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Abstract

The aim of this study was to assess how soil organic C (SOC) stocks and earthworm communities were modified in agroforestry systems compared to treeless control plots, and within the agroforestry plots (tree rows vs alleys). We used a network of 13 silvoarable agroforestry sites in France along a North/South gradient. Total earthworm abundance and biomass were significantly higher in the tree rows than in the control plots, but were not modified in the alleys compared to the control plots. Earthworm species richness, Shannon index, and species evenness were significantly higher in the tree rows than in the alleys. Total abundance of epigeic, epi-anecic, strict anecic and endogeic was higher in the tree rows. Surprisingly, earthworm individual weight was significantly lower in the tree rows than in the alleys and in the control plots. SOC stocks were significantly higher in the tree rows compared to the control plots across all sites. Despite higher SOC stocks in the tree rows, the amount of available C per earthworm individual was lower compared to the control. The absence of disturbance (no tillage, no fertilizers, no pesticides) in the tree rows rather than increased SOC stocks therefore seems to be the main factor explaining the increased total abundance, biomass, and diversity of earthworms. The observed differences in earthworm communities between tree rows and alleys may lead to modified and spatially structured SOC dynamics within agroforestry plots.

Introduction

Earthworms are a major component of the soil fauna in temperate climates (Lavelle 1988). They are usually classified into three main ecological categories having different morphology, physiology and behavior: epigeic, anecic, and endogeic (Bouché 1972, 1977; Potvin and Lilleskov 2017). Briefly, epigeic earthworms live and feed on surface organic matter, anecic make vertical or near-vertical burrows into which they incorporate varying amounts of surface organic matter and feed on a mix of surface and soil organic matter, and endogeic earthworms make horizontal or near-horizontal burrows and feed on humified soil organic matter. A distinction between epi-anecic and strict-anecic earthworms are sometimes made (Bouché 1972, 1977). Epi-anecic earthworms burrow few galleries and mainly feed on fresh surface organic matter whereas strict anecic earthworms mainly feed on soil humified organic matter burrowing a large network of galleries (Bouché and Kretzschmar 1974; Kretzschmar 1977; Ferrière 1980; Jégou et al. 1998, 2001a,b). Depending on their ecological category earthworms are involved in numerous ecosystem services such as pedogenesis, soil structure formation, nutrient cycling and climate regulation through soil organic carbon (SOC) sequestration (Lavelle et al. 2006; Blouin et al. 2013; Bertrand et al. 2015), through their burrowing activity and through their casts that are nutrient-rich compared to the bulk soil (Saharan and Singh 1988; Tian et al. 2000; Hmar and Ramanujam 2014).

The assembly of earthworm community is driven by several environmental factors, such as the biogeographical history of the region, broad habitat constraints (microclimate and soil properties), land use constraints and internal community constraints (competition or facilitation) (Decaëns et al. 2008). In agricultural landscapes, land use and land management can modify earthworm abundance and diversity (Decaëns et al. 2003; Smith et al. 2008b; Pelosi et al. 2009; Cluzeau et al. 2012; Frazão et al. 2017) and consequently impact ecosystem services provided by earthworms (Lavelle 1997, 2006; Jouquet et al. 2006). For example, Ponge et al. (2013) observed across 109 sites that agricultural fields exhibited a lower anecic earthworm abundance than grasslands. Slurry application only enhanced endogeic earthworm abundance whereas epigeic earthworm abundance was not influenced by neither land use nor management. At the plot scale and in cropping systems, Chan (2001) highlighted that anecic abundance tends to decline under tillage whereas endogeic abundance can increase especially under organic fertilization. A recent meta-analysis confirmed that epigeic and anecic earthworms were the most sensitive ecological groups to conventional tillage (Briones and Schmidt 2017). Several studies have observed that total earthworm abundance, biomass and richness were greater in field margins than in cultivated fields (Smith et al. 2008a; Nieminen et al. 2011; Roarty and Schmidt 2013; Crittenden et al. 2015).

Agroforestry systems include very diverse farming systems where trees and crops are grown in intimate combination (Nair 1993). In temperate regions, silvoarable systems associating parallel tree rows and annual intercrops, as well as silvopastoral systems combining trees, pastures and livestock, are the most widespread types of agroforestry. In temperate silvoarable systems, trees are planted in parallel rows, and the space between trees along the rows are usually untilled, unfertilized, and covered by a natural or sown herbaceous vegetation. In tropical systems, several authors have shown that total earthworm abundance, biomass and activity were increased in alley cropping compared to adjacent agricultural plots (Hauser 1993; Hauser et al. 1998; Fonte et al. 2010). In temperate regions, very few studies have been performed, but Price and Gordon (1999) observed in a silvoarable system in Canada a higher earthworm abundance and biomass in the tree row than in the cropped alley. Several explanations have been proposed to explain the higher occurrence of earthworms in agroforestry tree rows, especially the shading effect of trees, the lower soil temperature, the higher soil moisture (Tian et al. 2000), the lower level of soil disturbance (Hauser et al. 1998), and the higher amount of food, i.e., organic matter (Araujo and López-Hernández 1999; Frouz et al. 2009). SOC stocks are indeed usually increased in silvoarable systems compared to treeless agricultural fields (Chatterjee et al. 2018; de Stefano and Jacobson 2018; Feliciano et al. 2018; Shi et al. 2018, Cardinael et al. 2018a), especially in tree rows (Bambrick et al. 2010; Wotherspoon et al. 2014; Cardinael et al. 2015a, 2017). This additional food supply could positively affect earthworm individual weight (Shipitalo et al. 1988).

Due to the lower level of soil disturbance, the higher amount of food and buffered microclimatic conditions, tree rows could therefore represent favorable habitats for earthworm communities' development, especially for epigeic and anecic earthworms, potentially enabling them to colonize the cropped alleys. However, previous studies on earthworm communities in agroforestry systems have never taken into account the earthworm ecological categories or species susceptible to respond differently to specific properties in agroforestry system.

The objectives of this study were thus to i) compare earthworm communities and SOC stocks between agroforestry systems and treeless control plots, and to ii) compare the distribution of earthworm communities and SOC stocks between tree rows and alleys within the agroforestry plots.

Firstly, we hypothesized that total earthworm abundance, biomass, diversity, and earthworm individual weight would be higher in the agroforestry plots compared to the control plots, especially in the tree rows. Secondly, we hypothesized that the abundance of epigeic and anecic earthworms would be higher in the tree rows than in the alleys and control plots.

Material and methods

Site description

We selected a network of 13 agroforestry plots in France along a North/South gradient. Soil properties as well as the soil use and management varied greatly across sites. Briefly, the age of agroforestry sites ranged from 6 to 41 years and tree density from 35 to 200 trees ha^{-1}. In addition, soil pH ranged from 5.8 to 8.4 while clay content ranged from 100 to 530 g kg^{-1}. (Table 1). Each site comprised an agroforestry plot, and an adjacent agricultural control plot. Agroforestry alleys and control plots have been managed strictly the same way (soil tillage, crop rotation, fertilization) since the tree planting. A detailed description of the sites can be found in the supplementary materials. Due to time and budget constraints, not all sites have been sampled for both earthworms and SOC (see below).

Quantification of soil organic carbon stocks

SOC stocks at the CH, ME, RE, SJ and VZ sites were measured in a previous study using an intensive soil sampling (Cardinael et al. 2017). In this study, we measured SOC stocks at BE, BO, LB, PS, SJM and VER sites using a simplified sampling protocol. The SA and SM sites were not sampled for SOC stocks (Table 1). At the BE and PS sites, only the agroforestry plots were sampled for SOC (Table 1), but these sites still remain relevant to study the spatial

Table 1. Description of the agroforestry sites.

Site	Location	Soil texture clay/silt/sand (g kg^{-1})	Soil pH	Age (yrs)/ Planting date	Tree row/Alley width (m)	Density (trees ha^{-1})	Crop management	Tree species	Crops	Sampling locations C	Earthworms
BE	0°58'37.5"E, 46°32'24.4"N	297/325/378	7.1	8/2007	2/26	48	Conventional-Reduced tillage	Mixed species	Rapeseed, Wheat, Barley	AF	AF, C
BO	0°07'45.4"E, 45°12'39.4"N	447/346/207	8.1	8/2007	3/27	48	Conventional, Tillage	Poplar	Maize	AF, C	AF
CH	1°17'58"E, 48°06'08"N	195/705/100	7.0	6/2008	2/24	34	Conventional, Tillage	Hybrid walnut	Wheat, Rapeseed	AF, C	AF, C
LB	2°03'52.5"E, 49°28'25.6"N	246/603/151	8.0	6/2009	2/28	83	No pesticides, reduced tillage	Mixed species	Rapeseed, Wheat, Barley	AF, C	AF, C
ME	0°10'37"W, 46°11'54"N	250/645/105	5.8	6/2008	2/27	35	Conventional, Tillage	Hybrid walnut	Wheat, Rapeseed, Sunflower	AF, C	AF, C
PS	0°12'58.9"W, 47°49'18.1"N	235/247/518	-	8/2007	3/27	67 or 33	Conventional, No-tillage	Mixed species	Rapeseed, Wheat, Vetch-Peas, Barley, Sorghum	AF	AF, C
RE	04°01'E, 43°43'N	175/410/415	8.0	18/1995	2/11	110	Conventional, Tillage	Hybrid walnut	Durum wheat, Rapeseed, Chickpea	AF, C	AF
SA	0°02'53.9"W, 45°27'06.8"N	-	-	6/2007	5/20	65	Direct seeding, cover crops	Mixed species	Cereals	-	AF, C
SJ	0°13'57"W, 46°00'39"N	530/390/80	7.7	41/1973	2/12	102	Conventional, Tillage	Black walnut	Sunflower, Wheat, Barley	AF, C	AF, C

SJM	0°02'28.7"W, 46°54'19.0"N	329/355/316	8.4	9/2006	3/24	35	Conventional, Tillage	Mixed species	Maize	AF, C	AF
SM	0°30'42.9"W, 46°23'57.6"N	240/612/148	8.0	5 or 7/ 2008 or 2010	2/25	40	Organic, No-tillage	Mixed species	Cereals	-	AF
VER	2°48'56.4"E, 49°40'03.3"N	199/684/117	8.1	7/2008	2/28	46	Conventional, reduced tillage	Mixed species	Beetroot, Wheat, Field bean, Rapeseed	AF, C	AF, C
VZ	4°06'37"E, 44°03'29"N	100/390/510	8.3	18/1995	2/9	100	Organic, Tillage	Hybrid walnut	Rapeseed, Wheat, Potato, Garlic	AF, C	AF

The age correspond to the age of the agroforestry plot at the time of soil sampling for C analysis, except for the sites with no soil C data where the age corresponds to the time of earthworm sampling. Tree density corresponds to the agroforestry tree density. The crop management was the same in both the alleys and control plots.

AF: agroforestry plot, C: control plot (treeless).

BE, Béthines; BO, Bonnes; CH, Châteaudun; LB, Lasalle Beauvais; ME, Melle; PS, Parcé-sur-Sarthe; RE, Restinclières; SA, Saint-Aulaix-la-Chapelle; SJ, Saint-Jean-d'Angély; SJM, Saint-Jouin-de-Marnes; SM, Saint-Maxire ; VER, Verpillères; VZ, Vézénobres.

SOC data for the CH, ME, RE, SJ and VZ sites were taken from Cardinael et al., (2017).

heterogeneity within agroforestry plots. In total, SOC stocks were therefore measured on 11 agroforestry sites, with 9 sites sampled in both agroforestry and control plots.

Soil samples were taken every 10 cm from the surface to a depth of 30 cm using 500-cm^3 cylinders. In the tree rows of silvoarable systems, soil samples were taken at 1 m from a randomly chosen tree and at the half distance between two trees (Fig. 1). In the alleys, soil samples were taken at 1 m from the tree row and in the middle of the alley (Fig. 1). This sampling protocol was repeated three times in the agroforestry plots, around three different trees. In treeless agricultural plots, soil samples were collected at three to six different points spaced of 15 m. At each site, the bulk density (g cm^{-3}) was measured at tree sampling points, one in the tree row, one in the middle of the alley, and one in the control plot.

