Applied Soil Ecology 218 (2026) 106763

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Research paper

Intraspecific trait shift reflects earthworm response to land-use intensification in peat grasslands

Lianne C. Woudstra [a,*], Jacintha Ellers [a], Mariet M. Hefting [a], Taylor B. Craft [b,c], Matty P. Berg [a,b]

[a] Amsterdam Institute for Life and Environment (A-LIFE), Vrije Universiteit Amsterdam, De Boelelaan 1108, 1081, HZ, Amsterdam, the Netherlands
[b] Groningen Institute for Evolutionary Life Sciences (GELIFES), Groningen University, Nijenborgh 7, 9747, AG, Groningen, the Netherlands
[c] BirdEyes, Centre for Global Ecological Change at the Faculties of Science and Engineering and Campus Fryslân, University of Groningen, the Netherlands

ARTICLE INFO

Keywords:
Ecosystem engineer
Lumbricidae
Body size
Land use intensity
Productivity
Peat grassland

ABSTRACT

Peatland grasslands are ecologically valuable ecosystems that support biodiversity and provide key functions, such as carbon storage and water regulation. However, agricultural intensification can degrade these ecosystems by altering soil conditions and belowground communities. Earthworms, as important ecosystem engineers and prey for meadow birds, play a central role in soil processes and trophic interactions, yet their responses to land-use intensity in peat soils remain poorly understood. In this study, we examined how land management, soil physicochemical properties, and vegetation characteristics influence earthworm communities in 19 Dutch peat meadows. We assessed abundance, biomass, species richness, body size and species community composition in relation to land management variables and remote sensing indicators of land-use intensity (S2REP). Earthworm abundance and biomass increased with grass yield and S2REP, suggesting that more productive meadows support larger populations. Species richness, however, did not vary with land-use intensity. Average individual body size declined significantly under more intensive management, independent of juvenile proportions, indicating potential constraints on growth or condition. Communities were overall dominated by generalist, disturbance-tolerant species, while variation in species composition was more strongly linked to soil salinity than land-use intensity. Our findings show that land-use intensity primarily affects earthworm abundance and functional traits, particularly body size, rather than taxonomic diversity. These shifts may impact soil functioning and reduce the energetic value or accessibility of earthworms for meadow birds. Incorporating trait-based approaches alongside taxonomic assessments offers a more mechanistic understanding of how agricultural practices influence belowground biodiversity and ecosystem function in peatland grasslands.

1. Introduction

Peatlands are biodiversity hotspots, supporting specialized species communities adapted to their unique hydrological and nutrient conditions. Beyond their ecological distinctiveness, peatlands provide vital ecosystem services, including carbon sequestration, water regulation, and food production (Fluet-Chouinard et al., 2023; Lamers et al., 2015). Peatland ecosystems face mounting pressures from human activity and climate change. Their degradation, driven by land-use changes, agricultural intensification and urban expansion, poses severe environmental and ecological challenges (Fluet-Chouinard et al., 2023; UNEP, 2022). A major driver of peatland degradation is the drainage of peat soils, which accelerates peat oxidation, greenhouse gas emissions, and soil subsidence (Erkens et al., 2016). Furthermore, the widespread use of high amounts of manure and artificial fertilizers alters soil chemistry, increases nutrient runoff to surface water, and, along with excessive land use by heavy machinery, contributes to soil compaction (Batey, 2009; Luna Juncal et al., 2023; Rayne and Aula, 2020). The combination of these factors has resulted in a strong decline in biodiversity in peatlands, further diminishing the ecological integrity of peat meadows (Lamers et al., 2015).

Recognizing the challenges of maintaining peat grassland integrity, a range of restoration and regenerative agricultural practices are increasingly being adopted to reconcile conservation and land-use demands. These practices such as raising water tables, reducing livestock density, limiting nutrient inputs by applying manure, and modifying mowing regimes not only aim to reduce soil subsidence and greenhouse gas emissions, but also to shape favourable conditions for both

* Corresponding author.
E-mail address: l.c.woudstra@vu.nl (L.C. Woudstra).

https://doi.org/10.1016/j.apsoil.2025.106763
Received 19 June 2025; Received in revised form 22 December 2025; Accepted 24 December 2025
Available online 30 December 2025

aboveground and belowground biodiversity (Andersen et al., 2017; Girkin et al., 2023; Zak and McInnes, 2022). In Northwestern Europe, many peat meadows are managed extensively to support breeding populations of meadow birds, with policies that prioritize high water tables, low-input management, resulting in flower-rich meadows (Kleijn et al., 2004). While primarily designed to benefit bird species, such measures also affect soil conditions and belowground communities, particularly key invertebrates such as earthworms.

Earthworms (Lumbricidae) are key ecosystem engineers in soils, driving nutrient cycling, organic matter decomposition, and the formation of soil structure, which affects soil life via the creation of pores and the aeration of soils (Blouin et al., 2013; Pulleman et al., 2012). Through these processes, they also strongly influence plant production (van Groenigen et al., 2014). Simultaneously, earthworms serve as important bioindicators due to their sensitivity to land-use intensity and environmental change (Bartz et al., 2013; Pulleman et al., 2012). This dual role, as both biobuilders and bioindicators, places them at the centre in soil ecosystems. Moreover, as a major prey item for many meadow bird species, they form a crucial link between belowground biodiversity and aboveground higher trophic levels (Vickery et al., 2001).

Conventional agricultural practices, such as conventional tillage and monoculture cropping, typically reduce earthworm abundance and diversity (Briones and Schmidt, 2017). In clay soils, decline of earthworm communities are often associated with soil compaction and disruption of soil structure, whereas in sandy soils, reduced moisture retention and lower organic matter inputs make earthworm communities susceptible to land-use intensification (Bartz et al., 2013; Betancur-Corredor et al., 2024; Mamabolo et al., 2024). The effects of manure application on earthworm communities are variable. While manure can increase organic matter availability and serve as a food resource, positive effects on earthworm biomass and abundance appear to be species-specific and potentially favouring a limited number of responsive species (Curry et al., 2008; Murchie et al., 2015). The subsequent changes in community composition and trait expression may alter earthworm contributions to soil structure and nutrient cycling.

While responses of earthworms to land-use intensity are well documented in mineral soils (Didden, 2001; Hoeffner et al., 2024; Timmerman et al., 2006; Van Vliet and de Goede, 2006), it remains unclear whether the same patterns translate to peat soils, where high organic matter content and distinct hydrological conditions may alter key ecological drivers. In this study, we address this gap by examining how management of peat grasslands shapes soil properties and vegetation characteristics and how these factors jointly structure earthworm communities. Specifically, we assessed how key biodiversity metrics (species richness, abundance, biomass and functional traits) relate to variation in land management, soil conditions, and vegetation attributes, with a particular focus on body size as a functional trait linked to both soil structuring activity and trophic interactions. We hypothesise that low intensity management will be associated with higher earthworm abundance and species richness, particularly through improvements in soil moisture, physiochemical properties, and vegetation diversity. Although peat grassland soils in general contain high organic matter stocks (Schothorst, 1977), much of this material is poorly decomposed and of low nutritional quality for earthworms, which preferentially exploit microbially conditioned, nutrient-rich organic resources rather than bulk soil organic matter (Curry and Schmidt, 2007). Increased manure inputs under intensive management may therefore increase average earthworm body size via intraspecific growth responses to enhanced nutrient accessibility and/or interspecific turnover toward larger, more opportunistic and stress-tolerant taxa. By combining biodiversity metrics with trait-based responses, our study aims to provide a more nuanced understanding of how land-use practices shape belowground communities in peatland grasslands.

2. Methods

2.1. Study area

This study was conducted in the Vereenigde Binnenpolder near Spaarnwoude, the Netherlands (52.415° N, 4.711° E). The area is a lowland peat polder, characterized by grassland that is managed through an extensive system of ditches and dikes, where meadows within the polder were subject to water-level management by drainage (van der Aar, 1984). The Vereenigde Binnenpolder is typical of lowland peat areas used primarily for grassland-based agriculture, including dairy farming. The polder is located within a predominantly urbanized landscape (Atlas Leefomgeving, 2023). This peatland is classified as a minerotrophic (fen) peat (sedge-peat with reed) polder (Bodemdata, n.d.; van 't Veer, 2022).

