



Original article

The effects of agricultural practices on earthworm communities in Estonia

Merit Sutri^{a,*}, Mari Ivask^{a,b}, Annelly Kuu^a, Jordi Escuer-Gatius^a, Endla Reintam^a, Merrit Shanskiy^a

^a Estonian University of Life Sciences, Institute of Agricultural and Environmental Sciences, Chair of Soil Science, Kreutzwaldi Str. 5, Tartu, 51006, Estonia

^b Tallinn University of Technology, Tartu College, Puiestee Str. 78, Tartu, 51008, Estonia



ARTICLE INFO

Keywords:

Earthworms
Farming systems
Soil tillage
Sustainable agriculture
Soil texture
Agroecosystems

ABSTRACT

Earthworms support and mediate the provision of many processes in the soil. They are therefore important in maintaining soil functioning and contribute towards the sustainability of soil management systems. Assessment of earthworm communities can provide answers regarding the land management conservation efforts and insight on soil quality. The main aim of this study was to assess the impact of farming (organic vs conventional) and tillage (no-tillage vs minimum tillage vs conventional tillage) systems on earthworm communities under varying soil conditions in arable fields across Estonia. To achieve this, we compiled data from studies carried out over a period of 21 years on Estonian arable fields. While organic farming and conventional farming showed a similar earthworm abundance, earthworm diversity was significantly higher ($p < 0.05$) under the organic system. Higher abundance, species richness, and the proportion of anecic species suggest that a no-tillage system creates the most favourable habitat conditions for earthworms. Soil texture further influenced the effect of management system on earthworm abundance and diversity indexes. For example, the differences in earthworm abundance and diversity between the management systems increased from lighter textured to heavier textured soils. Our results suggest that soil texture is a major factor influencing earthworm communities in Estonian agricultural fields and emphasizes the importance of including different soil texture classes when assessing the effects of agricultural management practices in field-scale studies.

1. Introduction

Intensive agriculture is considered as one of the major threats to soil biodiversity [1]. Soil organisms mediate a great range of soil processes such as nutrient transformation, bio-accumulation and food-web assimilation [2]. Therefore, higher abundance and biodiversity can be associated with good soil quality [3] and the ability to recover after any disturbance. Earthworms, commonly described as *ecosystem engineers*, have been shown to contribute to water regulation and purification, nutrient cycling, carbon sequestration and climate regulation, aggregation, bioturbation, fragmentation, and macropore formation [4]. Since soil quality is essential to agriculture, the search for bioindicators for the assessment of soil management has been a major focus of soil quality research [5]. Earthworms have been widely recognised as bioindicators for agroecosystem management [6–8] and soil quality [9,10] because of their sensitivity to changes in their environment [11] and crucial role in soil functioning [4]. Agricultural management practices such as farming approach (organic vs. conventional) and tillage system

can greatly influence the soil environment and therefore change the habitat of soil biota [12]. Organic farming is often assumed to benefit earthworm communities because it typically relies on the usage of animal and green manures and diversified crop rotations to maintain soil health and fertility and does not involve the application of synthetic pesticides [13]. However, as reviewed by Hole et al., 2005 [14], there have been reports of organic farming having both positive and negative effects on earthworms. The main method to control pests and weeds in organic farming is usually soil tillage, which can counteract the positive influence of not using synthetic pesticides and relying on organic inputs for plant nutrition. Conversely, less intensive tillage can impact earthworms differently under conventional farming than organic farming because of interactions between tillage and organic matter management [12]. It may also be affected by the duration of the specific management type [12]. Furthermore, earthworms might not have enough food sources to support large populations under organic farming systems that do not involve sufficient organic fertilisation and plant residue input.

Reducing tillage intensity to the point of no-tillage has been widely

* Corresponding author.

E-mail address: merit.sutri@emu.ee (M. Sutri).

<https://doi.org/10.1016/j.ejsobi.2024.103662>

Received 19 July 2023; Received in revised form 20 March 2024; Accepted 12 August 2024

Available online 19 August 2024

1164-5563/© 2024 Elsevier Masson SAS. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

recognised to benefit earthworm communities [15]. Tillage injures earthworms directly, destroys their permanent burrows and changes their habitat and food accessibility [16]. However, the impact of tillage can differ between ecological groups, and it has been found that no-tillage [17] and reduced tillage benefit principally the deep burrowing anecic and surface-dwelling epigeic species [18], whereas endogeic species can be less responsive. In some cases, endogeic species can increase under conventional tillage as a result of the better food supply [16]. However, no-tillage systems have the disadvantage of increased dependence on pesticides to fight weeds [19] and have been shown to lead to soil compaction [20], both of which are factors that could negatively affect earthworms. Therefore, reduced tillage intensity cannot be said to always favour earthworm abundance relative to conventional soil ploughing [21] and the impact of tillage can be influenced by confounding factors such as soil texture, farming system, and crop rotation.

Although a large number of studies have determined the effects of farming and tillage systems [14,18], most studies have dealt with field experiments on a specific soil type. Moreover, relatively few studies have investigated the differences in community composition across different soil texture classes in large-scale farming systems under field conditions [22,23]. We combined data from multiple studies carried out on farm fields across Estonia to examine how earthworm communities are affected by contrasting agricultural management systems. The dataset consisted of earthworm community data collected from arable fields located in 12 of the 15 Estonian counties over a period of 21 years, covering a wide spatial and temporal range at a national level. By compiling site-level earthworm data, we aimed to collect information on how different agricultural management impacts the earthworm communities across and under different soil texture classes. We hypothesised that (i) the abundance and diversity of earthworm communities are promoted under organic farming relative to conventional farming, (ii) that less intensive tillage systems (no-tillage and minimum tillage) favour earthworm communities relative to conventional tillage, and (iii) the response of earthworm communities to management depends on soil texture. The additional aim was to study which soil properties contributed to characterising earthworm communities in arable landscapes.

2. Material and methods

2.1. Dataset

The data used for this study were gathered from several soil survey programs and research projects conducted in Estonia (a list of the included studies can be found in Annex 1). The main inclusion criteria for studies was that earthworms were collected from arable farm fields and that the study either reported farming or tillage systems. We attempted to include all available data comprising all possible combinations of farming or tillage systems on arable crop fields with different soil textures. We did not include studies based on field plot experiments, because of drastic differences in earthworm communities compared to data from research programmes based on farm fields. The distribution of sampling points is shown in Fig. 1.

Each site was categorized according to the farming system as organic or conventional and then assigned to the following soil texture classes: sand (<10 % clay), loamy sand (10%–20 % clay), loam (20%–50 % clay), and clay (>50 % clay). When the texture was not mentioned in the study, it was obtained from the Estonian Soil Map [24]. When known, the fields were classified according to the tillage system as no-tillage, minimum tillage (shallow non-inversion tillage), or conventional tillage (inversion tillage). The dataset did not include the complete combinations of all farming, tillage and, texture classes; therefore, we carried out our analyses in two steps: first, we analysed the effect of farming system irrespective of the tillage system; and then, tillage system was included in the analysis (see Section 2.3 for more details). We were also able to partially compile information regarding the usage of manure, mineral fertilizers, tillage frequency and study their relationships (Fig. S1) with the earthworm community parameters (abundance, species richness, Shannon – Wiener index, Simpson’s diversity index, proportion of dominant species, proportions of ecological groups).

