44.7	<0.001	25.1	<0.001
Soils*earthworms	3	5.2	<0.005	2.1	NS
Residuals (MS)	32	84825		478560	
<i>Soil bulk density</i>					
Soils	1	167.3	<0.001	158.8	<0.001
Earthworms	3	7.1	<0.001	18.2	<0.001
Soils*earthworms	3	2.2	NS	1.2	NS
Residuals (MS)	32	0.0		0.0	

mineralization were observed in the studied urban and alluvial soils with respect to earthworm activity, available phosphorus content did not increase in the urban soil material after one and three months of incubation. In the literature, it is generally admitted that in many soils earthworms increase available phosphorus content through the stimulation of soil microorganisms (Suarez et al., 2004; Milleret et al., 2009; Le Bayon et al., 2011) but little is known about the effect of earthworm activity on soil processes in urban soils. Stroo and Jenks (1982, in Bullock and Gregory, 1991) reported similarly lower available phosphorus content in mine soils compared to native soils after twenty years of soil reclamation. In our case, this difference of available phosphorus content compared to the alluvial soil material can be mainly explained by history, management, parental material composition or other environmental factors which modified soil properties in the urban context (Fresquez and Lindemann, 1983, in Bullock and Gregory, 1991).

Except for the available phosphorus, biophysicochemical processes seemed to run faster in the urban soil compared to the alluvial soil and especially when the two species were combined. After three months of incubation, the total length of burrows (21197 \pm 1810 mm) was significantly higher in the urban compared to the alluvial soil (15834 \pm 1598 mm) and probably explains the increase of SOM dynamics (cumulative C-CO₂ emission) and the fast nitrogen mineralization (N-NH₄⁺ and N-NO₃⁻). Studies reported also that in low fertile soils, the response of endogeic earthworms – which do not usually form permanent galleries (Bouché, 1972, 1977; Lavelle et al., 1992) – on organic matter dynamics is particularly marked (Lofs-Holmin, 1983; Steinberg et al., 1997; Lowe and Butt, 2007). However, little is known about the response of endogeic earthworms on soil structuring process in disturbed soils over time. In our study, even if an important part of burrows was probably backfilled (pers. obs.; Capowiez et al., 2011), a general increase of earthworm burrowing activity was observed in the urban compared to the alluvial soil material leading to a possible acceleration of soil processes in the urban context. The comparison with a natural reference such as alluvial soils remains therefore highly useful in order to better characterize soil processes and their speed in urban soils.

5. Conclusions

Under controlled conditions, our study showed that the burrowing activity of endogeic earthworms on the SOM dynamics and the soil structure was rather similar between urban and alluvial soil materials even if some differences were observed. Endogeic earthworms, and especially *A. chlorotica*, showed a good aptitude to live in the urban soil material and the combination of both species seemed to accelerate biophysicochemical processes. Except for available phosphorus,

