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Lumbricus terrestris abundance in grasslands on sandy soils in relation to soil texture, hydrology and earthworm community

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A B S T R A C T

Deep-burrowing (anecic) earthworm *Lumbricus terrestris* contributes to the crucial ecosystem service of water regulation. Their deep, vertical burrows facilitate water flow and deeper rooting, the former supporting the prevention of flooding and waterlogging, the latter improving drought tolerance. In Europe, these earthworms occur in agricultural grasslands on various soil types. However, their distribution pattern can be very heterogeneous. There is no conclusive set of soil biotic or abiotic factors that determines whether *L. terrestris* occurs or not. Through a better understanding of the *L. terrestris* distribution patterns we hope to gain more insight into their potential for climate adaptive water regulation.

We executed a field inventory (n = 62) to assess the relationship between *L. terrestris* population density in grassland on sandy soils and soil silt content (loaminess), gley depth, epigeic earthworm population density and grassland age.

We found positive correlations between soil silt concentrations and *L. terrestris* population densities. Gley depth slightly correlated with population density when presented in a model with silt concentration as a predictor. Presence and population density of *L. terrestris* correlated negatively with *L. rubellus* abundance. The number of years without mechanical soil disturbance and *L. terrestris* population density were not significantly related. Unexpectedly, we found *L. terrestris* in some very sandy soils. Our data was fitted into an existing predictive model based on land use and texture (by Lindahl et al., 2009), yielding 63% accuracy. Overall, this correlative study provides further insights into *L. terrestris* habitat selection, which helps us understand the species' potential for water regulation in the widespread grassland agro-ecosystems.

1. Introduction

Global climate changes are characterised by prolonged dry periods and intensified peak rainfall [1,2]. Although the former has gained more attention until now, the latter could also entail major impacts on plant growth, biogeochemical cycles and nutrient losses [3,4]. For example, flooding and waterlogging on grasslands reduces oxygen diffusion in soils, thus depriving plant roots of adequate oxygen supply. The resulting oxygen deficiency (hypoxia) or even completely anaerobic conditions (anoxia) in the rhizosphere enhance N_2O emissions and inhibit nutrient uptake and, thus, plant growth [5,6]. Additionally, changing precipitation patterns cause societal problems, including damage to buildings and infrastructure in the case of flooding, but also leads to water shortages [7,8].

As ecosystem engineers, earthworms provide various ecosystem services [9]. In permanent grasslands, where mechanical soil disturbance is low (e.g. no chisel ploughing), earthworms play an important role in soil bioturbation and thus improve water regulation [10]. Deep-burrowing earthworms (*anecics,* sensu Bouché [11]) such as *Lumbricus terrestris* and *Apporectodea longa* play an important role in the ecosystem service of water regulation [3,12,13]. They create vertical, semi-permanent burrows, reaching depths up to 2 m, thus enhancing soil macroporosity. This behaviour increases both the infiltration rate and capacity of the soil and avoids waterlogging and flooding [14–19]. Furthermore, earthworm activity increases rooting space, which is beneficial for plant growth and promotes drought tolerance [13,20]. Several factors are known to play a role in facilitating the presence of anecic earthworms:

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1. Soil texture: Positive interactions have been found between anecic earthworm density and soil silt and clay content [19,21–25]. Guild [21] found the highest population densities of *L. terrestris* and *A. longa* adults under permanent pastures in alluvial and loamy soils, respectively. Furthermore, within-field heterogeneity in terms of soil clay contents (>8%) was found to correlate with *A. longa* found in higher densities in the more clayey parts [24]. Nordström and Rundgren [23] suggested close positive interrelations between soil clay content and other soil factors stimulating earthworm population establishment, such as organic matter content and water retention. Hawkins et al. [26] used a soil column experiment to show that sand layers complicate *L. terrestris* burrowing activity, which is assumed to relate to the abrasive coarse texture of sandy soils compared to loamy soils. Both susceptibility to drought in soils with low clay contents and compaction and waterlogging in heavy clay soils could be detrimental to earthworms in general [19,23,27] and *L. terrestris* in particular [27].

2. Ground water levels: Very few studies assessed whether groundwater levels (wholly or partly) define anecic earthworm population density and its corresponding biomass. Decaëns et al. [28] observed lower anecic earthworm densities in both periodically flooded sandy soils (fluviosols) and soils with peat layers (histosols) than in more clayey plateaus. This finding may indicate that these earthworms escape environments with periodic water excess. At the field scale, Nuutinen et al. [29] found higher *L. terrestris* burrow and population densities above tile subdrains located at 1-m depth in sandy clay soil. This finding could either mean that reproduction rates are higher in these positions or that *L. terrestris* is able to select a suitable habitat whilst moving over the soil surface [30]. Although current research is inconclusive, favourable soil hydrological conditions are likely to play a role in successful anecic earthworm settlement [30,31].