After air-drying in the lab, soil cores were sieved to 2 mm and weighed without coarse particles >2 mm. Sub-samples for bulk density determination were oven-dried at 105°C for 48 h. The bulk density (g cm^{-3}) was calculated as the ratio of the dry mass of fine soil (<2 mm) to the cylinder volume. Sub-samples for organic C concentrations were dried at 40°C and ball milled until they passed through a 200 mm mesh sieve. These sub-samples were then analyzed using a CHN elemental analyzer. SOC stocks were calculated on an equivalent soil mass basis (Ellert and Bettany 1995).

Earthworm collection and laboratory analyses

To fulfill the first objective, earthworms were collected at 8 silvoarable sites (BE, CH, LB, ME, PS, SA, SJ, VER) in both the agroforestry and the adjacent control plots (Table 1). In addition, to complete the second objective, five other sites (BO, RE, SJM, SM, VZ) were also sampled in the agroforestry plot only. Therefore, 13 sites were used to study the spatial heterogeneity of earthworm communities within agroforestry plots.

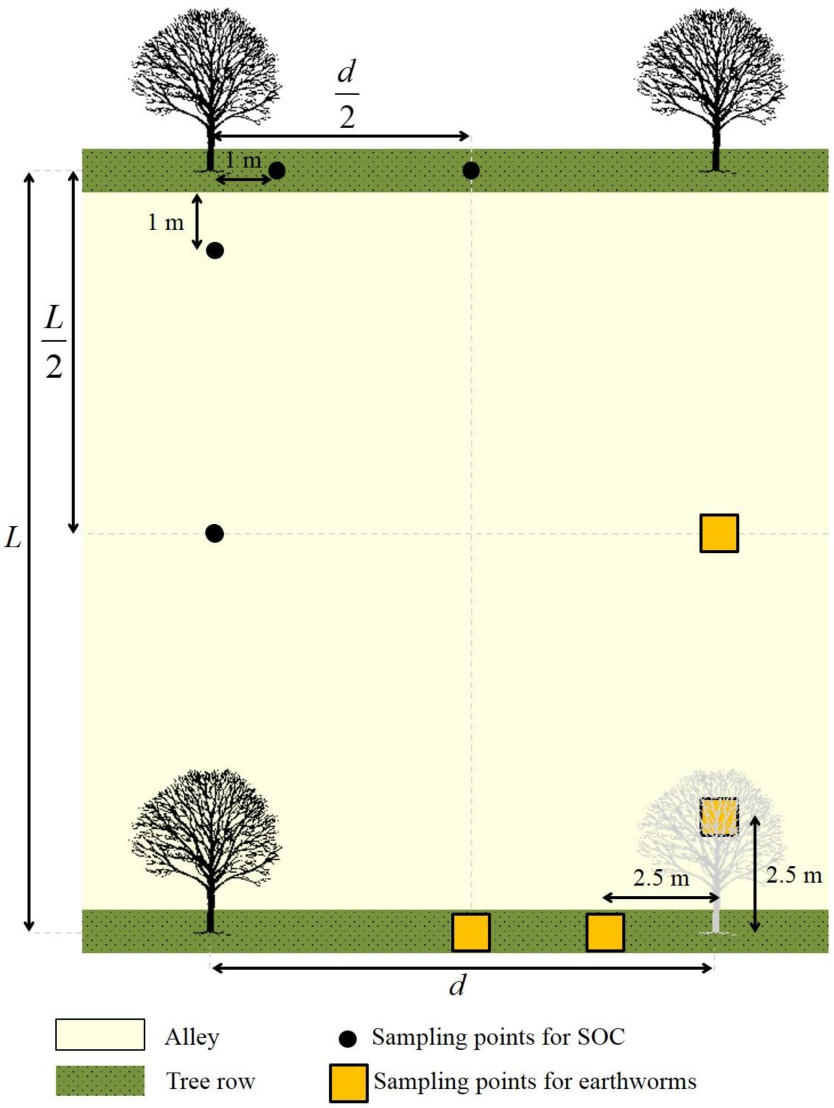


Figure 1. Sampling design for the silvoarable sites. This sampling protocol for earthworm communities and SOC was repeated three times in the agroforestry plots, around three different trees. *L* is the distance between tree rows, *d* is the distance between trees on the rows. SOC: soil organic C.

Earthworms were collected at each site during their maximum biological activity in March/April. In the tree rows of silvoarable systems, earthworms were sampled in the same direction at 2.5 m from a randomly chosen tree and at the mid-distance between two trees (Fig. 1). If spacing between trees along the tree rows was lower than 5 m, only the point at 2.5 m was sampled (it only happened at the LB site). In the alleys, earthworms were sampled at 2.5 m from the tree and in the middle of the alley (Fig. 1). These sampling points were repeated three times (around three different trees). Therefore, earthworms were sampled at 6 different points per site in the tree rows and alleys. In treeless agricultural plots, earthworms were collected in the middle of the plot, at three different points at 6 m distance.

Earthworms were sampled following the normalized protocol ISO 23 611-1, that was modified and validated during the RMQS BioDiv programme (Cluzeau et al. 2012). It combined a chemical and manual extraction. Briefly, three watering phases with 10 L of an increasing concentration of formaldehyde (0.25, 0.25 and 0.4%) were applied on 1 m^2 delimited with a frame. After each watering, earthworms were collected during 15 minutes. To recover earthworms that have not reached the surface, a manual hand sorting inside the sample square was then carried out on a soil cube (25 × 25 × 20 cm, length × width × depth) corresponding to a surface of 1/16 m^2. Earthworms were fixed and stored in formaldehyde (0.4%) at room temperature.

Earthworms were identified to the species level based on morphological criteria (Bouché 1972), and classified into ecological categories defined by Bouché (1972, 1977): epigeic, endogeic, and anecic with a distinction between epi-anecic and strict-anecic earthworms.

Each earthworm individual was then weighted +/- 10 mg (fresh formalin weights, full digestive tract) and assigned a stage of development, juvenile, sub-adult or adult. In total, about 24 000 earthworms were collected, identified at the species level and weighted. The number of hand sorted earthworms (HS) was multiplied by 16 to estimate the correct number per square meter. It was then added to the number of earthworms counted with the formaldehyde (F) to obtain the total amount of earthworms (FHS, Eq.1):

$$\mathrm{FHS} = \mathrm{F} + 16 \times \mathrm{HS} \qquad (\mathrm{Eq.}\,1)$$

Earthworm diversity was analyzed through three indices, total richness, Shannon index, and the species evenness.

Statistical analysis

One silvoarable site (VZ) associated organic vegetables, while all the other sites concerned arable crops. These sites were analyzed separately. To study the spatial distribution (tree rows vs alleys) of SOC or earthworms within silvoarable sites, we included all sites where the agroforestry plot was measured. When comparing agroforestry and control plots in terms of SOC or earthworms, we only included sites where both plots were sampled. No significant differences were found between SOC stocks and earthworm communities sampled at different distances from the tree, either in the tree rows or in the alleys (data not shown). Samples were therefore combined, and analyses were performed for three distinct modalities: tree rows, alleys, and controls.

We used statistical analyses commonly applied in meta-analysis or experimental network analysis (Makowski et al. 2018). For each location (tree row, alley, control) at each site, we calculated means and standard deviations of the different sampling points for SOC stocks, earthworm total abundance and biomass, earthworm ecological category abundance, total richness, Shannon index, and the species evenness. These means and standard deviations were used to calculate for each site the following effect sizes and their associated confidence intervals. The first one was the ratio of a given variable observed in the tree row to the one observed in the control. The second effect sizes compared alleys to control plots. A last effect size was calculated to study spatial heterogeneity within the agroforestry plot, and was the ratio of a given variable observed in the tree row to the one observed in the alley. A logarithm conversion was then applied to each effect size to center the values around zero. In order to estimate the mean effect size and its confidence interval across sites, we applied a random-effect model and a restricted maximum likelihood (REML) approach the using the *nlme* package (Pinheiro et al. 2013). Each site was considered as a random factor, making the results obtained on this experimental network more generalizable.

For the earthworm individual biomass, we only selected sites where species were represented by at least three individual adults in at least two of the three locations (tree row, alley and agricultural plot). Differences in earthworm individual biomass were compared species by species, location by location, and site by site. As the individual biomass of earthworms depends on each species, it is not relevant to compare absolute values between locations and sites. The individual weight of each earthworm species in the alleys and control at a given site were compared to the weight of same species in the tree rows, and expressed as a relative weight. The difference relative weights of each species were then averaged for each ecological category, location and site. For each earthworm ecological category, we used a linear mixed-effects model using *lme4* package (Bates 2010) with sites as a random factor, followed by Tukey HSD tests for post hoc pairwise comparisons to test differences in earthworm individual biomass between tree rows, alleys and control plots. The full list of earthworm species identified per site and location is available in Table S1 in the supplementary materials.

Statistical analyses were performed using R software, version 3.1.1 (R Development Core Team 2013). Significance was evaluated in all cases at p-value<0.05.

Results

Agroforestry effect on SOC stocks

The SOC stocks varied greatly between sites, reflecting various soil types and historical management (Fig. 2). Mean SOC stocks in 0-30 cm were significantly higher in tree rows compared to control plots across the sites (p-value = 0.004). No significant difference was found between alleys and control plots across the sites (p-value = 0.07). Mean SOC stocks in 0-30 cm were significantly higher in the tree rows than in the alleys across the silvoarable sites (p-value = 0.003) (Fig. 3). Site-specific log effect sizes for SOC can be seen in the supplementary materials (Fig. S1).

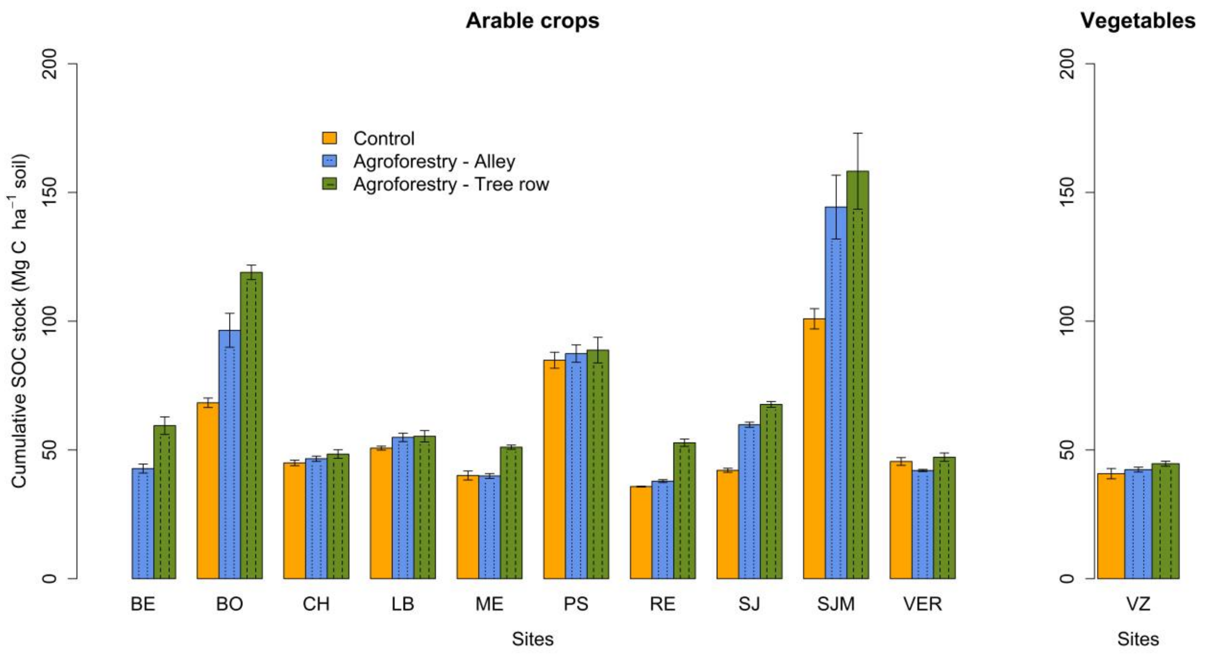


Figure 2. Soil organic C stock (Mg C ha^{-1}) in 0-30 cm at the different agroforestry sites. Error bars represent standard errors.

