Resilience of Earthworm and Soil Microbial Communities to Agricultural Intensification and Climatic Extremes
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A Case Study in the North German Lowlands

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Content

List of Tables

List of Figures

Summary

High demands for agricultural goods such as food, fiber and fodder and at the same time a decreasing farmland area result in an ongoing intensification of agricultural production. This is accompanied by high environmental costs such as pollution of soils and water bodies, biodiversity loss and greenhouse gas emissions. Since especially arable soils are a major nexus that links the fluxes of energy, carbon, water, and food, their conservation is a key challenge of the twenty-first century. A sustainable management of soils aims at maintaining its resilience, that is the soil's capacity to absorb disturbances and continue to function in the established way. Soil organisms mediate core ecosystem processes, therefore focusing on them allows us to study the soil's resilience. Since soil organism groups are known to not all respond in the same way to their environment, this dissertation focuses on two very different organism groups: on soil microbes and on earthworm communities. The long-term effect of intensive cropland management on soil organisms is studied in the North German Plains. They experienced a transition to intensive agricultural management half a century ago and currently rank among the most productive areas globally. In order to capture a picture across this area, four study sites with different natural landscape and cultivation history in the North German Plains were selected. To ensure consistent management in study site, three to four cropped fields of the same farm were sampled.

The first objective of this dissertation was to assess to what extent intensive agricultural management as a permanent stress factor impacts earthworm and soil microbial communities, by comparing cropped fields with permanent field margins with same natural background as the cropped field. Our data indicate that intensive agricultural management simplifies soil organism communities in two ways – crop management and soil cultivation reduce the size and activity of soil microbial and earthworm populations. Furthermore, this treatment reduces the diversity of earthworm communities and levels out geographical variation. In contrast, permanent field margins in intensively managed farmlands preserve a greater biomass and diversity of earthworm populations.

In addition to the long-term pressure of land-use intensification, cropland soils must buffer extra stressors such as droughts, as one example of climatic extremes whose frequency will increase due to global warming. Resilient arable soils exhibit a high resistance to stresses and/or a quick recovery to a pre-disturbed state after perturbation. Therefore, in the second part of this dissertation, earthworms and microbes were sampled in the year before, during and after the two years of the exceptional 2018/19 Central European drought. To disentangle the effect of drought and intensive management, soil organisms of arable fields were compared to soils of adjacent permanent, grassy field margins. We show that in the short-term, the drought reduced earthworm biomass and abundances in both field and margins. In margins, earthworms recovered quickly after the drought, however, in fields they did not recover during the study period. The drought reduced microbial biomass and activity in margins, but not in the fields. In fields, microbial biomass and activity were overall lower, but stayed at a constant level during and after the drought.

This dissertation contributes to a better understanding of biotic resilience in intensively managed soils. It provides evidence that intensive farming in the North German Plains simplifies and the homogenizes soil microbial and earthworm communities in cropped fields. Margins, however, continue to host a greater diversity and abundance of earthworms and are therefore valuable for earthworm conservation efforts in farmlands. Intensive farming reduces the resilience of earthworms to cope with drought as an additional stress. Soil microbial populations in fields were smaller and less active than those in field margins, however, these communities were resistant to drought, presumably because intensive agricultural practices selected for stress tolerators.

Thus, this dissertation underlines the importance of semi-natural habitats such as permanent field margins in intensive farmlands for the conservation of diverse and resilient soil communities. With the prospect of increasing frequency of drought events due to climate change, margins may serve as refuges for recolonization of cropped fields by soil organisms. So, with increasing attention on sustainable agriculture, the protection of existing, and creation of new, semi-natural habitats such as permanent field margins should become a priority. Future research should inform this further by assessing how quickly soil communities recover once taken out of management. Furthermore, more detailed analysis of microbial functional groups would allow to also determine the impact of intensive agriculture and drought on the community structure. In this way, we can contribute to a more nuanced understanding of soil decomposer communities that considers the different responses of organism groups to global change drivers.

1. Chapter: General Introduction

Intensive farmlands in Germany, own picture

"Worms have played a more important part in the history of the world than most persons would at first suppose" (Darwin 1881)

Next to photosynthesis, decomposition of organic matter is a key driver of biogeochemical cycles in all ecosystems, which mainly take place in soils (Bardgett and van der Putten 2014). Although we rely on soils so fundamentally, they suffer from degradation due to the current global change processes. This dissertation focuses on the impact of two key global change drivers: agricultural intensification and climate change.

This dissertation was part of the project F.R.A.N.Z. (Für Ressourcen, Agrarwirtschaft und Naturschutz mit Zukunft: franz-projekt.de), a larger German federal state funded project on biodiversity conservation in intensively managed farmlands. This first chapter outlines why it is important to study the resilience of arable soil communities and then briefly presents the research approach and ends by giving an outline of this dissertation.

1.1. Arable soil communities in the context of global change

Global change processes such as climate change, dwindling availability and quality of fresh water, progressing desertification, loss of fertile land and increased nitrogen deposition all menace ecosystems and their capacity to provide goods and services to humans (Steffen et al. 2015; Wang-Erlandsson et al. 2022). All these environmental issues intersect around soils (Bardgett 2005). Soils are the uppermost biotic layer of the Earth's terrestrial crust, having evolved through the interaction of bedrock, topography, climate, vegetation and – in the last 5000 years – also through human activities. Soils consist of around 50 % solid matter (about 45 % non-organic, 5 % organic) and 50 % pores that are filled with gases and water (Amelung et al. 2018). Soil organisms regulate major ecosystem processes such as organic matter turnover and nutrient cycling, and play a key role in linking above-ground and below-ground processes (Bardgett 2005). However, arable soils continue to suffer from degradation: estimates assume that a third of global agricultural land has been lost since 1950 due to maladapted agricultural management (FAO - ITPS 2015; Gupta 2019). There are even calls to recognize soil degradation as a threat to the Earth's planetary boundaries that need to be respected in order to stay within a safe operating space for humanity (Kraamwinkel et al. 2021). Without doubt, the global challenge of a sustainable soil management is key to sustaining ecosystem functioning and human well-being (Amundson et al. 2015; Wall and Bardgett 2012).

1.1.1. Resilience of soil communities as a sustainable management objective

A sustainable management of soils maintains the soil's resilience (Ludwig, Wilmes, and Schrader 2018). The resilience perspective has become a key concept in the management of natural systems (Scheffer et al. 2001). Ecological resilience can be defined as the ability of a system to absorb disturbance, such as changes in temperature or water supply, and continue to function in the established way (Holling 1973). When disturbance becomes too strong, a system's threshold is crossed and it will shift to a new state, thereby potentially losing specific ecological functions. Soils may even gain undesirable functions, e.g. harboring soil organisms harmful for plants as slugs, root infesting nematodes or fungi-derived plant diseases that can survive in soils for a long time (Valverde et al. 2021). A resilient system therefore comprises a high resistance to disturbance and quick recovery to a pre-disturbed state after the perturbation, whereas the threshold to shifting to a new state is high (Côté and Darling 2010). Identifying such thresholds is central for measuring the resilience of a system (Standish et al. 2014). However, there can also exist an undesirable resilience of ecosystems, as a degraded ecosystem may have a high capacity to buffer perturbation as well. This buffering capacity might in some cases even be higher than in a non-degraded ecosystem (Troell et al. 2005) (Fig. 1.1).

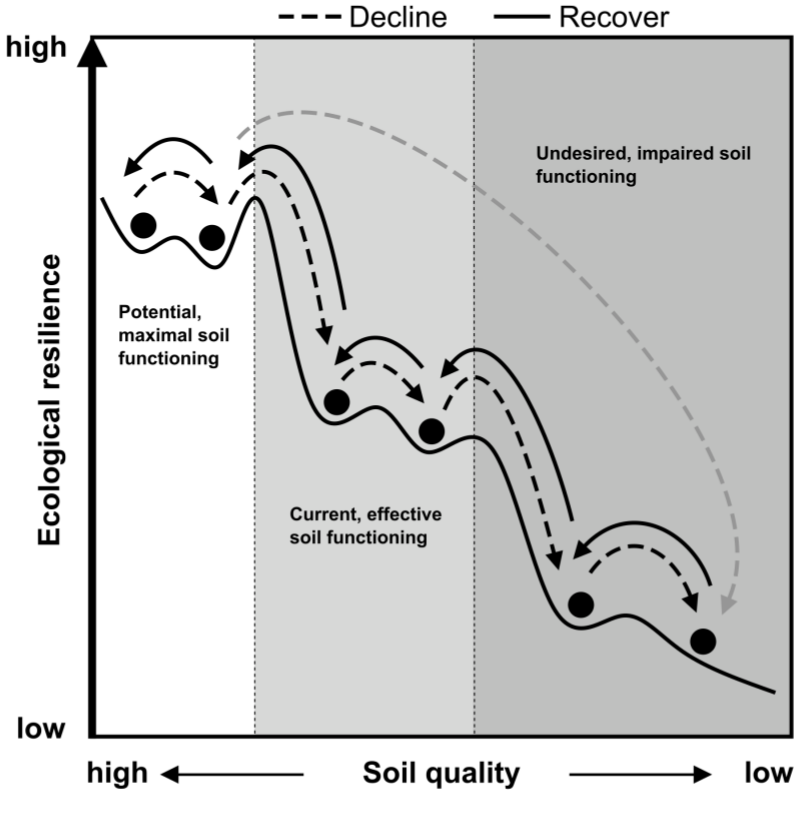

Figure 1.1: *Theoretical spectrum of ecosystem states in arable soils and their likely responses to disturbance (i.e., decline or recovery), adapted from a figure by Standish et al. (2014)*

As agricultural soils are the nexus of water, energy and food (Biggs et al. 2015), it is crucial to protect them from degradation and sustain their quality which ensures their provisioning, regulating and supporting ecosystem services (Amundson et al. 2015; Jónsson et al. 2016; Millenium Ecosystem Assessment 2005). Since intensive agriculture exerts major pressure on soil quality, this dissertation focusses on such practices as one important driver of global change, asking to what extent this permanent stress factor affects the soil's quality in the context of farming in Western Europe. Secondly, the resilience thresholds of arable soil systems are identified by studying the soil community's resistance to and recovery from an additional stress event, represented by a summer drought. Droughts are predicted to increasingly occur in the 21st century, due to climate change (Hari et al. 2020).

1.1.2. Microbes and earthworms as indicators of soil quality

The capacity of soils to "sustain biological activity, maintain environmental quality, and promote plant and animal health" was defined by Doran & Parkin (1994) as soil quality. Since soil quality varies naturally depending on differences in soil type, climate, and the type of vegetation growing on the soil, no universally applicable values exist for high soil quality. A way to monitor soil quality is by focusing on the soil organisms (Doran and Parkin 1994). Estimates assume around 3000 kg of fresh weight biomass of soil organisms in one hectare of agricultural soil (Bloem, Hopkins, and Benedetti 2006). The main taxonomic groups in the soil food web include earthworms, enchytraeids, mites, springtails, nematodes, protozoa, and soil microbes, mainly consisting of bacteria and fungi (Amelung et al. 2018). As both, soil microbes and earthworms, are sensitive to changes and relatively easily monitored, this dissertation focuses on the soil microbial community and on earthworms as well-suited indicators of soil quality.

Microorganisms are a common indicator for soil quality (ISO 2003). They are the smallest representatives among the main functional groups of the soil food web, including mostly bacteria, fungi and archaea (Lee et al., 2019). Microbial biomass carbon (C_{mic}) is defined as the living component of soil organic matter carbon (C_{org}), making up for around 0.2-4 % of C_{org} (Jenkinson and Ladd 1981). Relating C_{mic} to C_{org} (C_{mic}/C_{org}) allows to measure the vitality of soils, since a continuous supply of organic matter allows the share of C_{mic} in C_{org} to grow. It can be twice as high in grasslands as compared to arable land (Ottow 2011). C_{mic} is responsible for various metabolic processes such as nutrient mineralization or decomposition of anthropogenic inputs and is important for the soil's buffering capacity. Thus, the higher C_{mic}, the stronger the resilience of soils and their capacity of self-regeneration and -purification (Ottow 2011). The metabolic quotient (qCO_2) of soil respiration and soil microbial biomass is an indicator for the efficiency of nutrient turnover by the microbial community (Anderson and Domsch 1993); a high qCO_2 indicates that more microbial activity is necessary for self-maintenance and less is available for decomposition activity (Sechi et al. 2017).

The largest organisms in the soil invertebrate food web are earthworms; they constitute the major part of soil invertebrate biomass (Clive A. Edwards and Bohlen 1996). Earthworms play a crucial role in organic matter formation and decomposition, have a positive effect on soil aggregation as well as water infiltration and primary production (Blouin et al. 2013). The impacts of earthworms on soil processes differ among the species. Therefore, they were classified into three main ecological groups: Epigeic species dwell in and feed on the litter layer, anecic species create permanent vertical tunnels up to three meters deep and feed on a mixture of litter and soil organic matter, while endogeic species are geophagous and live in the upper soil layers (Bouché 1977; Bouché and Kretzschmar 1974). While these functional groups are widely referred to, Bouché proposed to conceptualize these groups as three gradients across which he attributed the individual species, rather than proposing three clearly separable classes (Bouché 1977). Since earthworms react quickly to changes in their environment, they are appreciated as key indicators of the ecological footprint of farming practices (Feledyn-Szewczyk et al. 2019; Fründ, Graefe, and Tischer 2011; Li, Wang, and Shao 2021).

1.1.3. Impact of intensive agricultural management on soils

Agricultural production is currently experiencing multiple and conflicting challenges: next to rising demands for classical agricultural goods, new demands have developed such as bioenergy production; meanwhile the global arable land area decreases and land prices rise (Gupta 2019; Potapov et al. 2022). In response, farming practices are increasingly intensified (Techen and Helming 2017). Intensified agriculture focuses on maximizing yields by shifting from diverse mixed cropping systems to highly specialized monocultures and low diversity systems. This is achieved by employing mechanized power, increasing water use for irrigation, and replacing organic manures and natural pest management strategies with agrochemical inputs (Giller et al. 1997). However, the intensification of agricultural production comes at high environmental costs (Kirschke, Häger, and Schmid 2021), putting major pressure on the ecological functioning of arable soils (Foley et al. 2005; Gardi, Jeffery, and Saltelli 2013).

The intensive management of croplands fundamentally affects water systems, local climate, and even soil formation (Lal 2015). Frequent soil cultivation through tillage produces new soil layers with a compacted subsoil horizon (Horn and Rostek 2000). It stimulates microbial activity; and regularly harvesting the total aboveground biomass of crops reduces input of organic matter into soils in fields. Both processes are main factors for the loss of soil organic carbon (Banwart, Noellemeyer, and Milne 2014). Furthermore, compaction of soils leads to a reduction of water infiltration as well as water holding capacity (Holden et al. 2017; Soane and van Ouwerkerk 1995). Together with temporarily bare soils between two crop cycles or when crops are still small, there is stronger surface runoff of precipitation (Chyba et al. 2014). The reduced organic matter content of the topsoil, soil compaction, and bare surfaces together support erosion of the topsoil. Topsoils can not only be eroded through water but also through wind, especially when soil cultivation occurs during dry weather (Smith et al. 2016).

Increased surface runoff, drainage and irrigation in croplands also change the water cycling fundamentally (Foster and Custodio 2019; Ilampooranan, Meter, and Basu 2022). Furthermore, surface- and ground-water bodies suffer from pollution through runoff and leaching of applied nutrients, pesticides and herbicides (Tsiafouli et al. 2015; UNCCD 2017). Finally, in favor of effective use of big machinery, large cropping areas were created at the cost of non-cropping landscape structures such as hedgerows or trees. This created vast open spaces in farming landscapes with little structural heterogeneity, which is a major driver of land biodiversity loss. Additionally, higher wind speed, less soil and plant shading, and frequently a total lack of vegetation cover outside the vegetation period change the local microclimate, supporting, for example, a quicker drying-out of soils (Haber 2014; Heißenhuber, Haber, and Krämer 2015).

There is little knowledge on how exactly these intensification processes impact soil organisms, though evidence suggests that the response to these changes depends on the soil organism group studied (Gessner et al. 2010). In general, earthworms are predicted to suffer from these changes, resulting in overall smaller and less divers communities (C. A. Edwards and Lofty 1977). Soil microbial communities are reduced in their size as well, and if there is no continuous input of easily available organic matter, their activity may also be reduced (Flohre et al. 2011; Postma-Blaauw et al. 2010).

1.1.4. Impact of the climatic extreme drought on soils

Droughts are one of the most jeopardizing climate-related disasters for both ecosystems and society (Cook et al. 2014). In general terms, a drought signifies a moisture deficit relative to a long-term baseline of rainfall and evapotranspiration of a particular area (Wilhite and Glantz 1985). Depending on the objective, several definitions of drought exist (Mishra and Singh 2010). Together they outline the vast spectrum of drought impacts (Mukherjee, Mishra, and Trenberth 2018). The onset of a drought is a prolonged precipitation deficit (meteorological drought) that with time propagates into lowered ground water levels and decreased discharge into streams (hydrological drought) as well as a soil moisture deficit (agricultural drought). Finally, a socio-economic drought occurs when water shortage affects economic activities and well-being of societies (access to water, food, fish, animal fodder, hydro-power) (Wilhite and Glantz 1985). While droughts have always occurred, climate change is expected to increase the frequency and severity of droughts (Cook, Mankin, and Anchukaitis 2018; Dai 2013). The improvement of our understanding of the impacts of droughts is therefore a critical area of climate change research and important for developing adequate mitigation and adaptation strategies (Dai 2011).

Especially the agricultural drought is at the interface of society and natural systems and therefore deserves special attention (van Hateren et al. 2021). An agricultural drought leads to lower yields or yields with poorer quality. This is due to the soil moisture deficit having an impact on both, soil functioning and crop growth. The impact of water deficit on crop growth ranges from smaller or less developed plants to plants not germinating, or, if germinated, to young plants dying of desiccation. As plants are weakened by water stress, the risk of pest infestation or plant disease outbreak is increased (Dalezios et al. 2014). A drought also affects directly and indirectly the environment of earthworms and microorganisms. A direct impact is a lower soil water content (Decaëns 2010), which reduces soil biological activity (Riutta et al. 2016; Thakur et al. 2018). The increased soil hardness and reduced water film on soil particles affects the soil organism's capacity to move (Or et al. 2007). An indirect effect of drought on soil organisms is the compromised plant growth (Franklin et al. 2016). Less or severely drought-affected plant biomass means on one hand less available feeding resources. On the other hand, a poorer plant development has a lower shading effect on the soil surface. This in return leads to further rising soil surface temperatures and evaporation, thus accelerating the dynamic of soil desiccation (Singh et al. 2019).

1.2. Methodology

1.2.1. Study design

This study was conducted in Western Europe, in the Federal Republic of Germany. Germany represents a country where the transformation to intensive agriculture happened in the 1960ies (Bauerkämper 2004). Due to the high agricultural yields that are achieved, Germany globally ranks as the third most important exporter of agricultural goods (Baumgarten 2018; Techen and Helming 2017).

The dissertation was part of the collaborative research project F.R.A.N.Z. (Für Ressourcen, Agrarwirtschaft und Naturschutz mit Zukunft: franz-projekt.de) funded by the Deutsche Rentenbank, Bundesministerium für Landwirtschaft and the Bundesamt für Naturschutz, Bundesministerium für Umwelt, Naturschutz und nukleare Sicherheit. It monitors farmland biodiversity on ten demonstration farms spread across Germany. Each farm is located in a different region that is distinct from the others in terms of natural landscape background and land-use history. All farms have in common that the transformation to intensive agricultural management has already taken place decades ago (Kuhlmann 2019). Four farms were chosen among these demonstration farms for this dissertation (Fig. 1.2). The farm-based approach ensured uniform management techniques across the sampled fields within each farm. In view of the research objectives, the four farms were well suited because each offered enough replicates, had not seen recent management changes, were easily accessible and provided a collaborative environment. Together, the four farms covered a wide range of intensive farming practices and thus data averaged across these farms can provide insights on the long-term resilience of soil organisms in intensive farming systems beyond regional specificities.

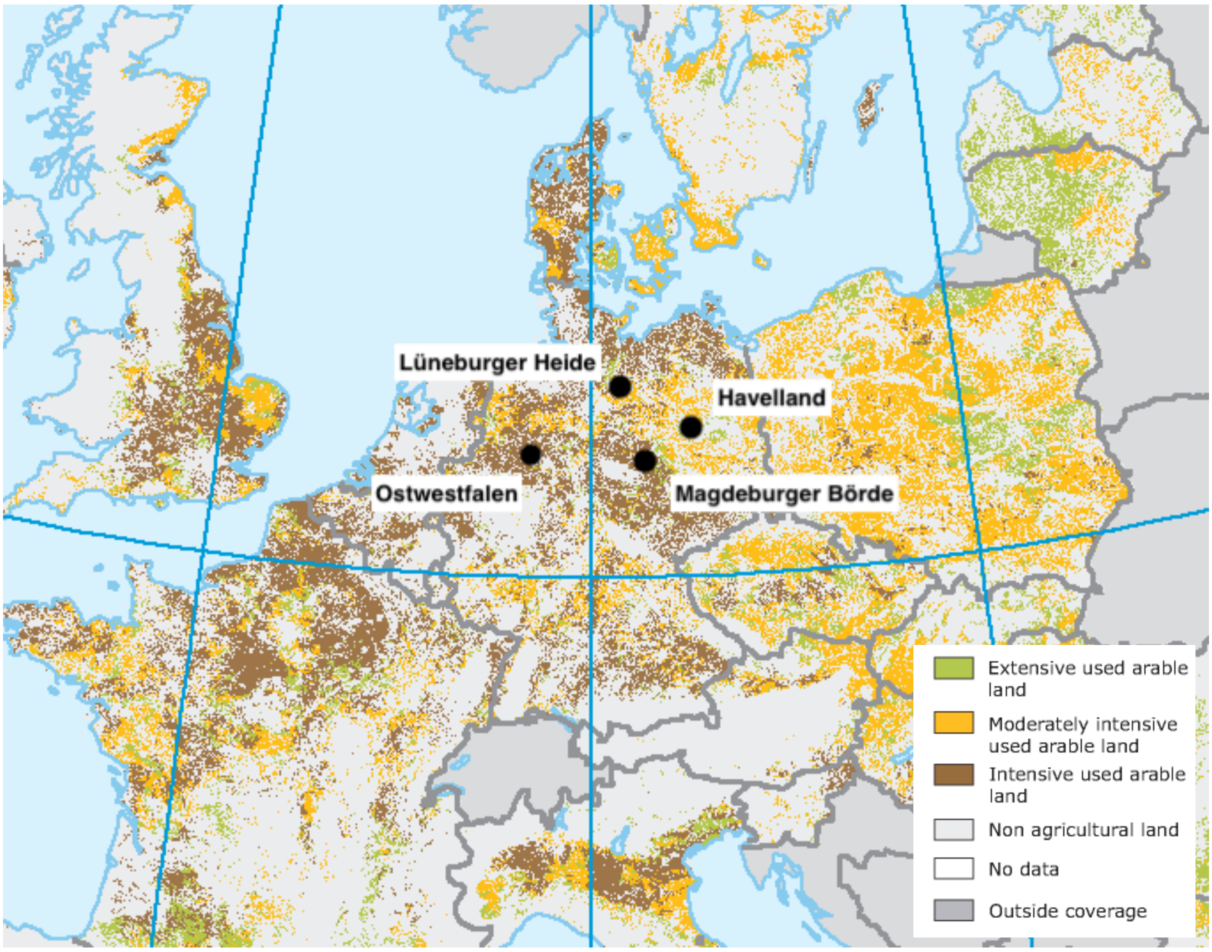

Figure 1.2: *Land use intensity on croplands in Central Europe and the four regions of the chosen demonstration farms for this study (map source: European Environment Agency, 2015).*

a) Study regions

Although the natural landscape background differs for each farm, they have some features in common. As intensive agriculture is difficult to realize in mountainous areas, the four farms are all situated outside the mountainous areas of the Central German Uplands (Deutsche Mittelgebirge) and lie within the North German Lowland plains. The two regions Magdeburger Börde and Ostwestfalen are at the Northern rim of the Central German Uplands. Ostwestfalen is part of the Lower Saxony Hills, marking the north-western rim of the Central German Uplands. Ostwestfalen lies in a periglacial moraine landscape with heterogeneous loamy to sandy soils where nowadays intensively managed arable fields and grasslands form small-structured patches with cattle and pig breeding playing a substantial role. Magdeburger Börde is part of the fertile loess belt found at the north-eastern rim of the Central German Uplands with deep Chernozem to Gleyic Chernozem soils where mainly wheat and sugar beet is grown.

Lüneburger Heide and Havelland both lie in the North German Lowland Plains that were formed during the Weichselian glaciation. Havelland is situated in a boggy and marshy lowland with Mollic Gleysols that formed under the ice sheets. Due to the poorer soils a substantial proportion is forest and grassland, mainly used for cattle. Especially in areas with high groundwater table, arable production takes place, traditionally of fruits and vegetables. Lüneburger Heide is the region with the poorest soils situated in a former heath landscape with sandy soils dominated by deposits of the Saalian glaciation on which Cambisols-Podsols developed. Potato and sugar beet cultivation play an important role (Glaser et al. 2007; Kuhlmann 2019; Meschede 2018).

Except for the farm in Magdeburger Börde, all other farms combined crop cultivation and livestock husbandry; therefore part of their cropped land is dedicated to fodder production. The farm in Magdeburger Börde operates a biogas plant, therefore some of their crop is produced for the power plant. According to the typical management in the respective region, tillage intensity ranges from ploughing yearly (Ostwestfalen) to every second year (Lüneburger Heide), every fifth year (Havelland) and never (Magdeburger Börde) (Table 1).

Table 1.1: *Climatic, soil, and tillage characteristics of the four farms (climate data obtained from local weather stations for the period 1991-2020; soil characterization from soil map BÜK 50).*

Farm	Mean annual precipitation (mm)	Mean annual temperature in °C	Dominating soil texture	Dominating soil type	Tillage intensity	Irrigation
Ostwestfalen	865	10.0	Loamy and sandy to silty clay	Cambisol to Gleysol	Yearly	no
Lüneburg	704	9.5	Sand	Cambisol-Podsol	Every second year	yes
Havelland	623	9.6	Loamy sand	Mollic Gleysols	Every fifth year	no
Magdeburger Börde	571	9.5	Silt	Chernozem	Never	yes

b) Study setup

On each farm, three or four fields were chosen for sampling, depending on suitability and consent of the farmer. To investigate the impact of cropping activities on soil organisms, each cropped field was paired with a neighbouring non-crop field margin. These 1 - 2 m wide strips next to the field border had the same characteristics as the cropped fields in terms of soil type, local climate, as well as topography. In all cases, the vegetation on the field margins only consisted of herbaceous plants, and the only treatment received was being mulched once a year, with biomass left on the field margins. Each pair of cropped field and field margin thus offered the same conditions for soil organisms, with the only difference being that the cropped field was a high input-output system (regular inputs like application of fertilizers, pesticides, herbicides as well as crops being sown and harvested regularly) with high disturbance (soil cultivation), whereas the field margins were low input-output systems (no intended inputs, permanent vegetation cover) with no intended soil disturbance (further details see Supplement 3).

Sampling took place from October 2017 onwards each year in October until 2020, as in Western Europe this moment in the year is considered best for monitoring long-term changes in soil communities (Schinner, Öhlinger, and Kandeler 1991). In each field and margin, four 0.25 m^2 plots were randomly chosen and sampled for earthworms. Pooled soil samples per plot for soil microbial analysis and soil chemical properties were taken from the upper 0 - 10 cm soil layer, after having removed the litter layer. Additionally, farmers were interviewed regarding their previous and current management activities (further details to the study setup see Supplement 3).

1.2.2. Methodological challenges

Much of current ecological knowledge on soil organisms has been gained through manipulative experiments (Kampichler, Bruckner, and Kandeler 2001). The value of experimental manipulation in a laboratory, greenhouse or an outdoor experimental field lies in being able to investigate specific factors or isolate effects by controlling conditions. However, the reduction of undesired sources of variability creates simpler systems. The artificial situation that is created in a manipulative experiment might even cause undesired side-effects.

Therefore, extrapolating findings from manipulative experiments to the real world can only be done cautiously (Carpenter 1996). In contrast, natural experiments study naturally assembled real world systems that have been shaped by environmental drivers and are continuously exposed to global change factors. Comparisons of manipulative and natural experimental findings even suggest that manipulative settings underestimate effects of global change for ecosystem functioning (Kröel-Dulay et al. 2022), for example the effect of warming on plant phenology (Wolkovich et al. 2012), or the effect of fire on soil microbial biomass (Dooley and Treseder 2012). Thus, *in-situ* natural experiments are crucial to complement manipulative experimental studies. Therefore, this dissertation analyses the resilience of arable soil communities with a natural experimental approach because knowledge on the impact of intensive agricultural practices and climate change in a real-world setting is crucial for developing sustainable management practices (Manning et al. 2019). However, a natural experiment faces the methodical challenge of high, uncontrolled variation of environmental factors that cannot be quantified entirely. At the same time, replication is often lower than in manipulative experimental settings. As natural experiments lack true control, observed relationships stay correlational. This limits the robustness of findings, whereas findings from manipulative experimental settings allow to develop a mechanistic understanding of nature (Kampichler, Bruckner, and Kandeler 2001; Manning et al. 2019).

Another challenge arises from the duration of studies. Most studies document short-term effects; however, long-term responses may differ substantially. For example, in a four-month earthworm experiment, there first occurred an increase in soil respiration and then a decrease (Borken, Gründel, and Beese 2000). To capture effects over longer periods, this dissertation documents four years of field observation. However, for some ecosystem responses, even four years is a very short period; in a 20-year study, for example, a distinct effect of earthworm exclusion on soil compaction only emerged after nine years (Clements, Murray, and Sturdy 1991).

1.3. Scope of this dissertation

This dissertation consists of chapter 2 and chapter 3 with research results followed up by a general discussion. The study focuses on the resilience of arable soil communities in the context of intensive cropland management and agricultural drought as the overarching research question.

The study's first objective was to understand how intensive agricultural management as a permanent stress factor impacts earthworm and soil microbial communities, by comparing cropped fields with long-term established field margins. We hypothesized that

1. Earthworm and microbial populations differ between the four farms located in four geographically different regions of North Germany
2. Regardless the geographical differences, earthworm and microbial populations are larger and more divers in margins than in the adjacent fields
3. There is an effect of the margins' permanent vegetation cover on earthworm communities
4. Neighbouring habitats bordering the margins have an effect on the earthworm communities in the margins

The first research chapter compares earthworm and soil microbial populations in intensively cropped fields with long-term established field margins in four geographically different regions. Earthworm biomass and abundances were reduced by 80 % in cropped fields, and microbial biomass and respiration by 50 %, compared to field margins. We did not detect strong geographical variation. In margins, high soil fertility was associated with large earthworm populations dominated by four species, and low fertility was associated with a more diverse vegetation cover and smaller but species-rich (eleven species) earthworm populations. There was no impact of neighbouring habitat type on earthworm populations in the margins. Our data indicate that intensive agricultural management simplifies soil organism communities in two ways – crop management and soil cultivation of fields reduce the size of both soil microbial and earthworm populations. Furthermore, this treatment reduces the diversity of earthworm communities and levels out geographical variation. However, our findings suggest that long-term established field margins in intensively managed croplands continue to be able to preserve biomass and diversity of earthworm populations.

The second objective was to study a drought event as an example of a climatic stressor. It additionally affects the soil communities that are already permanently stressed by intensive agricultural management. We hypothesized that

5. The 2018 – 2019 drought has an overriding effect compared with other environmental factors
6. The impact of the 2018 – 2019 drought on earthworms is stronger than on microbial populations
7. The drought influences earthworm community composition. It reduces species richness, whereas epigeic species are more strongly affected than anecic species
8. Earthworm and soil microbial communities are more strongly affected by the drought in cropped fields and recover more slowly compared to the adjacent field margins

The second research chapter documents the impact of the 2018 – 2019 Western and Central European drought on soil communities by comparison with the pre- and post-drought years 2017 and 2020. The study asked whether the impact differed between cropped field and permanent margin. The findings suggest that in cropped fields the resilience of earthworm communities is impaired presumably due to the consequences of intensive agricultural management. The populations were not resistant to an additional stress factor such as the drought and did not recover within the studied period. In long-term established field margins, the resilience of earthworm communities appeared not to be impaired by intensive agricultural management of the adjacent field: Even though earthworm population size and diversity was reduced by the drought, they recovered within the study period. Microbial communities in intensively managed fields continue to be resilient, though. They were fairly resistant to the additional stress factor drought. In margins, microbial biomass was overall higher compared to the cropped fields. However, these communities were not resistant to the additional stress event as constituted by the drought. Nonetheless, they recovered within the study period to pre-drought levels.

1.4. Literature

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2. Chapter: The long-term influence of intensive farming for earthworm and soil microbial populations in North German arable fields and permanent field margins

Autumn landcape in Lüneburg, own picture

“The plough is one of the most ancientand most valuable of man’s invention; but long before he existed the land was in fact regularly ploughed, and still continues to be thus ploughed by earth-worms.“ (Darwin 1881)

2.1. Abstract

Agricultural intensification is a global threat for biodiversity. However, its impact on soil organisms is not fully understood. In four different regions of North Germany where the transformation to intensive agriculture had taken place decades ago, we studied in October 2017 (a) the long-term effect of intensive agricultural practices on earthworm and soil microbial communities by comparing cropped fields with permanent margins. Furthermore, we studied (b) what factors are beneficial for earthworm conservation in margins by focusing on (1) soil properties, (2) land-use, (3) vegetation cover and (4) neighbouring habitat.

Soil chemical properties were the most important variables for explaining the variation of earthworm and microbial communities. However, we did not detect clear geographical differences between the four regions. In fields, earthworm biomass and abundances were reduced by 80 %, and microbial biomass and respiration by 50 %, compared to margins. In margins, vegetation cover added explanatory power, together with soil properties it explained 51 % of the variation in earthworm and microbial data. Two patterns emerged in the earthworm data: high soil fertility was associated with large earthworm populations dominated by four species, and low fertility associated with diverse plant cover and smaller but more diverse (eleven species) earthworm populations. There was no impact of neighboring habitat type on earthworm populations in margins.

Our data indicate that the long-term effect of intensive agricultural management is a simplification of soil organism communities – cultivation of cropped fields not only reduces the size of communities but also levels out geographical variation. Margins preserve biomass and diversity of earthworm populations. However, small-scale changes of soil and vegetation have a greater impact than the neighboring landscape context. Our findings suggest that less fertile soils support more diverse plant communities and in return species-rich earthworm populations. This study emphasizes the importance of semi-natural habitats between fields as reservoirs for soil biodiversity in intensively managed farmlands.

Keywords: earthworms, soil microbes, biodiversity conservation, intensive agriculture, long-term soil fauna surveys, landscape simplification

2.2. Introduction

Intensive agriculture is recognized as one of the major drivers of biodiversity loss in the twenty-first century (Gámez-Virués et al. 2015a; Sala et al. 2000). Current rates of biodiversity loss are 100 to 1000 times greater than natural extinction rates and still continue to increase (Ceballos et al. 2015; Pimm et al. 1995). Biodiversity loss at this rate is of concern as a decrease in the diversity of genes, species and functional organism groups is considered to diminish the efficiency of ecosystem processes and reduces the stability of ecosystems (Cardinale et al. 2012). This is of particular importance for Europe, where about 50 % of the land cover is farmland (Graf et al. 2015).