Composite soil samples were collected alongside earthworms at almost all sites, making it possible to also compile information on soil properties (soil total nitrogen, soil organic carbon, plant available soil phosphorus, plant available soil potassium, pH, and soil moisture content). If soil properties were measured at different depths, the average

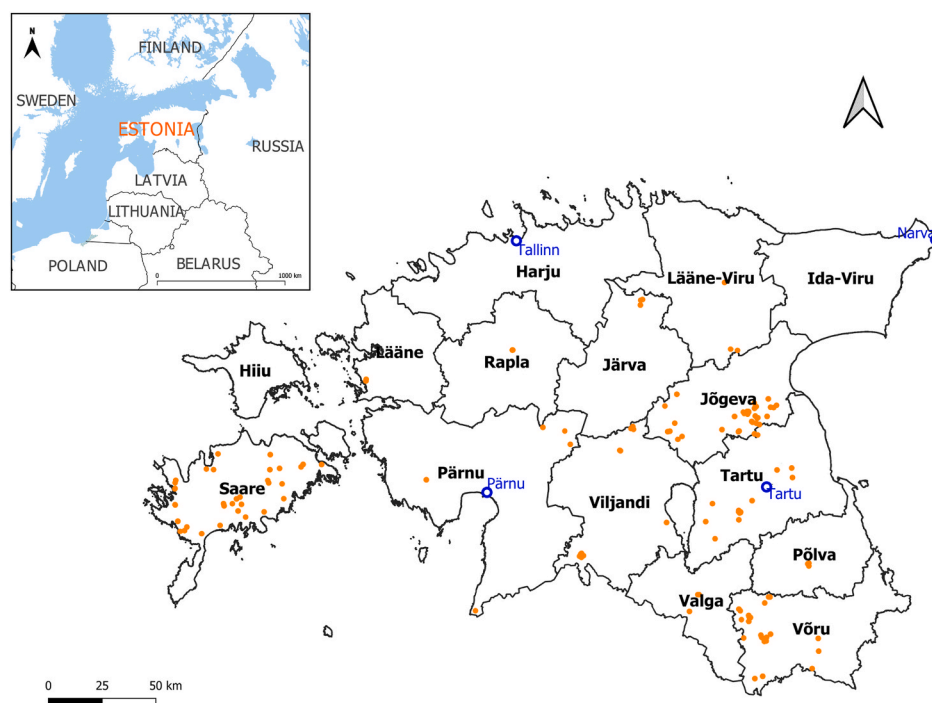


Fig. 1. Location of the sampling sites included in this study (orange dots). Estonian county names are indicated by bold type and the four main cities by population are indicated in blue.

value was used. When the soil organic matter was measured, we used the 1.724 conversion factor to convert it to soil organic carbon content.

2.2. Earthworm sampling and classification

The earthworms were typically collected from three randomly selected sampling points (0.5 m × 0.5 m) on each site in September or October, during the period when earthworms were active. The earthworm extraction method differed depending on the study. The method was either hand-sorting a 0.5 m × 0.5 m × 0.4 m soil monolith [25], vermifuge with 15 % mustard solution, or hand-sorting a soil monolith followed by vermifuge of the bottom of the soil pit (the methodology used in each study can be found in Annex 1). All studies followed the same protocol after earthworm extraction. This included washing the earthworms, keeping them in refrigeration for 48 h and fixing them in 70 % ethanol. All the studies followed Graff [26] and Timm [27] to identify earthworm species. In most cases studies reported the number of adults and juveniles. We then calculated the adult/juvenile ratio. Earthworms were also classified into three morpho-ecological groups (epigeic, anecic, and endogeic) to assess morpho-ecological community composition following Hill [28]. More specifically anecic species included *Lumbricus terrestris* (Linnaeus, 1758) and *Aporrectodea longa* (Ude, 1885). Epigeic species included *Lumbricus rubellus* (Hoffmeister, 1843), *Lumbricus castaneus* (Savigny, 1826), *Eiseniella tetraedra* (Savigny, 1826) and *Bimastos rubidus* (Savigny, 1826). Endogeic species included *Aporrectodea caliginosa* (Savigny, 1826), *Aporrectodea rosea* (Savigny, 1826), *Octolasion cyaneum* (Savigny, 1826), *Octolasion lacteum* (Orley, 1881) and *Allolobophora chlorotica* (Savigny, 1826).

To compare earthworm community across different agricultural managements, we used earthworm abundance (individuals per m²) and species diversity using the Shannon–Wiener index and Simpson's diversity index [29,30]. The function 'diversity' from the 'vegan' package [30] for the R programming language was used to calculate the diversity indexes. Species richness indicates the number of species present in each sampling point (species per sample). The proportion of the dominant species represents the proportion of *Ap. caliginosa* in the earthworm community.

2.3. Statistical analysis

All statistical analyses were carried out in the R programming language [31]. A mixed-effects model was fitted to study the effect of farming systems with soil texture as an additional fixed factor and with collection method, crop, year, study and field (nested under study) as random factors. Since the dataset did not include any organic no-tillage fields, we excluded all no-tillage fields from the farming system comparison. A second mixed model was fitted to study the effect of tillage system with the same fixed and random factors as the previous but also including the tillage system. The mixed-effects models were fitted using the function 'lmer' from the 'lme4' package [32]. Two different models were fitted in order to maximize the amount of data used in each model, as the tillage system was not available for all fields. The significance of the different factors in the mixed-effects models was determined with analysis of variance (ANOVA Type III). A post-hoc Tukey HSD (honest significant difference) was used to analyse the difference between the levels of the factors, using the package 'emmeans' [33]. Non-metric multidimensional scaling (NMDS) was used to analyse the variability among the different species, and to relate it to soil chemical properties and management practices. Soil properties were added post-hoc to the NMDS plot as vectors according to the relationship between soil properties and the NMDS scores. For the NMDS analysis, the soil texture was coded as a numerical variable according to the mean of the clay content interval in proportion for the soil texture (sand, 5; loamy sand, 15; loam, 35; clay, 75 based on the intervals as described in Section 2.1). The significance of soil properties in the NMDS analysis is determined based on 999 random permutations. Spearman's rank correlation coefficient

was used to study the relationships between earthworm community parameters and soil chemical properties. The box plots follow the conventions of Tukey [34], representing the minimum, the 25th percentile, the median, the 75th percentile, and the maximum values (excluding outliers).

3. Results

3.1. Overview of the earthworm population on arable fields

A total of 13 species have been identified in Estonia including *L. terrestris*, *Ap. longa*, *L. rubellus*, *L. castaneus*, *E. tetraedra*, *B. rubidus*, *Dendrobaena octaedra* (Savigny, 1826), *Eisenia fetida* (Savigny, 1826), *Ap. caliginosa*, *Ap. rosea*, *O. cyaneum*, *O. lacteum*, and *A. chlorotica* [27]. *B. rubidus* was previously recorded as *Dendrodriulus rubidus* (Savigny, 1862), but recently it has been discovered that *Dendrodriulus* is nested within the *Bimastos* clade, therefore they are treated as synonyms [35]. Overall, 11 out of these 13 species were identified on the arable fields in the studies included in this review (Fig. 2). The most abundant species was *Ap. caliginosa*, followed by *Ap. rosea*, *L. rubellus*, *Ap. longa*, *A. chlorotica*, *L. terrestris* and *L. castaneus*. It was found that *O. cyaneum*, *O. lacteum*, *E. tetraedra* and *B. rubidus* were quite rare in fields included in this study and are not typical for Estonian arable soils in general, since these species prefer high-moisture habitats [36–38]. In particular, *E. tetraedra* is a semi-aquatic species and is found mostly in riverbanks and *B. rubidus* is more frequent in forests with high amounts of leaf litter [39,40]. *O. cyaneum* is a relative newcomer to Estonia, and has been sighted only in a few locations [41].

3.2. The impact of farming system on earthworm communities

Overall, the farming system had a significant impact on the two considered diversity indexes (for Shannon's index $F = 8.25$, $p = 0.004$; for Simpson's diversity index $F = 8.62$, $p = 0.003$), proportion of the dominant species ($F = 11.18$, $p = 0.001$) and for the anecic individuals $F = 11.43$, $p = 0.001$; Table S1). Since soil texture had a significant impact on almost all earthworm community parameters we compared the impact of management within the soil texture class (Figs. 3 and 4). The means of additional earthworm community parameters (biomass, adults/juvenile ratio and proportions of adult and juvenile earthworms) can be found in Table S3 and species composition can be found in Table S4. When including the interaction effect in the model, soil texture and the interaction of farming and texture described a large amount of the variability in the dataset and the effect of the farming system alone

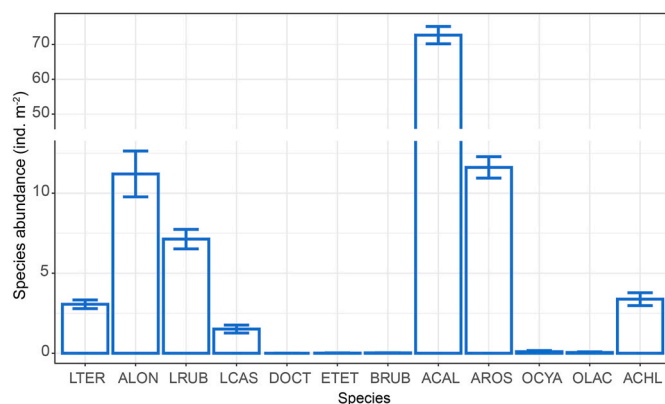


Fig. 2. Mean species abundance across all the fields included in the dataset. Error bars represent standard error. Earthworm species: LTER – *Lumbricus terrestris*, ALON – *Aporrectodea longa*, LRUB – *Lumbricus rubellus*, LCAS – *Lumbricus castaneus*, ETET – *Eiseniella tetraedra*, BRUB – *Bimastos rubidus*, ACAL – *Aporrectodea caliginosa*, AROS – *Aporrectodea rosea*, OCYA – *Octolasion cyaneum*, OLAC – *Octolasion lacteum*, ACHL – *Allolobophora chlorotica*.

