university of groningen

Grappling with greppels: How historical soil relief structures of grassland affect earthworm abundance and reproductivity

A time series throughout the meadow bird breeding season

Meri Hut
s3510867

14-10-2024

Supervised by Renée Veenstra & Prof. Dr. Theunis Piersma

Abstract

The disappearance of *greppels,* microrelief structures in the landscape, due to the intensification of agriculture in the Netherlands may significantly impact earthworms and their ecosystem functions, such as soil improvement and serving as a food source for higher trophic levels. This study compares earthworm populations across different ecotypes in grasslands with intact *greppel* structures and intensively managed fields. The research was conducted during the meadow bird breeding season, a period when Dutch grassland soils typically become drier due to evaporation rates exceeding precipitation.

The results show a stronger decline in earthworm populations, particularly among epigeic and endogeic ecotype species, in intensive fields compared to *greppelland*. The more rapid drying of soils in intensive fields hinders earthworm survival and reproduction. In contrast, *greppelland* retains more moisture, especially around water-retaining *greppels*, supporting higher reproductive activity. Earthworms in these areas exhibit prolonged fertility, which is crucial for sustaining populations.

Different ecotypes, such as epigeic and endogeic species, adopt various survival strategies during drought conditions. However, their overall functionality in nutrient cycling and soil health will decrease in extended periods of drought. This study highlights *greppelland* as a critical refuge for earthworms during drought, helping to preserve their ecological functions, which are essential for sustainable agriculture and the ecosystem.

Cover image: Crónica

Table of contents

Introduction

With large parts of the country lying below sea level, proper water management has always been a major challenge for farmers in the Netherlands. The water must be kept at distance to prevent flooding and ensure proper growth and harvest of crops, while in times of drought water needs to be retained. Before the 1940s, the solution for managing water in agricultural grassland was man-made microrelief structures, called *greppels*. These *greppels* functioned as a system for transporting excess water to ditches and could temporarily retain water in the fields during dryer conditions (figure 1). The *begreppeling* (construction of *greppels* in a field) of farming plots likely dates back to 1540 or even earlier (Breuker, 2017; van Slochteren, 2021; Priester, 1991). There are multiple *greppel* systems known in different parts of the northern Netherlands. The directions and depth of the landscaped *greppels* vary per region and time in history. Terms within this kind of water management differ as well, because this study focuses on the northern Netherlands we will use the word *greppel* when referring to the 20-60 deep man-made gutters within a dairy farm grassland serving to manage the water level. The most simple *greppelland* structure is a field with *greppels* going in the same direction with a similar depth and the same distance between them, commonly in Friesland. These *greppels* drain the water directly from the land to the surrounding ditch (figure 2) (Breuker, 2017; van Slochteren, 2021; Priester, 1991).

Figure 1, *Historical dutch greppelland (van Slochteren, 2021).*

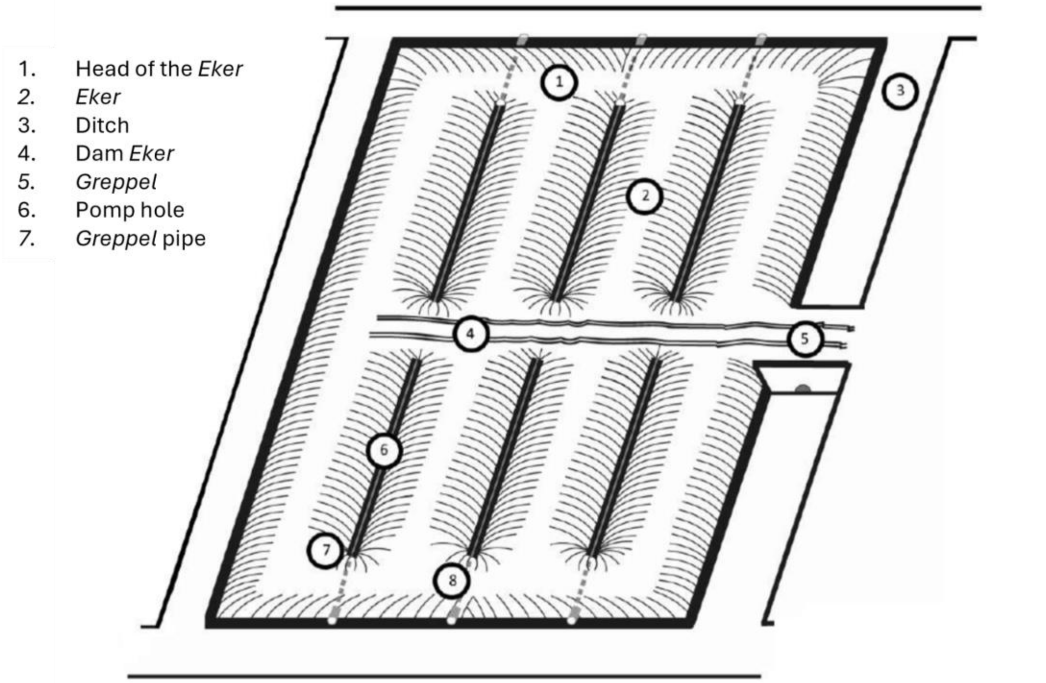

***Figure 2**, Schematic overview of a simple greppelland system (van Slochteren, 2021).*

The process of making these *greppels* is called *greppelen*. *Greppelen* was done by hand in late winter and early spring, when the soil was easier to cut and no harvest could be made. Ropes were stretched over the length of the field, along these lines the triangular shape of the *greppel* was cut with a cutting scythe. After this process the loose ground was dug out, forming the *greppel*. Later in time, horses were harnessed to a plough to accelerate the cutting process of the *greppels* as seen in figure 3 (van Slochteren, 2021).

Figure 3*, Imagery of the farmer cutting greppels with the help of a scythe and horsepower (Fries Film & Audioarchief, z.d.).*

Earlier in history, *greppels* reached fully to the slope of the connecting ditch. Later, the part of the *greppel* at the end of the parcel was closed, making it possible for larger machines to turn the end of the mowing strip. To maintain the drainage capacity of the *greppels*, ceramic pipes were placed underground to transport the water from the end of the *greppel* to the ditch. These ceramic pipes became available in the Netherlands from 1851 and were essential to farmers as agricultural machinery increased (van Slochteren, 2021; Priester, 1991).

Farming practices in the Netherlands kept on evolving over time. Despite the large-scale use of the ceramic pipes, the construction was labor intensive and expensive (Priester, 1991). Besides that, agricultural machines got bigger and heavier, making it hard to process the grass on the traditional *greppelland*. A new innovation using plastic pipes deeper in the ground ensured that *greppels* were not needed anymore to manage the water in the agricultural fields of the northern Netherlands. This new drainage technology required less maintenance compared to *greppels*, gained land (*greppels* causing 5-12% land surface loss) and bigger machines could be used because the modern underground drainage system could actively lower the water level in the field (Zander, 1963). All of this resulted in a higher yield for farmers.

The increase of yield was motivated by Dutch politics at that time, the aim of high profitability got more and more important. Intensive use of the agricultural land was motivated by subsidies and investments (Van de Bergh, 2004). Between 1950 and 1980 the consolidation process that involved the reorganizations and redistribution of agricultural parcels took place, significantly changing the landscape. This process was called the *ruilverkaveling*, where agricultural land had turned into flat, large fields with deep underground drainage systems. By the end of the 20th century the majority of the *greppelland* in the northern landscape had disappeared, and thereby the microrelief once formed by the *greppels* was lost (Van de Bergh, 2004; van Slochteren, 2021).

Besides the removal of *greppels,* other management practices changed too during this intensification process. Herb rich seed mixtures made place for a monoculture consisting of English ryegrass (*Lolium perenne*), a robust, protein-rich species. The soil is more disturbed because of the higher amount of plowing, mowing and harvesting. Instead of farmyard manure used in the extensively managed *greppelland*, grasslands are fertilized by injecting slurry (liquid dairy cattle manure) into the soil. The soil is used as a substrate for maximum yield, rather than a foundation for a properly working ecosystem, with biodiversity loss as a consequence (Neeteson, 2000).

Because *greppels* create small variances in height, they are forming a micro-relief in the landscape. As they drain water from the land in periods of high rainfall, but retain water or moisture in the *greppels* during drought, they create a gradient of moisture in the field. This functions as a valuable habitat for all kinds of species. One species group that is particularly influenced by soil moisture (and drought) are earthworms.

Earthworms are eco-system engineers, which means that they play a crucial role in delivering numerous ecosystem services (Blouin *et al.,* 2013; Lavelle *et al*., 2006). First of all, earthworms burrow channels and pores in the soil. Some species burrow small and temporary channels, while others make deeper, permanent ones. Earthworm burrowing activities contribute to the soil permeability, leading to improvement of the soil's aeration and water infiltration. Secondly, earthworms take organic litter from the soil surface deeper into the soil, where they increase the soil organic matter (SOM) by further breaking down the plant material into available nutrients. Deeper in the soil other species of earthworms, geophages, feed on soil. By this process they mix the soil and more nutrients become available deeper in the soil (Edwards & Arancon, 2022). Thirdly, castings of earthworms consist of nitrogen, phosphorus, potassium, carbon and calcium, known as primary macronutrients for plant growth (Clements *et al.*, 1991). The calcium present in the earthworm castings act as a natural pH buffer, helping to maintain a more stable pH in the soil. Moreover, earthworms increase microbial diversity by releasing diverse microorganisms through castings and creating microhabitats. With an increased microbial diversity, nutrient cycling is improved and the soil microbiome has a higher resilience against diseases (Edwards & Arancon, 2022). Finally, besides contributing to a fertile soil, earthworms play a crucial role in the food chain. Serving as a key component in the food chain, forming a link between plant-based material and higher trophic predators. They form a food source for a variety of other animals in higher trophic levels, like birds, foxes and badgers (Laird *et al*., 1981). Therefore, a healthy earthworm population boosts the local above-ground biodiversity and ensuring healthy earthworm populations is therefore vital for both agriculture and nature (Blouin *et al.,* 2013; Darwin, 1881; Macdonald, 1983; Van Groeningen *et al.*, 2015).

Based on their behaviour, earthworm species can be divided into three different groups, see figure 4 and 5 (Sanchez-Hernandez *et al.*, 2023). These three ecotypes of earthworms (anecic, endogenic, and epigeic) differ significantly in various aspects such as phenotype, diet, habitat, and response to drought (Bouché *et al.*,1977). Anecic earthworms are typically larger, and have a darker pigmentation. They feed on surface litter and organic matter, creating vertical burrows that can reach deep into the soil. These burrows help them access moisture during dry periods, making them more resilient to drought conditions (Edwards & Arancon, 2022). Endogeic earthworms are generally smaller and paler in color, often light pink or gray. They live within the soil and feed on soil organic matter and mineral particles, creating horizontal burrows. Once the soil moisture reaches a critical level, it will extract water from the earthworm's body, causing first their diapause. When endogenic earthworms enter the state of diapause, they curl up in a knot to reduce the contact with the surrounding dry soil (figure 6) (Edwards & Arancon, 2022; Holmstrup, 2001). Epigeic earthworms are usually small and often reddish-brown colored. They live near the soil surface and primarily consume decomposing organic matter. Due to their surface-dwelling nature, epigeic earthworms are highly sensitive to drought and rely on moist conditions to survive. Therefore the epigeic earthworm strategy to avoid drought, is to form eggs protected in cocoons, which have a higher survivability than the active stage (Edwards & Arancon, 2022). Each group's distinct characteristics reflect their adaptations to different ecological niches and environmental conditions.

Earthworms reproduce sexually, as they are hermaphrodites, meaning each worm has both male and female reproductive organs. During mating, two earthworms exchange sperm by aligning their bodies and secreting mucus from the clitellum. After mating, the clitellum produces a mucus cocoon, into which the fertilized eggs are deposited. The clitellum, a thick glandular band, is thus the important organ for the reproductivity of earthworms. Its presence indicates that the earthworm is mature and capable of reproducing (Edwards & Arancon, 2022).

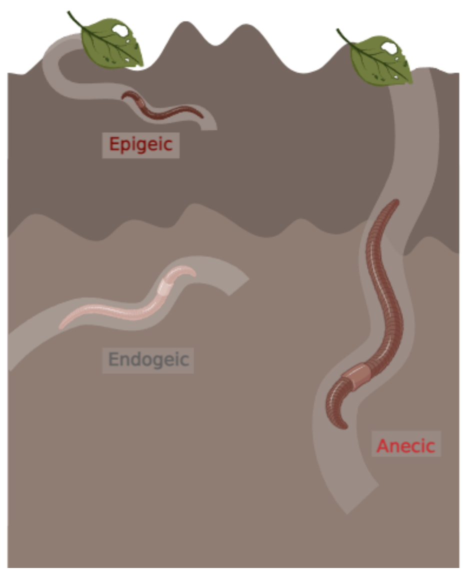

Figure 4*, Schematic overview of the three different earthworm eco-types. Made in Biorender.*

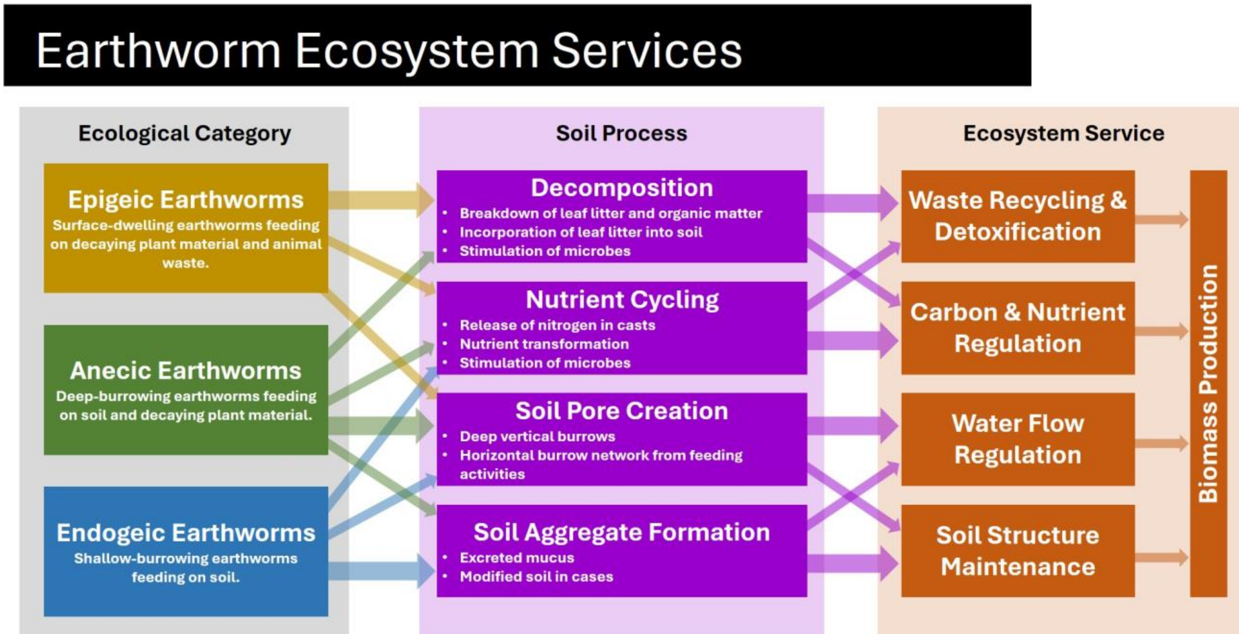

Figure 5*, overview of the different earthworm ecotypes and their role in the ecosystem (Keith & Robinson, 2012).*

Figure 6*, A. Caliginosa in diapause during drought, forming a knot (Friis et al., 2004).*

The management of agricultural grasslands affects earthworm communities in several ways. By altering the plant species for example, earthworm abundance and biomass reduces with less plant species richness (Eisenhauer *et al.*, 2011; Milcu *et al.*, 2008). High fertilizer input has been shown to reduce earthworm biomass and abundance compared to low fertilizer input. However, completely stopping the fertilization leads to long-term decrease in earthworm biomass and abundance (Bekker *et al.*, 2006; Clements *et al.*, 1991; Timmerman *et al.*, 2006). Anecic and epigeic earthworm species are more abundant in grasslands fertilized with farmyard manure than fields fertilized with slurry manure, while endogeic species are unaffected by the fertilization method (Onrust & Piersma, 2019). The cutting (typically 3–5 cm deep with slits 15–25 cm apart) of the topsoil to inject the slurry manure is disturbing the soil and reducing the abundance of earthworm species living in the top of the soil (De Goede *et al.*, 2003). Similarly, Timmermans *et al*. (2006) showed earthworm abundance decreased in grassland fertilized with slurry manure compared to grasslands fertilized with farmyard manure or not fertilized at all. However, completely stopping fertilization in the long-term leads to a decrease in earthworm biomass and abundance (Bekker *et al.*, 2006; Clements *et al*., 1991). Moreover, because of the importance of moisture on the survival of all earthworm species, the lowered water tables in intensive agricultural practices decrease earthworm activity (Carroll *et al.*, 2011; Onrust *et al.,* 2019).