Across the 9 silvoarable sites (average age 12.1 years) where the three modalities where sampled (BO, CH, LB, ME, PS, RE, SJ, SJM, VER) for SOC, the mean (± 95% confidence intervals) delta SOC stocks were 19.46 ± 13.77 and 10.66 ± 10.35 tC ha^{-1} between tree rows and control plot, and between alleys and control plot, respectively.

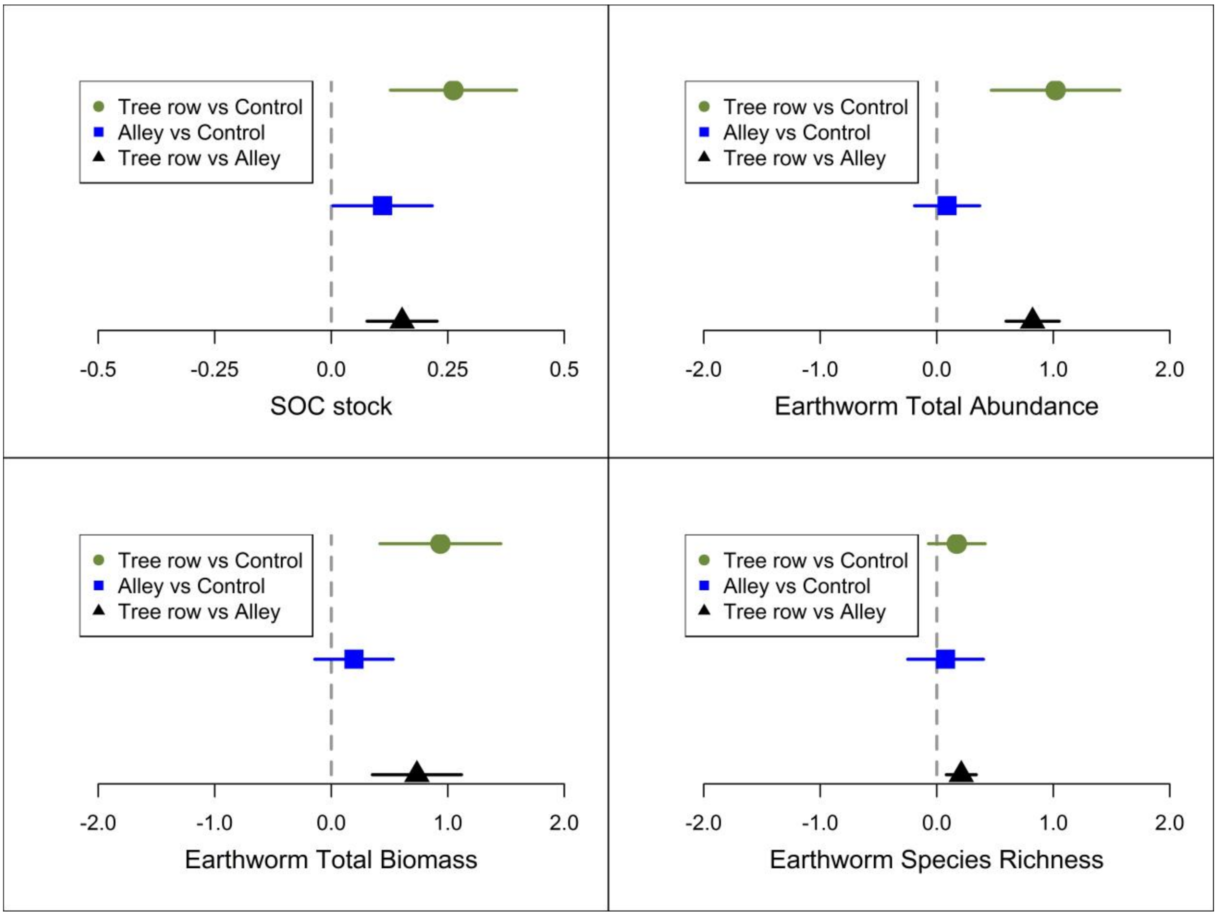


Figure 3. Mean log effect sizes of SOC stocks (0-30 cm), earthworm total abundance and biomass, and earthworm species richness between tree rows and control plots, alleys and control plots, and tree rows and alleys at the different silvoarable sites (excluding the VZ site with organic vegetables). Error bars represent confidence intervals.

Total earthworm abundance and biomass

Total earthworm abundance varied a lot between sites (Fig. 4). In general, the total earthworm abundance followed the same patterns across the silvoarable sites: tree rows >> alleys ≥ controls. At the VZ site (organic vegetables), earthworm total abundance was higher in the alleys than in the tree rows.

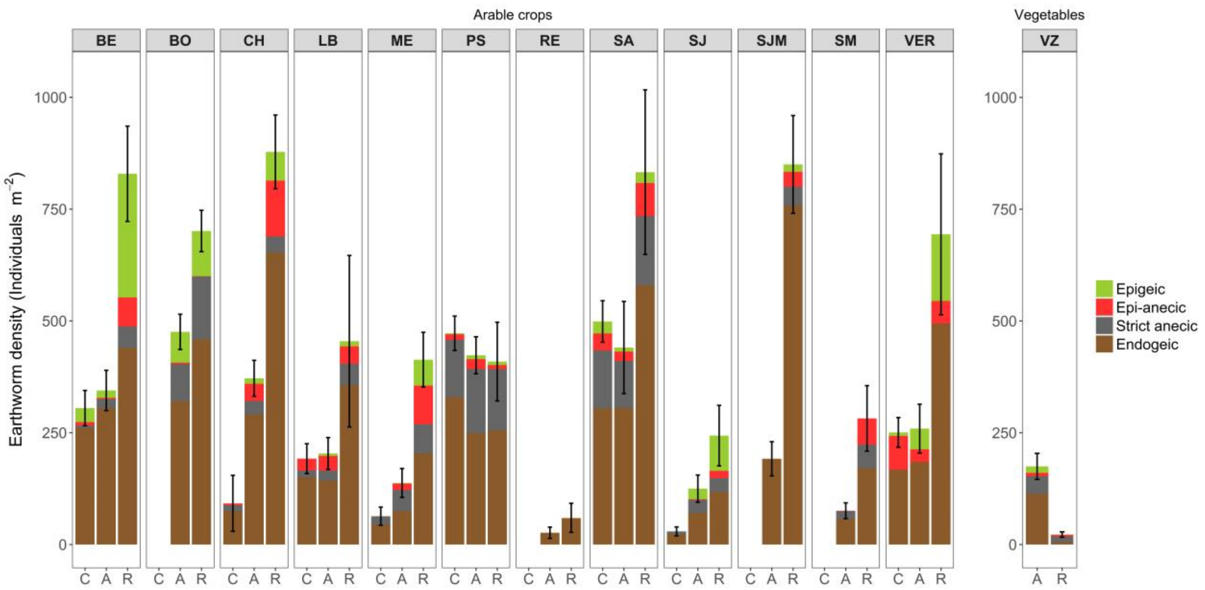
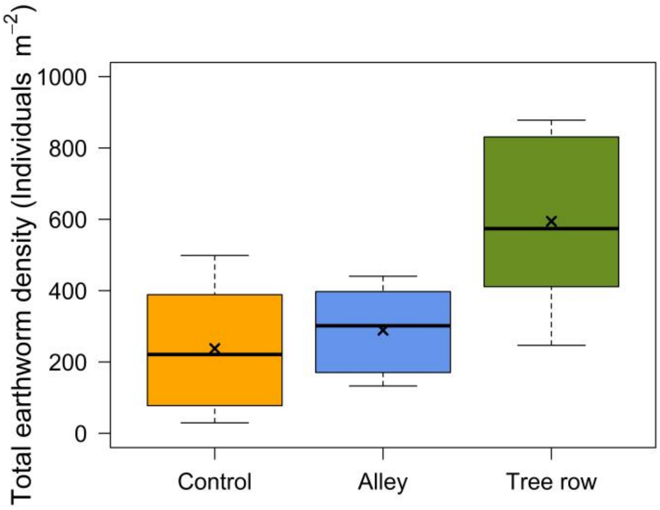


Figure 4. Distribution of earthworm mean total abundance in the four ecological categories at the different agroforestry sites and modalities. C, Control; A, Alley; R, Tree row. Error bars represent standard errors for total earthworm abundance. For the sites BO, RE, SJM, SM and VZ, the control plots were not sampled for earthworms (see Table 1).

For the eight silvoarable sites where the three modalities (control, alley, tree row) were sampled, the mean total earthworm abundances and associated 95% confidence intervals were 238 ± 124, 289 ± 85, and 595 ± 168 individuals m^{-2} in the control, alleys, and tree rows of silvoarable sites, respectively (Fig. 5). Mean total earthworm abundance in the tree rows was therefore 150% higher than in the control, 106% than in the alleys, and earthworm abundance in the alleys was 21% higher than in the control. The corresponding mean total earthworm biomasses and associated 95% confidence intervals were 77 ± 44, 96 ± 34, and 152 ± 58 g m^{-2}, respectively (Fig. 5).

Mean earthworm total abundance and total biomass were not significantly different between alleys and control plots across the sites (p-value = 0.55 and 0.29, respectively). However, they were significantly higher in the tree rows than in the control plots across all sites (p-value = 0.007 and 0.008, respectively) (Fig. 3). Mean earthworm total abundance and total biomass were also significantly higher in the tree rows than in the alleys across the agroforestry sites (p-value < 0.001 and p-value = 0.003, respectively) (Fig. 3). Site-specific effects are detailed in the supplementary materials (Fig. S2).



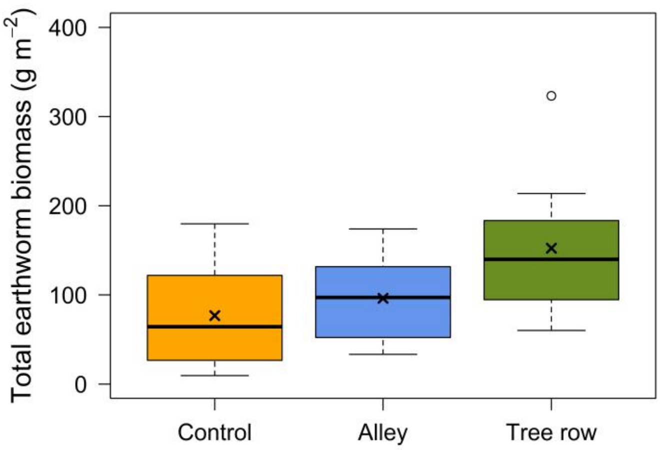


Figure 5. Total earthworm abundance and biomass in the control, alleys, and tree rows of the 8 silvoarable sites where the three modalities (control, alley, tree rows) were sampled. The following sites are concerned: BE, CH, LB, ME, PS, SA, SJ, VER. Upper and lower edges of boxes indicate 75th and 25th percentiles, horizontal lines within boxes indicate median, whiskers below and above the boxes indicate the 10th and 90th

percentiles, and crosses indicate arithmetic means. Outliers are plotted as individual points.

Earthworm ecological categories

A total of 20 species of Lumbricidae were identified across the agroforestry sites, with several representatives of the four ecological categories (Table S1). Total abundance was largely dominated by endogeic species such as *Allolobophora chlorotica chlorotica* or *Aporrectodea caliginosa caliginosa*, whereas total biomass was mainly driven by large-sized anecics (such as *Aporrectodea longa*).

Endogeic were the most abundant earthworms across all sites (Fig. 4). Across the eight silvoarable sites (BE, CH, LB, ME, PS, SA, SJ, VER) where the three modalities were sampled, mean endogeic abundances and associated 95% confidence intervals were 169.2 ± 82.3, 202.7 ± 68.6, and 387.6 ± 130.0 ind m^{-2} in the controls, alleys and tree rows, respectively. Mean epigeic abundances and associated 95% confidence intervals were 8.6 ± 9.0, 15.5 ± 9.9, and 83.8 ± 62.6 ind m^{-2} in the controls, alleys and tree rows, respectively. The abundance of epigeic, strict anecic, and endogeic was significantly higher in the tree rows than in the control plots across the silvoarable sites (p-values = 0.02, 0.006, and 0.009, respectively) (Fig. S3), but no difference was observed for the epi-anecic (p-value = 0.16). In the alleys, only the abundance of the strict anecic was significantly higher than in the control plots (p-value = 0.03). Within silvoarable plots, the mean abundance of each earthworm ecological category was significantly higher in the tree rows than in the alleys (p-values = 0.01, 0.009, 0.007, and <0.0001 for epigeic, strict anecic, epi-anecic, and endogeic earthworms, respectively) (Fig. S3).