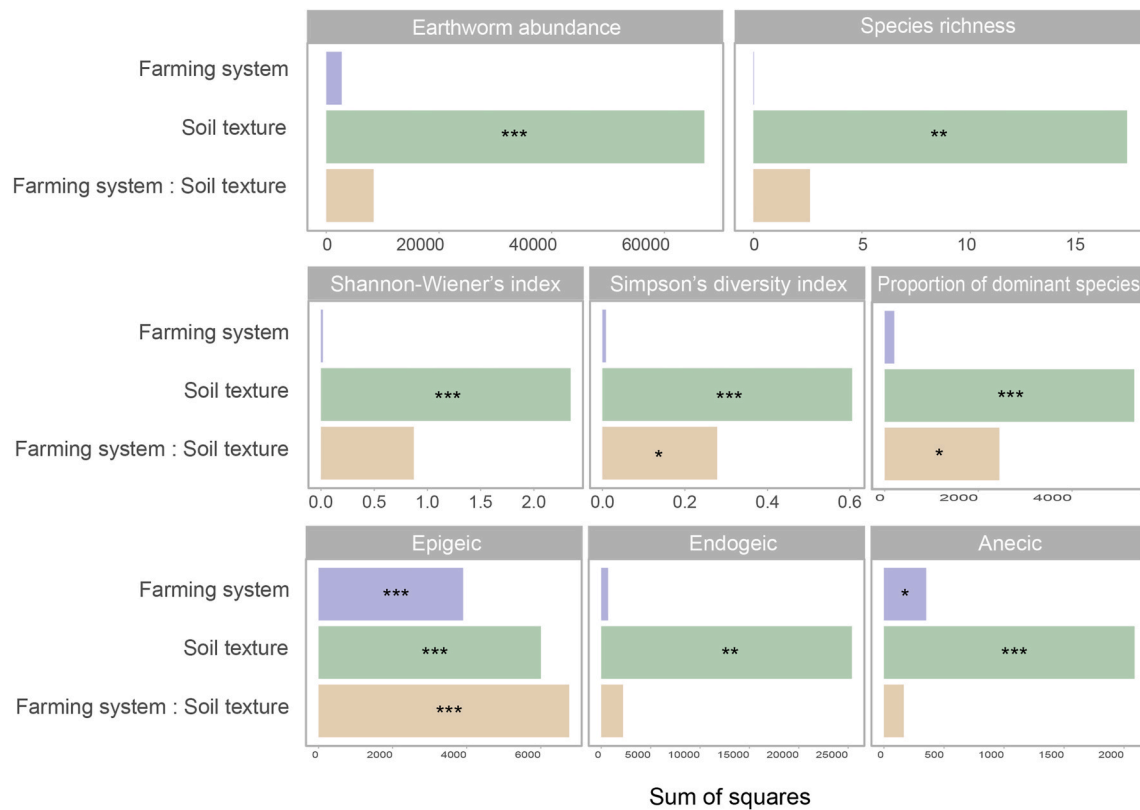


Fig. 3. The effects of farming system and texture and their interaction on the earthworm community based on an analysis of variance (ANOVA) of the mixed effects model including these two factors. Significance levels are indicated as follows: *** $p < 0.001$, ** $p = 0.01$, * $p = 0.05$. A complete summary of the ANOVA output can be found in [Supplementary Table S2](#).

remained significant only for the abundance of epigeic and anecic species. Earthworm abundance did not differ significantly between organic and conventional farming (Table 1), although when constrained by soil texture, we found that the mean earthworm abundance tended to be lower for organic farming on sandy and clay soils (Fig. 4). However, fields under organic farming had significantly higher earthworm diversity and proportion of epigeic and anecic species compared with conventional farming (Table 1). The dominance of *Ap. caliginosa* and proportion of endogeic species was lower under organic farming compared with conventional farming. The means of additional earthworm community parameters can be found in Table S6 and species composition can be found in Table S7.

Farming systems were next compared within different soil texture classes. The proportion of dominant species (60 %) was significantly lower under organic farming compared with conventional (73.16 %) on loam soil. Moreover, both diversity indexes (with a mean Simpson's diversity index of 0.533 and a mean Shannon's index of 1.027) were higher for organic farming compared with conventional (0.413 and 0.799, respectively) on loam soil. The opposite trend was found for clay soil, with a significantly lower proportion of dominant species on conventional fields (46.3 %) compared with organic (88 %). The diversity indexes tended to be higher under organic farming across all soil texture classes except clay. In general, the abundance of earthworms and the values of diversity indexes tended to increase, and the proportion of dominant species to reduce, as the soil texture became heavier (finer soil particles).

The abundance of anecic species was significantly higher in organic fields with a loam texture (Fig. S2), whereas the opposite trend was apparent for clay soils for epigeic species. The abundance of anecic species was generally very low in sandy and clayey soils. No significant differences in morpho-ecological group composition were observed when comparing farming system within the sand and loamy sand texture

classes.

3.3. The impact of tillage system on earthworm communities

The tillage system had a significant effect on almost all parameters of the earthworm community (Fig. 5). Earthworm abundance was significantly higher in the no-tillage system compared with conventional tillage with loam texture (Fig. 6). The proportion of dominant species tended to be lower among less intensive tillage systems across all sites but was significantly lower on minimum tillage fields (46.3 %) compared with conventional tillage (94.7 %) with a clay texture. Furthermore, significantly higher earthworm diversity was found on no-tillage fields compared with minimum tillage fields with a loam texture. Species richness and Simpson's diversity index were also significantly lower under conventional tillage compared with minimum tillage in fields with a clay soil.

The abundance of epigeic species was significantly higher under minimum tillage compared with conventional tillage on clay soil (Fig. S4). The abundance of anecic species was significantly higher under the no-tillage system compared with minimum tillage and conventional tillage on loam soil. Endogeic species were significantly more abundant in the no-tillage system compared with conventional system on loam soil. However when looking at the proportion of the endogeic species in the community (Fig. S5), the proportion of endogeic species was significantly lower under the no-tillage system compared with conventional tillage.

3.4. Relationships between earthworm communities, soil properties and management

Soil moisture and phosphorus content were significantly correlated to most of the parameters describing the earthworm community on