Estimates of biodiversity loss mainly rely on above-ground taxa. A European survey documented a 55 % decline of farmland birds (Heldbjerg, Sunde, and Fox 2018; Tarjuelo, Margalida, and Mougeot 2020). Also the documented 75 % decline in German insect biomass is attributed to be caused by practices of intensive agriculture (Hallmann et al. 2017). Estimates of belowground biodiversity loss are scarcer and how a belowground biodiversity loss affects ecosystem functioning is debated (Bardgett and van der Putten 2014). Within soil communities, functional redundancy is high due to generalized feeding habits of many soil organisms (Setälä, Berg, and Jones 2005). Yet, less belowground activity and a reduction in community complexity appears to have an impact on ecosystem functioning, e.g. it reportedly slows down the cycling of litter carbon and nitrogen (Handa et al. 2014). This study therefore aims at assessing the long-term impact of intensive agricultural practices on soil organisms and possible conservation measures.

Estimates assume around 3000 kg of fresh weight biomass of soil organisms in one hectare of agricultural soil (Bloem, Hopkins, and Benedetti 2006). The main functional groups in the soil food web include earthworms, enchytraeids, mites, springtails, nematodes, protozoa and soil microbes mainly consisting of bacteria and fungi (Amelung et al. 2018). As both soil microbes and earthworms are sensitive to land use changes and relatively easily monitored, this study outlines the soil biological community by focusing on the soil microbial community and on earthworms.

Microorganisms include mostly bacteria, fungi and archaea (Lee et al., 2019). They are a common indicator for soil quality (ISO 2003); Microbial biomass carbon (C_{mic}) is defined as being the living component of soil organic matter carbon (C_{org}) making up for around 0.2 - 4 % of C_{org} (Jenkinson and Ladd 1981). Relating C_{mic} to C_{org} (C_{mic} / C_{org}) allows to measure the vitality of soils – continuous supply of organic matter allows the share of C_{mic} in C_{org} to grow. It can be twice as high in grasslands compared to fields (Ottow 2011). C_{mic} is responsible for various metabolic processes such as nutrient mineralization or decomposition of anthropogenic compounds and is important for the soil's buffering capacity. Thus, the higher C_{mic}, the stronger the resilience of soils and its capacity of self-regeneration and -purification (Ottow 2011). The metabolic quotient (qCO_2) where soil respiration is related to soil microbial biomass stand as an indicator for the efficiency of nutrient turnover by the microbial community (T.-H. Anderson and Domsch 1993), high qCO_2 indicates that more microbial activity is necessary for self-maintenance and less available for decomposition activity (Sechi et al. 2017).

Earthworms constitute the major part of soil invertebrate faunal biomass (Edwards and Bohlen 1996a). These ecosystem engineers play a crucial role in organic matter formation and decomposition, have a positive effect on soil aggregation as well as water infiltration and primary production (Blouin et al. 2013). The impacts of earthworms on soil processes differ among the species that are classified into three main ecological groups (Edwards 2004): Epigeic species dwell in and feed on the litter layer, anecic species create permanent vertical tunnels up to 3 m deep and feed on a mixture of litter and soil organic matter, while endogeic species are geophagous and live in the upper soil layers (Bouché 1977a; Bouché and Kretzschmar 1974). Since earthworms react quickly to changes in their environment they are appreciated as key indicators of the ecological footprint of farming practices (Feledyn-Szewczyk et al. 2019; Fründ, Graefe, and Tischer 2011; Li, Wang, and Shao 2021).

There is scarce data on the long-term impact of intensive agriculture on earthworms. A long-term Swiss trial, where since 1978 conventional cropping was compared with organic cropping systems, reported 30 % lower earthworm abundances and biomass in conventional compared to organic cropping systems (Pfiffner and Mäder 1997). A recent study from Great Britain (Blakemore 2018) attempted to give a starting reference similar to the reports on insect biomass (Hallmann et al. 2017). They present data from a long-term experiment that suggests an on average decline of 80 % in earthworm biomass during the last century due to agricultural intensification (Blakemore 2018). Yet, to our knowledge there is no study addressing the long-term impact of intensive agriculture on earthworms in the North German Lowlands.

One product of today's intensive agricultural practices are simplified farmland landscapes. This simplification is considered to be a main driver of farmland biodiversity loss (Gámez-Virués et al. 2015b), especially the loss of structural landscape elements (Dudley and Alexander 2017; Tscharntke et al. 2005). Another effect of intensive agriculture, however, is also a homogenization of soil conditions in fields via inorganic and organic fertilizers, agrochemicals and fertilizing (Jänsch et al. 2013; Thiele-Bruhn et al. 2012). To date, there is little focus on the potential impact of decreased spatial variability in soil conditions on soil biological communities across different intensively managed agricultural regions. Knowledge on how soil organisms are distributed across farmland landscapes continues to be poor (Holden et al. 2019). Yet, soil biological communities are directly and most strongly influenced by the physical and chemical characteristics of the soils they dwell in (Edwards and Bohlen 1996a). The soil chemical properties pH, C_{org}, and soil nutrients, as well as the physical properties soil moisture and clay content have a particularly strong impact (Curry, 2004; Lee, 1985).

Intensive agricultural techniques primarily affect cropped areas. Field margins (henceforth: "margins") are uncropped stretches of land of 1-2 m width adjacent to cropped fields (henceforth: "fields"). As margins are perceived as one of the most important non-crop landscape elements for conservation of natural biodiversity in intensely cultivated landscapes, increasing their multifunctional value is crucial (Hackett and Lawrence 2014; Haddaway et al. 2016). The beneficial effect of margins for farmland biodiversity has been well documented for above-ground biota (Mansion-Vaquié et al. 2017; Wiggers et al. 2016). However, a recent meta-analysis revealed that only about 5 % of literature on margins considered their effect on below-ground biological communities (Mkenda et al. 2019). Generally, most studies reported that margins host more earthworm communities compared to the adjacent fields (Crittenden et al. 2015; Hof and Bright 2010; Roarty and Schmidt 2013; Jo Smith, Potts, and Eggleton 2008), although not all studies reported significant differences (Frazão et al. 2017). Differences are reported to be more pronounced in permanent, long established margins (Noordijk et al. 2010). Permanent field margins offer habitats that were not disturbed for a long time. No or low disturbance of soils (Jo Smith et al. 2009) and the development of a litter layer (J. Smith et al. 2007) lead to larger soil organism communities in terms of abundances and diversity in margins (Crittenden et al. 2015; Rutgers, Wouterse, et al. 2016). We therefore assume earthworm and microbial communities in permanent, undisturbed margins dominated by herbaceous grass-mixes to be a good estimate of the potential size and structure of these organism communities within the local soil, topographic and climatic conditions. The *a priori* assumption of this study is that these permanent margins support earthworm and microbial populations not dissimilar in composition, size and activity to those that would exist without agricultural intensification in the cropped fields. They are therefore employed as local reference sites for quantifying the impact of intensive agricultural practices on soil organisms in cropped fields.

Since field margins are seen as beneficial also for earthworm conservation in intensively managed farmlands (Nieminen et al. 2011), it is relevant to gain a better understanding of what factors make margins valuable for earthworms. Vegetation cover is a relevant factor for soil communities (Scherber et al. 2010), since plant canopy and litter deposition shape the local microclimate (Lavelle et al. 1997). Moreover, many soil organisms feed on plant exudates or decomposing plant material (Curry 2004). Therefore, changes in the quantity or quality of plant cover likely affect soil organisms. Studies from experimental settings report a positive effect of plant species richness on soil microbial biomass as well as abundance and diversity of soil meso- and macrofauna (Beugnon et al. 2019). The quality of plant roots appears to be important for decomposer communities (Milcu et al. 2006; Zaller and Arnone 1999). As the composition of roots correlates with plant functional groups (Crotty et al. 2015; Gastine, Scherer-Lorenzen, and Leadley 2003), perhaps rather the identity of plant functional groups impacts soil communities than species richness per se (Spehn et al. 2000). This is debated, however, whereas others report stronger impact of species richness than of functional groups (Eisenhauer et al. 2013).

Soil properties and vegetation are characteristics of the margins themselves. As margins are not isolated elements, the influence of the landscape context has been studied as well. While generally there is a positive correlation between habitat heterogeneity and species diversity, this effect varies considerably depending on the organisms studied (Tews et al. 2004). On the one hand, landscape heterogeneity seems to be of rather subordinate relevance for earthworms in margins (Decaëns et al. 2008; Frazão et al. 2017; Kovacs-Hostyanszki et al. 2013; Lüscher et al. 2014). On the other hand, margins positively affect earthworm abundances in fields according to some studies (Hof and Bright 2010; van Schaik et al. 2016). Vice versa, there might be an effect of the cultivation technique applied in the neighboring cropped field on the margin's earthworm population. For instance, a recent meta-analysis showed that tillage consistently decreased earthworm abundance and biomass in fields (Briones and Schmidt 2017).

This study was conducted in Western Europe, in the North German Lowland Plains. Germany represents a country where the transformation to intensive agriculture happened in the 1960ies (Bauerkämper 2004). Due to the high agricultural yields that are achieved, Germany globally ranks as the third most important exporter of agricultural goods (Baumgarten 2018; Techen and Helming 2017).

The study had two objectives. First, we studied the long-term impact of intensive agricultural practices on soil organism communities in four different intensive farming regions. Permanent margins were used as local control sites that do not receive cropping treatments. Second, we studied characteristics (soil chemical properties, vegetation cover and influence of neighbouring habitat type) that make these long-term established, permanent field margins valuable for earthworm conservation.

More specifically, we had the following hypotheses: (1) Earthworm biomass, abundance and species numbers as well as soil microbial basal respiration and biomass-C differ between the four farms since important soil physical and chemical properties for soil biological activity differ distinctly between the regions due to landscape background and land-use history. (2) Despite the regional differences earthworm biomass, abundance and diversity as well as soil microbial basal respiration and biomass-C are higher in margins than in the adjacent fields. We will to compare the results of this hypothesis with historical records on earthworms in North German cropped fields from before or during the transition to intensive agriculture between 1950 and 1980 in the discussion section. (3) There is an effect of the margins' vegetation cover on their earthworm biomass, abundance, species number and community structure because plants are the main trophic source for earthworms. Thereby, functional group composition (share of forbs, legumes, and graminoids) is more important than number of plant species *per se* (diversity). (4) Neighbouring non-crop habitats bordering the margin on the one side as well as tillage intensity of the adjacent field on the other side have an effect of the earthworm communities in the margins.

2.3. Methods

This study was conducted in the context of the project “Für Ressourcen, Agrarwirtschaft & Naturschutz mit Zukunft” (FRANZ) funded by Landwirtschaftliche Rentenbank and the Federal Ministries for Agriculture and for Environment. It aims at developing and evaluating agri-environmental measures in cooperation with ten farmers each in a different region spread across Germany.

2.3.1. Study area

The German Lowlands are part of the North European Lowland plains – bordered by the Central European Highlands to the south and the coasts of North and Baltic Sea to the north – stand out today as being among the most intensified agricultural landscapes throughout Europe (European Environment Agency 2015). They were formed during the Weichselian glaciation, by ice sheets and their impact on the surrounding areas. Four regions were chosen within the North German Lowlands that are each distinct in terms of natural landscape background and land-use history. Within each region, we chose three to four fields from the same farmer. The farm-based approach ensured uniform management techniques across the sampled fields within one region. All farms had in common that the transformation to intensive agricultural management had taken place decades ago (Kuhlmann 2019) (Fig. 1.2).

The four sites cover a wide range of farming landscape types, typical for intensive farming in Central Europe: the climate is temperate sub-continental to sub-oceanic with mean annual temperature varying from 9.5 to 10.0 °C and mean annual precipitation from 571 to 865 mm (Table 1.1). Especially Ostwestfalen and Lüneburger Heide are exposed to a relatively high mean annual precipitation due to proximity to the coast. The sites Havelland and even more so Magdeburger Börde have much drier climates. Since Magdeburger Börde is situated in the lee of the Harz mountains, the Börde belongs to the driest regions of Germany. The studied farms in Magdeburger Börde (due to its sub-continental climate) and Lüneburger Heide (due to the sandy soils) both irrigate fields (Table 1.1). All selected farms are located below 125 m a.s.l. in a planar to slightly undulating topography. Yet, geology and soil types are quite variable, with two farms being located mostly on loess-derived soils (Magdeburger Börde, Ostwestfalen) with relatively high fertility, and the other two on more sandy soils on Pleistocene basal moraines (Havelland, Lüneburg). The soils are quite variable ranging from Cambisols-Podsols to Chernozems and Gleysols under more natural vegetation (Table 1.1). All sites have in common that they have been shaped by agricultural land use for centuries with only little near-natural, non-managed vegetation being left (Bundesanstalt für Geowissenschaften und Rohstoffe 2016; Don and Prietz 2019).

2.3.2. Farming Practices

In each region, one conventionally-managed farm was selected for study. The farm-based approach allowed to establish uniform management techniques across the sampled fields. The four farms have been chosen, since they have followed conventional cropping practices for decades. According to the typical regional crop field management schemes in the respective region, tillage intensity varied between annual ploughing (Ostwestfalen) to tillage every second year (Lüneburger Heide), every fifth year (Havelland) and never (no-tillage; Magdeburger Börde) (Table 1.1). All farmers were interviewed regarding their crop management schemes and field margin management. We thus obtained information on soil cultivation techniques, fertilizer use, irrigation and harvesting practices as well as main and cover crop rotation on the studied fields. We also asked about recent changes in farming techniques (soil cultivation methods, crop rotation, fertilizer types, irrigation). Crop rotations were dominated on all farms by wheat/barley and fodder/biogas maize cultivation. A detailed description of farming practices is given in the Supplement 3.

2.3.3. Study design

On each farm, we chose three or four fields for sampling, depending on suitability and consent of the farmer. Cropped areas had to have either maize or wheat/barley as main crop in the year of analysis (2017). We thus reduced the variety of cultivated main crops in 2017 to the two distinctive plant functional types maize and cereals. For all four farms, these two represent the dominating crops within today's crop rotations of North Germany's Lowlands. The differing photosynthetic pathways - temperate cereals having a C3 metabolism and maize a C4 metabolism – do not affect soil communities (Dornbush et al. 2008; Mellado-Vázquez, Lange, and Gleixner 2019).

The selected 1-2 m wide permanent field margins as reference sites were characterized by the same soil type and topography as the corresponding sampled fields. The vegetation on the field margins consisted of grass or herb-dominated communities, which was mown once a year with the biomass left on the field margins. The margins were not seeded, fertilized or treated with pesticides; yet, some chemicals applied to the adjacent fields may well have drifted to the margins. Each pair of arable field and field margin thus offered similar pedologic conditions for soil life, with the main difference being the management scheme of the field. The cropped fields represent high input-output systems with regular addition of fertilizers, pesticides including herbicides as well as crops being sown and harvested regularly and (in part of the farms) with high soil disturbance through tillage, whereas the field margins were low input-output systems without intended substance inputs, permanent vegetation cover, and no intended soil disturbance (for details see Supplement 3). As there were no recent changes in field management schemes and all margins existed in their present form for at least 10 years, we assumed both the arable field and the field margins to represent steady-state systems.

In order to assess the impact of neighbouring non-crop habitat type on earthworms in margins, we chose field margins where the non-crop neighboring side of the margin had one of the following semi-natural habitat types: (a) stand of woody vegetation (3 margins), (b) grassy verge (4 margins), (c) water influenced area, i.e. a ditch (3 margins), (d) non-habitable infrastructure for soil dwellers, i.e. paved road (three margins). The chosen semi-natural habitat types represented a broad range of non-arable landscape features typical for farmlands in the North German Lowlands (Table 2.1).

Table 2.1: *Neighboring non-crop habitats of field margins included in the study. Each x stands for one margin.*

Neighbouring habitat

Farm	Woody vegetation stand	Ditch	Road	Grassy verge
Ostwestfalen	x	x	x	x
Havelland	x	x		x
Magdeburger Börde		x	x	x
Lüneburger Heide	x		x	x

2.3.4. Field and laboratory work

Fieldwork took place each year in October 2017. In the study regions, this season offers most favorable conditions for monitoring long-term changes of arable fields, as there is no immediate effect of management practices at this time with all main activities like fertilizing, harvesting and soil cultivation having ceased. This season is also best suited for monitoring earthworm activities and soil microbial activity, because soils usually have rewetted after summer, but soil temperatures have not yet dropped below 5°C (Schinner, Öhlinger, and Kandeler 1991). In conditions earlier or later in the year that are either too dry or too cold, earthworms tend to persist in a dormant state (Bouché 1977b). Dormant, they are not susceptible to the application of extracting fluids (Edwards and Bohlen 1996b) such as hot mustard (Plum and Filser 2005). Earthworms are most active in spring and autumn, where highest biomass is reported from extractions (Singh et al. 2021a). Similarly, soil microbes in arable fields exhibit a seasonal pattern of activity with reduced levels in summer when the soil is dry and in winter when the soil freezes. They further show a strong reaction after fertilizer application and higher amounts of root exudates in late spring (Rutgers, Wouterse, et al. 2016).

50-m transects were established and positioned to ensure comparable pedologic conditions in each pair of field and margin transect. Areas within 10 m of a field corner were excluded as being unrepresentative. The start and end points were documented with GPS-coordinates. Each 50-m transect was split into 4 blocks. Within each block, 2 sampling points were randomly chosen, always keeping them at least 4 m apart. This ensured a roughly even distribution of randomly positioned sampling points along each transect. We ensured that a sampling point was neither in a tramline nor in another spot not representative for the field or margin (e.g., log, puddle or power pole) (Fig. 2.1).

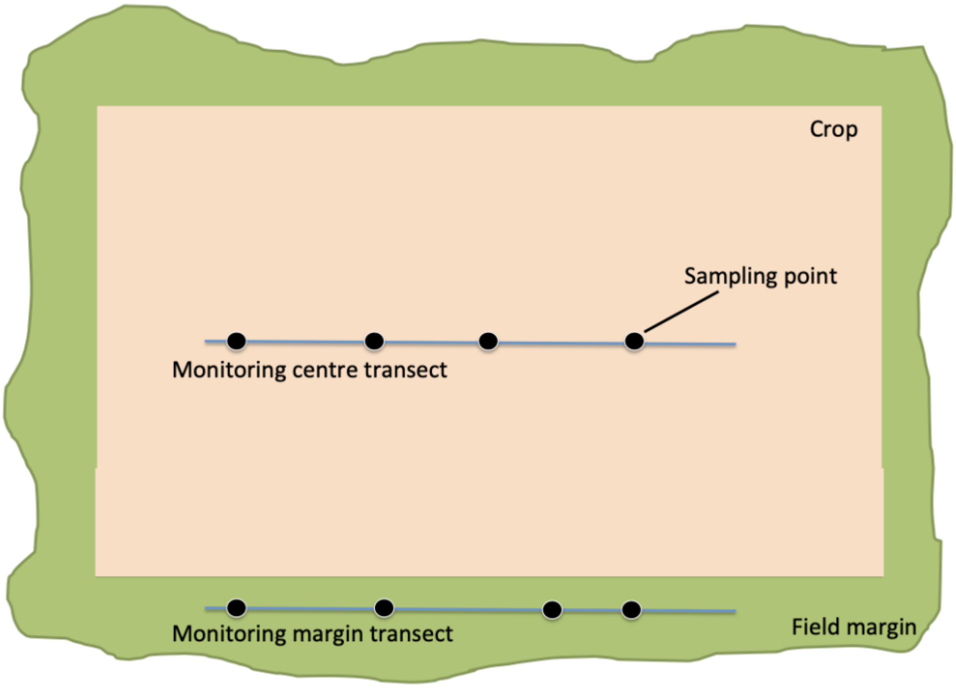


Figure 2.1: *Sampling setup for each pair of cropped field and field margin.*

a) Sampling of Earthworms

Extraction, transportation and storage

Earthworms were extracted with the hot mustard powder method, which has proven to be not harmful to the environment but still efficient (Sandor et al. 2015; Singh, Singh, and Vig 2016). 70 g of mustard powder (Semen Sinapis, Caelo) was mixed with 150 ml of water approximately 12 hrs before extraction, in order to let the hotness of the mustard develop. Just before sampling, the prepared mustard mash was diluted with 7 l of water.

For each sampling point, on 0.25 m2, standing vegetation was cut away and litter was carefully removed, taking care not to miss litter-feeding earthworms. The exposed ground allows to quickly see the appearing earthworms. In order to assure that the applied mustard percolated into the soil only on these 0.25 m2, a steel frame of 10 cm height was slightly pressed into the ground on each prepared spot.

We then slowly poured the 7 l of mustard water into each frame, taking care that the mustard-water percolated well into the soil. In cases where soils were so moist that the mustard-water ceased to drain away, we did not pour the 7 l to avoid water ponding in the frame. These cases were noted. The bulk of appearing earthworms within each frame could be extracted during 25 min. Meanwhile, soil temperature of every spot was recorded (Carter and Gregorich 2008). Extracted earthworms were carefully picked up with blunt tweezers and preserved in ethanol (70 %).

Laboratory analysis

Prior to analysis, earthworms were carefully washed and freed of remaining soil. All earthworms were counted and weighed. For species identification, every individual was put into a petri dish and placed on a dark sheet underneath a binocular (ZEISS, ‘Stemi 2000’). Species determination of adult earthworms was conducted by considering the position and constellation of setae, male pores, clitellum, tubercula pubertis and prostomium. As the clitellum is not yet developed in juvenile earthworms, they can only be distinguished by their colour, setae and structure of prostomium, which only partly allows assigning them to species (Christian and Zicsi 1999; Müller and Bährmann 2015; Sims and Gerard 1985).

b) Sampling of soil microbial data

Sample collection, transportation and storage

At each sampling point, soil coring was done with a split stainless-steel tube of 3 cm inner diameter to a depth of 10 cm. Within a radius of one meter, four samples were randomly taken and pooled together. In this manner we retrieved 4 samples on each transect. Samples were stored in plastic bags and transported to the laboratory of Göttingen University in cooling boxes. They were deep frozen at -20 °C on the day of sampling and analysed within a year (Anderson & Paulsen, 2017).

Laboratory analysis

In each pooled sample we made one analysis of microbial biomass and both basal respiration with an O_2 - micro-compensation apparatus (Scheu 1992). Prior to analysis, samples were left to thaw at 4 °C for at least 48 hrs, then plant residues were carefully removed. Samples were sieved through a mesh with pore size < 2 mm and left to rest at 4°C for a minimum of 5 days (Dilly 2001). Afterwards, we carefully placed an amount of fresh soil corresponding to 4 g of dry soil weight into about 10 ml volume glass vessels of the apparatus and left the soil to rest overnight at room temperature (about 20°C). Thereby the vessels were covered with a moist cloth in order not to lose soil moisture in the meantime (Dilly 2001). Before starting the basal respiration measurement, samples were left to acclimatize at 22 °C (J. P. E. Anderson and Domsch 1978) in the open vessels for at least 60 min. Basal respiration (µl O_2·h−1·g soil dry mass−1) was recorded for at least 24 hrs in 10-min intervals.

Microbial biomass was determined by measuring the substrate induced respiration (SIR) triggered by the response to D-glucose addition (Anderson & Domsch, 1978). An amount of 4 mg glucose per g soil dry weight at a water holding capacity of 50 % has been shown to saturate the catabolic enzymes of the microorganisms in agricultural soils (Beck et al. 1997). After addition of glucose and de-ionized water to the samples, they were left to rest for 20-30 min and subsequently the respiration was recorded for at a 10-minute interval for at least 12 h. The average over the lowest three recordings is defined as the maximum initial respiratory response

[MIRR µg O_2 g^{-1} dry weight soil h^{-1}]. As the O_2 - micro-compensation apparatus is very sensitive and prone to errors, around 20 % of samples had to be analyzed a second time. Even after re-measurements, we had to deal with around 10 % missing data.

Anderson & Domsch (1978) documented a correlation of substrate-induced maximal respiratory rate to microbial biomass carbon (C_{mic}) to be 1 ml CO_2 h^{-1} to 40 mg C_{mic} at 22 °C. This conversion factor was established on the basis of middle European soils, with a pH between 3.8 to 7.1.

c) Sampling of soil Chemical and Physical Properties

Sample collection, transportation and storage

Composite soil samples were taken by retrieving four soil cores at each sampling point within a circle of 1 m radius around the squares of earthworm sampling. Soil cores (0-10 cm depth) were extracted with a split steel tube corer of 33 mm inner radius. Additionally, one separate sample bulk density determination was taken on each sampling point. Samples were stored in plastic bags and rapidly transported to the laboratory of Göttingen University in cooling boxes. There they were kept at 8 °C until analysis.

Laboratory analysis

Prior to measurements, all soil samples were homogenized, and plant roots removed by sieving them with a mesh of < 2 mm pore size.

For bulk density analysis, the whole sample was oven-dried at 105°C until constant weight was reached (approx. 24 h). Subsequently, its mass was determined and related to the sample's volume.

For soil acidity determination, 10 g fresh soil was diluted in 25 ml de-ionized water. After 10-12 h of equilibration, pH(H2O) was measured. Afterwards KCl was added up to a concentration of 1 M KCl to determine pH(KCl).

For measuring soil water content, samples were weighed, oven-dried at 70 °C until constant weight was reached (approx. 48 h) and weighed again, and soil water content was calculated by subtracting dry weight from fresh weight.

Total soil carbon (C) and nitrogen (N) contents were analysed by first milling the dried samples. In order to quantify the amount of inorganic carbon content, 500 mg of ground soil was combusted at 600 °C for 5 h. Of the non-combusted and combusted soil samples, an aliquot each of 20 mg was weighed into tin capsules and analysed with a C/N elemental analyser (Vario EL III, Elementar, Hanau, Germany). For calculating soil organic carbon C_{org}, inorganic C was subtracted of total C.

Available phosphorus (P) and potassium (K) contents in soils were determined with the calcium-acetate-lactate (CAL) method (Schüller 1969), which extracts readily soluble and exchangeable phosphates as well as potassium and is suitable for soils with a pH of 6 or higher. A sample of 5 g sieved fresh soil was added to 100 ml of extracting solution (0.1 M Ca-lactate, 0.1 M Ca-acetate, 0.3 M acetic acid). Subsequently, the suspension was put on a shaker for 90 min and then immediately filtered. K was determined directly in the extract by measuring the absorbance at 767 nm with a flame photometer (BWB Technologies, Berkshire, UK). For determining P concentrations, 4 ml of a freshly prepared Murphy-Riley blue-dying solution (Murphy and Riley 1962) was added to 5 ml of the filtered extract and filled up to 25 ml with de-ionized water. After thoroughly mixing the solution by manually shaking it, the 25 ml were left to rest for 30 min for colour development. Afterwards, absorbance was measured at 882 nm with a spectrophotometer (Libra S 21, Biochrom, Cambridge, UK). For each sample, one analysis of all soil chemical and physical properties was undertaken.

2.3.5. Data Analysis

Data analysis was performed using the software package R, version 4.1.2 (R Core Team 2021) with R studio (R Studio Team 2022), if not indicated differently. Figures were produced using the packages ggplot2 (Wickham 2007) and ggpubr (Kassambara 2020). Differences were defined as significant with $p < 0.05$. The data was neither normally distributed (Shapiro-Wilk normality test) nor did it meet the assumption of homogeneity of variance (Levene test) using R package “car” (3.0-10, 2019).

Differences between the farms were analyzed with the Kruskal-Wallis test. The main analysis was followed up with post-hoc tests that are corrected for multiple testing as described by Siegel & Castellan (1988) using R package “pgirmess” (version 1.6.9 , 2018). Differences between fields and margins were analyzed with the Wilcoxon rank sum test. As data was nonnormally distributed, correlations between earthworm, soil microbial and soil abiotic variables were analyzed with the method of Spearman’s ranks using R package “Hmisc” (version 4.4-2, 2020).

In order to examine relationships between species composition and environmental characteristics, we performed a redundancy analysis (RDA) (Rao 1964), which we implemented in CANOCO (TerBraak, 1988–1992). RDA allows to relate qualitative environmental variables to a set of linear response variables. The RDA thus produces an ordination of the response variables constrained by the explanatory variables. From this analysis, canonical axes emerge that are formed by linear combinations of explanatory variables. Since our response variables are influenced by various factors, we expect several independent structures to concur in the dataset. Should those structures be linearly independent, they will appear on different axes (P. Legendre and Legendre 1998).

We used earthworm and microbial data as response variables and soil abiotic properties as explanatory variables. Farms and treatments (cropped field and field margin) were projected post-hoc into RDA space. We only determined the first four axes. As RDA assumes a linear relationship between response and explanatory variables, we log transformed (+1) the response data prior to analysis. Since the data has different units, we also standardized the data prior to analysis. Although it is not necessary to test the significance of RDA axes when there are only few (Pierre Legendre, Oksanen, and Braak 2011), it may help to distinguish the most important axes for explaining the variation in the data. We determined a significance value for the overall RDA solution and for each axis by Monte-Carlo permutation. As the overall solution was significant (pseudo-F = 4.1, p = 0.002) we can examine the significance of the first axis (pseudo-F = 22.9, p = 0.002).

We performed a second RDA as described above for closer analyzing the effect of vegetation cover and soil chemical properties on soil biological variables in margins. We could only include earthworms as response variables and had to exclude soil microbial data, as due to laboratory issues around 15 % of the microbial field margins data was missing. Since the missing data was not evenly distributed across the farms, including them would have led to an unbalanced field margin dataset for this analysis. Response variables were field margin earthworm variables and explanatory variables were soil properties and vegetation cover of each field margin. Prior to analysis, data was log-transformed (+1) and standardized. Analysis was constrained to compute merely the 4 first axes. A permutation test over all axes was significant (pseudo-F = 3.4, p=0.002) and the first axis was significant (pseudo-F = 11.1, p=0.002).

We performed a principal component analysis (PCA) with field margin earthworm variables as response, in order to analyze the impact of neighboring non-crop habitat and of tillage intensity in the neighboring cropped field (also implemented with CANOCO, TerBraak, 1988–1992). Prior to analysis, data was log-transformed (+1) and standardized. Analysis was constrained to compute merely the 4 first axes.

2.3.6. Search for historical records

We conducted a semi-structured search for historical literature on earthworms in agricultural contexts for North Germany, where we included records before 1980. The following search terms were employed: earthworm abundance, earthworm abundance Germany, earthworm agriculture Germany, historical record earthworm agriculture Germany. We searched on Google Scholar, Web of Science, Database of the Göttingen University Library, the Search Portal for Life Sciences (LIVIVO), Agricultural Online Access and on Open Agrar. Furthermore we conducted a search on the database “edaphobase” (https://portal.edaphobase.org/) and used the filters: Taxon: Lumbricidae Rafinesque-Schmaltz; Region: Nord- und Ostsee, Nordostdeutsches Tiefland, Nordwestdeutsches Tiefland; Date: before 01.01.1980

For data from the long-term monitoring sites run by the German Federal States we accessed their homepages and retrieved all reports that were accessible. Finally, we contacted experts of the field for recommendations to historical data, among these Prof. Dr. Rainer Jörgensen, University of Kassel and Dr Ricarda Lehmitz of the Senckenberg Museum für Naturkunde Görlitz.

Since results from earthworm studies tend to considerably differ regarding sampling method, soil or time of the year, we will only be able to compare the historical data with our sampling results.

2.4. Results

2.4.1. Variation across the four farms

a) Earthworm biomass, abundance and species number and percentage of juveniles

Averaged across fields and margins, earthworm biomass in Havelland (median 10.60 g m^{-2}) was significantly lower than in Ostwestfalen (median 23.86 g m^{-2}) and Magdeburger Börde (median 26.48 g m^{-2}) (H(3) = 13.6, p = 0.003). Lüneburger Heide (median 11.15 g m^{-2}) did not differ significantly from any of the other farms. Earthworm abundance in Lüneburger Heide (median 24 ind m^{-2}) was significantly lower than in Ostwestfalen (median 80 ind m^{-2}) (H(3) = 11.5, p = 0.009). Havelland (median 32 g m^{-2}) and Magdeburger Börde (median 40 ind m^{-2}) did not differ significantly from any other farm. Species number per sample was low with median values of 2-3 and not significantly different between the four farms (H(3) = 5.8, p = 0.12). Across all four sites, the median percentage of juvenile earthworms was 55 % in the samples. Havelland (median 40 %) had significantly lower percentages than Ostwestfalen (median 63.5 %) and Lüneburger Heide (median 65 %) (H(3) = 10.9, p = 0.012). Percentage of juveniles in Magdeburger Börde (median 53 %) did not differ significantly from any other farm (Fig. 2.2).

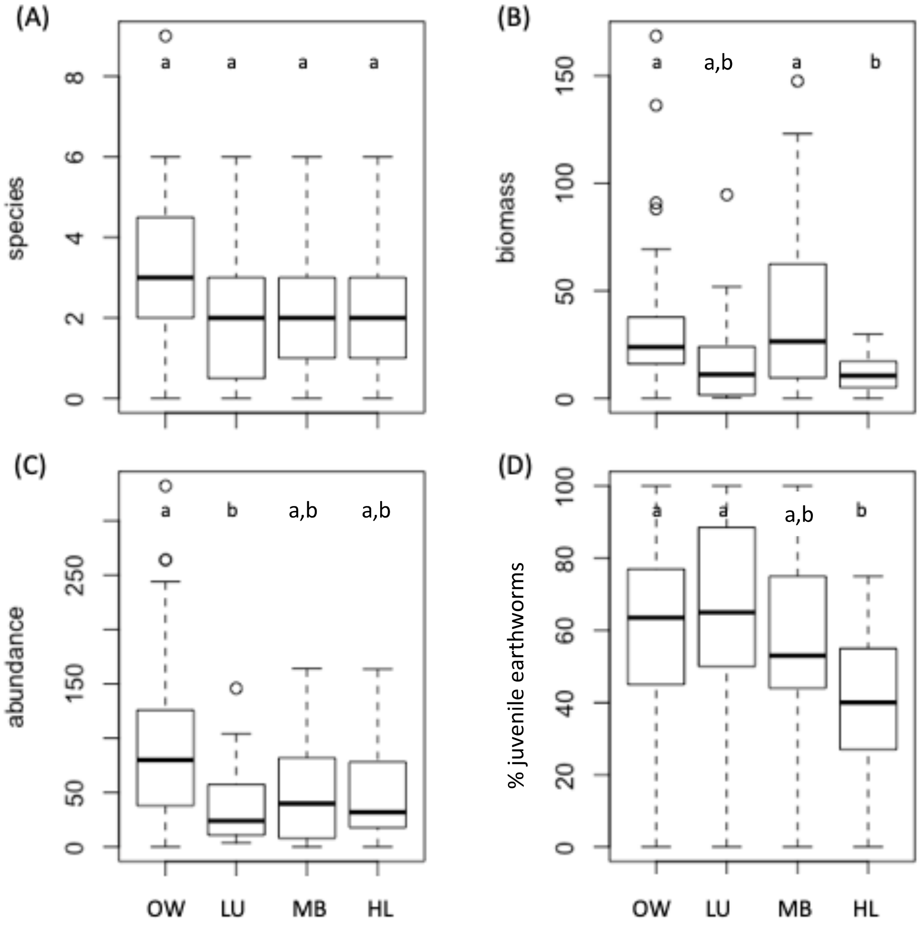


Figure 2.2: *Earthworm (A) species number (n sample^{-1}), (B) biomass (g m^{-2}), (C) abundance (n m^{-2}) and (D) percent juvenile per sample at the four farms. OW = Ostwestfalen, LU = Lüneburg, MB = Magdeburger Börde, HL = Havelland. Significant differences are marked wre 2.3: Earthworm (A) species number (n sample^{-1}), (B) biomass (g m^{-2}), (C) abundance (n m^{-2}) and (D) percent juvenile per sample at the four farms. OW = Ostwestfalen, LU = Lüneburg, MB = Magdeburger Börde, HL = Havelland. Significant differences are marked with different letters (non-parametric Kruskal Wallis rank sum test with post-hoc test according to Siegel & Castellan 1988; p < 0.05).*

b) Soil microbial respiration and biomass

Soil microbial respiration (MR) in Lüneburger Heide was significantly lower than in Ostwestfalen and in Havelland (median 1.82 vs 3.00 and 3.16 µg O_2 g^{-1} soil dry weight h^{-1}, respectively) (H(3) = 11.1, p = 0.01). Magdeburger Börde (median 2.96 µg O_2 g^{-1} soil dry weight h^{-1}) did not differ significantly from any other farm. Correspondingly, soil microbial biomass-C (C_{mic}) was lowest in Lüneburger Heide (median 353 µg g^{-1} soil dry weight), with a significant difference to Ostwestfalen, Havelland and Magdeburger Börde (median 520, 571 and 734 µg g^{-1} soil dry weight, respectively), whereas the difference between Magdeburger Börde and Ostwestfalen was significant, too (H(3) = 21.6, p <0.001). The percentage C_{mic} in

C_{org} (C_{mic}/C_{org}) was not significantly different at the four farms (H(3) = 1.9, p = 0.584). The metabolic quotient, qCO_2, i.e. respiration related to the available C_{mic}, in Magdeburger Börde was significantly lower than in Ostwestfalen, Havelland and Lüneburger Heide (median 2.43 vs 3.77, 2.90, 2.84 µg CO_2-C mg^{-1} C_{mic} h^{-1}, respectively) (H(3) = 23.93, $p < 0.001$) (see Fig. 2.3).