3. Interspecific competition: Decaëns et al. [32] concluded that local earthworm species assemblies are highly structured by interspecific competition. Under lab conditions, Butt [33] showed that *L. terrestris* growth rate was impaired through interspecific competition, which is probably related to resource depletion. According to Butt [33], a larger species like *L. terrestris* cannot keep up with smaller epigeic earthworms that have the advantage of a higher growth and reproduction rate. *Lumbricus rubellus* is an epigeic earthworm species that can be abundant in grassland and, in Europe, is often found to co-occur with *L. terrestris*. As L. *terrestris* and this epigeic species both feed on plant litter, interspecific competition for resources seems plausible.

4. Management: Soil physicochemical factors and groundwater levels could set limits for anecic earthworm population density, and thus field management could define local limitations [22,28]. Anecic earthworms have been found to prefer low soil disturbance conditions (e.g. no ploughing), which are characteristic of orchards, perennial cropland, permanent grasslands as well as field margins [19,22,28,34–36]. Population density recovery in grasslands after mechanical soil loosening may take at least two to three years [34,36,37]. Soil compaction has also been shown to impede burrow formation and maintenance by *L. terrestris* [12,38,39]. Benefits of high-quality (high N) plant litter and organic fertilizer inputs for population growth of anecic earthworms have frequently been demonstrated [19,35,37,40–43]. The rate of high-quality soil organic matter input is therefore an important determinant of anecic earthworm abundance.

Currently it is known that the distribution of *L. terrestris* is heterogeneous at the field and landscape scale. However, we lack a set of parameters that explains their occurrence, especially on grasslands on sandy soils, while the ecosystem service of water regulation in this land use and soil type combination is very important. This field inventory aims to improve our understanding of the factors that define *L. terrestris* presence and abundance in grasslands on sandy soil. Factors of importance are expected to be (1) soil texture characteristics, (2) groundwater level, (3) competitive interaction with resident earthworm species and (4) land use and management.

We hypothesised that anecic earthworm population densities are (1) positively correlated with soil silt concentration, (2) positively correlated with the depth of the highest groundwater level, (3) negatively correlated with epigeic earthworm abundance, and (4) positively correlated with the number of years without mechanical soil disturbance.

2. Materials & methods

2.1. Study area

Earthworm and soil sampling was carried out between March and May 2021 in an area with sandy soils south of the National Park Loonse and Drunense Duinen between Den Bosch and Tilburg in the province of Noord-Brabant, the Netherlands. This area was selected since it has a variety of sandy soils with different textures and is known to host *Lumbricus terrestris* (Linnaeus, 1758). The research area is a patchy landscape where small woodlands alternate with grassland, arable land and orchards, and it is heterogeneous in terms of its geomorphology, groundwater levels and soil texture. Geodata [44,45] was used to find grasslands of varying geomorphology interrelated with a range of soil types, texture classes and ground water stages (Table 1, Table 2). Grasslands were divided into age categories 'young' (≤3 years) and 'old' (>3 years), based on the number of years without disturbance (Table 1). The 'disturbance' was either direct grassland renewal in the form of ploughing followed by reseeding (grassland to grassland) or in the form of ploughing and seeding grassland after maize cultivation (maize to grassland). Ultimately, 31 grasslands that were distributed over 11 farms complied with the selection criteria. Because of the multiple selection criteria it was not possible to create a completely balanced set of grasslands with regard to age (11 young grasslands and 20 old grasslands).

Weekly rainfall during the earthworm and soil sampling period was higher in March 2021 than in April 2021 (Fig. 1).

2.2. Earthworm sampling and burrow counting

In each grassland, two plots (40 × 40 cm) were sampled (62 plots in total). The plots were located at representative locations at least 40 m apart from each other, distance to the border of the grassland was at least 10 m. We applied a combination of hand-sorting and AITC extraction [46]. From each plot, one cube of 20 × 20 × 20 cm was dug out and transported to the laboratory. The cube was then hand-sorted in order to identify all the earthworm species that it contained and to count their total numbers. Three more 20 × 20 × 20 cubes were dug out in order to create a pit of 20 cm deep and 40 × 40 cm in length and width. At the bottom of the 40 × 40 cm pit, the holes were counted that were assumed to be burrows of *L. terrestris* (ø >2 mm), to check for a correlation with *L. terrestris* abundance. Subsequently, approximately 4 L of 0.01% allyl-isothiocyanate (AITC) solution was applied to the bottom of the pit to collect *L. terrestris* from the deeper soil layers. All earthworms emerging at the pit surface within 20 min were collected, rinsed with water and stored in containers. The earthworms collected by hand-sorting and AITC extraction were washed with water, patted dry, weighed and stored in ethanol at 7 °C until further species identification was carried out. Earthworms were categorized as 'adult' if a clitellum was present and as 'juvenile' if a clitellum was absent. Adults were identified to species level [47], for juveniles it was checked whether they were *L. terrestris* or not. Juveniles of L. *rubellus* and *L. terrestris* were distinguished from each other by checking considerable thickenings of any septa, which, as described by Stöp-Bowitz, are absent for *L. rubellus* [48]. No other species that could have been interchanged with *L. rubellus* or *L. terrestris* were present in the samples.

