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A preliminary study of the effects of long-term potato monoculture on earthworm community

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Abstract
Earthworms are widely recognized as ecosystem engineers because their activities significantly modify soil properties and ecosystem functioning. Earthworm community composition is primarily determined by soil characteristics, land use, and climate. In agro-ecosystems, earthworm populations are strongly affected by management practices, particularly tillage intensity, crop rotation schemes, and the application of various agrochemicals. The aim of the present study was to investigate the effects of intensive potato (*Solanum tuberosum*) cultivation on earthworm community structure and diversity. Earthworm samples were collected by hand-sorting from long-term potato monoculture farms subjected to ploughing and the application of pesticides, fungicides, herbicides, and chemical fertilizers, as well as semi-natural, non-agricultural habitats used as reference sites. A total of eight anecic, epigeic, and endogeic earthworm species belonging to the family Lumbricidae were identified in the semi-natural habitats, namely *Aporrectodea caliginosa*, *A. longa*, *A. trapezoides*, *Dendrobaena hortensis*, *D. pentheri*, *D. semitica*, *Eisenia andrei*, and *Perelia kaznakovi*. In contrast, only a single anecic species (*A. longa*) was recorded in potato fields. These results indicate that intensive agricultural activities have adversely affected the earthworm community in potato fields, leading to species loss by eliminating epigeic and endogeic earthworms.

Keywords: Fauna, *Androctonus*, taxonomy, morphology, Azarbaijan, Iran.

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INTRODUCTION

Earthworms are recognized as ecosystem engineers due to their significant impact on soil biota, structure, and chemical properties. Consequently, earthworm abundance, biomass, and diversity have strong impacts on overall soil quality (Singh et al., 2021; Edwards & Arancon, 2022). Earthworms play a key role in improving soil structure and function through their burrowing and casting activities, which loosen the soil and enhance aeration. They also contribute to carbon and nutrient cycling through litter decomposition, support the maintenance of soil microbial community, and promote both the chemical and biological fertility of the soil (Edwards & Arancon, 2022; Vidal et al., 2023).

Agricultural monoculture has become a defining feature of modern intensive farming, often leading to soil degradation and loss of biodiversity (Foley et al., 2011; Lal, 2015). Potato monoculture, in particular, is widely practiced due to the crop's economic value and global demand, yet long-term cultivation of a single crop can substantially alter soil structure, nutrient dynamics, and microbial activity (Larkin, 2015). Such changes directly affect soil-dwelling organisms, especially earthworms, which play

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key roles in nutrient cycling, soil aggregation, and overall soil health (Edwards & Arancon, 2022). Because earthworm communities are highly sensitive to management practices and shifts in soil conditions (Bogužas et al., 2022), understanding the ecological consequences of prolonged potato monoculture is critical. This preliminary study therefore examines how long-term potato monoculture influences earthworm community structure and abundance.

The composition of earthworm communities is strongly shaped by the availability of soil nutrients and prevailing climatic conditions, both of which determine habitat suitability and resource accessibility. In agro-ecosystems, a variety of factors can influence their population dynamics, including tillage, cropping sequence, geographical location, fertilizer overuse, and climate (Edwards & Arancon, 2022). Regarding farming practices, the majority of the studies have shown that organic farming improves soil organic matter and increases earthworm abundance, biomass, and species diversity compared to conventional farming (Hole et al., 2005; Flohre et al., 2011; Crittenden et al., 2014). Incorporating organic matter during ploughing may enhance food availability for endogeic earthworm species (Ernst & Emmerling, 2009; van Capelle et al., 2012). However, tillage remains a major cause of earthworm mortality, particularly for epigeic and anecic species (Briones & Schmidt, 2017). In addition, soil compaction resulting from certain farming practices can adversely affect earthworm communities (Capowiez et al., 2009).

Inorganic fertilizers can exert adverse effects on the environment and pose a significant threat to the long-term sustainability of agricultural systems (Zhou et al., 2013). Soil pH is reduced by the use of inorganic fertilizers (Zhou et al., 2013; Ngosong et al., 2020), which results in detrimental effects on earthworm populations (Ngosong et al., 2020). In contrast, organic farming systems promote biodiversity (Suthar, 2009), and earthworm abundance, biomass, and diversity increase in organic farmlands (Crittenden et al., 2014). Jin et al. (2022) further demonstrated that organic fertilizers may positively affect the microbial diet of certain species, especially endogeic and anecic earthworms.

Pesticide application has been shown to reduce earthworm abundance (Bart et al., 2018). The sensitivity of earthworms to pesticides varies among species and is closely related to the efficiency of their xenobiotic detoxification systems (Lu et al., 2017). Anecic and endogeic earthworms are generally less tolerant to pesticide exposure than epigeic species (e.g. *Eisenia* spp.) (Robinson et al., 2021).

In the present study, the effect of long-term potato (*Solanum tuberosum* L., 1753) monoculture on the earthworm communities in agricultural lands was investigated. Because monoculture has been practiced for a long time in the study area, it is likely that the composition of the earthworm community has been significantly altered, leading to reduced diversity and biomass in potato monoculture fields compared to semi-natural habitats.