Aim of the research

The exact relationship between *greppel*s and earthworm populations remains unclear. Because extensively managed *greppelland* typically differs from intensively managed fields, not just in drainage systems but also in other practices such as fertilization, mowing and vegetation diversity, makes it challenging to determine the direct effect of *greppelland* on earthworm populations itself. This study tries to address this knowledge gap by setting up an in situ experiment mapping the earthworm population within the *greppelland* itself, and a comparison to intensive managed fields. The main question here is: How does the microrelief of the *greppelland* affects earthworm abundance and reproductivity? Due to their difference in ecology, we try to answer these questions for epigeic, endogeic and anecic species separately. To answer these questions, different variables were measured over the timespan of the meadow bird breeding season in Friesland (March to June). Comparing earthworm abundance, knot-forming and reproduction between *greppelland* and intensively managed grasslands and within *greppelland* itself.

Hypothesis

In early spring, higher rainfall can keep soil moist in both extensively managed *greppelland* and intensively managed fields. However, as rainfall decreases and temperature rises later in spring, intensively managed fields with underground drainage systems will dry out more quickly compared to the *greppelland* where water is retained (figure 7) (Carroll *et al.*, 2011; Onrust *et al.*, 2019). This will have a negative effect on the overall abundance and reproductivity of earthworms. Because of the different earthworm strategies to survive drought, abundance is expected to be dependent on the ecotype of the earthworm. Because of their robustness against drought, endogeic and anecic species are expected to still be present in the dry part of the season. In contrast, epigeic species are more sensitive to drought, therefore these species are expected to have a lower abundance as the season processes, especially in the intensive field type. As earthworms are capable of some degree of habitat selection (Caro *et al.*, 2012; Eijsackers, 2011; Kim *et al.*, 2017), we expect an overall higher abundance and reproductivity nearer to the wetter locations within the *greppelland* in the dry part of the season. Particularly for the drought-sensitive epigeic species, this *greppel* could be beneficial for their survival (Edwards & Arancon, 2022).

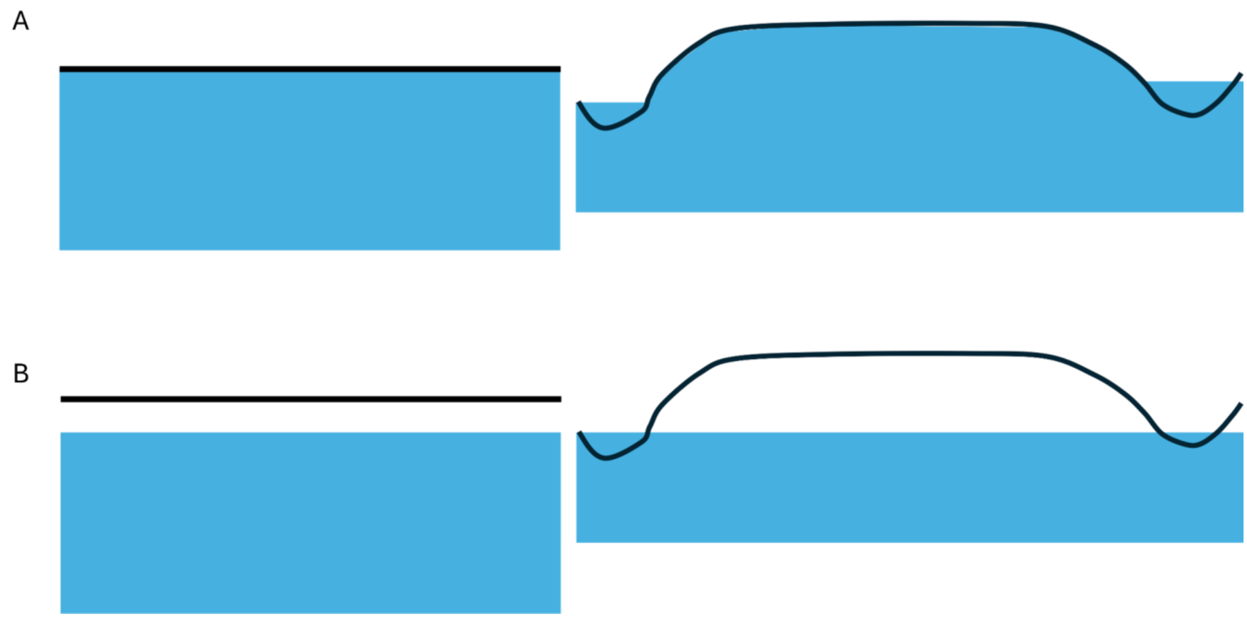

Figure 7, *schematic overview of the water level in the different field types. With A) representing the wet part of the season, and B) representing the dry part of the season.*

Materials & Methods

Study area

The observation period took place from March 20 to June 30 in the year 2023, coinciding with the meadow bird breeding season in the Netherlands. We gathered data from six parcels within a dairy farm located in the hamlet of Scharneburen, situated in Southwest of Friesland (52°59'43.2"N 5°26'08.2"E) (figure 8). This area is characterized by loamy soil, with a clay content ranging from 17,5% to 25%. Soil composition becomes progressively clayier towards the East, while the western side tends to be slightly sandier (*Bodemdata*, n.d.). Summer and winter water levels in the surrounding ditches are regulated by a nearby pumping station, maintaining consistent water levels across the area (S. Sterkenburgh, personal communication, June 30, 2023). For this study we examined a total of six parcels, half of which are intensively managed grassland (I1, I2, I3), while the remaining three fields are historical *greppelland* (G1, G2, G3) (figure 9).

***Figure 8**, Location of the research area.*

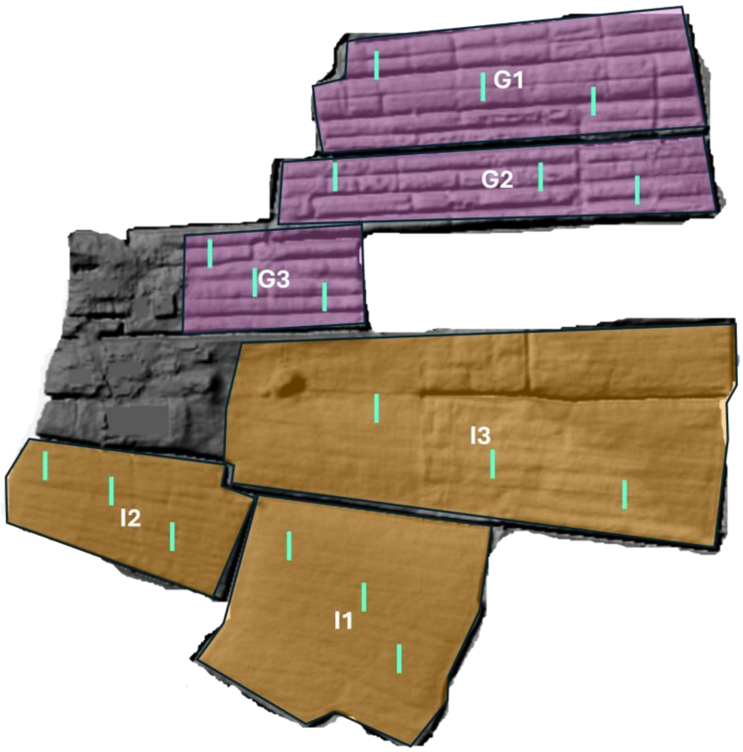

Figure 9, *Overview of the different parcels with transects.*

Water regulation in the *greppelland* is regulated via a *greppel* system, with ceramic pipes. These *greppel* fields are ancient, their exact date of origin remains unknown. Due to the historic nature of these fields, the vegetation naturally reseeds itself, resulting in a variety of plant species. Parcels G1 and G3 were fertilized with farmyard manure. And G1 was grazed by calves from June 16 onward. Mowing in these fields was postponed until June 15. In field G2 a solar powered pump is installed to create wetland. The selected intensively managed fields comprised a monoculture of english ryegrass (*Lolium perenne*), where water is regulated by an underground drainage system. The intensive fields were fertilized with injected slurry. Starting from May 30, cows grazed alternating parts of the intensive grassland. The first mowing of these grasslands took place around May 11 (S. Sterkenburgh, personal communication, June 30, 2023).

To answer the research question, abundance of different earthworm species is monitored in greppelland parcels biweekly. As a comparison this same monitoring scheme is conducted to intensively managed agricultural grasslands. Per field we took soil samples along three transects that encompass the variability within the parcel (table A1) (figure 9). Each transect comprises three locations, reflecting the differences in slope height within the *greppelland*. This entailed placing one location at the top of the *eker*, another halfway towards the *greppel*, and the last one near to the *greppel* itself (figure 10). Similar distances between locations were maintained in the intensive fields. Consequently, we have parallel datasets for both the *greppelland* and the intensive fields within this study.

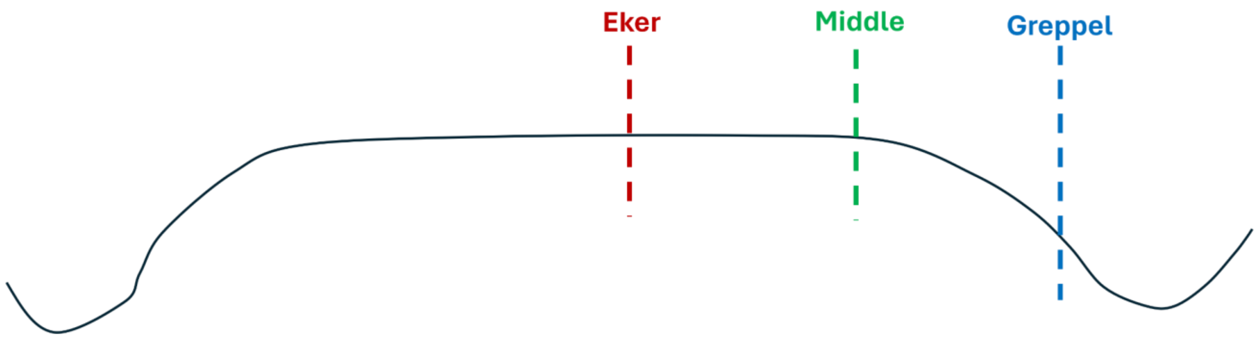

Figure 10*, Schematic overview of the different locations within a greppelland transect.*

Study species

Per point we took a 20 x 20 x 20 centimeter soil sample with a shovel. The top 10 centimeter was separated from the lower 10 centimeter. Per layer, all earthworms were collected by hand and taken to the field station. In the field, we counted the earthworms that formed a knot. We identified the earthworms alive to genus level and, if possible to species level. Per sample and per species, we counted the abundance and number of earthworms with a clitellum. The earthworm species were categorized into three ecological groups (Barois *et al.*, 1999), see table 1. The fraction of fertile earthworms was calculated by dividing the total number of earthworms with the total number of earthworms with a clitellum in a sample. The fraction of earthworms in diapause was calculated by dividing the total number of earthworms with the total number of earthworms forming a knot in a sample. To determine the abundance of earthworms per square meter, the following calculation was used.

$$Earthworm\ abundance\ per\ square\ meter = \frac{Earthworms\ found\ per\ sample}{Sample\ area\ (m^2)}$$

$$Earthworm\ abundance\ per\ square\ meter = \frac{Earthworms\ found\ per\ sample}{0{,}04}$$

$$Earthworm\ abundance\ per\ square\ meter = Earthworms\ found\ per\ sample\ * 25$$

Table 1, *The earthworm species found in this research, classified per ecotype.*

Ecotype	Species
Epigeic	*Eiseniella tetraedra*
	Lumbricus castaneus
	Lumrbicus rubellus
	Satchellius mammalis
Anecic	*Lumbricus terrestris*
	Apporrectodea longa
Endogeic	*Allolobophora chlorotica*
	Aporrectodea calignosa
	Aporrectodea rosea

Environmental measures

Per point, the moisture percentage of the soil was measured in triplo using a soil moisture sensor (models: SM150T, Delta-T Devices Ltd and Delta-T Devices Ltd, 2016). Measurements were conducted both at the soil surface (SM top) and at a depth of 10 cm (SM Bottom). This approach was adopted since it is hypothesized that the soil moisture readings at the top soil may be influenced by factors such as heavy rainfall or drought, potentially leading to more extreme values. Therefore, deeper soil measurements are suggested to provide a more reliable estimate of soil moisture percentages over an extended period in the field.

To show the change in rainfall during the meadow bird breeding season in 2023 at our study site, we gathered the precipitation deficit from the Koninklijk Nederlands Meteorologisch Instituut (KNMI), location 267: Stavoren (*Dagwaarden Van Weerstations*, KNMI). Precipitation deficit is a measure of drought that takes both precipitation and potential evaporation (evaporation and transpiration from plants) into account. Thereby refers precipitation deficit to the shortfall in the amount of precipitation in a period, measured in millimeters.

$$Precipitation\ Deficit\ (mm) = E\ (mm) - P\ (mm)$$

$E = The\ sum\ of\ daily\ reference\ vegetation\ evaporation\ over\ a\ specified\ time\ period$

$P = The\ sum\ of\ daily\ precipitation\ over\ a\ specified\ time\ period$

Statistical analysis

To analyze earthworm dynamics over time, the season was divided into three periods: Early (Julian Date 79 -104), Mid (Julian Date 114-137), and Late (Julian Date 157-181).

All statistical analyses were performed in R (v4.3.1, 16-06-2023) (R Core Team, 2023). The 'tidyverse' package (v2.0.0) (Wickham *et al*., 2019) and the 'dplyr' package (v1.1.2) (Wicham *et al*., 2023) were used for organizing and structuring the data. We ran generalized linear mixed models (glmm) with the 'glmmTMB' package (v1.1.8) (Brooks *et al.*, 2023), with different distributions (table 2). To explore the correlation between the predictor variables and the response variable we used the standard summary function from R and Post Hoc test from 'emmeans' package (v1.8.7) (Lenth, 2023). For the seasonal field description soil moisture content was used as the response variable. Between field types and within *greppelland* we tested multiple response variables: abundance (total and per ecotype) per square meter, reproductive earthworms and earthworms in diapause.

Due to the strong negative correlation between soil moisture and the progression of the season, it was not feasible to include both soil moisture and seasonal progression in our model. Given our focus on the trend of worm populations during the breeding season, we opted to include time in the model instead of soil moisture. We assume that the decline in worm numbers over time is driven by, or at least correlated with, the decrease in soil moisture.

All full models were stepwise reduced by removing a non-significant predictor variable and comparing models using the Akaike's information criterion (AIC). Where models with the lowest AIC, representing the model with the lowest information loss, were selected (Burnham *et al.*, 2011). If the difference between models was above the threshold of Δ7 AIC, we followed the rule of parsimony and selected the simplest model (Burnham *et al.*, 2011).

$$Akaike\ information\ criterion\ (AIC) = 2k - \ln(\hat{L})$$

$k = The\ number\ of\ estimated\ parameters\ in\ the\ model$

$\hat{L} = The\ maximized\ value\ of\ the\ likelihood\ function\ for\ the\ model$

Table 2, *Overview of the final models used, including response variables, significant fixed effects, random effects and the distribution family.*

	Response variable	Fixed effects	Random effect	Family link
Field descriptions	Soil moisture (%)	JD + Field type	FieldID	Tweedie
	Soil moisture (%)	JD + Point	FieldID	Negative binomial
Between field types	Abundance / m2	Field type * Period	FieldID	Negative binomial
	Reproductive earthworms	Field type * Period	FieldID	Beta binomial
	Earthworms in knot (late period)	Field type	FieldID	Beta binomial
	Abundance (ecotype) / m2	Field type + Period	FieldID	Negative binomial
Within *greppelland*	Abundance / m2	Field type * Period	FieldID	Negative binomial
	Reproductive earthworms	Field type * Period	FieldID	Beta binomial
	Earthworms in knot (late period)	Field type	FieldID	Beta binomial
	Abundance (ecotype) / m2	Field type + Period	FieldID	Negative binomial
Moisture	Abundance / m2	Soil moisture (%) * Field type	FieldID	Negative binomial
	Reproductive earthworms	Soil moisture (%) * Field type	FieldID	Beta binomial

Results

Seasonal description

To show the change in rainfall during the meadow bird breeding season in 2023 at our study site, we gathered the precipitation deficit from the Koninklijk Nederlands Meteorologisch Instituut (KNMI), location 267: Stavoren (KNMI, n.d.). Precipitation deficit refers to the shortfall in the amount of precipitation, measured in millimeters (mm), relative to the expected norm over a given period. A positive deficit indicates drier conditions than usual, while a negative value suggests wetter conditions. As shown in figure 11, the x-axis represents time in Julian Dates, which counts days sequentially throughout the year. Julian Date 100 corresponds to April 10, and Julian Date 180 is June 29. As observed in the graph, the deficit increases progressively as the season advances, indicating a decline in precipitation. This trend highlights the increasingly dry conditions towards the end of the breeding season.