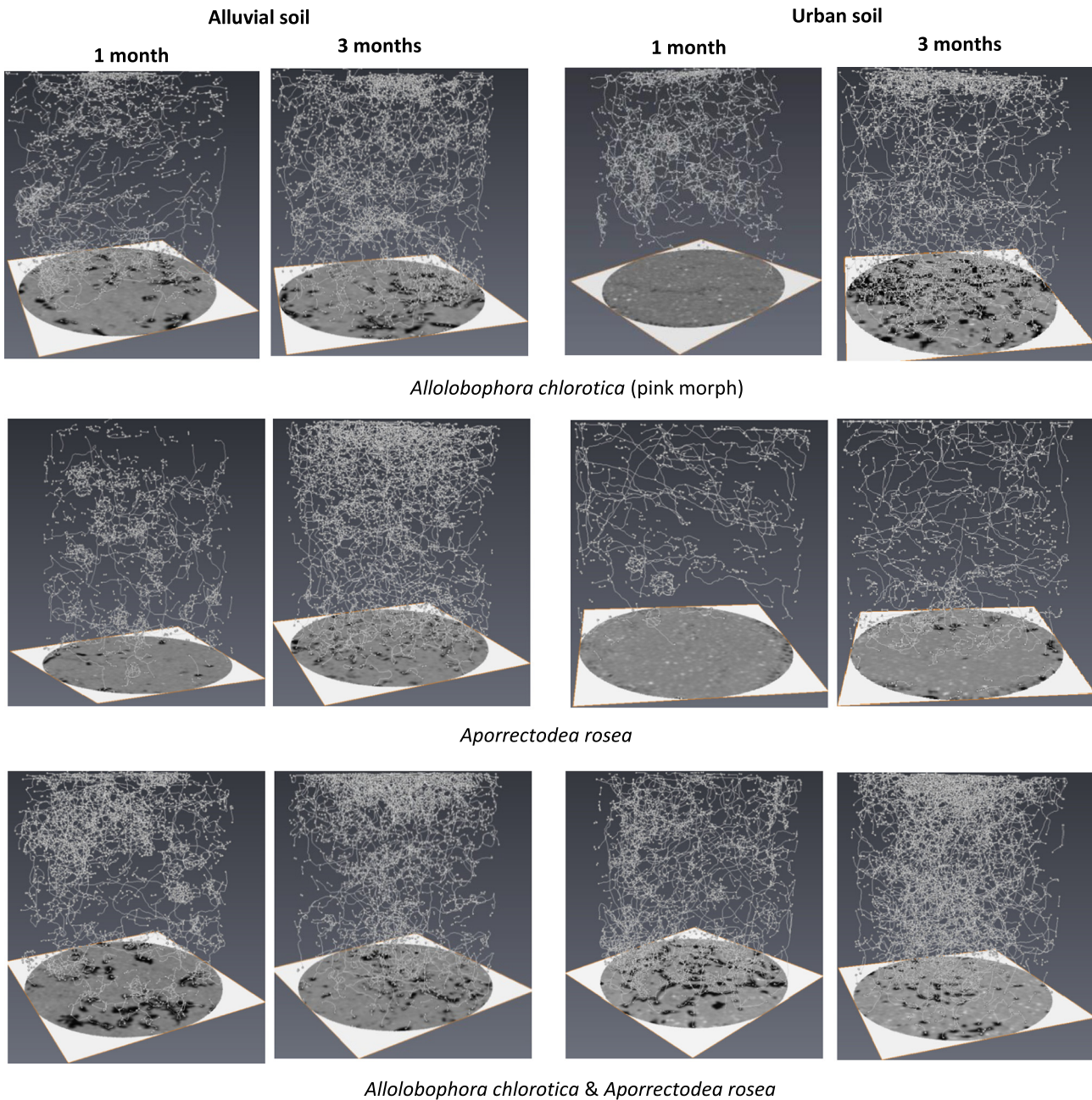


Fig. 4. 3D skeletonized burrows of endogeic earthworms for the alluvial and the urban soil after one and three months of incubation.

earthworm activity increased the SOM turnover (carbon and nitrogen mineralization) and the soil structure (burrow network) over time in the urban soil material creating favorable conditions for nutrient cycling, soil structure formation or water infiltration. Due to their abundance and their roles, endogeic earthworms appear as key actors of the soil functioning in the urban context.

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References

- Amossé, J., Le Bayon, R.-C., Gobat, J.-M., 2014. Are urban soils similar to natural soils of river valleys? *Journal of Soils and Sediments*, Special Issue SUITMA 7. <http://dx.doi.org/10.1007/s11368-014-0973-6>
- Baize, D., Girard, M.C., 2009. *Référentiel Pédologique 2008*. Editions Quae (405 pp.).
- Bastardie, F., Cannavacciuolo, M., Capowiez, Y., de Dreuzy, J.R., Bellido, A., Cluzeau, D., 2002. A new simulation for modelling the topology of earthworm burrow systems and their effects on macropore flow in experimental soils. *Biol. Fertil. Soils* 36, 161–169.
- Bernard, L., Chapuis-Lardy, L., Razafimbelo, T., Razafindrakoto, M., Pablo, A.-M., Legname, E., Poulain, J., Brûls, T., O'Donohue, M., Brauman, A., Chotte, J.-L., Blanchart, E., 2011. Endogeic earthworms shape bacterial functional communities and affect organic matter mineralization in a tropical soil. *ISME J.* 6, 213–222.