MATERIAL AND METHODS

Study area

The experimental design included 15 potato agricultural lands and 15 semi-natural fields in Hamedan Province, Iran, in May 2023 (Fig. 1). For more than 20 years, the potato fields have been used exclusively for the cultivation of potatoes without any crop rotation. The soil type of the farmlands is silty loam. The fields are ploughed three times a year using heavy machinery. The potato-growing areas have been irrigated by rain for the past 10 years; prior to that, flooding was used for irrigation. Chemical and organic fertilizers, pesticides, fungicides, and herbicides have been used on these farmlands (Table 1).

The semi-natural habitats examined in this study were located in the vicinity of potato fields. The vegetation in these areas comprises grassy and bushy plants, including *Avena fatua*, *Chenopodium album*, *Cynodon dactylon*, *Descurainia sophia*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Fumaria officinalis*, *Hordeum murinum*, *Papaver rhoeas*, and *Portulaca oleracea*. These habitats have been impacted by human activities such as soil compaction, vegetation cutting, vegetation burning, and grazing by sheep.

The climate of the study area is temperate. The average annual precipitation and air temperature in the area are about 325 mm and 11.2 °C, respectively (Mosammam et al., 2016; Talebmorad et al., 2021).

TABLE 1. Application of agrochemicals in potato farmlands (based on interviews with farmers).

Agrochemical inputs	Application rate (per hectare)	Applications/year (time)	Application time
Fertilizers			
Arcta NPK fertilizer	3-5 L	1-2	Spring
Phosphate (granular)	100-150 Kg	1	Fall
Poultry manure	6-10 t	1	Fall
Sulo potash (granular)	5-10 Kg	2-4	Spring
Urea (granular)	50-100 Kg	2-3	Spring
Pesticides			
Carbaryl	1-2 Kg	2-3	Spring
Chlorpyrifos	1-2 L	1-3	Spring
Diazinon	1-1.5 L	1-2	Spring
Imidacloprid	1-1.5 L	1	Early Spring
Metam-sodium	100-200 L	1	Fall
Thiacloprid	0.1-0.2 L	1-2	Spring
Fungicides			
Chlorothalonil	1.5-2 Kg	2-3	Spring
Mancozeb	2-2.5 Kg	3-5	
Nordox	2.5-3 Kg	1-2	Spring
Prochloraz	0.5-0.75 L	2-3	Spring
Signum	0.75-1 Kg	2-3	Spring
Thiabendazole	0.75-1 Kg	1-2	Spring
Herbicides			
Metribuzin	0.5-1 Kg	1	Early Spring
Paraquat	1-2 L	1-2	Early Spring
Pendimethalin	1-1.5 L	1	Early Spring
Rimsulfuron	20-40 gr	1	Mid-Spring

Earthworm sampling

Earthworms were hand-sorted in the field from three randomly selected replicates using quadrats (50 × 50 × 25 cm deep). Quadrats were arranged at 10-meter intervals along transects in each sampling site, with the starting point randomly selected. To determine the starting point, each station was divided into 16 sections, and one of them was selected using a random number table. In the potato fields, transects began at least 20 meters from the field margins, while in the semi-natural habitat quadrats were positioned at least 5 meters from the agricultural lands (Bartz et al., 2024; Mittmannsgruber et al., 2025). Sampling was conducted on sunny days between 9 a.m. and 12 p.m., with air temperatures ranging from 17 to 23 °C. The earthworm specimens were transported back to the laboratory in cool boxes, and their fresh weight was immediately measured. Thereafter, three adult specimens of each species were fixed in 80% ethanol for identification, and the rest of the specimens were returned to the sampling sites. Species identification was done based on Latif et al. (2021). The ecological categories of the earthworms were determined according to Latif et al. (2016), Reynolds and Mýsýrlýoðlu (2018), and Bottinelli et al. (2020).

Statistical analyses

The density of earthworms was expressed as the number of individuals per square meter (ind. m^{-2}). Biomass was defined as the fresh weight of worms per square meter (g. m^{-2}). For each species, the rate of occurrence was calculated as the percentage of stations in which the species was present. Relative abundance was calculated as the proportion of individuals of a given species relative to the total number of individuals observed at each station. These two metrics were treated separately to capture different aspects of species distribution: presence/absence patterns and the distribution of individual numbers across stations.