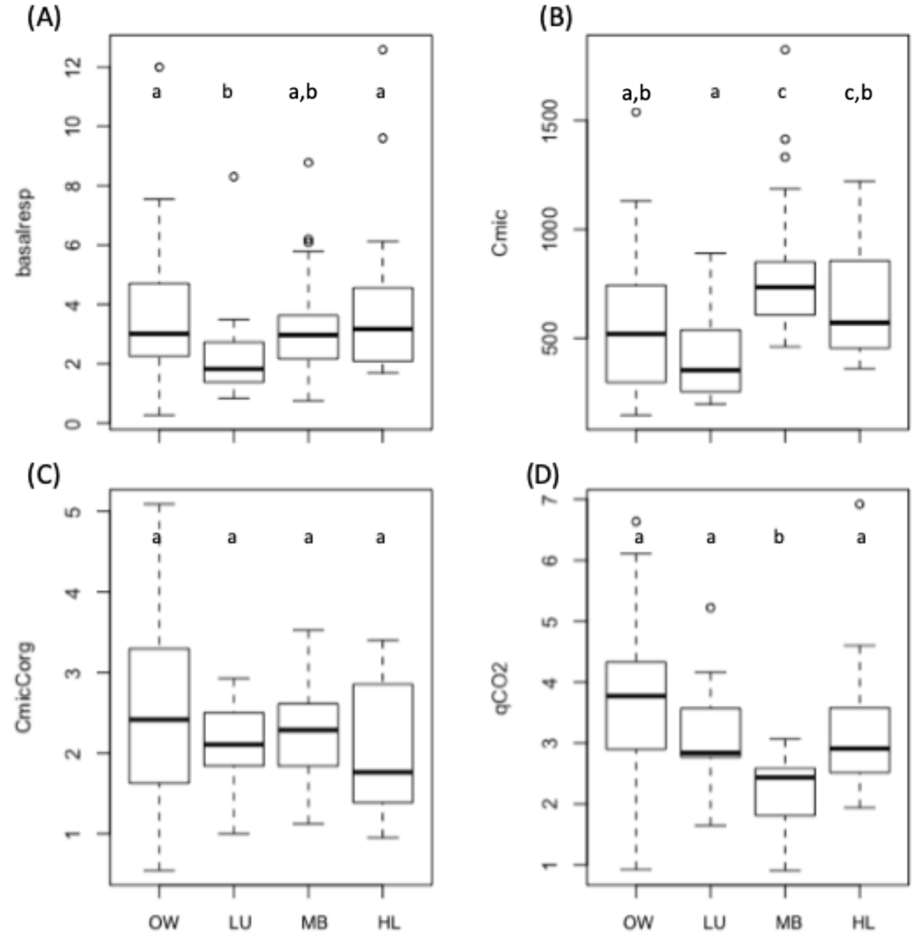


Figure 2.3: *Soil (A) microbial basal respiration (µg O_2 g^{-1} soil dry weight h^{-1}), (B) C_{mic} (µg g^{-1} soil dry weight), (C) percent C_{mic} of C_{org}, and (D) qCO_2 (µg C O_2-C mg^{-1} C_{mic} h^{-1}) at the four farms. OW = Ostwestfalen, LU = Lüneburger Heide, MB = Magdeburger Börde, HL = Havelland. Significant differences are marked with different letters (non-parametric Kruskal Wallis rank sum test with post-hoc test described by Siegel & Castellan 1988; $p < 0.05$).*

c) Soil properties

Soil properties differed significantly between the four farms (see Table 2.2). Soil moisture at the time of sampling in October was significantly higher in Magdeburger Börde than in Ostwestfalen and Lüneburger Heide. Soil moisture in Lüneburger Heide was significantly lower than in Havelland and in Magdeburger Börde (H(3) = 35.87, p < 0.001). Even though all sites had pH values >6, pH was significantly different between the four farms (H(3) = 40.84, p < 0.001); however, the difference between Magdeburger Börde and Havelland was non-significant. Both Magdeburger Börde and Havelland had significantly higher C_{total} contents than Lüneburger Heide (H(3) = 20.72, p < 0.001). Ostwestfalen and Lüneburg both had significantly lower N_{total} than Magdeburger Börde and Havelland (H(3) = 34.52, p < 0.001). The ratio of C to N differed significantly only between Lüneburger Heide and Magdeburger Börde (H3) = 8.78, p = 0.03). Magdeburger Börde had significantly higher P contents than all three other farms (H(3) = 41.29, p < 0.001). Also potassium contents in Magdeburger Börde were significantly higher than in all three other farms (H(3) = 13.06, p = 0.004). Bulk density differed only with marginal significance between the farms (H(3) = 7.75, p = 0.052).

Table 2.2: *Median (and interquartile range) of key soil variables in the whole dataset for the four farms and covering fields and margins. SDW = soil dry weight. Significant differences between the farms are marked with different letters in blue. Significant differences between the farms are marked with different letters in blue. Significant differences between field and margin in black letters (non-parametric Kruskal Wallis rank sum test with post-hoc test described by Siegel & Castellan 1988; p < 0.05).*

	Soil moisture (% water of SDW)	Bulk density (g cm^{-3})	pH (H_2O)	C_{tot} (mg g^{-1} SDW)	N (mg g^{-1} SDW)	C_{org} (mg g^{-1} SDW)	P (mg g^{-1} SDW)	K (mg g^{-1} SDW)
Overall (n=104)	24 (13)	0.95 (0.35)	7.1 (1.1)	28.6 (28)	2.5 (2.0)	27.6 (24)	0.066 (0.06)	0.16 (0.14)
Havelland (n=24)	26 (14) a,c	0.91 (0.34)	7.5 (0.92) a	41.1 (39) a	3.7 (2.1) a	40.8 (34)	0.07 (0.05) a	0.12 (0.10) a
Lüneburg (n=24)	18 (6.3) b	1.1 (0.16)	6.4 (0.74) b	15.1 (16) b	1.4 (1.4) b	15.0 (16)	0.06 (0.02) a	0.16 (0.08) a
Ostwestfalen (n=32)	20 (12) a,b	0.98 (0.36)	7.0 (1.3) c	27.2 (18)	2.2 (1.3) b	25.8 (17)	0.06 (0.02) a	0.15 (0.13) a
M. Börde (n=24)	32 (7.9) c	0.86 (0.18)	7.5 (0.27) a	38.1 (19) a	3.1 (0.10) a	36.2 (17)	0.17 (0.07) b	0.29 (0.41) b
Field (n=52)	19 (16) a	1.0 (0.30) a	7.1 (0.91) a	19.1 (20.1) a	1.67 (1.7) a	18.4 (16) a	0.066 (0.03)	0.13 (0.11) a
Margin (n=52)	26 (8.5) b	0.88 (0.33) b	7.0 (1.3) b	33.3 (22.4) b	2.91 (1.18) b	32.8 (19) b	0.072 (0.09)	0.21 (0.17) b

2.4.2. Differences between margins and fields

a) Earthworm biomass, abundance, species number and percentage of juveniles

Across all farms, earthworm biomass was just around a quarter in fields (median 6.39 g m^{-2}) of what margins (median 25.56 g m^{-2}, $W = 503.5$, $p < 0.001$) hosted. Similarly, earthworm abundance was on average roughly a fifth in fields (median 16 ind m^{-2}) compared to margins (median 88 ind m^{-2}, $W = 339.5$, $p < 0.001$). Species number per sample was also significantly lower in fields (median 1 species per sample) than in margins (median 3 species per sample) ($W = 379$, $p < 0.001$) (Fig. 2.4).

However, these effects differed between the four farms. Earthworm biomass and abundance were significantly higher in margins compared to fields at Ostwestfalen (biomass: $W = 57$, $p = 0.01$; abundance: $W = 21.5$, < 0.001), Lüneburger Heide (biomass: $W = 4$, $p < 0.001$, abundance: $W = 0$, $p < 0.001$) and Magdeburger Börde (biomass: $W = 8$, $p < 0.001$, abundance: $W = 5$, $p < 0.001$), but this was not the case in Havelland ($W = 56$, $p = 0.972$).

b) Soil microbial respiration and biomass

MR was significantly lower in fields compared to margins (median 2.03 vs 4.33 µg O_2 g^{-1} soil dry weight h^{-1}) ($W = 223$, $p < 0.001$). C_{mic} in fields was significantly lower than C_{mic} in margins as well (median 392.6 vs 743.0 µg g^{-1} soil dry weight, $W = 241$, $p < 0.001$). Also, the ratio of C_{mic} to C_{org} was significantly lower in fields compared to margins (median 2.05 vs 2.45 %, $W = 771$, $p = 0.055$), but qCO_2 was not significantly different between field and margin (median 2.80 vs 2.91 µg CO_2-C mg^{-1} C_{mic} h^{-1}, $W = 913$, $p = 0.447$) (Fig. 2.4).

As for earthworms, these effects differed between the four farms. MR was significantly higher in margins compared to fields in Ostwestfalen ($W = 7$, $p < 0.001$), in Lüneburger Heide ($W = 0$, $p<0.001$) and in Havelland ($W = 23$, $p = 0.007$), but not in Magdeburger Börde ($W = 20$, $p = 0.139$). C_{mic}/C_{org} was significantly higher in margins compared to fields in Ostwestfalen ($W = 39$, $p < 0.001$) and Magdeburger Börde ($W = 3$, $p < 0.001$), however not in Lüneburger Heide ($W = 61$, $p = 0.117$) and Havelland ($W = 83$, $p = 0.316$).

c) Soil properties

Soil chemical properties differed significantly between margin and field (Fig. 2.4). Significantly higher in margins than in fields were C_{total} (W = 714, $p < 0.001$), N_{total} (W = 643, $p < 0.001$) and K (W = 745, $p < 0.001$). Bulk density was significantly lower in margins than in fields (W = 1756, p = 0.001). However, not significantly different were P (W = 1158, p = 0.269) and soil C/N ratio (W = 1262, p = 0.675). Also, pH did not differ significantly (W = 1506.5, p = 0.235).

Nonetheless, these effects differed between the farms. C_{total} did not differ significantly between margin and field in Ostwestfalen (W = 82, p = 0.140) and in Magdeburger Börde (W = 58, p = 0.443) as did not N_{total} (W = 56, p = 0.378) and bulk density (W = 52, p = 0.266) in Magdeburger Börde. K did not differ significantly between field and margin in Lüneburger Heide (W = 56, p = 0.378) and in Ostwestfalen (W = 107, p = 0.626). However, P content in margins were significantly lower than in fields in Ostwestfalen (W = 192, p = 0.003). On the contrary, in Havelland P contents were significantly higher in margins than in fields (W=24, p = 0.004). pH was significantly lower in margin than in fields in Ostwestfalen (W=184, p = 0.01).

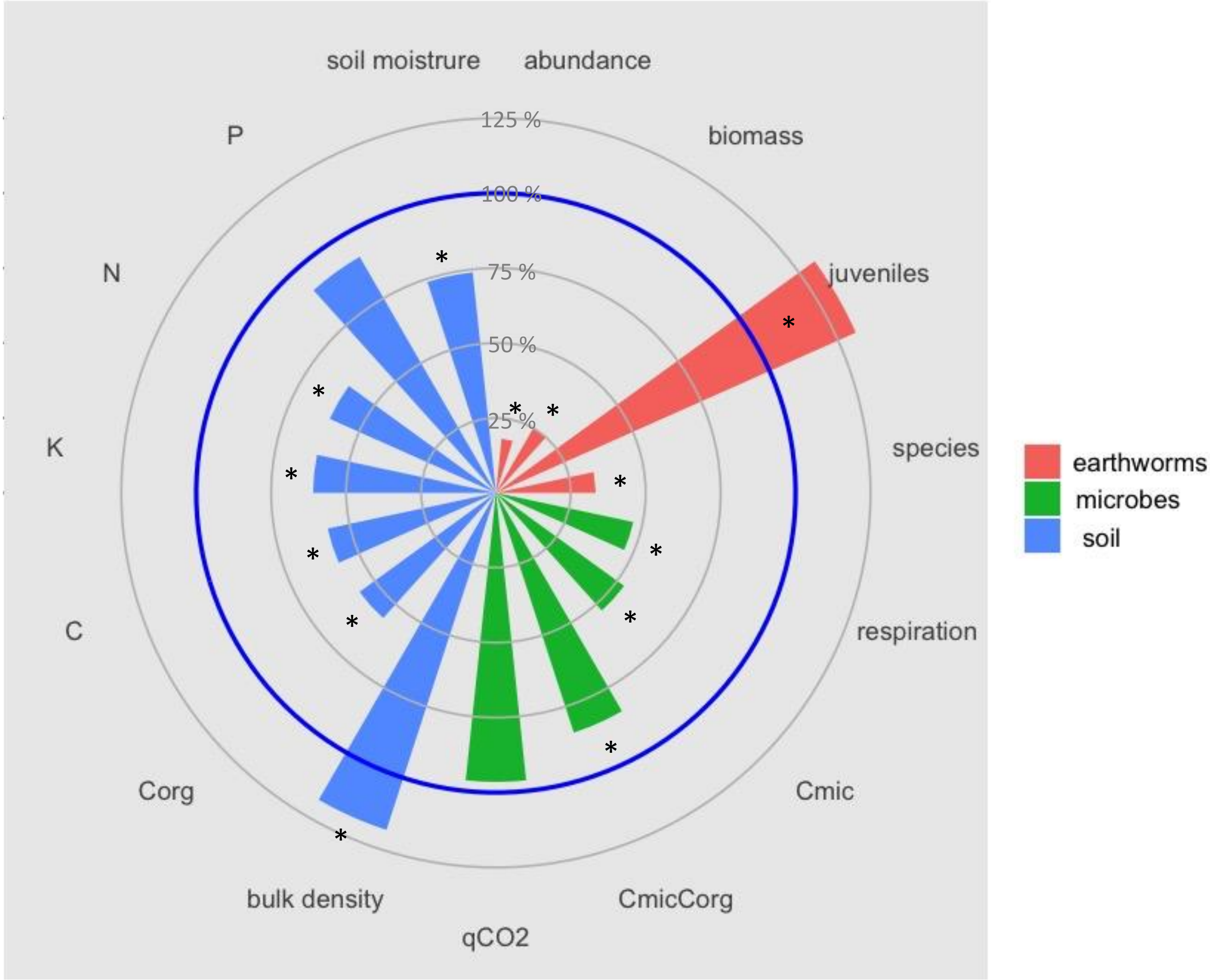


Figure 2.4: *Median of earthworm, soil microbial and soil chemical properties in fields, relative to those in the reference (margins) in bold blue circle, which is set to 100 %. Asterisks mark statistically significant differences between margins and fields (Wilcox on rank sum test, p < 0.05).*

d) Dependence of earthworm community patterns and soil microbial variables on soil chemical properties and site

15 earthworm species occurred at all four sites (Table 2.3). However, only nine species occurred in the fields of these sites. The most frequently recorded species in fields were *Aporrectodea caliginosa* (Savigny, 1826) (38 recordings), *Lumbricus terrestris* (Linné, 1758) (30 recordings), *Allolobophora chlorotica* (25 recordings) and *Aporrectodea rosea* (Savigny, 1826) (10 recordings). The least abundant species were *Aporrectodea longa* (Ude 1885), *Dendrobaena octaedra* and *Octolasion cyaneum* (Savigny, 1826) (each one recording), *Lumbricus rubellus* (Hofmeister 1843) (4 recordings) and *Lumbricus castaneus* (Savigny, 1826) (3 recordings). Exclusively recorded in margins were *Dendrodrilus rubidus* (30

recordings), *Octolasion tyrateum* (6 recordings), *Eisenia fetida* (3 recordings) *Aporrectodea icterica*, *Eiseniella tetraedra* (each 1 recording), (Savigny, 1826) and *Lumbricus eiseni* (Levinsen 1884) (2 recordings).

***Table 2.3**: List of earthworm species recorded at the sites Lüneburger Heide (LU), Ostwestfalen (OW), Havelland (HL) and Magdeburger Börde (MB)*

Total recorded individuals	Species	Individuals recorded in margins		Ecologcial group	feeding
838	*Juvenile earthworms*	608	(all sites)		
243	*Aporrectodea caliginosa*	205	(all sites)	endogeic	soil
95	*Lumbricus castaneus*	92	(all sites)	epigeic	litter
86	*Lumbricus terrestris*	56	(all sites)	anecic	litter
79	*Allolobophora chlorotica*	54	(all sites)	endogeic	soil
52	*Aporrectodea rosea*	42	(all sites)	endogeic	soil
40	*Lumbricus rubellus*	36	(only OW, LU, HL)	epigeic	litter
32	*Dendrobaena octaedra*	31	(only OW, LU, HL)	epigeic	litter
30	*Dendrodrilus rubidus*	30	(all sites)	epigeic	litter
14	*Aporrectodea longa*	13	(only LU, HL)	anecic	litter
6	*Octolasion tyrateum*	6	(all sites)	endogeic	soil
4	*Octolasion cyaneum*	3	(only OW, HL)	endogeic	soil
3	*Eisenia fetida*	3	(only LU)	epigeic	litter
2	*Lumbricus eiseni*	2	(only LU)	epigeic	litter
1	*Eisenia tetraedra*	1	(only HL)	epigeic	litter
1	*Aporrectodea icterica*	1	(only OW)	epigeic	litter

In margins, endogeic species held a share of median 50.8 % of the recorded earthworm individuals, while epigeics reached 33.7 % and anecics 15.4 %. In fields, the average share of epigeics was with 9.6 % significantly lower compared with margins (W= 424.5, $p < 0.001$), while the average share of anecics in fields shifted to 30.3 % and the share of endogeics increased to 60 %, though not significantly different from margins (W = 981.5, p = 0.381; W= 1054, p = 0.150, respectively) (Fig. 2.5).

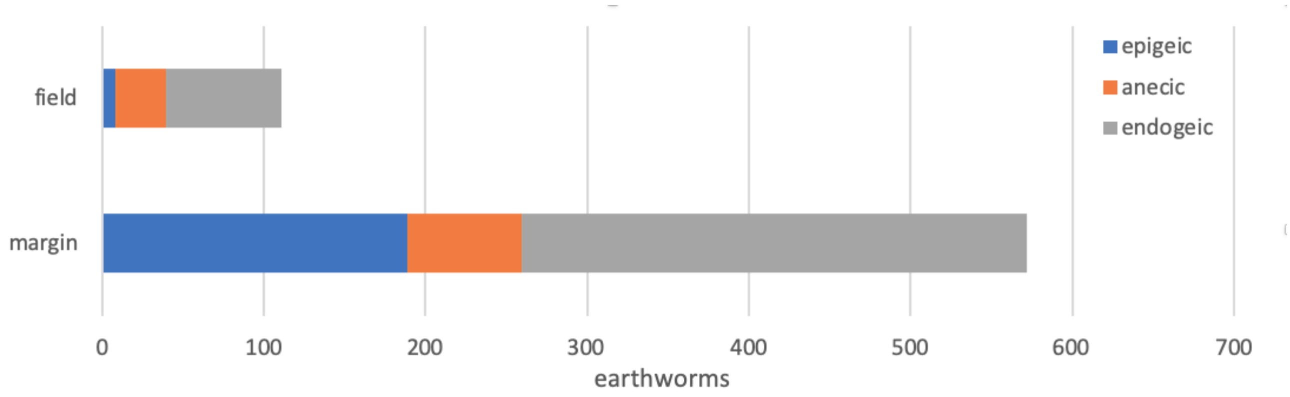


Figure 2.5: *Total number of recorded earthworm individuals in the fields and margins separated into three ecological groups.*

Soil chemical properties (soil moisture, pH, bulk density, C, N, P, K) explained 31.7 % of the variation of the soil biological data and significantly affected earthworm biomass, abundance, species numbers and community structure as well as soil microbial biomass and respiration according to the redundancy analysis (eigenvalues of axis 1 = 0.227 and axis 2 = 0.053; pseudo-F = 4.1, p = 0.002). The first axis was significant (pseudo-F = 22.9, p = 0.002) and separated fields from margins (Fig. 2.6). Margins were associated with higher soil C, N and K contents as well as pH and higher soil moisture. All earthworm-related variables (biomass, abundance, species number, abundance of juvenile earthworms) as well as C_{mic}, microbial respiration rate, and C_{mic}/C_{org} associated with margins. Fields associated with a wider C/N ratio, higher bulk density as well as higher P content. Among the soil biological variables, only qCO_2 associated with fields.

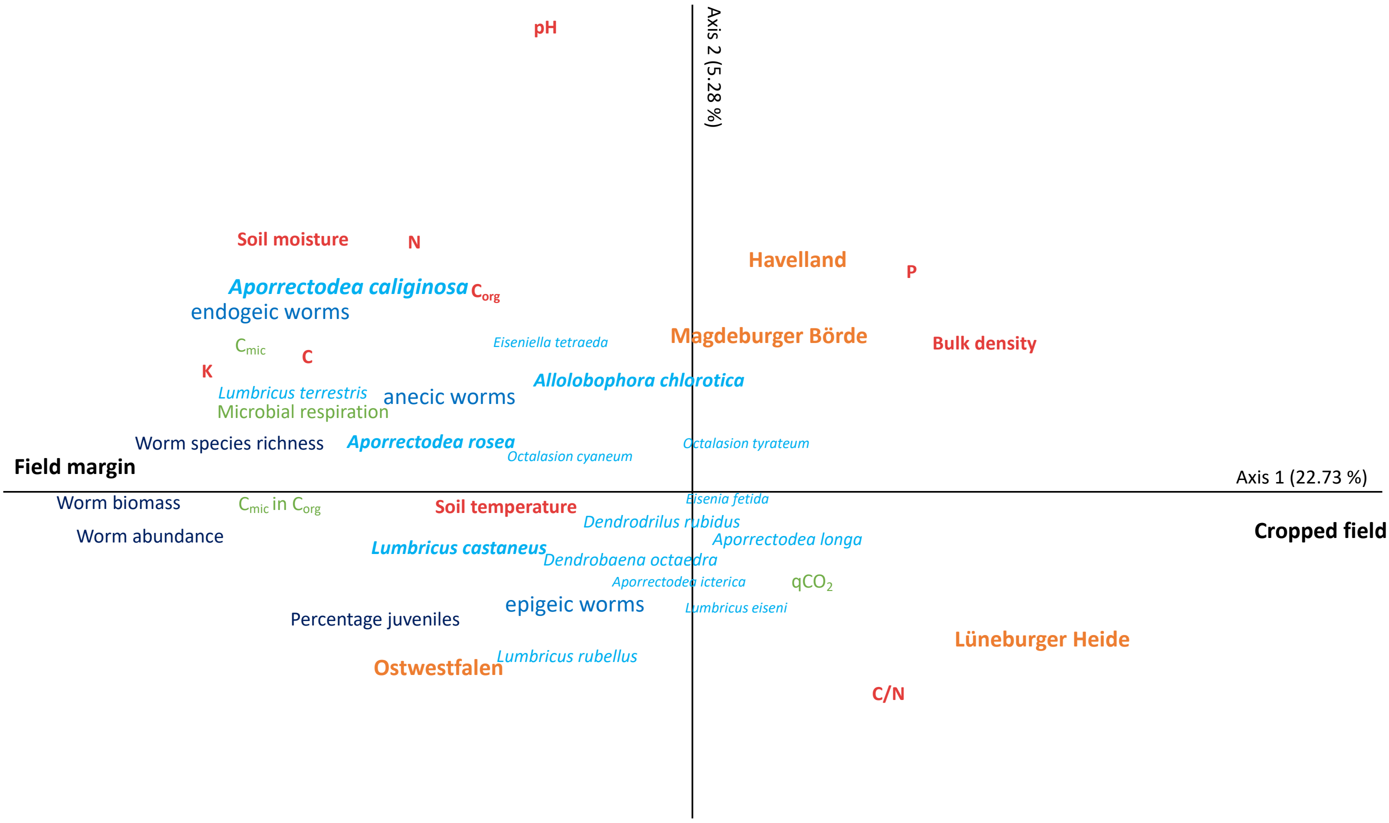


Figure 2.6: *Redundancy analysis (RDA) summarizing the variation in the composition of earthworm (blue) and microbial (green) communities with respect to soil properties (red) between margin and field (black) on all four farms (orange). A permutation test on all axes ($F = 4.1$, $p = 0.002$) and the first axis were significant ($F = 22.9$, $p = 0.002$).*

C and N content and soil moisture correlated positively with each other. Bulk density was significantly negatively correlated with C (Pearson's r = -0.73, $p < 0.001$), N (Pearson's r = -0.71, $p < 0.001$) and soil moisture (Pearson's r = -0.68, $p < 0.001$). Earthworm biomass, abundance and species number significantly positively correlated with each other. However, direct correlations of earthworm-related variables with soil chemical variables were non-significant or weak. Only with soil K content earthworm biomass (Pearson's r = 0.45, $p < 0.001$) and abundance (r = 0.37, $p < 0.001$) correlated directly. C_{org}, C_{mic} and microbial respiration rate were significantly positively related to each other. Microbial respiration rate significantly correlated positively with soil moisture and negatively bulk density (soil moisture: Pearson's r = -0.59, $p < 0.001$, bulk density: Pearson's r = -0.55, $p < 0.001$). C_{mic} correlated significantly negatively with soil moisture (Pearson's r = -0.77, $p < 0.001$) and bulk density (Pearson's r = 0.60, $p < 0.001$) as well. There were significant, direct correlations between microbial respiration and earthworm abundance (Pearson's r = 0.52, $p < 0.001$), species number

(Pearson’s r = 0.50, $p < 0.001$) and biomass (Pearson’s r = 0.40, $p = 0.001$). There were also significant correlations between C_{mic} and earthworm abundance (Pearson`s r = 0.53, $p < 0.001$), species number (Pearson’s r = 0.51, $p < 0.001$), and biomass (Pearson’s r = 0.47, $p < 0.001$).

2.4.3. Effect of vegetation and soil to earthworm community structure in margins

Vegetation cover characteristics (plant species number, plant height, plant functional groups legumes, graminoids and forbs) together with soil chemical properties (soil moisture, pH, bulk density, C, N, P, K content) explained 51.06 % of the variation of earthworm variables in field margins and significantly affected earthworm biomass, abundance, species number and community structure (RDA, eigenvalues of axis 1 = 0.288 and axis 2 = 0.123; pseudo-F = 3.3, $p < 0.01$). The first RDA axis was significant (pseudo-F = 13.7, $p < 0.01$) (Fig. 2.7). Soil chemical properties were associated with the first axis. Plant variables were associated with the second axis and with lower soil nutrient contents (N, P, K) as well as lower pH. Field margin plant communities were dominated by graminoids with an average coverage of 75 %. Forbs had an average coverage of only 36 % and Fabacae merely made up 1.5 %. Due to this dominance of graminoids, it was not possible to disentangle the effect of the three functional groups. While therefore the variable plant height must have mainly been determined by tall grasses, species richness also appears to be influenced by forbs.

Along the first axis, earthworm variables (as abundance, biomass and earthworm species number) clustered with the four most frequently recorded earthworm species *Aporrectodea caliginosa, Allolobophora chlorotica, Lumbricus terrestris* and *Aporrectodea rosea*. These comprised about 75 % of the recorded adult individuals. The remaining 25 % of adult individuals clustered with plant variables. This cluster included all eleven less frequently recorded taxa – the majority being epigeic species. A higher share of juvenile earthworms also associated with plant cover variables.

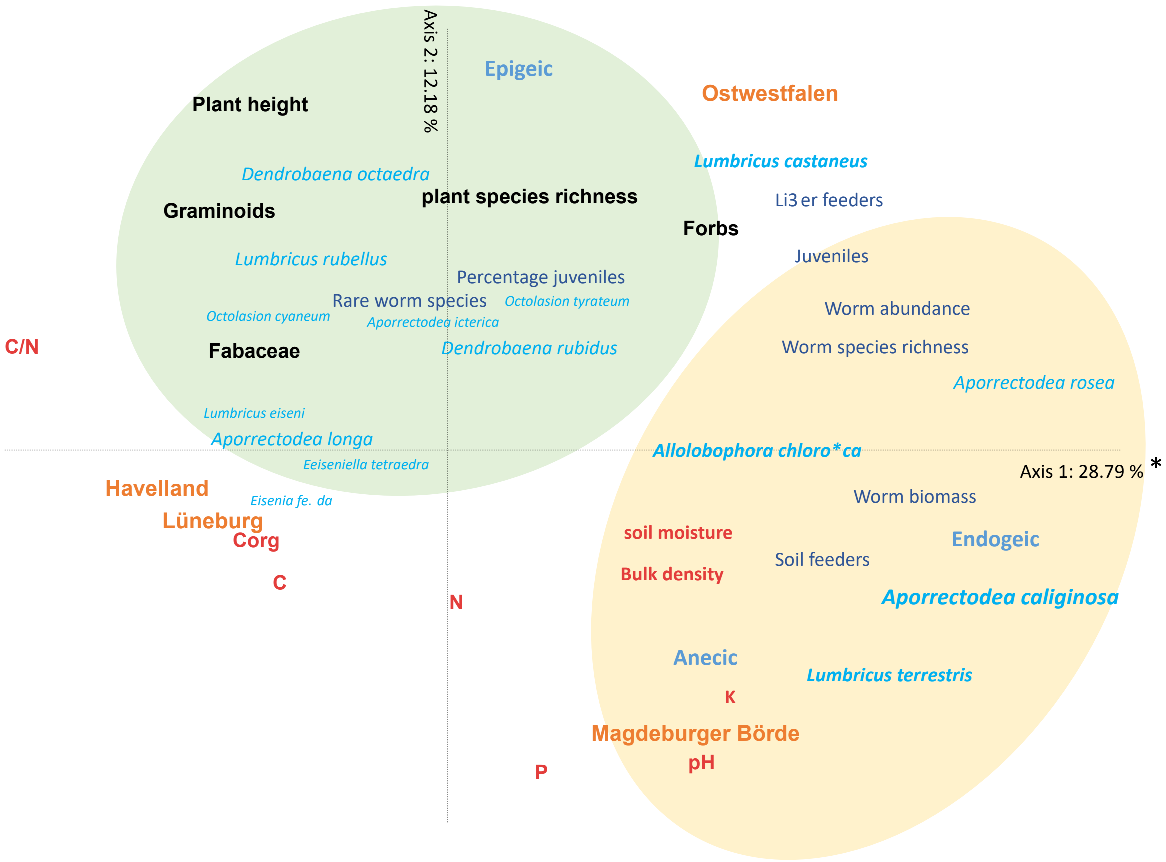
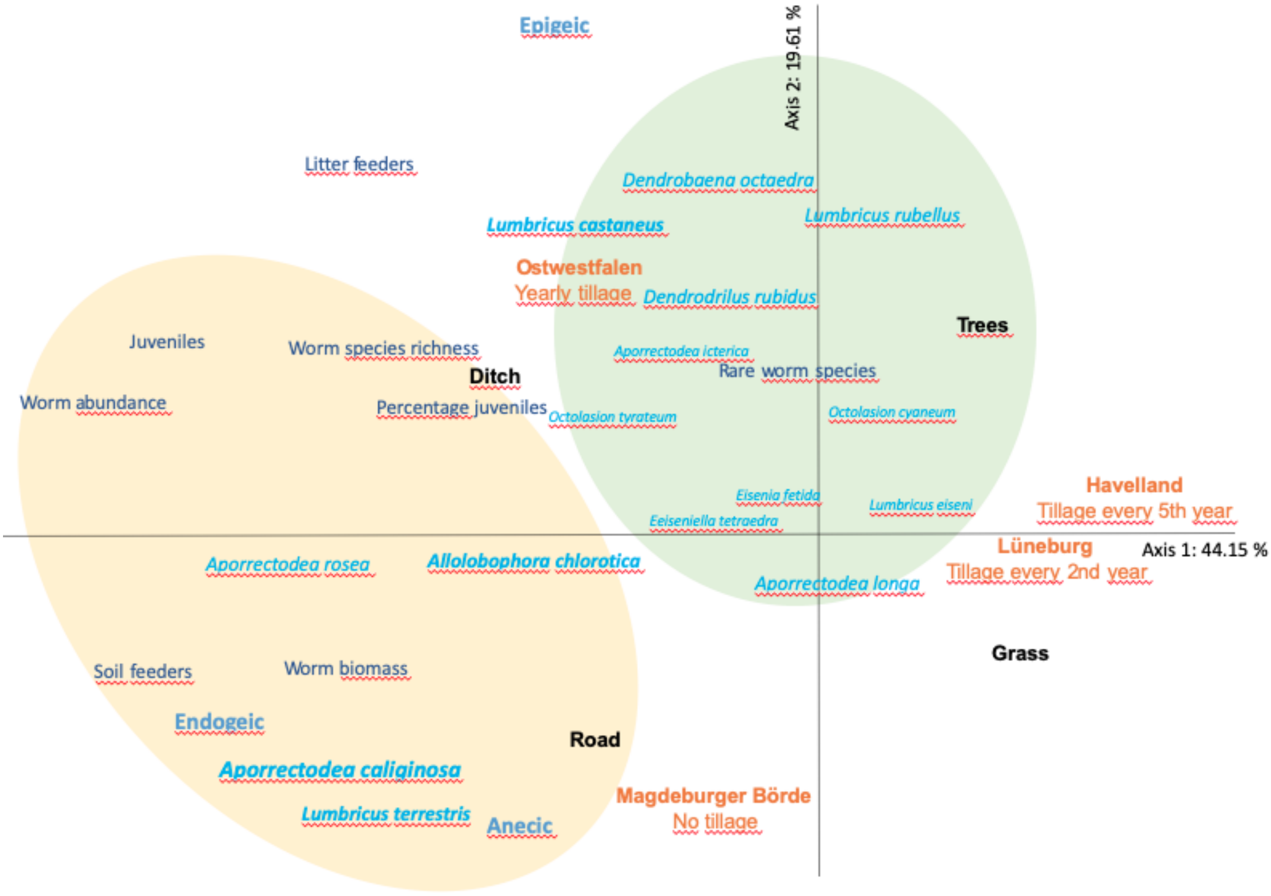


Figure 2.7: *Correlation biplot of the first two axes of redundancy analysis (RDA) that summarize variation in the composition of earthworm communities in margins (blue) with respect to soil properties (red) and vegetation cover (black) on all farms (orange). Two clusters of earthworm species could be distinguished (yellow and green backgrounds). A permutation test on all axes was significant (F = 3.3, p<0.01) as was the first axis (F=13.7, p<0.01).*

2.4.4. Effect of neighbouring landscape elements of the on the earthworm communities in the margins

A principal components analysis of the type of non-crop landscape element (road, ditch, trees, grassy verge) in the direct neighborhood and tillage intensity in the adjacent arable field (every year, every second year, every fifth year, never) explained 80.43 % of the earthworm community's variation in margins (Fig. 2.8).