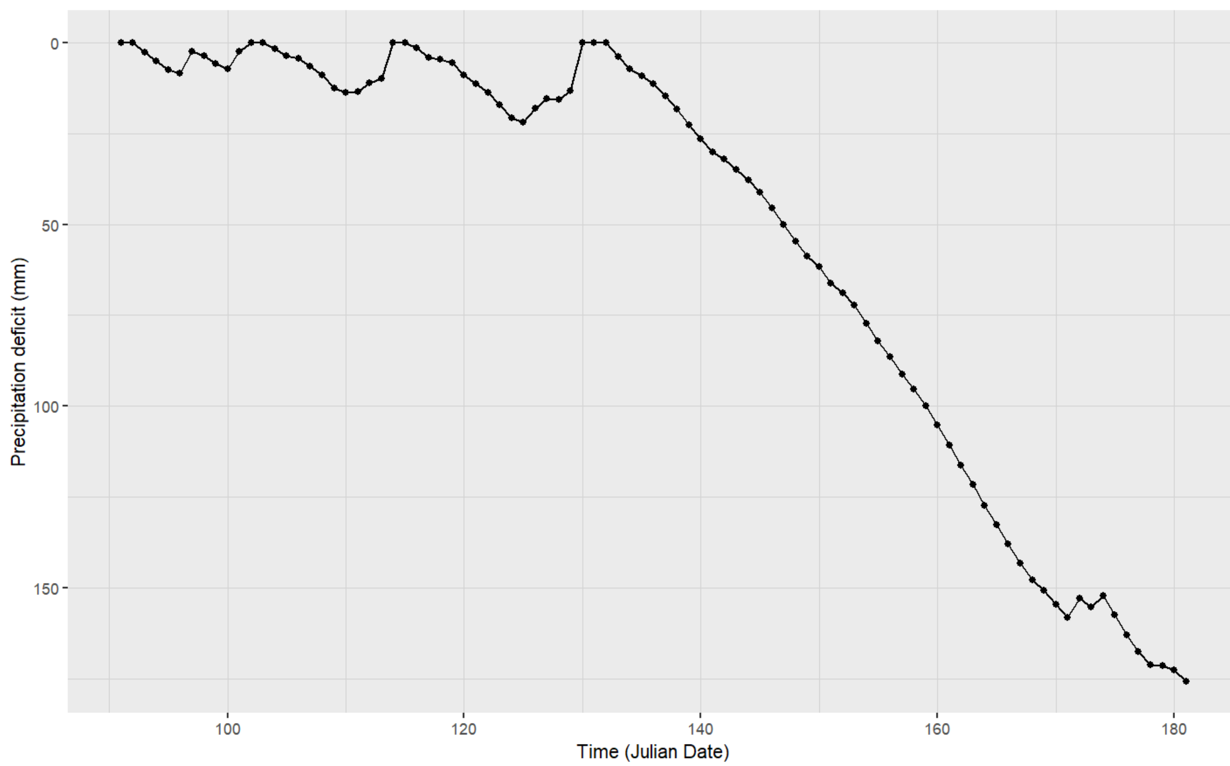

Figure 11*, Precipitation deficit in millimeters over the season (KNMI, Dagwaarden Van Weerstations, location location 267: Stavoren).*

The graph in figure 12 represents the soil moisture percentage over time, measured in the two different field types: *greppelland* and intensively managed grassland. Both trends exhibit a peak in soil moisture around Julian Date 106 (April 16). followed by a significant decline as time progresses (β=-0.017, SE=0.001, z=-13.108, p<0.001, table A6). Overall, the soil moisture percentages are lower in intensive fields compared to the *greppelland* (β=-0.28, SE=0.037, z=-7.565, p<0.001, table A6).

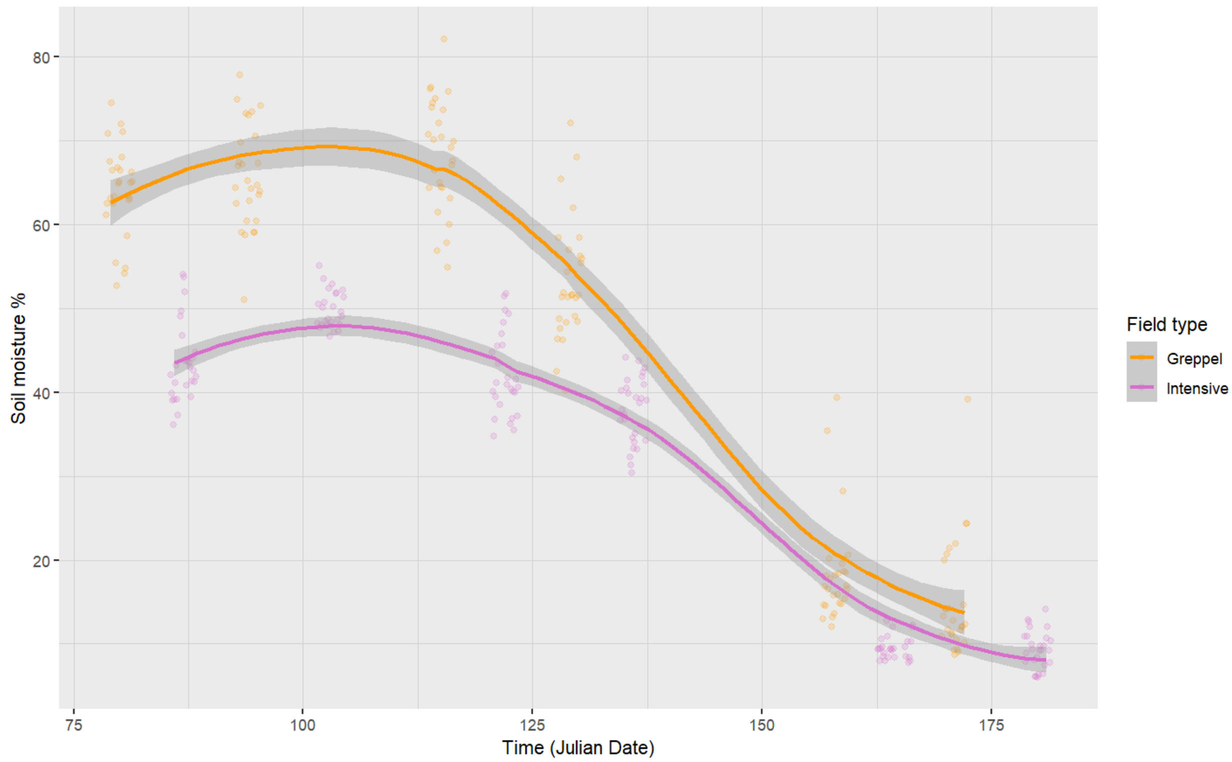

***Figure 12**, Soil moisture percentage measured in both field types over the season.*

The graph in figure 13 depicts the soil moisture percentage over time (Julian Date) at the three different locations within the *greppelland* (*eker*, middle and *greppel*). The soil moisture starts at approximately 60% for all three locations and exhibits a similar trend over time: an initial slight increase followed by a decline.

Overall the soil moisture percentage is decreasing while time progresses (β=-0.017, SE=0.001, z=-19.268, p<0.001, table A7). Where the location the nearest to the *greppel* consistently shows higher soil moisture compared to the other locations in the field (β=0.199, SE=0.062, z=3.186, p=0.001, table A7).

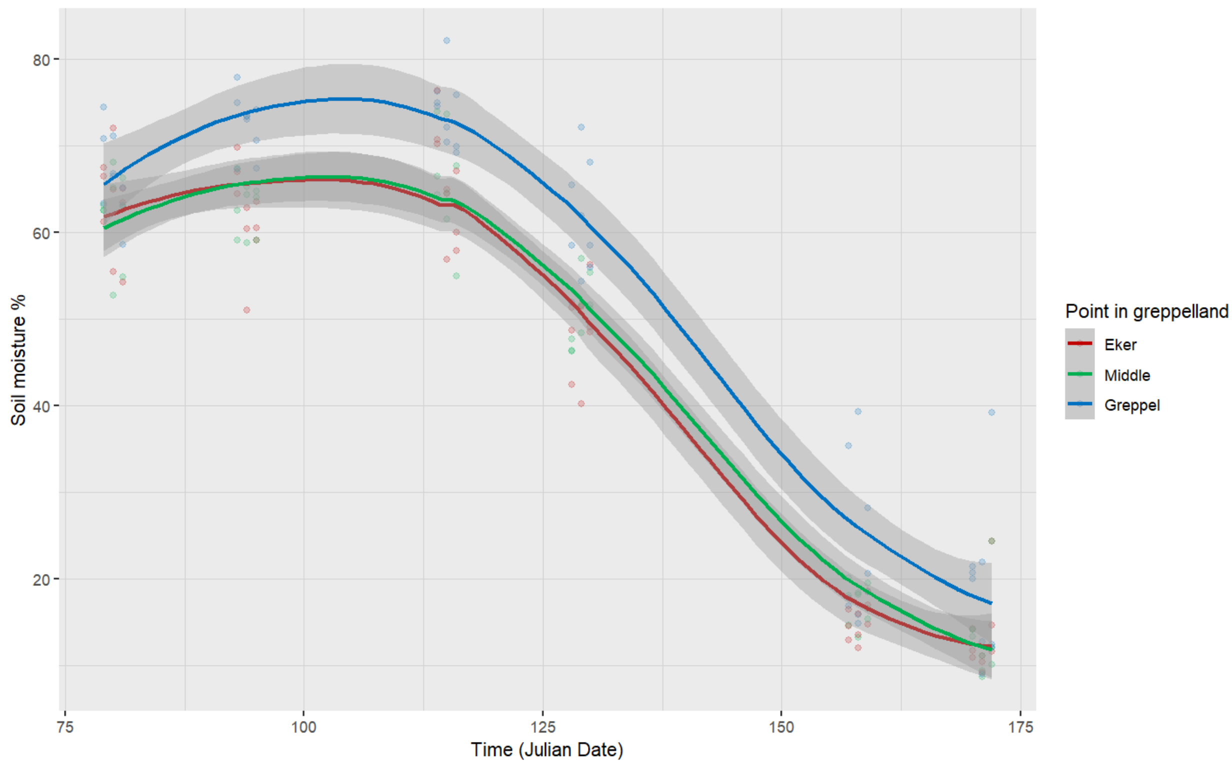

Figure 13*, Soil moisture percentage for the different locations within the greppelland.*

Between greppelland and intensive field

In both field types, the abundance of earthworms per square meter decreases as the season progresses (figure 14), but this decline is stronger in intensively managed grassland than in *greppelland* (β=-0.65, SE=0.15, z=-4.39, $p<0.001$, table A9).

In *greppelland*, there is no significant difference in earthworm abundance between the early and middle period, but there is a significant decrease from the early or mid to the late period (table A11). In intensively managed grassland however, there is already a significant decrease from the early to the middle period, as well as from the middle to the late period (table A11).

Moreover, in the early period of the meadow bird breeding season, there is no significant difference in earthworm abundance in *greppelland* and intensively managed fields (table A10). However, in the middle period, there are more earthworms in *greppelland* than in intensively managed grasslands but the difference is not significant yet (table A10). In the late period, the difference in earthworm abundance between the field types increases and becomes significant (β=0.79, SE=0.22, z=3055, $p<0.001$, table A10).

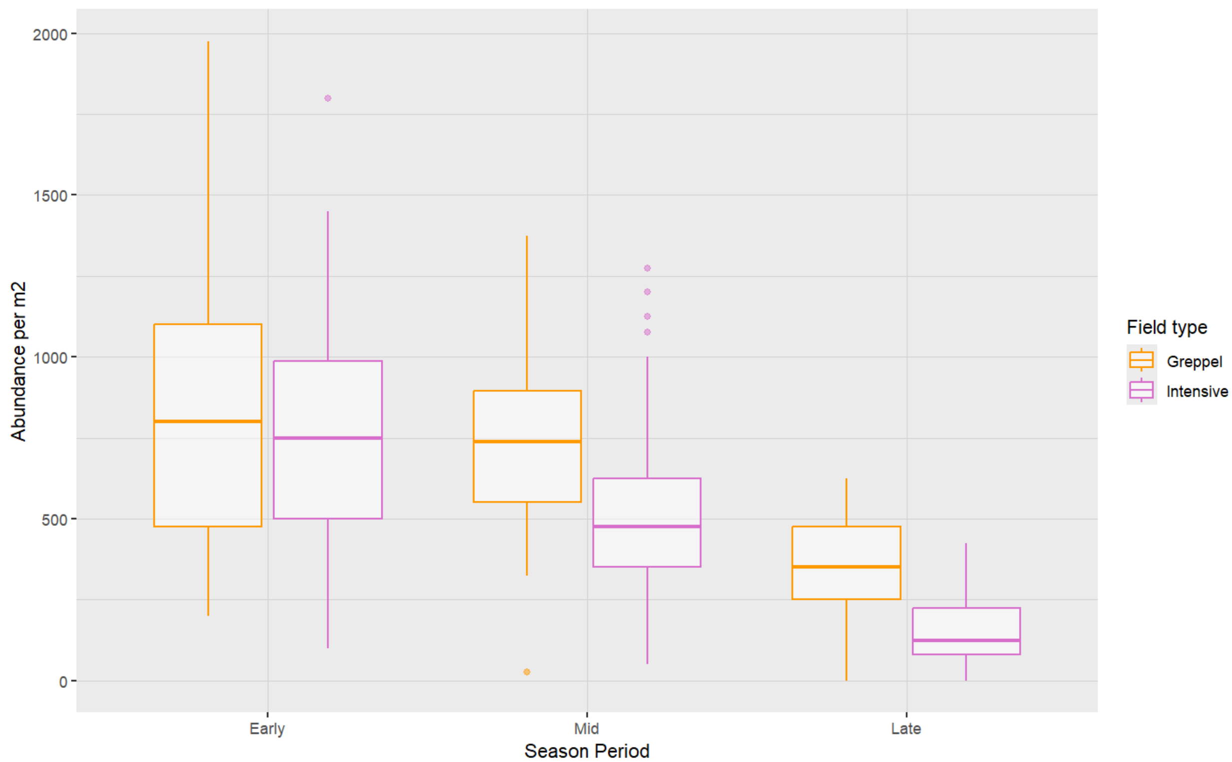

Figure 14, *Earthworm abundance per square meter over the season for different field types.*

When dividing the abundance of earthworms per square meter into the three different ecotype groups, we can observe differences in abundance between the *greppel*- and intensive fields for the ecotypes epigeic and endogeic earthworms (figure 15 and 16). For the anecic ecotype a general decline over the season was found, but no difference between field types (table A15).

When testing the epigeic earthworm group, again, an overall decline in abundance per square meter was observed over time, which was stronger in the intensive fields (β=-0.85, SE=0.34, z=-2.48, p=0.013, table A16) (figure 15). Additionally, intensively managed grasslands showed a significantly lower epigeic earthworm abundance in both the mid (β=0.92, SE=0.29, z=3.17, p=0.002, table A17) and late (β=1.34, SE=0.29, z=4.55, p<0.001, table A17) period of the season, compared to the *greppelland*.

In the endogeic earthworm group, a stronger overall decline over time was found in the intensive field type (β=-0.68, SE=0.17, z=-4.01, p<0.001, table A19) (figure 16). In the late part of the season, less endogeic earthworms are found in intensive grassland compared to *greppelland* β=0.73, SE=0.28, z=2.59, p=0.01, table A20) (figure 16).