Table 1
Categorisation of sampling points (number of sampling points between brackets) by soil type, soil texture class, landscape geomorphology, ground water stage (based on highest [HGL] and lowest [LGL] groundwater levels throughout the season) and grassland age.

Soil type[1]		Soil texture class[2]		Geo-morphology	Groundwater stage		Grassland age
	A-horizon		*Texture (%)*		*HGL (cm)*	*LGL (cm)*	
Sandy thick earth soil (19)	≥50 cm	Loamy sand (43)	Sand: 50-82.5; Clay: ≤8; Silt: 17.5-50	Plateau (26)	<25 (13)	120-180 (13)	≤3 years (22)
Sandy hydro-earth soil (31)	<50 cm	Light loamy sand (13)	Sand: 82.5-90; Clay: ≤8; Silt: 10-17.5	Plain (34)	<25 (6)	>180 (6)	>3 years (40)
Sandy xero-earth soil (12)	<50 cm	Loam-poor sand (6)	Sand: 90-100; Clay: ≤8; Silt: 0-10	Slope (2)	40-80 (13)	>180 (13)	
					80-140 (12)	>180 (12)	
					>140 (18)	140-180, >180 (18)	

[1] [51]; [2] [49], [50]

Table 2
Range of soil physico-chemical parameter values measured in the sampled grasslands, at 0–10 cm and 30–40 cm depth; mineral percentages are calculated as fraction of total mineral weight; SOM percentages are calculated as fraction of total soil weight.

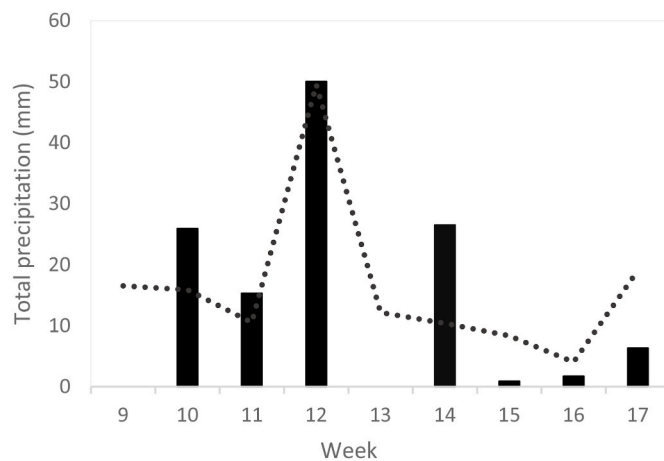|	0–10 cm depth			30–40 cm depth			
	Min.	Max.	Mean	Min.	Max.	Mean	
Clay (%)	1	9	3	1	10	3	
Silt (%)	7	42	25	7	42	24	
Sand (%)	52	91	71	50	92	70	
SOM (%)	2.5	16.0	5.2	1.1	7.4	2.6	
pH-KCl	4.5	6.9	5.4	4.6	7.4	5.4	

Fig. 1. Bars indicate total precipitation per week measured at Tilburg weather station in March and April 2021 (KNMI, n. d.). Trendline (dots) represents the 10-year precipitation average (2011–2020).

2.3. Assessing soil profile and soil sampling

An auger (10 cm diameter) was used to assess the soil profile (0–120 cm) and the soil type of each earthworm sampling plot. Information was recorded on A-horizon thickness, depth of clay layers and hydromorphic characteristics. Based on the results of texture analysis, soils were categorized as loam-poor, light loamy or loamy sands, according to a Dutch texture classification [49,50] (Table 1). Furthermore, they were classified as Earth soils (Fimic Anthrosols/gleysols), and most were characterised by an anthropogenic A-horizon, with or without the formation of hydromorphic features [51] (Table 1). Moreover, gley depth in cm was recorded as a measure for temporary maximum groundwater or pseudo-groundwater tables. Gley layers are characterised by a pattern of rust spots resulting from seasonal water table fluctuations.

Field-moist soil samples were taken from the 0–10 and 30–40 cm soil layer with a gouge auger (2.5 cm diameter) from 15 spots within a 2-m radius from the earthworm sampling plot to realise composite samples of approximately 200 g. Soil samples were stored at 7 °C until further analysis. Samples were analysed at Eurofins Wageningen for soil physical and organo-chemical characteristics. Clay (<2 μm diameter) content were determined through density fractionation (NEN 5753, 2018). Soil clay, silt and sand content was determined by the pipette method and sieving (resp. fractions <2, 2–50 and > 50 μm) and calculated as a fraction of mineral soil weight. Soil organic matter (SOM) was determined by loss-on-ignition [52]: after drying at 105 ± 5 °C, the soil sample was ignited at 550 ± 25 °C after which soil organic matter (SOM) was calculated as a fraction of the 105 °C dried soil. Soil acidity (pH) was measured after extraction in a 0.01 M $CaCl_2$ solution (Table 2).

2.4. Grassland management

Data about the history of land use (grassland age and prior crop to grassland) and fertilisation (e.g. type of organic manure applied - slurry or solid) were obtained from the farmer.