The first axis explained 44.15 % of the variation, and earthworm variables (biomass, abundance, species number, percent juveniles) were associated with this axis. The second axis added 19.61 % of explained variation and separated fields that were ploughed every year (as in Ostwestfalen) from fields that were never ploughed (as in Magdeburger Börde), with tillage every fifth year (Havelland) and tillage every second year (Lüneburger Heide) ranging in between. Two clusters of earthworm associations emerged, first the four most frequently recorded species *Aporrectodea caliginosa, Allolobophora chlorotica, Lumbricus terrestris* and *Aporrectodea rosea,* and second the eleven other earthworm species. The presence of trees as neighbouring habitat associated with the second cluster, ditches with high percentage of juveniles, roads with the first cluster, while grassy verges were related to none of the variables.



	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.4415	0.1961	0.1137	0.0530
Explained cumulated variation	44.15	63.76	75.13	80.43

***Figure 2.8**: Principal components analysis (PCA) of earthworm community composition (blue) with respect to neighbouring non-crop habitat (black) as well as with tillage intensity in the adjacent field on the four farms (orange). Two clusters of earthworm species could be distinguished (yellow and green backgrounds).*

2.4.5. Historical records of earthworm populations in North German cropped fields

The search for historical records was not very successful. Each German federal state runs long-term soil monitoring sites (Bodendauerbeobachtungsflächen) in selected land-use types, among these are agricultural sites. Since the 1990ies earthworms are included in the long-term monitoring. Furthermore, two single studies were found (Finck 1990; Graff 1953). They will be discussed in detail along with our findings in the discussion.

2.5. Discussion

This study had the objective to determine the long-term impact of intensive agricultural practices on earthworms as well as soil microbes and analyse the conservation value of permanent margins for earthworm populations.

2.5.1. Variation across the four farms

Contrary to our hypothesis, earthworm communities and microbial biomass and activity were similar across all farms. We did not detect pronounced geographical differences; on-farm variation of these soil organisms tended to exceed the variation between the farms. Among the earthworm species, we only recorded generalists and did not detect considerable differences between the farms. We also documented overall differences in topsoil physico-chemical properties on the different farms to vary only within a narrow range. Soils on all farms were rich in N, P and K, had on average pH-values close to neutral, and topsoils were well aerated with low bulk densities. Our findings indicate that regional differences in soil type, climate and cultivation history have only limited effects on soil physico-chemical and soil biological properties in intensively cropped fields. Probably, intensive farming practices override local differences, which explains the similarity of earthworm and microbial patterns across the regions, as will be discussed in detail in the following.

A key characteristic of intensified agriculture is the fundamental regulation of soil functions by chemical and mechanical inputs (Giller et al. 1997; Lüscher et al. 2014) namely tillage, high fertilizer as well as agrochemical inputs and controlling soil acidity via liming (Thiele-Bruhn et al. 2012). This results in a reduced complexity of soil food webs (Banerjee et al. 2019; Bloor et al. 2021) with mainly generalist species surviving (Tsiafouli et al. 2015). Indeed, our most frequently recorded four species *A. caliginosa, L. terrestris*, *A. chlorotica* and *A. rosea* not only generally belong to the most common species reported in Germany (Lehmitz et al. 2014) but are common specifically for agricultural sites in North Germany (Tischer 2007). Our by far most often recorded species *A. chlorotica* is characterized as the earthworm having the most pronounced preference for crop fields and grassland in Germany. It typically occurs in croplands together with the endogeic *A. caliginosa* and the two anecic taxa *A. longa* and *L. terrestris* (Jänsch et al. 2013).

Intensive agriculture simplified formerly heterogeneous landscapes with fewer crop and non-crop habitats (Landis 2017) resulting in biotic homogenization (McKinney and Lockwood 1999). Similar to our findings, previous studies also reported only minor differences in earthworm populations across different intensively managed arable sites within a region (Joschko et al. 2006; Regulska and Kołaczkowska 2016; Wirth 1999). Also on a national scale, a study on earthworm communities in intensive arable soils across Finland reported higher variation within the localities than between and did not detect a geographical trend (Nieminen et al., 2011). The variation of soil microbial communities in agricultural soils in Australia was reported to be reduced even on a continental scale as well (Xue et al., 2018). However, evidence is mixed and other studies from intensive arable soils in different regions reported significant differences between regions (Roarty and Schmidt 2013). Where differences were documented, these were mostly explained by differing physico-chemical soil conditions (Plassart et al. 2019; Xue et al. 2018). Overall, our earthworm assemblages are typical for North German intensified agricultural landscapes. Apparently, one aspect of agricultural intensification being so far less discussed in literature, is the homogenization of soil conditions, which has as consequence a homogenization of soil organisms as well.

At the farm Lüneburger Heide, microbial biomass and respiration were lowest as well as earthworm biomass and abundance values. Lüneburger Heide farm stood out with driest soils, lowest pH and lowest soil carbon content and high proportion of sand in the soils. This finding suggests that where field management practices cannot override differences in physico-chemical properties entirely, they continue to locally determine earthworm and soil microbial communities.

Since soil acidity causes epidermal damage (Chen, Zhang, and Wei 2020), earthworms respond quickly to changes in soil acidity with a preference between 5 and 7.4 (Curry and Schmidt 2007), and abundances and biomass were observed to be scarce towards pH values of 4.5 (McCallum et al. 2016). Being their food base, soil organic matter content and quality is considered to be a good predictor of earthworm populations (Edwards and Bohlen 1996a). Furthermore, medium textured soils are preferable because they have best soil moisture conditions, while soils with high clay content are prone to becoming anaerobic with rainfall and in sandy soils the risk of drought increases (Curry 2004). A study on conventionally cropped sites in North German Lowlands proposed that earthworm and microbial communities are mainly shaped by differences in soil pH and total nitrogen availability in soils (Joschko et al. 2006; Wirth 1999). Our pH values were all well above 5, therefore it is questionable if the impact of pH was of primary importance in our study. Soil organic matter and nitrogen values in Lüneburger Heide were low, however. We argue that in Lüneburger Heide agricultural activity on soils with a high share of sand led to lower soil organic matter and available nitrogen contents.

We conclude that for North Germany, while soil properties and climatic factors generally set the limits for soil organisms, intensive agricultural management is nowadays able to override these limits and simplifies the organism communities.

2.5.2. Differences between margins and fields

Our findings support the second hypothesis since soil organisms show distinct patterns for margins and fields. In margins, most earthworm and soil microbial variables were two to four times greater than what we recorded in fields, e.g. averaged earthworm abundances were 80 ind / m^2 in margins and only 16 ind / m^2 in fields. Fields were also associated with higher soil bulk density, wider topsoil C/N ratios and higher qCO_2 values, while we documented higher nutrient contents and soil organic matter in margin soils. Yet, soil properties were only able to explain about a third of the variation of earthworm and soil microbial variables. Also, direct correlations of soil chemical properties with soil biological variables were only weak. We suggest the pronounced reduction of earthworm and soil microbial populations in fields compared to margins is a consequence of intensive management. The fact that we did not document a strong correlation between soil properties and soil organism variables underlines the overriding effect of intensive arable management.

Other studies also reported low numbers in fields compared to margins for earthworms and soil microbes (Cluzeau et al. 2012; Crittenden et al. 2015; Hof and Bright 2010; Sechi et al. 2017; Jo Smith, Potts, and Eggleton 2008). An extensive survey of arable fields in north-western France measured on average 350 to 215 earthworm ind / m^2 in margins compared to fields (Cluzeau et al. 2012), in the Netherlands on average 541.3 in margins to 414 in fields (Frazão et al. 2017) and in Ireland 470 to 174 ind / m^2 (Roarty and Schmidt 2013). Direct comparisons with other countries must be done cautiously, though. The named studies were from countries that were distinguished as one of the main global hotspots for earthworm abundance and diversity (Phillips et al. 2019). For Germany, rather 114 earthworm ind / m^2 are expected on average (Rutgers et al., 2016). Thus, earthworm abundances even in margins were merely half of what would be expected to occur in German soils. Sampled margins were with 1-2 m width narrow though, which could explain the low values, as earthworm occurrences depend on the area studied (Judas 1988).

A review from 1952 on earthworms in Germany reports abundances of 100-1200 ind./m^2 in cropped soils (Graff 1953). These numbers are much higher than recent reports from the long-term monitoring sites in Brandenburg (0-307 ind./m^2) (Krück et al. 2006), Niedersachsen (5-126 ind./m^2) (Höper and Meesenburg 2021) or Sachsen-Anhalt (1-300 ind./m^2) (Langer et al. 2012). Indeed, on the long-term monitoring sites in Bavaria they reported already four decades ago how the combined effect of mineral fertilizer and pesticide use reduced earthworm abundances from 222 to 39 ind / m^2 in agricultural fields (Bauchhenss 1986). In line with the review from Great Britain that found a 80 % decline of earthworm biomass due to long-term intensive agriculture (Blakemore 2018), this would suggest a decline of earthworms in North German conventional croplands within the last decades. Supporting this view, after conversion from grassland to cropland, a 90 % decline in earthworm biomass was monitored 5 years after on the long-term monitoring sites in North Germany (Beylich and Graefe 2009).

These comparisons need to be made cautiously, though, as results differ considerably depending on sampling method, soil types or season of sampling. Contrasting findings exist as well. For example, within fifteen years of monitoring in North-Eastern German croplands between 1994 and 2009 earthworm biomass did not change (Langer et al. 2012), meanwhile also in this period cropping further intensified in Germany (Kirschke, Häger, and Schmid 2021). In line with this observation, a 40-year study on the effect of intensive agriculture on earthworms in North Germany reported no decrease in earthworm abundances (Finck 1990). At the first sampling date (1952), the sites were still under extensive cropping practices and at the second date (1988) under intensive cropping practices. The transition had taken place between 1960 to 1970. On both dates, abundances of 100-200 ind./m^2) are reported, which are similar to the abundance that we documented. Finck argues that a presumably negative effect of intensified practices as pesticide use or intensified tillage is compensated with improved soil nutrient supply. However, as comparisons with historical records are scarce, it stays unclear whether Finck documented a general pattern or a special situation.

We detected a significant correlation between microbial biomass and respiration rate and earthworm biomass, abundance, and species number, suggesting both populations react similarly to stresses of intensive agricultural management. The correlation of earthworm and microbial variables supports the findings of other studies (Flohre et al. 2011; Postma-Blaauw et al. 2010). Earthworm casts host higher fungal and bacterial populations (Liu et al. 2019), which might explain the reported correlation. Nevertheless, agricultural intensification appears to have the most detrimental effect on larger-sized soil organisms as earthworms than smaller organisms as microbes (Postma-Blaauw et al. 2010; Tsiafouli et al. 2015). This might explain why we recorded much more pronounced differences between field and margin for earthworms than for soil microbes.

Next to reduced numbers of soil organisms in fields, our results confirm the second hypothesis as well in the sense that the share of earthworm ecological groups shifted dramatically from margins to fields. While among the adult earthworm individuals, epigeic species accounted for about a third of all individuals in margins, they represent only 10 % of the total of adult individuals recorded in fields. For instance, the second most frequently recorded species *L. castaneus* is epigeic and occurred mostly in margins (only 3 recordings in fields). Our findings indicate that intensive agricultural management in fields does not impact all earthworms similarly but that epigeic species suffer disproportionally.

This is in line with what Finck reported in his 40-year study: he documented a reduction in anecic species with epigeic species staying constant at around 10 % (Finck 1990). Also the long-term soil monitoring sites in North-Eastern Germany documented for agricultural soils on average 80 percent endogeics, around 20 percent anecic species (we recorded around 60 %

endogeic and 30 percent anecic species) and almost no epigeic species (Tischer 2007). Other studies also document significant decreases in the share of anecic species from margin to field (Nieminen et al. 2011). Pesticide and herbicide use is documented to have negative effects (Céline Pelosi et al. 2014) in particular surface-dwelling species as epigeic and anecic species are disproportionally affected (C. Pelosi et al. 2013). A study on the effect of glyphosate on earthworms demonstrated that endogeic species as the frequently recorded *A caliginosa* are much less impaired by this herbicide (Gaupp-Berghausen et al. 2015). Next to the impact of pesticides, the negative effect of ploughing notably on anecic and epigeic earthworm species is demonstrated in a global meta-analysis (Briones and Schmidt 2017). Endogeic species are much less impaired by regular perturbation (Ekschmitt and Griffiths 1998) like ploughing (Chan 2001; Beylich and Graefe 2009). Some authors even argue that communities with a strong dominance of endogeic species serve as indicators overly disturbed soils (Stroud 2019).

The shift in functional group composition may also have consequences on soil formation processes. As epigeic worms produce casts more enriched in organic carbon in form of residues of the digested litter than the other functional groups (Zhang and Hendrix 1995), their reduction in the total share of earthworm composition might potentially impact soil carbon cycling (Singh et al. 2019) and degradation of fresh organic matter (Bertrand et al. 2015). The lack of deep-burrowing anecic species has consequences not only for soil aeration and drainage of water, but also for organic matter that is less incorporated and mixed into the soil profile (Briones and Schmidt 2017). Furthermore, the reduction of surface casting species alters soil microbial biomass and activity and thus impacts nutrient cycling (Briones and Schmidt 2017). An increase in diversity of endogeic species would not be a compensation (Ekschmitt and Griffiths 1998). We reported less severe losses in the share of epigeics than what was previously documented for North Germany. In contrast to other studies, we did not find a significant decrease in the share of anecic species from margin to field. However, we recorded in total only around 100 individuals in fields, while we documented in margins more than adult 550 individuals. The overall reduction of earthworms must have a strong impact on soil formation processes already in itself.

Our study supports the view that margins are refuges for earthworms and show higher soil microbial populations. We conclude that margins therefore serve well as local reference sites for monitoring the impact of intensive agriculture and the success of conservation measures for soil organisms. Particularly, earthworms appear to be easy to monitor indicators for the soil biological community.

2.5.3. Effect of vegetation and soil on earthworm community structure in margins

Our results confirm the third hypothesis in so far as including plant variables into the analysis of earthworms in margins added explanatory value in the RDA. Nonetheless, soil variables primarily explained earthworm and plant community structure. Fertile soils with less soil acidity supported large earthworm population in terms of high biomass and abundance. These populations were dominated by only few species, though. Less fertile soils with lower pH supported smaller earthworm populations but with high earthworm species richness. Also, plant variables associated with less soil nutrients and lower pH. Our results suggest that less fertile soils allow the existence of more diverse plant communities, which in turn support more species-rich earthworm communities.

For plant communities it is well documented that fertilizing increases standing biomass at the cost of species loss. Contrarily, nutrient-poor sites restrict the dominance of a few very competitive species and thus allow the existence of more species that each are less competitive (Bakelaar and Odum 1978; Inouye and Tilman 1995; Leuschner and Ellenberg 2017). Therefore, next to explaining low earthworm populations with unfavorable soil conditions like a high share of sand in soils (Lapied, Nahmani, and Rousseau 2009), another explanation for lower earthworm populations may be that plant tissues from grasses are relatively nitrogen-poor and therefore sustain overall smaller earthworm populations (Singh et al. 2021b). A positive effect of plant species diversity notably of grasses and legumes on soil organisms was also documented in other studies (Birkhofer et al. 2011; Gormsen et al. 2004). Particularly on sandy soils, plant diversity has a positive effect on soil food webs (Eisenhauer et al. 2013). The authors argue that this is the case because of the accumulation of organic matter in sandy soils. On the other hand, for nutrient rich soils, a study in grasslands in Brittany, France, reported that an increase of soil organic matter content and pH were the most important factors for high earthworm abundance and biomass. Particularly endogeic species were able to profit from these favorable soil conditions (Hoeffner et al. 2021). Indeed, it is well documented that soil texture, pH, and soil organic matter are the most important factors for large earthworm populations (Curry 2004; K. E. Lee 1985).

We recorded both, a high share of sand in soils and a high share of grasses with diverse earthworm assemblages. Therefore, it is difficult to disentangle what the effect may have been in our case. Certainly, the share of legumes played a subordinate role. In contrast to the findings of Eisenhauer et al. (2013), C_{org} was lowest in Lüneburger Heide, the farm with highest share of sand in soils. Thus, the accumulation of soil organic matter was not the driver of diverse earthworm assemblies. On the contrary, in accordance with Hoeffner et al. (2021) we documented high soil organic matter content to associate with high earthworm populations, dominated by endogeics.

Our results show that the species-diverse earthworm assemblages were dominated by epigeic – and thus litter feeding – species. Plant cover was important for earthworm reproduction as well.

This indicates that plant cover is important particularly for epigeic species and on earthworm reproduction. Epigeic species are especially dependent on the litter layer (Bouché and Kretzschmar 1974). A recent meta-analysis revealed that only a minority of studies have a focus on juvenile earthworms (Briones and Schmidt 2017), although they may represent up to 70-90 % of the population (Domínguez and Bedano 2016). Juvenile earthworms occupy different niches regardless of their ecological group they belong to and mainly feed on the surface soil layers and on roots (Gerard 1967). Our findings support the given literature that a permanent vegetation cover producing a litter layer is important notably for epigeic species and for earthworm reproduction.

Thus, from a sustainable farming perspective the question arises whether it is preferable to have high earthworm abundances with lower species richness, as high abundances improve many soil processes. Alternatively, our findings suggest that lower earthworm abundances allow more species to be present, in our case namely epigeic species. The latter ecological earthworm group profits from a well-developed litter layer. This might conflict with farmland wildlife conservation aims of margins that target species with a need for gaps in the vegetation layer (Jo Smith et al. 2009; Vickery, Feber, and Fuller 2009). Yet, particularly epigeic species appear to be of special importance as a food source for farmland wildlife. For instance, some farmland birds depend on soil-dwelling invertebrates benefit from higher epigeic abundances as was documented for the Northern Lapwing, *Vanellus vanellus* (McCallum et al. 2016).

We conclude by highlighting the multifunctional value of margins, where species-rich plant communities are viewed to be the basis for multifunctionality (Holland et al. 2012; Verhoeven et al. 2022). Given the widespread disappearance of oligotrophic and mesotrophic sites and their characteristic communities in Central Europe in the course of eutrophication (Leuschner and Ellenberg 2017), it may be argued that decreasing the nutrient load on field margins is a more straightforward management strategy to increase agrobiodiversity than fertilizing the margins for bird fodder.

2.6.4. Effect of neighboring landscape elements on earthworm communities in margins

We cannot confirm the fourth hypothesis that neighboring habitat type has a strong impact on earthworm populations in margins. Concerning the effect of neighboring field on the margin, it was not possible to differentiate between regional impact and the effect of tillage intensity, as soil cultivation methods were always the same across one farm. We assume that the primary effect visible in our results was due to soil properties, namely the share of sand in soils. Concerning the neighboring non-crop habitat, trees associating with diverse earthworm assemblies and ditches were associated with earthworm reproduction. Next to this, no strong effect was visible on earthworm communities in margins. As the studied field margins were narrow with 1-2 m width, our study suggests that earthworm communities are structured at a fine scale and that small-scale changes in soil and vegetation factors had a greater impact than the neighboring landscape context.

Contrary to other taxa as bees where landscape context matters a lot (Coutinho et al. 2021), landscape context appears to be of subordinate importance for earthworm communities (Lüscher et al. 2014). The degree of landscape simplification did not matter either: neither in intensively managed areas as in Dutch polders (Frazão et al. 2017) nor in an Hungarian low-input farming system, a landscape composition effect on earthworms could be detected (Kovacs-Hostyanszki et al. 2013). An effect of directly neighboring landscape elements was documented in some studies, however. A study on grassy field margins between forests and cropped fields reported an increase of earthworm biomass and species from inside the forest to the forest edge and a decrease into the field again (Zeithaml et al., 2009). Also, a recent study that sampled earthworms in grasslands next to hedgerows reported a positive influence of hedgerows, especially on the diversity of anecic and epigeic species (Hoeffner et al. 2021). We also documented most earthworm species (and the majority being epigeic) to associate with trees as non-crop neighboring habitat. Some authors argue, that the diversity of soil organisms is explained because ecotones, as in this case the shift from forest to field, offer small-scale differing soil environments (Cardinael et al. 2019). However, these were the species of which we recorded low abundances, perhaps due to drier soil conditions. In line with this, a study from agroforestry windbreaks into agricultural fields reported lowest earthworm abundances at the edge of the windbreak hedges and a subsequent increase into the field (Rivest, Whalen, and Rivest 2019). Earthworm growth and survival depends strongly on soil moisture (Curry 2004; Wever, Lysyk, and Clapperton 2001). This may explain why earthworm reproduction was positively influenced by ditches as neighboring habitat.

As the spill-over effect from neighboring habitats is small in case of earthworms, in the context of the land sharing/land sparing debate (Grass, Batáry, and Tscharntke 2021), developing soil management practices in cropped areas that are able to sustain soil organisms should be supported especially in intensive arable landscapes.

2.6. Conclusion

This study aimed to assess the long-term impact of intensive agricultural practices on earthworms as well as microbes. It furthermore discussed the potential of permanent field margins for conservation of earthworms in the North German Plains.

We demonstrated how intensive farming substantially levels out regional differences. Hereby, our results support existing concerns that biotic homogenization due to agricultural intensfication may turn out to be an even more fundamental threat to farmland biodiversity than local diversity loss (Gossner et al. 2016). While the threat to farmland biodiversity through landscape simplification is well documented for other taxa (Landis 2017), there is yet much less attention to the consequences of homogenization of soils. In future research, we therefore suggest focussing on soil homogenization as a consequence of intensive agricultural practices.

Furthermore, we documented a much stronger depletion of earthworm populations than expected, not only in cropped fields but also in margins.

We stress the point that long-established, permanent margins with a well-developed litter layer serve well as refuges for earthworms. Our study revealed the strong small-scale response of earthworms to changes in their environment, filling a major gap in knowledge on the distribution of soil organisms across farmland landscapes. While in cropped fields regional differences in soil type are levelled out by cultivation, they still shape belowground communities in margins. We emphasize the importance of permanent vegetation cover, notably for earthworm reproduction and for the presence of epigeic earthworm species.

Ultimately, our study revealed the urgent need for developing soil management practices that cease to destroy but support these key “soil ecosystem engineers” (Blouin et al. 2013). Promoting vibrant earthworm communities in fields may also be beneficial for yields, as a meta-analysis reported an 18 % increase in yield with the presence of epigeic and even an 32 % increase in yield with the presence of anecic species (van Groenigen et al. 2014). We demonstrated that margins serve well to locally quantify the state of soil quality in cropped fields. Finally, our findings support a pilot study with farmers where they employed earthworms to assess the situation of soil health in their fields. Our findings suggest that direct comparisons of cropped fields with margins are useful indicators for farmers to decide on soil conservation measures and then monitor their success (Stroud 2019).

2.7. Literature

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3. Chapter: Resistance and resilience of earthworm and soil microbial communities to the exceptional 2018/19 drought in intensive cropland

Soil profiel in Havellenad, own picture

"It may be doubted whether there are many other animals which have played so important a part in the history of the world than these lowly-organized creatures" (Darwin 1881)

3.1. Abstract

Land-use intensification and climate warming are two key global change drivers that may act as stressors in agricultural systems. There is a lack of thorough observational studies addressing the combined effect of both stressors on soil organisms. We conducted a four-year study on earthworm and soil microbial populations in four intensively managed cropland landscapes in the North German Lowlands, measuring biomass, abundance, and activity before, during and after the exceptional 2018/19 Central European drought. To disentangle the effect of drought and intensive management, soils of arable fields were compared to soils of adjacent permanent, grassy field margins.

Averaged over field and margin, the drought reduced earthworm biomass, abundances and species richness in 2018 by 66 %. All functional groups suffered losses in 2018. However, endogeic and anecic earthworms recovered already in 2019, while epigeic species remained suppressed until 2020. Earthworm population recovery was faster in margins (until 2019) than in fields (not achieved till 2020). The drought reduced microbial biomass (C_{mic}) and basal respiration (BR) by 15 % in 2018 and 2019 compared to 2017 and 2020. The drought had a different effect on fields than on margins: while in margins earthworms recovered in the study period, they did not in fields. In contrast, soil microbes were reduced in margins by the drought, whereas they stayed unaffected in fields, where C_{mic} and BR were maintained at a lower, but constant level throughout the drought.

Our results suggest that intensive farming reduces the drought-resilience of earthworm populations and decreases C_{mic} and BR. The drought-induced loss of epigeic earthworms may have implications for carbon cycling and decomposition, which can last in the fields for more than two years. We conclude that different soil biota show group- and species-specific responses to intensive management and drought. Further studies must show whether long-term responses to drought differ from the demonstrated short-term effects.

Keywords: soil ecology, earthworms, soil microbes, ecological resilience, climate change, intensive agriculture, natural experiment

3.2. Introduction

Agricultural production is currently exposed to multiple and conflicting challenges. Rising demands for agricultural goods as the production of bioenergy and other products for bio-economy increase the pressure on cropland, whereas the area of productive cropland is decreasing globally (Kraamwinkel et al. 2021) and land prices are rising (Potapov et al. 2022). The consequential intensification of agricultural production burdens the environment with high costs (Kirschke, Häger, and Schmid 2021). Agricultural intensification impacts not only surface and groundwater bodies, the atmosphere and biodiversity, but exerts also major pressure on arable soils (Foley et al. 2005). Soil ecological functions such as carbon storage, decomposition, nutrient cycling, water filtration and climate regulation are reduced under intensive management compared to the potential functioning that would be possible under the local climatic, edaphic, topographic and historical settings (FAO - ITPS 2015). For instance, regular ploughing may reduce soil carbon (C) storage and compact the subsoil, thereby reducing water infiltration (Smith et al. 2016).

As especially arable soils are the nexus that links the fluxes of energy, carbon, water, and food (Biggs et al. 2015), it is crucial to protect them from degradation (Amundson et al. 2015; Jónsson et al. 2016). A sustainable arable management for fertile soils maintains the soil's resilience (Ludwig, Wilmes, and Schrader 2018). The resilience perspective has become a key concept in the management of natural systems (Scheffer et al. 2001) and thus should also be applied to arable soils. Ecological resilience can be defined as the ability of a system to absorb disturbance, such as changes in temperature or water supply, and continue to function in the established way (Holling 1973). When disturbance becomes too strong, a system's threshold is crossed and it will shift to a new state, while potentially losing functions or even gaining undesirable functions. A resilient system therefore comprises a high resistance to disturbance and quick recovery to a pre-disturbed state after the perturbation. Furthermore, its threshold is is high (Côté and Darling 2010). Locating thresholds is central for measuring the resilience of a system (Standish et al. 2014). However, also a degraded ecosystem may be resilient: that is, its capacity may be high to buffer perturbation and might in some cases even be higher than in a non-degraded ecosystem (Troell et al. 2005). This requires experimental or observational data on disturbance events and the subsequent recovery pathway (Pimm 1984).

Severe droughts are among the disturbances with highest relevance for agricultural production, and their frequency is predicted to increase with climatic warming in many regions on Earth (Barbosa et al. 2021; Hari et al. 2020; van Hateren et al. 2021). To our knowledge, no observational study has explicitly documented the response of intensively managed arable soils to a severe natural drought in a normally humid climate. Results from experimental settings suggest that the interactive effects of climatic warming and intensive agriculture reduce soil organism biomass (Siebert, Eisenhauer, et al. 2019; Yin et al. 2020). Should these experimental findings hold true also for real-life systems, it would be alarming, as soil organisms regulate key ecosystem functions (Amelung et al. 2018). It is unclear whether such climate manipulation experiments can simply be extrapolated to natural systems for predicting their response to climate warming. Yet, a recent meta-analysis suggests that experimental findings usually even underestimate the effect of drought on ecosystem functioning (Kröel-Dulay et al. 2022). Therefore, understanding how intensively managed arable soils respond to climatic extreme events is becoming increasingly important, as rising temperatures and an increasing atmospheric evaporative demand are associated with a higher frequency and severity of hot summer droughts in many regions on Earth (Hari et al. 2020; IPCC 2021).

We here explore the effects of the exceptional 2018/19 drought episode in Central and Western Europe on soil biota in intensively managed arable soils. This drought was the most extreme drought event in the region since more than 2000 years (Büntgen et al. 2021). In summer 2018, the region suffered from large precipitation deficits and a heat wave that caused agricultural yield reductions up to 50 % (A. Bastos et al. 2020; Toreti et al. 2019). The drought persisted in winter 2018/19 and also in summer 2019 (Hari et al. 2020), and was followed by a further dry spell in spring 2020 (Barbosa et al. 2021). In previous decades, soil moisture deficits that developed in Germany in one year usually were compensated already in the following year. This was different in the 2018/19 episode, as the consecutive dry years 2018 and 2019 led to a deficit that persisted into 2020.

To investigate the effects of this drought on the resilience of soil biota, we analyze observational data from intensively managed arable soils in four regions of North Germany, which have been subjected to intensive agricultural management for decades (Kirschke, Häger, and Schmid 2021). A widely used indicator for soil biological activity and soil quality are soil microorganisms (ISO 2003); earthworms are another frequently employed key biotic indicator (Edwards and Bohlen 1996; Pelosi et al. 2014). The latter serve especially as an indicator for the management intensity of arable land (Siebert, Eisenhauer, et al. 2019). We thus choose these two groups and report their biomass, abundance and activity dynamics from 2017 to 2020, exploring the change from 2017 (average moisture conditions) to 2018 (extremely dry) as a measure of population resistance to drought, and from 2018 to 2019 (dry) and 2020 (moderately dry) as a measure of recovery from the drought.

Drought can influence soil biota both directly and indirectly. Low soil water contents and soil water potentials can impair the tissue and cell water status of soil organisms (Decaëns 2010), which may reduce their metabolic activity, growth and fertility (Riutta et al. 2016; Thakur et al. 2018). Increased soil compactness upon drying and reduced water filling of soil pores affects the soil organism's mobility (Or et al. 2007). An indirect drought effect on soil organisms is reduced plant growth and associated carbon release to the soil (Franklin et al. 2016). Reduced vegetation cover and biomass means lower food supply for soil biota and less thermal isolation of the soil, which heats up more and dries out more excessively than under closed vegetation (Singh et al. 2019).

Different soil organism groups are known to react differently to drought, with invertebrates generally being more susceptible than soil microorganisms (Manzoni, Schimel, and Porporato 2012). Higher temperatures tend to increase earthworm biomass and abundance up to a critical threshold. However, this is only the case when soil moisture conditions are favorable (Lowe and Butt 2005). Extreme events such as droughts and floods are expected to have deleterious effects on earthworm communities (da Silva et al. 2020; Plum and Filser 2005). However, not much empirical data exist that demonstrate the response of earthworm communities to such extreme events in more detail (Singh et al. 2019). Soil moisture appears to be the most influential environmental factor for earthworm distribution, abundance and activity (Phillips et al. 2019). Earthworms possess a water-permeable skin and are thus strongly dependent on the soil moisture of the medium (Edwards and Bohlen 1996). Optimum soil moisture is species-specific, but in general, earthworms are most active in soils close to field capacity. Earthworms have a certain dehydration tolerance, as they can lose up to 70 % of their maximal water content without lethal effects. Strategies to escape desiccation are hiding in deeper soil layers or entering diapause (Bouché 1977). Prolonged droughts have shown to decrease earthworm abundances markedly, and worm populations take several years to recover to pre-disturbance numbers after the event (Edwards and Bohlen 1996).

The main ecological groups of earthworms differ in their strategies to cope with drought. The litter-dwelling epigeic species have the least capacity to protect themselves against desiccation. Adult epigeic earthworms therefore usually do not survive severe droughts. However, they possess a short reproduction cycle and have a high cocoon production, a life stage that is much less sensitive to drought (Martin Holmstrup and Loeschcke 2003). Epigeic worm communities therefore are rapidly recovering after drought (Bouché 1977). The topsoil-dwelling endogeic species endure a drought by entering aestivation in soil layers that are less affected by moisture deficits (Rundgren 1975). Finally, the deep-burrowing anecic species are expected to be least affected by a drought, as they can retreat to deeper soil layers and are observed to generally enter diapause in summer (Bouché 1977). As droughts impact the earthworm's fecundity (Edwards and Bohlen 1996), summer drought periods are expected to impact the age structure of earthworm populations as well. When earthworms fall inactive during a summer drought, reproduction becomes restricted to spring and autumn. Cocoons appear to hatch only at certain soil moisture levels (Martin Holmstrup 2001). Juvenile earthworms were reported to be especially drought-vulnerable (Singh et al. 2021), probably because they have not yet achieved their full capacity to avoid desiccation (Edwards and Bohlen 1996), and as they are more susceptible to food limitations than adults (Curry and Schmidt 2007).

Many soil microorganisms are strongly dependent on the soil moisture status (Orchard and Cook 1983). Adaption to drier soil can be achieved through the accumulation of osmotic protectants (Harris 1981), a process which consumes ATP and resources that are not available for growth or metabolic activity. A conservative estimate suggests that the total C cost for drought acclimation of microbes via osmolyte accumulation may consume 3-6 % of total annual microbial biomass production (Schimel, Balser, and Wallenstein 2007). When soil desiccation becomes too severe, microorganisms can enter anhydrobiosis (García 2011). In soils, typically the bulk of microbial biomass is dormant, and merely 0.1 – 2% of cells are active, which represents the subset of the whole microbial community that is adapted to the specific local environmental conditions (Blagodatskaya and Kuzyakov 2013). As a consequence, the response of the active microbe fraction to soil water deficits may differ from that of the entire microbial community. Indeed, a recent meta-analysis has revealed that microbial biomass usually does not change upon a reduction in precipitation (Zhang and Xi 2021).

There is a shortage of studies on the combined effect of anthropogenic and environmental stresses on soil fauna (Singh et al. 2019), as exemplified by the impact of drought in intensively managed cropland. It is currently debated under which conditions multiple environmental stresses have an exacerbating or relieving effect on organisms. For instance, some studies observe the toxicity on earthworms of applied pesticides to be increased under higher temperatures (Friis, Damgaard, and Holmstrup 2004; Owojori and Reinecke 2010), while other studies argue that under dry conditions earthworms become inactive and hide in deeper soil layers. They are thus less exposed to pesticide application on the soil surface and therefore, toxicity is reduced (Johnston et al. 2015). The impact of drought on soil fauna is suggested to be strongly land-use dependent (Singh et al. 2019), with reports that soil biological activity is especially vulnerable to drought in extensively managed systems (Siebert, Thakur, et al. 2019).

Our objective was to study the short-term response of earthworm and soil microbial communities to the combined effect of the severe 2018/19 drought in relation to the stress imposed by intensive agricultural management in different regions of North Germany. In order to disentangle the impacts of drought and intensive agricultural management on soil organisms, we compare soils of arable fields (henceforth: “fields”) with those under long-established field margins (henceforth: “margins”) dominated by annually cut perennial herbaceous vegetation, which exists under the same soil and topographic conditions as the fields but is not intentionally treated with fertilizers and pesticides and not ploughed.