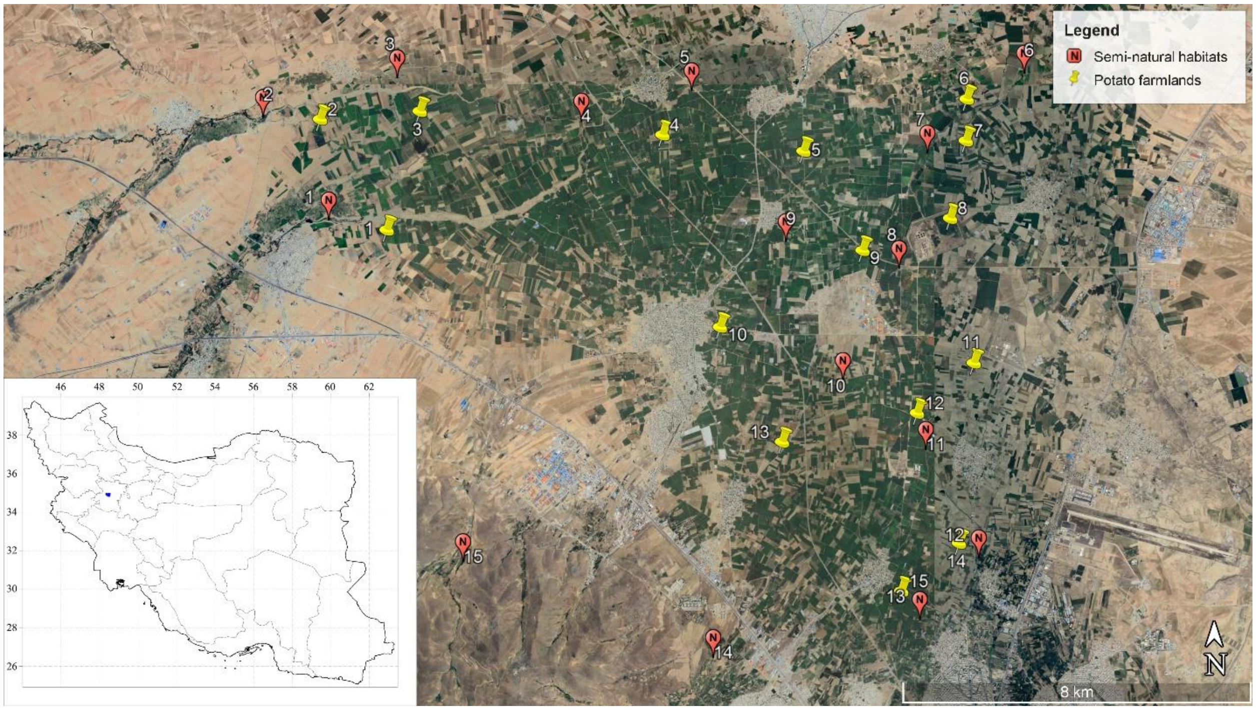

FIGURE. 1. Locations of sampling sites. Yellow markers indicate potato farms, and red markers indicate semi-natural habitats.

The Menhinick diversity index (D_{Mn}), Shannon-Wiener diversity index (H′), Simpson index (D), and Jaccard similarity index were used for biodiversity assessment (Singh et al., 2020).

Normality of variables was examined using the Kolmogorov-Smirnov test and the homogeneity of variances assessed using Levene's test. Independent-Samples t-test was used to compare earthworm abundance, weight, biomass, and diversity between agricultural and non-agricultural habitats (Student's t-test was applied when variances were equal, and Welch's t-test was used when variances were unequal). Kruskal-Wallis H test was conducted to detect differences among relative abundance and biomass, and Mann–Whitney U test was used for pairwise comparisons. Chi-square test (χ^2) was used to compare the distribution of species among stations. Data are presented as mean ± standard error (SE). Statistical analyses were performed using SPSS version 22 at a significance level of 0.05.

RESULTS

A total of eight earthworm species belonging to the family Lumbricidae were found at the semi-natural habitats, namely *Aporrectodea caliginosa* (Savigny, 1826), *A. longa* (Ude, 1885), *A. trapezoides* (Dugés, 1828), *Dendrobaena hortensis* (Michaelsen, 1890), *D. pentheri* (Rosa, 1905), *D. semitica* (Rosa 1893), *Eisenia andrei* Bouché, 1972 and *Perelia kaznakovi* (Michaelsen, 1910). In contrast, at the potato farmlands, only one species was observed: *A. longa*.

The total abundance of earthworms was very similar between the two land uses —agricultural and semi-natural habitats ($t = 1.513$, $df = 28$, $p = 0.141$), although it was slightly higher in the farmlands (19.20 ± 1.522 ind. m^{-2}) than in the non-agricultural habitats (16.27 ± 1.201 ind. m^{-2}). The abundance of different earthworm species was significantly different between treatments ($\chi^2 = 62.534$, $df = 8$, $p < 0.0005$). Specifically, the density of *A. longa* in agricultural lands was about six times higher than in semi-natural habitats, and this difference was statistically significant (pairwise Mann-Whitney U, $p < 0.0005$). Moreover, its density was also significantly higher than that of all other species (pairwise Mann-Whitney U, $p < 0.0005$). No statistically significant differences were found between densities per species in semi-natural habitats (Fig. 2 and Table 2).