- Binet, F., Kersanté, A., Munier-Lamy, C., Le Bayon, R.C., Belgy, M.J., Shipitalo, M.J., 2006. Lumbricid macrofauna alter atrazine mineralization and sorption in a silt loam soil. *Soil Biol. Biochem.* 38, 1255–1263.
- Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Pérès, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J., 2013. A review of earthworm impact on soil function and ecosystem services. *Eur. J. Soil Sci.* 64, 161–182.
- Bolton, P.J., Philipson, J., 1976. Burrowing, feeding, egestion and energy budgets of *Allolobophora rosea* (Savigny) (Lumbricidae). *Oecologia* 23, 225–245.
- Bouché, M.B., 1972. *Lombriciens de France: écologie et systématique*. Institut National de la Recherche Agronomique, Paris (671 pp.).
- Bouché, M.B., 1977. Stratégies lombriciennes. *Ecol. Bull.* 25, 122–132.
- Brown, G., 1995. How do earthworms affect microfloral and faunal community diversity? *Plant Soil* 170, 247–269.
- Bullock, P., Gregory, P.J., 1991. *Soils in the Urban Environment*. Blackwell Scientific Publications, Oxford (174 pp.).
- Capowiez, Y., Pierret, A., Daniel, O., Monestiez, P., Kretzschmar, A., 1998. 3D skeleton reconstructions of natural earthworm burrow systems using CAT scan images of soil cores. *Biol. Fertil. Soils* 27, 51–59.
- Capowiez, Y., Sammartino, S., Michel, E., 2011. Using X-ray tomography to quantify earthworm bioturbation non-destructively in repacked soil cores. *Geoderma* 162, 124–131.
- Capowiez, Y., Sammartino, S., Cadoux, S., Bouchant, P., Richard, G., Boizard, H., 2012. Role of earthworms in regenerating soil structure after compaction in reduced tillage systems. *Soil Biol. Biochem.* 55, 93–103.
- Carter, M.R., Gregorich, E.G., 2007. *Soil Sampling and Methods of Analysis*. CRC Press, Boca Raton (1264 pp.).
- Conseil fédéral de Suisse, 2008, 1998. Ordonnance sur les atteintes portées aux sols (OSol) du 1er juillet, état le 1er juillet 2008, Suisse (12 pp.).
- R Development Core Team, 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Edwards, C.A., 2004. *Earthworm Ecology*. In: Lavoisier (Ed.), second edition. ISBN: 978-0-203-99823-6 (456 pp.).
- Edwards, C.A., Bohlen, P.J., 1996. *Biology and Ecology of Earthworms*. 3rd ed. Chapman and Hall, London (426 pp.).
- Fonte, S.J., Winsome, T., Six, J., 2009. Earthworm populations in relation to organic matter dynamics and management in California tomato cropping systems. *Appl. Soil Ecol.* 41 (2), 206–214.
- Fresquez, P.R., Lindmann, W.C., 1983. Greenhouse and laboratory evaluations of amended coal mine spoils. *Reclamation and Revegetation Research* 2, 205–215.
- Gerard, B.M., 1967. Factors affecting earthworms in pastures. *J. Anim Ecol.* 36, 235–252.
- Glasstetter, M., 2012. Earthworm diversity in urban habitats of Basel. *Oligochaeta: Lumbricidae, Nothwerstern Switzerland*.
- Gobat, J.-M., Aragno, M., Matthey, W., 2013. *Le Sol vivant, Bases de pédologie, biologie des sols, Troisième édition revue et augmentée*. Presses polytechniques et universitaires romandes, Suisse (519 pp.).
- Harris, D., Horwath, W.R., van Kessel, C., 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. *Soil Sci. Soc. Am. J.* 65, 1853–1856.
- Havlicek, E., 2012. Soil biodiversity and bioindication: from complex thinking to simple acting. *European Journal of Soil Biology, Special Issue "Bioindication in Soil Ecosystems"* 49, pp. 80–84.
