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Influence of light availability and ungulate browsing on earthworms in temperate forests.

A manipulative experimental study in the University Forest Würzburg.

Von Johanna Maria Hieber
Johanna.Hieber@student.uibk.ac.at
12234439
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Betreut von
Clemens Geitner,
Christian Ristok &
Ludwig Lettenmaier

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Abstract

Earthworms are of high importance in European forest ecosystems. They are considered to be ecosystem engineers because they impact the structure and characteristics of soils, affect the soil food web and with this both organisms below- and above-ground as well as vegetation. Forests as a climate mitigation entity are at the same time under high risks due to climate and global change. Disturbance factors such as tree mortality leading to canopy gaps as well as the overabundant roe deer impacting vegetational compositions are common. Below-ground mechanisms are very complex and still largely ambiguous and there is only little knowledge of influencing factors to earthworm communities. Most existing studies investigated impacts on invasive earthworm compositions in the United States.

The aim of this research is to determine whether canopy gaps and deer browsing have an impact on the native German earthworm populations. An experimental study was conducted to gain new insights into this question.

The 75 plots are located at the University Forest of the Julius-Maximilians-University of Würzburg near Sailershausen and are part of the BETA-FOR project of the DFG and MainPro. The experimental design consists of two treatments. Exclosure subplots were set up with a fence, control subplots without a fence. 21 plots were subjected to an aggregated tree removal resulting in sunny sites due to canopy openness, whereas 54 plots with a distributed treatment showed shady sites.

Earthworms were sampled with mustard-solution expulsion and hand sorted on 25 x 25 x 10 cm excavations and further weighed, identified to species level and assigned to their functional groups. In addition, I assessed soil pH-values and water stable soil aggregates (WSA).

Results of the experiment showed that earthworm abundance and biomass were affected by canopy gaps and deer exclosure. Regarding my hypotheses, I expected both canopy gaps and deer exclosure to result in lower total earthworm abundance and biomass. However, my hypothesis could only partially be accepted as I found a significant positive effect of canopy, soil pH-value and the interaction of canopy and fence but none for fence on the total earthworm abundance. Hence, total abundance increased with sunny sites resulting from canopy gaps and with higher soil pH-values. Total earthworm biomass was also significantly affected by canopy and soil pH-value. It was marginally affected by fence and the interaction of canopy and fence, i.e., biomass was increased by canopy gaps as wells as by higher soil pH-values and slightly by deer exclosures. However, it seems that roe deer only decrease the abundance of earthworms if regarded independent of light availability. Given the interaction of both treatments, deer browsing had opposite results as it increased earthworm abundance and biomass in sunny forests compared to shady forests. Thus, highest abundance and biomass were found in sunny plots with deer present.

My hypothesis of an increased water stable soil aggregate amount with higher earthworm abundance or biomass could not be proved as no significant differences were identified. Possible mechanisms causing these outcomes are discussed with potential future forest management consequences.

KEYWORDS

Earthworms – ecosystem engineer – ungulates – roe deer – temperate forest – canopy gaps – linked disturbance – above-ground below-ground interactions – ecosystem services – climate change – forest management

Zusammenfassung

Regenwürmer sind in den europäischen Waldökosystemen von großer Bedeutung. Sie gelten als Ökosystemingenieure, da sie die Struktur und die Eigenschaften des Bodens verändern, sich auf das Nahrungsnetz des Bodens auswirken und damit sowohl die unter- und oberirdischen Organismen als auch die Vegetation beeinflussen können. Wälder sind Teil der Klimaanpassung, gleichzeitig aber hohen Risiken durch den Klimawandel und globalen Wandel ausgesetzt. Störfaktoren wie das Absterben von Bäumen, das zu Lücken im Kronendach führt, sowie das übermäßig häufig vorkommende Rehwild, das die Vegetationszusammensetzung beeinträchtigt, sind weit verbreitet. Die unterirdischen Mechanismen sind sehr komplex und noch weitgehend unklar, wobei nur wenige Erkenntnisse über die Einflussfaktoren auf Regenwurmgemeinschaften existieren. Die meisten bisherigen Studien haben lediglich die Auswirkungen auf die Zusammensetzung invasiver Regenwürmer in den Vereinigten Staaten untersucht.