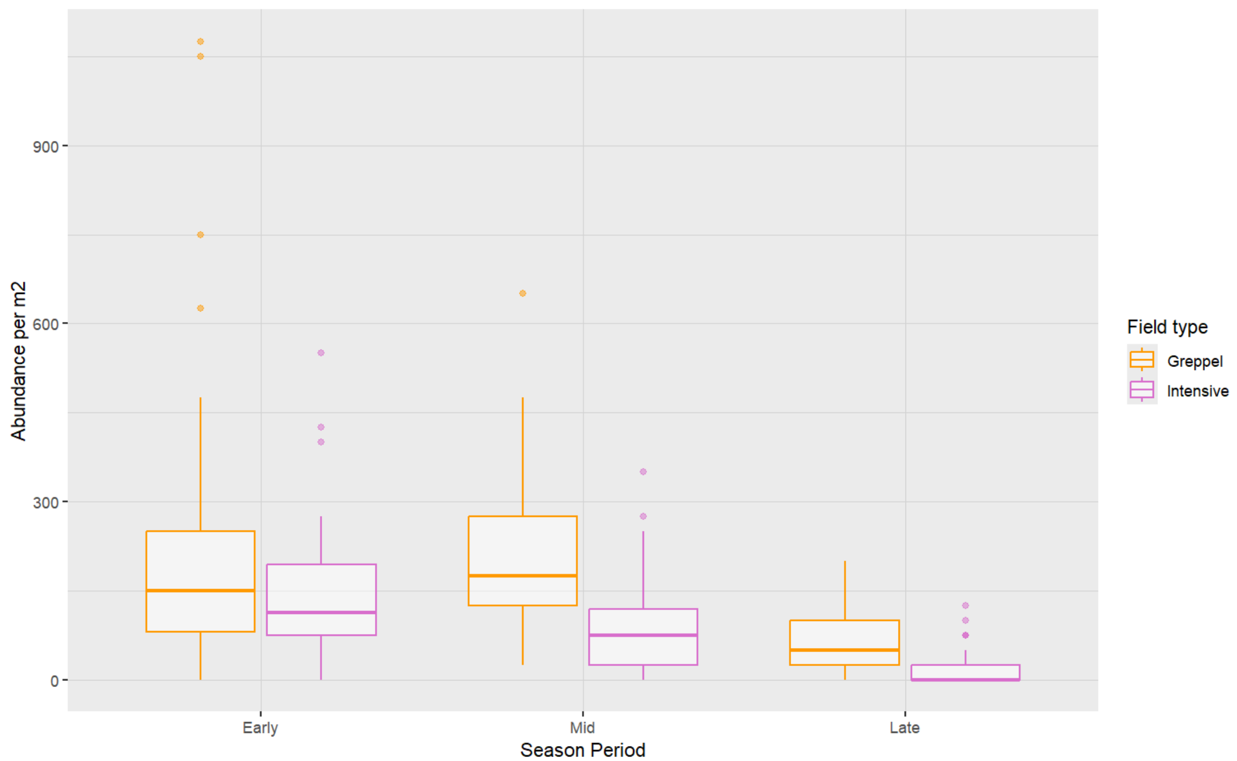

Figure 15*, Abundance per square meter for epigeic earthworms over the season.*

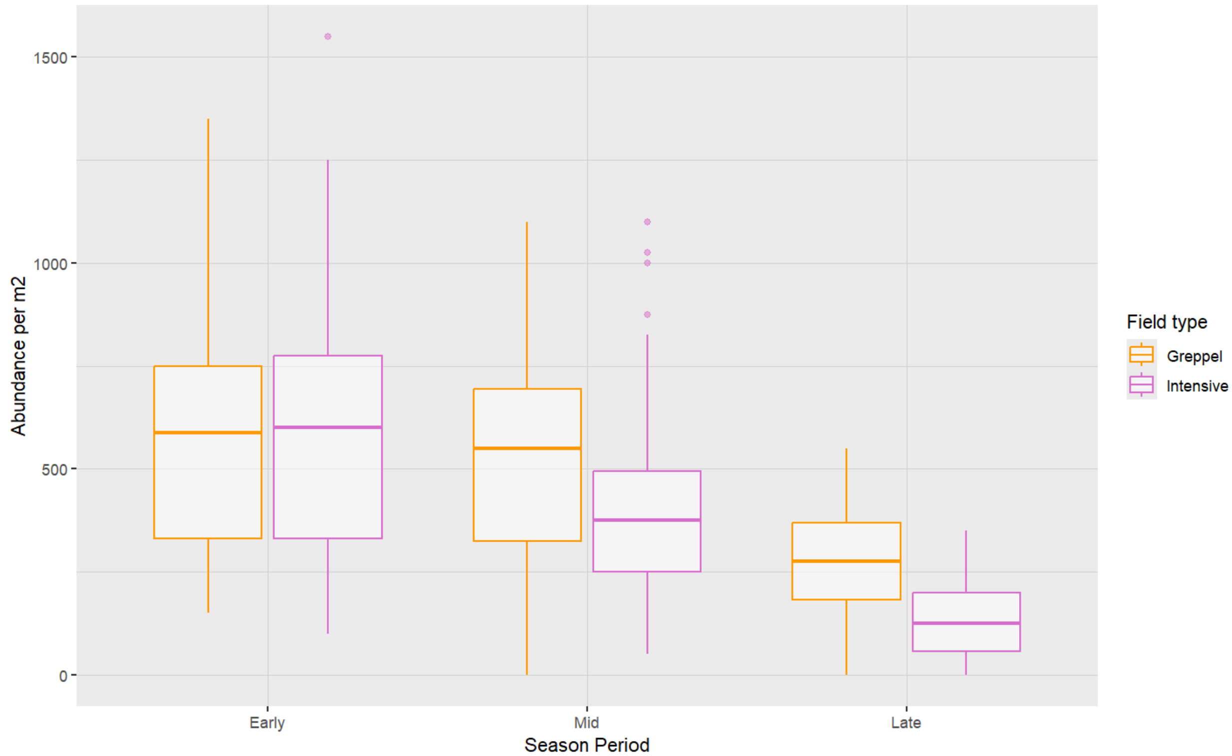

Figure 16*, Abundance per square meter for endogeic earthworms over the season.*

The amount of earthworms found in a state of diapause, forming a knot, were only present in the late period of the season. Comparing the fraction of earthworms in a knot in this period, shows that there are significantly more earthworms in diapause found in the intensively managed grasslands (β=1.98, SE=0.68, z=2.9, p=0.004, table A14) (figure 17).

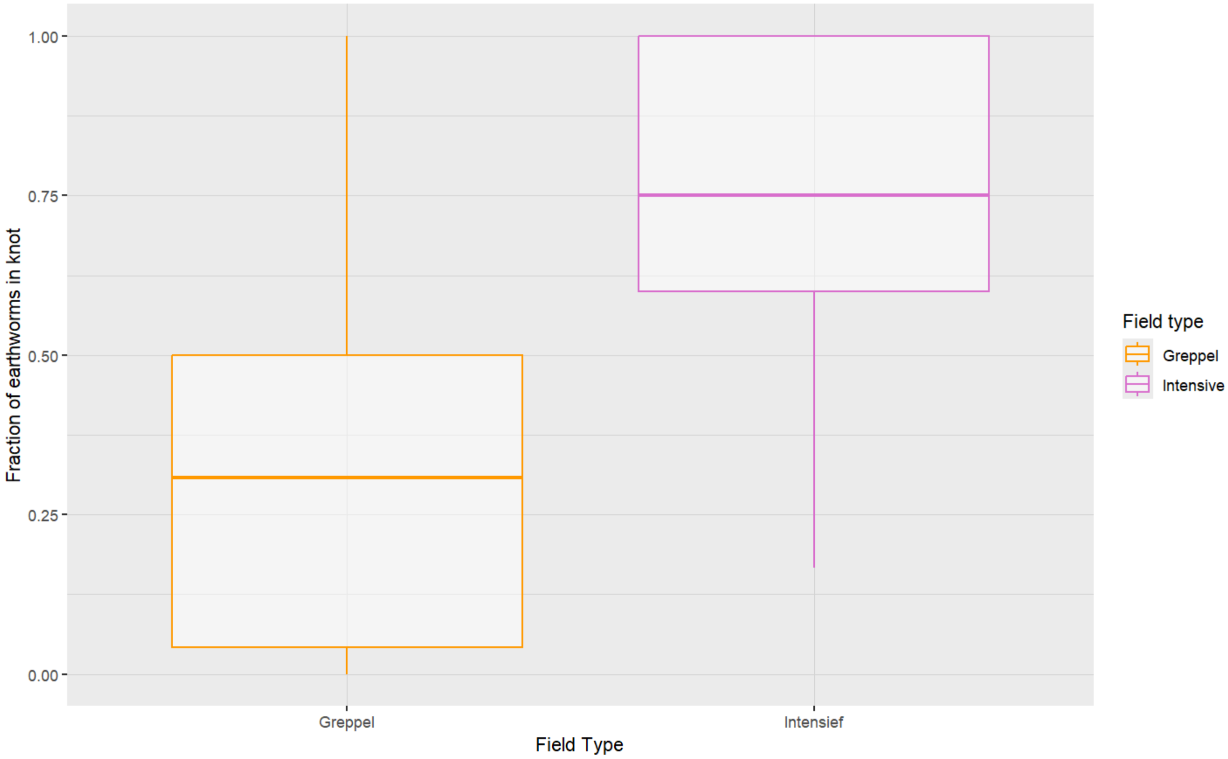

Figure 17*, The fraction of earthworms which formed a knot in the late period of the season for different field types*.

In both field types, the proportion of reproductive earthworms is decreasing over the season, but this decline is stronger in intensively managed grassland than in *greppelland* (β=-1.26, SE=0.35, z=-3.62, p<0.001, table A12) (figure 18).

Between *greppelland* and intensive fields, there is no difference in the proportion of reproductive earthworms in the early and mid-season (table A14), but in the late period, a significantly higher proportion of fertile earthworms is found in *greppelland* (β=1.65, SE=0.39, z=4.22, p<0.001, table A14).

In *greppelland*, there is no difference in the proportion of reproductive earthworms between the early and mid period of the season or between the early and late period (table A13), but a significant difference is observed between the mid and late season (β=-0.63, SE=0.15, z=-4.17, p<0.001, table A13), suggesting a slight peak in earthworm reproductivity during the mid-season. In intensive fields, no difference is observed between the early and mid period of the season (table A13), but there is a significant decrease in the proportion of reproductive earthworms in the late period compared to the mid period of the season (β=-1.84, SE=0.32, z=-5.83, p<0.001, table A13).

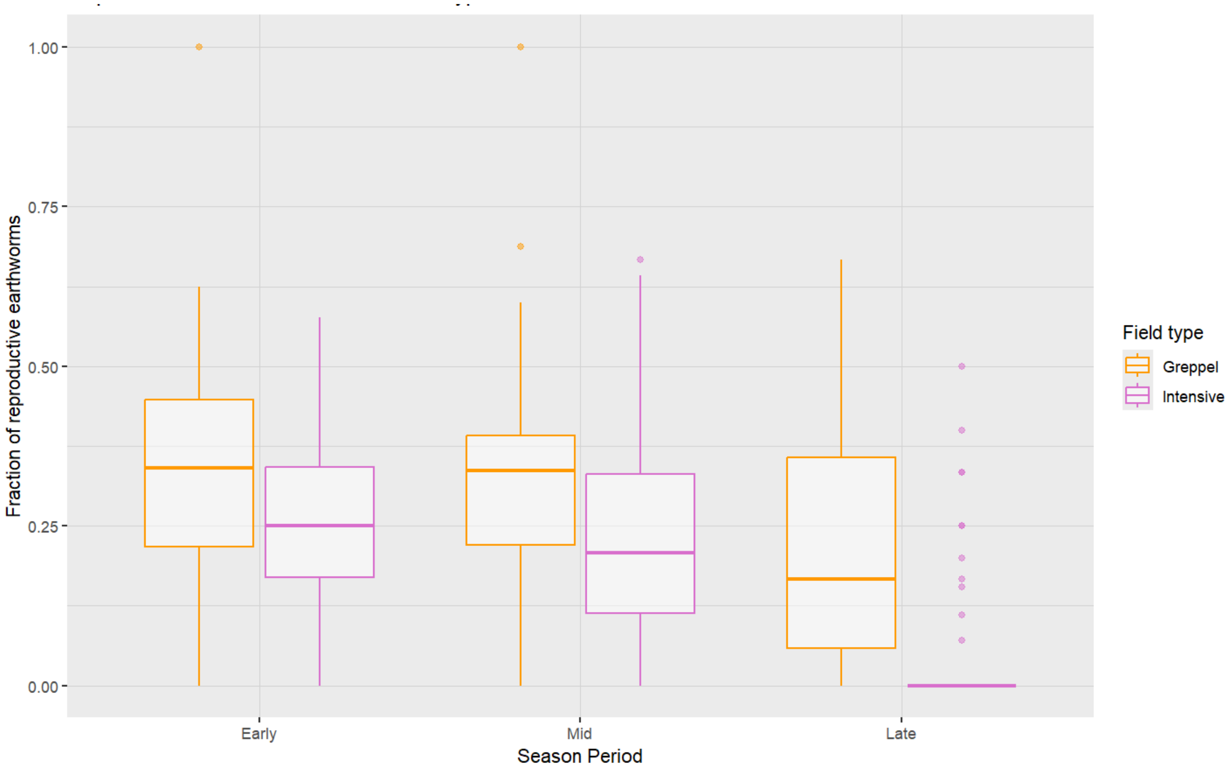

Figure 18*, The fraction of reproductive earthworms over the season for different field types*.

Within greppelland

Now we zoom in to the different locations within the *greppelland* itself: the *eker*, the middle and the location nearest to the *greppel*. Although there is a overall decline in earthworm abundance per square meter over time (β=-0.88, SE=0.10, z=-8.57, p<0.001, table A23), there is no significant difference between the locations within the *greppelland* (table A23) (figure 19).

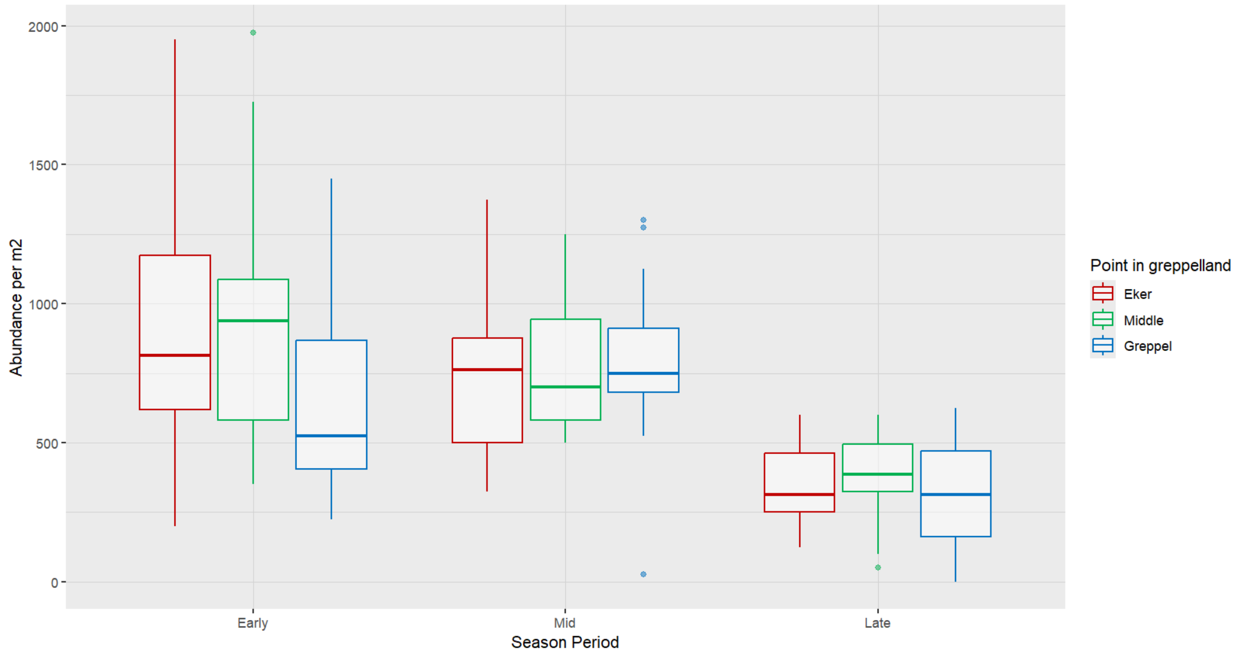

Figure 19*, Earthworm abundance per square meter for different locations within the greppelland over the season*.

For all earthworm ecotypes, a lower abundance per square meter was observed in the late part of the season compared to earlier periods (tables A30, A32 and A34). There was no significant difference in anecic and endogeic earthworm abundance between the different locations within the *greppelland* (tables A30 and A34). Although we measured a higher epigeic earthworm abundance in the mid and late parts of the season for the location the closest to the *greppel*, this difference was not statistically significant (table A32) (figure 20).

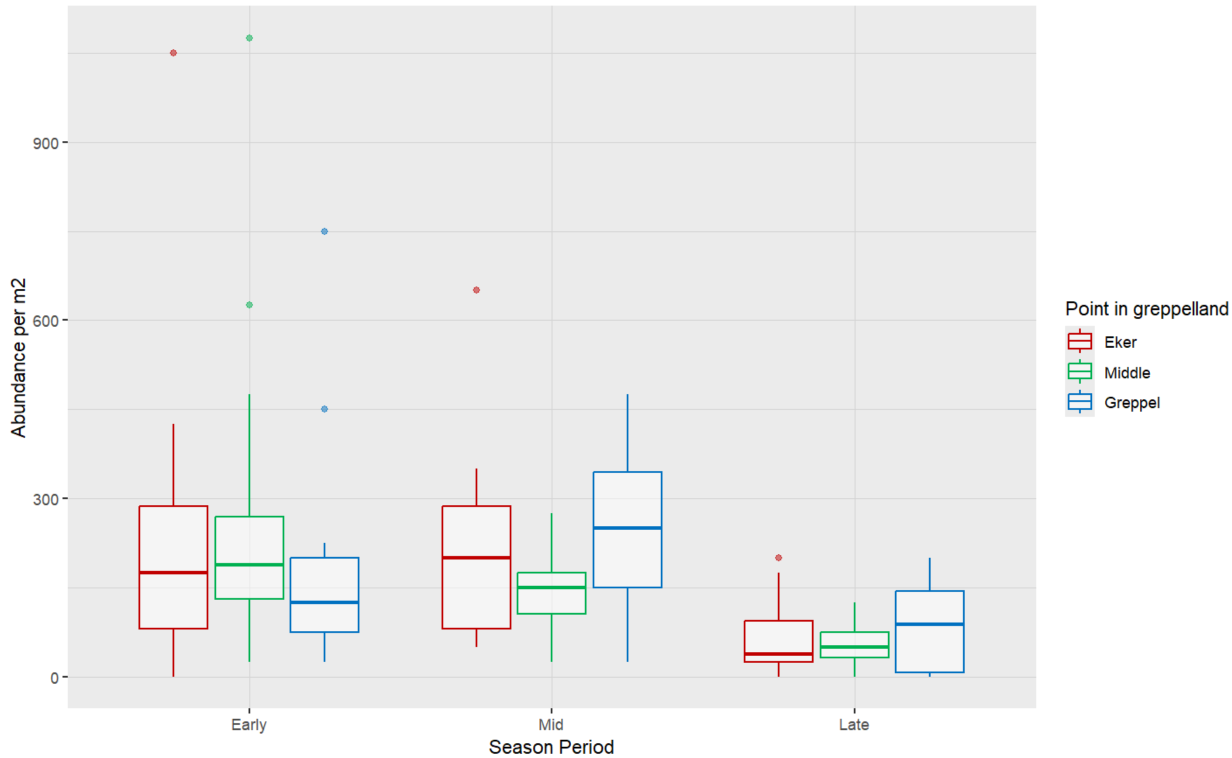

Figure 20, *Abundance per square meter of epigeic earthworms for different locations within the greppelland over the season.*

There were less earthworms in diapause, forming a knot, found at the location closest to the *greppel* in the late part of the season, but no significant difference between the other locations within the *greppelland* (table A28 and A29) (figure 21).