- Hazelton, P., Murphy, B., 2011. *Understanding Soils in Urban Environments*. CSIRO Publishing, Paperback 9780643091740 (160 pp.).
- Hirth, J.R., 1996. Volume density of earthworm burrows in compacted cores of soil as estimated by direct and indirect methods. *Biol. Fertil. Soils* 21 (3), 171–176.
- IUSS Working Group, 2007. *World reference base for soil resources*. *World Soil Resources Reports* 103. FAO, Rome (145 pp.).
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jouquet, P., Dauber, J., Lagerlof, J., Lavelle, P., Lepage, M., 2006. Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Appl. Soil Ecol.* 32, 153–164.
- Jouquet, P., Plumere, T., DoanThu, T., Rumpel, C., TranDuc, T., Orange, D., 2010. The rehabilitation of tropical soils using compost and vermicompost is affected by the presence of endogeic earthworms. *Appl. Soil Ecol.* 46, 125–133.
- Lapied, E., Nahmani, J., Rousseau, G.X., 2009. Influence of texture and amendments on soil properties and earthworm communities. *Appl. Soil Ecol.* 43, 241–249.
- Lavelle, P., 1981. Stratégies de reproduction chez les vers de terre. *Acta Oecol. Oecol. Gen.* 2, 117–133.
- Lavelle, P., Spain, A.V., 2001. *Soil Ecology*. Hardbound, 0792371232p. GBP200 (654 pp.).
- Lavelle, P., Zaidi, Z., Schaefer, R., 1983. Interactions between earthworms, soil organic matter and microflora in an African savanna soil. In: Lebrun, P., André, H.M., De Mets, A., Grégoire-Wibo, C., Wauthy, G. (Eds.), *New Trends in Soil Biology. Proceedings of the VIII International Colloquium of Soil Zoology Dieu-Brichart; Louvain-la-Neuve*, (253–259 pp.).
- Lavelle, P., Melendez, G., Pashanasi, B., Schaefer, R., 1992. Nitrogen mineralization and reorganization in casts of the geophagous tropical earthworm *Pontoscolex corethurus* (glossoscolocidae). *Biol. Fertil. Soils* 14, 49–53.
- Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.P., 2006. Soil invertebrates and ecosystem services. ICSZ — soil animals and ecosystems services, proceedings of the XIVth International Colloquium on Soil Biology. *Eur. J. Soil Biol.* 42, 3–15.
- Le Bayon, R.-C., Matera, V., Kohler-Milleret, R., Degen, C., Gobat, J.-M., 2011. Earthworm activity alters geogenic arsenic and soil nutrient dynamics. 9th International Symposium on Earthworm Ecology/Pedobiologia 54S, S193–S201.
- Le Bayon, R.-C., Bullinger-Weber, G., Gobat, J.-M., Guenat, C., 2013. Chapter 3: Earthworm Communities as Indicators for Evaluating Floodplain Restoration Success in Floodplains, Environmental Management, Restoration and Ecological Implications. *Environmental Research Advances*. Enner Herenio Alcantara, Nova publishers, New York (241 pp.).
- Lee, K.E., 1985. *Earthworms, Their Ecology and Relationship With Soils and Land Use*. CSIRO Division of Soils Adelaide, Academic Press, New York (441 pp.).
- Levene, H., 1960. In: Olkin, Ingram, Hotelling, Harold, et al. (Eds.), *Contributions to Probability and Statistics: Essays in Honor of Harold Hotelling*. Stanford University Press (278–292 pp.).
- Lofs-Holmin, A., 1983. Earthworm population dynamics in different agricultural rotations. In: Satchell, J.E. (Ed.), *Earthworm Ecology — From Darwin to Vermiculture*. Chapman and Hall, London, pp. 151–160.