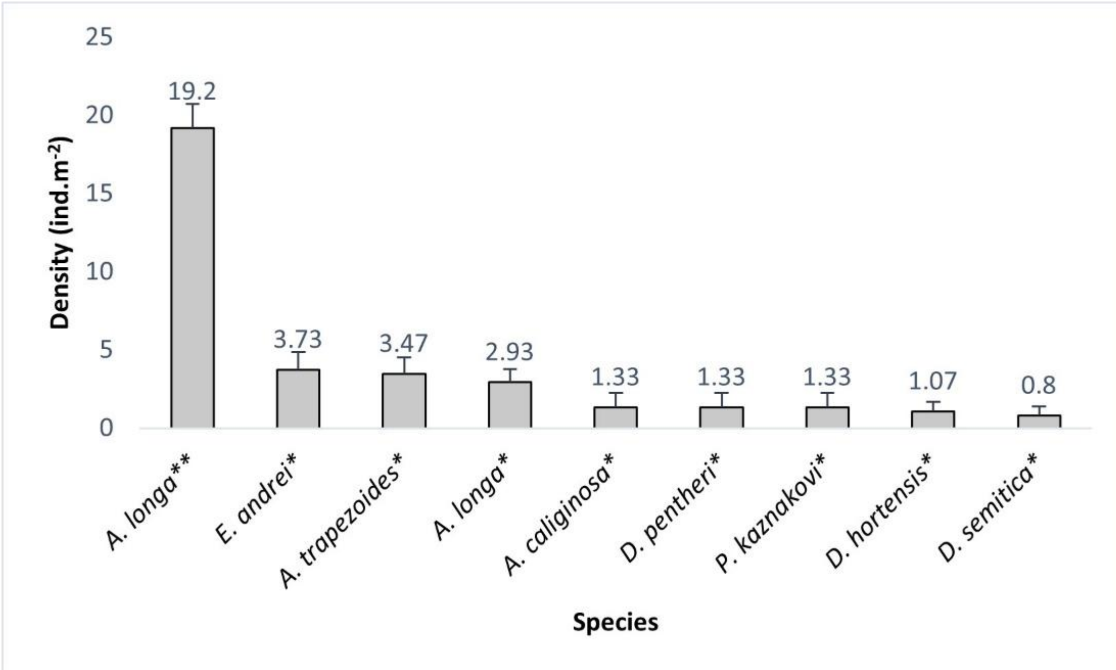

FIGURE. 2. Earthworm density per species in potato farmlands (**) and semi-natural (*) habitats. Data are presented as mean ± standard error (SE).

TABLE 2. Comparison of earthworm species densities among different stations.

Species	χ^2 (H)	df	p-value	η^2	Cohen's d	Effect Size Interpretation
A. longa	12.80	14	0.543	0.059	0.48	small-medium
A. caliginosa	18.00	14	0.210	0.084	0.42	small-medium
A. trapezoides	16.40	14	0.290	0.076	0.64	small-medium
D. hortensis	14.00	14	0.450	0.065	0.46	Small
D. pentheri	22.00	14	0.078	0.102	0.42	medium
D. semitica	20.00	14	0.130	0.093	0.38	small-medium
E. andrei	15.20	14	0.367	0.071	0.64	small-medium
P. kaznakovi	19.10	14	0.280	0.112	0.42	small-medium

In the semi-natural habitats, species composition (both the type and number of species, as well as the number of individuals of each species) varied among different stations. *A. longa*, *A. trapezoides*, and *E. andrei* occurred more frequently than other species at these atations (Fig. 3). The differences in the rate of species occurrence among stations were statistically significant ($\chi^2 = 91.551$, df = 7, $p < 0.0005$). These same three species also showed higher relative abundance in non-agricultural habitats compared to other species, although the pattern of abundance differed among stations (Fig. 4). The differences in relative abundance of species in non-agricultural habitats across stations were statistically significant ($\chi^2 = 30.535$, df = 7, $p < 0.0005$).

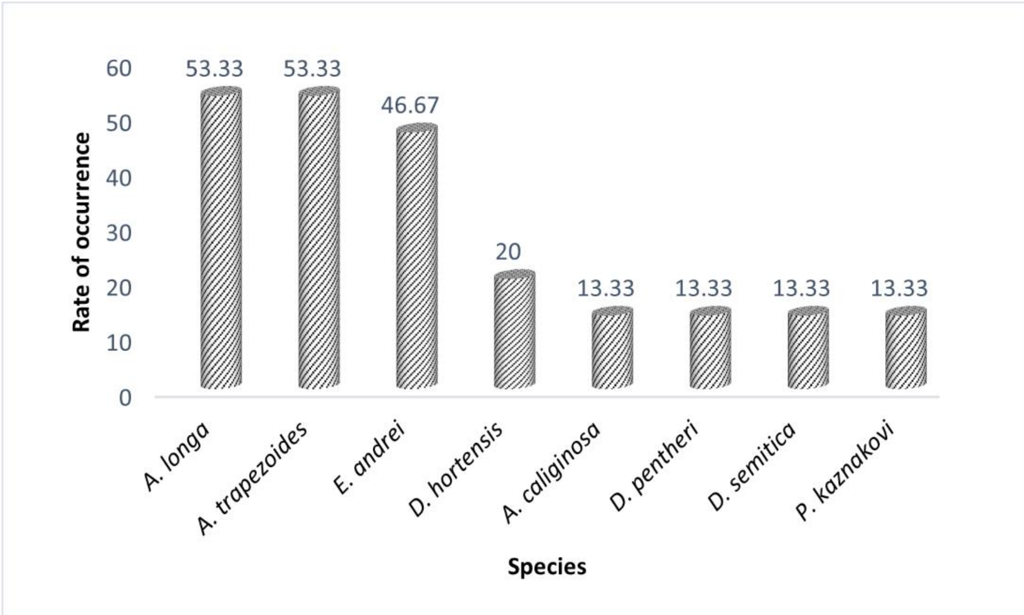

FIGURE 3. Rate of species occurrence in semi-natural stations.