Ziel meiner Forschung war es daher, ein besseres Verständnis der Reaktion einheimischer deutscher Regenwürmer auf die zwei Störungen in Wäldern der gemäßigten Zonen zu erlangen, nämlich Rehverbiss und Lücken im Baumkronendach.

Die 75 Versuchsflächen befinden sich im Universitätswald der Julius-Maximilians-Universität Würzburg bei Sailershausen und sind Teil des BETA-FOR-Projekts der DFG und Main-Pro. Das Versuchsdesign besteht aus zwei Eingriffen. Je Plot gab es einen umzäunten Subplot, sowie einen Subplot ohne Zaun. 21 Plots wurden einer aggregierten Baumentfernung unterzogen, die aufgrund der offenen Baumkronen zu sonnigen Standorten führte, wohingegen 54 Plots mit einer verteilten Entfernung von Bäumen schattige Standorte aufwiesen.

Während der Feldarbeit wurden Regenwürmer von 25 x 25 x 10 cm großen Ausgrabungen mit Senflösung ausgetrieben und per Hand gesammelt, später gewogen, auf Artebene identifiziert und funktionellen Gruppen zugeordnet. Darüber hinaus wurde der pH-Wert des Bodens und die wasserstabilen Bodenaggregate (WSA) bestimmt.

Die Ergebnisse des Experiments zeigten, dass Regenwurmvorkommen und deren Biomasse durch Lücken im Kronendach und den Ausschluss von Rehen beeinflusst werden. Hinsichtlich meiner Hypothesen erwartete ich, dass sowohl die Baumkronenlücken als auch der Ausschluss von Rehen zu einer geringeren Gesamtregenwurmabundanz und -biomasse führen würden. Meine Hypothesen konnte jedoch nur teilweise bestätigt werden, da eine signifikant positive Auswirkung des Kronendachs, des Boden-pH-Werts und der Wechselwirkung zwischen Kronendach und Zaun, jedoch keine Auswirkung des Zauns auf die Gesamtmenge der Regenwürmer festgestellt werden konnte. Die Gesamtabundanz nahm also bei sonnigen Standorten, die aus Kronenlücken resultierten, und bei höheren pH-Werten des Bodens zu. Die Gesamtbiomasse der Regenwürmer wurde ebenfalls signifikant vom Baumkronendach und dem pH-Wert des Bodens beeinflusst. Sie wurde marginal durch den Zaun und durch die Wechselwirkung von Kronendach und Zaun beeinflusst, d.h. die Biomasse wurde durch Lücken im Kronendach sowie durch höhere Boden-pH-Werte und geringfügig durch Rehausschlüsse erhöht. Es scheint jedoch, dass Rehe die Abundanz von Regenwürmern nur dann verringern, wenn sie unabhängig von der Lichtverfügbarkeit betrachtet werden. Bei einer Wechselwirkung beider Eingriffe führte der Rehwildverbiss zu anderen Ergebnissen, da er die Abundanz und Biomasse von Regenwürmern in sonnigen Wäldern im Vergleich zu schattigen Wäldern erhöhte. Die höchste Abundanz und Biomasse wurden daher in sonnigen Plots mit Rehvorkommen gefunden.

Meine Hypothese einer erhöhten wasserstabilen Bodenaggregatmenge mit höherer Regenwurmabundanz sowie Biomasse konnte nicht bestätigt werden, da keine signifikanten Unterschiede festgestellt wurden.

Potentielle Mechanismen, die diese Ergebnisse verursachen, werden mit möglichen zukünftigen Folgen für die Waldbewirtschaftung diskutiert.