A total of 19 fields were selected for sampling (supplementary fig. S1), distributed across the study area (7.6 km^2). The selected fields represented a gradient of land-use intensity, ranging from regenerative managed grasslands with no input of manure to regenerative fields only using farmyard manure, which contains a lower amount of nitrogen per unit, to more conventional managed fields using slurry manure and artificial fertilizer. Field selection was based on management information provided by farmers organised in a local agricultural nature collective.

2.2. Earthworm sampling

Earthworm collection took place on March 20, 2024. In each selected meadow, eight soil blocks measuring 20 × 20 × 20 cm were excavated using a stratified sampling approach (Jiménez et al., 2006; van der Laan et al., 2025). We did not applied additional sampling techniques (e.g. mustard solution) to collect specific groups of deeper-burrowing earthworms (Singh et al., 2016) as they are rare in our wet meadow ecosystem (Onrust and Piersma, 2017). The soil blocks were collected at a minimum of 10 m distance from each other and kept at least 10 m away from any water bodies, such as ditches, to ensure consistency between the replicate sample blocks. Each collected soil block was placed in a separate plastic bag and transported to a central place, where they were taken apart and all earthworms could be collected. Soil blocks that could not be processed the same day were transported to the Vrije Universiteit, Amsterdam, and stored in a dark cooling cell at 5 °C to prevent decomposition and mortality of earthworms prior to processing. All soil blocks were processed within one week of collection to maintain sample integrity. After extraction, collected earthworms were preserved in tubes containing 96 % ethanol to ensure proper preservation for subsequent identification and body measurements. The eight samples were combined into a single composite sample per field for data analysis. This approach was taken to account for spatial heterogeneity within the fields, while ensuring consistent sample sizes across sites.

2.3. Earthworm identification, biomass and body volume

Each earthworm was individually identified using the Dutch earthworm identification key of Krediet and Kimpel (2024). Specimens were examined under a stereomicroscope (30× magnification) to reliably determine the presence or absence of a clitellum. Adult earthworms (with a clitellum) were identified to species level, while individuals lacking a clitellum were classified as juveniles. Although juveniles could not be identified to species level, they were included in analyses of total abundance, total biomass, and body size to ensure comprehensive data coverage. Fragmented earthworms were identified to the species level if the body remained intact from the head to the end of the clitellum as this allowed reliable identification. These individuals were also included in the total abundance analyses. In contrast, body fragments that could not be used to reconstruct individuals, which were mainly tail ends, were excluded from the total abundance analyses. However, these body fragments were included in total biomass calculations to account for their contribution to total biomass.

After identification, earthworm body width and length were measured with a precision of 1 mm with a hand ruler. To determine the body size of each identified individual, we calculated body volume using the following formula, where width and length were measured in cm:

$$Volume\ (cm^3) = Width^2 * Length * \pi$$

This formula assumes a cylindrical body shape, providing an estimate of the earthworm's volume based on its body width and length.

Earthworm biomass was determined by measuring the dry weight of each individual. Prior to drying, each earthworm was patted dry with a paper towel to remove any excess ethanol. The individuals were then frozen at −21 °C for a minimum of 24 h. After freezing, the earthworms were freeze-dried for at least 48 h (*Edwards Modulyo* freeze dryer) to ensure all remaining moisture was removed. The dried individuals were then weighed using a *Sartorius R160P Analytical Balance* with a precision of 0.1 mg.

Body volume was used as the primary indicator of body size in subsequent analyses, as it is less affected by variation in the amount of organic content in the gut, that can make up to 20 % of the weight of an earthworm (Edwards et al., 1996). To assess comparability with previous studies that use weight, we also tested the correlation between the two metrics using a Pearson correlation test.

2.4. Soil and vegetation variables

Soil samples were collected using a stratified sampling approach to ensure representativeness. At each field, soil was taken from the topsoil layer (0–20 cm) using a stainless-steel auger to avoid contamination. Between 15 and 25 cores were randomly collected and homogenized to form a composite sample per field. Samples were placed in clean plastic bags, labelled, and stored in cool conditions before being sent to the laboratory for analysis. Plant-available nutrients were extracted using the Mehlich 3 method. Concentrations of extractable phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), ammonium (NH_4+), nitrate (NO_3^-), sodium (Na), sulphur (S) and aluminium (followed Mehlich (1984)). Soil organic matter content (SOM%) was measured by loss-on-ignition at 550 °C for 4 h. Soil pH was measured in a 1:1 soil-to-demiwater slurry using a profiline pH set and WTW pH electrode. Cation exchange capacity (CEC) was calculated as the sum of extractable base cations (Ca^{2+}, Mg^{2+}, K^+, and Na^+) from the Mehlich 3 extract (M3-CEC), reflecting the effective nutrient-holding capacity under field conditions. Total exchangeable capacity (TEC) was determined using the $BaCl_2$ method (Schwertfeger and Hendershot, 2009). (Supplementary table S1).

Vegetation structure and plant diversity were assessed in each field using a single 10 × 10 m plot, located at least 10 m from adjacent water bodies. Within this plot, vegetation height was measured at ten randomly chosen points where a ruler was placed against the stem or leaf of the plant measuring the maximum plant height. The average of ten measurements was calculated to represent mean vegetation height for the field. In the same plot, plant species richness was determined by identifying and counting all vascular plant species present. Each plot was considered representative of the overall vegetation structure and composition of the field and used as a field-level covariate in subsequent analyses.

2.5. Meadow management

Information on land management practices of each sampled meadow was collected directly from the farmers by the local agricultural nature collective. This included data on fertilizer application, as well as early season grass yield (expressed in kg dry matter ha^{-1}). Fertilizer and manure application rates were expressed as kg N ha^{-1}, since many fields received a mixture of slurry, rough manure, and artificial fertilizer rather than a single consistent type. To account for variation in soil moisture content between fields, the relative land height above the water height in the surrounding ditches was calculated based on the georeferenced locations where earthworm sampling took place and averaged per field. The coordinates of these sampling points were used to extract elevation data from the Actueel Hoogtebestand Nederland (AHN, 2020) a high-resolution national digital elevation model. The mean surface elevation per field was then calculated from eight points in each field. Surface water level date of surrounding ditches, indicating the target water table height, were obtained from the regional water board Rijnland and were subtracted from average land height to calculate land height above surface water level.

2.6. Land-use intensity (S2REP)

In the Netherlands, large-scale grass mowing generally begins in late April, when swards reach a height of around 20 cm. Fields with high pre-mowing biomass typically reflect conventional management and are dominated by perennial ryegrass *(Lolium perenne*). In contrast, fields with lower biomass are often situated on nutrient-poor soils or are managed under regenerative regimes, supporting a more diverse mix of grasses, herbs, and other plant species.

To assess grassland production in our study area, we used the Sentinel-2 Red Edge Position Index (S2REP) (Frampton et al., 2013), a remote sensing-based vegetation index. Imagery was acquired, processed, and analysed using Google Earth Engine (GEE) (Gorelick et al., 2017) for the spring seasons of 2024, covering the period from April 4 to May 1, depending on cloud conditions. Due to persistent cloud cover over the study area, additional preprocessing steps were required. No single date provided cloud-free coverage, so we constructed a mosaic using images from April 4, April 14, April 24, April 29, and May 1.

A key spectral feature in vegetation monitoring is the "red edge," spanning the 680–780 nm region of the electromagnetic spectrum, where reflectance increases sharply due to chlorophyll presence. Sentinel-2 includes three dedicated red edge bands: Band 5 (705 nm), Band 6 (740 nm), and Band 7 (783 nm). Chlorophyll absorbs strongly in the blue (~450 nm) and red (~670 nm) regions, while reflecting green (~550 nm) and NIR light (above 700 nm), creating a distinct red edge signal in dense, photosynthetically active vegetation. We computed S2REP for each pixel using the following formula:

$$705 + 35 * ((B4 + B7)/2 - B5)/(B6 - B5)$$

where B4 is the reflectance at 665 nm, B5 at 705 nm, B6 at 740 nm, and B7 at 783 nm. Higher S2REP values are associated with areas of dense, actively growing vegetation and typically reflect higher management intensity (Bekkema and Eleveld, 2018).