Specifically, we hypothesized (1) that the 2018/19 drought would have an overriding effect over other environmental parameters known to be important for shaping earthworm and soil microbial populations such as soil pH, C and N content (Amelung et al. 2018; Curry 2004). Secondly, we hypothesized (2) that the 2018/19 drought would reduce earthworm populations in 2018 and in 2019 compared to the pre-drought year 2017 and that they would not recover to pre-drought levels in 2020. However, we expected that the drought would affect microbial biomass to a lesser extent. We expected the basal respiration to be reduced in years 2018 and 2019, as the active part of microbial populations is more sensitive to a drought than the total (Bastida et al. 2017). As soil microorganisms are able to quickly adapt to changed environmental conditions (Schimel, Balser, and Wallenstein 2007), we expected microbial activity to regain pre-drought levels immediately after soil moisture levels were back to normal. Furthermore, we hypothesized (3) that the drought would alter earthworm community composition with fewer species present during the drought. We expected that epigeic species should suffer most but would also recover rapidly, while the abundance of anecic species should change only little; endogeic taxa were expected to be reduced when drought in the topsoil is strongest but to recover quickly afterwards. We expected to find a smaller share of juvenile earthworms in the drought years due to less hatching in dry conditions and juvenile earthworms being more vulnerable. Finally, we hypothesized that (4) earthworms and soil microbes would be more strongly affected by drought in arable fields and would recover more slowly than in the adjacent field margins, which are protected by permanent vegetation cover.

3.3. Methods

3.3.1. Study area

To capture a more general picture of earthworm community responses beyond regional specificities, we collected samples in four intensively managed farmland regions across the North Germany Lowlands (Fig. 1.2). The four sites cover a wide range of farming landscape types, typical for intensive farming in Central Europe: the climate is temperate sub-continental to sub-oceanic with mean annual temperature varying from 9.5 to 10.0 °C and mean annual precipitation from 571 to 865 mm (Table 1.1). Especially Ostwestfalen and Lüneburger Heide are exposed to a relatively high mean annual precipitation due to proximity to the coast. The sites Havelland and even more so Magdeburger Börde have much drier climates. Since Magdeburger Börde is situated in the lee of the Harz mountains, the Börde belongs to the driest regions of Germany. The studied farms in Magdeburger Börde (due to its sub-continental climate) and Lüneburger Heide (due to the sandy soils) both irrigate fields (Table 1.1). All selected farms are located below 125 m a.s.l. in a planar to slightly undulating topography. Yet, geology and soil types are quite variable, with two farms being located mostly on loess-derived soils (Magdeburger Börde, Ostwestfalen) with relatively high fertility, and the other two on more sandy soils on Pleistocene basal moraines (Havelland, Lüneburg). The soils are quite variable ranging from Cambisols-Podsols to Chernozems and Gleysols under more natural vegetation (Table 1.1). All sites have in common that they have been shaped by agricultural land use for centuries with only little near-natural, non-managed vegetation being left (Bundesanstalt für Geowissenschaften und Rohstoffe 2016; Don and Prietz 2019).

3.3.2. Farming practices

In each region, one conventionally-managed farm was selected for study. The farm-based approach allowed to establish uniform management techniques across the sampled fields. The four farms have been chosen, since they have followed conventional cropping practices for decades. According to the typical regional crop field management schemes in the respective region, tillage intensity varied between annual ploughing (Ostwestfalen) to tillage every second year (Lüneburger Heide), every fifth year (Havelland) and never (no-tillage; Magdeburger Börde) (Table 1.1). All farmers were interviewed regarding their crop management schemes and field margin management. We thus obtained information on soil cultivation techniques, fertilizer use, irrigation and harvesting practices as well as main and cover crop rotation on the studied fields. We also asked about recent changes in farming techniques (soil cultivation methods, crop rotation, fertilizer types, irrigation). Crop rotations were dominated on all farms by wheat/barley and fodder/biogas maize cultivation. A detailed description of farming practices is given in the Supplement 3.

3.3.3. Monitoring of agricultural drought intensity

The data on regional soil drought magnitude was kindly provided by the German Drought Monitor (GDM), an information platform for agricultural droughts in Germany available under www.ufz.de/droughtmonitor. It offers simulated soil moisture in a 4 x 4 km^2 spatial resolution (Zink et al. 2016). The calculated magnitude is based on meteorological data collected by the German Weather Service. Soil moisture for the upper soil layer (0-25 cm depth) and for the total soil column (locally defined, on average to 180 cm depth) is simulated with the mesoscale hydrologic model mHM (Samaniego, Kumar, and Zink 2013). The simulated soil moisture has been found to be well in agreement with observed data especially for the vegetation period (April-October) (Boeing et al., 2021, under review). In a next step, a soil moisture index (SMI) [0-1] is calculated for every grid cell. Four drought classes are defined based on the probability of damage to crops and pastures. Moderate drought is defined from an upper threshold of SMI 0.2, meaning that these conditions were observed in less than 20% of cases between 1954 and 2013 for a specified time of the year and grid cell. Events assigned to the most severe drought class have a probability of occurrence of only once in 50 years (SMI <0.02). In order to compare the degree of droughts between different years, the GDM proposes to use the drought magnitude (DM), a dimensionless unit. The DM is an aggregated drought signal that considers the length of the drought period and the absolute dryness between April and October. The DM value increases with increasing drought duration and with negative deviation of the lower 20th percentile of the SMI (0.2) (Samaniego, Kumar, and Zink 2013).

Next to the regional estimate of drought magnitude for each year, we also quantified the drought severity at each earthworm and soil microbial sampling plot. In parallel to the sampling for soil microbial analysis in the topsoil (0-10 cm) in October of the study years, we also measured soil moisture in the 0 – 10 cm layer gravimetrically and measured soil temperature.

3.3.4. Study design

Sampling took place on 15 fields spread across the four farms. On each farm, we chose three or four arable fields for sampling, depending on suitability and consent of the farmer. As reference sites, the selected 1-2 m wide permanent field margins that were characterized by the same soil type and topography as the corresponding sampled fields. The vegetation on the field margins consisted of grass or herb-dominated communities, which was mown once a year with the biomass left on the field margins. The margins were not seeded, fertilized or treated with pesticides; yet, some chemicals applied to the adjacent fields may well have drifted to the margins. Each pair of arable field and field margin thus offered similar pedologic conditions for soil life, with the main difference being the management scheme of the field. The arable fields represent high input-output systems with regular addition of fertilizers, pesticides including herbicides as well as crops being sown and harvested regularly and (in part of the farms) with high soil disturbance through tillage, whereas the field margins were low input-output systems without intended substance inputs, permanent vegetation cover, and no intended soil disturbance (for details see Supplement 3 1).

As there were no recent changes in field management schemes and all margins existed in their present form for at least 10 years, we assumed both the arable field and the field margins to represent steady-state systems.

3.3.5. Field and laboratory work

Fieldwork took place each year in October from 2017 to 2020. In the study regions, this season offers most favorable conditions for monitoring long-term changes in arable fields, as there is no immediate effect of management practices at this time with all main activities like fertilizing, harvesting and soil cultivation having ceased. This time of the year is also best suited for monitoring earthworm activities and soil microbial activity, because soils usually have rewetted after summer, but soil temperatures have not yet dropped below 5°C (Schinner, Öhlinger, and Kandeler 1991). In conditions earlier or later in the year that are either too dry or too cold, earthworms tend to persist in a dormant state (Bouché 1977). In this state, they are not susceptible to the application of extracting fluids (Edwards and Bohlen 1996) such as hot mustard (Plum and Filser 2005). Earthworms are most active in spring and autumn, where highest biomass is reported from extractions (Singh et al. 2021). Similarly, soil microbes in arable fields exhibit a seasonal pattern of activity with reduced levels in summer when the soil is dry and in winter when the soil freezes. They further show a strong reaction after fertilizer application and higher amounts of root exudates in late spring (Bloem, Hopkins, and Benedetti 2006a).

Sampling of earthworm, soil microbial and soil chemical and physical variables took place along 50 m transects. One 50 m transect was in the field, the second was established in the adjacent field margin. The exact position of the transects was randomly chosen and then documented with GPS coordinates. Each transect was split into four blocks. Within each block, one sampling point was randomly chosen, thus guaranteeing a roughly even distribution of randomly positioned sampling points along each transect. We ensured that a sampling point was neither in a tramline nor in another spot not representative for the field or margin (e.g., log, puddle or power pole).

a) Earthworms

Extraction, transportation and storage

Earthworms were extracted with the hot mustard powder method, which has proven to be not harmful to the environment but still efficient (Sandor et al. 2015; Singh, Singh, and Vig 2016). 70 g of mustard powder (Semen Sinapis, Caelo) was mixed with 150 ml of water approximately 12 hours before extraction, in order to let the hotness of the mustard develop. Just before sampling, the prepared mustard mash was diluted with 7 liters of water.

For each sampling point, the standing vegetation was cut away on 0.25 m^2 and litter was carefully removed, taking care not to miss litter-feeding earthworms. The exposed ground allows to quickly recognize the appearing earthworms. In order to assure that the applied mustard percolated into the soil only on these 0.25 m^2, a steel frame of 10 cm height was slightly pressed into the ground on each prepared spot.

We then slowly poured the 7 l of mustard water into each frame, taking care that the mustard-water percolated well into the soil. In cases where soils were so moist that the mustard-water ceased to drain away, we did not pour the 7 l to avoid water ponding in the frame. These cases were noted. Earthworms appearing at the surface within 25 minutes of the mustard application were removed with blunt tweezers and preserved in ethanol (70 %). We observed that very few earthworms appeared after the 25-minute time period. Meanwhile, soil temperature of every spot was recorded (Carter and Gregorich 2008).

Laboratory analysis

Prior to analysis, earthworms were carefully washed and freed of remaining soil. All earthworms were counted and weighed. For species identification, every individual was put into a petri dish and placed on a dark sheet underneath a binocular (ZEISS, 'Stemi 2000'). Species determination of adult earthworms was conducted by considering the position and constellation of setae, male pores, clitellum, tubercula pubertis and prostomium as described in Brohmer and Schaefer (2010), Christian and Zicsi (1999a) as well as in Sims and Gerard (1985). Species nomenclature followed Sims and Gerard (1985). As the clitellum is not yet developed in juvenile earthworms, they cannot be identified to species level.

b) Soil microbial data

Sample collection, transportation and storage

At each sampling point, soil coring was done with a split stainless-steel tube of 3 cm inner diameter to a depth of 10 cm. Within a radius of one meter, four samples were randomly taken and pooled for further analysis. In this manner, we retrieved four samples on each transect. Samples were stored in plastic bags and transported to the laboratory of Göttingen University in cooling boxes. They were deep frozen at -20 °C on the day of sampling and analyzed within a year (Anderson & Paulsen, 2017).

Laboratory analysis

In each pooled sample we made one analysis of microbial biomass and both basal respiration with an O_2 - micro-compensation apparatus (Scheu 1992). Prior to analysis, samples were left to thaw at 4 °C for at least 48 hours, then plant residues were carefully removed. Samples were sieved through a mesh with pore size < 2 mm and left to rest at 4 °C for a minimum of 5 d (Dilly 2001). Afterwards, we carefully placed an amount of fresh soil corresponding to 4 g of dry soil weight into glass vessels of about 10 ml volume of the apparatus and left the soil to rest overnight at room temperature (about 20 °C). During this period, the vessels were covered with a moist cloth in order not to lose soil moisture through evaporation (Dilly 2001). Before starting the basal respiration measurement, samples were left to acclimatize at 22 °C (Anderson & Domsch, 1978) in the open vessels for at least 60 min. Basal respiration (expressed in $\mu l\ O_2\ h^{-1}$ g soil dry mass^{-1}) was recorded for at least 24 h in 10-min intervals.

Microbial biomass was determined by measuring substrate-induced respiration (SIR) triggered by the response to D-glucose addition (Anderson & Domsch, 1978). An amount of 4 mg glucose per g soil dry weight at a water holding capacity of 50 % has been shown to saturate the catabolic enzymes of the microorganisms in agricultural soils (Beck et al. 1997). After addition of glucose and de-ionized water to the samples, they were left to rest for 20-30 min and subsequently the respiration rate was recorded for a 10-min interval for at least 12 h. The average over the lowest three recordings is defined as the maximum initial respiratory response [MIRR $\mu g\ O_2\ g^{-1}$ dry weight soil h^{-1}]. As the O_2 - micro-compensation apparatus is very sensitive and prone to errors, around 20 % of samples had to be analyzed a second time. Even after re-measurements, we had to deal with around 10 % missing data.

Anderson & Domsch (1978) documented the correlation of substrate-induced maximal respiration rate to microbial biomass carbon (C_{mic}) to equal 1 ml $CO_2\ h^{-1}$ to 40 mg C_{mic} at 22 °C. This conversion factor was established based on measurements in Central European soils with a pH between 3.8 and 7.1, which corresponds well to our conditions. We therefore used this conversion factor to calculate C_{mic} from our results.

c) Soil chemical and physical properties

Sample collection, transportation and storage

Composite soil samples were taken by retrieving four soil cores at each sampling point within a circle of 1 m radius around the squares of earthworm sampling. Soil cores (0-10 cm depth) were extracted with a split steel tube corer of 33 mm inner radius. Additionally, one separate sample for determining soil bulk density was taken on each sampling point. Samples were stored in plastic bags and rapidly transported to the laboratory of Göttingen University in cooling boxes. There they were kept at 8 °C until analysis.

Laboratory analysis

Prior to measurements, all soil samples were homogenized and plant roots removed by sieving them with a mesh of < 2 mm pore size.

For soil bulk density analysis, the whole sample was oven-dried at 105°C until constant weight was reached (approx. 24 h). Subsequently, its mass was determined and related to the sample's volume.

For soil acidity determination, 10 g fresh soil was diluted in 25 ml de-ionized water. After 10-12 h of equilibration, pH(H_2O) was measured. Afterwards KCl was added up to a concentration of 1 M KCl to determine pH(KCl).

For measuring soil water content, samples were weighed, oven-dried at 70 °C until constant weight was reached (approx. 48 h) and weighed again, and soil water content was calculated by subtracting dry weight from fresh weight (% dry wt.).

Total soil carbon (C) and nitrogen (N) contents were analysed by first milling the dried samples. In order to quantify the amount of inorganic carbon content, 500 mg of ground soil was combusted at 600 °C for 5 h. Of the non-combusted and combusted soil samples, an aliquot each of 20 mg was weighed into tin capsules and analysed by gaschromatography with a C/N elemental analyser (Vario EL III, Elementar, Hanau, Germany). For calculating soil organic carbon C_{org}, inorganic C was subtracted from total C.

Available phosphorus (P) and potassium (K) contents of the soil were determined with the calcium-acetate-lactate (CAL) method (Schüller 1969), which extracts readily soluble and exchangeable phosphates as well as potassium and is suitable for soils with a pH of 6 or higher. A sample of 5 g sieved fresh soil was added to 100 ml of extracting solution (0.1 M Ca-lactate, 0.1 M Ca-acetate, 0.3 M acetic acid). Subsequently, the suspension was put on a shaker for 90 min and then immediately filtered. K was determined directly in the extract by measuring the absorbance at 767 nm with a flame photometer (BWB Technologies, Berkshire, UK). For determining P concentrations, 4 ml of a freshly prepared Murphy-Riley blue-dying solution (Murphy and Riley 1962) was added to 5 ml of the filtered extract and filled up to 25 ml with de-ionized water. After thoroughly mixing the solution by manually shaking it, the 25 ml were left to rest for 30 min for colour development. Afterwards, absorbance was measured at 882 nm with a spectrophotometer (Libra S 21, Biochrom, Cambridge, UK). For each sample, one analysis of all soil chemical and physical properties was undertaken.

Further details and specific deviations from the above described are documented in Supplement 3.

3.3.6. Data analysis

Data analysis was performed using the software package R, version 4.1.2 (R Core Team 2021) with R studio (R Studio Team 2022), if not indicated differently. In text and figures, always means and standard error are given with untransformed data. Figures were produced using the packages ggplot2 (Wickham 2007) and ggpubr (Kassambara 2020).

a) Ordination

In order to determine the impact of drought on earthworm and soil microbial communities in the context of other environmental variables, a redundancy analysis (RDA) was performed (Rao 1964) using Canoco 5.02 (Microcomputer Power, Ithaca, New York) (Šmilauer and Lepš 2014). Response variables were earthworm species, numbers and biomass as well as C_{mic}. Soil moisture and temperature, pH and soil C and N content were included as explanatory variables. Year, farm and treatment (field vs. margin) were projected post-hoc into RDA space as supplementary, passive variables. Prior to analysis, response variables were log(+1) transformed and standardized to harmonize the different units. By means of Monte-Carlo permutation, a significance value for the global RDA solution and for the first axis was determined. Via forward selection, we determined how much each single environmental variable was able to contribute to the global explained variation (sum of squares of the regression) in response variables. The significance of each variable was determined by Monte-Carlo permutation (TerBraak and Smilauer 1998).

b) Parametric analysis

In order to approximate normal distribution and to control for outliers, soil microbial respiration and percent C_{mic} in C_{org} were log(+1) transformed. C_{mic} and qCO_2 were 1/(x+1)-transformed prior to analysis, topsoil moisture was square-root(+1) transformed prior to analysis. A one-way analysis of variance (ANOVA) was performed to compare the effect of drought on microbial response variables. The assumption of sphericity was automatically checked during the computation of the ANOVA test using the Mauchly's test. The Greenhouse-Geisser sphericity correction was automatically applied to factors violating the sphericity assumption. Where significant, post-hoc multiple pairwise paired t-tests between years were applied with Bonferroni correction for multiple testing. A two-way repeated measures ANOVA was performed to test whether there was a statistically significant interaction between drought (as between-subject-factor) and treatments (margin, field as within-subject factor). In case of significant interactions, this analysis was followed up by a Tukey's Honestly Significant Difference (Tukey's HSD) post-hoc test for pairwise comparisons with Bonferroni adjustment of p-values for multiple testing. This analysis was performed using the packages rstatix (Kassambara 2021) and moments (Komsta & Novomestky 2015).

c) Non-parametric analysis

Since earthworm data did not meet homoscedasticity and normality requirements for parametric tests, we performed non-parametric analyses (Shah & Madden, 2004), which are robust with outliers and show a good performance also in relatively small sample sizes (Brunner, Domhof, and Langer 2002). For comparison of earthworm variables between the years, a Friedman test was used to assess whether there were any statistically significant differences between the distributions. This was followed by pairwise Wilcoxon signed-rank tests for identifying which groups were different. P-values were adjusted using the Bonferroni multiple testing correction method. To test whether there was a statistically significant interaction between drought and treatments (margin, field), non-parametric ANOVA-type test statistics (ATS) of ranked data were performed using the package nparLD (Noguchi et al. 2012). In case of a significant interaction, a post-hoc signed pairwise Mann–Whitney–Wilcox test was performed. In case treatment as main effect was significant, the analysis was followed with a one-tailed Mann–Whitney–Wilcox test to test for differences between treatments within each year.

With respect to the interaction term years x treatment, for the ATS, only the numerator degrees of freedom of the F distribution are given, as the denominator degrees of freedom are set to infinity. For the main effect treatment, however, ATS gives both the numerator and the denominator degrees of freedom of the F distribution. Post-hoc p-values were adjusted with the Benjamini-Hochberg correction for multiple testing (Benjamini & Yekutieli, 2001).

d) Community structure analysis

To investigate if the community structure of earthworms differed between the years, a discriminant function analysis (DFA) was conducted with earthworm abundance data. Prior to the analysis, a non-metric Multidimensional Scaling (NMDS) was applied to reduce the number of dimensions (i.e. earthworm species) (Legendre and Legendre 1998). Only adult individuals were considered, as only they can be determined to species level. NMDS reduced the number of dimensions to three. Subsequently, the NMDS coordinates were used in the discriminant function analysis (DFA) with years as grouping variable. Squared Mahalanobis distances between group centroids were calculated to evaluate significant differences between years. This analysis was performed using STATISTICA 7.1 (Statsoft, Tulsa, USA).

3.4. Results

3.4.1. Spatial and temporal variation of soil drought intensity

According to calculations based on the water balance, the pre-drought year 2017 was characterized in the upper 25 cm of the soil by drought intensities close to the 60-year mean at all sites except for Ostwestfalen, where soil drought intensity exceeded the average. At all study sites, the soil drought magnitude in the topsoil was strongest in 2018 and less pronounced in 2019. However, soil drought magnitude levels in the topsoil did not return to pre-drought levels in 2020 at any study site. When considering the whole soil profile (typically 0-180 cm), the drought magnitude was at most sites higher than average in all study years (2017-2020) with highest severity in 2019. The drought magnitude in 2020 continued to be higher than the 60-year mean at all sites, even though regional variation was large (Supplement 1: Fig. S1).

Topsoil moisture (0-10 cm) as determined in October at the study sites dropped from 2017 to 2018 by 50 % (mean of the four sites in 2017: 25.0 ± 0.81 vol. %, 2018: 13.2 ± 0.42 %; $F_{(2.74, 317.64)} = 135.50$, $p < 0.0001$), and reached in 2019 and 2020 about 20 % lower values than before the drought (2019: 20.8 ± 0.82 %, 2020: 21.7 ± 0.90 %; Fig. 6). No significant differences existed in the topsoil moisture of fields and margins (Supplement 1: Table S1; $F_{(3,460)} = 1.78$, $p = 0.15$). The water balance-derived drought magnitude correlated closely with the topsoil moisture data taken at the study sites in the four study years (Pearson's rho = -0.631, $p < 0.001$).

3.4.2. Dependence of earthworm biomass and abundance and soil microbial activity on environmental factors

Climatic and edaphic variables (soil moisture, soil temperature, soil pH and C and N content) explained together 15.4 % of the variation in earthworm species composition and biomass and microbial biomass-C (C_{mic}) (eigenvalues of axis 1 = 0.146 and axis 2 = 0.005; pseudo-F = 88.8, p = 0.002). The soil properties had a narrow range, with soil acidity between 4.3 and 8.3 and C:N ratios between 7 to 16. Of the explained variation, 84.2 % was attributable to the effect of topsoil moisture (Table 3.1). Even though soil pH varied between 4.3 and 8.3 and soil C/N ratio between 7 and 16, soil chemical variables contributed with only 10.3 % to the explained variance. The first axis largely separated the year 2018 from 2019 and 2020 and was most closely associated with the soil moisture and earthworm biomass gradient (pseudo-F = 19.1, p = 0.002). Earthworm biomass and abundance were significantly positively correlated with topsoil moisture levels (Spearman's correlation coefficient rho biomass: 0.34, abundance: 0.31). The different earthworm species varied in their relatedness to topsoil moisture. Among the most frequently recorded species, *A. caliginosa* and *A. chlorotica* were most strongly associated soil moisture (Fig. 3.5).

While soil microbial basal respiration (BR) and soil microbial biomass-C (C_{mic}) were significantly positively correlated with topsoil moisture (Spearman's rho: 0.5, C_{mic}: 0.68), C_{mic} was most closely associated with soil carbon and nitrogen content and not with soil moisture, which contrasts with earthworm biomass.

Table 3.1: *Contribution of each environmental variable to the explained variation in earthworm variables and microbial biomass-C. p values were adjusted for multiple testing.*

Variable	Contribution to explained variation (%)	p-value
Topsoil moisture	84.2	**0.01**
Soil temperature	5.6	**0.05**
pH (H_2O)	4.6	0.06
C	3.9	0.10
N	1.8	0.66

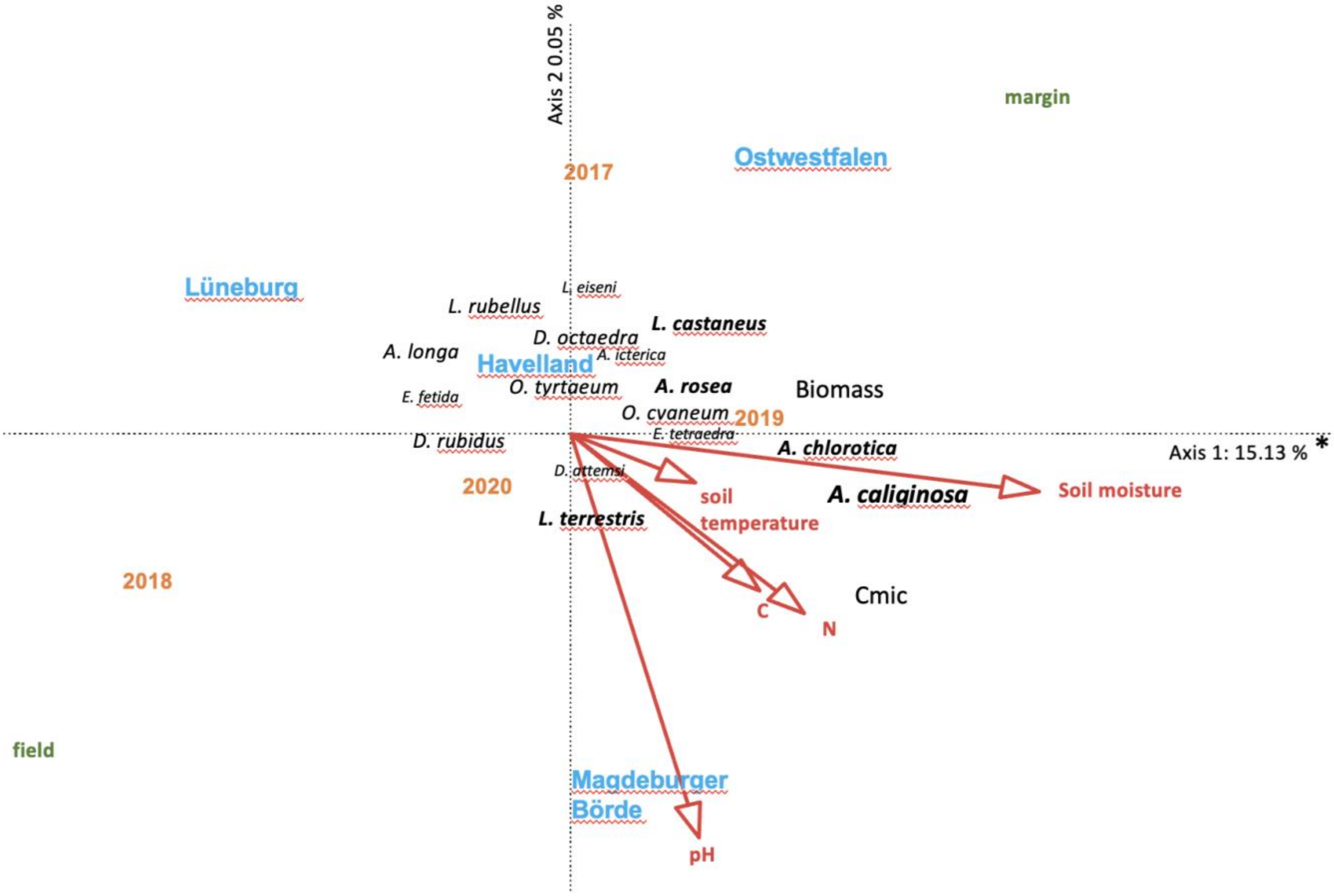

Figure 3.1: *Redundancy analysis (RDA) of the occurrence of earthworm species, total earthworm biomass and soil microbial biomass-C (C_{mic}) in cereal fields and unmanaged field margins ('treatment') at the four study sites (farms) in the four study years. Topsoil moisture, temperature and soil pH and C and N content were included as environmental variables. All earthworm species were included in the analysis. Treatment (green), farms (blue) and years (yellow) were included as passive variables not affecting the ordination. The letter size of the species indicates how often they occurred in the dataset (big letters: the most frequent species, small letters: rare species). The five most abundant earthworm species are marked in bold. For full names of species see table 3.2. Length of gradient: 2.9. Permutation tests on all axes and the first axis were significant (marked with an asterisk).*

3.4.3. Response of earthworm and soil microbial populations to the drought

Earthworm biomass averaged over the four sites was significantly lower in 2018 (9.9 ± 1.9 g m^{-2}) than in all three other years (2017: 27.4 ± 3.1 g m^{-2}; 2019: 27.3 ± 3.6 g m^{-2}; 2020: 23.0 ± 3.0 g m^{-2}) (χ^2 (3) = 59.88, $p < 0.0001$). Similarly, earthworm abundances were significantly lower in 2018 (23.0 ± 4.0 ind. m^{-2}) than in the three other years (2017: 55.6 ± 5.1 ind. m^{-2}; 2019: 63.4 ± 8.0 ind. m^{-2}; 2020: 57.6 ± 6.4 ind. m^{-2}) (χ^2 (3) = 59.33, $p < 0.0001$) (Fig. 3.2).

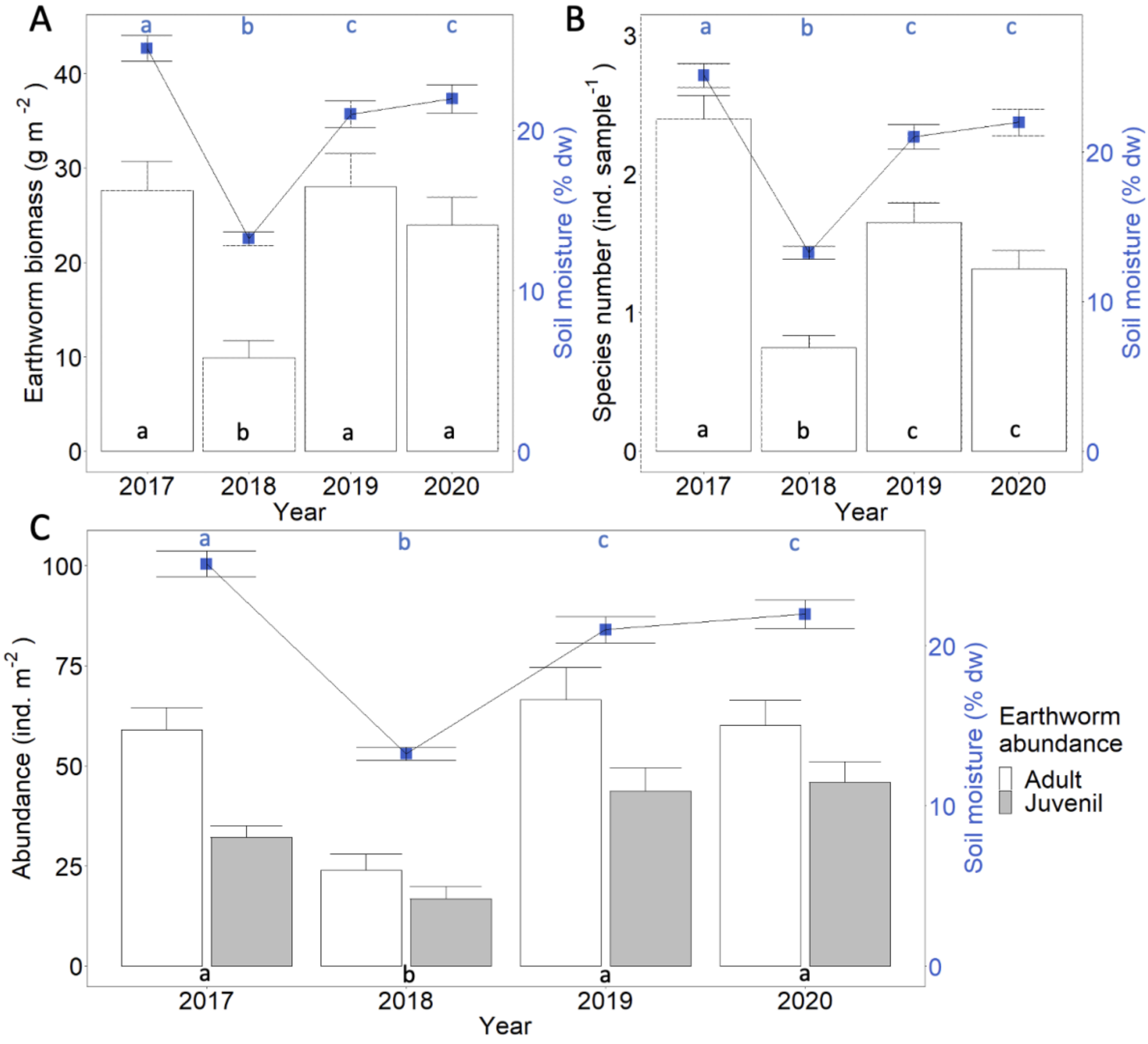

Figure 3.2: *(A) Earthworm biomass and (B) species number per sample as well as (C) earthworm abundances (adults: white bars, juveniles: grey bars) in the four study years averaged over all four study sites (fields and margins; bars, left y-axis) and topsoil moisture content (0-10 cm) (blue squares, right y-axis). Given are means ± SE. Significant differences in earthworm parameters between years are marked by different black letters (Friedman test, post-hoc pairwise Wilcoxon signed-rank tests with Bonferroni correction for multiple testing; $p < 0.05$). Significant differences in soil moisture levels between years are marked with different blue letters (ANOVA, post hoc paired t-tests with Bonferroni correction for multiple testing, $p < 0.05$).*

In the drought years 2018 and 2019, microbial basal respiration was with 1.7 ± 0.09 and 1.9 ± 0.1 µg O_2 g^{-1} soil dry weight h^{-1}, respectively, significantly lower than in 2017 (2.3 ± 0.16 µg O_2 g^{-1} d.w. h^{-1}) and in 2020 (2.6 ± 0.1 µg O_2 g^{-1} d.w. h^{-1}) ($F_{(2.67, 277.81)} = 21.90$, $p < 0.0001$). Basal respiration in 2019 was already a little increased compared to 2018 and therefore not significantly different to 2017 anymore. Microbial biomass-C (C_{mic}) was in 2018 and 2019 (0.50 ± 0.03 and 0.52 ± 0.03 mg g^{-1} d.w., respectively) significantly lower than in 2017 and 2020 (0.62 ± 0.03 and 0.61 ± 0.03 mg g^{-1} soil dry weight, respectively) ($F_{(2.38, 226.2)} = 18.19$, $p < 0.0001$) (Fig. 3.3).