2.5. Data analysis

Prior to data analysis, earthworm abundance data was converted to number of individuals m^{-2}. For L. *terrestris*:

$$Individuals \left(\frac{\#}{m^2}\right) = Hand\ sorted\ cube * \left(\frac{1}{0.2 * 0.2}\right)(m^2) + AITC$$
$$* \left(\frac{1}{0.4 * 0.4}\right)(m^2)$$

Here, hand-sorted cube and AITC are the number of individuals retrieved with the methods described in section 2.2. The number of epigeics and endogeics retrieved from the hand-sorted cube in the laboratory were also converted to number of individuals m^{-2}. The number of burrows counted in the 40 × 40 cm pit was also converted to burrow density m^{-2}.

For all statistical analyses in this research, R version 4.0.3 (2020-10-10) and RStudio version 1.2.5042 [53–55] were used. The correlation between soil type, texture class, groundwater stage and grassland age categories (Table 1) and L. *terrestris* population density was analysed with the *lme4* package [56]. Linear mixed models were created in which the categorical data was used as a fixed effect and *farm* and *field* were used as random factors. Chi-square and Fisher's exact test were applied to assess the correlation between different factors and the absence/-presence of L. *terrestris*. Bonferroni corrections were applied when performing multiple comparisons.

For all correlative analyses, all 62 data points with and without

L. terrestris were used together. A general selection of variables correlating with *L. terrestris* population densities was retrieved by matrix-wise Pearson's r correlations of all the soil and earthworm community variables measured. Further selection candidate correlative variables took place by conducting stepwise Akaike's Information Criterion (AIC) forward selection. Variables that correlated significantly with *L. terrestris* population densities were used to perform a Principal Component Analysis (PCA) with the *stats package* [54] to ordinate *L. terrestris* population densities in a multidimensional space.

Furthermore, these selected variables were used for the creation of linear models to explore further the correlation with total, adult and juvenile densities of *L. terrestris*. Of each model presented, the coefficient of determination (R^2), $R^2_{adjusted}$ and the Root Mean Square Error (RMSE) are shown, along with significance levels of each variable within the model. Collinearity within the models was considered not to be an issue when the Variance Inflation Factor (VIF) values were <10. Additional correlation analyses were performed between *L. terrestris* density and burrow counts m^{-2}.

Normal distribution of linear model and mixed-model residuals was checked with the Shapiro-Wilk test and visually with histograms, quantile-quantile-plots (QQ), boxplots and residual plots. Log- and squared- and square root-transformations were applied if necessary for meeting the normality assumptions and performing regression analyses. When statistical analysis was performed on transformed data, this is mentioned in the figure and table captions. When normality assumptions could not be achieved for categorical data, the Kruskal-Wallis H test was applied if the assumption of equal variance (Levene's test) had been met.

The data, as obtained from the field inventory, was fitted into the existing classification tree for *L. terrestris* density m^{-2} as created by Lindahl et al. [27]. In accordance with Lindahl et al. [27], 'land-use type' was classified as 'perennial'. The percentage of lutum, sand and silt from the soil samples at 10 cm depth and 40 cm depth was used to determine the USDA soil texture classification of each sample. The obtained soil classifications were then translated into the categories (fine, medium, coarse) used by Lindahl et al. [27].

3. Results

3.1. General overview

Fig. 2 shows a general overview of the significant correlations between the *L. terrestris* population density and the parameters measured. *Lumbricus terrestris* population density (*TotalLT*) correlated with soil silt content at 30–40 cm depth and the presence of the epigeic species *L. rubellus*. Soil clay content and gley depth very slightly contributed to explaining the variation in *L. terrestris* population densities. Non-correlating factors (soil type, texture class, depth of A-horizon, groundwater stage, pH and SOM) were left out of the PCA for clarity (See Supp. Tables 5A and 5B for an overview of all tested correlations).

3.2. Soil abiotic characteristics and L. terrestris population density

Total, adult and juvenile *L. terrestris* densities did not differ significantly between soil texture classes. A range of 0–441 *L. terrestris* individuals m^{-2} was found in loamy sands, compared to 0–144 individuals m^{-2} in light loamy sands and 0–105 individuals m^{-2} in loam-poor sand (Table 3). Both adult and juvenile *L. terrestris* mean densities were highest in the loamy sand soil category (Table 3).