- Lowe, N.C., Butt, K.R., 2007. Life-cycle traits of the dimorphic earthworm species *Allolobophora chlorotica* (Savigny, 1826) under controlled laboratory conditions. *Biol. Fertil. Soils* 43, 495–499.
- MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. *Am. Nat.* 100 (916).
- McKenzie, B.M., Dexter, A.R., 1993. Size and orientation of burrows made by the earthworm *Aporrectodea rosea* and *Aporrectodea caliginosa*. *Geoderma* 56, 233–241.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. *Bioscience* 52 (10), 883–890.
- McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst.* 11, 161–176.
- Millennium Ecosystem Assessment (MEA), 2005. *Ecosystems and Human Well-being: Biodiversity Synthesis*. World Resources Institute, Washington, DC (86 pp.).
- Milleret, R., Le Bayon, R.-C., Gobat, J.-M., 2009. Root, mycorrhiza and earthworm interactions: their effects on soil structuring processes, plant and soil nutrient concentration and plant biomass. *Plant Soil* 316, 1–12.
- Nahmani, J., Capowiez, Y., Lavelle, P., 2005. Effects of metal pollution on soil macroinvertebrate burrow systems. *Biol. Fertil. Soils* 42 (1), 31–39.
- Nordström, S., Rundgren, S., 1974. Environmental factors and lumbricid associations in southern Sweden. *Pedobiologia* 14, 1–27.
- Pey, B., Cortet, J., Watteau, F., Cheynier, K., Schwartz, C., 2013. Structure of earthworm burrows related to organic matter of a constructed Technosol. *Geoderma* 202, 103–111.
- Phillipson, J., Abel, R., Steel, J., Woodell, S.R.J., 1976. Earthworms and the factors governing their distribution in an English beechwood. *Pedobiologia* 16, 258–285.
- Roithmeier, O., Pieper, S., 2009. Influence of Enchytraeidae (*Enchytraeus albidus*) and compaction on nutrient mobilization in an urban soil. *Pedobiologia* 53, 29–40.
- Satchell, C.J.E., 1967. Lumbricidae, in *Soil Biology*. In: Burgess, A., Raw, F. (Eds.), Academic Press, London (259–322 pp.).
- Satchell, J.E., 1980. Potential of the Silpho moor experimental birch plots as a habitat of *Lumbricus terrestris*. *Soil Biol. Biochem.* 12, 317–323.
- Scheiner, J.D., 2005. Spéciation du Carbone, de l'Azote et du Phosphore de différentes boues de stations d'épuration au cours de leurs incubations contrôlées dans deux types de sol. (Thesis report), Institut national polytechnique de Toulouse, France (218 pp.).
- Schlaghamerský, J., Pižl, V., 2009. Enchytraeids and earthworms (Annelida: Clitellata: Enchytraeidae, Lumbricidae) of parks in the city of Brno, Czech Republic. *Soil Org.* 81 (2), 145–173.
- Steinberg, D.A., Pouyat, R.V., Parmelee, R.W., Groffman, P., 1997. Earthworm abundance and nitrogen mineralization rates along an urban-rural land use gradient. *Soil Biol. Biochem.* 29 (3/4), 427–430.
- Stroo, H.F., Jencks, E.M., 1982. Enzyme activity and respiration in mine spoils. *Soil Sci. Soc. Am. J.* 46, 548–553.
- Suarez, E.R., Pelletier, D.M., Fahey, T.J., Groffman, P.M., Bohlen, P.J., Fisk, M.C., 2004. Effects of exotic earthworms on soil phosphorus cycling in two broadleaf temperate forests. *Ecosystems* 7, 28–44.
- United States Department of Agriculture (USDA), 1975. *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys*. Natural Resources Conservation Service, Washington DC pp. 436.
- Zangerlé, A., Pando, A., Lavelle, P., 2011. Do earthworms and roots cooperate to build soil macroaggregates? A microcosm experiment. *Geoderma* 167–168, 303–309.