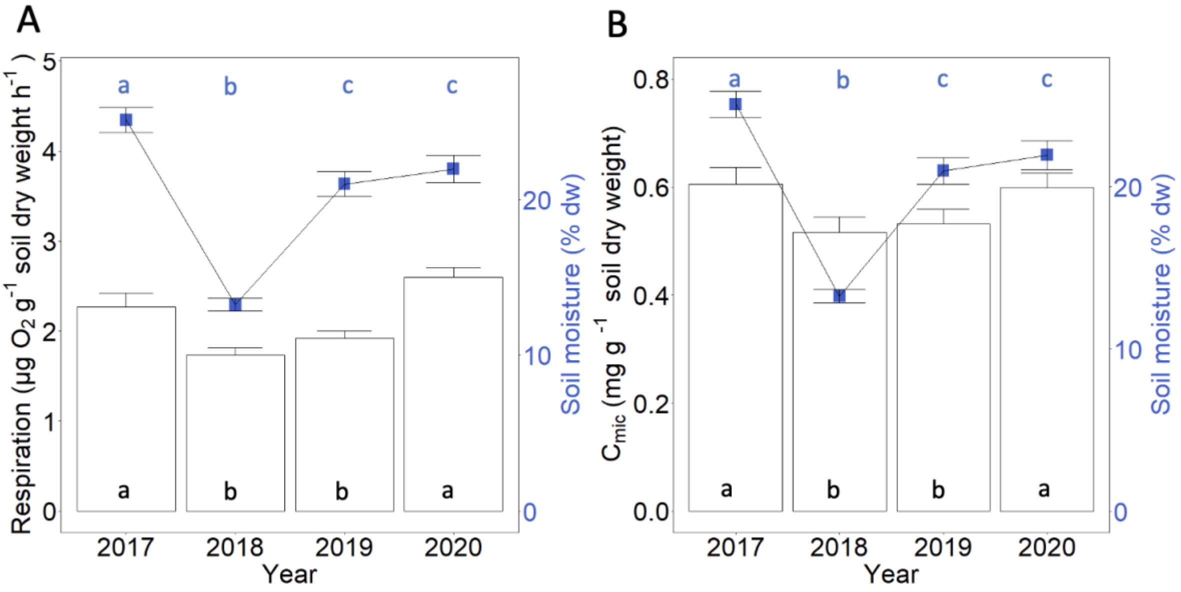

Figure 3.3*: (A) Microbial basal respiration (µg O_2 g^{-1} soil dry weight h^{-1}) and (B) microbial biomass-C C_{mic} (mg g^{-1} soil dry weight) in the four study years averaged over all four study sites (fields and field margins) (bars, left y-axis) and topsoil moisture content (0-10 cm) (blue squares, right y-axis). Given are means ± SE. Significant differences in earthworm parameters between years are marked by different black letters (Friedman test, post-hoc pairwise Wilcoxon signed-rank tests with Bonferroni correction for multiple testing; $p < 0.05$). Significant differences in soil moisture levels between years are marked with different blue letters (ANOVA, post hoc paired t-tests with Bonferroni correction for multiple testing, $p < 0.05$).*

The percent C_{mic} of C_{org} was not significantly different between the years, whereas the metabolic quotient (qCO_2), i.e. basal respiration per C_{mic}, was significantly higher in 2020 (3.62 ± 0.12 µg CO_2-C mg $C_{mic}{}^{-1}$ h^{-1}) than in all three other years (2017: 3.00 * 0.11; 2018: 3.44 ±0.29; 2019: 3.18 ± 0.12 µg CO_2-C mg $C_{mic}{}^{-1}$ h^{-1}) ($F_{(2.45, 232.90)} = 14.58$, $p < 0.0001$) (Fig. 3.4).

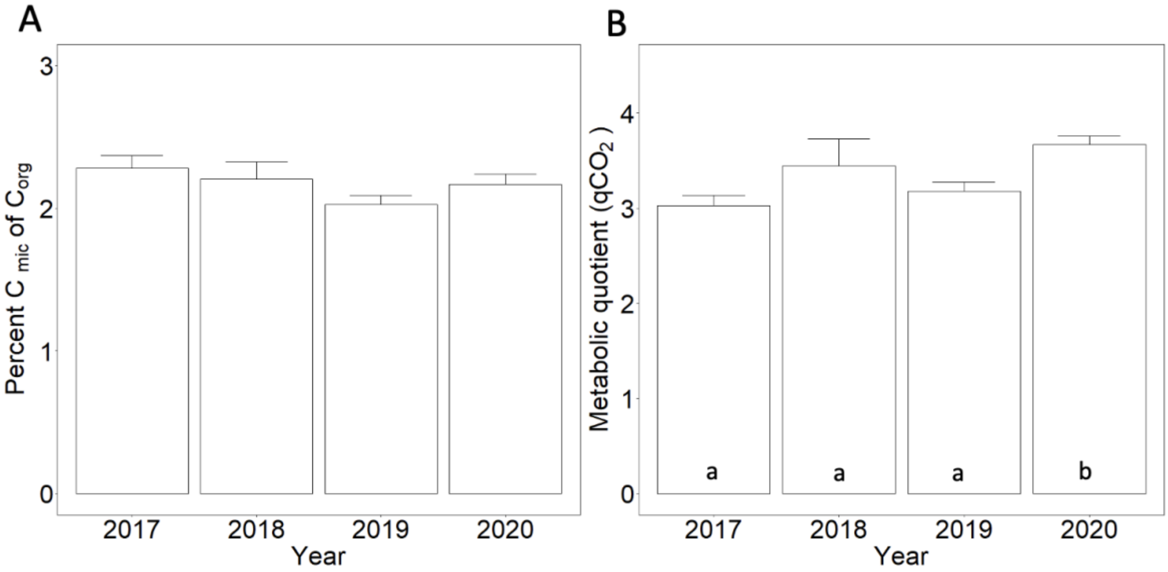

Figure 3.4: *(A) percent C_{mic} of C_{org},, and (B) metabolic quotient qCO_2 ($\mu g\ CO_2$-C mg^{-1} C_{mic} h^{-1}) in the four study years averaged over all four study sites (fields and field margins). Given are means ± SE. Significant differences between years in soil microbial variables are marked with different black letters (ANOVA, post hoc paired t-tests with Bonferroni correction for multiple testing, $p < 0.05$). Significant differences in soil moisture levels between years are marked with different blue letters (ANOVA, post hoc paired t-tests with Bonferroni correction for multiple testing, $p < 0.05$).*

3.4.4. Drought effects on earthworm community structure

In total, 16 earthworm species were recorded in the four years (Table 3.2). Earthworm community composition differed significantly between the four years (Wilks' lambda = 0.83; $F_{12,955} = 5.7$; $p < 0.001$); community differences were strongest between 2018 in comparison to 2017 and 2019 (Table 3.3).

Table 3.2*: Earthworm species recorded in the four years at the four sites (means of individuals per sample with standard error per sample for each year).*

	2017	**2018**	**2019**	**2020**
Aporrectodea caliginosa	2.27±0.39	0.18±0.05	2.01±0.29	0.87±0.15
Lumbricus castaneus	0.85±0.26	0.2±0.11	0.4±0.18	0.04±0.03
Lumbricus terrestris	0.84±0.14	0.48±0.11	0.64±0.14	0.53±0.1
Allolobophora chlorotica	0.72±0.13	0.52±0.13	1.61±0.29	1.12±0.2
Aporrectodea rosea	0.48±0.11	0.03±0.01	0.37±0.1	0.32±0.08
Lumbricus rubellus	0.4±0.1	0.06±0.03	0.22±0.06	0.21±0.1
Dendrodrilus rubidus	0.27±0.14	0.06±0.04	0.03±0.01	0.05±0.03
Aporrectodea longa	0.16±0.05	0.09±0.05	0.12±0.05	0.1±0.06
Octolasion cyaneum	0.03±0.02	0.01±0.01	0.02±0.01	0
Aporrectodea icterica	0.01±0.01	0	0.01±0.01	0.01±0.01
Eisenia fetida	0.04±0.03	0	0	0.01±0.01
Dendrobaena octaedra	0.28±0.09	0.03±0.01	0	0
Dendrobaena attemsi	0	0.03±0.03	0.02±0.01	0
Octolasion tyrtaeum	0.05±0.03	0	0	0.03±0.02
Lumbricus eiseni	0.02±0.01	0	0	0
Eisenia tetraedra	0.01±0.01	0	0	0

Table 3.3*: Squared Mahalanobis distances between group centroids of the four years for the earthworm community structure in the four study years.*

	2017	2018	2019	2020
2017	-	0.98 ***	0.30**	0.23**
2018	-	-	1.06***	0.40**
2019	-	-	-	0.26*

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Earthworm species richness (i.e. no. of species per sample) was significantly higher in 2017 (2.3 ± 0.16) than in 2018 (0.7 ± 0.09), 2019 (1.5 ± 0.14) and 2020 (1.3 ± 0.14) (χ^2 (3) = 93.51, $p < 0.0001$). Compared to 2018, the 2019 and 2020 samples were significantly species-richer, with no significant difference between 2019 and 2020 (Fig. 3.5). Earthworm species richness was significantly positively correlated with topsoil moisture (Spearman's rho: 0.26).

The five most frequently recorded species (*A. caliginosa, L. castaneus, L. terrestris, Al. chlorotica* and *A. rosea*) revealed species-specific abundance patterns across the years. The abundances of the endogeic spieces *A. caliginosa* was significantly lower in 2018 compared to all other years. Abundances in 2017 and in 2019 were significantly higher compared to 2020 (χ^2 (3) = 73.78, $p < 0.0001$). Abundances of *A. rosea* were significantly lower in 2018 compared to all other years, however, abundances of 2020 did not differ significantly from 2017 and 2019 (χ^2 (3) = 29.43, $p < 0.0001$). Abundances of *Al. chlorotica* 2017 and 2018 did not differ significantly, however, abundances in 2019 and 2020 were significantly higher than in 2018 (χ^2 (3) 19.65, $p = 0.0002$). The abundances of *L. castaneus* in 2017 were significantly higher compared to all three other years (χ^2 (3) = 33.76, $p < 0.0001$). In contrast, the abundance of *L. terrestris* was not significantly different between the four years. The eight rarest species were not recorded in all years. In 2017, seven out of the eight rare species were recorded, while in all other years, five of the eight rare species were missing (Table 3.2).

The mean number of endogeic earthworms per sample was significantly lower in 2018 (0.6 ± 0.1 ind. per sample) than in all other years. In 2020 we found with 2.3 ± 0.3 ind. per sample significantly fewer endogeic earthworms per sample than in 2017 and 2019 (3.4 ± 0.5, 3.9 ± 0.5 ind. per sample, respectively) (χ^2 (3) = 74.3, $p < 0.001$). The mean number of epigeic earthworms per sample was significantly higher in 2017 (1.6 ± 0.3 ind. per sample) than in all other years (2018: 0.4 ± 0.1; 2019: 0.6 ± 0.2; 2020: 0.3 ± 0.1 ind. per sample) (χ^2 (3) = 62.9, $p < 0.001$). Finally, the mean number of anecic earthworms per sample in 2018 (0.6 ± 0.1) was significantly lower compared to 2017 (1.0 ± 0.1) (χ^2 (3) = 12.6, $p = 0.006$) (Fig. 3.9).

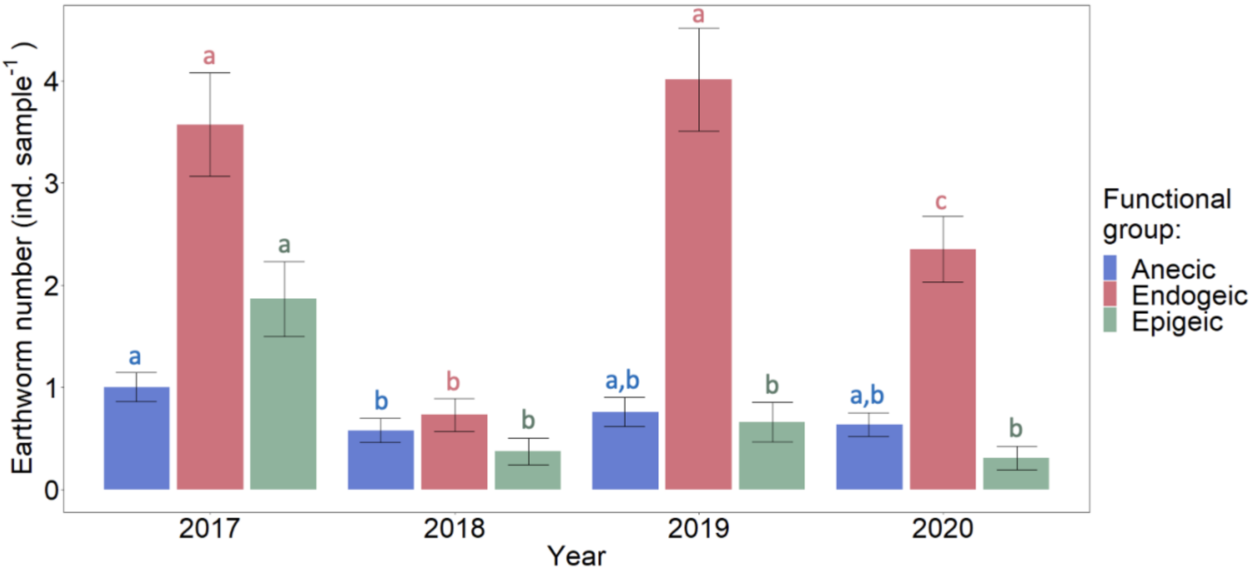

Figure 3.5: *Abundance of earthworm functional groups in the four study years expressed as individuals per sample (averaged over the four sites, cereal fields and field margins; means ± SE). Significance differences between years were tested for each functional gro group separately. Significant differences are marked with different letters in group-specific colors (Friedman test, post-hoc pairwise Wilcoxon signed-rank tests with Bonferroni correction for multiple testing; p < 0.05).*

As a measure of the drought effect on earthworm reproduction, the abundance of juvenile earthworms was significantly lower in 2018 (16.2 ± 3.1 juvenile ind. m^{-2}) than in all other years (2017: 30.9 ± 2.9 juvenile ind. m^{-2}; 2019: 41.0 ± 5.7 juvenile ind. m^{-2}; 2020: 44.0 ± 5.2 juvenile ind. m^{-2}) (χ^2 (3) = 40.32, p < 0.0001) (Fig. 3.5). The age structure of the earthworm communities expressed as the percentage of juvenile earthworms per m^2 differed significantly between 2020 (60.2 ± 3.6 %) compared to 2017 (52.2 ± 2.7 %) and 2019 (48.5 ± 3.2 %) (χ^2 (3) = 18.7, p < 0.001).

3.4.5. Combined effect of drought and land-use on earthworms and microorganisms

Earthworm biomass was significantly lower in the arable fields compared to the unmanaged field margin (non-parametric ANOVA-type statistics (ATP) $_{(1.00,\ 107.4)}$ = 94.0, p < 0.001). The drought effect on earthworm biomass in the fields differed significantly from the drought effect on earthworm biomass in the margins (ATS $_{(2.91)}$ = 3.02, p = 0.028). While earthworm biomass was significantly lower in 2018 than in all other years in both field and margin, biomass reached similar high (or higher) levels in 2019 and 2020 in the margins as compared to 2017, which was not the case in the fields. Here, earthworm biomass was significantly lower in 2019 and 2020 than in 2017 (Fig. 3.6, Supplement 2: Table S2), i.e. recovery was incomplete. Field and margin showed a contrasting temporal development of earthworm biomass despite similar topsoil moisture patterns (Supplement 1: Table S1 and Fig. S2).

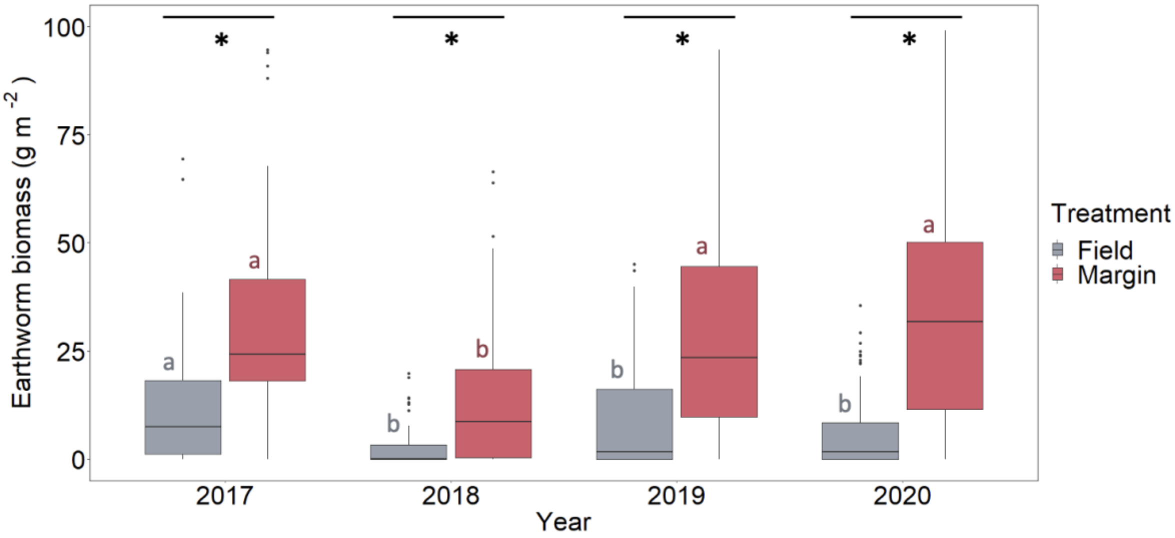

Figure 3.6: *Earthworm biomass in margin and field in the four study years, averaged over the four sites. Different letters indicate significant differences between years in black for field and in red for margin. Asterisks mark significant differences between treatments (field vs. margin) in each year (ANOVA-type statistics, post-hoc Mann–Whitney–Wilcox test with Benjamini-Hochberg correction for multiple testing, p < 0.05).*

Earthworm abundance averaged over all sites was significantly lower in fields than in margins (ATS $_{(1, 112)}$ = 84.00, p < 0.001). The effect of drought on earthworm abundance in fields was significantly different to the drought effect in margins (ATS $_{(2.97)}$ = 5.38, p = 0.001): In the latter, earthworm abundance was significantly lower in 2018 than in all other years, i.e. abundance recovered completely in 2019 and 2020. In the fields, earthworm abundance recovered only by 2020 (Fig. 3.7, Supplement 2: Table S3).

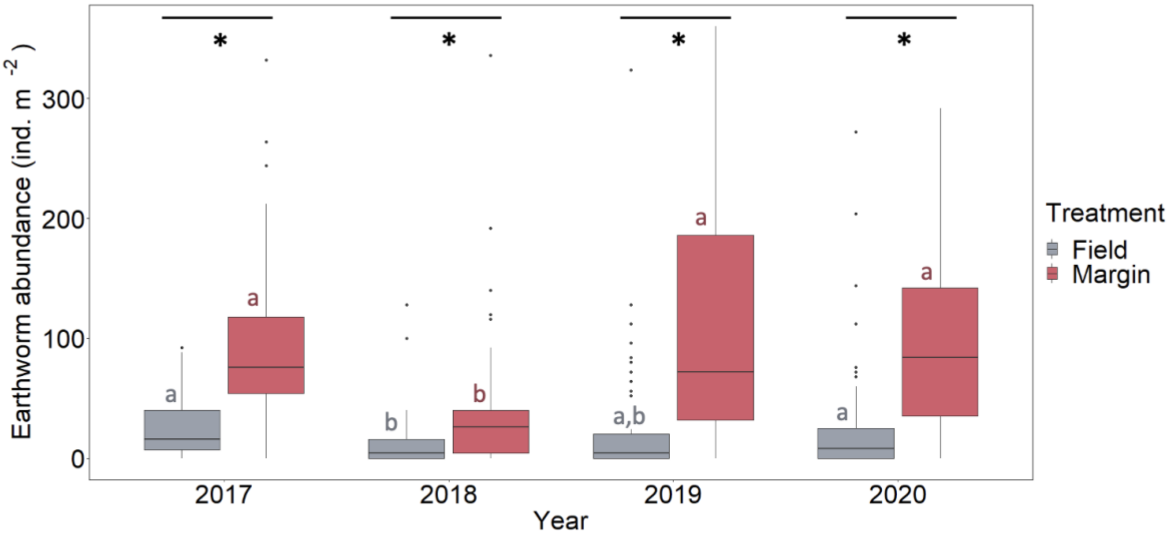

***Figure 3.7**: Earthworm abundance in margin and field in the four study years, averaged over the four sites. Different letters indicate significant differences between years in black for field and in red for margin. Asterisks mark significant differences between treatments (field vs. margin) in each year (ANOVA-type statistics, post-hoc Mann–Whitney–Wilcox test with Benjamini-Hochberg correction for multiple testing, $p < 0.05$).*

Earthworm species numbers per sample were significantly lower in the field than in the margin samples as an average over all sites ($ATS_{(1.00, 109.08)} = 113.85$, $p < 0.001$). Similarly to abundance, the drought effect on earthworm species number per sample in fields was significantly different to the drought effect in margins ($ATS_{(2.77)} = 4.37$, $p = 0.006$): In the latter, earthworm species number per sample was significantly lower in 2018 than in all other three years with species numbers approaching the 2017 level in 2019 and 2020. In contrast, earthworm species number per sample remained at a very low level in 2018-2020 in the fields (Fig. 3.8, Supplement 2: Table S4).

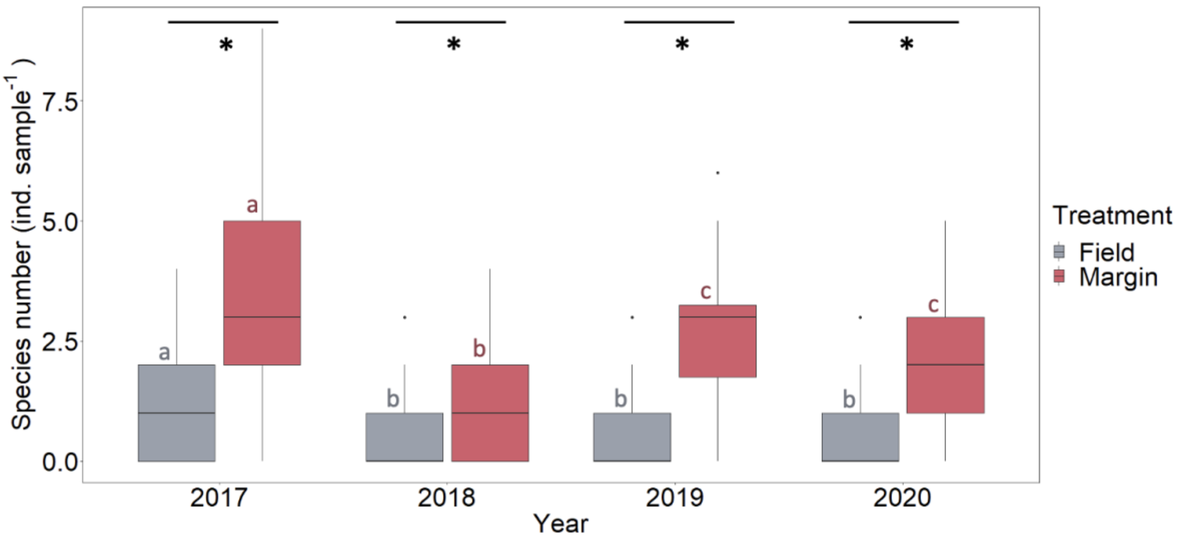

Figure 3.8: *Earthworm species number per sample in margin and field in the four study years, averaged over the four sites. Different letters indicate significant differences between years in black for field and in red for margin. Asterisks mark significant differences between treatments (field vs. margin) in each year (ANOVA-type statistics, post-hoc Mann–Whitney–Wilcox test with Benjamini-Hochberg correction for multiple testing, $p < 0.05$).*

Microbial biomass carbon (C_{mic}) was significantly lower in fields compared to margins ($F_{(1,376)} = 85.6$, $p < 0.001$), except in 2018. The effect of drought on soil microbial biomass-C (C_{mic}) in fields was significantly different to the effect of drought on C_{mic} in margins ($F_{(3,376)} = 2.99$, $p = 0.04$): in margins, C_{mic} was significantly lower in 2018 compared to 2017 and 2020. In fields, C_{mic} did not differ significantly between the years (Fig. 3.9, Supplement 2: Table S5).

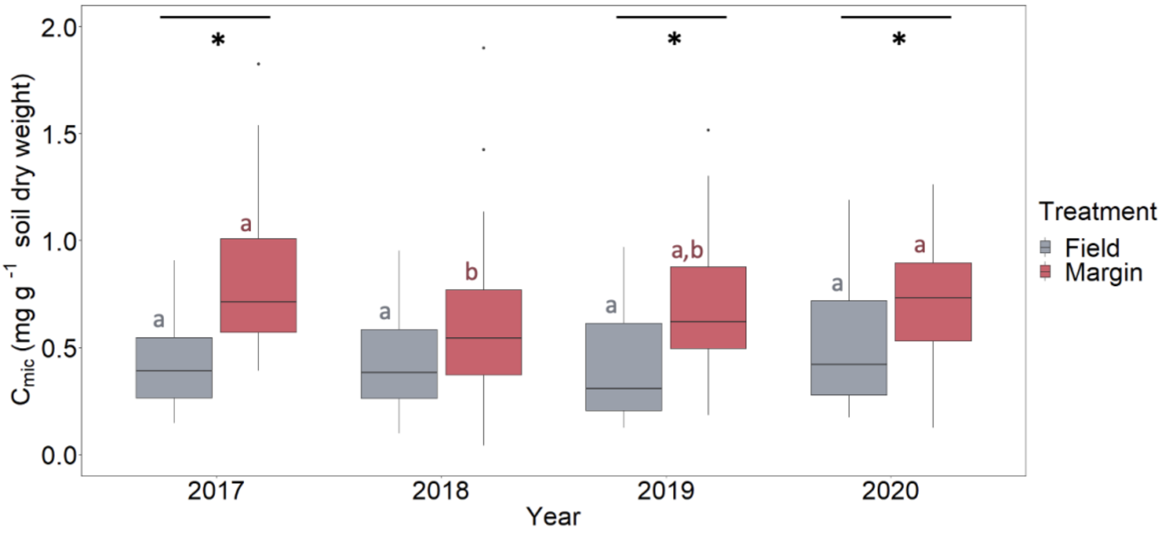

Figure 3.9: *Soil microbial biomass-C (mg C_{mic} g^{-1} soil dw) for field and margin samples in the four study years (averaged over all sites).Different letters indicate significant differences between years for margin in red and grey for field. Asterisks mark significant differences between treatments (field and margin) in each year (ANOVA, post-hoc Tukey's HSD test for pairwise comparisons with Bonferroni adjustment of p-values for multiple testing, $p < 0.05$).*

Soil basal respiration (BR) was significantly lower in fields than in margins ($F_{(1,396)} = 152.3$, $p < 0.001$) in all years except for in 2018. The effect of drought on BR in fields was significantly different to the effect of drought on BR in margins ($F_{(3,376)} = 5.67$, $p < 0.001$): in the latter, BR was significantly lower in 2018 and in 2019 compared to 2017 and 2020. In fields, in contrast, BR did not differ significantly between 2017 compared to the drought years 2018 and 2019. However, in 2020 BR was significantly higher compared to 2019 (Fig. 3.10, Supplement 2: Table S5).

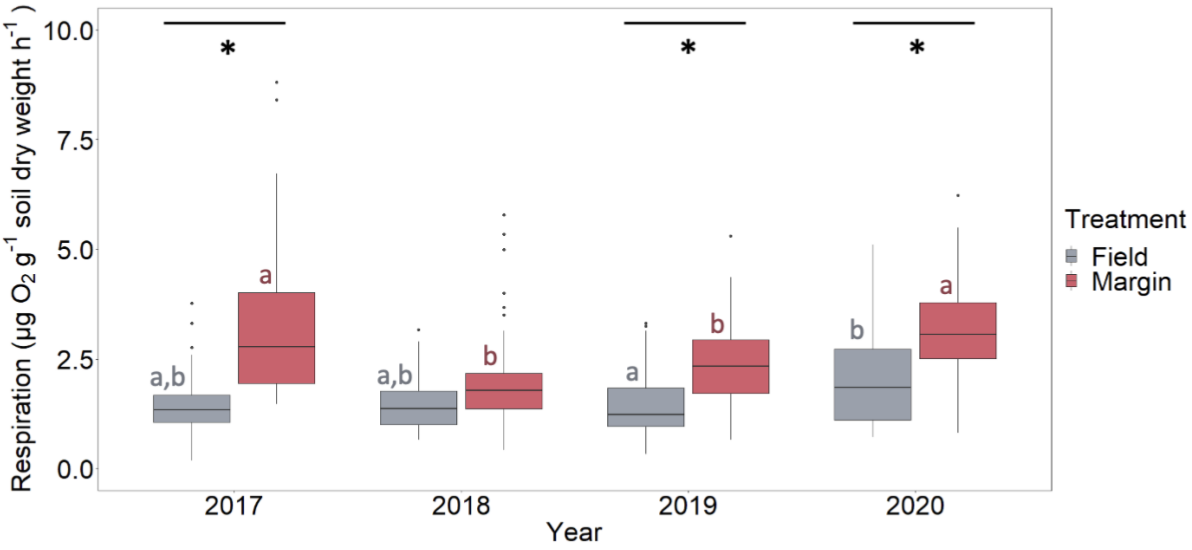

Figure 3.10: *Soil basal respiration (µg O_2 g^{-1} soil dry weight h^{-1}) for field and margin samples in the four study years (averaged over all sites).Different letters indicate significant differences between years for margin in red and grey for field. Asterisks mark significant differences between treatments (field and margin) in each year (ANOVA, post-hoc Tukey's HSD test for pairwise comparisons with Bonferroni adjustment of p-values for multiple testing, $p < 0.05$).*

3.5. Discussion

In this study, we explored the short-term resistance and resilience of earthworm and soil microbial populations in intensively managed arable soils to the exceptional 2018-2019 agricultural drought in Central Europe. Therefore, we first assessed the impact of drought compared to other soil properties and then the general response of earthworm and soil microbial populations to drought. We focused more specifically on how the drought altered earthworm community composition; and finally, we analyzed whether the impact of the drought was different in arable fields and in margins.

3.5.1. Strength of 2018-2019 drought effect compared to other abiotic drivers

The variation in earthworm and soil microbial populations that could be explained by soil abiotic variables was primarily determined by topsoil moisture levels and soil temperature, whereas soil acidity and soil C and N content did not contribute significantly to the explained variation. This supports our hypothesis that severe droughts as happened in 2018/19 have a profound influence on earthworm and microbial communities in arable fields, largely overriding the effects over other environmental factors. Our data further suggest that topsoil desiccation rather than water deficits in the whole profile is decisive for the negative impact on earthworms, since worm abundance suffered a larger drop in 2018 than in 2019, when the lower soil profile was even drier than in 2018. Our findings are in line with the general perception in the literature that soil moisture is a key factor for earthworm survival, growth and reproduction (Edwards and Bohlen 1996; Eggleton et al. 2009; Singh et al. 2019). Earthworms do not have mechanisms for effectively controlling tissue water content, rendering them largely dependent on the external moisture level (Kretzschmar and Bruchou 1991). For the microbial communities of arable soils, soil moisture is also a main activity-controlling factor (Orchard and Cook 1983), as was demonstrated, for example, in a study of the effect of a heat wave on soil microbial community composition in intensively managed cropland (Acosta-Martínez et al. 2014); this factor was clearly more influential than other environmental drivers in the study period.

Even though soil moisture was the dominant influencing abiotic factor, 85 % of the variation in earthworm and microbial populations remained unexplained by our models which further considered soil temperature, pH, and soil C and N content. The variation in soil pH and C:N ratio across the four sites was only moderate despite variable geology, which must be a consequence of decade-long fertilization and liming that has reduced soil chemical gradients (Arriaga, Guzman, and Lowery 2017; Helming et al. 2018). Other important environmental variables for earthworm and soil microbial populations that were not quantified in this study include soil texture, soil aeration and food supply for the soil organisms (Bloem, Hopkins, and Benedetti 2006b; Edwards and Bohlen 1996). Further, the application of specific combinations of pesticides at the study sites could explain part of the observed variation in soil biological activity. Influences of past management regimes on the fields could also be important. The interaction of abiotic and management-related factors as possible determinants of the composition and activity of soil biota is complex and thus only few studies have aimed at disentangling them (M. J. I. Briones, Mascato, and Mato 1992).

3.5.2. Response of earthworm and soil microbial populations to the 2018/19 drought

Earthworm biomass and abundances were reduced on average to 33 % in 2018 compared to the pre-drought year 2017. Topsoil desiccation reached its maximum in summer/autumn 2018 in the 2017-2020 period, supporting our hypothesis that soil drought is an important stressor of earthworm populations in arable soil. Interestingly, earthworm biomass recovered to pre-drought levels already in 2019, even though the winter 2018/19 and the summer 2019 were also dry and the cumulated soil moisture deficit thus increased from 2018 to 2019 and further to 2020. Earthworm abundances even exceeded the 2017 level by 15 % in 2019, even though the desiccation of lower soil layers was more pronounced in 2019 than in 2018. Thus, our hypothesis that earthworm populations would not recover to pre-drought levels by 2020, was not confirmed. We assume that the recovery of earthworm populations was mostly a consequence of partial topsoil rewetting in summer 2019, which approached pre-drought moisture levels, while the deeper soil layers remained dry.

Numerous studies have reported that droughts can markedly reduce earthworm populations (Singh, Singh, and Vig 2016; Thakur et al. 2018). However, our findings are surprising, as the deleterious effect of droughts is usually considered to increase over time (Ana Bastos et al. 2021; Eggleton et al. 2009). Our results support the view that abundances and distribution of earthworms are strongly determined by the temperature and moisture levels especially of the upper soil layers (Bessolitsyna 2012), while desiccation in the subsoil may harm crops, but seems to be less relevant for earthworms. In the four years of our study, soil drought magnitude was strongest in the upper soil layer (0-25 cm) in 2018, whereas the drought magnitude increased toward 2019, when the whole soil profile was affected (Supplement 1: Fig. S1). Studies on seasonal change in the vertical distribution of earthworms have found that the animals tend to stay in the upper soil layers and rather enter aestivation upon soil desiccation, at least in normal summers with only mild drought (Rundgren, 1975). However, during exceptional soil moisture deficits, earthworms seem to respond unanimously in the upper soil layer by retreating to deeper layers and then enter aestivation there (Edwards 2004). When deeper soil layers dry out, the response of earthworms is species specific (Gerard 1967). The differing response of earthworms to a soil moisture deficit in the topsoil and in deeper soil layers may be due to the fact that most species feed in the upper soil or litter layer and only anecic species burrow into deeper soil layers (Edwards 2004). Our results point at considerable resilience of the earthworm populations of arable fields to desiccation of lower soil layers, since increasing subsoil water deficits in a two-year period had not reduced population sizes after four years. Thus, contrary to other studies, we did not find a growing drought effect over time, but a close response to topsoil moisture only, while the dry subsoil apparently did not harm these communities additionally. We speculate that intense chemical and mechanical stress and increasing drought exposure in the past decades have selected in these fields earthworm communities with considerable stress tolerance.

Microbial biomass-C (C_{mic}) was reduced by 15 % in 2018 and 2019 compared to 2017 and 2020. We had expected only negligible drought effects on C_{mic} (hypothesis 2), assuming that microbial communities would respond to soil desiccation with a shift to more drought-tolerant taxa and perhaps activity stimulation through the release of mineral nitrogen and labile C-compounds from dying bacteria and physical disintegration of organic substances (Schimel, Balser, and Wallenstein 2007). Yet, microbial basal respiration was reduced by 15 % in 2018 and in 2019 compared to pre- and post-drought years (2017 and 2020) and the drop lasted until 2019, even though topsoil moisture levels in 2019 and 2020 had recovered to similar levels as in 2017. This suggests that the 2018/19 drought has significantly impaired microbial activity and it contradicts our hypothesis that microbial respiration would recover as soon as soil moisture is back to normal again. The latter finding suggests that the soil microbial community response to drought is not only driven by the soil moisture deficit itself, but by a more enduring additional drought-related effect as well. One could speculate that the drought has reduced the availability of readily available labile C compounds in the soil through reduced saprophytic activity, which may need longer to recover than earthworm populations that endured the drought through aestivation. The reduced activity of soil meso- and microfauna during drought may also lead to slower decomposition rates (Thakur et al. 2018), affecting soil organic matter cycling.

Evidence on the response of soil microbial communities to drought is mixed. In line with our findings, other studies also documented a reduction of microbial biomass in response to drought (Sheik et al. 2011). On the other hand, results from a meta-analysis that studied the effect of precipitation changes on both plants and soil microorganisms suggest no change in microbial biomass-C under reduced precipitation (Zhang & Xi, 2021). A reason for the diverging observations may be that findings from experimental studies do not necessarily reflect the complexity of real-life situations. A recent meta-analysis comparing data from experimental and real-life studies argues that experimental setups might often underestimate the detrimental effect of drought (Kröel-Dulay et al. 2022).