Earthworm diversity indicators

Across the eight silvoarable sites (BE, CH, LB, ME, PS, SA, SJ, VER) where the three modalities were sampled, earthworm species richness was 5.3, 6.1, and 7.3 for the controls, alleys and tree rows, respectively. This indicator was significantly higher in the tree rows than in the alleys within agroforestry plots (Fig. 3). However, it was not significantly different either between tree rows and control plots or between alleys and control plots across the sites (Fig. 3). The same results were obtained for the Shannon index and the species evenness (Fig. S4).

Earthworm individual weight

The ANOVA revealed that the earthworm individual weight did not significantly vary across sites (p-value = 0.629). However, the individual weight significantly depended on the location (p-value < 0.001) and on the ecological category (p-value = 0.002). The interaction between the location and the ecological category was also significant (p-value < 0.001). Adult individual mean weights of epigeic, epic-anecic, strict anecic and epigeic species ranged from 0.05 to 0.43 g, 0.41 to 8.80 g, 0.84 to 5.78 g, and 0.03 to 0.89 g, respectively. An example of earthworm individual weight across the sites and locations is shown in Figure S5 for *Allolobophora chlorotica chlorotica* species.

Adult individual mean weights of epigeic and epi-anecic species were significantly higher in the controls (+26 and +27%, respectively) and in the alleys (+14 and +13%, respectively) compared to the tree rows (Fig. 6). Adult individual mean weight of endogeic adults was significantly higher in the alleys and in the controls (+6 and +7%, respectively) than in tree rows (Fig. 6). Surprisingly, there was no difference between the adult individual weight of strict anecic species in the tree rows and the alleys (+6%) but they were significantly lighter than in the controls.

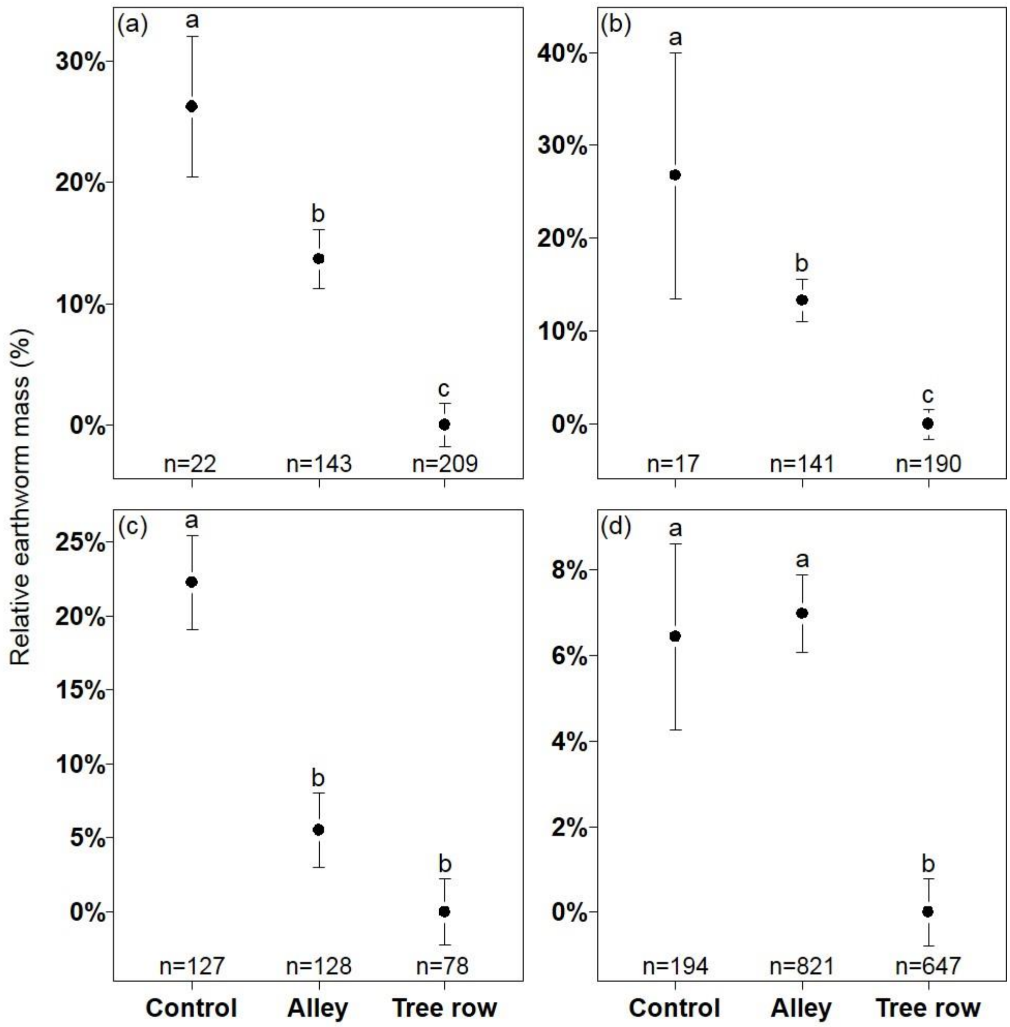


Figure 6. Relative adult earthworm weights in controls and alleys compared to tree rows according to the ecological category a) epigeic, b) epi-anecic, c) strict anecic and d) endogeic. Values are arithmetic means and error bars represent standard errors; n: number of individuals. Different letters denote significant differences among relative adult earthworm weight with a>b>c (Tukey test results).

Discussion

Spatial variation of SOC stocks

We found that SOC stocks were not significantly higher (p-value = 0.07) in the alleys than in control plots across the sites. This is probably the result of the high percentage of young sites within this experimental network (3 sites older than 15 years, 10 sites younger than 10 years). However, this study confirms previous results showing that SOC stocks in silvoarable systems are significantly higher in the tree rows than in the alleys and control plots (Bambrick et al. 2010; Cardinael et al. 2015a, 2017). Cardinael et al. (2018b) found that in an 18-year-old silvoarable system (110 trees ha^{-1}), tree rows received two times more organic C inputs compared to the control plot and 65% more than alleys. The additional organic inputs came from litterfall, from tree root mortality (Cardinael et al. 2015b; Germon et al. 2016), and also from the herbaceous vegetation growing between the trees (Cardinael et al. 2018b). In this study, SOC stocks in young silvoarable plots were found to be increased mainly in the tree rows, which could be ascribed to this herbaceous vegetation, analogous to grassland strips. Finally, tree rows are usually untilled, and a higher aggregate stability could contribute to SOC sequestration (Udawatta et al. 2008).

Higher earthworm abundance, biomass and richness in tree rows

In general, total earthworm abundance, biomass and richness were higher in the tree rows than in the alleys and in the control plots. Only the abundance of epi-anecic earthworms and the richness between tree rows and control plots were not different. These results are similar to those observed in grassy or hedge field-margins of arable fields. As previously observed by Smith et al. (2008a), Nieminen et al. (2011), Roarty and Schmidt (2013) and Crittenden et al. (2015), earthworm abundance, biomass and richness were often higher in field margin than further in the agricultural field. It is well known that soil disturbance, food supply and soil physical properties like soil moisture and compaction affect earthworm communities (Lee 1985; Curry 1998; Chan, 2001; Capowiez et al. 2009; Pelosi et al. 2014; van Capelle et al. 2012). It is therefore likely that the greater abundance, biomass and diversity in the tree rows was the result of the absence of cultivation and the provision of food resources as observed in grasslands compared to croplands (Curry 1998). However, with some agricultural practices such as manure addition, diversified rotations and reduced tillage, Lagerlöf et al. (2002) observed higher abundance in cropland than in field margins. Hof and Bright (2010) observed opposite results with a higher earthworm total abundance and biomass in croplands at 20 m from a grassy field margin than without grassy field margin. At the VZ silvoarable site associating hybrid walnut trees with organic vegetables, alleys were usually amended with poplar ramial chipped wood. This increase in the trophic resource for earthworms could explain their higher abundance in the alley than in the tree row at this site. Pérès et al. (1998) also found an increase in earthworm abundance after application of fresh poplar bark. In addition, the PS site was managed under no-tillage practices, which could explain the similar earthworm abundance between the alleys and tree rows (Chan 2001). Inter-site variability could also be explained others factors like soil characteristics, tree density and age, tree species composition, tree row plant community characteristics, management of the tree row (sown or spontaneous vegetation, mowing…), but due to a lack of data, we were unable to test it. Tree species composition and herbaceous tree row plant community could indeed result in quantitatively and qualitatively different litter inputs and varying plant effects on belowground conditions because of different root densities and characteristics.

Are tree rows an earthworm source for the cropped alleys?

In our study, earthworm communities were not very different between the alleys and the control plots. Moreover, no difference was found between the earthworm abundance collected in the alleys close to the tree rows or in the middle of the alleys. This finding is similar to results observed with field margins, suggesting that tree rows are a favourable habitat but do not serve as a source of earthworms for the alleys. Despite a higher earthworm abundance, biomass or richness in the field margins, Roarty and Schmidt (2013) and Crittenden et al. (2015) did not observe an increase of in-field earthworm populations as usually documented for more mobile, aboveground invertebrate taxa through colonization or spill-over effects. They therefore suggested that earthworm populations inside agricultural fields rely on residual, surviving in-field populations, rather than on immigration from surrounding land. Nevertheless, earthworms are also mobile species, their dispersal rate and distance vary between groups of earthworms (Eijsackers 2011) but this mobility is affected by other factors, such as agricultural practices (Nieminen et al. 2011) or climatic conditions (Cluzeau 1992). Nuutinen et al. (2011) found that margins could have importance as a source for epi-anecics when they invade a new arable habitat. The complexity of earthworm dispersion dynamics between the tree row and the alley could be further studied using molecular tools to distinguish sub-populations (Mathieu et al. 2010; Dupont et al. 2015, 2017) or earthworm tagging (Butt et al. 2009; Mathieu et al. 2018). Some studies have shown a earthworm species-related mobility, from 4.5 meters per year for *Lumbricus terrestris* (Hoogerkamp et al. 1983), 5.9-6.7 meters per year for *Aporrectodea longa* (Schon et al. 2014), up to 6.3 meters per year for all the earthworm community (Ligthart and Peek 1997). Zeithaml et al. (2009) and Hof and Bright (2010) observed an abundance of earthworms greater at 20 or 25 m from the field margin than at 5 or 10 m from the field margin but the reasons are not clear. Our results also revealed that strict-anecic earthworms abundance was overall higher in alleys than in control plots. This ecological category could potentially benefit from the local microclimate and organic matter brought by trees in the agroforestry system. Strict-anecic earthworms are geo-saprophagous, meaning that they consume highly humified soil organic but also decaying organic matter and could benefit from increased SOC stocks (Bouché and Kretzschmar 1974; Kretzschmar 1977; Ferrière 1980). In a previous study, Cardinael et al. (2015a) found that most of the additional SOC in agroforestry compared to control plots was made decaying particulate organic matter (200-2000 and 50-200 µm). This type of organic matter might be more palatable for strict-anecic than for endogeic earthworms which are more geophagous, and explain why the abundance of endogeic earthworm was not enhanced in alleys compared to control plots.