Schlüsselwörter

Regenwürmer – Ökosystemingenieur – Huftiere – Rehe – gemäßigte Wälder – Kronendachlücken – Verknüpfte Störungen – oberirdische und unterirdische Wechselwirkungen – Ökosystemdienstleistungen – Klimawandel – Waldbewirtschaftung

1.Introduction

1.1 Relevance of the study

Soils are of central importance for the entire terrestrial ecosystem and are an asset worth protecting since they show a rich biodiversity, consisting of microbes, microfauna, mesofauna and macrofauna (Anthony et al., 2023). Soils provide many different ecosystem services as outcomes of ecosystem functions which brings benefits to all other living organisms and is particularly important for human well-being (Brussaard, 2012; Haines-Young and Potschin, 2018; Wurst et al., 2012). Worldwide diversity losses are posing risks to the earth system as most of these ecosystem services are positively influenced by soil biodiversity, especially supplied by soil macrofauna (European Environment Agency, 2023; Wurst et al., 2012).

Among the group of macrofauna, classified as organisms with a body size larger than two mm or which are visible with the naked eye, earthworms play vital parts in the functioning of ecosystems and are considered ecosystem engineers (Blouin et al., 2013; Bottinelli et al., 2015; Wurst et al., 2012). These key species form habitats by physically changing abiotic or biotic resources and with it impact their availability to other organisms (Jones et al., 1994). Through earthworms' activities of burrowing, casting and mixing of organic and soil components, they affect soil composition, nutrient cycling, hydrology and above-ground plant communities (Edwards and Bohlen, 1996; Jones et al., 1994; Thompson et al., 1993). In addition, earthworms decompose litter through their mineralization of organic compounds, phosphor and nitrogen as well as through their changes to the environment which leads to stronger microbial activities (Heydari et al., 2014; Tsukamoto and Sabang, 2005).

Depending on their environment and behaviour, earthworms are categorized in three different ecological groups, namely anecic, endogenic, and epigeic due to their morphological adaptation to soil conditions (Bouché, 1977). Anecic earthworms are large-sized, reddish coloured and live up to two metres deep in vertical burrows where they find shelter and store or digest litter collected and pulled down from the soil surface. Endogeic species on the other hand are medium-sized, very light or rose-coloured, and live in subhorizontal, narrow burrows as geophagous organisms consuming mineral earth. Lastly, epigeic earthworms are small-sized and feed on plant litter remains. They live in the litter layer at the soil surface as well as in shallow burrows and are responsible for some mixing of organic and mineral strata. Hence, these different functional groups inhabit different niches and show different behaviours, especially on foraging, feeding and burrowing, which leads to different ecosystem services and influences to the environment (Bouché, 1977; De Wandeler et al., 2016; Eisenhauer, 2010).

The activities of earthworms and all other soil organisms are influenced by ecosystem structures which can be threatened naturally as well as by anthropogenic actions. Consequently, the detrimental impacts of global change on soil invertebrates such as high temperatures, droughts, heat waves and windblows are manifesting in manifold ecological and evolutionary processes below- and above-ground (Bardgett and Van Der Putten, 2014; Singh et al., 2019; Wirth et al., 2024).

Earthworm species are able to move actively and reach from ten to around 100 metres per year (Bardgett and Van Der Putten, 2014). Their mean abundance can count from ten to more than 1000 individuals per square metre (Edwards and Bohlen, 1996). Furthermore, earthworms have the biggest share of animal biomass in most terrestrial soils, especially in European forests (Lavelle and Spain, 2001). For this reason, they do have a great impact on forest ecosystems and any changes to their communities might as well affect the whole ecosystem functions of soil which depend a lot on the underground diversity of fauna (De Wandeler et al., 2016; Schröder, 2008). However, how forest management, forest wildlife, or climate change induced shifts in forest structure affect earthworms is scarcely known (Bardgett and Van Der Putten, 2014; Reed et al., 2023).