Silt (*%Silt40*) and clay (*%Clay10*) concentrations at a soil depth of 30–40 cm and 0–10 cm, respectively, were found to correlate significantly with *L. terrestris* total and adult population densities. Silt concentration correlated with *L. terrestris* total ($R^2 = 0.21$; $p < 0.001$) as well as adult ($R^2 = 0.33$; $p < 0.025$) and juvenile ($R^2 = 0.15$; $p < 0.025$) densities (Supp. Table 1). Clay concentration was only found to correlate significantly with total, adult and juvenile *L. terrestris* population
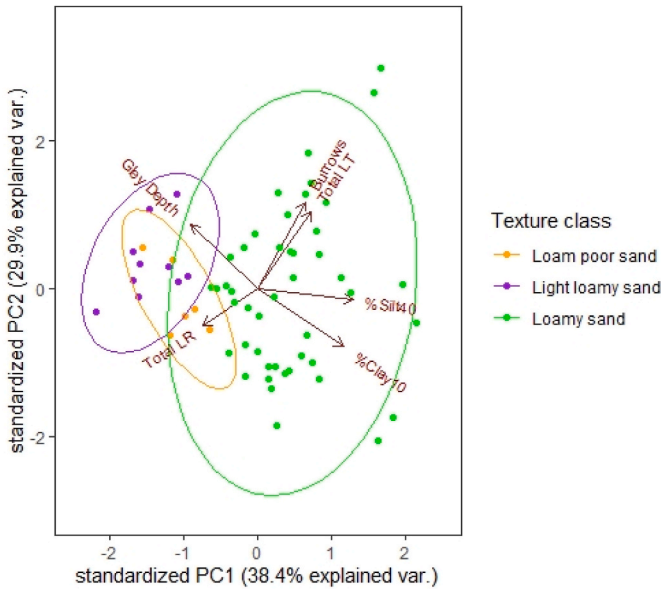

Fig. 2. Principal Component Analysis: ordination of sampling points in the plane shown along multiple soil textural and earthworm population correlation vectors, defined by Principal Components (PC) 1 and 2. Gley Depth = depth (cm) at which gley features start; burrows = number of vertical anecic earthworm burrows m^{-2}; Total LT = total *Lumbricus terrestris* (anecic) individuals m^{-2}; Total LR = total *Lumbricus rubellus* (epigeic) individuals m^{-2}; %Silt40 = percentage of silt in the soil at 40 cm depth; %Clay10 = percentage of clay in the soil at 10 cm depth.

Table 3
Lumbricus terrestris total, juvenile and adult number of individuals per texture class (# m^{-2}). In the 'Texture class' column, the number of sampling points is indicated between brackets. In the 'Mean' column, the standard deviation (SD) is indicated between brackets. Statistical analysis was applied to square root transformed data.

Lumbricus terrestris	Texture class (n)	Mean (SD)	P-value
Total	Loam-poor sand (6)	17 (43)	0.48
	Light loamy sand (10)	21 (48)	
	Loamy sand (46)	65 (97)	
Adults	Loam-poor sand (6)	1 (2)	0.28
	Light loamy sand (10)	6 (14)	
	Loamy sand (46)	14 (16)	
Juveniles	Loam-poor sand (6)	17 (41)	0.56
	Light loamy sand (10)	15 (39)	
	Loamy sand (46)	51 (88)	

densities as an added variable to silt concentration (Supp. Table 1).

Total population densities of *L. terrestris* were found to correlate positively with soil silt concentration at 30–40 cm and negatively with soil clay concentration at 0–10 cm depth (Fig. 3). Within the loamy sands, a strong positive trend was observed in *L. terrestris* population densities between a soil silt percentage of 20% and 40% (Fig. 3).

The results suggest that higher clay concentrations arising at 0–10 cm depth in loamy sands correlate with lower *L. terrestris* population densities. However, this correlation was only significant when modelled together with the soil silt concentration.

For 63% of the samples, fitting our data on texture into the classification tree by Lindahl et al. [27] (2009) resulted in an accurate estimation of *L. terrestris* density (low, medium, high; <3, 3–10, >10 m^{-2}, respectively). The accuracy of the classification tree for medium-textured soils was 51%, for coarsely-textured soils, it was 69%.
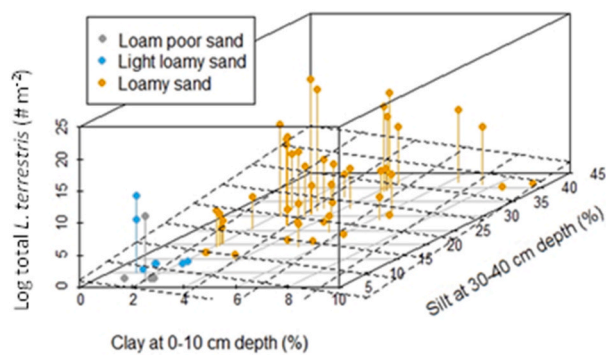
Fig. 3. Correlation between soil silt and clay concentration and total *Lumbricus terrestris* population densities m^{-2}. The plane represents the related linear model (Supp. Table 1). Texture classes based on a Dutch texture triangle [49, 50]. Total L. *terrestris* population densities are log transformed.

3.3. Gley depth and L. terrestris population density

Gley depth measured on site positively correlated with *L. terrestris* total densities when presented in a model with the silt concentration predictor ($R^2 = 0.25$; $p < 0.05$) (Supp. Table 2), Fig. 4 confirms this. Fig. 4 shows also that *L. terrestris* population densities tend to be slightly higher at the sample locations where gley was found deeper in the soil profile. It should be noted that gley depth correlated negatively with both silt and clay concentrations at 10 and 40 cm soil depth ($p < 0.05$) (Supp. Tables 5A and 5B).