Effect of earthworm density on individual weight

Within each ecological category, earthworm individual biomass was at the lowest in the tree rows. Tree rows were characterized by a high density of earthworms compared to the control plots. A similar pattern could be observed to a lesser extent between the tree row and the alley, as epigeic, epi-anecic and endogeic individual biomass were also smaller in the tree rows compared to the alley. The negative relationship between earthworm abundance and individual biomass, observed in our study, has already been shown in laboratory experiment with different earthworm density gradients (Neuhauser et al. 1980; Hartenstein and Amico 1983; Butt et al. 1994), but to our knowledge, this is the first study revealing this phenomenon *in situ*. Butt et al. (1994) suggested that this density effect was not a function of food deprivation as excess feed was provided. Here, despite increased SOC stocks, the amount of available total organic C per earthworm individual was lower in the tree rows than in the control plots due to their higher total abundance (Fig. 7, S6, S7). This suggests a higher intra and/or inter-specific competition in the tree rows. Similarly to what we observed in the tree rows, Butt et al. (1994) also showed in a laboratory experiment that a larger density of *Lumbricus terrestris* had a negative effect on growth rate and on final earthworm individual weight, but resulted in a greater total biomass. A lower earthworm individual weight could potentially impact their provision of ecosystem services, but also the population dynamics (Lavelle 1983). For instance, Hoeffner et al. (2018) observed that surface litter incorporation by epi-anecic earthworms was not dependent on the earthworm species but was highly correlated to the initial mean weight of earthworms.

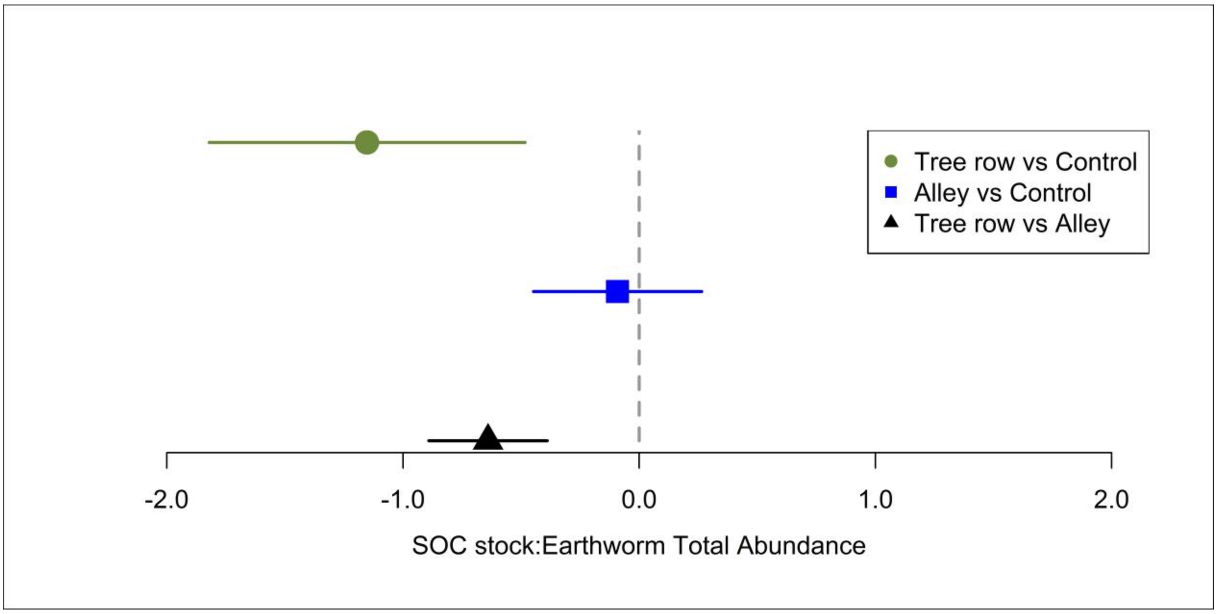


Figure 7. Log effect size of the ratio between SOC stocks (0-30 cm) and total earthworm biomass. Error bars represent confidence intervals.

Conclusions

This study showed that earthworm communities and SOC stocks were modified in agroforestry systems. More precisely, we found that earthworm total biomass and abundance were much higher in the tree rows than in the cropped alleys or than in the control plots. A similar results was observed for SOC stocks. However, tree rows did not seem to serve as a source of earthworms for the alleys. Finally, despite higher SOC stocks, adult earthworm individual weights were found to be lower in the tree rows than in the cropped alleys, probably due to intra and/or inter-specific competition. Further studies are needed to assess how earthworm activities and subsequent ecosystem services could be modified in agroforestry systems.

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Supplementary material

Site description

The BE silvoarable site was located in Béthines, in the department of Vienne (longitude 0°58'37.5"E, latitude 46°32'24.4"N, elevation 112 m a.s.l.). The soil was a Luvisol (IUSS Working Group WRB, 2007). Hybrid walnut trees (*Juglans regia* × *nigra*) were planted in 2007 at a density of 48 trees ha^{-1}. The trees were planted 8 m apart within the tree rows, with 26 m between rows. The rows of trees were two meters wide, and covered by spontaneous herbaceous vegetation. After tree planting, rapeseed (*Brassica napus* L.), wheat (*Triticum aestivum* L. subsp. *aestivum*) and barley (*Hordeum vulgare* L.) were grown in rotation following conventional practices in the control plot and in the inter-rows. Crop residues were left in the field after harvest. The soil was ploughed every three years to a depth of 10–20 cm in both the agroforestry inter-rows and the control plot.

The BO silvoarable site was located in Bonnes, in the department of Charente (longitude 0°07'45.4"E, latitude 45°12'39.4"N, elevation 34 m a.s.l.). The soil was a Fluvisol (IUSS Working Group WRB, 2007). Poplars (*Populus deltoides* x *nigra*) were planted in 2007 at a density of 48 trees ha^{-1}. The trees were planted 7 m apart within the tree rows, with 27 m between rows. The rows of trees were three meters wide and covered by spontaneous herbaceous vegetation. After tree planting, irrigated maize (*Zea mays* L.) was grown in monoculture following conventional practices in the control plot and in the inter-rows. Crop residues were left in the field after harvest. The soil was ploughed every year in both the agroforestry inter-rows and the control plot.

The CH silvoarable site was located in Châteaudun, in the department of Eure-et-Loir (longitude 1°17'58"E, latitude 48°06'08"N N, elevation 147 m a.s.l.). The mean temperature was 11.1 °C and the mean annual rainfall 595 mm (years 2001–2013, INRA CLIMATIK, https://intranet.inra.fr/climatik). The soil was a silty loam Luvisol (IUSS Working Group WRB, 2007). Hybrid walnut trees (*Juglans regia* × *nigra* cv. NG23) were planted in 2008 at a density of 34 trees ha^{-1}. The trees were planted 10 m apart within the rows, with 26 m between rows. A mix of ryegrass (*Lolium perenne* L.) and tall fescue (*Festuca arundinacea* Schreb.) was sown in 2007 in two meter wide strips along the tree rows. After tree planting, wheat (*Triticum aestivum* L. subsp. a*estivum*) and rapeseed (*Brassica napus* L.) were grown in rotation in the control plot and in the inter-rows following conventional practices. All crop residues were left in the field after harvest. The agroforestry inter-rows and the control plot were ploughed every three years.

The LB silvoarable site was located in Le Marquis, in the department of Oise (longitude 2°03'52.5"E, latitude 49°28'25.6"N, elevation 110 m a.s.l.). Mixed species of trees (hybrid walnut, sycamore maple, apple tree, cherrywood, wild service tree, common walnut) were planted in 2009 at a density of 83 trees ha^{-1}. The trees were planted 4 m apart within the tree rows, with 28 m between rows. The rows of trees were two meters wide and covered by spontaneous herbaceous vegetation. After tree planting, rapeseed (*Brassica napus* L.), wheat (*Triticum aestivum* L. subsp. *aestivum*) and barley (*Hordeum vulgare* L.) were grown in rotation without pesticides in the control plot and in the inter-rows. Crop residues were left in the field after harvest. The crops were directly sown on crop residues, with no tillage, in both the agroforestry inter-rows and the control plot.

The ME silvoarable site was located in Melle, in the department of Deux-Sèvres (longitude 0°10'37''W, latitude 46°11'54''N, elevation 107 m a.s.l.). The mean temperature was 11.7 °C and the mean annual rainfall 810 mm (years 1990–2013, INRA CLIMATIK, https://intranet.inra.fr/climatik). The soil was a silty loam Luvisol (IUSS Working Group WRB, 2007). Hybrid walnut trees (*Juglans regia* × *nigra* cv. NG23) were planted in 2008 at a density of 35 trees ha^{-1}. The trees were planted 8 m apart within the rows, with 29 m between rows. Sheep fescue (*Festuca ovina L.*) was sown in 2008 in two meter wide strips along the tree rows. After tree planting, wheat (*Triticum aestivum L. subsp. aestivum*), rapeseed (*Brassica napus L.*) and sunflower (*Helianthus annuus L.*) were grown in rotation, following conventional practices, in the control plot and in the inter-rows. Crop residues were usually exported, but this was counterbalanced by the application of manure in both the agroforestry inter-rows and the control plot. Before the spring crop (sunflower), a winter cover crop was sown to prevent soil erosion and nitrate leaching. This cover crop was a mix of radish (*Raphanus sativus* L.), phacelia (*Phacelia tanacetifolia* Benth.) and mustard (Sinapis alba L.). The soil was ploughed every year to a depth of 20 cm in both the agroforestry inter-rows and the control plot.

The PS silvoarable site was located in Parcé sur Sarthe, in the department of Sarthe (longitude 0°12'58.9''W, latitude 47°49'18.1''N, elevation 49 m a.s.l.). Mixed species of timber trees (hybrid walnut, wild service tree, common walnut, red oak, sorb tree) were planted in 2007 at two density (67 and 33 trees ha^{-1}). The trees were planted 5 or 10 m apart within the tree rows, with 27 m between rows. The rows of trees were three meters wide and covered by spontaneous herbaceous vegetation. In between timber trees, trees for biomass production were planted on the half of the site (hazel, black locust, sessile oak). Rapeseed (*Brassica napus* L.), wheat (*Triticum aestivum* L. subsp. *aestivum*), barley (*Hordeum vulgare* L.), sorghum (*Sorghum bicolor*), meslin were grown in rotation following conventional practices in the control plot and in the inter-rows. Cover crops are sown between the main crops. Crop residues were left in the field after harvest. The crops were sown after a reduced tillage in both the agroforestry inter-rows and the control plot.

The RE site was located in Prades-le-Lez, at the Restinclières experimental site, in the department of Hérault (longitude 04°01'E, latitude 43°43'N, elevation 54 m a.s.l.). The climate was sub-humid Mediterranean with a mean temperature of 15.4 °C and a mean annual rainfall of 873 mm (years 1995–2013, experimental site weather station). The soil was a deep carbonated sandy loam Fluvisol (IUSS Working Group WRB, 2007). Hybrid walnut trees (*Juglans regia* × *nigra* cv. NG23) were planted in 1995 and the density was 110 trees ha^{-1} at the time of the study. The trees were planted 4–8 m apart along the rows with 13 m between rows. The two meter wide tree rows were covered by spontaneous herbaceous vegetation. They were mainly intercropped with durum wheat (*Triticum turgidum* L. subsp. *durum*) but also with rapeseed (*Brassica napus* L.) and chickpea (*Cicer arietinum* L.). The soil was regularly ploughed to a depth of 20 cm in both the agroforestry inter-rows and the control plot.

The SA silvoarable site was located in Saint Aulais La Chapelle, in the department of Charentes (longitude 0°02'53.9''W, latitude 45°27'06.8''N, elevation 82 m a.s.l.). Mixed species of trees (Hybrid walnut, common walnut, sorb tree, sycamore maple, common apple, common pear, elm) were planted in 2007 at a density of 65 trees ha^{-1}. The trees were planted 6 m apart within the tree rows, with 20 m between rows. The rows of trees were five meters wide and sown with tall fescue (*Festuca arundinacea* Schreb.). After tree planting, cereal crops were grown in rotation with the minimum use of pesticides in the control plot and in the inter-rows. Crop residues were left in the field after harvest. The crops were directly sown under cover crops in both the agroforestry inter-rows and the control plot.