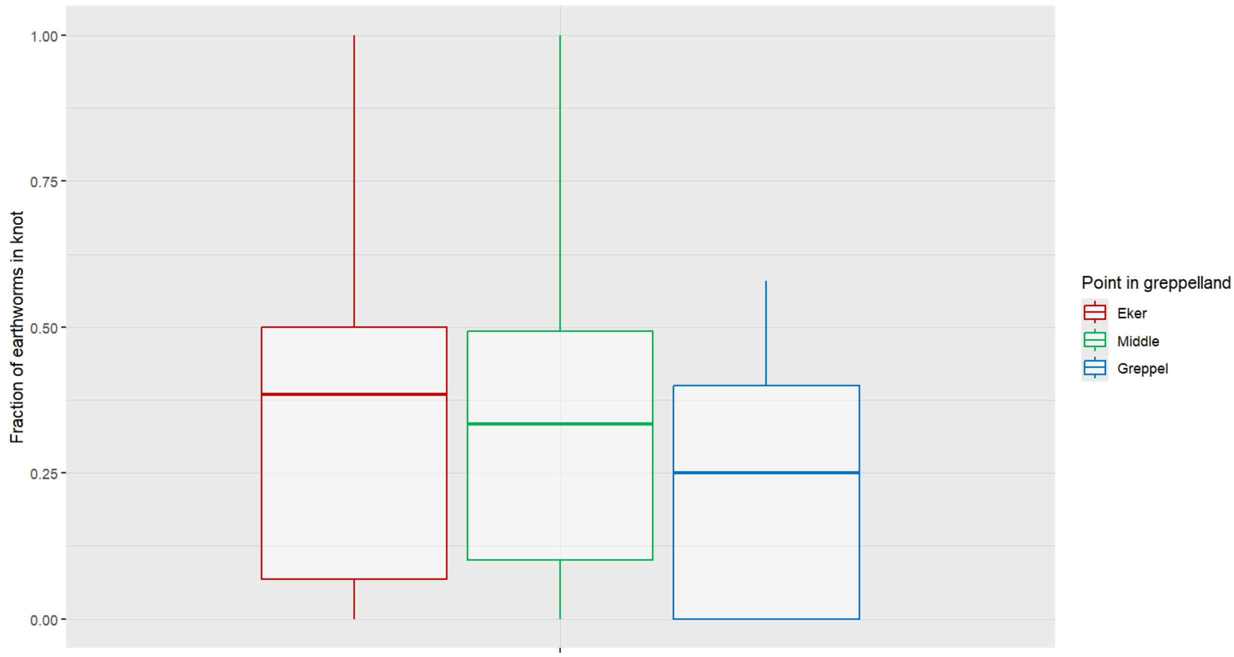

Figure 21, *Proportion of earthworms in knot for different locations within the greppelland for the late period of the season*.

Within the *greppelland*, the fraction of reproductive earthworms is better maintained throughout the season at the location the closest to the *greppel* (β=1.06, SE=0.37, z=2.83, p=0.005, table A25) (figure 22). In the mid part of the season this difference is significantly shown in comparing the *greppel* location to the middle location (β=-0.05, SE=0.21, z=-2.40, p=0.043, table A26). In the late part of the season, this difference is seen in comparing both the middle location (β=-0.77, SE=0.29, z=-2.63, p=0.023, table A26) and the *eker* location (β=-0.83, SE=0.30, z=-2.76, p=0.016, table A26) to the location the nearest to the *greppel*.

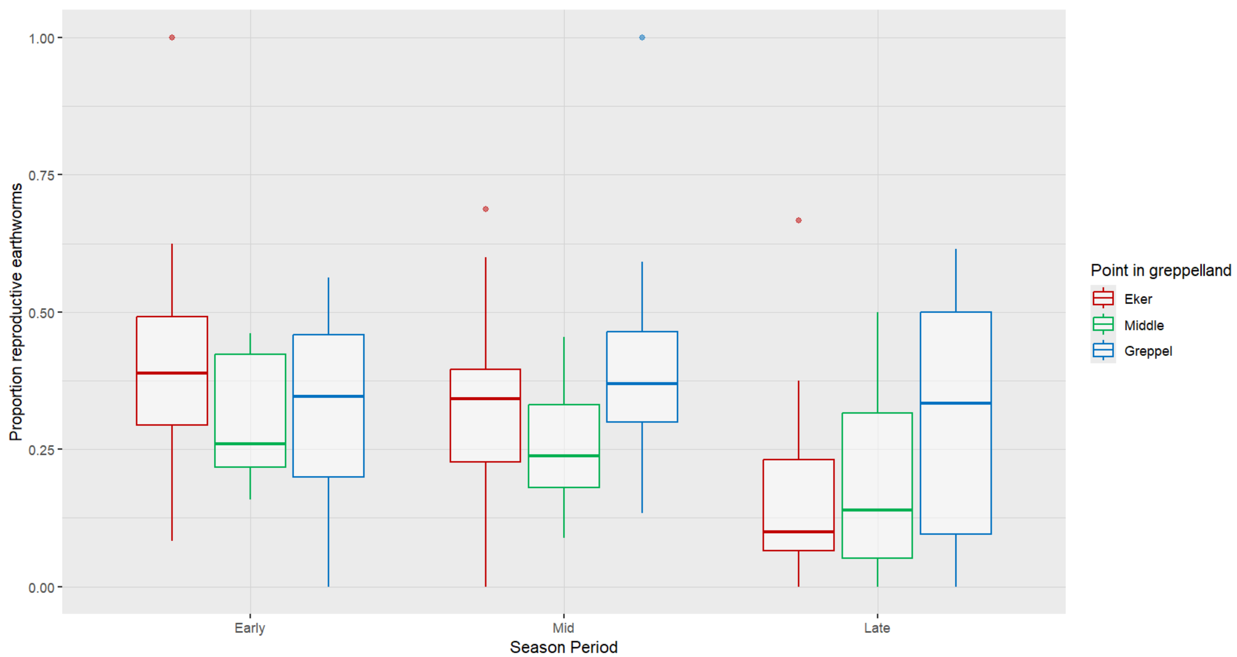

Figure 22*, Proportion of reproductive earthworms for different locations within the greppelland over the season.*

Earthworms and moisture

The graph below depicts the positive correlation between soil moisture and the abundance of earthworms per square meter (β=0.016, SE=0.002, z=8.66, p<0.001, table A36) (figure 22). This correlation varies across different management practices, the effect of soil moisture content on earthworm abundance is stronger within the intensive field type (β=0.023, SE=0.003, z=7.22, p<0.001, table A36).

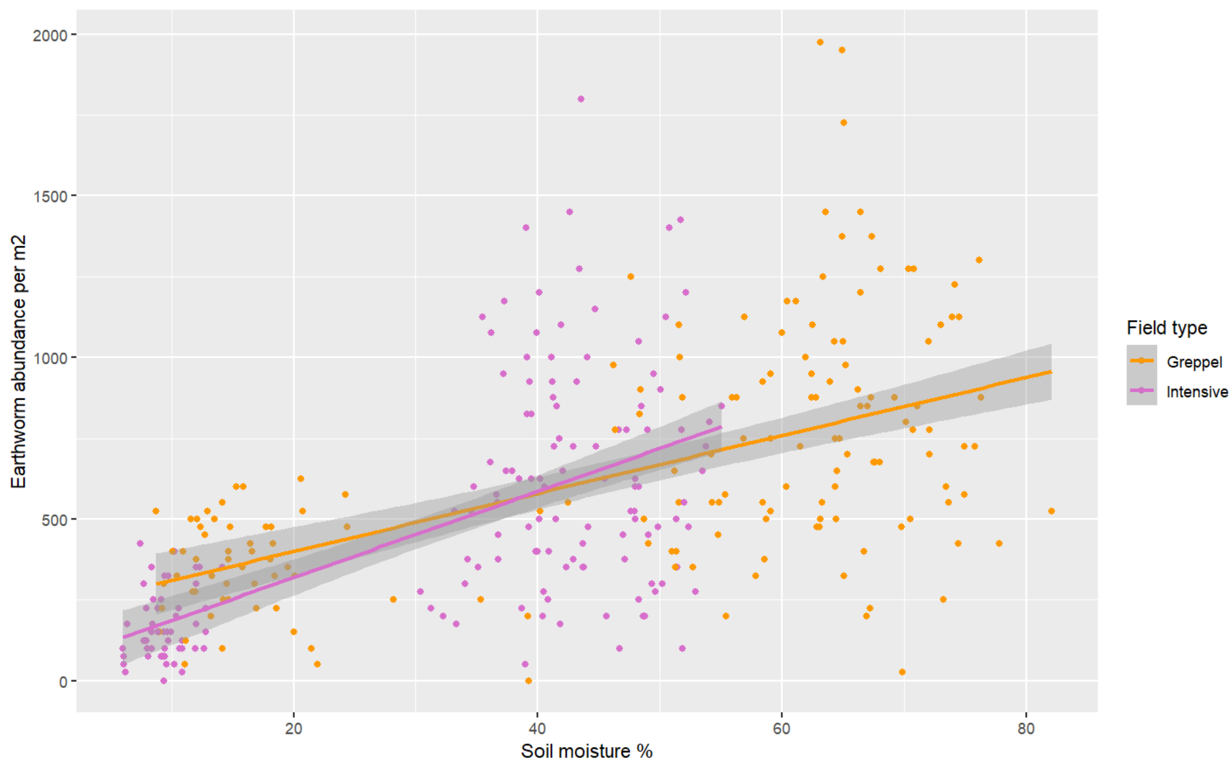

Figure 22*, Earthworm abundance per square meter plotted against soil moisture percentage of the soil.*

In addition, we can see a positive correlation between soil moisture and the proportion of reproductive earthworms (β=0.01, SE=0.003, z=5.24, p<0.001, table A37) (figure 23). This correlation varies between the different field types, the effect of soil moisture content on the proportion of reproductive earthworms is stronger within the intensive field type (β=0.03, SE=0.007, z=3.85, p<0.001, table A37).

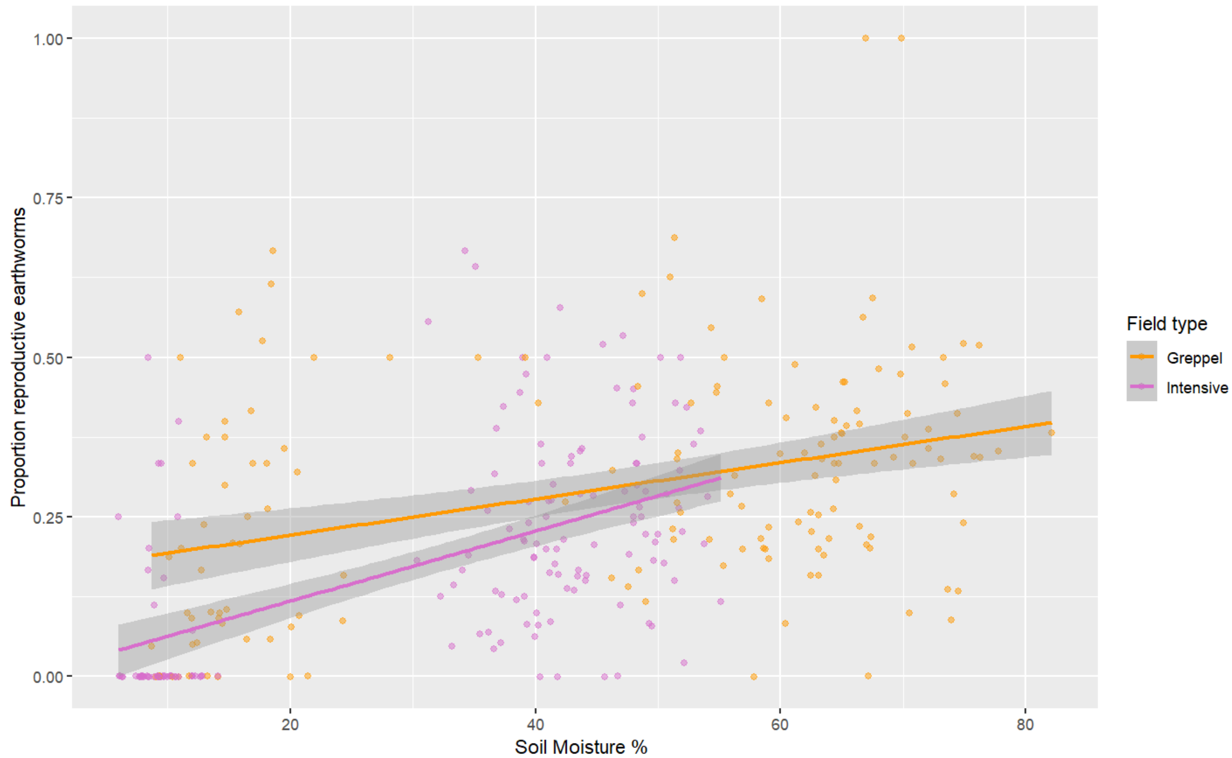

Figure 23, *Proportion of reproductive earthworms plotted against soil moisture percentage of the soil.*

Discussion

Earthworm population trends between greppelland and intensive fields

In this study, we showed that the decline of earthworm abundance throughout the meadow bird breeding season in Friesland is stronger in intensively managed grassland than in *greppelland*. This aligns with expectations, as intensively managed fields with underground drainage systems dry out more quickly when rainfall decreases and temperatures rise in spring, compared to *greppelland* where water is retained (Carroll *et al.*, 2011; Onrust *et al.*, 2019).

The correlation between earthworm survival and drought has been highlighted in several studies (Evans & Guild, 1947; Potvin & Lileskov, 2016; da Silva *et al.*, 2020; Walsh *et al*., 2019; Wood, 1974). As earthworms are highly dependent on moisture for survival, they adopt different strategies as the soil dries out during the season. Depending on their ecotype, earthworms may adopt various strategies, such as digging deeper (anecic), entering diapause (endogeic), or producing cocoons (epigeic), providing a higher survival rate during drought conditions (Edwards & Arancon, 2022).

In our study, intensively managed grasslands exhibited a significantly lower abundance of epigeic earthworms in both the mid and late periods of the season compared to *greppelland*, suggesting that in intensively managed fields, this ecotype is either dead or in the cocoon stage from the mid-season onward. Since the epigeic ecotype is living on the soil surface, which will dry up the fastest, especially in intensive fields (Onrust, 2019), this is a logical outcome.

Endogeic earthworm species in diapause, forming a knot, were significantly more abundant in the dry, late part of the season in intensive fields compared to *greppelland*, where fewer endogeic earthworms were experiencing drought stress. Furthermore, in the late season, a lower number of endogeic earthworms were found in the intensive fields, indicating that not all earthworms in diapause survived the prolonged drought. McDaniel *et al.* (2013) showed in a laboratory experiment that *A. caliginosa* individuals could survive for two weeks in diapause, but after three weeks 14% of the population died. This could mean that part of the endogeic earthworms in intensive fields did not survive in diapause during the prolonged drought period.

Anecic earthworm species are known for their ability to burrow deeper into the soil to survive periods of drought (Edwards & Arancon, 2022). In our study, we observed a significant decline in their numbers towards the end of the season, in both of the field types, with almost no individuals remaining. This suggests that the anecic worms may have burrowed deeper than the 20 cm depth of our sampling range.

In the late, driest part of the season, a higher proportion of fertile earthworms was found in *greppelland*, which aligns with studies indicating that soil moisture significantly influences earthworm fecundity. Specifically, decreased moisture levels lead to the production of fewer and lighter cocoons (Evans & Guild, 1948). Additionally, research by Holmstrup (2001) revealed that low soil moisture adversely affects cocoon production, growth, and development in the earthworm *A. caliginosa*. In our study, we observed a decrease in the proportion of reproductive earthworms with decreasing soil moisture content, with this decline being more pronounced in intensive fields than in *greppelland*. This could be attributed by the decline of soil moisture content being stronger in the intensive field throughout the season or additional factors present in this field type. Such as soil pH and the availability of organic matter, both of which can negatively impact earthworm health (Edwards & Arancon, 2022).