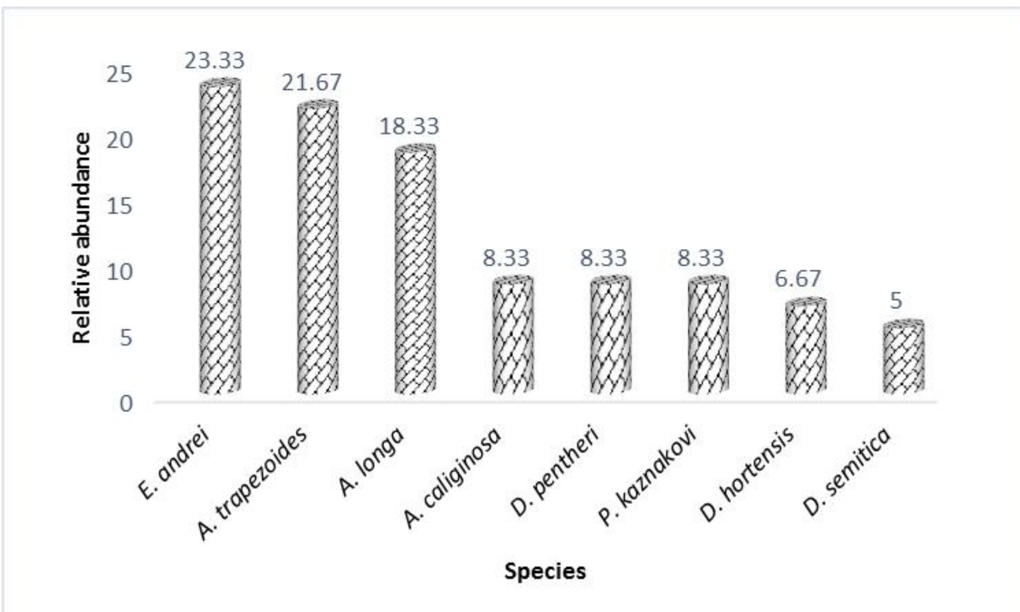

FIGURE 4. Relative abundance of species in semi-natural habitats.

The total biomass of earthworms in agricultural lands (82.15 ± 6.46 g. m^{-2}) was significantly higher than that of semi-natural habitats (28.16 ± 1.86 g. m^{-2}) ($t = 8.034$, $df = 16.294$, $p < 0.0005$). There was also a significant difference in relative biomass among the semi-natural habitats ($\chi^2 = 22.124$, $df = 7$, $p = 0.002$), with *A. longa* having the highest value, followed by *A. trapezoides* and *E. andrei*, respectively (Fig. 5). These three species differed significantly from each other and from other species. A significant difference ($t = 6.016$, $df = 14.504$, $P < 0.0005$) was also found in the mean fresh weight of *A. longa* between farmlands (4.28 ± 0.06 g) and non-agricultural habitats (3.43 ± 0.13 g).

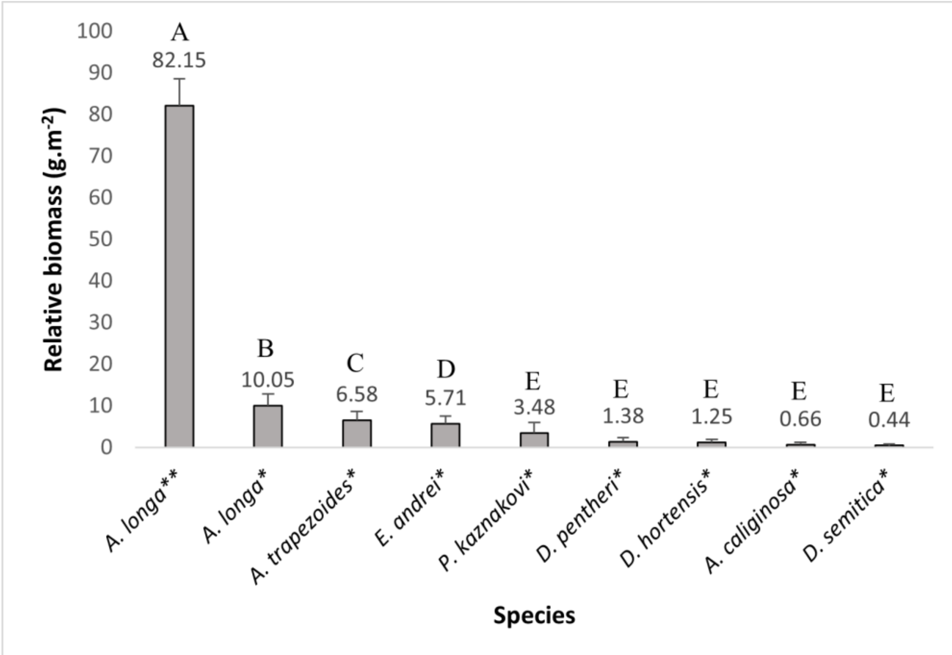

FIGURE 5. Species relative biomass in potato farmlands (**) and semi-natural (*) habitats. Data are presented as mean ± standard error (SE). Different letters above the bars indicate statistically significant difference at $p < 0.05$.

As shown in Table 3, biodiversity in potato fields is considerably lower than in semi-natural habitats, as indicated by Menhinick, Shannon-Wiener, and Simpson indices (0.24 vs 0.56, 0 vs 2.11, and 1 vs 0.48, respectively). Consequently, similarity between the two ecosystems is very low, as reflected by the Jaccard similarity index (0.11).