The SJ silvoarable site was located in Saint-Jean-d'Angély, in the department of Charente-Maritime (longitude 0°13'57"W, latitude 46°00'39"N, elevation 152 m a.s.l.). The mean temperature was 12.9 °C and the mean annual rainfall 850 mm (years 1990–2013, INRA CLIMATIK, https://intranet.inra.fr/clima- tik). The soil was a carbonated silty clay Luvisol (IUSS Working Group WRB, 2007). Black walnut trees (*Juglans nigra* L.) were planted in 1973 at a density of 102 trees ha^{-1}. The trees were planted 7 m apart within the tree rows, with 14 m between rows. The rows of trees were two meters wide, and covered by spontaneous herbaceous vegetation. After tree planting, sunflower (*Helianthus annuus* L.), wheat (*Triticum aestivum* L. subsp. *aestivum*) and barley (*Hordeum vulgare* L.) were grown in rotation following conventional practices, in the control plot and in the inter-rows. Crop residues were left in the field after harvest. The soil was ploughed every three years to a depth of 10–20 cm in both the agroforestry inter-rows and the control plot.

The SM silvoarable site was located in Saint Maxire, in the department of Deux Sèvres (longitude 0°30'42.9"W, latitude 46°23'57.6"N, elevation 44 m a.s.l.). Mixed species of trees (hybrid walnut, sorb tree, wild service tree) were planted in 2008 and 2010 at a density of 37 trees ha^{-1}. The trees were planted 9 m apart within the tree rows, with 28 m between rows. The rows of trees were two meters wide and sown with perennial ryegrass. After tree planting, cereal crops were grown in rotation following organic practices in the control plot and in the inter-rows. Crop residues were left in the field after harvest. The soil was never ploughed in both the agroforestry inter-rows and the control plot.

The SJM silvoarable site was located in Saint Jouin de Marnes, in the department of Deux Sèvres (longitude 0°02'28.7"W, latitude 46°54'19.0"N, elevation 59 m a.s.l.). Mixed species of trees (Hybrid walnut, alder, ash) were planted in 2006 at a density of 37 trees ha^{-1}. The trees were planted 10 m apart within the tree rows, with 24 m between rows. The rows of trees were three meters wide and sown with perennial ryegrass. After tree planting, maize (*Zea mays* L.) was grown in monoculture following conventional practices in the control plot and in the inter-rows. Crop residues were left in the field after harvest. The soil was ploughed every year in both the agroforestry inter-rows and the control plot.

The VER silvoarable site was located in Verpillières, in the department of Somme (longitude 2°48'56.4"E, latitude 49°40'03.3"N, elevation 81 m a.s.l.). Mixed species of trees (hybrid walnut, sorb tree, black locust, sycamore maple, common pear, common apple, norway maple) were planted in 2008 at a density of 42 trees ha^{-1}. The trees were planted 8 m apart within the tree rows, with 28 m between rows. The rows of trees were two meters wide and covered by spontaneous herbaceous vegetation. After tree planting, beetroot (Beta vulgaris subsp. vulgaris), wheat (*Triticum aestivum* L. subsp. *aestivum*), field bean (*Vicia faba*), rapeseed (*Brassica napus* L.) were grown in rotation following conventional practices in the control plot and in the inter-rows. Crop residues were left in the field after harvest. The crops were sown after a reduced tillage in both the agroforestry inter-rows and the control plot.

The VZ silvoarable site was located in Vézénobres, in the department of Gard (longitude 4°06'37"E, latitude 44°03'29"N, elevation 102 m a.s.l.). The climate was sub-humid Mediterranean with a mean temperature of 14.5 °C and a mean annual rainfall of 1037 mm (mean 1995–2007, experimental site weather station). The soil was a deep sandy loam alluvial

Fluvisol (IUSS Working Group WRB, 2007) originating from deposits from the granitic Cevennes mountain range and was, therefore, not calcareous. Hybrid walnut trees (*Juglans regia* × *nigra* cv. NG23) were planted in 1995 at a density of 100 trees ha^{-1}. The trees were planted 10 m apart with the rows, with 10 m between rows. The tree rows were two meters wide and were covered by spontaneous herbaceous vegetation. In the inter-rows, rapeseed (*Brassica napus* L.) and wheat (*Triticum aestivum* L. subsp. *aestivum*) were grown in rotation until 2010. In 2011, the farm changed over to organic farming and potatoes were planted (*Solanum tuberosum* L.). In 2012 garlic (*Allium sativum* L.) was grown in the inter-rows. In 2013 the inter-rows were left fallow and in 2014 sunflower (*Helianthus annuus* L.) was sown. The same crops were grown in the control plot, except in 2011 when wheat (*Triticum aestivum* L. subsp. *aestivum*) was sown and in 2012 when the control was left fallow. The soil was occasionally ploughed to a depth of 20 cm in both the agroforestry inter-rows and the control plot. The soil regularly amended with rameal chip wood.

Table S1. Mean earthworm species abundance across agroforestry sites and locations (T, Tree row; A, Alley; C, Control). Individual weights of adults are indicated in brackets when at least 3 adults were present on at least 2 different locations per sites.

	Ecological category	BE			BO			CH			LB		
		T	A	C	T	A	C	T	A	C	T	A	C
Eiseniella tetraedra	Epigeic					1							
Dendrobaena mammalis	Epigeic	98 (0.12)	2 (0.13)	2	101 (0.18)	68 (0.21)							
Lumbricus castaneus	Epigeic	178	15	30							12 (0.20)	6 (0.17)	
Lumbricus rubellus castanoides	Epigeic							64 (0.22)	12 (0.21)	1			
Lumbricus rubellus rubellus	Epi-anecic				1	3							
Lumbricus terrestris	Epi-anecic	60	2	7				125 (3.63)	38 (4.46)	4 (6.79)	39 (3.63)	33 (3.87)	27
Lumbricus festivus	Epi-anecic	5	1	1									
Lumbricus friendi	Epi-anecic												
Aporrectodea giardi	Strict-anecic	48	21	4	18 (2.64)	58 (1.97)					10	14	
Aporrectodea longa	Strict-anecic				122 (1.86)	11 (2.01)		36 (2.19)	30 (2.78)	13 (3.68)			
Aporrectodea nocturna	Strict-anecic		1			14					37	8	15
Aporrectodea caliginosa meridionalis	Strict-anecic												
Aporrectodea caliginosa caliginosa	Endogeic	212 (0.33)	89 (0.32)	80 (0.26)				392 (0.37)	189 (0.43)	29 (0.41)	180 (0.33)	76 (0.37)	45 (0.38)
Allolobophora chlorotica chlorotica	Endogeic	85 (0.18)	191 (0.15)	179 (0.15)	276 (0.18)	240 (0.22)		138 (0.18)	38 (0.22)	31 (0.24)	119 (0.18)	62 (0.18)	91
Allolobophora minima	Endogeic	119	11										
Allolobophora icterica	Endogeic							28 (0.63)	13 (0.74)				
Allolobophora rosea rosea	Endogeic	24	14	1	69			95 (0.20)	51 (0.19)	10 (0.18)	55 (0.21)	4.5 (0.20)	13
Allolobophora cupulifera	Endogeic				114 (0.16)	81 (0.18)							
Prosellodrilus fragilis	Endogeic												
Octalasium cyaneum	Endogeic									5	3	1	1
Other genus or species undetermined	NA											1	
	Total	829	345	303	701	476		878	372	92	455	204	192

	Ecological category	ME			PS			RE			SA		
		T	A	C	T	A	C	T	A	C	T	A	C
Eiseniella tetraedra	Epigeic												
Dendrobaena mammalis	Epigeic	20			4 (0.17)	4 (0.22)					24 (0.20)	9 (0.20)	27 (0.25)
Lumbricus castaneus	Epigeic				4 (0.24)	5 (0.28)	2 (0.34)	1					
Lumbricus rubellus castanoides	Epigeic	38 (0.18)	1 (0.26)				1						
Lumbricus rubellus rubellus	Epi-anecic												
Lumbricus terrestris	Epi-anecic	2						1			1		
Lumbricus festivus	Epi-anecic				9	22	13						
Lumbricus friendi	Epi-anecic	84	14								73 (1.97)	21 (1.95)	38 (1.80)
Aporrectodea giardi	Strict-anecic										21		
Aporrectodea longa	Strict-anecic	65 (1.11)	14 (1.31)	6	136 (1.36)	143 (1.50)	119 (1.89)				132 (1.69)	105 (1.60)	121 (1.86)
Aporrectodea nocturna	Strict-anecic		34	12									
Aporrectodea caliginosa meridionalis	Strict-anecic				1		9				2		9
Aporrectodea caliginosa caliginosa	Endogeic				165 (0.40)	155 (0.42)	120 (0.44)	21	9				
Allolobophora chlorotica chlorotica	Endogeic	188 (0.18)	63 (0.18)	45	30 (0.18)	31 (0.23)	134 (0.25)	36	18		573 (0.25)	232 (0.22)	235 (0.24)
Allolobophora minima	Endogeic											56	69
Allolobophora icterica	Endogeic	1											
Allolobophora rosea rosea	Endogeic	16	11		61 (0.24)	64 (0.24)	74 (0.25)				6	14	1
Allolobophora cupulifera	Endogeic										0.3	4	
Prosellodrilus fragilis	Endogeic												
Octalasium cyaneum	Endogeic		1				2						
Other genus or species undetermined	NA							1					
	Total	413	137	63	409	423	472	60	26		833	441	499

	Ecological category	SJ			SJM			SM			VER		
		T	A	C	T	A	C	T	A	C	T	A	C
Eiseniella tetraedra	Epigeic												
Dendrobaena mammalis	Epigeic	49	1		8								
Lumbricus castaneus	Epigeic	30 (0.20)	23 (0.17)		8						149 (0.12)	46 (0.16)	8
Lumbricus rubellus castanoides	Epigeic												
Lumbricus rubellus rubellus	Epi-anecic												
Lumbricus terrestris	Epi-anecic				33						51 (3.78)	29 (4.77)	75 (3.73)
Lumbricus festivus	Epi-anecic												
Lumbricus friendi	Epi-anecic	17	2					59	1				
Aporrectodea giardi	Strict-anecic		3					22	16				
Aporrectodea longa	Strict-anecic	30 (2.57)	21 (2.70)	7 (2.73)	42				2				
Aporrectodea nocturna	Strict-anecic												
Aporrectodea caliginosa meridionalis	Strict-anecic	1	5					31					
Aporrectodea caliginosa caliginosa	Endogeic				275	25					346 (0.33)	162 (0.37)	29 (0.35)
Allolobophora chlorotica chlorotica	Endogeic	42 (0.26)	69 (0.29)	23 (0.30)	358 (0.20)	125 (0.20)		170 (0.24)	57 (0.30)		1	1	122
Allolobophora minima	Endogeic	69			88	25							
Allolobophora icterica	Endogeic										1		6
Allolobophora rosea rosea	Endogeic	1	1		38	17		1	1		147 (0.25)	22 (0.22)	11
Allolobophora cupulifera	Endogeic												
Prosellodrilus fragilis	Endogeic												
Octalasium cyaneum	Endogeic	6	1								1		
Other genus or species undetermined	NA	3	8					1					
	Total	247	133	29	850	192		282	76		694	259	251

	Ecological category	VZ		
		T	A	C
Eiseniella tetraedra	Epigeic			
Dendrobaena mammalis	Epigeic			
Lumbricus castaneus	Epigeic			
Lumbricus rubellus castanoides	Epigeic	1	14	
Lumbricus rubellus rubellus	Epi-anecic	4 (0.55)	7 (0.52)	
Lumbricus terrestris	Epi-anecic		1	
Lumbricus festivus	Epi-anecic			
Lumbricus friendi	Epi-anecic			
Aporrectodea giardi	Strict-anecic			
Aporrectodea longa	Strict-anecic			
Aporrectodea nocturna	Strict-anecic	12 (1.87)	39 (1.78)	
Aporrectodea caliginosa meridionalis	Strict-anecic			
Aporrectodea caliginosa caliginosa	Endogeic	4	58	
Allolobophora chlorotica chlorotica	Endogeic	2	5	
Allolobophora minima	Endogeic			
Allolobophora icterica	Endogeic	1	33	
Allolobophora rosea rosea	Endogeic		11	
Allolobophora cupulifera	Endogeic			
Prosellodrilus fragilis	Endogeic		5	
Octalasium cyaneum	Endogeic			
Other genus or species undetermined	NA			
	Total	22	175	

BE, Béthines; BO, Bonnes; CH, Châteaudun; LB, Lasalle Beauvais; ME, Melle; PS, Parcé-sur-Sarthe; RE, Restinclières; SA, Saint-Aulaix-la-Chapelle; SJ, Saint-Jean-d’Angély; SJM, Saint-Jouin-de-Marnes; SM, Saint-Maxire ; VER, Verpillères; VZ, Vézénobres.