Earthworm population trends within greppelland

Within the *greppelland*, the location closest to the *greppel* retains more moisture throughout the season compared to the other locations. We hypothesized a higher earthworm abundance near the *greppel* in the dry part of the season, however, this was not supported by the results. In the late season, there was a decline in earthworm numbers across all locations, which may indicate that all the locations within the *greppelland* did provide a moderate habitat, reducing the need for earthworms to conduct a drought survival strategy. This is also supported by the results of earthworms in diapause, which is not significantly lower in the location closer to the *greppel*.

Despite the overall decline in earthworm abundance during the late part of the season, those found at the location near the *greppel* show a significantly higher proportion of reproductive individuals. This suggests that earthworms are able to retain a longer fertility period in moist conditions, as moisture is essential for successful mating between earthworms (Edwards & Arancon, 2022). Another possible explanation is that in the drier areas of the field, earthworms may take longer to reach maturity due to less favorable conditions (Edwards & Arancon, 2022; Murchie, 1960). To investigate this phenomenon further, laboratory studies could focus on different earthworm species to examine their reproductive strategies under drought conditions, to precisely answer the question why the *greppel* is so important for earthworm reproduction in dryer periods.

Importance of greppelland in the agricultural landscape

Fewer functional earthworms during dry periods create various problems for soil health and the food web. When epigeic earthworms only exist in cocoon stage, they no longer serve as a food source for higher trophic levels and do not contribute to the accumulation of soil organic matter (Blouin, 2013; Onrust *et al*., 2019). Additionally, the endogeic earthworms tangled up in knots during diapause are much harder for meadow birds to access, as they are enclosed in soil cells. And when anecic earthworms burrow deeper into the soil, it will make them inaccessible to the foraging beaks of meadow birds. These latter ecotypes also play crucial roles in promoting healthy soil by supporting nutrient cycling, enhancing moisture retention, and improving soil structure (Blouin, 2013; Edwards & Arancon, 2022; Sanchez-Hernandez *et al.*, 2023).

After prolonged droughts, such as those observed in Dutch agricultural grasslands, earthworm populations require time to recover before they can resume their essential ecosystem functions. Wet areas within the field are crucial for this recovery as earthworms can migrate to these more favorable spots when conditions elsewhere become less favorable (Mathieu *et al.*, 2010). Endogeic earthworms can only survive in diapause for up to three weeks (McDaniel *et al*., 2013; Roots, 1956), and epigeic earthworm cocoons require moisture to be produced and developed (Edwards & Arancon, 2022; Evans & Guild, 1948; Holmstrup, 2001; Owojori & Reinecke, 2010). Especially for population recovery, the presence of reproductive earthworms near *greppels*, during dry periods, is important.

Protecting the still existing historical *greppelland* and reintroducing *greppels* in agricultural grasslands could provide a sustainable solution for earthworm functionalities. Allowing earthworm ecotypes to recover from drought more effectively, maintaining their essential soil functions, and sustaining their vital role in the food web. Further research could explore the optimal type of *greppel* that balances the needs of both farmers and meadow birds, ensuring it supports agricultural productivity while benefiting biodiversity. Once viewed primarily as a tool for irrigating lowland grasslands, *greppels* could now be recognized as a natural solution that enhances biodiversity, boosts soil fertility, and supports conservation efforts. This multifunctional approach makes *greppels* not only valuable historical landscape features but also a key component of effective farming practices.

Acknowledgements

First of all, I would like to thank my supervisor, Renée Veenstra, for all the support and guidance throughout this project, I have learned a lot from her. I am also grateful to Theunis Piersma for the opportunity to conduct this research. My thanks go to Jeroen Onrust, Mohamed Henriques, Rienk Fokkema and the rest of team BirdEyes for their help with the statistical analysis and interpreting the results. I also want to thank everyone at the Workum field station for assisting with data collection. Finally, I thank the Sterkenburgh family for their hospitality and for allowing us access to their property for this research.

References

Barois, I., Lavelle, P., Brossard, M., Tondoh, J., Martinez, M., Rossi, J. P., Senapati, B. K., Angeles, A., Fragoso, C., Jimenez, J. J., Decaëns, T., Lattaud, C., Kanyonyo, J., Blanchart, E., Chapuis, L., Brown, G. G., & Moreno, A. (1999). Ecology of earthworm species with large environmental tolerance and extended distributions. *Earthworm management in tropical agroecosystems, 3, 57-84.*

Beintema, A. J., Moedt, O., & Ellinger, D. (1995). Ecologische atlas van de Nederlandse weidevogels. Schuyt & Co.

Bekker, R. M., Düttmann, H., de Vries, Y., Bakker, J. P., Buchwald, R., & Brauckmann, H. J. (2006). 30 years of hay meadow succession without fertilization: how does it affect soil and avifauna groups?. *Osnabrücker Nat. Mitt*, *32*, 145-155.

Blakemore, R. J. (2000) Ecology of Earthworms under the ‘Haughley Experiment’ of Organic and Conventional Management Regimes. Biological Agriculture & Horticulture 18:141–159.

Blouin, M., M. E. Hodson, E. A. Delgado, G. Baker, L. Brussaard, K. R. Butt, J. Dai, L. Dendooven, G. Peres, J. E. Tondoh, D. Cluzeau, and J.-J. Brun. (2010) A review of earthworm impact on soil function and ecosystem services: Earthworm impact on ecosystem services. *European Journal of Soil Science,* 64:161–182.

Bodemdata. (n.d.). https://bodemdata.nl/basiskaarten

Bouché, M. B., Lohm, U., & Persson, T. (1977). Soil organisms as components of ecosystems. *Ecol. Bull*, *25*, 122-132.

Breuker, P. (2017). *Het landschap van de Friese klei: 800-1800*. Wijdemeer. https://doi.org/10.18352/bmgn-lchr.10541

Brooks, M., Bolker, B., Maechler, M., Magnussen, A., McGillycuddy, M., Skaug, H., & Stouffer, D. B. (2023). Generalized linear mixed models using template model builder (version 1.1. 7).

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65:23–35.

Carroll, M. J., Dennis, P., Pearce-Higgins, J. W., & Thomas, C. D. (2011). Maintaining northern peatland ecosystems in a changing climate: Effects of soil moisture, drainage and drain blocking on craneflies. *Global Change Biology*, 17, 2991-3001.

Clements, R. O., P. J. Murray, and R. G. Sturdy. (1991). The impact of 20 years’ absence of earthworms and three levels of N fertilizer on a grassland soil environment. *Agriculture, Ecosystems & Environment* 36:75–85.

Colenbrander, H. J., Blumenthal, K. P., Cramer, W., & Volker, A. (1989) Water in the Netherlands. *Proceedings and Information.* The Hague, The Netherlands: TNO Committee on Hydrological Research.

Darwin, C. (1892). *The formation of vegetable mould, through the action of worms, with observations on their habits* (Vol. 37). J. Murray.

De Goede, R. G. M., L. Brussaard, and A. D. L. Akkermans. (2003). On-farm impact of cattle slurry manure management on biological soil quality. *NJAS: Wageningen Journal of Life Sciences*, 51:103–133.

Delta-T Devices Ltd. (2016). *User Manual for the SM150T Soil Moisture Sensor*.

Edwards, C. A., & Arancon, N. Q. (2022). Biology and Ecology of Earthworms. In *Springer eBooks*. https://doi.org/10.1007/978-0-387-74943-3

Eisenhauer, N., A. Milcu, A. C. W. Sabais, H. Bessler, J. Brenner, C. Engels, B. Klarner, M. Maraun, S. Partsch, C. Roscher, F. Schonert, V. M. Temperton, K. Thomisch, A. Weigelt, W. W. Weisser, and S. Scheu. (2011). Plant Diversity Surpasses Plant Functional Groups and Plant Productivity as Driver of Soil Biota in the Long Term. *PLoS ONE*, 6:e16055.

Evans, A. C., & Guild, W. J. M. (1947). Studies on the relationships between earthworms and soil fertility. I. Biological studies in the feld. *Annals of Applied Biology*, 34, 307–33

Evans, A. C., Guild, W. J., & Mc, L. (1948). Studies on the relationships between earthworms and soil fertility. IV. On the life cycles of some British Lumbricidae. *Annals of Applied Biology*, 35, 471–484.

Fries Film & Audioarchief. (z.d.). https://www.friesfilm-audioarchief.nl/

Friis, K., Damgaard, C., & Holmstrup, M. (2004). Sublethal soil copper concentrations increase mortality in the earthworm Aporrectodea caliginosa during drought. *Ecotoxicology and Environmental Safety, 57*(1), 65-73.

Holmstrup, M. (2001). Sensitivity of life history parameters in the earthworm Aporrectodea caliginosa to small changes in soil water potential. *Soil Biology and Biochemistry*, 33, 1217–1223.

Jacobs, A. F. G., Heusinkveld, B. G., & Holtslag, A. A. M. (2007). Seasonal and interannual variability of carbon dioxide and water balances of a grassland. *Climatic Change*, 82, 163–177. https://doi.org/10.1007/s10584-006-9182-7

Keith, A. M., & Robinson, D. A. (2012). Earthworms as natural capital: ecosystem service providers in agricultural soils. *Economology Journal*, 2, 91-99.

KNMI. Dagwaarden van weerstations. (n.d.). https://daggegevens.knmi.nl/

Laird, J. M., Kroger, M., & Heddleson, M. R. (1981). Earthworms. *Critical Reviews in Environmental Science and Technology*, 11(3), 189-218.

Lavelle, P., T. Decaëns, M. Aubert, S. Barot, M. Blouin, F. Bureau, P. Margerie, and P. Mora. (2006). Soil invertebrates and ecosystem services. *European Journal of Soil Biology*:13.

Lenth, R. V. (2023). emmeans: Estimated Marginal Means, aka Least-Squares Means (v1.8.7). https://CRAN.R-project.org/package=emmeans

Macdonald, D. W. (1983). Predation on earthworms by terrestrial vertebrates. *Earthworm ecology: From Darwin to vermiculture*, 393-414.

Mathieu, J., Barot, S., Blouin, M., Caro, G., Decaens, T., Dubs, F., Dupont, L., Jouquet, P., Nai, P., et al. (2010). Habitat quality, conspecifc density, and habitat pre-use affect the dispersal behaviour of two earthworm species, Aporrectodea icterica and Dendrobaena veneta, in a mesocosm experiment. *Soil Biology and Biochemistry*, 42, 203–209.

Matson, P. A., Parton, W. J., Power, A. G., & Swift, M. J. (1997). Agricultural intensification and ecosystem properties. *Science*, *277*(5325), 504-509.

McDaniel, J. P., Barbarick, K. A., Stromberger, M. E., & Cranshaw, W. (2013). Survivability of Aporrectodea caliginosa in response to drought stress in a Colorado soil. *Soil Science Society of America Journal*, 77(5), 1667-1672.

Milcu, A., S. Partsch, C. Scherber, W. W. Weisser, and S. Scheu. (2008). Earthworms and legumes control litter decomposition in a plant diversity gradient. *Ecology* 89:1872–1882.

Murchie, W. R. (1960). Biology of the oligochaete Bimastos zeteki Smith and Gittins (Lumbricidae) in northern Michigan. *American Midland Naturalist*, 64, 194–215.

Neeteson, J.J. (2000). Nitrogen and phosphorus management on Dutch dairy farms: legislation and strategies employed to meet the regulations. *Biology and Fertility of Soils*, 30, 566-572.

Onrust, J., and T. Piersma. (2019). How dairy farmers manage the interactions between organic fertilizers and earthworm ecotypes and their predators. *Agriculture, Ecosystems & Environment* 273:80–85.

Onrust, J., E. Wymenga, T. Piersma, and H. Olff. (2019). Earthworm activity and availability for meadow birds is restricted in intensively managed grasslands. *Journal of Applied Ecology* 56:1333–1342.

Owojori, O. J., & Reinecke, A. J. (2010). Effects of natural (flooding and drought) and anthropogenic (copper and salinity) stressors on the earthworm Aporrectodea caliginosa under field conditions. *Applied Soil Ecology*, 44(2), 156-163.

Potvin, L. R., & Lileskov, E. A. (2016). Introduced earthworm species exhibited unique patterns of seasonal activity and vertical distribution, and Lumbricus terrestris burrows remained usable for at least 7 years in hardwood and pine stands. *Biology and Fertility of Soils*, 53, 187–198

Priester, P.R. (1991) De economische ontwikkeling van de landbouw in Groningen 1800-1910. In: A.A.G. Bijdragen Deel 31. Wageningen: Landbouwuniversiteit Wageningen.

R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Roots, B. I. (1956). The water relations of earthworms. II. Resistance to desiccation and immersion and behaviour when submerged and when allowed choice of environment. *The Journal of Experimental Biology*, 33, 29–44.

Rutgers, M., Orgiazzi, A., Gardi, C., Römbke, J., Jänsch, S., Keith, A. M., & De Zwart, D. (2016). Mapping earthworm communities in Europe. *Applied Soil Ecology*, 97, 98–111.

da Silva, P. M., Nascimento, E., Reis, F., Briones, M. J., Brussaard, L., & Sousa, J. P. (2020). More frequent droughts slow down litter decomposition across European agroecosystems and increase the importance of earthworm functional diversity. *Applied Soil Ecology*, 153, 103628.

Slochteren, F. van (2021). Van greppel tot drainagebuis: een interdisciplinair onderzoek naar het verleden en de toekomst van detailontwatering in het noordelijke kleilandschap. Msc thesis, Rijkuniversiteit Groningen, Groningen.

Timmerman, A., D. Bos, and J. Ouwehand. (2006). Long-term effects of fertilisation regime on earthworm abundance in a semi-natural grassland area. *Pedobiologia* 50:427–432.

Tsiafouli, M. A., E. Thébault, S. P. Sgardelis, P. C. de Ruiter, W. H. van der Putten, K. Birkhofer, L. Hemerik, F. T. de Vries, R. D. Bardgett, M. V. Brady, L. Bjornlund, H. B. Jørgensen, S. Christensen, T. D. Hertefeldt, S. Hotes, W. H. Gera Hol, J. Frouz, M. Liiri, S. R. Mortimer, H. Setälä, J. Tzanopoulos, K. Uteseny, V. Pižl, J. Stary, V. Wolters, and K. Hedlund. (2015). Intensive agriculture reduces soil biodiversity across Europe. *Global Change Biology* 21:973–985.

Van den Bergh, S. (2004). Verdeeld land: de geschiedenis van de ruilverkaveling in Nederland vanuit een lokaal perspectief, 1890-1985. Wageningen University and Research.

Van Groenigen, J. W., Lubbers, I. M., Vos, H. M., Brown, G. G., De Deyn, G. B., & Van Groenigen, K. J. (2014). Earthworms increase plant production: a meta-analysis. *Scientific reports*, *4*(1), 6365.

Walsh, C., Johnson-Maynard, J. L., & Leslie, I. N. (2019). Seasonal variations in exotic earthworm populations in wheat felds of the inland Pacifc northwest, USA. *Pedobiologia*, *76*, 150569.

Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019). “Welcome to the tidyverse.” *Journal of Open Source Software*, 4(43), 1686. doi:10.21105/joss.01686.

Wickham H, François R, Henry L, Müller K, Vaughan D (2023). *dplyr: A Grammar of Data Manipulation*. R package version 1.1.4, https://github.com/tidyverse/dplyr,

Wood, T. G. (1974). The distribution of earthworms (Megascolecidae) in relation to soils, vegetation and altitude on the slopes of Mt Kosciusko, Australia. *The Journal of Animal Ecology*, 87–106.

Zander, J. (1963). Enige aspecten van de drainage. In: Rapporten van de afdeling mechanisatie cultuurtechniek. No. 30. Wageningen: Instituut voor Landbouwtechniek en Rationalisatie.