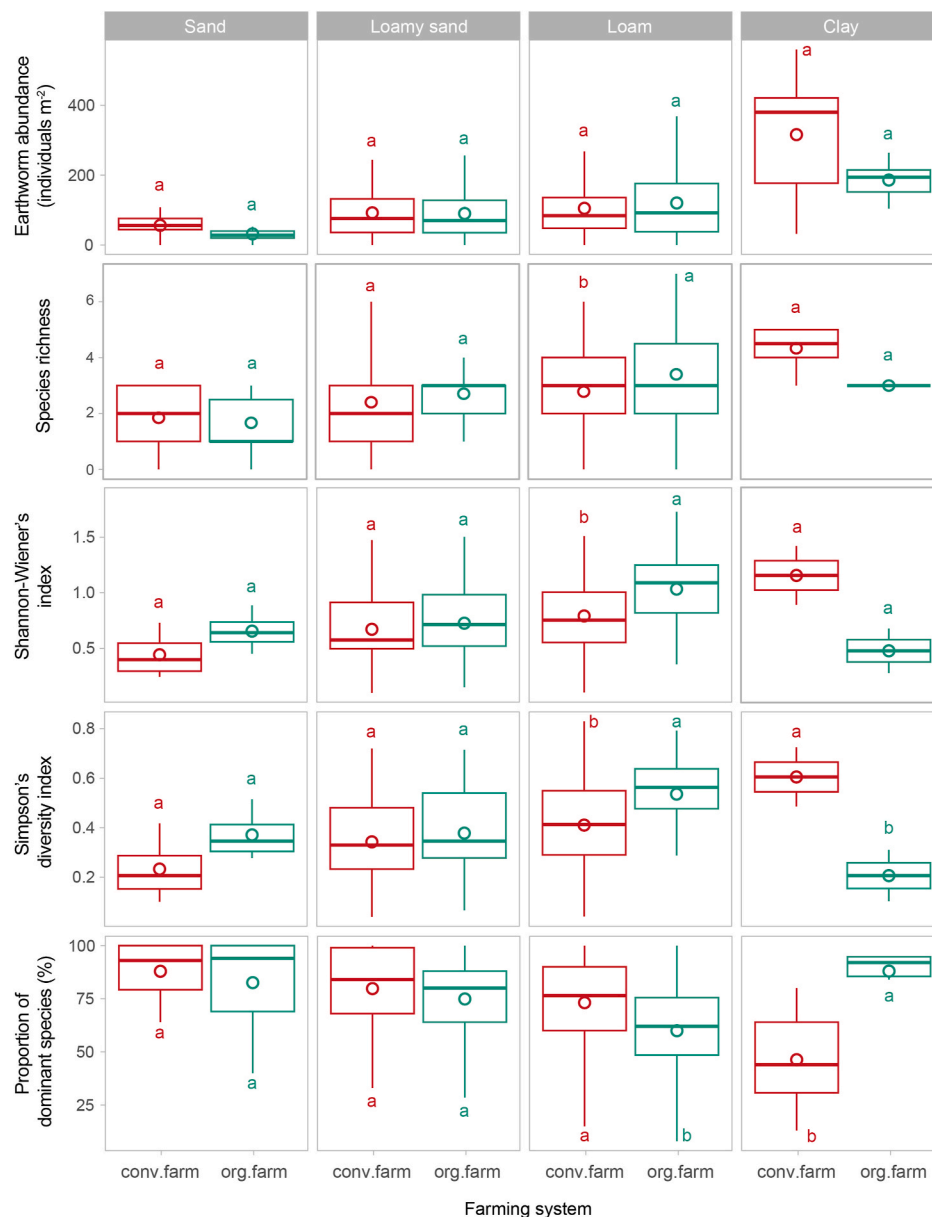


Fig. 4. Distribution of earthworm abundance, percentage of dominant species and diversity indexes across farming systems (conv.farm: conventional farming; org.farm: organic farming) within each soil texture class. The mean is represented with a circle. Different letters indicate significant differences ($p < 0.05$) according to a post-hoc Tukey HSD test.

Table 1

Mean (and standard error) earthworm community indices for the different farming systems. Different letters indicate significant differences ($p < 0.05$) according to a post-hoc Tukey HSD test.

	Conventional farming	Organic farming
Earthworm abundance, ind. m ⁻²	103.16 ± 4.83 ^a	104.64 ± 5.93 ^a
Species richness	2.65 ± 0.07 ^a	3.01 ± 0.1 ^b
Simpson's index	0.41 ± 0.02 ^a	0.46 ± 0.02 ^b
Shannon-Wiener index	0.80 ± 0.03 ^a	0.88 ± 0.04 ^b
Proportion of dominant species, %	75.43 ± 1.1 ^a	67.92 ± 1.43 ^b
Epigeic species, %	4.78 ± 0.53 ^a	6.84 ± 0.65 ^b
Endogeic species, %	88.41 ± 0.87 ^a	84.39 ± 1.08 ^b
Anecic species, %	6.81 ± 0.66 ^a	8.76 ± 0.89 ^b

arable fields (Fig. 7 and S6), while soil organic carbon and total nitrogen were the main controlling indicators related to species diversity and morpho-ecological community composition. Earthworm abundance was

positively correlated with soil moisture content ($\rho = 0.22$, $p < 0.001$) and in a negative relationship with soil pH ($\rho = -0.21$, $p = 0.002$) and phosphorus content ($\rho = -0.25$, $p < 0.001$). Biodiversity indexes were positively correlated with soil organic carbon (for Simpson's diversity index $\rho = 0.17$; $p = 0.010$; for Shannon's index $\rho = 0.19$, $p = 0.005$), total nitrogen (for Simpson's diversity index $\rho = 0.23$, $p < 0.001$; for Shannon's index $\rho = 0.24$, $p < 0.001$), pH ($\rho = 0.19$; $p = 0.006$) and soil moisture content (for Simpson's diversity index $\rho = 0.31$, $p < 0.001$; for Shannon's index $\rho = 0.33$, $p < 0.001$) and negatively with soil phosphorus content (for Simpson's diversity index $\rho = -0.30$; $p < 0.001$; for Shannon's index $\rho = -0.28$, $p < 0.001$). The NMDS analysis of earthworm abundance data did not show clear clustering of sites based on farming system (Fig. S7; $k = 2$, stress = 0.16); however, it revealed a slight differentiation between conventional tillage and no-tillage system. This trend was parallel with an increase in earthworm abundance. The main factors that grouped the no-tillage fields were species (i.e., *Ap. longa*, *L. rubellus*, and *L. terrestris*). Soil texture ($p = 0.001$), soil total

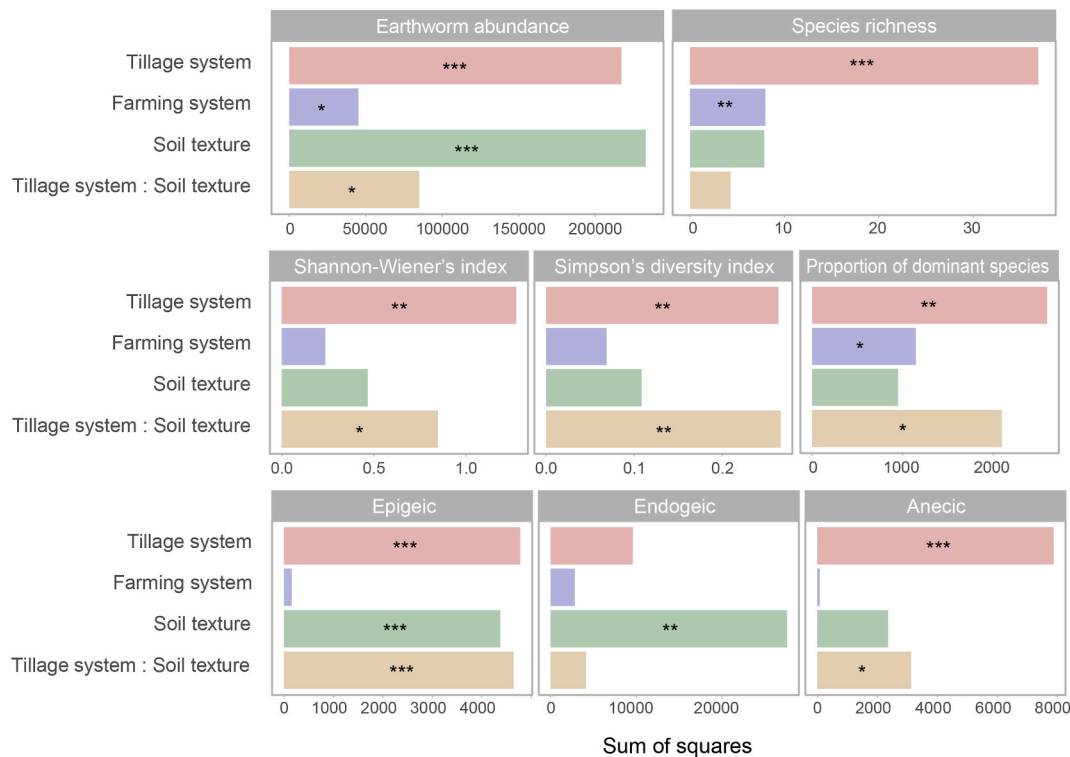


Fig. 5. The effects of tillage system, farming system, soil texture, and the interaction of tillage system and soil texture on earthworm community based on an analysis of variance (ANOVA) of the mixed effects model including these three factors. Significance levels are indicated as follows: *** $p < 0.001$, ** $p = 0.01$, * $p = 0.05$. A complete summary of the ANOVA output can be found in [Supplementary Table S5](#).

nitrogen ($p = 0.022$), soil pH ($p = 0.046$) and plant available phosphorus content ($p = 0.001$) were significant soil factors. Regardless of management, these data suggest that some species were sensitive to a very fine or coarse soil texture (Table S4, Table S7), as *L. terrestris* was rare and *Ap. longa* was absent in both soil texture classes and *L. castaneus* and *A. chlorotica* were absent only in sandy soils.