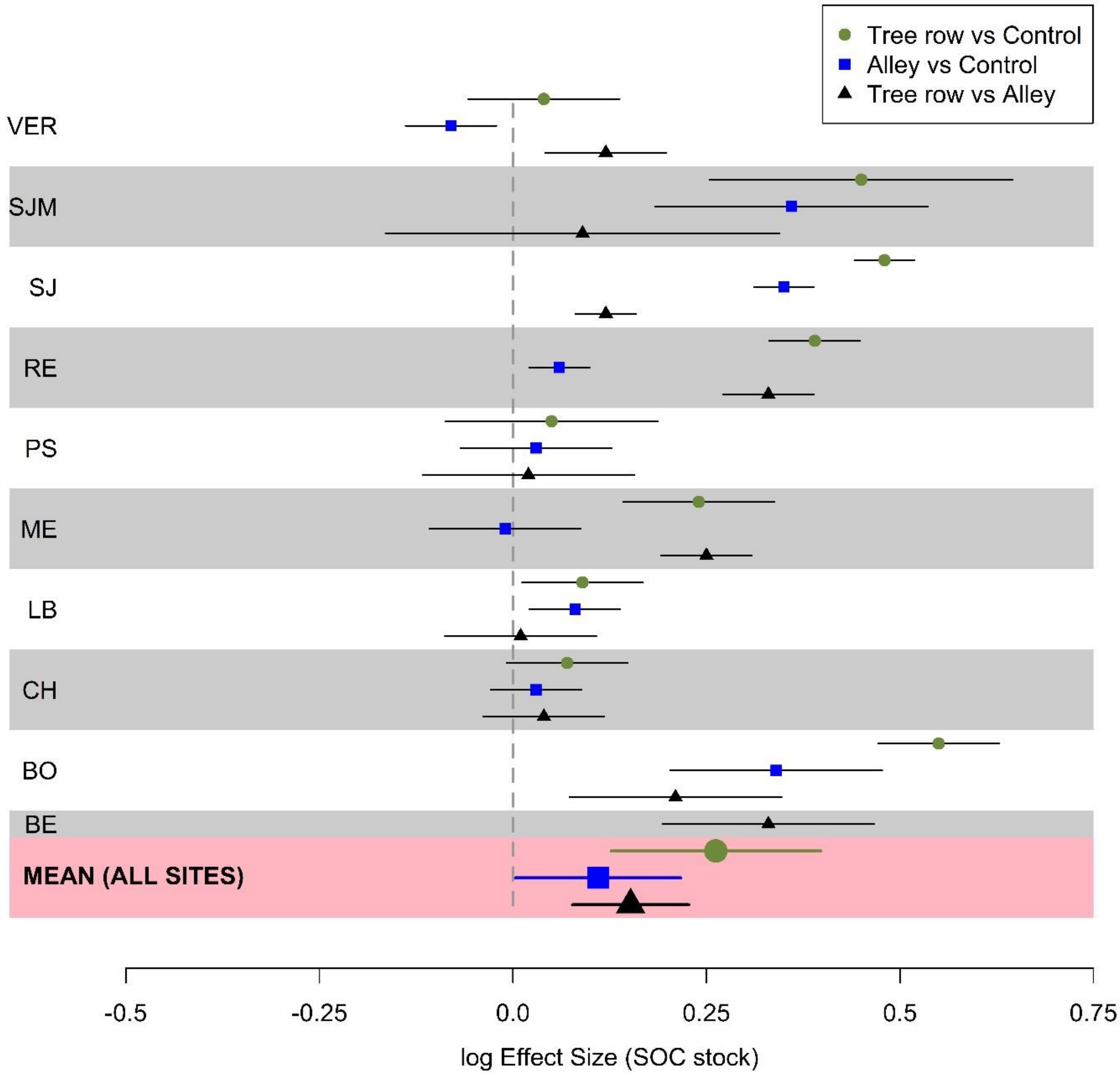

Figure S1. Site-specific log effect sizes of SOC stocks (0-30 cm) between tree rows and control plots, alleys and control plots, and tree rows and alleys for the silvoarable sites (excluding the VZ site with organic vegetables). Error bars represent confidence intervals.

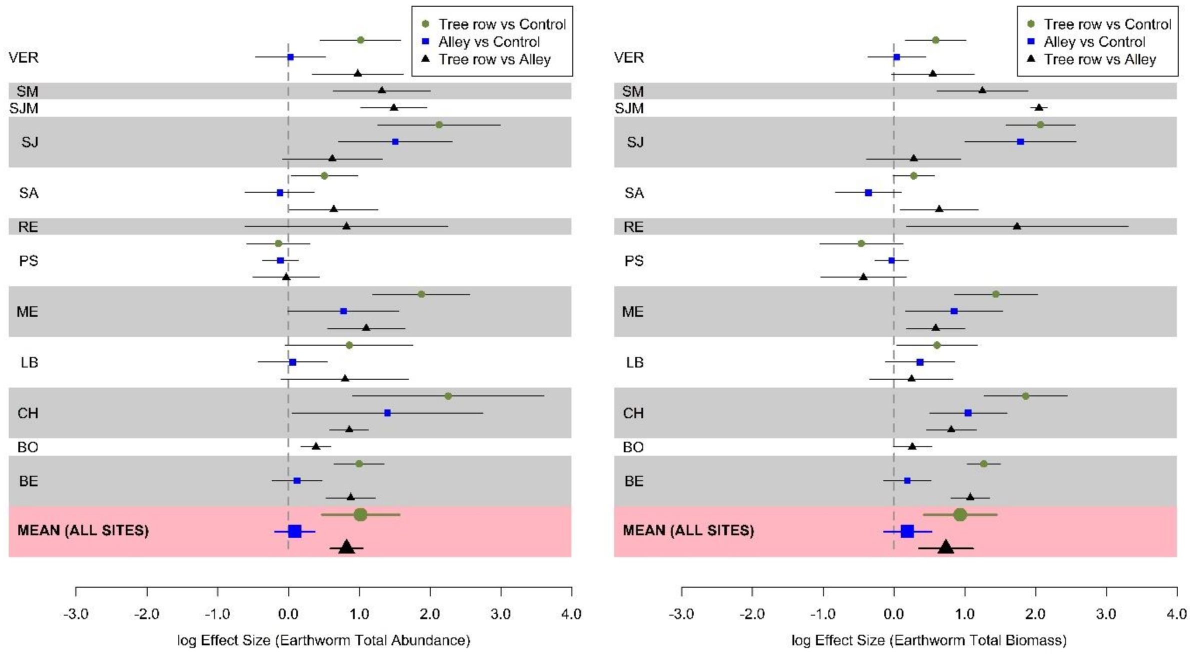

Figure S2. Site-specific log effect sizes of earthworm total abundance and biomass between tree rows and control plots, alleys and control plots, and tree rows and alleys for the silvoarable sites (excluding the VZ site with organic vegetables). Error bars represent confidence intervals.

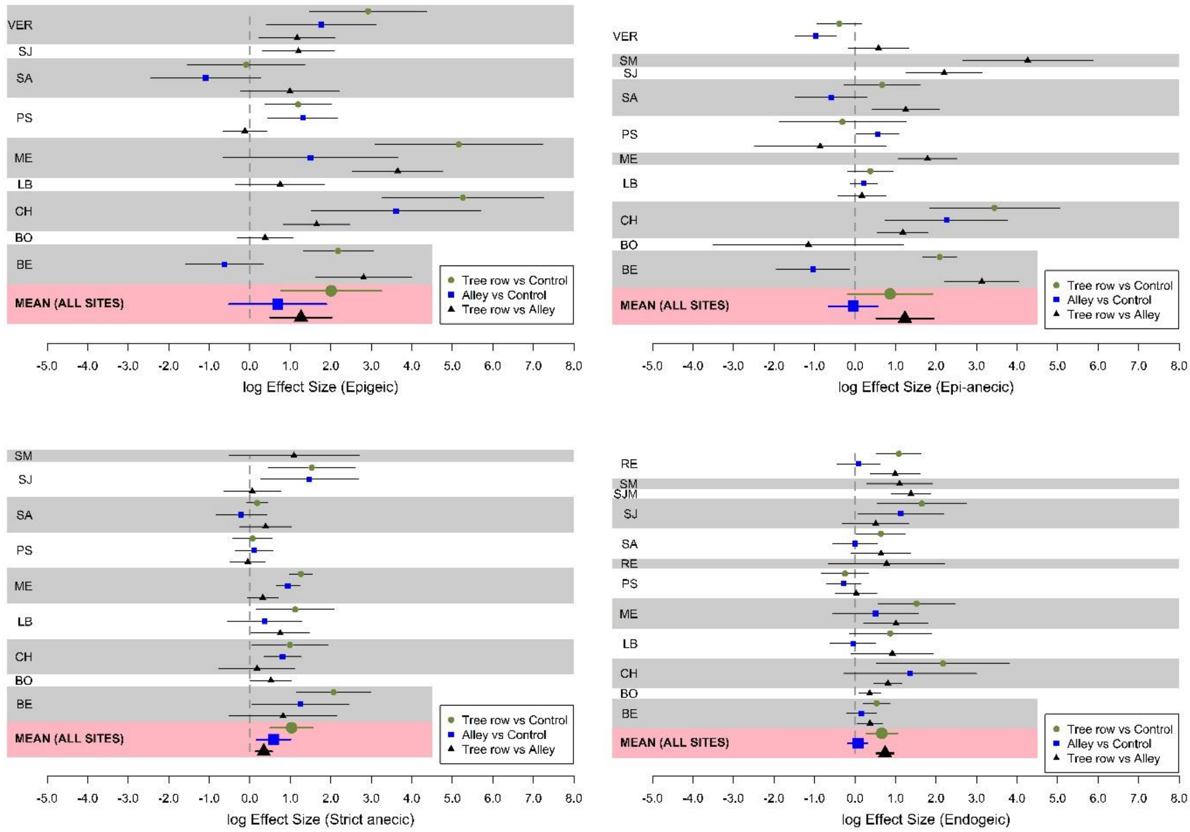

Figure S3. Site-specific log effect sizes of earthworm abundance per ecological category between tree rows and control plots, alleys and control plots, and tree rows and alleys for the silvoarable sites (excluding the VZ site with organic vegetables). Error bars represent confidence intervals. Missing sites between the four graphs correspond to an absence of this earthworm category in at least a modality (not possible to calculate a log ratio).