Appendix

***Table 1**, Location overview of transects across the research fields.*

Field	Transect	GPS coördinates
G1	1	52°59'50.4"N 5°26'37.6"E
	2	52°59'50.7"N 5°26'29.9"E
	3	52°59'51.3"N 5°26'22.7"E
G2	1	52°59'48.2"N 5°26'37.6"E
	2	52°59'48.4"N 5°26'26.2"E
	3	52°59'48.7"N 5°26'19.2"E
G3	1	52°59'44.5"N 5°26'20.9"E
	2	52°59'45.0"N 5°26'17.8"E
	3	52°59'46.1"N 5°26'14.6"E
I1	1	52°59'31.8"N 5°26'23.6"E
	2	52°59'34.9"N 5°26'20.7"E
	3	52°59'37.7"N 5°26'17.4"E
I2	1	52°59'36.4"N 5°26'12.7"E
	2	52°59'38.0"N 5°26'09.5"E
	3	52°59'39.0"N 5°26'07.9"E
I3	1	52°59'37.6"N 5°26'38.4"E
	2	52°59'39.8"N 5°26'32.3"E
	3	52°59'41.4"N 5°26'26.0"E

***Table 2**, Overview of the final models used to compare soil moisture content between greppelland and intensive field and within greppelland. Including response variables, significant fixed effects, random effects and the distribution family.*

1	Response variable	Fixed effects	Random effect	Family link
A	Soil moisture (%)	JD + Field type	FieldID	Tweedie
B	Soil moisture (%)	JD + Point	FieldID	Negative binomial

***Table 3**, Overview of models used to compare earthworm populations between greppelland and intensive grassland, including response variables, significant fixed effects, random effects and the distribution family.*

2	Response variable	Fixed effects	Random effect	Family link
A	Abundance / m2	Field type * Period	FieldID	Negative binomial
B	Reproductive earthworms	Field type * Period	FieldID	Beta binomial
C	Earthworms in knot (late period)	Field type	FieldID	Beta binomial
D anecic	Abundance / m2	Field type + Period	FieldID	Negative binomial
D epigeic	Abundance / m2	Field type + Period	FieldID	Negative binomial
D endogeic	Abundance / m2	Field type + Period	FieldID	Negative binomial

***Table 4**, Overview of models used to compare earthworm populations within greppelland, including response variables, significant fixed effects, random effects and the distribution family.*

3	Response variable	Fixed effects	Random effect	Family link
A	Abundance / m2	Period	FieldID	Negative binomial
B	Reproductive earthworms	Point * Period	FieldID	Beta binomial
C	Earthworms in knot (late period)	Point	FieldID	Beta binomial
D anecic	Abundance / m2	Point + Period	FieldID	Negative binomial
D epigeic	Abundance / m2	Point * Period	FieldID	Negative binomial
D endogeic	Abundance / m2	Point * Period	FieldID	Negative binomial

***Table 5**, Overview of the final models used to test the effect of soil moisture content on earthworm population. Including response variables, significant fixed effects, random effects and the distribution family.*

4	Response variable	Fixed effects	Random effect	Family link
A	Abundance / m2	Soil moisture (%) * Field type	FieldID	Negative binomial
B	Reproductive earthworms	Soil moisture (%) * Field type	FieldID	Beta binomial

Table 6, *Parameter estimates of the generalized linear model with tweedie family, analyzing the effect of field type (greppelland or intensively managed grassland) and time (Julian Date) on the soil moisture content. Field type greppelland is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 1A

	Mean_SM			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	5.865	0.159	36.847	**<0.001**
JD	-0.017	0.001	-13.108	**<0.001**
Field Type [Intensief]	-0.280	0.037	-7.565	**<0.001**
Random Effects				
σ^2	0.00			
$\tau_{00\ FieldID}$	0.00			
$N_{FieldID}$	6			
Observations	324			

Table 7, *Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of location within the greppelland (eker (A), middle (B) and greppel (C)) and time (Julian Date) on the soil moisture content. The eker location is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 1B

	Mean_SM			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	5.777	0.115	50.445	**<0.001**
JD	-0.017	0.001	-19.268	**<0.001**
Point [B]	0.020	0.063	0.318	0.751
Point [C]	0.199	0.062	3.186	**0.001**
Random Effects				
σ^2				
$\tau_{00\ FieldID}$	0.00			
$N_{FieldID}$	3			
Observations	162			

Table 8, *Post-hoc tests for model 1B, using the emmeans package with pairwise comparisons between within greppelland locations.*

contrast	Coef. β	SE (β)	df	z-value	p-value
A - B	-0.0199493	0.0627731	Inf	-0.3177998	0.9458507
A - C	-0.1985496	0.0623116	Inf	-3.1864004	0.0041140
B - C	-0.1786003	0.0622406	Inf	-2.8695150	0.0114576

***Table 9**, Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of field type (greppelland or intensively managed grassland) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the abundance of earthworms per square meter. Abundance in greppelland in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 2A

	abundanceperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	6.724	0.157	42.789	**<0.001**
Field Type [Intensief]	-0.147	0.222	-0.660	0.509
Season Period [Late]	-0.881	0.104	-8.502	**<0.001**
Season Period [Mid]	-0.092	0.103	-0.893	0.372
Field Type [Intensief] × Season Period [Late]	-0.645	0.147	-4.385	**<0.001**
Field Type [Intensief] × Season Period [Mid]	-0.249	0.146	-1.699	0.089
Random Effects				
σ^2	0.25			
$\tau_{00\ FieldID}$	0.06			
$N_{FieldID}$	6			
Observations	324			

Table 10, *Post-hoc tests for model 2A, using the emmeans package with pairwise comparisons between field types within each period.*

contrast	Season Period	Coef. β	SE (β)	df	z-value	p-value
Greppel - Intensief	Early	0.1466285	0.2222908	Inf	0.6596245	0.5094948
Greppel - Intensief	Late	0.7914190	0.2226624	Inf	3.5543449	0.0003789
Greppel - Intensief	Mid	0.3953653	0.2223370	Inf	1.7782253	0.0753669

Table 11, *Post-hoc tests for model 2A, using the emmeans package with pairwise comparisons between periods within each field type.*

contrast	Field Type	Coef. β	SE (β)	df	z-value	p-value
Early - Late	Greppel	0.8813095	0.1036594	Inf	8.5019727	0.0000000
Early - Mid	Greppel	0.0923435	0.1034305	Inf	0.8928074	0.6448522
Late - Mid	Greppel	-0.7889659	0.1036678	Inf	-7.6105227	0.0000000
Early - Late	Intensief	1.5261000	0.1042811	Inf	14.6344828	0.0000000
Early - Mid	Intensief	0.3410804	0.1036579	Inf	3.2904432	0.0028749
Late - Mid	Intensief	-1.1850197	0.1046144	Inf	-11.3274998	0.0000000

Table 12*, Parameter estimates of the generalized linear model with beta binomial family, analyzing the effect of field type (greppelland or intensively managed grassland) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the reproductive earthworms. Reproductive earthworms in greppelland in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 2B

	cbind(Sum_Clitellum, Sum_Total - Sum_Clitellum)			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	-0.665	0.181	-3.674	**<0.001**
Field Type [Intensief]	-0.392	0.256	-1.531	0.126
Season Period [Late]	-0.724	0.154	-4.714	**<0.001**
Season Period [Mid]	-0.098	0.126	-0.778	0.437
Field Type [Intensief] × Season Period [Late]	-1.256	0.348	-3.615	**<0.001**
Field Type [Intensief] × Season Period [Mid]	-0.043	0.188	-0.230	0.818
Random Effects				
σ^2	0.15			
τ_{00} FieldID	0.07			
$N_{FieldID}$	6			
Observations	316			

***Table 13**, Post-hoc tests for model 2B, using the emmeans package with pairwise comparisons between periods within each field type.*

contrast	Field Type	Coef. β	SE (β)	df	z-value	p-value
Early - Late	Greppel	0.7241922	0.1536141	Inf	4.7143590	0.0000072
Early - Mid	Greppel	0.0981677	0.1262339	Inf	0.7776652	0.7167699
Late - Mid	Greppel	-0.6260245	0.1500257	Inf	-4.1727828	0.0000892
Early - Late	Intensief	1.9806922	0.3118008	Inf	6.3524285	0.0000000
Early - Mid	Intensief	0.1415209	0.1397857	Inf	1.0124130	0.5689898
Late - Mid	Intensief	-1.8391713	0.3154765	Inf	-5.8298195	0.0000000

***Table 14**, Post-hoc tests for model 2B, using the emmeans package with pairwise comparisons between field types for different periods.*

contrast	Season Period	Coef. β	SE (β)	df	z-value	p-value
Greppel - Intensief	Early	0.3920526	0.2560729	Inf	1.531020	0.1257645
Greppel - Intensief	Late	1.6485525	0.3900249	Inf	4.226788	0.0000237
Greppel - Intensief	Mid	0.4354058	0.2584499	Inf	1.684682	0.0920500

Table 15, *Parameter estimates of the generalized linear model with beta binomial family, analyzing the effect of field type (greppelland or intensively managed grassland) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the earthworms in knot. Earthworms in knot in greppelland is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 2C

	cbind(Knots, Total_number_worms - Knots)			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	-0.999	0.479	-2.085	**0.037**
Field Type [Intensief]	1.982	0.683	2.902	**0.004**
Random Effects				
σ^2	0.17			
τ_{00} FieldID	0.61			
N FieldID	6			
Observations	106			

Table 16, *Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of field type (greppelland or intensively managed grassland) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the anecic ecotype. Anecic earthworms in greppelland in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 2D Anecic

	abundanceperecotypeperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	2.616	0.547	4.779	**<0.001**
Season Period [Late]	-1.534	0.428	-3.587	**<0.001**
Season Period [Mid]	0.222	0.443	0.501	0.616
Random Effects				
σ^2	2.27			
τ_{00} FieldID	1.24			
N FieldID	6			
Observations	324			

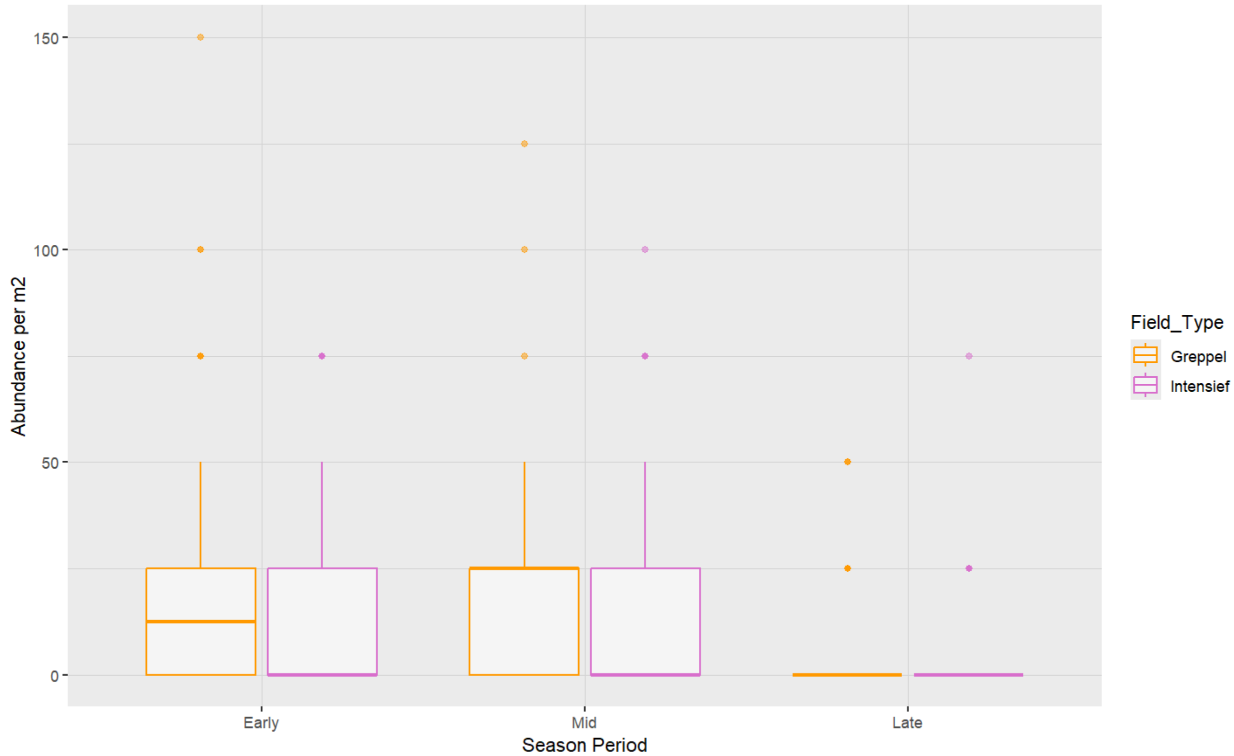

Figure 1*, Abundance per square meter for anecic earthworms between field types over the season.*

***Table 17**, Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of field type (greppelland or intensively managed grassland) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the epigeic ecotype. Epigeic earthworms in greppelland in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 2D Epigeic

	abundanceperecotypeperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	5.390	0.207	26.045	**<0.001**
Field Type [Intensief]	-0.496	0.293	-1.690	0.091
Season Period [Late]	-1.145	0.240	-4.771	**<0.001**
Season Period [Mid]	-0.068	0.239	-0.284	0.776
Field Type [Intensief] × Season Period [Late]	-0.846	0.341	-2.482	**0.013**
Field Type [Intensief] × Season Period [Mid]	-0.434	0.338	-1.283	0.200
Random Effects				
σ^2	0.93			
τ_{00} FieldID	0.04			
$N_{FieldID}$	6			
Observations	324			

Table 18, *Post-hoc tests for model 2D epigeic, using the emmeans package with pairwise comparisons between field types within each period.*

contrast	Season_Period	Coef. β	SE (β)	df	z-value	p-value
Greppel - Intensief	Early	0.4959567	0.2934212	Inf	1.690255	0.0909792
Greppel - Intensief	Late	1.3414924	0.2947484	Inf	4.551313	0.0000053
Greppel - Intensief	Mid	0.9296537	0.2934608	Inf	3.167897	0.0015355

Table 19, *Post-hoc tests for model 2D epigeic, using the emmeans package with pairwise comparisons between periods within each field type.*

contrast	Field_Type	Coef. β	SE (β)	df	z-value	p-value
Early - Late	Greppel	1.1448976	0.2399807	Inf	4.7707905	0.0000055
Early - Mid	Greppel	0.0678594	0.2389402	Inf	0.2840015	0.9565130
Late - Mid	Greppel	-1.0770382	0.2404845	Inf	-4.4786184	0.0000224
Early - Late	Intensief	1.9904332	0.2421178	Inf	8.2209284	0.0000000
Early - Mid	Intensief	0.5015563	0.2392620	Inf	2.0962645	0.0905837
Late - Mid	Intensief	-1.4888769	0.2418341	Inf	-6.1566056	0.0000000

Table 20*, Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of field type (greppelland or intensively managed grassland) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the endogeic ecotype. Endogeic earthworms in greppelland in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 2D Endogeic

	abundanceperecotypeperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	6.379	0.200	31.821	**<0.001**
Field Type [Intensief]	-0.058	0.283	-0.206	0.837
Season Period [Late]	-0.782	0.119	-6.570	**<0.001**
Season Period [Mid]	-0.105	0.119	-0.881	0.378
Field Type [Intensief] × Season Period [Late]	-0.676	0.169	-4.006	**<0.001**
Field Type [Intensief] × Season Period [Mid]	-0.202	0.168	-1.202	0.229
Random Effects				
σ^2	0.32			
τ_{00} FieldID	0.10			
N FieldID	6			
Observations	324			

Table 21*, Post-hoc tests for model 2D endogeic, using the emmeans package with pairwise comparisons between field types within each period.*

contrast	Season_Period	Coef. β	SE (β)	df	z-value	p-value
Greppel - Intensief	Early	0.0583950	0.2834979	Inf	0.2059802	0.8368064
Greppel - Intensief	Late	0.7338969	0.2838515	Inf	2.5854964	0.0097239
Greppel - Intensief	Mid	0.2605913	0.2835632	Inf	0.9189885	0.3581016

Table 22*, Post-hoc tests for model 2D endogeic, using the emmeans package with pairwise comparisons between periods within each field type.*

contrast	Field_Type	Coef. β	SE (β)	df	z-value	p-value
Early - Late	Greppel	0.7816138	0.1189680	Inf	6.5699510	0.0000000
Early - Mid	Greppel	0.1047252	0.1188166	Inf	0.8814019	0.6520630
Late - Mid	Greppel	-0.6768886	0.1189157	Inf	-5.6921703	0.0000000
Early - Late	Intensief	1.4571158	0.1195240	Inf	12.1909933	0.0000000
Early - Mid	Intensief	0.3069215	0.1190253	Inf	2.5786236	0.0268137
Late - Mid	Intensief	-1.1501943	0.1201117	Inf	-9.5760412	0.0000000

Table 23, *Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of location within greppelland (eker (A), middle (B) and greppel (C)) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the abundance of earthworms per square meter. Abundance in the eker location is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 3A

	abundanceperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	6.724	0.073	92.256	**<0.001**
Season Period [Late]	-0.879	0.103	-8.566	**<0.001**
Season Period [Mid]	-0.090	0.102	-0.876	0.381
Random Effects				
σ^2	0.25			
τ_{00} FieldID	0.00			
N FieldID	3			
Observations	162			

Table 24*, Post-hoc tests for model 3A, using the emmeans package with pairwise comparisons between periods.*

contrast	Coef. β	SE (β)	df	z-value	p-value
Early - Late	0.8785046	0.1025527	Inf	8.5663681	0.0000000
Early - Mid	0.0896665	0.1023954	Inf	0.8756884	0.6556704
Late - Mid	-0.7888381	0.1025109	Inf	-7.6951655	0.0000000

***Table 25**, Parameter estimates of the generalized linear model with beta binomial family, analyzing the effect of location within the greppelland (eker (A), middle (B) and greppel (C)) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the reproductive earthworms. Reproductive earthworms in teh eker location in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 3B

	cbind(Sum_Clitellum, Sum_Total - Sum_Clitellum)			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	-0.465	0.173	-2.691	**0.007**
Point [B]	-0.375	0.217	-1.724	0.085
Point [C]	-0.231	0.224	-1.033	0.302
Season Period [Late]	-1.209	0.272	-4.447	**<0.001**
Season Period [Mid]	-0.217	0.212	-1.023	0.306
Point [B] × Season Period [Late]	0.433	0.380	1.140	0.254
Point [C] × Season Period [Late]	1.058	0.373	2.834	**0.005**
Point [B] × Season Period [Mid]	0.002	0.304	0.007	0.994
Point [C] × Season Period [Mid]	0.363	0.304	1.193	0.233
Random Effects				
σ^2	0.12			
$\tau_{00\ FieldID}$	0.02			
$N_{FieldID}$	3			
Observations	155			