3.4. Correlation between L. terrestris and L. rubellus population density

A significant negative correlation was observed between *L. rubellus* population densities and *L. terrestris* total and adult population densities ($R^2 = 0.10$; $p < 0.025$ and $R^2 = 0.11$; $p < 0.025$ respectively) (Supp. Table 3). No significant correlations were found between *L. rubellus* population densities and *L. terrestris* juvenile population densities. The significant correlations are presented both in models with only *L. rubellus* population density as a factor and in models where soil silt concentration and gley depth are added as factors (Supp. Table 3).

A significant negative correlation was found between silt concentration and adult *L. rubellus* population density ($R^2 = 0.10$; $p < 0.025$). Mean *L. rubellus* total population densities were 79, 133 and 45 individuals m^{-2} in loam-poor, light loamy and loamy sands, respectively.
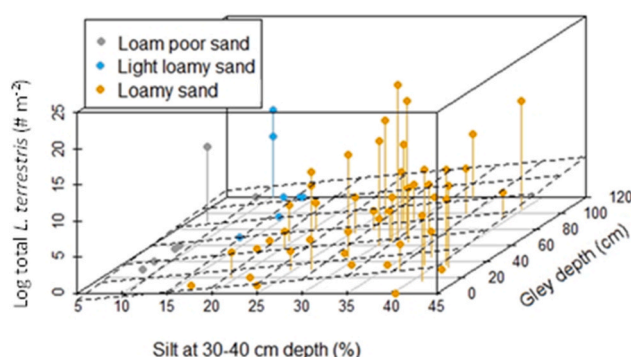
3.5. Grassland age and L. terrestris population density

Grassland age did not significantly correlate with *L. terrestris* population densities (Supp. Tables 5A and 5B). Furthermore, differences in *L. terrestris* population densities between grasslands classified as old (>3 years) and young (<3 years) were not significantly different.

3.6. Correlation between L. terrestris burrow density, soil texture and L. rubellus population density

The density of vertical burrows, which were assumed to be (formerly) inhabited by *L. terrestris* individuals, was linearly correlated with the total *L. terrestris* population density (Fig. 5). Burrow density also correlated with the factors discussed in the previous sections: it correlated positively with silt concentration and gley depth and negatively with clay concentration and *L. rubellus* population density (Supp. Table 4).

4. Discussion

4.1. Texture

Soil silt concentrations at 30–40 cm depth positively correlated with both *L. terrestris* adult and juvenile densities in grasslands. This finding supports our hypothesis that loamier grassland soils host higher *L. terrestris* population densities. Clay content at 0–10 cm depth correlated negatively with *L. terrestris* population densities (Table 2; Fig. 3). Moreover, *L. terrestris* was also present in some very sandy soils (Fig. 3; Table 3), which was not in line with our expectations.

Higher densities of *L. terrestris* in loamier (less sandy) soils were found in earlier research [21,28]. Hawkins et al. [26] and Lee et al. [19] suggested that earthworm survival is impeded by the coarse texture and drought proneness of sandy soils. However, Guild [21] did find *L. terrestris* in coarsely textured soil, albeit in lower densities than in medium-textured soils. So did Chamberlain and Butt [57] during their inventory in a sand dune ecosystem in NW England, they reported low numbers of *L. terrestris* at a car park with sandy soil and low organic matter content (0.9%). Apparently, *L. terrestris* can also survive in loam poor sand, as was confirmed by our finding of *L. terrestris* in very sandy
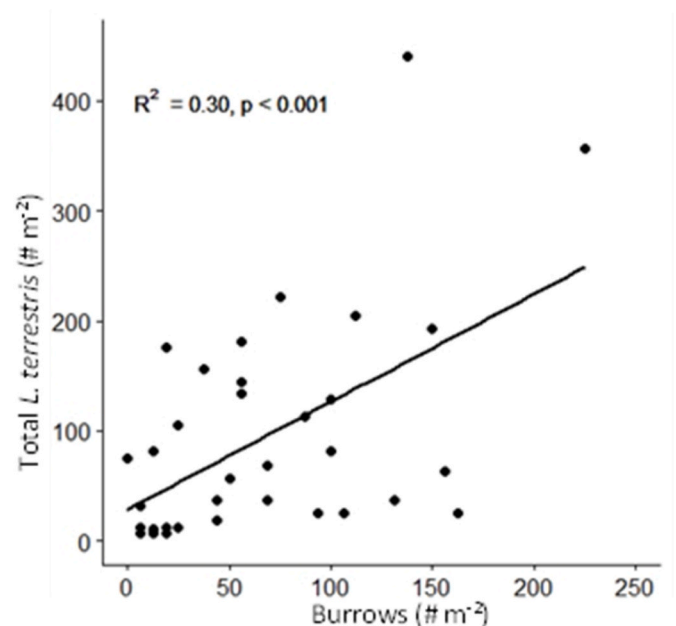

Fig. 4. Correlation between soil silt concentration at 30–40 cm depth, gley depth and total *Lumbricus terrestris* population densities m^{-2}. The plane represents the related linear model (Supp. 2); StartGley is the depth (cm) at which the gley starts. Texture classes based on a Dutch texture triangle [49,50]. Total L. *terrestris* population densities are square root transformed.