TABLE 3. Ecological indices for comparing biodiversity in semi-natural and agricultural habitats.

Ecological index	Mean ± SE		t/Z	df	p
	Potato fields	Semi-natural habitats			
Menhinick diversity index (D_{Mn})	0.24 ± 0.01	0.56 ± 0.04	-8.307	16.633	< 0.0005
Shannon-Wiener diversity index (H′)	0 ± 0	2.11 ± 0.34	-4.474	---	< 0.0005
Simpson diversity index (D)	1 ± 0	0.48 ± 0.06	-4.474	---	< 0.0005

DISCUSSION

In this study, four ecological categories of earthworms with a relatively even distribution were identified in non-agricultural environments: anecic (*A. longa*), endogeic (*P. kaznakovi*, *A. caliginosa*), epi-endogeic (*A. trapezoides*), and epigeic (*D. hortensis*, *D. pentheri*, *D. semitica*, *E. andrei*). In contrast, only the anecic species was found in the potato fields.

The single-species occurrence of *A. longa*, with higher density and biomass than in semi-natural habitats, observed in potato fields in this study is partly consistent with findings from other agricultural systems, where *A. longa* often dominates the anecic component of earthworm communities under intensive land use (Baker, 2002; Sutri et al., 2025). Several mechanisms may explain this pattern. As a deep-burrowing anecic species, *A. longa* can be partially buffered from short-term surface disturbances, including surface-applied agrochemicals and microclimatic extremes, reducing mortality relative to epigeic and endogeic species (Baker, 2002). Additionally, the species exhibits tolerance to various management regimes, including tillage and reduced organic-matter inputs, which often favor only a few resilient species in intensively managed soils (Sutri et al., 2025). The absence of other species in the potato fields has likely contributed to the increased abundance and biomass of *A. longa*, possibly due to reduced interspecific competition (Eriksen-Hamel & Whalen, 2007; Eijsackers, 2011). Because pesticide residues were not measured and species-specific toxicity tests were not conducted in this study, the relative contributions of these mechanisms cannot be determined. Future studies integrating residue analysis, laboratory toxicity assays, and comparative sampling across different management practices are therefore recommended to clarify whether pesticide tolerance, habitat suitability, or specific management practices drive the single-species occurrence of *A. longa* in this region.

In this study, natural habitats sustained a more diverse earthworm community —both in terms of species richness and ecological groupings —than intensively cultivated soils, as reflected in the diversity indices ($H' = 2.11 \pm 0.34$ vs. 0; $D_{Mn} = 0.56 \pm 0.04$ vs. 0.24 ± 0.01; $D = 0.48 \pm 0.06$ vs. 1.00, respectively). These values indicate that natural habitats support higher species richness and more even community structure, whereas cultivated soils exhibit extremely low diversity and complete dominance by a single species, highlighting the strong simplifying effect of intensive agricultural practices on earthworm communities.

A similar negative effect of potato cultivation systems on earthworms was observed by Curry et al. (2002) in silty loam to silty clay loam in Ireland. In their study, earthworm populations were almost eliminated from these agricultural lands within two years: five of the nine species disappeared during the first year after potato harvest, and three more were lost in the second year, leaving only a single species remaining, *Murchieona minuscula* (Rosa, 1906). The density of the remaining species in the second year after potato harvest was, however, higher than in the first year.

Important differences exist between the two studies. First, while Curry et al. (2002) monitored earthworm responses over a two-year period following the introduction of intensive potato cultivation, the potato fields in the present study have been subjected to more than 20 years of continuous monoculture without rotation, representing a much longer and more persistent disturbance regime. Second, soil management intensity at the study sites is substantially higher: fields are ploughed three times annually using heavy machinery and receive repeated inputs of fertilizers, pesticides, fungicides, and herbicides, whereas the Irish fields experienced intensive tillage primarily during potato establishment and mechanical harvesting. Finally, the climatic context differs markedly: Hamedan Province has a semi-arid temperate climate with an average annual precipitation of ~325 mm, whereas the Irish site has a temperate oceanic climate with 650–750 mm rainfall. These contrasts in long-term land use, management intensity, and climate likely contribute to the even stronger and more persistent reduction in earthworm diversity and abundance observed in the studied fields.

Although Curry et al. (2002) reported a slight rebound in the density of the single remaining species during the second year after potato harvest, the sampling design used here does not allow detection of comparable short-term fluctuations. Because earthworm sampling in the present study was conducted only once, in May, transient seasonal changes—whether increases or declines—may have occurred outside this sampling window. This temporal limitation is therefore acknowledged, and multi-season or multi-year sampling would be necessary to determine whether similar short-term recovery patterns occur in long-term potato monoculture systems. Future studies should incorporate repeated sampling across different seasons to capture potential temporal dynamics more accurately.

Furthermore, Buckerfield and Wiseman (1997) cropped pasture paddocks once and returned them to pasture. They applied sulphate of potash, lime, NPK fertilizer (Nitrogen, Phosphorus, and Potassium), urea or ammonium nitrate, liquid nitrogen, fungicide, herbicide, insecticide, and trace elements S, Cu, Zn, and Mo to the cropping fields. In the paddocks cultivated with potatoes, the population of earthworms was halved compared to the pasture in the year immediately following potato cropping. However, in the second year, the earthworm community was similar in the cultivated and non-cultivated paddocks. According to the researchers, the increase in earthworm density two years after potato harvest may be attributed to fertilizer use (increasing soil organic matter) and lime application (raising soil pH).