We extracted S2REP values for each sampling field using the coordinates of the eight sample points per field. This was done in RStudio using the *terra* package (Hijmans et al., 2023) S2REP values were extracted from the pre-processed mosaic image by overlaying the point coordinates onto the raster data. For each field, we calculated the average S2REP value across the eight sample points, yielding a single representative value per field; importantly, none of the fields had been mown prior to image acquisition. To facilitate model interpretability, these average S2REP values were then rescaled to a 0–1 range prior to subsequential analysis.

2.7. Statistical analysis

All statistical analyses were conducted in RStudio (Posit team, 2025), using generalized linear models (GLMs) and linear models to assess the relationships between earthworm community metrics (species richness, total abundance, proportion of juveniles, biomass, and individual average body volume), land management variables and soil and vegetation characteristics. Prior to model construction, we checked that model assumptions were met and screened explanatory variables for multicollinearity using Variance Inflation Factors (VIF < 3).

To mitigate issues of multicollinearity among soil and vegetation variables and to facilitate dimension reduction a Principal Component Analysis (PCA) was performed on collected soil and vegetation variables using the *vegan* package (Oksanen et al., 2013). Variables included in the PCA analysis were: vegetation height, plant species richness, pH, Ca, Mg, CEC, total exchangeable cations (TEC), SOM%, NH_4^+-N, phosphorus (P), potassium (K), sodium (Na), nitrate-N (NO_3^--N), sulphur (S), and aluminium (Al). The data was standardized by centring and scaling to unit variance prior to analysis to ensure comparability across variables with different units. PCA was conducted using standardized values, and the first two principal components were extracted to represent the main variance in the data.

To investigate differences in earthworm species composition among fields, we conducted a non-metric multidimensional scaling (NMDS) analysis, based on Bray-Curtis dissimilarities of relative species abundances. Juvenile and unidentified individuals were excluded from the analysis. Species counts per field were converted to relative abundances by dividing the number of individuals of each species by the total number of identified individuals per plot. NMDS was performed using the metaMDS() function in the vegan package (Oksanen et al., 2022), with two dimensions (k = 2), Bray-Curtis distance, and 100 random starts to ensure convergence on a stable solution. We tested for significant shifts in community composition using permutational multivariate analysis of variance (PERMANOVA) with the adonis2() function. Significance was assessed using 9999 permutations, and effect sizes were evaluated using R^2 values.

3. Results

3.1. General

A total of 4160 earthworm individuals and fragments were collected across all sampling plots, representing nine different species. The identified species were *Aporrectodea caliginosa, Allolobophora chlorotica, Lumbricus rubellus, Eiseniella tetraedra, Aporrectodea rosea, Octolasion lacteum, Lumbricus castaneus, Satchellius mammalis,* and *Aporrectodea longa* (supplementary fig. S3). A large proportion of the sample consisted of juveniles (2174 individuals; 52.3 %), while 688 individuals or fragments (16.5 %) could not be identified to species level and were recorded as “Unknown”. Among the 1298 individuals identified to species level, the most dominant species were *A. caliginosa* (534 individuals; 41.1 %), *A. chlorotica* (412 individuals; 31.4 %) and *L. rubellus* (144 individuals; 11.1 %). These three species represented the majority of the identified earthworm community. Across sampled plots, there was a large variation in the number of species, total number of individuals found, as well as in biomass, and the mean individual volume of earthworms (Table 1). Across all fields, the overall average per-soil block abundance was 24.3 ± 23.6 individuals, with a corresponding biomass of 0.85 ± 0.80 g and an average species richness of 2.26 ± 1.61 species (mean ± SD, N = 152 samples). (Supplementary table S2). Individual body volume and dry weight were strongly correlated (Pearson's $r = 0.85$, $p < 0.001$).

Table 1
Summary of earthworm community metrics (0–20 cm soil depth) across all sampling sites.

Metric	Range	Median	Mean ± SD
Earthworm abundance (ind/m^2, 0–20 cm)	56.25–1444	653.1	606 ± 438
Earthworm biomass (g/m^2, 0–20 cm)	2.81–55.4	19.9	22.0 ± 14.3
Species richness (no. of species)	3–7	5.0	4.95 ± 1.18
Mean volume per individual (cm^3)	0.53–1.20	0.74	0.77 ± 0.20

3.2. PCA on vegetation and soil characteristics

The first principal component (DIM1) accounted for 31 % of the total variance and primarily can be interpreted as a mineralisation and fertility gradient, with higher values indicating increased nutrient availability, base saturation, and potential for organic matter turnover, and lower values associated with more acidic soils, greater plant species richness, and taller vegetation likely reflecting more regenerative conditions. The second principal component (DIM2) explained 17.7 % of the variance and represents a gradient of soil salinization, with higher values reflecting increased concentrations of Na, S, and TEC, consistent with brackish conditions or salt-affected soils (supplementary fig. S2).

3.3. Relationships between land management and soil and vegetation characteristics

Overall, there was no clear relationship between vegetation characteristics or soil gradients and the tested land management variables. For DIM1, the model showed no significant relationships with height above ditch water level (estimate = −2.67, p = 0.757), manure application (estimate = 0.0054, p = 0.367), and grass yield (estimate = 0.22, p = 0.403) (supplementary fig. S4). Similarly, the model for DIM2 showed no significant relationships for height above ditch water level (estimate = −5.97, p = 0.366), manure application (estimate = 0.004, p = 0.372), and grass yield (estimate = −0.1, p = 0.611) (supplementary fig. S5).

3.4. Relationships between land management, soil and vegetation characteristics and earthworm community metrics

Total earthworm abundance was associated with early-season grass yield (negative binomial model: estimate = 0.176, $p < 0.05$; fig. 1 A) and manure application (estimate = 0.0032, $p < 0.05$; fig. 1B), which were retained as explanatory variables. The model, however, explained only a small proportion of variation (McFadden's $R^2 = 0.039$).

Higher early season grass yield appears to support not only more worms, but also a higher total biomass of earthworms. The final model retained a reduced model including grass yield and manure application, which explained a greater proportion of variation in earthworm biomass (adjusted $R^2 = 0.39$) compared to total abundance. Grass yield had a significant positive effect on biomass (estimate = 0.176, $p < 0.05$; fig. 2 A), while manure application had no significant effect (estimate = 0.003, p = 0.077; fig. 2B) on total biomass of earthworms.

In contrast, the proportion of juveniles within the different earthworm populations was not associated with any of the directly measured land management variables, soil nor vegetation characteristics. Stepwise model selection did not retain any predictors, indicating no clear relationship between these factors and the proportion of juveniles. Similarly, species richness was not related to either height above ditch water level and manure application, or soil and vegetation characteristics. Stepwise model selection resulted in a reduced model including only grass yield as a predictor. The model explained a small proportion of the variation in species richness across fields (adjusted $R^2 = 0.0766$). The relationship between grass yield and species richness was not statistically significant (estimate = 0.19, p = 0.133) (supplementary fig. S6).

Earthworm body size (average volume of an individual) was not affected by any of the directly measured land management variable or soil and vegetation characteristics. Although DIM1 was maintained in the final model, it explained only a small proportion of variation in individual body volume (adjusted $R^2 = 0.08$). DIM1 showed no significant effect (estimate = −0.073, p = 0.122) (supplementary fig. S7).

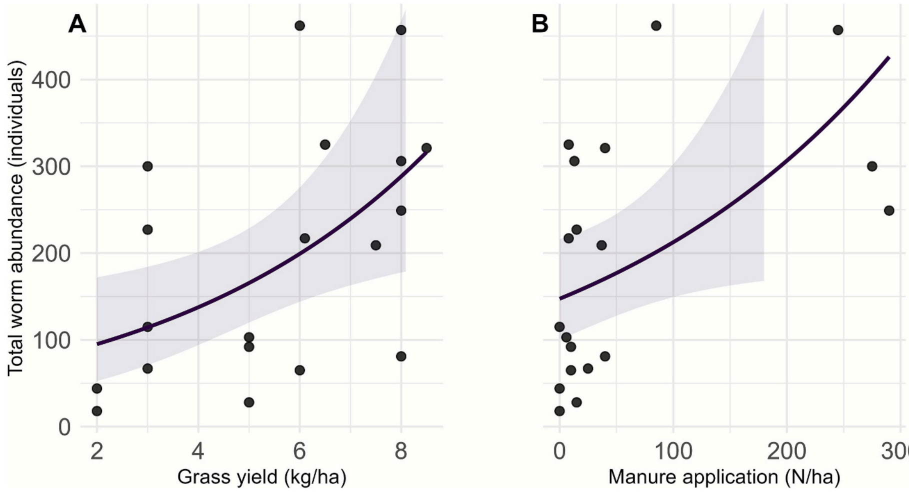

Fig. 1. Relationships between total earthworm abundance and (A) grass yield (kg dry matter/ha^{-1}) and (B) manure application (N/ha^{-1}). Solid lines represent best-fit models with 95% confidence intervals (shaded area in A). Dotted lines indicate non-significant relationships (B).