4. Discussion

4.1. The effect of farming system on earthworm communities

Earthworm abundance was not significantly different between conventional and organic farming systems. This supports the findings of previous studies [23,42] that the farming system had no clear effect on earthworm abundance or diversity. The contradictory findings for the effects of farming system on earthworms present in the literature might be related to differences in the use of organic amendments [23,42] and the possibility that responsible pesticide use does not have a harmful effect on earthworms [23]. Although the abundance was not significantly different between farming systems, we found that the diversity of earthworm species was higher under organic than under conventional farming, partially confirming our hypothesis. Several authors have found higher earthworm diversity in organic systems compared with conventional systems [8,14,43]. This could be because species such as *L. castaneus* and *A. chlorotica* are more common in organic systems as these species are known to be sensitive to pesticide use [44].

The endogeic species *Ap. caliginosa* was dominant in both farming systems across different texture classes, but their dominance was lower in organic farming than in conventional farming. Another possible explanation is that the high disturbance of earthworm habitat causes the community to shift towards a simpler composition. This community consists of only a few stress-tolerant species, mainly comprising *Ap. caliginosa* but also *Ap. rosea* and *L. rubellus* [8,45]. This suggests that, despite the similar earthworm numbers, the widespread adoption of

conventional farming system in Estonia could possibly lead to a slightly less diverse earthworm community, with a higher proportion of dominant species that are adapted to pesticides and other stressors.

Our results also suggest that the farming system had modified the morpho-ecological group composition of the earthworm community, since organic fields had a significantly higher proportion of epigeic and anecic species. This supports the results of Henneron et al. [46]. Epigeic and anecic species are likely to be the most sensitive to pesticide applications and other intensive agricultural operations since they feed mostly on plant litter [47]. Furthermore, the higher proportion of epigeic species in organic farming could be related to the potentially higher use of green and animal manure and more frequent inclusion of leys in crop rotations, increasing earthworm food supply and generally creating more favourable habitat conditions [47,48]. Since morpho-ecological groups of earthworms support different soil functions, lower proportions of epigeic and anecic species in conventional fields could also impact provision of the ecosystem services they support [49]. However, we found that on clay soils the proportion of epigeic species was relatively high on fields under conventional farming. This could be related to differences in soil tillage since tillage frequency can be higher on organic fields, as it is one of the main measures to fight weeds and plant pathogens.

4.2. The effect of tillage system on earthworm communities

The tillage system had a significant impact on both earthworm abundance and diversity, with higher abundance in less intensive tillage systems, confirming our hypothesis. No-tillage also had significantly higher diversity of earthworms. The means of diversity and the proportion of dominant species under no-tillage and minimum tillage followed the same trend when compared with conventional tillage; however, the differences were not significant, likely due to the high variability in these fields. This agrees with previous studies that showed intensive tillage has a negative effect on earthworm communities [16,

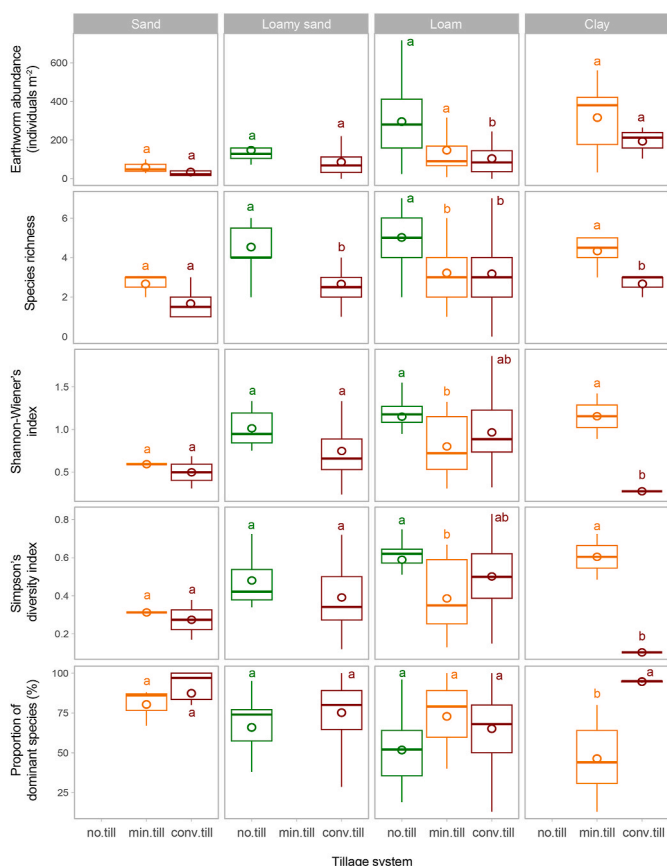


Fig. 6. Distribution of earthworm abundance, percentage of dominant species, and diversity indexes across tillage systems (conv.till: conventional tillage; min.till: minimum tillage; no.till: no-tillage) within texture class. Mean is represented with a circle. Different letters indicate significant differences ($p < 0.05$) according to a post-hoc Tukey HSD test.

18]. Besides injuring earthworms directly, tillage changes the habitat and relocates food sources. Furthermore, the layer of plant residues on no-tillage fields protects the soil from moisture loss during periods of drought [50], therefore also prolonging the period during which earthworms can be active and reproduce.

When examining the morpho-ecological groups of earthworms, we found that the proportion of epigeic species tended to be larger in less intensive tillage systems (with significant differences among tillage systems on clay soils) compared with conventional tillage. In addition, the proportion of anecic species was significantly higher on loam soil with no-tillage compared with minimum and conventional tillage. The main contributors to this finding were the epigeic species *L. rubellus* and the anecic species *Ap. longa* and *L. terrestris*, which tended to be more abundant under the no-tillage system. This agrees with the results of several authors who have found that reducing tillage intensity was beneficial, especially for the epigeics and anecics [18,51], mostly due to better food availability, but also likely because these morpho-ecological groups are the most vulnerable towards mechanical soil disturbance [52].

The accumulation of plant residues at the soil surface mainly benefits epigeic species and anecic species. However, some studies have associated a higher abundance of endogeic species, including the dominant species *Ap. caliginosa*, with the incorporation of plant residues under conventional tillage [53]. In these cases, conventional tillage is likely to have, increased the food availability for this morpho-ecological group that feed on soil organic matter by ingesting soil. Insufficient food resources could also partially explain the lower proportion of endogeic species in no-tillage fields, since it has been well documented that no-tillage does not always translate into a higher organic carbon stock compared with conventional tillage [54,55]. Therefore, the stratification of organic matter or higher soil density under no-tillage could potentially result in a shift in the proportions of the different earthworm morpho-ecological groups [53].

4.3. Earthworm communities and soil properties

It is well known that soil pH is one of the main soil factors influencing earthworm abundance and activity [56], and in general, earthworm abundance tends to increase with soil pH [57–59]. However, we found a



Fig. 7. Spearman's rank correlation analysis between earthworm community indices and soil properties. The vertical legend on the right indicates correlation coefficients, where blue is for positive and red for negative correlations. Parameters included are as follows: pH_{KCl} (pH), plant available soil phosphorous content (P), plant available soil potassium content (K), soil organic carbon (C_{org}), soil total nitrogen content (N_{tot}). Empty circles indicate non-significant correlations. Significance levels are indicated as follows: ***p < 0.001, **p < 0.01, *p < 0.05.

negative correlation between earthworm abundance and soil pH when looking at the associations of the indicators throughout the whole dataset (Fig. 7). Moreover, as shown in the NMDS analysis (Fig. S7), pH was a significant factor determining species composition. In an extensive global meta-analysis, Briones et al. [18] similarly found higher earthworm numbers in the most acidic soils category with a pH below 5.5. The authors attributed this to higher organic matter accumulation in reduced tillage systems, which might result in soil acidification and explained that a lower pH might not have a detrimental effect on earthworms because the chemical bonding of organic substrates and clay particles can improve nutrient availability. Similarly, the negative relationship between earthworm abundance and soil phosphorus was probably not because of a causal relationship between the two parameters, but a consequence of differences in management. While the no-tillage system favoured large earthworm populations, the value of the soil phosphorus content and soil pH tended to be lower on these fields (Fig. S8), leading to this negative relationship.