In 2024, Germany’s land area was covered by around 11.5 million hectares of forest which equals 32% forest area, having slightly increased within the last decade, and the state of Bavaria even shows 37% of forest area. Although Germany’s forests have a high diversity, there are still many flora and fauna species on the red list. Half of the forests are privately owned, and the most frequent tree species are pine, spruce, beech and oak. Starting from the 1980s, mixed forest stands have been gaining at the expense of coniferous monocultures due to forest conversion strategies. However, the high deer population since the last 50 years is counteracting (BMEL, 2024; Wirth et al., 2024). Further, calamities such as droughts have disturbed the forest structure and intensified forest composition dynamics, particularly leading to a decline of spruce. Climate change also impacts site-related factors such as water balance or vegetation period which shifts the original communities. Positively, young forests mainly develop from natural rejuvenation with near-natural tree species in half of the tree composition (BMEL, 2024).

Small-scale events such as the death of single trees or on the large-scale level droughts, windstorms and fires, mainly induced by severe climate catastrophes, but also insect infestations and diseases or logging can generate forest canopy gaps and deadwood. Canopy gaps, any empty spot resulting in sunny areas within the forest, are a main disturbance factor in most forests and are likely to increase in the future according to climate scenarios (Muscolo et al., 2014; Reed et al., 2023; Seidl et al., 2017). These gaps bring drastic changes not only to the microclimate of the ground floor environment as light availability, irradiance and with this temperature increase. The special microclimate created by forest canopies which has a buffering effect of temperature, partially gets lost with canopy gaps (De Frenne et al., 2019; Denslow, 1987; Thom et al., 2023). But also, soil moisture content of the soil surface gets higher due to

reduced plant transpiration. These environmental shifts increase the soil microbial activities which alter soil characteristics and lead to more nutrients being available (Denslow, 1987).
Almost half of the German forest area is extensively cultivated without tree removal. The rise of deadwood within the last ten years, now accounting for 29.4 cubic metre per hectare in Germany, stresses the climate vulnerability of forests but on the other hand also increases the forest's closeness to nature (BMEL, 2024). Promoting pest outbreaks, forest management has aimed to pull out deadwood since the 19th century. However, deadwood enhances structural diversity and fosters biodiversity through presenting heterogenous habitats. Many species, like fungi, beetles, birds and particularly saproxylic species are dependent on deadwood as a nutrient source or for breeding. Deadwood is altering the microclimate and fulfils important ecosystem functions. Its induced soil formation, nutrient and carbon cycling and storage as well as the prevention of soil erosion might also impact soil biota (BMEL, 2024; Graf et al., 2022; Müller et al., 2023).

Given the continuously growing numbers of the European roe deer (*Capreolus capreolus L.*) since the 20th century, they have reached overabundant occurrences with negative impacts on woody ecosystems and biodiversity in some areas of Europe (Carpio et al., 2021). Because of their behaviour, deer are impacting forests by browsing on twigs as well as on seeds, by stripping and peeling bark, fraying, uprooting, by helping germination through spreading seeds and by altering nutrient-cycling through trampling and scraping and through their droppings (Carpio et al., 2021; Ramirez et al., 2018; Reimoser, 2003). As deer have special preferences on their food, they are browsing selectively which results in a different tree species composition in subsequent successional years because of a modified competition between plants (Boulanger et al., 2009; Gill and Beardall, 2001; Reimoser, 2003). Therefore, higher deer densities can alter the understory plant communities, often cause lower tree species diversity and richness and are a disturbance not to be neglected (Gill and Beardall, 2001; Reed et al., 2023). Moreover, owing to their browsing, digested plants often have altered chemical structures, uneaten plants remain which will constitute in a different litter quality and finally soil microenvironments are changed (Augustine and McNaughton, 1998). Regarding the developments in forest ecosystems due to deer, it seems very likely that earthworms will be influenced by these changed habitat conditions.
Furthermore, the study of Tondoh et al. (2011) suggested that earthworm abundance can be connected to soil pH-value which decreases after forest disturbances (Heydari et al., 2014).