Fig. 5. Correlation between total *Lumbricus terrestris* population density and vertical burrows counted at the same sample site.

soil on one of the farms.

It may instead be that the *indirect* advantages of finer textured, loamy sand play a role in facilitating higher *L. terrestris* densities: these could create a niche with preferable water regulation compared to coarser textured soils [58,59]. Better moisture and nutrient retention in loamy sand has been suggested to provide a more favourable environment for earthworms than loam poor sand [19,23,60]. Furthermore, loamy sands are less sensitive to compaction and partly anaerobic conditions due to waterlogging than soils that are higher in silt and clay content [61,62] and badly drained (Rachel Creamer, pers. comm., 2021). This could also favour better *L. terrestris* settlement, despite the coarser soil texture.

In recent studies, soil compaction has been related to more superficial burrowing by *L. terrestris* [63], which indicates the plasticity of their behaviour. As a result, macroporosity in compacted soils is decreased [64]. Soil texture and its susceptibility to compaction could strongly affect water regulation, therefore we think they are very important factors in *L. terrestris* settlement in more sandy soils.

Fig. 5 shows the correlation between the number of burrows and the number of *L. terrestris* found is positive ($R^2 = 0.30$). *Lumbricus. terrestris* is known to create burrows that sometimes –not always [65,66]- branch below the soil surface [67,68], which could have resulted in varying numbers of *L. terrestris* per hole counted. Additionally, burrows can survive longer than their inhabitants [69]. For this reason it was decided not to discuss burrow abundance in relation to the measured variables. We consider burrow counting a useful quick scan method for assessing *L. terrestris* presence and activity in the field. However, the method does not generate reliable data about the current actual *L. terrestris* population density.

4.2. Predictive power of a land use and texture model

Although *L. terrestris* population density was not significantly related to soil texture class, when fitting our population density data into the Lindahl et al. [27] land use and texture model, we found an overall accuracy of 63%. In medium-textured soils, the accuracy of the model was 51%; in coarsely textured soils, the accuracy of the model was 69%. Eight of our samples (out of a total of 62) could not be fitted into the model as their difference in texture between 10 cm depth and 40 cm depth did not allow us to assign them to the texture classes that were defined by Lindahl et al. [27]. They report a 71% accuracy of their classification tree for predicting *L. terrestris* density based on land use and soil texture.

The accuracy of the classification tree appeared limited in medium-textured soils for our data, we present three possible explanations. First, in the Lindahl et al. [27] paper, the classification tree is correct in for fine and medium textured soils in 90% of the cases. It could be that in coarsely-textured soils, it is mainly texture or effects of texture that prevent high *L. terrestris* densities, whereas in medium-textured soils, soil texture and its direct implications are not paramount. Second, we think that the textural classes that were used in our inventory may have been too broad to bring to light existing associations between earthworms and soil texture. This might explain why we did not find significant correlations between texture classes and *L. terrestris* population density. We recommend to increase the resolution of soil textural classes in future earthworm research. Third, the addition of an extra predictor after soil texture could possibly improve the predictive power of the classification tree. However, it is difficult to determine which parameter qualifies. We found that gley levels and grassland age do not explain enough variation. Holmstrup et al. [58] tried to find associations between soil texture, soil water characteristics and earthworm populations. They found that none of the investigated parameters explained the earthworm population, the parameters being: texture, pH, bulk density, water holding capacity and total C. Possibly the addition of a step regarding soil water regulation through the soil profile (e.g. water levels, infiltration capacity, penetration resistance) could improve the predictive power of the classification tree.

4.3. Gley levels

Gley depth was found to have low predictive power for *L. terrestris* total population densities, and only when added to models with soil silt concentration as a predictor (Fig. 4; Supp. Table 2). As gley depth is an indicator of the highest groundwater levels, we expected this correlation to be stronger.

The absence of compaction layers prone to waterlogging and associated formation of temporal shallow 'groundwater' levels (pseudo-groundwater) indicates well-structured soils. Previous research suggests that well-structured, porous and deep-drained soils are suitable for anecic earthworms [28,29,31,39,70]. In deeper soil layers, anecics possibly avoid predation and highly fluctuating soil moisture and temperatures in the top layers.

To better understand the relationship between *L. terrestris* population density and groundwater dynamics, we recommend researchers in the future measure both the highest and lowest soil groundwater levels as well as subsoil bulk density to assess susceptibility to waterlogging, which could affect *L. terrestris* population densities.

4.4. Earthworm species interactions

We hypothesised a negative correlation between *L. rubellus* abundance and *L. terrestris* abundance, and the results confirmed this. Both these species feed on surface organic material; therefore, interspecific competition between these species may arise when food sources are limited. This could have contributed to the negative correlation between *L. terrestris* and *L. rubellus* population densities. *Lumbricus rubellus* has a higher reproduction and growth rate than *L. terrestris* and may therefore outcompete the latter for limited aboveground food sources [33,71].