Soil texture was a major factor determining earthworm communities on Estonian arable fields. The overall mean earthworm abundance and diversity tended to increase, and the proportion of dominant species reduced towards finer soil texture. This was likely because of the higher water-holding capacity [60] and organic matter content [61] in fine-textured soils, which provided food sources and better habitat conditions for earthworms supporting large and diverse earthworm communities [62]. This supported the results of the correlation analysis, which showed that soils with higher organic carbon and total nitrogen content had higher earthworm diversity, a lower proportion of the dominant species, and a higher proportion of epigeic species in the community. Therefore, the relationships between soil properties and the earthworm community can also be largely attributed to the effect of soil texture, since fine-textured soils are able to store and protect more organic carbon and nitrogen [63]. Anecic species were observed to be sensitive to soil texture as they were almost absent in very coarse and fine-textured arable soils. This could be related to moisture dynamics as fine-textured soils are more prone to periods of waterlogging and compaction, leading to anaerobic conditions [64]. Epigeic species *L. castaneus* and endogeic *A. chlorotica* were absent in coarse-textured soils as they are known to be more sensitive to drier conditions [56,65,66].

Differences in earthworm community parameters between contrasting farming systems tended to increase as soil texture became finer, suggesting that the ecological tolerance of agricultural activity in the earthworm community can vary with soil texture. Although it was not possible to compare all the combinations of tillage systems and soil texture, we noticed that, similarly to the trend observed for farming system, the differences in earthworm abundance between less intensive (no-tillage or minimum tillage) and conventional tillage increased as the soil texture became finer. This supports the findings of Briones et al. [18] and Joschko et al. [67], that the earthworm community benefits from reducing soil tillage more notably in fine-textured soils. The more pronounced response of the earthworm population to differences in management in fine-textured soils could be related to the interaction between soil texture and management and the differences in community composition of earthworms. Soil physical properties are more responsive to tillage systems in fine-textured soils [50], which could partly explain the significance of the interaction between soil texture and management and earthworm abundance/diversity. Moreover, earthworm communities are less diverse in sandy soils, consisting of only a few tolerant species, while finer soils are more likely to provide suitable habitat conditions for sensitive species [62]. It is also possible that in sandy soils, the effect of other management practices such as crop rotation [59] or other soil properties might have a greater influence on earthworm communities than tillage or farming system.

5. Conclusions

This study combined data from multiple studies carried out within a

period of 21 years on Estonian arable fields. It was found that while differences in earthworm communities between organic and conventional farming were small, higher diversity, the proportion of epigeic and anecic species and lower proportion of the dominant species *Ap. caliginosa* suggest better ecological conditions under organic farming. Furthermore, the effect of farming systems on earthworm communities was different depending on soil texture, with larger differences in more fine-textured soil classes. A similar trend was observed when comparing fields with different tillage systems, in which differences between the tillage systems increased towards heavier textured soils. No-tillage fields had higher earthworm abundance, species richness and proportion of anecic species in the community indicating favourable habitat conditions compared to other tillage systems. Comparing the effect of management practice across different soil texture classes revealed the resilience of earthworms to agricultural activity, implying that the effects of farming and tillage systems on the earthworm community is dominated by soil texture. Therefore, our results emphasize the importance of including different soil texture classes in future monitoring schemes that use earthworms as bioindicators when assessing the land management conservation efforts as the earthworm community in some areas might be less resilient towards intensive management systems.

CRediT authorship contribution statement

Merit Sutri: Writing – review & editing, Writing – original draft, Visualization, Data curation, Conceptualization, Formal analysis, Investigation, Methodology, Project administration. **Mari Ivask:** Writing – review & editing, Supervision, Investigation, Data curation, Conceptualization, Funding acquisition, Methodology, Project administration, Resources. **Annely Kuu:** Writing – review & editing, Data curation, Conceptualization, Investigation, Methodology, Project administration, Supervision. **Jordi Escuer-Gatius:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation, Conceptualization, Supervision. **Endla Reintam:** Writing – review & editing, Supervision. **Merrit Shanskiy:** Writing – review & editing, Supervision, Conceptualization, Investigation, Project administration, Resources.

Declaration of competing interest

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

Data availability

The authors do not have permission to share data.

Acknowledgements

The data used for this research originates from the following research projects/survey programmes: National Environmental Monitoring Programme of Estonia (Estonian Environment Agency), monitoring for Estonian Rural Development Plan, Estonian Science Foundation Grant No. 5571 and European Union's Horizon 2020 project SoilDiverAgro (Grant No 817819). This research was partly funded by European Union's Horizon 2020 project SoilDiverAgro (Grant No 817819).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ejsobi.2024.103662>.