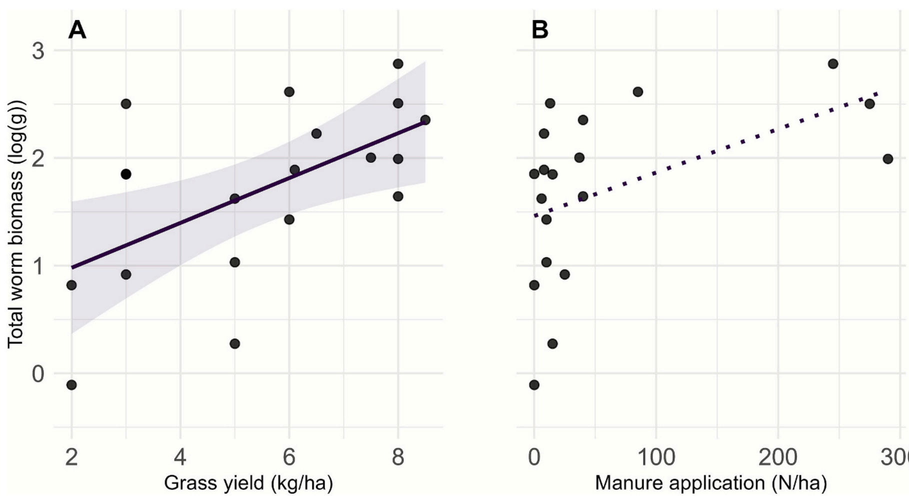

Fig. 2. Relationships between total earthworm biomass and (A) grass yield (kg dry matter/ha^{-1}) and (B) manure application (N/ha^{-1}). Solid lines represent best-fit models with 95% confidence intervals (shaded area in A). Dotted lines indicate non-significant relationships (B).

3.5. Linking remote-sensing data to land management, soil and vegetation characteristics and earthworm community metrics

Plots with a higher early season grass yield were associated with higher land use intensity. Grass yield had a significant positive effect on S2REP (estimate = 0.28, $p < 0.05$; fig. 3). Stepwise selection resulted in a model including DIM2, height above ditch water level and grass yield, which together explained a moderate proportion of the variation in S2REP across fields (adjusted R^2 = 0.31, F(3, 15) = 3.643, $p < 0.05$), height above ditch water level showed no significant effect (estimate = 7.65, p = 0.1), and neither did DIM2 (estimate = 0.24, p = 0.18).

Total earthworm abundance increased significantly with S2REP (Negative binomial model, estimate = 0.38, $p < 0.001$), indicating that meadows with higher land use intensity supported higher worm densities (fig. 4 A). However, this explained only a small proportion of the variation in abundance (McFadden's R^2 = 0.039). Log-transformed total worm biomass was positively associated with S2REP (estimate = 0.33, p = 0.012), explaining a moderate proportion of the variation (adjusted R^2 = 0.28). This suggests that not only worm numbers were higher in fields with a higher land use intensity, but their combined biomass was also greater (fig. 4B). In contrast, worm species richness was not significantly related to S2REP (estimate = 0.10, p = 0.629), and the model explained little variation (R^2 = 0.01), suggesting that land use intensity affects worm quantity more than diversity (fig. 4C). Finally, there was a clear and significant negative relationship between S2REP and average worm volume (estimate = −0.09, $p < 0.01$), with the model explaining a substantial portion of the variation (adjusted R^2 = 0.34). This indicates that although total abundance and biomass increased with land use intensity, individual worms tended to be smaller in more intensively managed plots (fig. 4D).

3.6. Linking management, soil and vegetation variables and remote-sensing data to species community composition

Species community composition was significantly associated with variation along DIM2, indicating a change in species community composition along a gradient of soil salinization. PERMANOVA indicated that DIM2 explained a significant portion of the variation in species composition (R^2 = 0.13, $p < 0.05$), while any management variables or S2REP were not significant predictors of change in species composition (fig. 5).

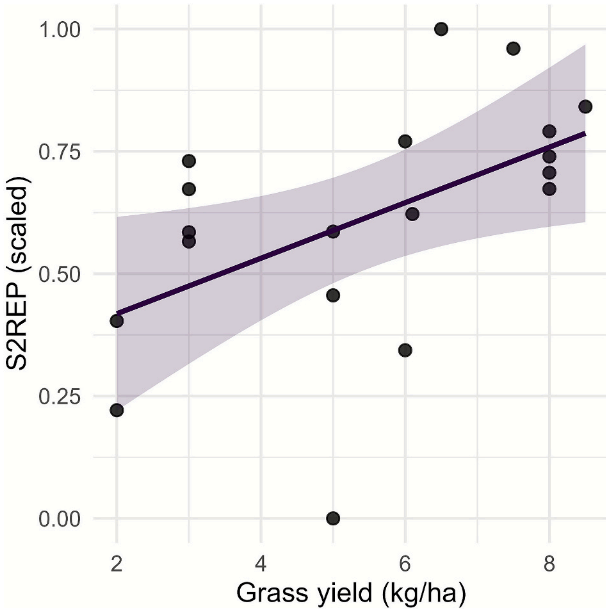

Fig. 3. Relationship between grass yield (kg dry matter/ha^{-1}) and S2REP (scaled), a remote sensing indicator of land use intensity. The solid line represents the best-fit model with 95% confidence intervals (shaded area).

4. Discussion

Earthworm communities in these peat grasslands responded to land management intensity in ways that were partly consistent with our expectations, but also revealed important deviations. While species richness remained relatively stable across fields, earthworm abundance and biomass increased with land-use intensity, particularly in relation to grass yield and remote sensing indicators (S2REP) of land-use intensity, suggesting that productive grasslands supported higher worm densities. Although the direct management variables explained only a small proportion of the variation in abundance and biomass. Contrary to our expectation that intensive management might favour larger-bodied individuals due to increased food availability, average body size declined with land use intensity. Juvenile proportion varied across fields but was not significantly associated with management variables, suggesting that observed trait shifts in body size reflect changes intraspecific rather than through demographic structure. Lack of a relationship between species composition and land management intensity, and its association instead with soil salinization (DIM2), underscores the importance of abiotic soil properties in shaping species community composition.

The average number of 606 individuals m^{-2} is notably higher than values reported for comparable grassland ecosystems on clay or sandy soils. For instance, Didden (2001) reported an average 384 individuals m^{-2} in Dutch lowland grassland meadows, Cluzeau et al. (2012) recorded 350 individuals m^{-2} in French lowland grasslands, and Hoeffner et al. (2024) found on average 214 individuals m^{-2} in managed grasslands in central France. These elevated densities may be partly attributed to drained peat soils, which typically retain more moisture