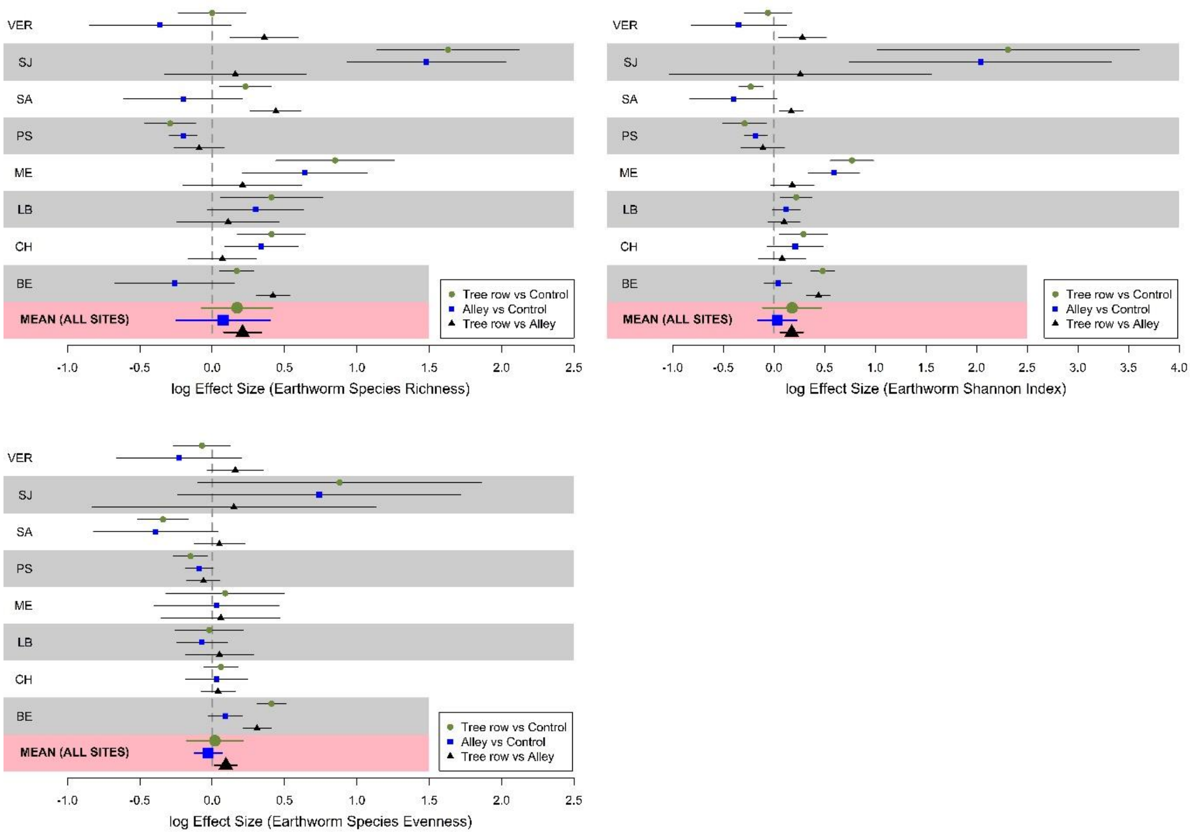

Figure S4. Site-specific log effect sizes of earthworm species richness, Shannon index and species evenness between tree rows and control plots, alleys and control plots, and tree rows and alleys for the silvoarable sites (excluding the VZ site with organic vegetables). Error bars represent confidence intervals.

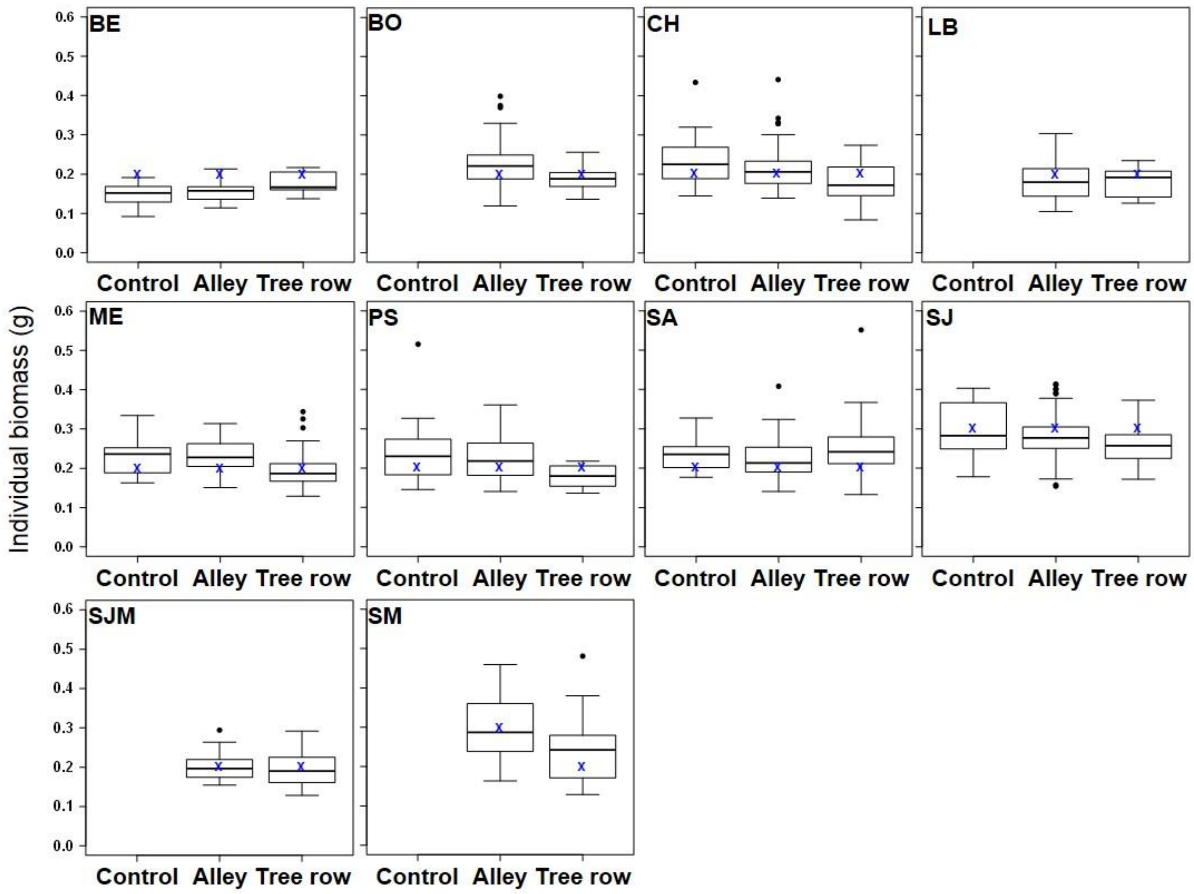

Figure S5. Individual weight of *Allolobophora chlorotica chlorotica* across agroforestry sites and locations.

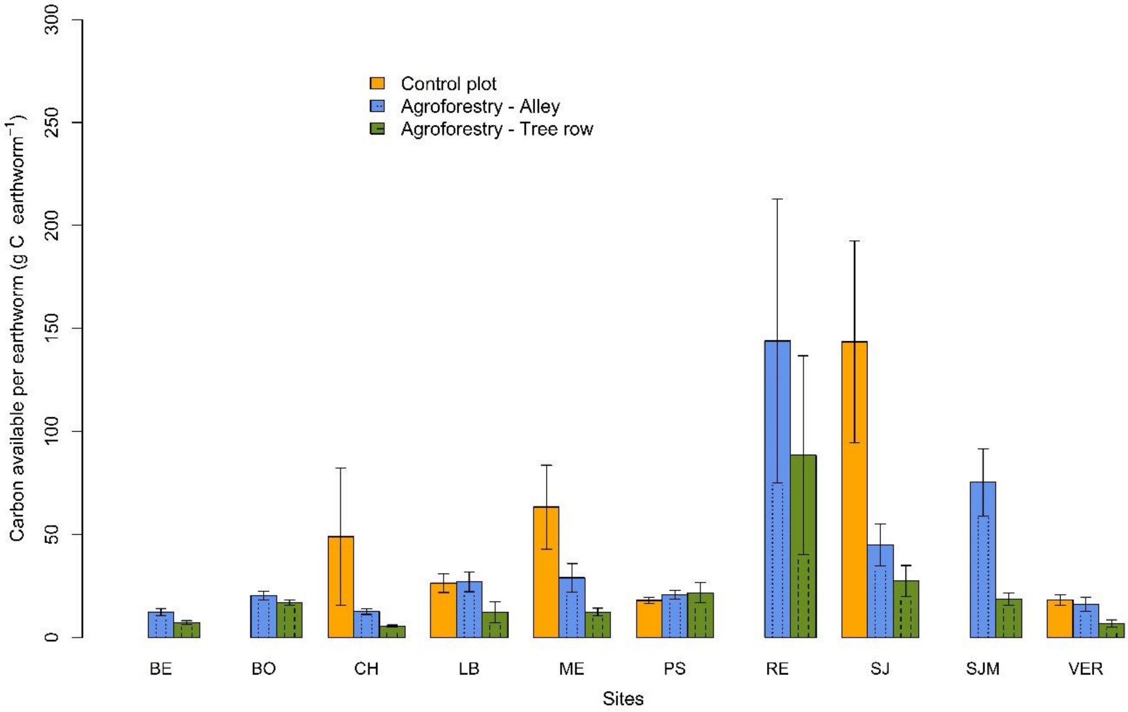

Figure S6. Ratio between SOC stocks (0-30 cm) and total earthworm abundance at the silvoarable sites (excluding the VZ site with organic vegetables). Error bars represent standard errors.

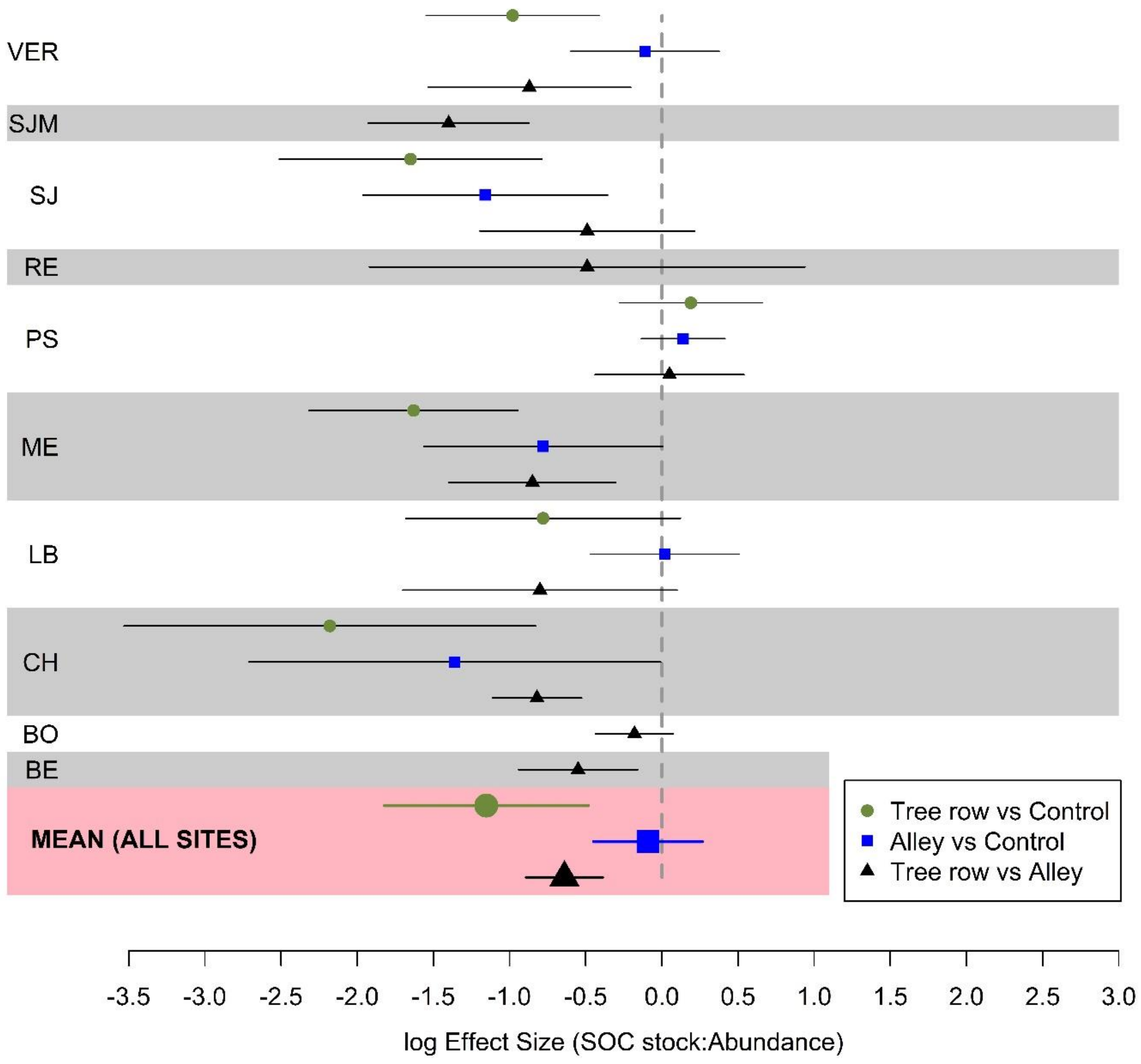

Figure S7. Site-specific log effect sizes of the ratio between SOC stocks (0-30 cm) and total earthworm abundance at the silvoarable sites (excluding the VZ site with organic vegetables). Error bars represent standard errors.