Drought impacts soil microorganisms not only directly by reducing the available water in their immediate soil environment (Schimel, Balser, and Wallenstein 2007) but also indirectly via effects on the plant community (Bardgett, Freeman, and Ostle 2008). Under moderate drought stress, plants allocate more carbon to roots (Karlowsky et al. 2018; Sanaullah et al. 2011). Increased release of root exudates under drought might buffer adverse effects of soil desiccation on microorganisms (Bloor, Zwicke, and Picon-Cochard 2018), possibly explaining why some studies they did not find a response of soil microbes to drought. The overall effect of drought on below-ground plant carbon supply to microbes may vary strongly in dependence of drought magnitude and it likely is strongly context-dependent (Preece and Peñuelas 2016). Impaired plant growth as a consequence of drought led to reduced belowground allocation of easily mineralizable C via both plant litter and root exudates (Fuchslueger et al. 2014). The fact that cropland and managed grasslands suffered reduced productivity in Europe during the severe 2018/19 drought (A. Bastos et al. 2020; Ana Bastos et al. 2021; Buras, Rammig, and Zang 2020) suggests that a lower input of plant-derived C-compounds to the soil has also limited soil microbial growth and activity (Ciais et al. 2005). We thus speculate that microbial biomass and activity were reduced during the drought primarily due to the indirect effect of poorer vegetation development in field and field margin reducing the availability of labile C compounds for soil microbes.

It appears that the earthworm communities of the cropland responded directly to topsoil moisture levels and quickly recovered once the soil water content was back to normal. In contrast, the soil microbes may have been more indirectly affected by topsoil desiccation through impaired plant growth. It is likely that subsoil desiccation had a pronounced negative effect on the plants, while the harm to earthworm populations apparently was of minor importance.

3.5.3. Drought effects on earthworm community structure

The drought in 2018 reduced earthworm species richness per sample by 66 % in comparison to the pre-drought year 2017. Earthworm species numbers per sample did not regain pre-drought values in 2019 and 2020, in contrast to biomass and abundances. This confirms our hypothesis that drought reduces earthworm species richness in cropland. A closer look shows that, while anecic earthworm abundances were less affected (40 % reduction) by the drought, the abundance of endogeic and epigeic species was reduced in 2018 by 80 % compared to 2017. Endogeic earthworms recovered in 2019, even exceeding pre-drought values by 15 %. This confirms our hypothesis that the sensitivity to drought varies among the earthworm ecological groups, with endogeic earthworms being able to recover quickly after drought and anecic taxa being less affected. We could not confirm our hypothesis that epigeic earthworms recover quickly after drought. A likely explanation for the different response of the three ecological groups is that the dependence on topsoil moisture levels and vegetation cover varies among the groups, resulting in abundance shifts between the groups.

It is well established that the resistance and resilience of earthworms to drought differs among the three ecological groups (Bouché 1977; Edwards and Bohlen 1996). In line with our findings, other studies also reported anecic species to be unaffected by drought (da Silva et al. 2020). Endogeic populations usually survive droughts but in smaller abundance, while drought is most detrimental to epigeic species (María Jesús Iglesias Briones et al. 2009; Plum and Filser 2005). Endogeic species avoid mortality by entering aestivation in desiccated soil (Gerard 1967; Martin Holmstrup 2001; Rundgren 1975). Anecic species retreat to deeper soil layers; from example, *L. terrestris* burrows deeper under dry conditions (Daniel 1991). The strategy of epigeic species is focused on a short reproduction cycle with formation of drought-resistant cocoons (Bouché 1977; Martin Holmstrup and Loeschcke 2003; Petersen et al. 2008). However, the drought tolerance of epigeic species such as *D. octaedra* may vary in dependence on regional climate, with cocoons in humid regions being much less desiccation-resistant (Martin Holmstrup and Loeschcke 2003). Furthermore, growth and survival of juvenile earthworms are largely dependent on readily available food. In contrast to endogeic juveniles that feed also on soil, epigeic juveniles rely only on litter as feeding source (Curry and Schmidt 2007). It can be assumed that the overall reduced productivity of the vegetation in Europe during the 2018/19 drought (Hari et al. 2020) has increased the mortality especially of epigeic hatchlings.

The high number of endogeic earthworms found in autumn 2019 must result from cocoons that hatched sometime in the first half of the year 2019, as endogeic juveniles take three to six months to mature (Butt, Frederickson, and Morris 1997; Lowe and Butt 2008). This suggests that in contrast to epigeic juveniles, especially endogeic juveniles have successfully survived the 2019 summer drought. The ability to not just feed on litter but also on mineral soil material (Curry and Schmidt 2007) and reduced competition with epigeic earthworms may explain the high numbers of endogeic earthworms in 2019. This is, however, in contrast to observations, where growth and cocoon production of endogeic earthworms were negatively affected by drought (Martin Holmstrup 2001).

The response to drought on a species level differed within a given ecological group. For instance, in the most frequently recorded endogeic species, the means per sample of both *A. caliginosa* and *A. rosea* dropped by 90 % in 2018 compared to 2017 but regained pre-drought levels in 2019. In contrast, the mean per sample of the endogeic *A. chlorotica* dropped in 2018 only by 30 %, and in 2019 and 2020 it exceeded pre-drought levels by 100 %. This does not confirm our hypothesis of an unanimous response to drought within a given ecological group. These findings suggest that the tolerance range to drought within the same ecological group is largely species-specific. Species-specific responses within a given ecological group have been reported in the literature, however, with mixed results. In contrast to our observation, *A. caliginosa* recovered quickly, while the abundance of *A. rosea* decreased after drought (Mariotte et al. 2016; Plum and Filser 2005), possibly because *A. rosea* forms aestivation chambers closer to the soil surface (Gerard 1967) whereas the chambers of *A. caliginosa* are found below 10-20 cm (McDaniel et al. 2013). Briones et al. (2009) report that within the epigeic group, *L. rubellus* recovered within a year after a summer drought, while *D. octaedra* did not regain pre-drought abundance levels even after several years, suggesting that *L. rubellus* is more drought tolerant. Consequently, while there is some similarity in the drought response of each ecological group, the exact response seems to be largely determined by specific life history traits of the individual species.

The drought seems to have changed the age structure of the earthworm communities: 50 % of earthworm individuals were juveniles in the pre-drought year, whereas in 2020 this proportion was at 60 %. This is opposite to our hypothesis that juvenile earthworms are disproportionally affected by drought. These findings are surprising, as other published studies have shown that even moderate drought levels strongly reduce reproduction, probably because hatching of cocoons is only successful under favorable soil moisture levels (M. Holmstrup and Westh 1995; Maraldo et al. 2009; Wever, Lysyk, and Clapperton 2001).

We conclude that while earthworm abundances and biomass swiftly regained pre-drought levels after the drought, the community composition was affected for longer with species numbers generally reduced. The shift in earthworm community composition may exacerbate the impact of drought on soils: Anecic earthworms can accelerate soil desiccation by both their burrowing activity that aerates the soil and by their feeding habit that removes protective litter from the soil surface. In contrast, the activity of epigeic earthworms usually increases soil water storage in the upper soil layers (da Silva et al. 2020; Ernst et al. 2009). The evidence of functional group-specific earthworm activities on soil desiccation is mixed, though. For instance, some endogeic species have been found to decrease the soil water holding capacity by their compacting effect, whereas other endogeic species had the opposite effect (Blouin et al., 2013).

3.5.4. Combined effect of drought and land-use on earthworms and soil microorganisms

On average, earthworm biomass was 80 % and abundances 70 % lower in the managed field than in the adjacent field margins on similar substrate. Species numbers per sample were reduced by 70 % compared to margins. Moreover, the impact of the 2018/19 drought on earthworm biomass, abundances and species richness differed between margin and field. While the drought reduced earthworm biomass, abundances and species richness in both habitats in 2018 relative to 2017, earthworm biomass and abundances recovered in the margins to pre-drought levels already by 2019, but in fields did not regain pre-drought levels even by 2020. Earthworm species richness started to recover in the post-drought years in the margins, but did not so in the fields.

This confirms our hypothesis that earthworm populations are affected by the drought in both habitats but are recovering more slowly in the managed fields. We assume that the main reason for the more lasting impact of drought in fields is that the drought stress is exacerbated by the additional chemical and mechanical stress imposed through intensive agriculture. Our results suggest that earthworm community resilience is weakened in managed fields in comparison to field margins with much lower management impact.

In line with our findings, it is well established that intensive agricultural management of arable soils reduces the resistance and resilience of earthworm communities to stress (Bloor et al. 2021). This applies to both flooding (Kiss et al. 2021) and droughts (Yin et al. 2020) as common abiotic stress factors. The commonly practiced intensive agriculture exposes earthworm populations and other soil biota to multiple stresses though the combined application of e.g. herbicides, insecticides and fungicides in combination with heavy metals (Pelosi et al. 2014; Uwizeyimana et al. 2017), which may act synergistically. Earthworms may be more drought-vulnerable when exposed to harmful chemical compounds (Friis, Damgaard, and Holmstrup 2004).

Next to soil disturbance, the absence of permanent soil cover through a closed vegetation and litter layer in arable fields is a principal factor reducing earthworm abundance, as it limits food availability (Curry 2004) and may desiccate the topsoil. Food limitation is especially constraining immature earthworms (Curry and Schmidt 2007), which offers a possible explanation for the observation that earthworm communities in our fields did not to recover as rapidly as they did in the margins, as juveniles contributed a large fraction of the populations. Another factor most likely is the reduced soil organic matter content in the fields, which was 50% higher in the margins, that may have retarded earthworm population recovery (Johnston et al. 2015). When conditions are favorable, earthworm populations can grow and expand within only a few years (Edwards 2004), which is consistent with our observation of a swift recovery in the margins. After the 2003 summer drought, two observational studies on grasslands in Great Britain and Germany documented earthworm population recovery within less than a year (Eggleton et al., 2009, Plum & Filser, 2005). After the 2006 summer drought, earthworm populations regained pre-drought abundance values in a grassland, as soon as topsoil moisture (0 - 5 cm) was back to normal, which happened within less than a year (Eggleton et al. 2009). This fits our observations on earthworm population recovery in the margins.

In conclusion, climate-change effects such as droughts on earthworm populations in farmland are strongly context-dependent. The deleterious impact of drought is stronger on earthworm populations that already suffer from unfavorable conditions. Earthworm community recovery may benefit from increased soil organic matter content and from soil management practices that return a high proportion of crop residues to the soil (Bot and Benites 2005; Johnston et al. 2015). For instance, cereal-legume intercropping supports larger earthworm communities than cereal fields (Schmidt, Clements, and Donaldson 2003). Management activities that promote higher earthworm densities in arable fields can have beneficial cascading effects on the soil meso- and micro-fauna as well: When soil biota are exposed to dry conditions, overall soil species richness of the soil fauna is positively related to earthworm abundance, with especially micro-arthropod communities benefitting most (Siebert et al., 2019). Thus, larger earthworm populations can buffer the negative impact of drought on the overall soil decomposer community.

In fields, microbial biomass (C_{mic}) was 40 % lower and basal respiration (BR) lower by 30 % than in margins. Moreover, the impact of drought on microbial biomass and basal respiration differed between margin and field. In the margins, the drought significantly reduced C_{mic} and BR in 2018 compared to 2017. This was not the case in the fields, where the drought did not affect microbial biomass and basal respiration. This contradicts our hypothesis that microbial populations are more strongly affected by the drought in fields than in margins. Our findings suggest that in the managed fields microbial communities are smaller but stable and apparently largely resistant to the extra stress associated with the drought, while in margins, microbial populations are larger but more vulnerable to drought.

There is consensus in the literature that soil microbial biomass and activity vary with the type of land use (Ahmed et al. 2019) and so does their response to drought (Sünnemann et al. 2021; Vries et al. 2012; Yin et al. 2020). Microbial respiration has been found to be more sensitive to warmer and drier conditions under extensive compared to intensive land-use management (Siebert, Thakur, et al. 2019). In line with our findings for fields, an experimental drought on conventional cropland did not reduce soils microbial activity in the short-term (Sünnemann et al. 2021). On the other hand, a summer drought reduced microbial communities in grasslands (Alster et al. 2013). Yet, evidence on the impact of drought on the microbiome of grasslands is mixed, as other studies do not report droughts to reduce microbial biomass (Fuchslueger et al. 2014) or, on the contrary, even found increasing microbial populations under drought (Sanaullah et al. 2011).

Differing microbial community structures may be a possible explanation for the land use dependency of the drought response of microbial communities (Vries et al. 2012). Fungal communities usually are more drought-tolerant than bacterial communities (Acosta-Martínez et al. 2014; Harris 1981), although there is great variability in drought tolerance among different fungal species. Many fungi can accumulate osmoregulatory substances to protect their metabolism under drought (Blomberg and Adler 1992). Furthermore, their filamentous structure allows them to reach and continue exploiting the soil also in very dry conditions (Griffin 1981). Since grassland soils tend to have more fungal-based and cropland soils more bacteria-based communities (Bardgett and McAlister 1999; Vries et al. 2012), we had expected to find a negative effect of drought on the microbial communities of the fields and not in the margins which are more similar to grasslands. Yet, a meta-analysis revealed that the fungi-bacteria ratio in soil is not associated with the community-level drought stress threshold (Manzoni, Schimel, and Porporato 2012). It appears that the relative contribution of fungi and bacteria of the soil microbiome seems to depend less on water availability than on soil pH and C:N ratio (Fierer et al. 2009). As soil pH is close to neutral in both fields and margins of our study, we expected a contribution of both bacteria and fungi to the microbial communities in the two habitats (Ottow 2011).

Besides soil chemical factors, vegetation cover certainly will influence soil microbial communities and their stress tolerance. The margins usually have a permanent vegetation cover of a mixture of grasses and herbs which should offer soil microbial communities continuous supply of easily mineralizable organic substances via leaf and root litter production and root exudation. In conjunction with the absence of soil disturbance, these conditions must favor a higher microbial biomass and biological activity than in intensively managed cropland soils (Ottow 2011). In contrast, the cropping practices might have selected for stress tolerators in fields. More detailed analysis of microbial communities as determining microbial functional groups would allow to assess more in detail the impact of intensive agriculture and droughts on the microbial community structure. Furthermore, part of the fields had been bare of vegetation for several weeks at the time of soil microbiological sampling in October, which must have reduced the supply of plant-derived labile C compounds. Thus, it is likely that C limitation was more pronounced at the time of sampling in the fields than in the margins. Drought likely has reduced the productivity of the margin vegetation and thus the flow of carbon to the soil, while the C transfer from the vegetation had already ceased at the time of harvest in the fields. One possible explanation of the missing drought effect on microbes in the fields is therefore the fact that a drought effect on the C flow from the plants immediately before sampling is likely in the margins but absent in harvested fields. Sampling in June before crop harvest might well have reflected a drought effect on C_{mic} and BR in the fields as well.

Comparing the drought response of fields and margins and earthworms and soil microbes highlights the large effect of land-use type and vegetation cover and phenology as well as the contrasting behavior of different groups of soil biota to defined stress. The decomposer communities of intensively managed cropland and non-cultivated habitat islands in the farmland do not respond in an unanimous manner to a severe drought, thereby increasing the diversity of stress responses on the landscape level.

3.6. Conclusion

In this study, we document the effect of the exceptional 2018/19 drought in Central Europe on two components of the decomposer food web in intensively managed arable soils, i.e. earthworms and soil microbial communities. The drought had an overriding impact on the abundance and/or activity of these soil organism groups compared to other environmental factors. Intensively managed fields represent stressful environments for soil biota which is reflected in lowered densities and/or activities of earthworms and soil microbes compared to less affected farmland habitats on similar soil as permanent margins. Severe droughts as they are predicted to happen more frequently in future with climate warming, represent additional stressors with the potential to further weaken ecosystem functions provided by the decomposer food web in arable soils.

Here, we documented the short-term response (one to two years) of microbial and earthworm communities to a severe drought. The long-term response (several years to decades) to drier soil may differ substantially. To our knowledge, there is a lack of studies addressing the long-term impact of climate-change-related drought and heat on soil biota in farmland soils. When droughts occur more regularly over extended periods of time, a shift to more drought-tolerant soil biological communities may take place. Existing evidence shows that soil microbial as well as earthworm communities are able to adapt to drought stress in the long run (Allison, Wallenstein, and Bradford 2010; Cordero et al. 2021; Martin Holmstrup and Loeschcke 2003), either through a community shift to more drought tolerant species (Edwards and Bohlen 1996; Vries et al. 2012) or, within populations, by a shift to more drought-tolerant individuals (Martin Holmstrup and Loeschcke 2003; Walker, Palmer, and Voordouw 2006). Physiological adaptation within the lifespan of an individual or a strain is also an option, as observed in microbes that produce thicker cell walls (Schimel, Balser, and Wallenstein 2007), or earthworms that increase their alanine concentration (Bayley et al. 2010; Martin Holmstrup et al. 2016) and accumulate more osmolytes like sorbitol in their cocoons (Petersen et al. 2008).

As both earthworms and soil microbes are important for various crucial ecosystem functions and are valuable bioindicators, we underline that (1) observational studies are crucial to complement the insights gained from experimental settings, (2) future investigations should take into account the land-use and organism-group dependency of drought effects on soil biota in farmlands, and (3) there is a lack of studies considering the long-term response of soil decomposers to climate change.

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4. Chapter: General discussion

Field margin in Magdeburger Börde, own picture

„You could call these earthworms the miners of our garden and the system of many tunnels a miniature mine. Except that the earthworm doesn't get anything out of the ground.“
(Franke 2019)

This dissertation investigated the impact of two important global change drivers on the resilience of arable soil communities: the long-term impact of intensive agricultural management and the short-term additional impact of a severe drought. In this synopsis, I first discuss the implications of the main findings from the second chapter that dealt with the effect of intensive agricultural management on earthworms and microbes (section 4.1.) and then I focus on the role of field margins for soil organisms in the context of farmland biodiversity conservation (section 4.2.). Moreover, I review the consequences of the main findings from the third chapter that dealt with drought as one consequence of climate change on soil organisms (section 4.3.) and discuss its effect as an additional stress factor in intensive agriculture (section 4.4). I conclude by returning to the main objective and ask what could be learnt regarding the resilience of arable soil communities in intensive farmlands (section 4.5.).

4.1. Intensive agriculture as a permanent stress factor for earthworms and soil microbes

In a first step, the impact of intensive agricultural management on earthworms and soil microbial populations was investigated by comparing cropped fields with long-term established, grassy field margins. Our findings indicated that there was surprisingly little geographical differentiation in earthworm communities between the studied regions. In cropped fields, earthworm and soil microbial communities were smaller and less active than in permanent field margins, and earthworm communities were less diverse.

Our results imply that the long-term effect of intensive agriculture in Germany is two-fold: it simplifies soil organism communities and renders them similar across landscapes. These findings are alarming, since simplification and homogenization narrow down the response range of these communities to disturbance events and to changing environmental and management conditions (Olden et al. 2004). According to the insurance hypothesis (Yachi and Loreau 1999), when communities are small and reduced to few species, they have a more limited set of possible responses to disturbances. Then, the risk of being impaired is greater than when there are larger and more diverse communities that differ from site to site.

While for above-ground taxa, it is widely recognized that intensive agriculture reduces population sizes and the complexity of organism groups, the change in belowground organism community structure and possible consequences for ecosystem functioning is, however, less studied (Bardgett and van der Putten 2014). Our findings contribute to filling this knowledge gap. We reported simplified soil communities in the sense that microbial activity was lower and earthworm abundances were reduced, as well as that earthworm community composition was reduced to a few generalists (Jänsch et al. 2013). This confirms the observation that the reducing impact of intensive management is not random; Gámez-Virués et al. (2015) argue that it selects against species with specialized feeding habits, shorter activity period and relatively smaller body size. A reduction of population size and species richness under intensive agriculture in Europe not only for earthworms but also for Collembolans and oribatid mites was documented as well (de Vries et al. 2013). Indeed, a consistent negative impact of intensive agriculture is reported over the whole soil food web (Tsiafouli et al. 2015).

While losses in local agrobiodiversity are well documented (Newbold et al. 2015), the similarity of communities across geographical sites as documented in our findings highlights a second much less studied long-term consequence of intensive agriculture. Indeed, this homogenization across landscapes is assumed to be a major threat to beta diversity (Gossner et al. 2016). This loss in beta diversity in intensive farmlands is well studied for different above-ground taxa, e.g. for plant communities (Clough et al. 2007; Gabriel et al. 2006; Wietzke et al. 2020), insects (Ekroos, Heliölä, and Kuussaari 2010) or birds (Karp et al. 2012). Evidence for a homogenization effect on below-ground organism groups of intensive agriculture is scarcer. However, our findings are in line with other studies that found a loss in beta diversity not only for earthworms and microbes, but also for soil arthropod communities (Diekötter et al. 2010; Flohre et al. 2011). This suggests that intensive management has a consistent homogenization effect across both above- and belowground organism groups (Gossner et al. 2016).

Our findings confirm the general observation that intensive agriculture is a major driver of biodiversity loss, which in turn is rated to be among the most pressing challenges of the twenty-first century (Gámez-Virués et al. 2015; Sala et al. 2000). Current rates of biodiversity loss are 100 to 1000 times greater than natural extinction rates and still continue to increase (Ceballos et al. 2015; Pimm et al. 1995). Biodiversity loss at this rate is of concern as a decrease in the diversity of genes, species and functional organism groups is considered to diminish the efficiency of ecosystem processes and reduces the stability of ecosystems (Cardinale et al. 2012). This is of particular significance for Europe, where about 50 % of the land cover is farmland (Graf et al. 2015). However, estimates of biodiversity loss mainly rely on aboveground taxa. A European survey documented a 55 % decline of farmland birds (Heldbjerg, Sunde, and Fox 2018; Tarjuelo, Margalida, and Mougeot 2020). Also the documented 75 % decline in German insect biomass is thought to be mainly caused by practices of intensive agriculture (Hallmann et al. 2017). Estimates of belowground biodiversity loss are scarcer. A study reported intensive agriculture to reduce earthworm biomass by 80 % (Blakemore 2018). Yet, how belowground biodiversity loss affects ecosystem functioning is debated (Bardgett and van der Putten 2014). Within soil communities, functional redundancy is high due to generalized feeding habits of many soil organisms (Setälä, Berg, and Jones 2005). Still, less belowground biological activity and a reduction in community complexity as we documented it appears to have an impact on ecosystem functioning. For example, it reportedly slows down the cycling of litter carbon and nitrogen (Handa et al. 2014). Therefore, in the next section, I will focus on what can be learnt from our findings regarding farmland biodiversity conservation.

4.2. The value of field margins for below-ground biodiversity conservation in farmlands

In a second step we focused on the permanent field margins and studied the effect of soil, vegetation, and neighboring habitat on earthworm communities. Our findings indicated that earthworm populations were sensitive to local soil and vegetation factors in margins. Earthworm population size was larger in more fertile soils. On less fertile soils, we documented more diverse plant communities. At the same time, earthworm populations were smaller but they were far more species rich. We did not document an influence of neighboring habitat type on earthworms in margins.

While the value of field margins in the context of farmland biodiversity conservation for above-ground organisms is well documented, its value for below-ground organisms is less studied (Hyvonen et al. 2021). Our findings that in margins earthworm communities include four times as many species and that microbial biomass is two times larger compared to cropped fields, suggest a capacity of permanent field margins to serve as refuges for soil organisms. While also other studies report larger earthworm and microbial communities in permanent margins (Prendergast-Miller et al. 2018; Roarty and Schmidt 2013), there is ongoing debate what properties field margins should have to maximize their conservation value for belowground organisms (Mansion-Vaquié et al. 2017; Smith et al. 2009; Verhoeven et al. 2022).

Our findings suggest that there is a trade-off: We documented largest earthworm populations in fertile soils. They were, however, dominated only by a few species. In contrast, we documented most diverse earthworm communities in margins with most diverse plant communities. Yet, these communities had small population sizes and they were associated with less fertile soils. The complexity of interdependencies between aboveground and belowground ecosystem components such as plants, soil organisms and abiotic soil properties is enormous and a matter of ongoing debate (Eisenhauer and Powell 2017; David A Wardle 2002). Higher plant species richness is suggested to increase soil decomposer community diversity because they provide more varied organic matter input to soils and this more reliably (Eisenhauer 2012; Milcu et al. 2010). It is also well recognized that species-rich plant communities are associated with lower soil fertility (Michalet et al. 2002; Roem and Berendse 2000). Therefore, our findings support the view that less fertile soils have a positive impact on the species richness of soil organisms and plants. It is well established for plant communities that while soil fertility reduces species richness, it increases biomass (De Schrijver et al. 2011; Leuschner and Ellenberg 2017). On fertile soils, fast growing plant species with fewer natural defenses and tissues of a higher N-content tend to dominate, which again may be favorable for larger decomposer communities (van der Putten et al. 2009). Therefore, our findings indicate that soil fertility supports both a larger plant biomass and larger soil decomposer biomass, however, with the trade-off that these assemblies are dominated by few species.

Should our findings reflect a general pattern, then for farmland biodiversity conservation the following question arises: should earthworm biomass and abundances or earthworm species richness be maximized in field margins? The fact that earthworm species richness is heavily reduced in cropped fields stresses the importance of field margins as a refuge for high earthworm diversity in intensive farmlands. For the objective of maximizing species richness, our findings suggest reducing soil fertility in margins. In contrast to this, fertilizing is a recommended conservation measure for increasing earthworm abundances as food source for farmland birds (Brandsma 2004; McCallum et al. 2016). This is in line with our findings of large earthworm populations in margins with high soil fertility. Yet, promoting fertilization for increasing earthworm abundances as food source for farmland birds has recently been contested as an appropriate conservation measure (Onrust et al. 2019; Verhoeven et al. 2022).

Instead, the multifunctional value of margins is stressed, where species-rich plant communities are viewed to be the basis for multifunctionality (Holland et al. 2012; Verhoeven et al. 2022). Given the widespread disappearance of oligotrophic and mesotrophic sites and their characteristic communities in Central Europe in the course of eutrophication, it may be argued that decreasing the nutrient load on field margins is a more straightforward management strategy to increase agrobiodiversity than fertilizing the margins for bird fodder.

There is ongoing debate whether there is a positive spill-over effect from margins into cropped fields. While for above-ground taxa a spill-over from margins into fields is documented (Hof and Bright 2010; Holland et al. 2012), evidence for a possible spill-over of earthworms into arable fields is mixed (Frazão et al. 2017; Hof and Bright 2010; Roarty and Schmidt 2013). Exact knowledge on how soil organisms are distributed and what factors determine their distribution is still poor (Holden et al. 2019; Wu et al. 2011). Our finding that neighboring habitat type did not have an influence on earthworm communities in margins suggests that there is little spill-over effect. In the context of the debate whether farmland biodiversity conservation is best achieved by measures that are integrated into farming practices (land sharing) or by setting aside parts of the farmland that is then solely dedicated to conservation (land sparing) (Grass, Batáry, and Tscharntke 2021), our findings support the first approach for earthworm conservation. Should our findings represent a general pattern, then conservation measures that target earthworms on a broader scale would need to address also farming practices in arable fields.

4.3. Drought as one consequence of climate change for soil organisms

In a third step, we documented the resistance and short-term recovery of earthworms and soil microbes to the Western and Central European 2018 – 2019 summer drought and compared it with the pre-drought year 2017 and the post-drought year 2020. The drought had an overriding impact over other environmental parameters as soil pH, soil C and N content. The drought reduced earthworm biomass, abundances and species richness by 66 %, whereas it reduced soil microbial biomass and respiration by 15 %. It also affected earthworm community structure; while abundances of the deep burrowing anecic earthworms were little affected by the drought, it reduced the topsoil-dwelling endogeic and the litter-dwelling epigeic abundances by 80 % in 2018. Abundances of endogeic species recovered by 2020, whereas epigeic did not.

The Western and Central European 2018 – 2019 drought was the most extreme episode for the last two millennia (Büntgen et al. 2021). The probability of such a drought to occur is expected to increase in the 21rst century due to climate change (Hari et al. 2020). Our findings indicate that a drought leads to a reduction in earthworm and microbial abundance and activity. This is in line with other reports of a decline in earthworm and microbial abundances and activity in response to drought (Sheik et al. 2011; Singh et al. 2019). This is of concern as the reduced activity of the soil fauna slows down decomposition rates, which may have consequences for organic matter cycling (Thakur et al. 2018). While abundances and activity recovered quickly, the shift in earthworm community structure towards more endogeic species at the cost of epigeic species may exacerbate the negative impact of the drought. The activity of epigeic species on top of the soil and in the upper soil layers increases soil water storage (da Silva et al. 2020; Ernst et al. 2009) and their loss may affect carbon cycling (Zhang and Hendrix 1995).

Our study investigated the short-term response of earthworms and soil microbes to a drought. Further studies on the long-term effect of climate change on soil organisms are needed (Singh et al. 2019). Climate change in Central Europe will have a general impact on seasonal patterns with e.g. earlier start of spring (Rannow et al. 2010), which is expected to affect the life cycle and nutrition of soil animals (Geisen, Wall, and van der Putten 2019). Higher mortality of soil organisms is expected due to higher temperatures, which increases the metabolic demand of soil organisms (Thakur et al. 2018). Projected increased frequencies of extreme events such as heat waves, floods or storm surges may lead to higher erosion rates, which would deteriorate the living conditions for soil organisms (Nearing, Pruski, and O’neal 2004). The interaction of these climate change factors and drought for soil organisms needs to be considered in future studies, as they might exacerbate the impact of a drought on soil organisms.

4.4. Drought as an additional stress factor for soil organisms in intensive agriculture

In a fourth step we studied the impact of drought for margins and fields separately. Earthworm abundances and diversity were reduced in both fields and margins in 2018 compared to 2017. However, earthworms recovered quickly in margins, whereas in fields they did not recover within the studied period. In fields, soil microbial biomass was smaller compared to margins. Nonetheless, the soil microbial community was largely resistant to drought in fields. In contrast, in margins, the drought reduced microbial biomass and activity; but biomass and activity also recovered within the studied period.

Knowledge on the combined effect of different global change drivers on soil organisms is still poor (Singh et al. 2019). Our findings indicate that the short-term combined effect of intensive agriculture and drought is different for earthworms and for soil microbes. Our findings suggest that the permanent stress of intensive agricultural management in arable fields reduced the resilience of earthworm communities: their capacity to buffer the additional stress event was impaired and they did not recover within the study period. Soil microbial biomass and activity were affected by intensive agricultural management, as both parameters were reduced in fields compared to margins. However, the intensive agricultural management appears to have created microbial communities in fields that are largely resistant to an additional stress event (drought), at least in terms of biomass and activity, whereas in margins the microbial communities were affected by the drought, presumably because they are less stress-tolerant. In line with our findings of a differing response of microbes and earthworms, other studies also report that the effect of intensive agriculture is not consistently harmful to all soil organism groups (D. A. Wardle et al. 1999); e.g. fungal diversity was reported to increase with intensive management (de Graaff et al. 2019). Nonetheless, studies on soil food webs in agroecosystems suggest that intensive agricultural management reduces complexity and connectivity of whole soil food webs, which in return makes decomposer communities more prone to suffer from additional disturbances (Bloor et al. 2021; de Vries et al. 2013).

Our findings support predictions that soil organism groups show individual responses to global change (Sünnemann et al. 2021). This encourages further studies of soil biotic responses to natural hazards that consider multiple soil organism groups, which will then allow a comprehensive understanding of the consequences of drought for soil decomposer communities in intensive farming.

4.5. Concluding remarks: Resilience as a sustainable management perspective

This dissertation investigated the long-term effect of intensive farming in Germany and asked whether it reduces the resilience of decomposer communities by studying two different soil organism groups: soil microbes and earthworms. We assumed that a comparison of earthworm and microbial communities in cropped fields with undisturbed field margins will allow to assess the impact of intensive agriculture. Our findings demonstrated that intensive agriculture is a permanent stress factor for both organism groups and thus, the current, effective earthworm and microbial community size and activity is reduced compared to the potential maximal size and activity under the given edaphic and climatic conditions.

Then, we investigated whether this permanent stress factor impairs the resilience of earthworm and microbial communities in arable fields by studying how earthworms and microbes respond to an additional stress event such as a drought. According to ecological resilience theory, earthworm and microbial communities with strong resilience will show high resistance to disturbance and if perturbed will swiftly return to the pre-disturbed state. In contrast, when earthworm and microbial communities with low resilience are exposed to an additional stress, it will strongly impair their activity and abundance and they have difficulties to return to the pre-disturbed state. An additional stress may easily even push the communities over a threshold, beyond which they will not return to the pre-disturbance state again but find equilibrium in a new stability. This new stability, however, may be a degraded ecological state, possibly providing reduced ecosystem functions and services (Côté and Darling 2010; Holling 1973; Standish et al. 2014). This dissertation suggests that microbial communities in long-term intensively managed arable fields of Germany exhibit a high resilience, as they are resistant to the additional stress event of a drought. We assume that the harsh environment has selected a rather small number of microbial taxa that are well adapted to mechanical and chemical disturbance and to a strongly seasonal supply of organic matter. In contrast, the resilience of earthworms in long-term intensively managed arable fields of Germany was weak, as the drought reduced abundances, biomass and species number and they did not recover to the pre-disturbance state. It might even be possible that earthworms irreversibly crossed the threshold to a new degraded stability during the severe 2018-2019 drought episode. However, to determine this, longer-term investigations would have been necessary (Fig. 4.1).

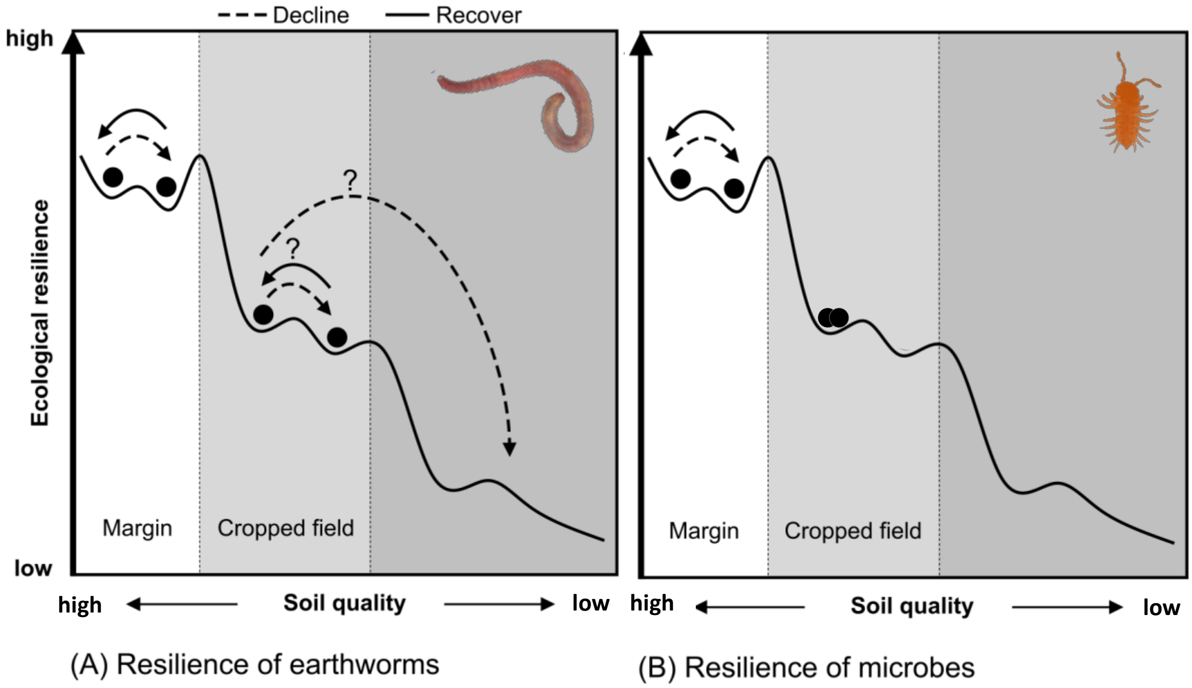

Figure 4.1: *Decline and recovery in response to the 2018-19 drought of (A) earthworms and (B) microbes in permanent field margins and in cropped fields. While in margins, both earthworms and microbes declined during the drought, immediately after they recovered again. In fields, microbial and earthworm communities were overall smaller than in margins. Microbes in fields were resistant to the drought while earthworms declined. Within our study period we could not determine whether earthworms were long-term impaired (dashed arrow to the dark grey area) or would only need more years to recover (black arrow) (figure adapted from Standish et al. 2014).*

We suggest investigating in future research, how rapidly earthworm and microbial communities are able to recover to their “maximal potential”: that is to abundances and activities that the local climate, soil and topography would allow. We propose to investigate a secondary succession by taking plots of these long-term intensively managed arable soils out of management and compare their recovery trajectory with undisturbed, permanent field margins. The latter may serve as a local estimate of the “maximal potential”, even though it is likely that also the margins are affected by spray-drift of pesticides and irregular fertilizer input. If earthworm as well as microbial abundance and activity do not recover quickly towards their maximal potential, this will be an indication of the so-called “undesired resilience” (Troell et al. 2005): the long-term intensive management produced a new quasi-stable state that is not so easily changed. This information along with the findings of this dissertation may have important implications for a sustainable management of arable soils.