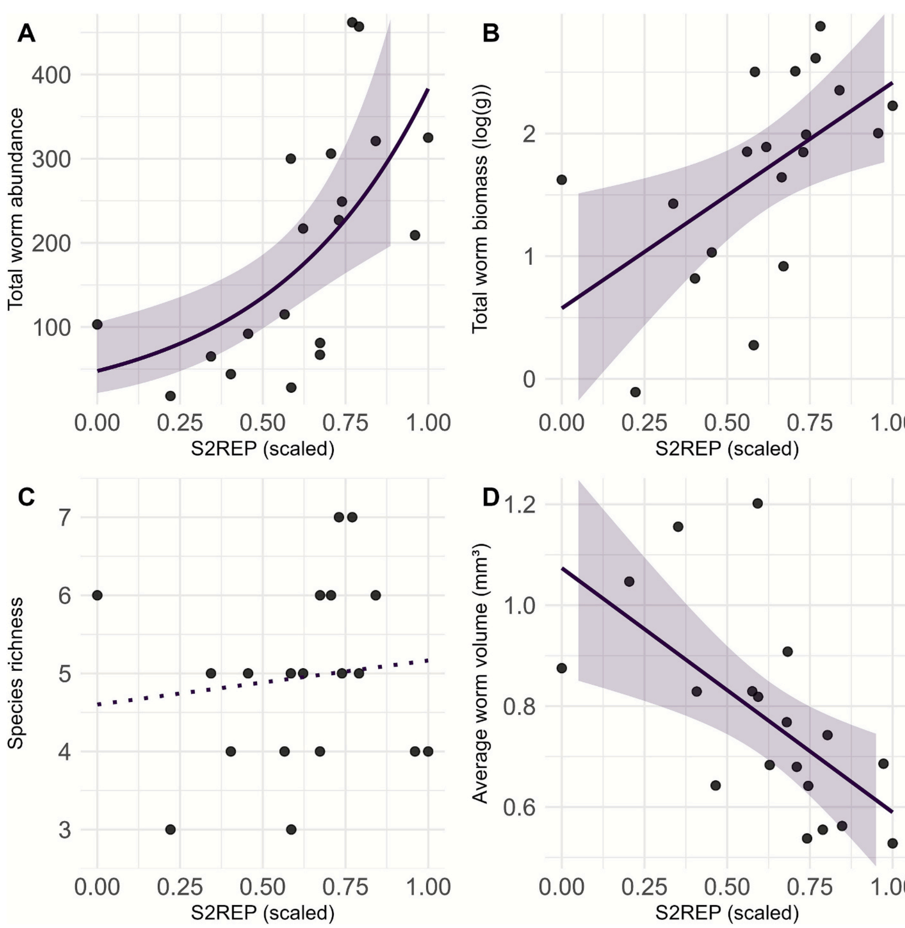

Fig. 4. Relationship between S2REP (scaled), a proxy for land-use intensity and total worm abundance (A), Total worm biomass (log(g) (B), the number of observed unique species (C), individual average worm volume (mm^3) (D). Solid lines represents the best-fit model with 95% confidence intervals (shaded area) and a significant relation. Dotted lines indicate non-significant relationships.

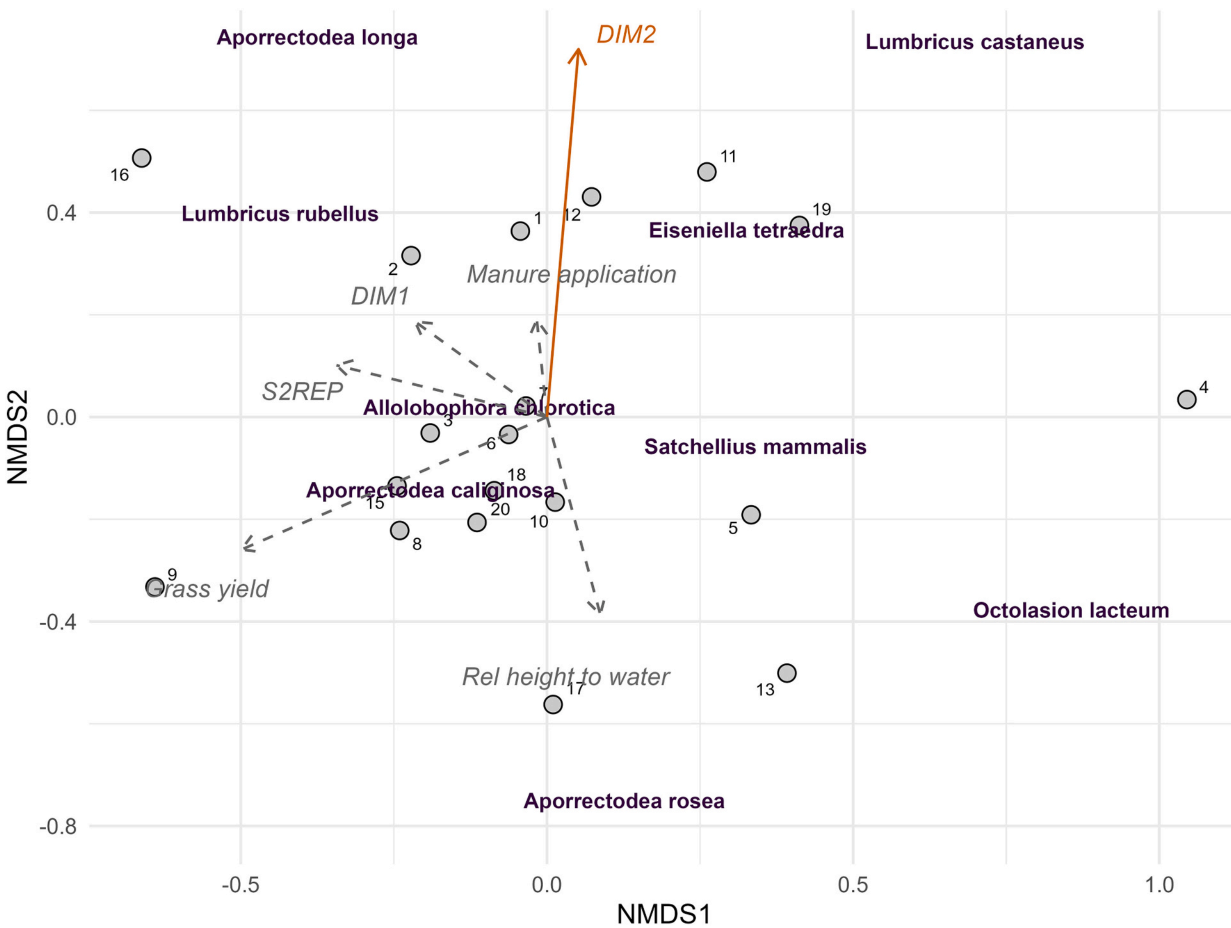

Fig. 5. NMDS ordination of earthworm community composition based on Bray–Curtis dissimilarity. Each grey dot represents a sampling field. Species are plotted as weighted averages of their abundances across fields. The orange arrow indicates a significant environmental vector (DIM2), suggesting a gradient associated with variation in community structure. Grey arrows represent non-significant environmental variables included in the PERMANOVA model, plotted for reference but not statistically associated with community variation. Species abbreviations: A. longa – *Aporrectodea longa,* A. rosea – *Aporrectodea rosea,* A. caliginosa – *Aporrectodea caliginosa, A. chlorotica* – *Aporrectodea chlorotica,* L. rubellus – *Lumbricus rubellus,* L. castaneus – *Lumbricus castaneus,* E. fetida – *Eisenia fetida,* E. tetraedra – *Eiseniella tetraedra,* S. mammalis – *Satchellius mammalis,* O. lacteum – *Octolasion lacteum.*

and soil organic matter than mineral soils, offering favourable conditions for earthworm activity and reproduction (Torppa et al., 2024). In addition, regular inputs of manure and the absence of tillage likely support surface-dwelling and endogeic species by maintaining a stable food supply and physical structure (Chan, 2001). Although in our study, it remains difficult to disentangle whether these effects act indirectly through increased grass productivity or directly through the type of manure applied, which can either provide an immediate food source (rough manure containing straw) (Onrust and Piersma, 2019) or cause stress (slurry application with increased mortality by cutting the soil) (Van Vliet and de Goede, 2006). Furthermore, our sampling was conducted in early spring, when soil moisture and earthworm activity are generally high, providing an indication of relative differences among fields under different management conditions, though seasonal dynamics may alter abundances later in the year with changes in soil moisture content and temperature (Eggleton et al., 2009; Ligrone et al., 2024).

High earthworm abundance is often regarded as beneficial because of their roles in soil aeration, structural stability, and organic matter decomposition (Blouin et al., 2013; Sharma et al., 2017). However, these contributions vary among functional groups, as different groups of earthworms influence these processes in distinct ways (Ernst et al., 2009; Huang et al., 2020). Earthworm communities across the studied peat meadows were dominated by a number of generalist species, reflecting patterns commonly observed in agriculturally managed grasslands (Hoeffner et al., 2021; Onrust and Piersma, 2019). The high prevalence of generalist taxa suggests that frequent disturbance and nutrient inputs may favour species with broad ecological tolerances, resulting in a simplified community structure. A possible explanation for the absence of functionally distinct groups such as anecic earthworms, particularly *Lumbricus terrestris*, is a combination of methodological and ecological constraints. Earthworms in this study were sampled by excavating soil blocks to a depth of 20 cm, potentially underrepresenting deep-burrowing anecic species, which typically inhabit deeper layers (Pelosi et al., 2009). However, in peat soils, deeper layers are often saturated or waterlogged, creating conditions that are less favourable to anecic earthworms (Decaëns et al., 2003; Onrust and Piersma, 2019). Their apparent absence may therefore reflect both limited sampling depth and genuinely unsuitable habitat conditions.