References

- [1] M.A. Tsiafouli, E. Thébault, S.P. Sgardelis, P.C. de Ruiter, W.H. van der Putten, K. Birkhofer, L. Hemerik, F.T. de Vries, R.D. Bardgett, M.V. Brady, L. Bjornlund, H. B. Jørgensen, S. Christensen, T.D. Hertefeldt, S. Hotes, W.H. Gera Hol, J. Frouz, M. Liiri, S.R. Mortimer, H. Setälä, J. Tzanopoulos, K. Uteseny, V. Pizil, J. Stary, V. Wolters, K. Hedlund, Intensive agriculture reduces soil biodiversity across Europe, *Glob Chang Biol* 21 (2015) 973–985, <https://doi.org/10.1111/gcb.12752>.
- [2] R.E. Creamer, J.M. Barel, G. Bongiorno, M.J. Zwetsloot, The life of soils: integrating the who and how of multifunctionality, *Soil Biol. Biochem.* 166 (2022) 108561, <https://doi.org/10.1016/j.soilbio.2022.108561>.
- [3] S. Fusaro, F. Gavinelli, F. Lazzarini, M.G. Paoletti, Soil Biological Quality Index based on earthworms (QBS-e). A new way to use earthworms as bioindicators in agroecosystems, *Ecol. Indic.* 93 (2018) 1276–1292, <https://doi.org/10.1016/j.ecolind.2018.06.007>.
- [4] M. Blouin, M.E. Hodson, E.A. Delgado, G. Baker, L. Brussaard, K.R. Butt, J. Dai, L. Dendooven, G. Peres, J.E. Tondoh, D. Cluzeau, J.-J. Brun, A review of earthworm impact on soil function and ecosystem services, *Eur. J. Soil Sci.* 64 (2013) 161–182, <https://doi.org/10.1111/ejss.12025>.
- [5] R. Zornoza, J.A. Acosta, F. Bastida, S.G. Domínguez, D.M. Toledo, A. Faz, Identification of sensitive indicators to assess the interrelationship between soil quality, management practices and human health, *SOIL* 1 (2015) 173–185, <https://doi.org/10.5194/soil-1-173-2015>.
- [6] M.G. Paoletti, The role of earthworms for assessment of sustainability and as bioindicators, *Agric. Ecosyst. Environ.* 74 (1999) 137–155, [https://doi.org/10.1016/S0167-8809\(99\)00034-1](https://doi.org/10.1016/S0167-8809(99)00034-1).
- [7] K. Sepp, M. Ivask, A. Kaasik, M. Mikik, A. Peepson, Soil biota indicators for monitoring the Estonian agri-environmental programme, *Agric. Ecosyst. Environ.* 108 (2005) 264–273, <https://doi.org/10.1016/j.agee.2005.02.007>.
- [8] M. Ivask, A. Kuu, E. Sizov, Abundance of earthworm species in Estonian arable soils, *Eur. J. Soil Biol.* 43 (2007) S39–S42, <https://doi.org/10.1016/j.ejsobi.2007.08.006>.
- [9] Z. Bai, T. Caspari, M.R. Gonzalez, N.H. Batjes, P. Mäder, E.K. Bünemann, R. de Goede, L. Brussaard, M. Xu, C.S.S. Ferreira, E. Reintam, H. Fan, R. Mihelić, M. Glavan, Z. Tóth, Effects of agricultural management practices on soil quality: a review of long-term experiments for Europe and China, *Agric. Ecosyst. Environ.* 265 (2018) 1–7, <https://doi.org/10.1016/j.agee.2018.05.028>.
- [10] D. Cluzeau, M. Guernion, R. Chaussois, F. Martin-Laurent, C. Villenave, J. Cortet, N. Ruiz-Camacho, C. Pernin, T. Mateille, L. Philippot, A. Bellido, L. Rougé, D. Arrauays, A. Bispo, G. Pérès, Integration of biodiversity in soil quality monitoring: baselines for microbial and soil fauna parameters for different land-use types, *Eur. J. Soil Biol.* 49 (2012) 63–72, <https://doi.org/10.1016/j.ejsobi.2011.11.003>.
- [11] M.B. Postma-Blaauw, R.G.M. de Goede, J. Bloem, J.H. Faber, L. Brussaard, Soil biota community structure and abundance under agricultural intensification and extensification, *Ecology* 91 (2010) 460–473, <https://doi.org/10.1890/09-0666.1>.
- [12] S.J. Crittenden, T. Eswaramurthy, R.G.M. de Goede, L. Brussaard, M.M. Puleman, Effect of tillage on earthworms over short- and medium-term in conventional and organic farming, *Appl. Soil Ecol.* 83 (2014) 140–148, <https://doi.org/10.1016/j.apsoil.2014.03.001>.
- [13] P. Maeder, A. Fliessbach, D. Dubois, L. Gunst, P. Fried, U. Niggli, Soil fertility and biodiversity in organic farming, *Science* 296 (2002) 1694–1697, <https://doi.org/10.1126/science.1071148>.
- [14] D.G. Hole, A.J. Perkins, J.D. Wilson, I.H. Alexander, P.V. Grice, A.D. Evans, Does organic farming benefit biodiversity? *Biol. Conserv.* 122 (2005) 113–130, <https://doi.org/10.1016/j.biocon.2004.07.018>.
- [15] I. Dekemati, B. Simon, S. Vinogradov, M. Birkás, The effects of various tillage treatments on soil physical properties, earthworm abundance and crop yield in Hungary, *Soil Tillage Res.* 194 (2019) 104334, <https://doi.org/10.1016/j.still.2019.104334>.
- [16] K.Y. Chan, An overview of some tillage impacts on earthworm population abundance and diversity — implications for functioning in soils, *Soil Tillage Res.* 57 (2001) 179–191, [https://doi.org/10.1016/S0167-1987\(00\)00173-2](https://doi.org/10.1016/S0167-1987(00)00173-2).
- [17] K.A. Torppa, A.R. Taylor, Alternative combinations of tillage practices and crop rotations can foster earthworm density and bioturbation, *Appl. Soil Ecol.* 175 (2022) 104460, <https://doi.org/10.1016/j.apsoil.2022.104460>.
- [18] M.J.I. Briones, O. Schmidt, Conventional tillage decreases the abundance and biomass of earthworms and alters their community structure in a global meta-analysis, *Glob Chang Biol* 23 (2017) 4396–4419, <https://doi.org/10.1111/gcb.13744>.
- [19] J. Bijttebier, G. Ruyschaert, R. Hijbeek, M. Werner, A.A. Pronk, L. Zavattaro, L. Bechini, C. Grignani, H. ten Berge, F. Marchand, E. Wauters, Adoption of non-inversion tillage across Europe: use of a behavioural approach in understanding decision making of farmers, *Land Use Pol.* 78 (2018) 460–471, <https://doi.org/10.1016/j.landusepol.2018.05.044>.
- [20] M. Sutri, M. Shanskiy, M. Ivask, E. Reintam, The assessment of soil quality in contrasting land-use and tillage systems on farm fields with stagnic luvisol soil in Estonia, *Agriculture* 12 (2022) 2149, <https://doi.org/10.3390/agriculture12122149>.
- [21] V. Nuutinen, Earthworm community response to tillage and residue management on different soil types in southern Finland, *Soil Tillage Res.* 23 (1992) 221–239, [https://doi.org/10.1016/0167-1987\(92\)90102-H](https://doi.org/10.1016/0167-1987(92)90102-H).
- [22] M. Nieminen, E. Ketoja, J. Mikola, J. Terhivuo, T. Sirén, V. Nuutinen, Local land use effects and regional environmental limits on earthworm communities in Finnish arable landscapes, *Ecol. Appl.* 21 (2011) 3162–3177, <https://doi.org/10.1890/10-1801.1>.
- [23] C. Pelosi, M. Bertrand, J. Roger-Estrade, Earthworm community in conventional, organic and direct seeding with living mulch cropping systems, *Agron. Sustain. Dev.* 29 (2009) 287–295, <https://doi.org/10.1051/agro/2008069>.
- [24] Land Board, Estonian Soil Map, (n.d.). <https://geoportaal.maaamet.ee/eng/Spatial-Data/Estonian-Soil-Map-p316.html> (accessed October 25, 2023).
- [25] E. Meyer, *Methods in soil biology*, in: Springer Lab Manual, Springer, Berlin, Heidelberg, 1996.
- [26] O. Graff, *Regenwürmer Deutschlands. Aus dem Institut für Humuswirtschaft der Forschungsanstalt für Landwirtschaft Braunschweig, Völknerode, Hannover, 1953.* Verlag M. & H. Schaper.
- [27] T. Timm, *A Guide to the Estonian Annelida, Looduseuurija Käsiraamatud 1, Eesti Looduseuurijate Seltsi Väljaanne, Teaduste Akadeemia Kirjastus, Tartu-Tallinn, 1999.*
- [28] M.B. Bouché, Soil organisms as components of ecosystems, in: U. Lohm, T. Persson (Eds.), *Ecological Bulletin, Ecological Bulletin, Stockholm, 1977*, pp. 122–132.
- [29] M.O. Hill, Diversity and evenness: a unifying notation and its consequences, *Ecology* 54 (1973) 427–432, <https://doi.org/10.2307/1934352>.
- [30] J. Oksanen, *Vegan: ecological diversity*, 1–12, <https://cran.r-project.org/web/packages/vegan/vignettes/diversity-vegan.pdf>, 2022. (Accessed 19 October 2023).
- [31] R Core Team, *R: a Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, 2016.
- [32] D. Bates, M. Maechler, B. Bolker, S. Walker, R.H.B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, J. Fox, A. Bauer, P.N. Krivitsky, *Linear Mixed-Effects Models Using “Eigen” and S4*, 2023.
- [33] R.V. Lenth, B. Bolker, P. Buurker, I. Giné-Vázquez, M. Herve, M. Jung, J. Love, F. Miguez, H. Riebl, H. Singmann, *Estimated Marginal Means, Aka Least-Squares Means*, 2023.
- [34] J.W. Tukey, *Exploratory Data Analysis*, 1977.
- [35] C. Csuzdi, C.-H. Chang, T. Pavlíček, T. Szederjesi, D. Esopi, K. Szlávecz, Molecular phylogeny and systematics of native North American lumbricid earthworms (Clitellata: megadrillii), *PLoS One* 12 (2017) e0181504, <https://doi.org/10.1371/journal.pone.0181504>.
- [36] M. Ivask, J. Truu, A. Kuu, M. Truu, A. Leito, Earthworm communities of flooded grasslands in Matsalu, Estonia, *Eur. J. Soil Biol.* 43 (2007) 71–76, <https://doi.org/10.1016/j.ejsobi.2006.09.009>.
- [37] M. Ivask, M. Meriste, A. Kuu, S. Kutti, E. Sizov, Effect of flooding by fresh and brackish water on earthworm communities along Matsalu Bay and the Kasari River, *Eur. J. Soil Biol.* 53 (2012) 11–15, <https://doi.org/10.1016/j.ejsobi.2012.08.001>.
- [38] M. Ivask, A. Kuu, J. Truu, S. Kutti, M. Meriste, J. Raamets, Earthworm communities in soils of Estonian wooded meadows, *Balt. For.* 18 (2012) 111–118.
- [39] M. Ivask, J. Truu, K. Lõhmus, M. Truu, I. Ostonen, Earthworm lumbricidae community in alder and aspen forest: three case studies, *Balt. For.* 6 (2000) 74–77.
- [40] M. Ivask, J. Truu, M. Truu, K. Lõhmus, I. Ostonen, The earthworm communities and microbial activities in coniferous forests of Estonia, *Balt. For.* 5 (1999) 32–36.
- [41] A. Kuu, M. Ivask, Distribution of octolasion cyaneum (savigny, 1826) in Estonia 1993–2008, *Zool. Middle East* 51 (2010) 75–81, <https://doi.org/10.1080/09397140.2010.10638460>.
- [42] V. Nuutinen, J. Haukka, Conventional and organic cropping systems at Suitia VII: earthworms, *Agric. Food Sci.* 62 (1990) 357–367, <https://doi.org/10.23986/afsci.72910>.
- [43] A. Flohre, M. Rudnick, G. Traser, T. Tschardtke, T. Eggers, Does soil biota benefit from organic farming in complex vs. simple landscapes? *Agric. Ecosyst. Environ.* 141 (2011) 210–214, <https://doi.org/10.1016/j.agee.2011.02.032>.
- [44] C. Pelosi, L. Toutous, F. Chiron, F. Dubs, M. Hedde, A. Muratet, J.-F. Ponge, S. Salmon, D. Makowski, Reduction of pesticide use can increase earthworm populations in wheat crops in a European temperate region, *Agric. Ecosyst. Environ.* 181 (2013) 223–230, <https://doi.org/10.1016/j.agee.2013.10.003>.
- [45] M. Ivask, A. Kuu, M. Meriste, J. Truu, M. Truu, V. Vaater, Invertebrate communities (Annelida and epigeic fauna) in three types of Estonian cultivated soils, *Eur. J. Soil Biol.* 44 (2008) 532–540, <https://doi.org/10.1016/j.ejsobi.2008.09.005>.
- [46] L. Henneron, L. Bernard, M. Hedde, C. Pelosi, C. Villenave, C. Chenu, M. Bertrand, C. Girardin, E. Blanchart, Fourteen years of evidence for positive effects of conservation agriculture and organic farming on soil life, *Agron. Sustain. Dev.* 35 (2015) 169–181, <https://doi.org/10.1007/s13593-014-0215-8>.
- [47] C. Pelosi, S. Barot, Y. Capowiez, M. Hedde, F. Vandenbulcke, Pesticides and earthworms. A review, *Agron. Sustain. Dev.* 34 (2014) 199–228, <https://doi.org/10.1007/s13593-013-0151-z>.
- [48] M. Bertrand, S. Barot, M. Blouin, J. Whalen, T. de Oliveira, J. Roger-Estrade, Earthworm services for cropping systems. A review, *Agron. Sustain. Dev.* 35 (2015) 553–567, <https://doi.org/10.1007/s13593-014-0269-7>.
- [49] H.J. Escudero, A. Domínguez, J.C. Bedano, Large-scale ecologically-based farming systems foster earthworm communities and their contribution to ecosystem processes, *Appl. Soil Ecol.* 185 (2023) 104800, <https://doi.org/10.1016/j.apsoil.2022.104800>.
- [50] H. Blanco-Canqui, S.J. Ruis, No-tillage and soil physical environment, *Geoderma* 326 (2018) 164–200, <https://doi.org/10.1016/j.geoderma.2018.03.011>.
- [51] C. Pelosi, B. Pey, M. Hedde, G. Caro, Y. Capowiez, M. Guernion, J. Peigné, D. Piron, M. Bertrand, D. Cluzeau, Reducing tillage in cultivated fields increases earthworm functional diversity, *Appl. Soil Ecol.* 83 (2014) 79–87, <https://doi.org/10.1016/j.apsoil.2013.10.005>.
- [52] C.A. Edwards, J.R. Lofly, The effect of direct drilling and minimal cultivation on earthworm populations, *J. Appl. Ecol.* 19 (1982) 723, <https://doi.org/10.2307/2403277>.