Efforts to promote higher earthworm densities in arable fields may be a key to more resilient soil decomposer communities in arable soils, as earthworms are suggested to have a beneficial effect for the soil fauna in general; larger earthworm populations were documented to be able to buffer the negative impact of drought on the soil decomposer community. This was observed in an experimental setting, where soil fauna exposed to drought comprised highest belowground species richness with highest earthworm abundances; where especially micro-arthropod communities were maintained also under dry conditions (Siebert et al. 2019). It has been suggested that earthworm community recovery benefits from increased soil organic matter content and from soil management practices that return a high proportion of crop residues to soils (Bot and Benites 2005; Johnston et al. 2015). Cereal-legume intercrops support higher earthworm abundances as well (Schmidt, Clements, and Donaldson 2003). There is evidence that a continuous and varied plant cover could improve living conditions for earthworms (Singh et al. 2019). To assess the success of such conservation measures that farmers or other stakeholders may implement, we suggest field margins as a local reference for determining the state of soil communities. Its applicability was already tested in a citizen science study in Great Britain (Stroud 2019).

The twenty-first century will bring many challenges and among these, tackling global environmental change is unquestionably one of the greatest concerns. Since decomposition is next to photosynthesis a key process that ensures life on this planet, a careful management of soils will always be at the heart of a sustainable use of the Earth's natural resources. In this context my dissertation contributed to a better understanding of decomposers in intensively managed soils, by providing evidence that the resilience of earthworm communities in intensive fields of Germany is currently impaired. However, the microbial communities of arable soils exhibit a more resilient behaviour. Thus, this dissertation calls for a nuanced perspective on soil decomposer communities that considers the different responses of organism groups to global change drivers.

4.6. Literature

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Supplementary Material

Supplement 1:
Drought magnitude and soil moisture

Content:

1.1. Drought Magnitude for each farm

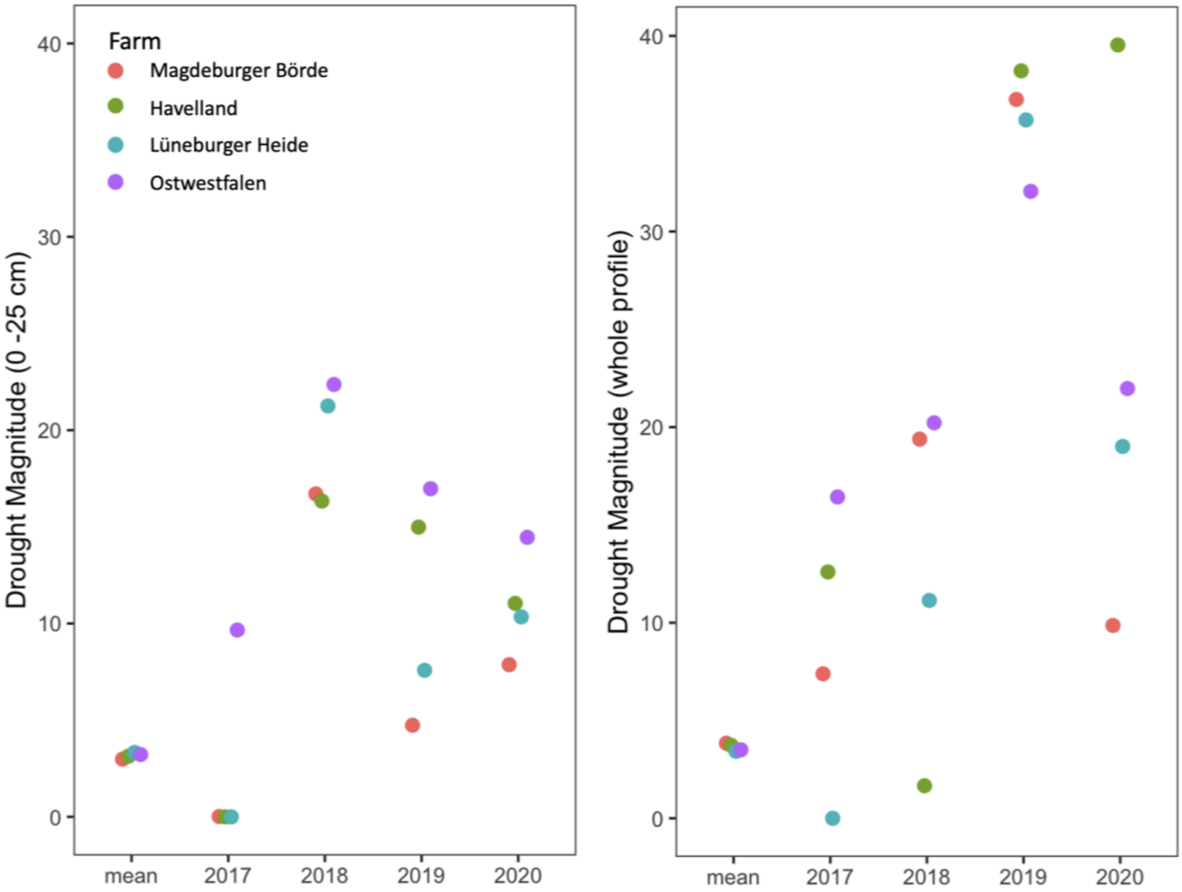

Figure S1: Soil drought magnitude for the upper soil layer (0 - 25 cm) and whole soil profile (on average 80 cm) for each farm between 2017 and 2020.

1.2. Soil moisture and drought magnitude in margin and field

Table S1: Mean and standard error of topsoil (0-10 cm deep) moisture (vol. %) for field and margin samples in the four study years (averaged over all sites).

	Field	**Margin**
	Mean (±SE)	Mean (±SE)
	19.1 ± 0.6	**21.3 ± 0.6**
2017	22.6 ± 1.13	27.5 ± 1.07
2018	12.9 ± 0.50	13.4 ± 0.67
2019	19.7 ± 1.18	21.9 ± 1.12
2020	21.0 ± 1.12	22.4 ± 1.39

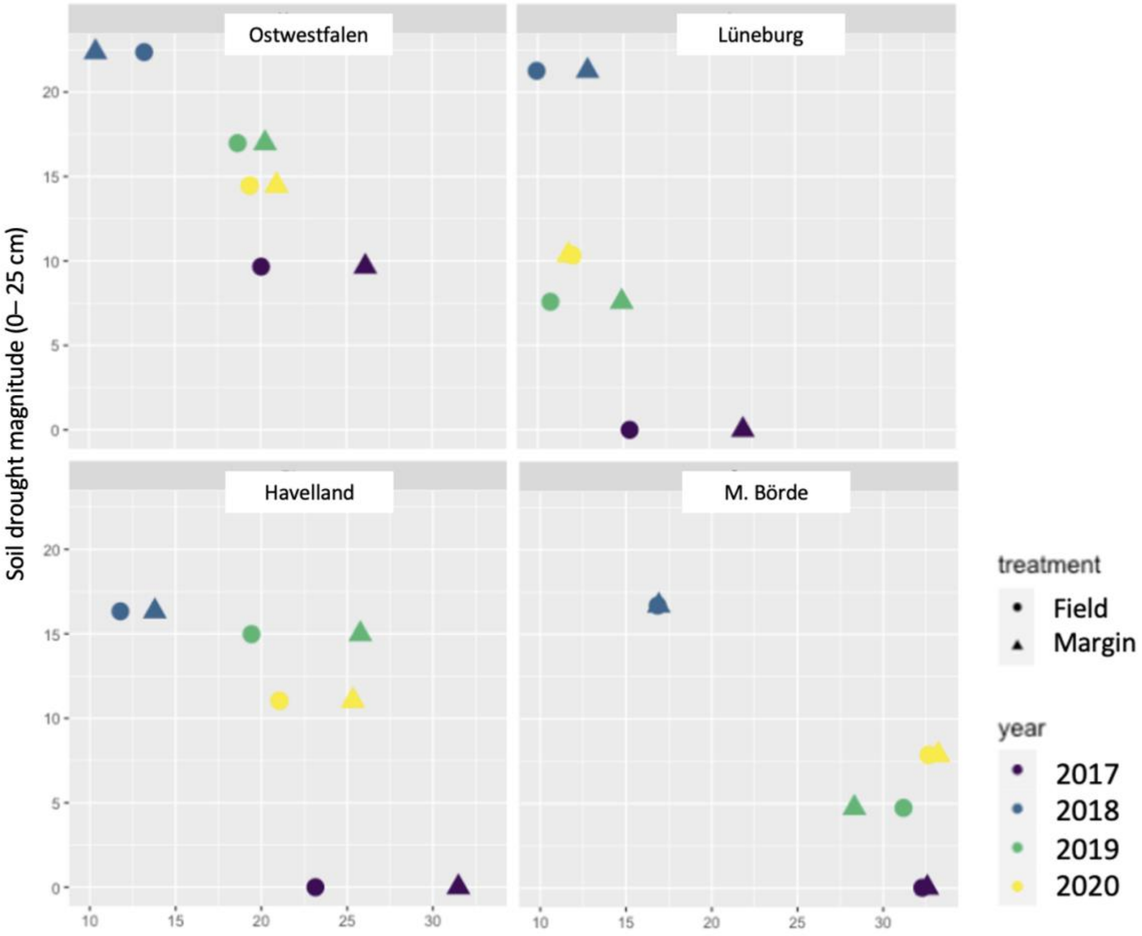

Figure S2: Soil drought magnitude of the upper soil layer (0 - 25 cm) for each year, differentiated in field (circle) and margin (triangle).

Supplement 2: Combined effect of intensive agriculture and drought

Table S2: Mean and standard error of earthworm biomass (g m^{-2}) along with ANOVA-type statistics (ATS) rank means for field and margin samples in the four study years (averaged over all sites). The significance level of differences between field and margin for each year was determined with a one-sided pairwise Wilcoxon test with Benjamini-Hochberg multiple testing correction.

	Field		**Margin**		**Significance of difference**
	Mean (±SE)	Rank mean	Mean (±SE)	Rank mean	p
	7.8 ± 0.7	**165**	**37.3 ± 2.6**	**298**	**<0.001**
2017	13.0 ± 1.9	219	43.3 ± 5.2	334	<0.001
2018	2.9 ± 0.5	117	17.2 ± 3.4	219	<0.001
2019	9.0 ± 2.4	168	47.0 ± 5.8	326	<0.001
2020	6.3 ± 1.2	156	41.5 ± 4.8	314	<0.001

Table S3: Mean and standard error of earthworm abundance (ind. m^{-2}) along with ANOVA-type statistics rank means for field and margin samples in the four study years (averaged over all sites). The significance level of differences between field and margin for each year was determined with a one-sided pairwise Wilcoxon test with Benjamini-Hochberg multiple testing correction.

	Field		**Margin**		**Significance of difference**
	Mean (±SE)	Rank mean	Mean (±SE)	Rank mean	p
	22.9 ± 2.6	**166**	**79.9 ± 5.1**	**297**	**<0.001**
2017	26.0 ± 3.2	208	89.0 ± 8.1	340	<0.001
2018	11.6 ± 2.8	125	35.8 ± 7.6	207	<0.001
2019	25.3 ± 6.5	159	105.8 ± 13.0	327	<0.001
2020	28.8 ± 7.0	169	89.6 ± 9.3	318	<0.001

Table S4: Mean and standard error of earthworm species richness (species no. per sample) along with ANOVA-type statistics rank means for field and margin samples in the four study years (averaged over all sites). The significance level of differences between field and margin for each year was determined with a one-sided pairwise Wilcoxon test with Benjamini-Hochberg multiple testing correction.

	Field		Margin		Significance of difference
	Mean (±SE)	Rank mean	Mean (±SE)	Rank mean	p
	0.72 ± 0.06	**167**	**2.29 ± 0.11**	**296**	**<0.001**
2017	1.28 ± 0.14	227	3.44 ± 0.21	371	<0.001
2018	0.38 ± 0.07	132	1.13 ± 0.15	209	<0.001
2019	0.71 ± 0.12	166	2.48 ± 0.19	319	<0.001
2020	0.52 ± 0.10	145	2.11 ± 0.21	285	<0.001

Table S5: Mean and standard error of soil microbial biomass-C (mg C_{mic} g^{-1} soil dry weight) and of soil microbial basal respiration (µg O_2 g^{-1} soil dry weight h^{-1}) for field and margin samples in the four study years (averaged over all sites). Significance level of differences in field and margin for each year was determined with Tukey's HSD post-hoc test for pairwise comparisons with Bonferroni adjustment of p-values for multiple testing.

		Field	Margin	Significance of difference
		Mean (±SE)	Mean (±SE)	*p*
C_{mic}				
	Per treatment	**0.44 ± 0.02**	**0.69 ± 0.02**	**<0.001**
	Per year 2017	0.44 ± 0.03	0.82 ± 0.04	<0.001
	2018	0.43 ± 0.03	0.58 ± 0.05	0.219
	2019	0.39 ± 0.03	0.65 ± 0.04	<0.001
	2020	0.50 ± 0.04	0.73 ± 0.04	<0.001
Basal respiration				
	Per treatment	**1.60 ± 0.06**	**2.70 ± 0.08**	**<0.001**
	Per year 2017	1.46 ± 0.10	3.21 ± 0.25	<0.001
	2018	1.48 ± 0.08	2.00 ± 0.15	0.114
	2019	1.43 ± 0.12	2.37 ± 0.13	<0.001
	2020	2.01 ± 0.15	3.29 ± 0.15	<0.001

Supplement 3:
Detailed description of sampled permanent margins and arable fields

Content:

3.1. Methodological approach

Selection of permanent margins and cropped fields

Prior to field work, interviews were conducted with all farmers and asked about their management and recent changes regarding cropped fields and permanent margins adjacent to the fields (transcript see supplement 2.3 a, 2.3. b). On each farm, soil type and topographical conditions of the included fields were as similar as was possible by the natural conditions. The chosen permanent field margins were chosen according to their similarity to the respective field.

Changes in transect position

In five cases, changes in management between years meant that transects needed to be substituted (see appendix 1.2). In this case, new transect positions with as similar conditions as possible to the old ones were selected.

Between 2017 and 2018 we changed the transect sampling positions in most of the arable fields from the field interior (c. 20 m from the crop edge) to the field edge (c. 2 m from the crop edge). This was to reduce disturbance caused in the cropped area due to sampling. We assume no significant changes in the results due to this small shift in position.

3.2. Sampled transects

Table S6: Soil and topographical parameters of each sampled transect (information from Bodenübersichtskarten (BÜK50).

Farm	Field ID	Original transect	Soil type	Soil texture	Topography	Adapted transect	Soil type	Soil texture	Topography
Westfalen	104	Ha104AM4	Cambisol	Loamy sand	Flat	Ha9AR1	Cambisol	Loamy sand	Flat
Westfalen	74	Ha74AM4	Stagnosol	Loamy sand	Flat	Ha94AR1	Podzolic gley	Sand	Flat
Westfalen	102	Ha102AM4	Podzolic gleysol, gleysol	Sand	Flat	Ha99AR1	stgnosolic podzol	Sand	Flat
Westfalen	7	Ha7AM4	Cambisol	Silty loam	Slope	Ha5AR7	Stagnosol	Clayic silt	Depression
Havelland	28	Ri28AM6	Humus gleysol - mollic gleysol	Loamy sand	Flat	Ri28AR6	Humus gleysol	Loamy sand	Flat
Havelland	37	Ri37AM1	Humus gley - mollic gleysol	Loamy sand	Flat	Ri25AR3	Humus gleysol	Loamy sand	Flat
Havelland	23	Ri23AM1	Humus gley - mollic gleysol	Loamy sand	Depression	Ri24AR3	Humus gleysol	Loamy sand	Depression
Magdeburger Börde	350	Os350AM3	Gleyic chernozem	Carbonatic fluvic silt	Flat	Os350AR5	Gleyic chernozem	Carbonatic fluvic silt	Flat
Magdeburger Börde	324	Os324AM6	Chernozem	Silt (loess)	Depression	Os322AR3	Gleyic chernozem	Carbonatic fluvic silt	Depression
Magdeburger Börde	350	Os350AM3	Gleyic chernozem	Carbonatic fluvic silt	Flat	Os291AR4	Gleyic chernozem	Carbonatic silt	Flat
Magdeburger Börde	450	Os450AM5	Gleyic chernozem	Carbonatic silt	Flat	Os510AR1	Chernozem	Silt (loess)	Flat
Lüneburger Heide	30	Lu30AM3	Podzolic cambisol	Sand	Flat	Lu9AM4	Podzolic cambisol	Loamy sand	Flat
Lüneburger Heide	3	Lu3AM3	Podzolic cambisol	Sand	Flat	Lu27AM5	Podzolic cambisol	Loamy sand	Flat
Lüneburger Heide	47	Lu47AM2	Podzolic cambisol	Sand	Flat				Flat
Lüneburger Heide	9	Lu30AM3	Podzolic cambisol	Loamy sand	Flat	2019 and 2020:	Podzolic cambisol	Loamy sand	Flat
Lüneburger Heide	7	Lu47AM2	Podzolic cambisol	Sand	Flat	Lu5AR3	Podzolic cambisol	Loamy sand	Flat

Table S6 continued

Farm	**Field ID**	**Original transect**	**Soil type**	**Soil texture**	**Neighboring non-crop habitat type**	**Topography**	**Margin width [cm]**	**Adapted transect**	**Soil type**	**Soil texture**	**neighboring non-crop habitat type**	**Topography**	**Margin width [cm]**
Ostwestfalen	7	Ha7R1	Cambisol	Siltic loam	Ditch	Depression	500	Ha5R2	Luvisol	Clayic silt	Ditch	Depression	>800
Ostwestfalen	104	Ha104R3	Cambisol	Loamy sand	Road	Flat	200						
Ostwestfalen	74	Ha74R1	Cambisol	Loamy sand	Trees	Flat	>800						
Ostwestfalen	102	Ha102R2	Gleyic Podzol, Gleysol	Sand	Pasture	Flat	250						
Havelland	28	Ri28R4	Humus Gleysol	Loamy sand	Pasture	Flat	>800	Ri28R2	Gleysol	Loamy sand	Ditch	flat	300
Havelland	37	Ri37R1	Humus Gleysol	Loamy sand	Trees	Flat	500						
Havelland	35	Ri35R1	Humus Gleysol	Loamy sand	Ditch	Flat	500						
Havelland	23	Ri23R1	Humus Gleysol	Loamy sand	Ditch	Depression	300						
Magdeburger Börde	350	Os350R3	Gleyic Chernozem	Carbonatic fluvic silt	Pasture	Flat	>800						
Magdeburger Börde	324	Os324R2	Gleyic Chernozem	Carbonatic fluvic silt	Ditch	Depression	200						
Magdeburger Börde	350	Os350R3	Gleyic Chernozem	Carbonatic fluvic silt	Pasture	Flat	>800	Os350R4	Gleyic Chernozem	Carbonatic fluvic silt	Trees	Flat	>800
Magdeburger Börde	450	Os450R2	Gleyic Chernozem	carbonatic silt	Road	Flat	250						
Lüneburger Heide	30	Lu30R1	Podzolic Cambisol	Sand	Trees	Flat	300						
Lüneburger Heide	3	Lu3R1	Podzolic Cambisol	Sand	Pasture	Flat	150						
Lüneburger Heide	47	Lu47R2	Podzolic Cambisol	Sand	Road	Flat	100	Lu9R9	Cambisol	Sand	Pasture	Flat	300
Lüneburger Heide	47	Lu47R2	Podzolic Cambisol	Sand	Road	Flat	100	Lu7R3	Cambisol	Sand	Trees	Flat	100

3.3. Coordinates of sampled fields and margins

Table S7: Coordinates of each transect for chapter 2.

			Coordinates	
Farm	**Field numer**	**Field**	**x**	**y**
Ostwestfalen	7	Ha7AM4	8.30623789	52.09421740
	104	Ha104AM4	8.26477000	52.10121990
	74	Ha74AM4	8.25332221	52.05396450
	102	Ha102AM4	8.31186520	52.05813140
Havelland	28	Ri28AM6	12.74411380	52.63947800
	37	Ri37AM1	12.75933250	52.63510400
	23	Ri23AM1	12.74399150	52.63047970
Magdeburger Börde	350	Os350AM3	11.37386060	51.99021460
	324	Os324AM6	11.39032700	51.98998250
	450	Os450AM5	11.30689600	52.02982720
Lüneburger Heide	30	Lu30AM3	10.37788560	53.19976640
	3	Lu3AM3	10.37391100	53.20216300
	47	Lu47AM2	10.38684550	53.19823340
Ostwestfalen	7	Ha7R1	8.30703712	52.09400060
	104	Ha104R2	8.26352800	52.10075600
	74	Ha74R1	8.25581900	52.05450000
	102	Ha102R2	8.31136500	52.05782200
Havelland	28	Ri28R4	12.74471910	52.63907250
	37	Ri37R2	12.75992110	52.63564150
	23	Ri23R1	12.74477805	52.63063781
Magdeburger Börde	350	Os350R3	11.37433000	51.99075900
	324	Os324R2	11.39028080	51.99023844
	450	Os450R2	11.30569270	52.02945020
Lüneburger Heide	30	Lu30R1	10.37795549	53.19957073
	3	Lu3R1	10.37354743	53.20260240
	47	Lu47R2	10.38764690	53.19969660

Table S8: Coordinates of each sampled transect for chapter 3.

2017				
			Coordinates	
Farm	**Field number**	**Field**	**x**	**y**
Ostwestfalen	104	Ha104AM4	8.26477000	52.10121990
	74	Ha74AM4	8.25332221	52.05396450
	102 / 99	Ha102AM4	8.31186520	52.05813140
	5	Ha7AM4	8.30623789	52.09421740
Havelland	28	Ri28AM6	12.74411380	52.63947800
	37	Ri37AM1	12.75933250	52.63510400
	23	Ri23AM1	12.74399150	52.63047970
Magdeburger Börde	350	Os350AM3	11.37386060	51.99021460
	324	Os324AM6	11.39032700	51.98998250
	350	Os350AM3	11.37386060	51.99021460
	450	Os450AM5	11.30689600	52.02982720
Lüneburger Heide	30	Lu30AM3	10.37788560	53.19976640
	3	Lu3AM3	10.37391100	53.20216300
	9	Lu30AM3	10.37788560	53.19976640
	7	Lu47AM2	10.38684550	53.19823340
Ostwestfalen	104	Ha104R3	8.26352800	52.10075600
	74	Ha74R1	8.25581900	52.05450000
	102 / 99	Ha102R2	8.31180200	52.05744400
	5	Ha7R1	8.30703712	52.09400060
Havelland	28	Ri28R4	12.74411380	52.63947800
	37	Ri37R1	12.75933250	52.63510400
	23	Ri23R1	12.74440956	52.63072920
Magdeburger Börde	350	Os350 R3	11.37433000	51.99075900
	324	Os324R2	11.39028080	51.99023844
	350	Os350 R3	11.37433000	51.99075900
	450	Os450R2	11.30569270	52.02945020
Lüneburger Heide	30	Lu30R1	10.37795549	53.19957073
	3	Lu3R1	10.37354743	53.20260240
	9	Lu47R2	10.38684550	53.19823340
	7	Lu47R2	10.38684550	53.19823340

Table S8 continued

2018				
			Coordinates	
Farm	**Field number**	**Field**	**x**	**y**
Ostwestfalen	104	Ha9AR1	8.28277490	52.09239187
	74	Ha94AR1	8.25557532	52.05137143
	102 / 99	Ha99AR1	8.30786643	52.05664786
	5	Ha5AR7	8.30271455	52.10898257
Havelland	28	Ri28AR6	12.74628952	52.64004598
	37	Ri25AR3	12.74516505	52.63635612
	23	Ri24AR3	12.74463640	52.63342762
Magdeburger Börde	350	Os350AR5	11.36723671	51.98618459
	324	Os322AR3	11.39010975	51.99036152
	350	Os291AR4	11.38614932	52.00484075
	450	Os510AR1	11.29817581	52.02971392
Lüneburger Heide	30	Lu9AM4	10.37292867	53.20259796
	3	Lu27AM5	10.37428504	53.20346473
	9	Lu9AR5	10.37338180	53.20203100
	7	Lu5AR3	10.37007235	53.19921921
		Margin		
Ostwestfalen	104	Ha104R3	8.26352800	52.10075600
	74	Ha74R1	8.25581900	52.05450000
	102 / 99	Ha102R2	8.31180200	52.05744400
	5	Ha5R2	8.30301284	52.10983612
Havelland	28	Ri28R4	12.74471910	52.63907250
	37	Ri37R1	12.75992110	52.63564150
	23	Ri23R1	12.74477805	52.63063781
Magdeburger Börde	350	Os350 R3	11.37433000	51.99075900
	324	Os324R2	11.39028080	51.99023844
	350	Os350R4	11.36714506	51.98610303
	450	Os450R2	11.30569270	52.02945020
Lüneburger Heide	30	Lu30R1	10.37795549	53.19957073
	3	Lu3R1	10.37354743	53.20260240
	9	Lu9R9	10.36759842	53.20528620
	7	Lu7R7	10.36615257	53.20383386

Table S8 continued

2019				
			Coordinates	
Farm	**Field number**	**Field**	**x**	**y**
Ostwestfalen	104	Ha9AR1	8.28277490	52.09239187
	74	Ha94AR1	8.25557532	52.05137143
	102 / 99	Ha99AR1	8.30786643	52.05664786
	5	Ha5AR7	8.30271455	52.10898257
Havelland	28	Ri28AR6	12.74628952	52.64004598
	37	Ri25AR3	12.74516505	52.63635612
	23	Ri24AR3	12.74463640	52.63342762
Magdeburger Börde	350	Os350AR5	11.36723671	51.98618459
	324	Os322AR3	11.39010975	51.99036152
	350	Os291AR4	11.38614932	52.00484075
	450	Os510AR1	11.29817581	52.02971392
Lüneburger Heide	30	Lu9AM4	10.37292867	53.20259796
	3	Lu27AM5	10.37428504	53.20346473
	9	Lu110AR3	10.36881540	53.20131320
	7	Lu5AR3	10.37007235	53.19921921
		Margin		
Ostwestfalen	104	Ha104R3	8.26352800	52.10075600
	74	Ha74R1	8.25581900	52.05450000
	102 / 99	Ha102R2	8.31180200	52.05744400
	5	Ha5R2	8.30301284	52.10983612
Havelland	28	Ri28R2	12.74038369	52.64114740
	37	Ri37R2	12.75989581	52.63554953
	23	Ri23R1	12.74477805	52.63063781
Magdeburger Börde	350	Os350 R3	11.37433000	51.99075900
	324	Os324R2	11.39028080	51.99023844
	350	Os350R4	11.36714506	51.98610303
	450	Os450R2	11.30569270	52.02945020
Lüneburger Heide	30	Lu30R1	10.37795549	53.19957073
	3	Lu3R1	10.37354743	53.20260240
	9	Lu9R9	10.36759842	53.20528620
	7	Lu7R7	10.36615257	53.20383386

Table S8 continued

2020				
			Coordinates	
Farm	**Field number**	**Field**	**x**	**y**
Ostwestfalen	104	Ha9AR1	8.28277490	52.09239187
	74	Ha94AR1	8.25557532	52.05137143
	102 / 99	Ha99AR1	8.30786643	52.05664786
	5	Ha5AR7	8.30271455	52.10898257
Havelland	28	Ri28AR6	12.74628952	52.64004598
	37	Ri25AR3	12.74516505	52.63635612
	23	Ri24AR3	12.74463640	52.63342762
Magdeburger Börde	350	Os350AR5	11.36723671	51.98618459
	324	Os322AR3	11.39010975	51.99036152
	350	Os291AR4	11.38614932	52.00484075
	450	Os510AR1	11.29817581	52.02971392
Lüneburger Heide	30	Lu9AM4	10.37292867	53.20259796
	3	Lu27AM5	10.37428504	53.20346473
	9	Lu110AR3	10.36881540	53.20131320
	7	Lu5AR3	10.37007235	53.19921921
		Margin		
Ostwestfalen	104	Ha104R3	8.26352800	52.10075600
	74	Ha74R1	8.25581900	52.05450000
	102 / 99	Ha102R2	8.31180200	52.05744400
	5	Ha5R2	8.30301284	52.10983612
Havelland	28	Ri28R2	12.74038369	52.64114740
	37	Ri37R2	12.75989581	52.63554953
	23	Ri23R1	12.74477805	52.63063781
Magdeburger Börde	350	Os350 R3	11.37433000	51.99075900
	324	Os324R2	11.39028080	51.99023844
	350	Os350R4	11.36714506	51.98610303
	450	Os450R2	11.30569270	52.02945020
Lüneburger Heide	30	Lu30R1	10.37795549	53.19957073
	3	Lu3R1	10.37354743	53.20260240
	9	Lu9R9	10.36759842	53.20528620
	7	Lu7R7	10.36615257	53.20383386

3.4. Transcript of interviews regarding management of fields and margins

Table S9: Transcript of the farmer's interviews regarding the management of the cropped fields.

	Soil cultivation			**crop rotation**	
Farm	**Are you applying soil-turning ploughing? If so, how deep does your plough go? Only for a certain crop or always?**	**Are you applying soil cultivaton techniques that do not turn the soil? If so, how often and how deep?**	**Was there a change in soil cultivation techniques during the last 15 years? What changed?**	**What is your typical crop rotation?**	**Was there a change of crop rotation in the past 15 years?**
Westfalen	yearly ploughing in preparation of each main crop. 30 cm deep.	on the Greening areas we only work with the chisel plough.	no	maize, wheat, maize, barley, potatoes	yes, increase of maize in the crop roatation
Magdeburger Börde	no tillage	yearly with the chisel plough, 20-25 cm deep	Since 2001 no tillage any more	rape seed, winter wheat, winter barley, summer barley	no change in crop rotation
Havelland	every fifth year before rape seed, 38 cm deep	every year 0-15 cm deep with a chisel plough	since 2007 reduced soil cultivation	maize, cereal with undersown grass, maize, cereal, winter rape seed, intercrop	since 2010 more maize for bio gas energy
Lüneburger Heide	every second year, 28 cm deep	twice a year, 15-28 cm deep. After wheat two times, with disc harrow (5-8 cm)	Trend towards ploughing less	potatoe, summer barley, sugar beet, winter cereal	we cultivate more sugar beet

Table S9 continued

	fertilizing			**irrigation**		
Farm	**Do you apply mineral fertilizer?**	**Do you apply organic fertilizer? If so, what exactly?**	**Was there a change in the way you applied fertilizer within the last 15 years?**	**Do some fields receive irrigation?**	**Do you always irrigate or only specific crops?**	**Since how many years to you irrigate?**
Westfalen	yes, additionally	cattle slurry, fermentation residues from biogas production NAWARO	increas in fermentation residues	no	no	stopped 15 years ago
Magdeburger Börde	yes	fermentation residues of different origin	reduction of fermentation residues within the framework of the fertilizer regulations	yes	Only on fields with potatoes.	Since 1998
Havelland	yes	solid and liquid fermentation residues	since 2011 fertilizung with fermentation residues	no	never	-
Lüneburger Heide	yes	no	since 2 years we started with fertilizung following the Kinsey propositions, we increased chalking	yes	always	since 40 years

Table S10: Transcript of the farmer's interviews regarding the management of the permanent field margins.

Field margin ID	farmer's own field ID	Establishement of field margins		management of field margins	
		In the last 15 years, were field margins newly esablished, altered or changed?	if so, when, how often?	How often are field margins mowed?	In what months?
Ha7R1	**Hamlingdorf Unten**	yes	in 2017 newly established	once a year	no reply
Ha104R3	**Berghausen**	no	-	once a year	no reply
Ha74R1	**Boeggemeier Casum gross**	no	-	once a year	no reply
Ha102R2	**Helmut Guenther**	no	-	once a year	no reply
Ha5R2	**Nato FFW rechts**	no	-	once a year	no reply
Ri28R4	**Hinter den Elsen**	no	-	once a year	August/September
Ri37R1	**Das Unterluch**	no	-	once a year	August/September
Ri23R1	**Unter der Kleinbahn**	no	-	once a year	August/September
Os350R3		yes	since 2015 newly established with grass/clover mix as part of EU Greening	twice a year	01.07 and 31.10.
Os324R2	**Drostenberg**	yes	since 2015 newly established with grass/clover mix as part of EU Greening	twice a year	01.07 and 31.10.
Os350R4		yes	since 2015 newly established with grass/clover mix as part of EU Greening	twice a year	01.07 and 31.10.
Os450R2		yes	Until 2017 each year worked with chisel plough for grass and weed control, not in 2017.	twice a year	01.07 and 31.10.
Lu30R1	**Neuland 4**	no	-	never	-
Lu3R1	**Neuland 1-3**	no	-	once a year	August
Lu47R2	**Dierssen 1**	no	-	every second year	August

Table S10 continued

Field margin ID	farmer's field ID	management oif field margins	Comment by the farmer
		The cut biomass is left on the field margins?	
Ha7R1	**Hamlingdorf Unten**	mulching, biomass stays on the field margin	
Ha104R3	**Berghausen**	mulching, biomass stays on the field margin	
Ha74R1	**Boeggemeier Casum gross**	mulching, biomass stays on the field margin	
Ha102R2	**Helmut Guenther**	mulching, biomass stays on the field margin	
Ha5R2	**Nato FFW rechts**	mulching, biomass stays on the field margin	
Ri28R4	**Hinter den Elsen**	biomass stays on the field margin	sometimes used to drive with the car on it
Ri37R1	**Das Unterluch**	biomass stays on the field margin	
Ri23R1	**Unter der Kleinbahn**	biomass stays on the field margin	
Os350R3		until 2016, biomass left on field margin, since 2016 taken away	Because of lasting dryness in the past years the biomass is taken down and given to livestock holdings.
Os324R2	**Drostenberg**	biomass stays on the field margin	
Os350R4		until 2016, biomass left on field margin, since 2016 taken away	
Os450R2		until 2016, biomass left on field margin, since 2016 taken away	
Lu30R1	**Neuland 4**	-	
Lu3R1	**Neuland 1-3**	biomass stays on the field margin	
Lu47R2	**Dierssen 1**	biomass stays on the field margin	
Lu9R9	**Brandwiese**	biomass stays on the field margin	
Lu7R7	**Hühnerglück 7**	biomass stays on the field margin	