Negative interactions between the two species were already suggested in previous research under semi-controlled conditions but not yet in a field inventory like ours. Lowe and Butt [72] found lower growth rates of *L. terrestris* individuals when grown together with *L. rubellus* adults than when grown together with *L. terrestris* adults. Laboratory experiments by Eriksen-Hamel and Whalen [73] indicated that heavier earthworms (like *L. terrestris*) show a stronger reduction in growth rate than smaller earthworms in a multispecies setting. Van de Logt et al. [74] observed a negative correlation between *L. rubellus* population density and *L. terrestris* population density when both species were present in a mesocosm set-up.

Differences in habitat preferences of anecics and epigeics may also have played a role in the negative correlation observed between *L. terrestris* and *L. rubellus* population densities in sandy grasslands. Decaëns et al. [28] observed dominance of epigeics and endogeics in low-lying soils (histosols, fluvisols) with periodic water excess, while anecics were more prevalent in higher-located, better-drained soils (reductisols). They indicate that land use and specific soil properties may also explain the distribution of earthworm ecological groups (e.g. peat layer in histosols and sandy texture of fluvisols) [28]. In a modelling study based on empirical data by Palm et al. [75], it was suggested that epigeics prefer lower elevations, in contrast with anecics. This suggestion was based on the deep-burrowing activity of anecics, avoiding high groundwater levels, and the preference of epigeics for moist soils. Nordstrom and Rundgren [23] indicated that *L. rubellus* is less confined to soils with a certain pH and texture range than *L. terrestris*. This finding corresponds with our observation that considerable abundances of *L. rubellus* where found in loam poor and light loamy sand as well as loamy sand, while for *L. terrestris* they were especially found in the latter. Despite slight differences in habitat preference, it is very common for *L. rubellus* and *L. terrestris* to co-occur in European grasslands. We think it is likely that competition for food plays a role in the observed negative correlation between *L. terrestris* and *L. rubellus*.

4.5. Grassland age

Grassland age did not significantly correlate with *L. terrestris* population densities. This could be due to a relatively low number of young grasslands (≤3 years) in our dataset (n = 31), 11 young grasslands versus 20 old grasslands. We expected to find a positive correlation between the number of years without soil disturbance and the abundance of *L. terrestris*, as the negative influence of soil disturbance on earthworm population densities is broadly accepted [19,22,28,34–37]. After disturbance by mechanical soil loosening, earthworm population density was found to recover within three years [34,36]. Only Lees et al. [34] specifically looked at anecics, which they found to recover three years after deep mechanical soil loosening.

Van Eekeren et al. [76] argued that recovery of earthworm population density after disturbance is not only a function of time but also of the quality and amount of organic matter input (e.g. plant litter, manure) and the presence of an insulating vegetation layer. Also, the presence of low-disturbance, resource-rich field margins hosting *L. terrestris* could improve the recovery of populations in the field after disturbance [30,77]. Lower numbers of *L. terrestris* found in some young grasslands in our study could have been a combined result of recent soil disturbance, low organic matter input from the previous crop (maize) and, in some cases, a large distance from undisturbed field margins. Future research could further disentangle the effects of the pre-crop, management and semi-natural landscape elements in temperate grassland landscapes on anecic earthworm population density.

5. Conclusions

In this earthworm inventory in grasslands on sandy soil, we found that *L. terrestris* was more abundant in soils with a higher silt percentage, likely because of positive relationships between loaminess and other soil factors like soil moisture and nutrient retention, resulting in favourable living conditions. Unexpectedly, *L. terrestris* was also present in a grassland on loam-poor sand. Demonstrating the ability of the species to establish itself in sandy soil. The classification tree by Lindahl et al. [27] correctly predicted the level of *L. terrestris* abundance based on land use and soil texture in 63% percent of our data points. A weak positive correlation was observed between *L. terrestris* population densities and gley depth. Gley depth is an indicator of maximum groundwater levels. Higher groundwater levels or soil profiles with temporarily waterlogged layers could create less hospitable, oxygen-poor environments for the deep-burrowing *L. terrestris*. Additionally, a negative correlation with epigeic earthworm *L. rubellus* abundance was shown. We suspect this is caused by competition for soil surface food resources, perhaps combined with slightly diverging soil habitat preferences. Overall, this correlative study provides further insights into *L. terrestris* habitat selection, which helps us understand the species' potential for water regulation in the widespread grassland agro-ecosystems.

6. Statements & declarations

This work was supported by the Public-Private Partnership KLIMAP. 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. Authors Roos van de Logt and Thom van der Sluijs contributed equally to the creation of the manuscript. Experimental design, data collection, writing and revision were done by Roos van de Logt and Thom van der Sluijs. Data analysis was performed by Thom van der Sluijs. Experimental design, writing and revision of the manuscript were done by Nick van Eekeren. All authors read and approved of the final manuscript. The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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