This limited functional composition may restrict the range of ecological roles performed by the earthworm community, such as vertical mixing and deep burrowing, which are typically associated with the presence of anecic species (Andriuzzi et al., 2015; Huang et al., 2020). However, in peat grassland systems, such functions may not necessarily benefit the ecological integrity of peatlands (Lubbers et al., 2013; Wu et al., 2017). Vertical mixing and deep burrowing by earthworms causes increased oxygenation which can enhance organic matter decomposition, contributing to higher CO_2 emissions (van Groenigen et al., 2014).

In addition to functional simplification, changes in body size revealed another dimension of community response with potential consequences for soil functioning. Average individual body volume declined significantly with increasing S2REP, a proxy for land-use intensity. Importantly, this decline in size was not driven by a higher proportion of juveniles in intensive fields, as the proportion of juveniles was not significantly associated with S2REP or other management variables. This suggests that land use intensity may constrain growth or body condition, rather than altering demographic structure. To our knowledge, there is no literature that clearly explains the mechanism behind decreasing body size under more intensive land management. One possible explanation is that earthworms exposed to stressful conditions (e.g. nutrient imbalance, disturbance, or soil compaction) may need to allocate resources toward tolerance and maintenance mechanisms, thereby limiting investment in growth (Aira et al., 2007; Congdon et al., 2001). Such effects may act indirectly through variation in land use intensity influencing growth rates; for example, Onrust and Piersma (2019) demonstrated differences in earthworm growth rate under different types of manure application. Growth rates are also known to depend on environmental conditions such as soil temperature and moisture (Eriksen-Hamel and Whalen, 2006; Whalen and Parmelee, 1999). As earthworm weight and body volume were strongly correlated in our study, our observed decline in body volume likely reflects a reduction in growth and body condition under more intensive management. Soil temperature and moisture can vary with land use practices (Mayel et al., 2021) that underly in complex management effects likely captured by S2REP. Such environmental differences may contribute to variation in earthworm body size.

This reduction in body size may further impact ecological functions related to soil porosity or nutrient cycling and potentially limiting the energetic value as food source available to meadow birds. Furthermore, in more intensively managed fields, drier summer conditions may reduce the accessibility of earthworms to foraging meadow birds, despite higher worm densities at the start of the breeding season. Hardened soils limit prey availability, raising questions about the actual foraging value of these fields compared to fields with a higher water table. This aligns with findings by Verhoeven et al. (2022), who found no evidence for a relationship between earthworm abundance and the presence of breeding godwits.

Surprisingly, typical land management variables, such as height above ditch water level, manure application, and grass yield were not strongly associated with the main ecological gradients in vegetation or soil physiochemical composition. This disconnection likely reflects the temporal dynamics of soil processes and nutrient availability, which arise from fluctuating inputs and outputs as well as legacy effects of past fertilization and short-term, non-linear responses following manure application, all of which are strongly modulated by factors such as pH, moisture, temperature, and organic matter quality (Bouwman et al., 2017; Rieke et al., 2018). Consequently, it is challenging to identify which individual soil elements drive nutrient availability, as their effects are masked by these interacting temporal processes and, in our study, were also highly correlated in the PCA. This makes it difficult to directly connect single soil variables to land management and to disentangle their independent contributions to earthworm community patterns. To address these issues we integrated a comprehensive remote sensing indicator, that might capture broader or more complex association with land management intensity. S2REP proved to be a useful proxy of land-use intensity, correlating strongly with grass yield and was positively associated with total earthworm abundance and biomass. These findings support the use of remote sensing to assess belowground responses to management. However, S2REP did not explain variation in species richness or community composition, reinforcing the notion that alteration in land management alters earthworm quantity and species traits more than diversity or species identity.

5. Conclusions

Together, these findings highlight that land management intensity influences earthworm communities in peat grasslands primarily through changes in community structure and functional traits, such as individual body size, rather than through shifts in species richness or community composition. The dominance of endogenic and disturbance-tolerant generalists and the decline in adult body size under more intensive management suggest a shift toward a functionally simplified community. Moreover, reduced body size of earthworms in more intensively managed fields may lower their energetic value and potentially may be less accessible to foraging meadow birds later in the season due to drier soil conditions. These results underscore the importance of interpreting belowground biodiversity within the specific ecological context of peat soils. Incorporating trait-based approaches alongside taxonomic data provides a more nuanced and mechanistic understanding of how land-use practices affect soil biota, ecosystem processes, and trophic interactions in these agricultural landscapes.

CRediT authorship contribution statement

Lianne C. Woudstra: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Jacintha Ellers:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Mariet M. Hefting:** Writing – review & editing, Validation, Supervision, Methodology. **Taylor B. Craft:** Writing – review & editing, Resources, Methodology. **Matty P. Berg:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT4o in order to check grammar and improve readability. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

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.

Acknowledgements

This study was supported by the research program VeenVitaal funded by the Nationale Wetenschapsagenda – Onderzoek op Routes door Consortia (NWA-ORC, NWA.1389.20.125).

We are grateful to Provincie Noord-Holland, Agrarisch Collectief Noord-Holland Zuid, and Koningshoeve-Ettingen BV, particularly Nico Jonker, Andries Kamstra, and Gertjan van Tunen, for their support in co-organizing the one-day event that enabled data collection. We thank Wij.land, and especially Siem Vlaanderen, for coordinating soil core extraction and funding the physicochemical analyses. We also sincerely appreciate the contributions of the VeenVitaal volunteers and students from Vrije Universiteit Amsterdam and Aeres University of Applied Sciences, Almere, who assisted with soil sample processing and earthworm collection.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2025.106763.

Data availability

Data will be made available on request.

References

AHN, 2020. Dataroom Algemeen Hoogtebestand Nederland (DTM). https://www.ahn.nl/dataroom. (Accessed 20 May 2025).

Aira, M., Domínguez, J., Monroy, F., Velando, A., 2007. Stress promotes changes in resource allocation to growth and reproduction in a simultaneous hermaphrodite with indeterminate growth. Biol. J. Linn. Soc. 91, 593–600. https://doi.org/10.1111/j.1095-8312.2007.00822.x.

Andersen, R., Farrell, C., Graf, M., Muller, F., Calvar, E., Frankard, P., Caporn, S., Anderson, P., 2017. An overview of the progress and challenges of peatland restoration in Western Europe. Restor. Ecol. 25, 271–282. https://doi.org/10.1111/rec.12415.

Andriuzzi, W.S., Pulleman, M.M., Schmidt, O., Faber, J.H., Brussaard, L., 2015. Anecic earthworms (Lumbricus terrestris) alleviate negative effects of extreme rainfall events on soil and plants in field mesocosms. Plant Soil 397, 103–113. https://doi.org/10.1007/s11104-015-2604-4.

Atlas Leefomgeving, 2023. https://www.atlasleefomgeving.nl/kaarten?config=3ef897de-127f-471a-959b-93b7597de188&gm-x=155564.49238446465&gm-y=463685.7445560462&gm-z=9&gm-b=1544180834512,true,1;1553433974269,true,0.8;&activateOnStart=info&deactivateOnStart=layercollection. (Accessed 13 January 2025).

Bartz, M.L.C., Pasini, A., Brown, G.G., 2013. Earthworms as soil quality indicators in Brazilian no-tillage systems. Appl. Soil Ecol. Progress and Priorities in Latin American Oligochaete Research 69, 39–48. https://doi.org/10.1016/j.apsoil.2013.01.011.

Batey, T., 2009. Soil compaction and soil management – a review. Soil Use Manag. 25, 335–345. https://doi.org/10.1111/j.1475-2743.2009.00236.x.