Table 26, *Post-hoc tests for model 3B, using the emmeans package with pairwise comparisons between locations within greppelland for each period.*

contrast	Season_Period	Coef. β	SE (β)	df	z-value	p-value
A - B	Early	0.3745406	0.2171888	Inf	1.7244929	0.1959948
A - C	Early	0.2313888	0.2239704	Inf	1.0331220	0.5559115
B - C	Early	-0.1431518	0.2269214	Inf	-0.6308430	0.8031411
A - B	Late	-0.0581897	0.3123246	Inf	-0.1863117	0.9810456
A - C	Late	-0.8266473	0.2990818	Inf	-2.7639501	0.0157561
B - C	Late	-0.7684576	0.2918459	Inf	-2.6330936	0.0230186
A - B	Mid	0.3723528	0.2137704	Inf	1.7418353	0.1896807
A - C	Mid	-0.1314393	0.2056436	Inf	-0.6391610	0.7984850
B - C	Mid	-0.5037922	0.2095668	Inf	-2.4039699	0.0428461

Table 27, *Post-hoc tests for model 3B, using the emmeans package with pairwise comparisons between each period for the locations within greppelland.*

contrast	Point	Coef. β	SE (β)	df	z-value	p-value
Early - Late	A	1.2093488	0.2719479	Inf	4.4469865	0.0000259
Early - Mid	A	0.2170898	0.2122056	Inf	1.0230161	0.5622885
Late - Mid	A	-0.9922591	0.2696615	Inf	-3.6796461	0.0006834
Early - Late	B	0.7766186	0.2655900	Inf	2.9241256	0.0096736
Early - Mid	B	0.2149021	0.2181016	Inf	0.9853301	0.5861458
Late - Mid	B	-0.5617165	0.2647360	Inf	-2.1217988	0.0854485
Early - Late	C	0.1513128	0.2565522	Inf	0.5897934	0.8256017
Early - Mid	C	-0.1457383	0.2187549	Inf	-0.6662175	0.7831142
Late - Mid	C	-0.2970511	0.2426381	Inf	-1.2242557	0.4387767

***Table 28**, Parameter estimates of the generalized linear model with beta binomial family, analyzing the effect of location within the greppelland (eker (A), middle (B) and greppel (C)) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the earthworms in knot. Earthworms in knot in greppelland is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 3C				
	cbind(Knots, Total_number_worms - Knots)			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	-0.807	0.499	-1.619	0.106
Point [B]	-0.064	0.388	-0.164	0.870
Point [C]	-0.440	0.412	-1.067	0.286
Random Effects				
σ^2	0.47			
τ_{00} FieldID	0.51			
N FieldID	3			
Observations	53			

Table 29, *Post-hoc tests for model 3C, using the emmeans package with pairwise comparisons between locations within greppelland.*

contrast	Coef. β	SE (β)	df	z-value	p-value
A - B	0.0635405	0.3883791	Inf	0.1636042	0.9853521
A - C	0.4399731	0.4122038	Inf	1.0673680	0.5343928
B - C	0.3764327	0.4128263	Inf	0.9118428	0.6327947

Table 30*, Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of location within the greppelland (eker (A), middle (B) and greppel (C)) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the anecic ecotype. Anecic earthworms in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 3D Anecic

	abundanceperecotypeperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	3.181	0.387	8.221	**<0.001**
Season Period [Late]	-1.466	0.550	-2.668	**0.008**
Season Period [Mid]	-0.101	0.547	-0.185	0.853
Random Effects				
σ^2				
τ_{00} FieldID	0.00			
N FieldID	3			
Observations	162			

Table 31, *Post-hoc tests for model 3D anecic, using the emmeans package with pairwise comparisons between periods within greppelland.*

contrast	Coef. β	SE (β)	df	z-value	p-value
Early - Late	1.4663371	0.5495564	Inf	2.6682195	0.0208274
Early - Mid	0.1010961	0.5472933	Inf	0.1847202	0.9813650
Late - Mid	-1.3652409	0.5496308	Inf	-2.4839235	0.0347078

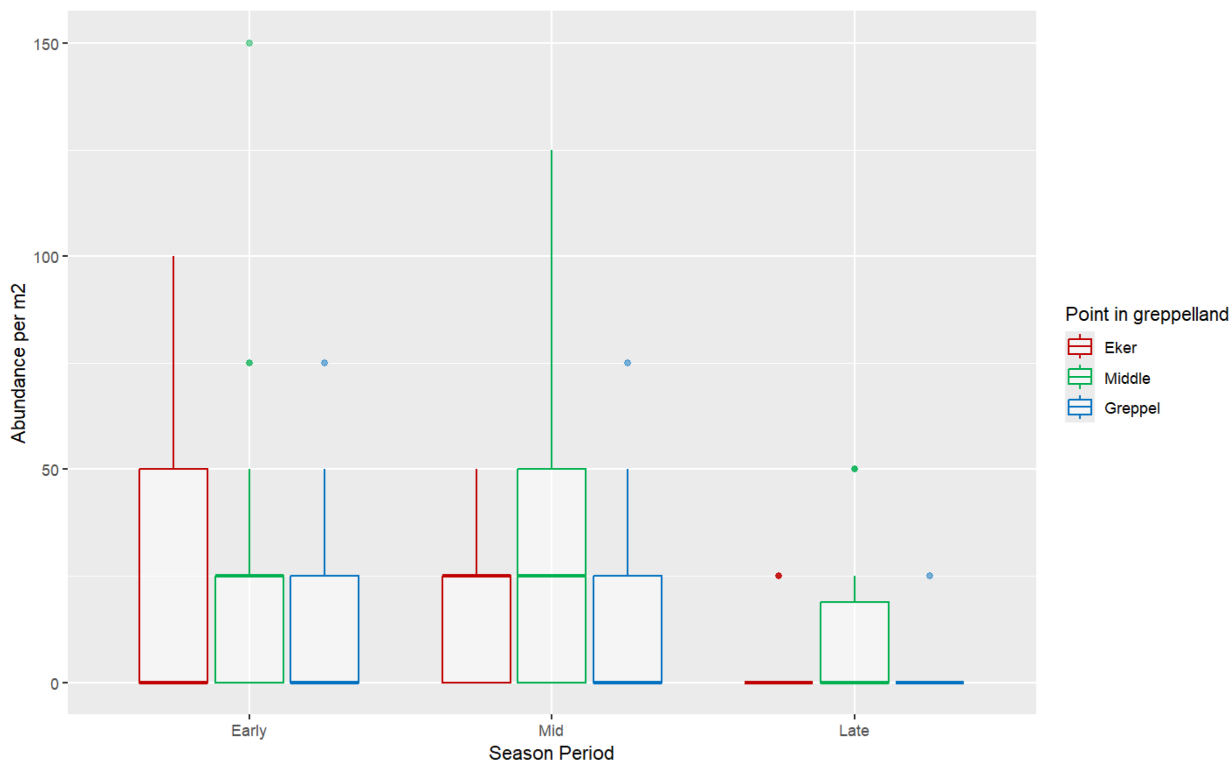

Figure 2, *Abundance per square meter for anecic earthworms within greppelland over the season.*

Table 32, *Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of location within the greppelland (eker (A), middle (B) and greppel (C)) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the epigeic ecotype. Epigeic earthworms in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 3D Epigeic

	abundanceperecotypeperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	5.395	0.131	41.084	**<0.001**
Season Period [Late]	-1.155	0.186	-6.201	**<0.001**
Season Period [Mid]	-0.067	0.186	-0.363	0.717
Random Effects				
σ^2				
$\tau_{00\ FieldID}$	0.00			
$N_{FieldID}$	3			
Observations	162			

Table 33, *Post-hoc tests for model 3D epigeic, using the emmeans package with pairwise comparisons between periods within greppelland.*

contrast	Coef. β	SE (β)	df	z-value	p-value
Early - Late	1.1547826	0.1862113	Inf	6.2014643	0.0000000
Early - Mid	0.0673436	0.1857360	Inf	0.3625769	0.9301042
Late - Mid	-1.0874390	0.1862270	Inf	-5.8393200	0.0000000

***Table 34**, Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of location within the greppelland (eker (A), middle (B) and greppel (C)) and the period in of sampling (early, mid or late in the meadow bird breeding season) on the endogeic ecotype. Endogeic earthworms in the early sampling period is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 3D Endogeic

	abundanceperecotypeperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	6.377	0.084	75.572	**<0.001**
Season Period [Late]	-0.777	0.115	-6.736	**<0.001**
Season Period [Mid]	-0.099	0.115	-0.860	0.390
Random Effects				
σ^2	0.31			
τ_{00} FieldID	0.00			
N FieldID	3			
Observations	162			

Table 35*, Post-hoc tests for model 3D endogeic, using the emmeans package with pairwise comparisons between periods within greppelland.*

contrast	Coef. β	SE (β)	df	z-value	p-value
Early - Late	0.7765060	0.1152758	Inf	6.7360720	0.0000000
Early - Mid	0.0990082	0.1151600	Inf	0.8597445	0.6657175
Late - Mid	-0.6774978	0.1151405	Inf	-5.8840955	0.0000000

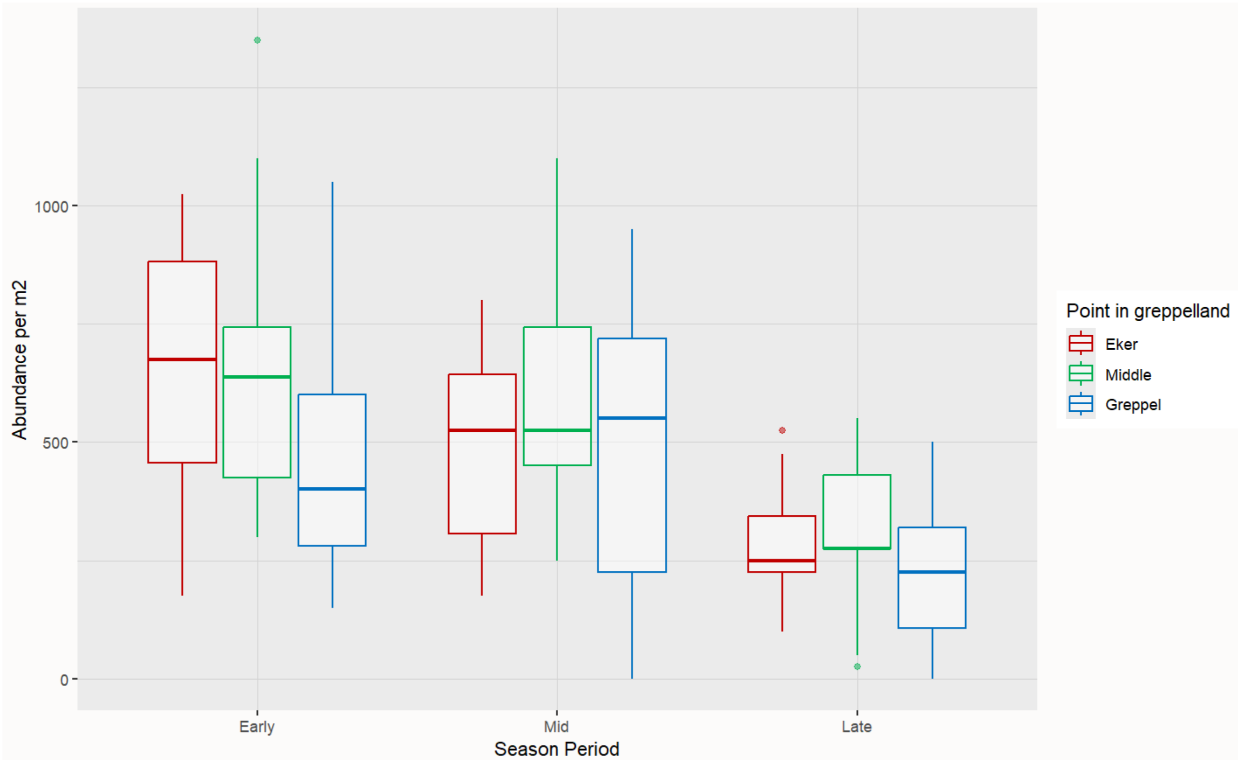

Figure 3, *Abundance per square meter for endogeic earthworms within greppelland over the season.*

Table 36, *Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of soil moisture content and field type (greppelland or intensively managed grassland) on earthworm abundance per square meter. Earthworm abundance in greppelland is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 4A

	abundanceperpointm2			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	5.639	0.195	28.961	**<0.001**
Mean SM	0.016	0.002	8.657	**<0.001**
Field Type [Intensief]	-0.948	0.274	-3.459	**0.001**
Mean SM × Field Type [Intensief]	0.023	0.003	7.217	**<0.001**
Random Effects				
σ^2	0.26			
$\tau_{00\ FieldID}$	0.08			
$N_{FieldID}$	6			
Observations	324			

Table 37, *Parameter estimates of the generalized linear model with negative binomial family, analyzing the effect of soil moisture content and field type (greppelland or intensively managed grassland) on reproductive earthworms. Reproductive earthworms in greppelland is used as the intercept. Results of the best model are shown, and significant predictors are marked in bold.*

Model Summary 4B

	cbind(Sum_Clitellum, Sum_Total - Sum_Clitellum)			
Predictors	*Coef. β*	*SE (β)*	*z-value*	*p-value*
(Intercept)	-1.611	0.192	-8.371	**<0.001**
Mean SM	0.014	0.003	5.244	**<0.001**
Field Type [Intensief]	-1.352	0.354	-3.814	**<0.001**
Mean SM × Field Type [Intensief]	0.027	0.007	3.850	**<0.001**
Random Effects				
σ^2	0.16			
$\tau_{00\ FieldID}$	0.04			
$N_{FieldID}$	6			
Observations	316			

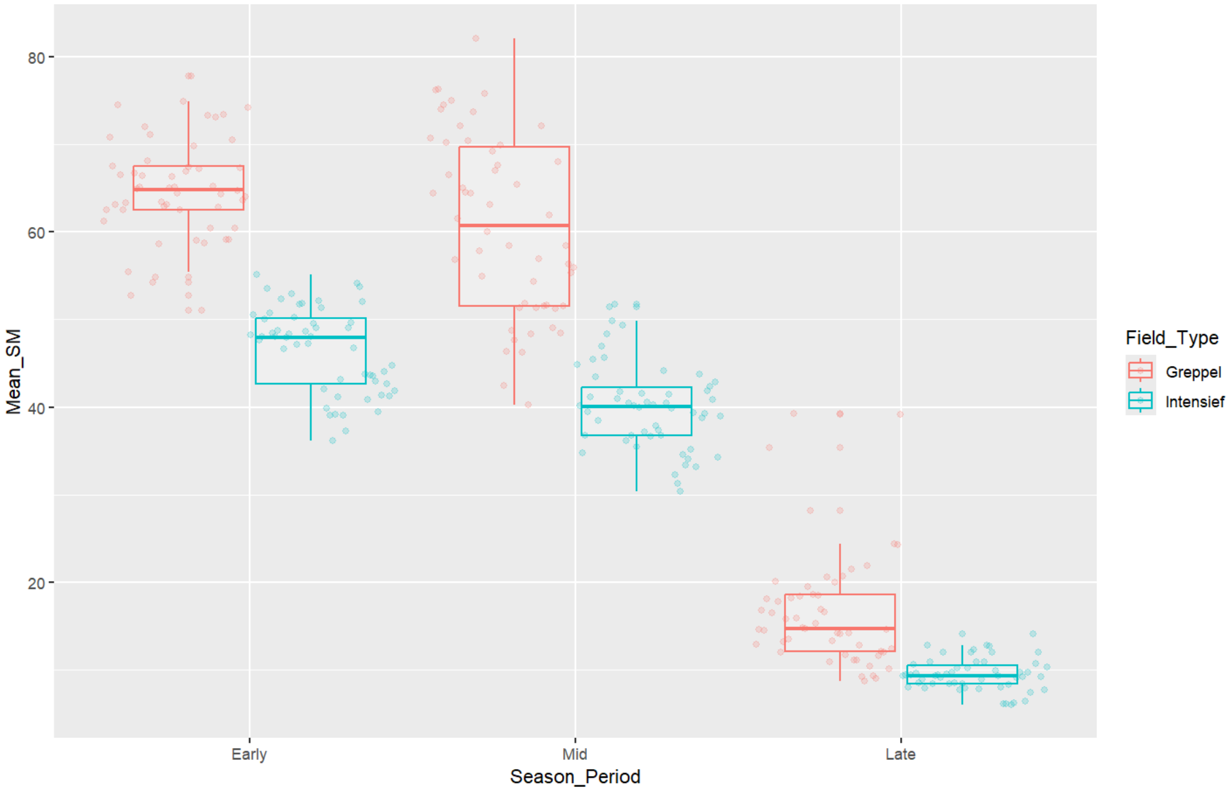

***Figure 4**, Soil moisture content for each field type over the season.*