Unlike the transient rebound observed by Buckerfield and Wiseman (1997) following short-term potato cultivation, earthworm populations in the long-term monoculture fields studied showed no signs of recovery. This persistent decline is likely driven by repeated tillage, continuous application of agrochemicals, and prolonged habitat simplification. Analyses of station-level heterogeneity confirmed that this pattern was consistent across all fields, with no significant deviations, highlighting the long-term negative effects of intensive management on earthworm communities.

Physicochemical factors (e.g., soil temperature, moisture, pH, inorganic salts, aeration, and texture) and food availability (herbage, litter composition, dung, consolidated organic matter) are known to influence earthworm community composition (Shakir & Dindal, 1997; Edwards & Arancon, 2022). However, these variables were not measured in the present study, and thus direct inference of their effects on the observed patterns is not possible. Future studies should include measurements of soil pH, organic matter, total nitrogen, available phosphorus and potassium, electrical conductivity, texture, and bulk density or penetration resistance to better understand their influence on earthworm communities.

The loss of diversity in the potato farmlands could be related to the findings of Lagerlöf et al. (2002) and Singh et al. (2016). They reported that declines in epigeic species diversity in farmland result from physical soil disturbances during ploughing and intensive pesticide use, as these species do not enter diapause under adverse conditions, leading to higher mortality during warm and dry periods. These authors also stated that the diversity of endogeic species in agricultural fields is reduced by heavy soil cultivation, which destroys their burrows. In the potato fields studied here, heavy machinery is used for harvesting and soil preparation, which can lead to soil compaction. This may contribute to restrictions on earthworm burrowing activity (Marinissen, 1992; Capowiez et al., 2012).

Soil nutrients are known to influence earthworm diversity (Edwards & Arancon, 2022); however, nutrient levels were not measured in this study, and future work should include such measurements to better interpret community differences. In potato farmlands, herbicides and fungicides are applied to control weeds and fungi, which may limit the diversity of plant litter inputs. By contrast, semi-natural habitats receive organic material from a wider variety of plants, particularly grasses. The observed differences between earthworm populations in these habitats may therefore be related to the quantity and quality of available food, depending on litter composition (Shakir & Dindal, 1997), although this remains a hypothesis that requires direct measurement of litter inputs.

Steroidal glycoalkaloids, which serve as chemical protectants against plant pathogens and herbivores, are commonly found in the Solanaceae plant family. In *Solanum tuberosum*, the main glycoalkaloids are α-solanine and α-chaconine, present in all plant parts at varying concentrations, with the highest levels in sprouts, followed by flowers, leaves, berries, and tubers. These compounds are released into the soil during plant senescence and through the decomposition of residues and leftover tubers after harvest. Although glycoalkaloid concentrations were not measured in the present study, their presence could potentially influence soil biota, including earthworms. Reported topsoil concentrations in potato fields suggest that glycoalkaloids are largely bound to organic matter. While data on annelid-specific toxicity remain limited, future studies should investigate whether the observed levels approach toxicity thresholds for earthworms (Jensen et al., 2009a; Jensen et al., 2009b; Milner et al., 2011).

Both α-solanine and α-chaconine are toxic to a wide range of organisms, including mollusks, amphibians, and mammals, particularly embryos and juveniles (Milner et al., 2011; Akiyama et al., 2021). The potential effects of these toxins on earthworm populations in potato fields remain untested, but they may represent one of several factors influencing community composition, alongside tillage, soil compaction, pesticide use, and soil moisture conditions. Even deep-dwelling anecic species such as *A. longa*, which feed at the soil surface, may be exposed to these compounds.

Another factor influencing earthworm survival is soil moisture (Edwards & Arancon, 2022). Moreover, ploughing at the appropriate time of year is crucial, as early-spring ploughing negatively affects earthworm populations, while autumn ploughing has comparatively little impact (Chan, 2001). In the potato fields examined here, ploughing occurs during harvest, and in many cases the fields are ploughed twice in summer to prepare the land for the following season. Although soil moisture was not measured, management records indicate that irrigation ceases after harvest, which may accelerate topsoil drying. Such conditions are known to be detrimental to earthworms (Marinissen, 1992), potentially placing epigeic and endogeic species at risk when humidity becomes insufficient. By contrast, anecic species such as *A. longa* can burrow down to 50 cm, enabling them to enter aestivation or quiescence during adverse periods (Lagerlöf et al., 2002; Jiménez & Decaëns, 2004; Singh et al., 2016).

Soil pH is a key determinant of earthworm community structure, as earthworms are highly sensitive to acidic conditions and are unable to persist below species-specific pH thresholds (Edwards & Arancon, 2022). Acidic soils—often associated with elevated concentrations of soluble metal ions—limit earthworm survival, feeding, and burrowing activity (Springett & Syers, 1984; Lagerlöf et al., 2002). Most species reach their highest abundances in near-neutral soils (Gerard & Hay, 1979; Nair et al., 2005; Stoscheck et al., 2012; Singh et al., 2016).