Due to continuous increasing impacts of environmental change, such influencing factors on earthworms should be taken into account to get a better understanding of their relationships, to predict the distribution of the different functional earthworm groups and to improve scenarios of affected ecosystem services (Schröder, 2008). The further aim is to work intradisciplinary and to revise land management practices into more sustainable approaches in order to keep soil fertile, to make forests future climate-resilient and to assure forest multifunctionality. This is especially important for biomass production but also for diminishing climate change impacts (Bardgett and Van Der Putten, 2014; Müller et al., 2023).

However, until now there is only few research investigating how individual disturbing events are connected and linked to earthworm populations (Reed et al., 2023). Reed et al.'s study from 2023 in northern Wisconsin, North America, could prove a connection between disturbance events in forests and the invasion of earthworms. Being motivated by this study I investigated the impacts of deer browsing and canopy gap creation in a local temperate forest in Germany on native European earthworms since North America is colonised by invasive earthworms only (Reed et al., 2023).

1.2 Hypothesis and overview of the thesis

The main purpose of this study is to get a better understanding of influences on earthworms in order to be able to develop guidelines for protecting their communities and for encouraging their activities. They have plenty of positive effects but run the risk of being destroyed (Lavelle, 1988). Especially the relationship between earthworm compositions and the two disruptive factors of the opening of tree canopies which results in more light exposure and the ungulate browsing which alters plant communities are investigated.

This leads to my tested hypotheses, the first of them being earthworms are negatively influenced by openness of tree canopies in forests resulting in a lower abundance, which was the outcome of the study of Reed et al. (2023) in North America. However, the effects might also be positive since sunny areas will result in a different vegetation composition, likely showing higher rejuvenation rates and supporting the ground with more litter and nutrients. The denser vegetation can prevent soil from too much light and from drying out.

My second hypothesis states that earthworms are positively influenced by deer presence, as well based on the results of Reed et al.'s study (2023). Deer dung might lead to nutrient enrichment of the soil which can attract earthworms and influence the vegetation communities positively as well, which in turn impacts earthworms through a different habitat. On the other hand, through herbivory attacks plants produce secondary metabolites as chemicals for defence and warning which influences the below-ground organisms and may therefore impact earthworms. Deer trampling might be a disturbance to earthworms (Bardgett and Van Der Putten, 2014).

Both hypotheses are thought to be connected to soil pH, stating that a higher soil pH-value meaning less acidic will lead to an increased earthworm abundance and biomass.

The third hypothesis postulates that higher earthworm abundance produces an increased amount of water stable soil aggregates thanks to earthworms' activities.

The study was conducted within the framework of the BETA-FOR experiment (Müller et al., 2023) and MainPro (University Würzburg, Geographie und Geologie). 75 experimental plots for my bachelor thesis are situated at the University Forest of Würzburg, near Sailershausen. For the research, earthworms were hand sorted on all subplots with the use of mustard solution for expulsion, later identified, categorized in their three ecological groups and weighed to determine their biomass. Furthermore, soil samples were taken of which soil pH-value and water stable soil aggregates were measured.

2. Research status

Amongst soil organisms, earthworms are very well studied with a lot of literature about their functions and traits existing. Since the last 20 years, the impacts of macrofauna on soil properties have been approved and published. Soil ecologists acknowledge the macrofauna as ecosystem engineers. Through their bioturbation they can regulate microbiological, chemical and physical soil characteristics as well as other living beings, and thus impact whole landscapes' architectures due to their abundant occurrence (Blouin et al., 2013; Jones et al., 1994; Wurst et al., 2012). Some scientists as well as policy makers lately recognize earthworms as bioindicators for soil quality and generally, more awareness is put on their importance amongst the public (Bardgett and Van Der Putten, 2014; Bottinelli et al., 2015). In contrast, many scientists still do not consider macrofauna in soil functioning models (Lavelle et al., 2022).