- [53] G. Ernst, C. Emmerling, Impact of five different tillage systems on soil organic carbon content and the density, biomass, and community composition of earthworms after a ten year period, *Eur. J. Soil Biol.* 45 (2009) 247–251, <https://doi.org/10.1016/j.ejsobi.2009.02.002>.
- [54] S. Hermle, T. Anken, J. Leifeld, P. Weiskopf, The effect of the tillage system on soil organic carbon content under moist, cold-temperate conditions, *Soil Tillage Res.* 98 (2008) 94–105, <https://doi.org/10.1016/j.still.2007.10.010>.
- [55] I. Martínez, A. Chervet, P. Weiskopf, W.G. Sturny, A. Etana, M. Stettler, J. Forkman, T. Keller, Two decades of no-till in the Oberacker long-term field experiment: Part I. Crop yield, soil organic carbon and nutrient distribution in the soil profile, *Soil Tillage Res.* 163 (2016) 141–151, <https://doi.org/10.1016/j.still.2016.05.021>.
- [56] C.A. Edwards, P.J. Bohlen, *Biology and Ecology of Earthworms*, third ed., Chapman & Hall, London, 1996.
- [57] H.M. McCallum, J.D. Wilson, D. Beaumont, R. Sheldon, M.G. O'Brien, K.J. Park, A role for liming as a conservation intervention? Earthworm abundance is associated with higher soil pH and foraging activity of a threatened shorebird in upland grasslands, *Agric. Ecosyst. Environ.* 223 (2016) 182–189, <https://doi.org/10.1016/j.agee.2016.03.005>.
- [58] K. Hoeffner, M. Santonja, C. Monard, L. Barbe, M. Le Moing, D. Cluzeau, Soil properties, grassland management, and landscape diversity drive the assembly of earthworm communities in temperate grasslands, *Pedosphere* 31 (2021) 375–383, [https://doi.org/10.1016/S1002-0160\(20\)60020-0](https://doi.org/10.1016/S1002-0160(20)60020-0).
- [59] M. Joschko, C.A. Fox, P. Lentzsch, J. Kiesel, W. Hierold, S. Krück, J. Timmer, Spatial analysis of earthworm biodiversity at the regional scale, *Agric. Ecosyst. Environ.* 112 (2006) 367–380, <https://doi.org/10.1016/j.agee.2005.08.026>.
- [60] Z. Libohova, C. Seybold, D. Wysocki, S. Wills, P. Schoeneberger, C. Williams, D. Lindbo, D. Stott, P.R. Owens, Reevaluating the effects of soil organic matter and other properties on available water-holding capacity using the National Cooperative Soil Survey Characterization Database, *J. Soil Water Conserv.* 73 (2018) 411–421, <https://doi.org/10.2489/jswc.73.4.411>.
- [61] B. Sarkar, M. Singh, S. Mandal, G.J. Churchman, N.S. Bolan, Clay minerals—organic matter interactions in relation to carbon stabilization in soils, in: *The Future of Soil Carbon*, Elsevier, 2018, pp. 71–86, <https://doi.org/10.1016/B978-0-12-811687-6.00003-1>.
- [62] S. Krück, M. Joschko, R. Schultz-Sternberg, B. Kroschewski, J. Tessmann, A classification scheme for earthworm populations (*Lumbricidae*) in cultivated agricultural soils in Brandenburg, Germany, *J. Plant Nutr. Soil Sci.* 169 (2006) 651–660, <https://doi.org/10.1002/jpln.200521903>.
- [63] G.S. Richardson, M.D. Ruark, T. Radatz, A. Radatz, E. Cooley, E.M. Silva, A. J. Augarten, J. Zhu, C.H. Zegler, The influence of inherent soil factors and agricultural management on soil organic matter, *Ecosphere* 14 (2023), <https://doi.org/10.1002/ecs2.4459>.
- [64] N. Plum, Terrestrial invertebrates in flooded grassland: a literature review, *Wetlands* 25 (2005) 721–737, [https://doi.org/10.1672/0277-5212\(2005\)025\[0721:TIIFGA\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2005)025[0721:TIIFGA]2.0.CO;2).
- [65] M. Ivask, J. Truu, The relationship of Estonian earthworms to local habitat and soil factors, *Pedobiologia* 42 (1998) 378–384.
- [66] C.N. Lowe, K.R. Butt, Life-cycle traits of the dimorphic earthworm species *Allolobophora chlorotica* (Savigny, 1826) under controlled laboratory conditions, *Biol. Fertil. Soils* 43 (2007) 495–499, <https://doi.org/10.1007/s00374-006-0154-x>.
- [67] M. Joschko, R. Gebbers, D. Barkusky, J. Rogasik, W. Hohn, W. Hierold, C. Fox, J. Timmer, Location-dependency of earthworm response to reduced tillage on sandy soil, *Soil Tillage Res.* 102 (2009) 55–66, <https://doi.org/10.1016/j.still.2008.07.023>.