Within this general framework, species-specific tolerance thresholds become important for interpreting habitat-level patterns. The anecic species *A. longa* has an acid-tolerance threshold around pH 4.4–4.6, below which it is unable to burrow (Laverack, 1960; Baker & Whitby, 2003). Although *A. longa* generally prefers near-neutral soils (Bouché, 1972, as cited in Baker & Whitby, 2003), laboratory observations indicate relatively weak discrimination between soils of pH 4.5 and 7.0, with only slight avoidance of soils above pH 7.0 (Baker & Whitby, 2003). Its deep-burrowing lifestyle may further reduce exposure to acidity in surface layers compared to epigeic and endogeic species.

These physiological and ecological differences help contextualize the management practices in the potato fields examined in this study. Poultry manure and NPK fertilizers are commonly applied, together with fungicides, herbicides, and insecticides. Poultry manure—neutral to moderately alkaline (pH 6.9–8.0; Ravindran et al., 2017) and nutrient-rich (Burton et al., 2004)—is generally considered beneficial for earthworm populations (Ngosong et al., 2020). Nitrogen-rich amendments can enhance earthworm abundance, biomass, and cocoon production, and NPK fertilizers may increase biomass through elevated soil N and P availability (Shipitalo et al., 1988; Edwards & Arancon, 2022). However, these potentially positive nutrient-driven effects coexist with the well-documented acidifying influence of long-term inorganic nitrogen application, which can disadvantage epigeic and endogeic species (Haynes & Naidu, 1998; Timmerman et al., 2006; Ngosong et al., 2020). Accordingly, organic farming systems—where acidification pressures are lower—consistently show higher earthworm abundance, biomass, and diversity than conventional systems (Crittenden et al., 2014).

The earthworm patterns observed in the studied potato fields may therefore reflect the interplay of multiple, potentially opposing processes: nutrient enrichment from poultry manure and NPK, long-term soil acidification, species-specific pH tolerance, and functional-group differences in exposure pathways. While *A. longa* may be comparatively less affected by surface acidification and may benefit from nutrient inputs and deep organic matter placement, epigeic and endogeic species are likely to be more vulnerable. However, soil pH was not measured in this study; therefore, all pH-related interpretations should be considered provisional until field-specific measurements become available.

Chemical pesticides can disrupt enzyme activities, reduce fecundity and growth, alter behaviors such as feeding rate, and ultimately decrease the biomass and density of earthworm communities. Insecticides and fungicides, in particular, pose high toxicity risks by impairing survival and reproduction (Pelosi et al., 2013; Pelosi et al., 2014). Singh et al. (2016) reported high earthworm diversity in fields receiving low levels of inorganic pesticides and noted that burrowing earthworms are generally less directly affected by these chemicals. In the potato fields examined here, epigeic and endogeic species are likely more intensively exposed to pesticides due to their surface activity, whereas *A. longa*, as a deep-burrowing anecic species, may be less exposed, although surface feeding still brings them into contact with treated residues. Exposure pathways include contact with soil-active compounds and plant residues containing pesticides. According to our pesticide inventory (Table 1), the active ingredients commonly applied in these fields include carbaryl, chlorpyrifos, diazinon, imidacloprid, metam-sodium, and thiacloprid, which could differentially affect earthworm functional groups.

The findings of this study on the abundance and biomass of the large-bodied anecic species *A. longa* contradict previous reports on anecic earthworm populations in farmlands (e.g., Gerard & Hay, 1979; Edwards & Lofty, 1982; Capowiez et al., 2009; Ernst & Emmerling, 2009; De Oliveira et al., 2012; Crittenden et al., 2014; Briones & Schmidt, 2017). Wyss and Glasstetter (1992) reported that in minimally tilled cornfields, *A. longa* abundance exceeded that of endogeic species, whereas in conventionally tilled fields, endogeic species were abundant. In contrast, in the potato fields examined here, both the abundance and biomass of *A. longa* were higher than in adjacent semi-natural habitats (mean biomass difference: 53.99 g. m^{-2}, 95% CI: 40.23-67.76; mean fresh weight difference: 0.85 g, CI: 0.55-1.16; Welch's t-test was used for comparisons due to unequal variances). This conflict may be explained by several hypothesized mechanisms, including (i) the contribution of poultry manure, (ii) the absence of competing species, and (iii) the increased availability of food resulting from the burial of organic matter into deeper soil layers during ploughing. These hypotheses require targeted testing, such as measuring soil OM, N, P, and pH; quantifying bulk density, compaction, and the vertical distribution of organic matter; conducting microcosm experiments manipulating manure inputs; and applying community-level analyses (e.g., PERMANOVA, NMDS) to relate species composition to measured soil properties. An additional possibility is that the collapse of earthworm diversity may have reduced interspecific competition, allowing *A. longa* to attain higher biomass and body size even without substantial increases in absolute resource availability.

CONCLUSIONS

The study revealed a significant reduction in earthworm diversity in long-term monoculture potato fields compared to semi-natural habitats. This decline is likely attributable to intensive agricultural practices, including deep ploughing with heavy machinery during periods of earthworm vulnerability, as well as the application of chemical fertilizers, herbicides, fungicides, and pesticides.

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