Bekkema, M., Eleveld, M., 2018. Mapping grassland management intensity using Sentinel-2 satellite data. GI_Forum 1, 194–213. https://doi.org/10.1553/giscience2018_01_s194.

Betancur-Corredor, B., Zaitsev, A., Russell, D.J., 2024. The impact of multiple agricultural land uses in sustaining earthworm communities in agroecosystems - a global meta-analysis. Sci. Rep. 14, 30160. https://doi.org/10.1038/s41598-024-81676-5.

Blouin, M., Hodson, M.E., Delgado, E.A., Baker, G., Brussaard, L., Butt, K.R., Dai, J., Dendooven, L., Peres, G., Tondoh, J.E., Cluzeau, D., Brun, J.-J., 2013. A review of earthworm impact on soil function and ecosystem services. Eur. J. Soil Sci. 64, 161–182. https://doi.org/10.1111/ejss.12025.

Bodemdata, n.d. https://bodemdata.nl/basiskaarten (accessed 13 January 2025).

Bouwman, A.F., Beusen, A.H.W., Lassaletta, L., van Apeldoorn, D.F., van Grinsven, H.J.M., Zhang, J., Ittersum van, M.K., 2017. Lessons from temporal and spatial patterns in global use of N and P fertilizer on cropland. Sci. Rep. 7, 40366. https://doi.org/10.1038/srep40366.

Briones, M.J.I., Schmidt, O., 2017. Conventional tillage decreases the abundance and biomass of earthworms and alters their community structure in a global meta-analysis. Glob. Chang. Biol. 23, 4396–4419. https://doi.org/10.1111/gcb.13744.

Chan, K.Y., 2001. An overview of some tillage impacts on earthworm population abundance and diversity — implications for functioning in soils. Soil Tillage Res. 57, 179–191. https://doi.org/10.1016/S0167-1987(00)00173-2.

Cluzeau, D., Guernion, M., Chaussod, R., Martin-Laurent, F., Villenave, C., Cortet, J., Ruiz-Camacho, N., Pernin, C., Mateille, T., Philippot, L., Bellido, A., Rougé, L., Arrouays, D., Bispo, A., Pérès, G., 2012. Integration of biodiversity in soil quality monitoring: baselines for microbial and soil fauna parameters for different land-use types. Eur. J. Soil biol. Bioindication in Soil Ecosystems 49, 63–72. https://doi.org/10.1016/j.ejsobi.2011.11.003.

Congdon, J.D., Dunham, A.E., Hopkins, W.A., Rowe, C.L., Hinton, T.G., 2001. Resource allocation-based life histories: a conceptual basis for studies of ecological toxicology. Environ. Toxicol. Chem. 20, 1698–1703. https://doi.org/10.1002/etc.5620200811.

Curry, J.P., Doherty, P., Purvis, G., Schmidt, O., 2008. Relationships between earthworm populations and management intensity in cattle-grazed pastures in Ireland. Appl. Soil Ecol. 39, 58–64. https://doi.org/10.1016/j.apsoil.2007.11.005.

Curry, J.P., Schmidt, O., 2007. The feeding ecology of earthworms – a review. Pedobiologia 50, 463–477. https://doi.org/10.1016/j.pedobi.2006.09.001.

Decaëns, T., Bureau, F., Margerie, P., 2003. Earthworm communities in a wet agricultural landscape of the Seine Valley (upper Normandy, France): the 7th international symposium on earthworm ecology · Cardiff · Wales · 2002. Pedobiologia 47, 479–489. https://doi.org/10.1078/0031-4056-00217.

Didden, W.A.M., 2001. Earthworm communities in grasslands and horticultural soils. Biol. Fertil. Soils 33, 111–117. https://doi.org/10.1007/s003740000297.

Edwards, C.A., Bohlen, P.J., Hendrix, P., Arancon, N., 1996. Biology and Ecology of Earthworms. Springer.

Eggleton, P., Inward, K., Smith, J., Jones, D.T., Sherlock, E., 2009. A six year study of earthworm (Lumbricidae) populations in pasture woodland in southern England shows their responses to soil temperature and soil moisture. Soil Biol. Biochem. 41, 1857–1865. https://doi.org/10.1016/j.soilbio.2009.06.007.

Eriksen-Hamel, N.S., Whalen, J.K., 2006. Growth rates of Aporrectodea caliginosa (Oligochaetae: Lumbricidae) as influenced by soil temperature and moisture in disturbed and undisturbed soil columns. Pedobiologia 50, 207–215. https://doi.org/10.1016/j.pedobi.2005.10.008.

Erkens, G., van der Meulen, M.J., Middelkoop, H., 2016. Double trouble: subsidence and CO2 respiration due to 1,000 years of Dutch coastal peatlands cultivation. Hydrogeol. J. 24, 551–568. https://doi.org/10.1007/s10040-016-1380-4.

Ernst, G., Felten, D., Vohland, M., Emmerling, C., 2009. Impact of ecologically different earthworm species on soil water characteristics. Eur. J. Soil Biol. 45, 207–213. https://doi.org/10.1016/j.ejsobi.2009.01.001.

Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., Malhotra, A., Melton, J.R., Poulter, B., Kaplan, J.O., Goldewijk, K.K., Siebert, S., Minayeva, T., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A.M., Davidson, N., Finlayson, C.M., Lehner, B., Jackson, R.B., McIntyre, P.B., 2023. Extensive global wetland loss over the past three centuries. Nature 614, 281–286. https://doi.org/10.1038/s41586-022-05572-6.

Frampton, W.J., Dash, J., Watmough, G., Milton, E.J., 2013. Evaluating the capabilities of Sentinel-2 for quantitative estimation of biophysical variables in vegetation. ISPRS J. Photogramm. Remote Sens. 82, 83–92. https://doi.org/10.1016/j.isprsjprs.2013.04.007.

Girkin, N.T., Burgess, P.J., Cole, L., Cooper, H.V., Honorio Coronado, E., Davidson, S.J., Hannam, J., Harris, J., Holman, I., McCloskey, C.S., McKeown, M.M., Milner, A.M., Page, S., Smith, J., Young, D., 2023. The three-peat challenge: business as usual, responsible agriculture, and conservation and restoration as management trajectories in global peatlands. Carbon Manag. 14, 2275578. https://doi.org/10.1080/17583004.2023.2275578.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google earth engine: planetary-scale geospatial analysis for everyone. Remote Sens. Environ. Big Remotely Sensed Data: tools, applications and experiences 202, 18–27. https://doi.org/10.1016/j.rse.2017.06.031.

Hijmans, R.J., Bivand, R., Dyba, K., Pebesma, E., Sumner, M.D., 2023. Terra [R Package] (R Programming Language).

Hoeffner, K., Louault, F., Lerner, L., Pérès, G., 2024. Management of grassland: a necessary tool to maintain plant and earthworm diversity. Eur. J. Soil Biol. 120, 103589. https://doi.org/10.1016/j.ejsobi.2023.103589.

Hoeffner, K., Santonja, M., Monard, C., Barbe, L., Moing, M.L., Cluzeau, D., 2021. Soil properties, grassland management, and landscape diversity drive the assembly of earthworm communities in temperate grasslands. Pedosphere 31, 375–383. https://doi.org/10.1016/S1002-0160(20)60020-0.

Huang, W., González, G., Zou, X., 2020. Earthworm abundance and functional group diversity regulate plant litter decay and soil organic carbon level: a global meta-analysis. Appl. Soil Ecol. 150, 103473. https://doi.org/10.1016/j.apsoil.2019.103473.

Jiménez, J.J., Lavelle, P., Decaëns, T., 2006. The efficiency of soil hand-sorting in assessing the abundance and biomass of earthworm communities. Its usefulness in population dynamics and cohort analysis studies. Eur. J. Soil biol. ICSZ 42, S225–S230. https://doi.org/10.1016/j.ejsobi.2006.07.031.

Kleijn, D., Berendse, F., Smit, R., Gilissen, N., Smit, J., Brak, B., Groeneveld, R., 2004. Ecological effectiveness of Agri-environment schemes in different agricultural landscapes in the Netherlands. Conserv. Biol. 18, 775–786. https://doi.org/10.1111/j.1523-1739.2004.00550.x.

Krediet, A., Kimpel, N., 2024. De Nederlandse regenwormen. Jeugdbondsuitgeverij.