Despite terrestrial ecosystems' functioning with its above-ground biodiversity is co-influenced by earthworms on any places where they naturally occur, many mechanisms within ecosystem processes are still largely unknown. The focus has mainly been laid to aboveground biodiversity as the producing part, following in a lack of knowledge of the below-ground diversity as the decomposing counterpart. This should be solved with more and more new studies since the last decade to get a holistic understanding of these feedback systems (Bardgett and Van Der Putten, 2014; Bardgett and Wardle, 2003). However, existing studies have different outcomes and conclusions on different sites to date. So far, it is clear that soil organisms are distributed non-homogeneously. They show a temporal patchy and fragmentary composition due to their slow movement and adapt to available nutrients and to soil properties, depending a lot on prevailing tree species and their litter quality (Bardgett and Van Der Putten, 2014; Lavelle, 1988).

Because of global change with climate change as well as land use change there are shifts in habitats of earthworms (Wardle et al., 2004). Two thirds of all forest habitat types in Germany are at risk due to land development according to Faktencheck Artenvielfalt (Wirth et al., 2024). Given the importance of earthworms as a vital part of soil biodiversity, the globally declining species number is alerting (Bardgett and Van Der Putten, 2014). Soil biodiversity losses are likely on more than 40% of the soils within the EU (Orgiazzi et al., 2016), however until now, knowledge about impacts or adaption possibilities of soil organisms to new environments is confined (Wardle et al., 2001, 2004). Ecosystem management therefore has the goal to keep biodiversity high, while at the same time ensure the provision of ecosystem services for human well-being. For tackling this challenge and being able to show better reactions, a broad knowledge of all changes within an ecosystem is necessary, particularly the disturbance regimes (Thom and Seidl, 2016).

The land climate is subject to severe shifts due to the human-caused climate change through an increased atmospheric CO_2-level. Land temperatures were around 1.65 °C warmer between 2013 and 2022 than in the period of 1850 to 1900 and the "[m]ean surface air temperature over land […is] about 40% larger than global mean warming" (Calvin et al., 2023a, 47). Observed facts since the 1950s are an increased frequency and intensity of hot extremes, heatwaves, droughts as well as heavy rainfall events. These effects will likely be even stronger and more complex with higher degrees of temperature, which is problematic as global warming is modelled to reach 3.2 °C by 2100 based on present policies (Calvin et al., 2023a). This is with high likelihood accompanied by "changes in ecosystem structure", "species range shifts" and "changes in seasonal timing (phenology)" (Calvin et al., 2023a, 49).

Forests are a "climate-exposed sector" (Calvin et al., 2023b, 6) and might therefore face challenges and harms induced by climate change, already visible with land degradation. Alarming are the IPCC's (Intergovernmental Panel on Climate Change) outcomes stating an increased likelihood of tree mortality, wildfire damages, as well as carbon loss, irreversible biodiversity loss and species extinction in forest ecosystems with rising temperatures (Figure A 2). If any ecosystem service gets lost, there will be cascading and long-term detrimental effects to people worldwide (Calvin et al., 2023a).

The ecosystem services are "defined as the contributions that ecosystems make to human well-being", by the Common International Classification of Ecosystem Services, thus "they are the outputs of ecosystems" (Haines-Young and Potschin, 2018, iii&3). 29 of the total 83 ecosystem service classes are connected to soil and they can be structured in supporting, regulating, provisioning and cultural services according to the Millennium Ecosystem Assessment of 2005 (Figure A (Appendix) 1) (Millennium Ecosystem Assessment, 2005; Paul et al., 2021). Soil provides functions by improving soil structure, filtration and storage of water, decomposing and cycling of nutrients, balancing the soil food web and diseases, providing habitats and affecting primary productivity by plant growth. With this they balance other living communities and counteract climate warming by carbon storage (Table A 1) (European Environment Agency, 2023; Wurst et al., 2012).