Lamers, L.P.M., Vile, M.A., Grootjans, A.P., Acreman, M.C., van Diggelen, R., Evans, M.G., Richardson, C.J., Rochefort, L., Kooijman, A.M., Roelofs, J.G.M., Smolders, A.J.P., 2015. Ecological restoration of rich fens in Europe and North America: from trial and error to an evidence-based approach. Biol. Rev. 90, 182–203. https://doi.org/10.1111/brv.12102.

Ligrone, A., Alvarez, M., Jorge-Escudero, G., Piñeiro, G., 2024. Seasonal dynamics of agricultural land use impacts on earthworm communities: insights into diversity, abundance, and functional composition. Eur. J. Soil Biol. 120, 103588. https://doi.org/10.1016/j.ejsobi.2023.103588.

Lubbers, I.M., van Groenigen, K.J., Fonte, S.J., Six, J., Brussaard, L., van Groenigen, J.W., 2013. Greenhouse-gas emissions from soils increased by earthworms. Nat. Clim. Chang. 3, 187–194. https://doi.org/10.1038/nclimate1692.

Luna Juncal, M.J., Masino, P., Bertone, E., Stewart, R.A., 2023. Towards nutrient neutrality: a review of agricultural runoff mitigation strategies and the development of a decision-making framework. Sci. Total Environ. 874, 162408. https://doi.org/10.1016/j.scitotenv.2023.162408.

Mamabolo, E., Pryke, J.S., Gaigher, R., 2024. Soil macrofauna are important bioindicators of soil quality in agroecosystems under different management. Ecol. Indic. 167, 112723. https://doi.org/10.1016/j.ecolind.2024.112723.

Mayel, S., Jarrah, M., Kuka, K., 2021. How does grassland management affect physical and biochemical properties of temperate grassland soils? A review study. Grass Forage Sci. 76, 215–244. https://doi.org/10.1111/gfs.12512.

Mehlich, A., 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Commun. Soil Sci. Plant Anal. 15, 1409–1416. https://doi.org/10.1080/00103628409367568.

Murchie, A.K., Blackshaw, R.P., Gordon, A.W., Christie, P., 2015. Responses of earthworm species to long-term applications of slurry. Appl. Soil Ecol. 96, 60–67. https://doi.org/10.1016/j.apsoil.2015.07.005.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2013. Package vegan. Community Ecol. Package Version 2, 1–295.

Oksanen, J., Simpson, G.L, Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2022. vegan: Community Ecology Package (R package version 2.6-2). The Comprehensive R Archive Network (CRAN). https://CRAN.R-project.org/package=vegan.

Onrust, J., Piersma, T., 2017. The hungry worm feeds the bird. Ardea 105, 153–161. https://doi.org/10.5253/arde.v105i2.a4.

Onrust, J., Piersma, T., 2019. How dairy farmers manage the interactions between organic fertilizers and earthworm ecotypes and their predators. Agric. Ecosyst. Environ. 273, 80–85. https://doi.org/10.1016/j.agee.2018.12.005.

Pelosi, C., Bertrand, M., Capowiez, Y., Boizard, H., Roger-Estrade, J., 2009. Earthworm collection from agricultural fields: comparisons of selected expellants in presence/absence of hand-sorting. Eur. J. Soil Biol. 45, 176–183. https://doi.org/10.1016/j.ejsobi.2008.09.013.

Posit team, 2025. RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA.
Pulleman, M., Creamer, R., Hamer, U., Helder, J., Pelosi, C., Pérès, G., Rutgers, M., 2012. Soil biodiversity, biological indicators and soil ecosystem services—an overview of European approaches. Curr. Opin. Environ. Sustain. Terrestrial systems 4, 529–538. https://doi.org/10.1016/j.cosust.2012.10.009.
Rayne, N., Aula, L., 2020. Livestock manure and the impacts on soil health: a review. Soil Syst. 4, 64. https://doi.org/10.3390/soilsystems4040064.
Rieke, E.L., Soupir, M.L., Moorman, T.B., Yang, F., Howe, A.C., 2018. Temporal dynamics of bacterial communities in soil and leachate water after swine manure application. Front. Microbiol. 9. https://doi.org/10.3389/fmicb.2018.03197.
Schothorst, C.J., 1977. Subsidence of low moor peat soils in the western Netherlands. Geoderma 17, 265–291. https://doi.org/10.1016/0016-7061(77)90089-1.
Schwertfeger, D.M., Hendershot, W.H., 2009. Determination of effective cation exchange capacity and exchange acidity by a one-step BaCl2 method. Soil Sci. Soc. Am. J. 73, 737–743. https://doi.org/10.2136/sssaj2008.0009.
Sharma, D.K., Tomar, S., Chakraborty, D., 2017. Role of earthworm in improving soil structure and functioning. Curr. Sci. 113, 1064–1071.
Singh, J., Singh, S., Vig, A.P., 2016. Extraction of earthworm from soil by different sampling methods: a review. Environ. Dev. Sustain. 18, 1521–1539. https://doi.org/10.1007/s10668-015-9703-5.
Timmerman, A., Bos, D., Ouwehand, J., de Goede, R.G.M., 2006. Long-term effects of fertilisation regime on earthworm abundance in a semi-natural grassland area. Pedobiologia 50, 427–432. https://doi.org/10.1016/j.pedobi.2006.08.005.
Torppa, K.A., Castaño, C., Glimskär, A., Skånes, H., Klinth, M., Roslin, T., Taylor, A.R., Viketoft, M., Clemmensen, K.E., Maaroufi, N.I., 2024. Soil moisture and fertility drive earthworm diversity in north temperate semi-natural grasslands. Agric. Ecosyst. Environ. 362, 108836. https://doi.org/10.1016/j.agee.2023.108836.
UNEP, 2022. Global Peatlands Assessment: The State of the World's Peatlands - Evidence for Action toward the Conservation, Restoration, and Sustainable Management of Peatlands.
van 't Veer, 2022. Groeiend Veen in Laag Holland. Landschap Noord-Holland. https://www.researchgate.net/publication/361276186_Groeiend_Veen_in_Laag_Holland_versie_augustus_2022_Definitieve_versie.
van der Aar, J.M., 1984. 550 Jaar Vereenigde Binnenpolder onder Haarlemmerliede en Spaarnwoude.
van der Laan, A., van Eekeren, N., Wassen, M.J., Rebel, K.T., van Dijk, J., 2025. Soil biota response to raised water levels and reduced nutrient inputs in agricultural peat meadows. Appl. Soil Ecol. 207, 105932. https://doi.org/10.1016/j.apsoil.2025.105932.
van Groenigen, J.W., Lubbers, I.M., Vos, H.M.J., Brown, G.G., De Deyn, G.B., van Groenigen, K.J., 2014. Earthworms increase plant production: a meta-analysis. Sci. Rep. 4, 6365. https://doi.org/10.1038/srep06365.
Van Vliet, P.C.J., de Goede, R.G.M., 2006. Effects of slurry application methods on soil faunal communities in permanent grassland. Eur. J. Soil biol. ICSZ 42, S348–S353. https://doi.org/10.1016/j.ejsobi.2006.09.004.
Verhoeven, M.A., McBride, A.D., Hooijmeijer, J.C.E.W., Piersma, T., Senner, N.R., 2022. Earthworm abundance and availability does not influence the reproductive decisions of black-tailed godwits in an agricultural grassland. Ecol. Solut. Evid. 3, e12125. https://doi.org/10.1002/2688-8319.12125.
Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., Brown, V.K., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647–664. https://doi.org/10.1046/j.1365-2664.2001.00626.x.
Whalen, J.K., Parmelee, R.W., 1999. Growth of Aporrectodea tuberculata(Eisen) and Lumbricus terrestris L. under laboratory and field conditions. Pedobiologia 43, 1–10.
Wu, X., Cao, R., Wei, X., Xi, X., Shi, P., Eisenhauer, N., Sun, S., 2017. Soil drainage facilitates earthworm invasion and subsequent carbon loss from peatland soil. J. Appl. Ecol. 54, 1291–1300. https://doi.org/10.1111/1365-2664.12894.
Zak, D., McInnes, R.J., 2022. A call for refining the peatland restoration strategy in Europe. J. Appl. Ecol. 59, 2698–2704. https://doi.org/10.1111/1365-2664.14261.