Plants and especially tree growth are vital for the health of our planet. As for the most important functions, forests support and provide by producing wood through photosynthesis. Water filtration, climate regulation and carbon fixation are regulating functions while cultural benefits are provisioned by giving space for recreation or cultural identity (Ring and Bundesamt für Naturschutz, 2021). Most forests show multifunctionality meaning they "need to fulfill a multitude of functions and services simultaneously, including but not limited to serving as habitat, protecting the soil from erosion, […] etc." (Thom and Seidl, 2016, 762). Hence, within Germany the Bundeswaldgesetz, a sustainable guideline for forestry has been active since 1975 in order to equally meet the utility, protection and recreational functions of forests (Ring and Bundesamt für Naturschutz, 2021).

As recently as the last 20 years it has been recognized that vegetation not only depends on abiotic and above-ground biotic factors but also on interactions with soil organisms. Especially the earthworm plays a vital role for nutrients and soil properties, hence it can influence the plant community composition and succession (Bardgett and Van Der Putten, 2014; Wardle et al., 2004). Next to being influenced by soil organisms, plant growth itself also influences indirectly the soil biota as a feedback system through its provision of plant resources, such as different tree species' litter.

Further, foliar herbivores need plants, mainly juvenile tree species, as a food source but they also alter these vegetational resources both in quality and quantity and to close the loop, this influences the soil biota again (Augustine and McNaughton, 1998; Bardgett and Wardle, 2003; Wardle et al., 2004). Deer browsing effects on tree regeneration has been studied mainly motivated by forestry economic reasons (Speed et al., 2013). The European roe deer, belonging to the cerevides, are rather small ruminants and the most widespread herbivores in Europe (Linnell et al., 2020). They could increase up to overpopulation thanks to higher regulations on hunting, winter feeding, due to the existence of plenty of suitable habitats and because natural predators have become rare (Ramirez et al., 2018; Reimoser, 2003). Their increase is likely going to grow on account of climate warming with milder winters, and further depending on predators, such as the return of the wolves (Bardgett and Wardle, 2003; Frelich et al., 2012).

This forest ecological topic has strong relevance to the field of geography and above-mentioned aspects are touching physical geographical disciplines such as soil geography, landscape ecology or zoogeography and even economic among social geography.

Thanks to forests' provision of a variety of ecosystem services with great social benefits, many different stakeholders are involved in a sustainable management of forests in order to meet the versatile utilization concepts. Acting as an intermediary, Geography plays a vital role herby (Walz and Steinhardt, 2024). The alteration of landscapes by humans is the main focus of landscape ecology. Through their demands on nature, humans affect every ecological interaction and given the resulting environmental problems, landscape ecology is working holistic, multidisciplinary and human-centred (With, 2019). It is a scientific basis for landscape planning and for sustainable environmental management, therefore engaging in the challenge of land use, land degradation and more detailed e.g. forests as multifunctional landscapes (Walz and Steinhardt, 2024; With, 2019). This also engages regional and spatial planning which has a more political perspective on forests as resources (Goeke et al., 2015).

Even though soil has plenty of functions, human and social sciences only saw it as “a stock of resources” (Granjou and Meulemans, 2023, 1) for societies. Soil science however has acknowledged humans’ ability and power to shape soil formation especially since the end of the 20th century, resulting in proposals of a new discipline as anthropedology or in the Technosol, a new soil group in the World Reference Base for Soil Resources of the Food and Agriculture Organization (Granjou and Meulemans, 2023; Richter et al., 2011). As human activities are severely affecting soil genesis, soil sciences are now at the intersection of natural and human sciences. Owing to climate change soil geography has become more prominent, investigating the dependence of soil biota on environment and vice versa. Thus, the interaction of a healthy forest, deer and earthworms, all influenced by societies’ activities, is part of the human-environment-relationship, a main topic of Geography (De Vries and Bardgett, 2012; Fierer et al., 2009; Granjou and Meulemans, 2023).

Furthermore, soils are an integral sphere of the global water cycle. Hydrogeography, an essential sub-discipline of geography, explores the different water resource distributions controlled by the physical geosphere and investigates its impacts to humans. Anthropogenic activities are drivers and together with climate change induced forces it might cause drastic alterations of regional and global water availability. Water flows are investigated by hydrologists not only above-ground but also below-ground with soil properties of different strata (Karthe et al., 2018). Water infiltration is depending a lot on the soil structure and pore size and gets enhanced through earthworm activity (Lavelle, 1988). Thus, one might argue that soil biota activities should be considered in water management and hydrogeography as a sustainable tool in terms of heavy rain events and water erosion.

The University Forest is situated at the Steigerwald, a temperate forest within southern Germany. Regarding its tree diversity serving as a role model for a mixed forest of the future, it is a suitable woodland for studying disturbance interactions to earthworms. Thus, understanding its ecological functions and processes is of high importance in terms of forest restructuring. Experimentation is hereby a key tool of landscape ecology. However, since forest ecosystems work as large extent systems, research upon them with the right experimental set up remains challenging. Here, an in-situ experiment distributed over a certain area, accompanied by an ex-situ experiment with samples from the field analysed at a laboratory were conducted. As a manipulative experiment, two parameters were actively affected, while control plots were identical except for the manipulation (Wiersma, 2022).

3. Material and Methods

3.1 Study area

3.1.1 Location & Experimental Design

The experimental plots of my bachelor thesis are based at the University Forest owned by the Julius-Maximilians-University of Würzburg since 1821. It is situated near Sailershausen (50° 4′ N, 10° 27′ O), in the administrative district of Landkreis Haßberge, in Lower Franconia, Bavaria, in the south of Germany (Figure 4). Sailershausen is located around 70 km northeast of the city of Würzburg and east of the Wässernach, a confluent of the river Main, on a ridge at 320 to 380 m above sea level, which is part of the high plateau Schweinfurt Rhön (Bartsch, 2024). The forest has long been used as a silvicultural testing area, for excursions and for scientific research taking samplings of environmental variables to determine ecosystem functions. Nevertheless, it also serves as an economic working forest through the sale of timber and seeds by the University Forestry Office (Müller et al., 2023; University Würzburg).
The research took place at the experimental plots of BETA-FOR, a project of the DFG (German Research Foundation) called “Enhancing the structural diversity between patches for improving multidiversity and multifunctionality in production forests” (Müller et al., 2023). The project aims to understand the impacts of homogenisation of German temperate forests due to human activities, especially monocultures for timber production. Its focus is on the question, how structural diversity in forests affects their biodiversity and multifunctionality. The University Forest Sailershausen is one of eleven experimental forest sites within Germany (Müller et al., 2023). It is also part of MainPro, the Maintal project of risks, potentials and prospects for Bavaria, which intends to develop preventions against climate consequences in habitats of the Main valley due to climate change (University Würzburg, Geographie und Geologie).

For the experimental design silvicultural treatments were undertaken in winter 2018 to 2019 in order to increase structural heterogeneity and diversity by canopy opening and gap felling. The clearance encompassed around 30 % of the trees within one patch. This altered light availability and the amount of deadwood in the patches. The deadwood was not removed as typically done in modern silviculture but remained on the sites as stumps, snags, logs or combinations of snags and logs. The spatial arrangement of the cutting was either distributed with only single trees being removed or aggregated where interventions removed clustered trees resulting in a central canopy gap (Figure 1) (Müller et al., 2023).

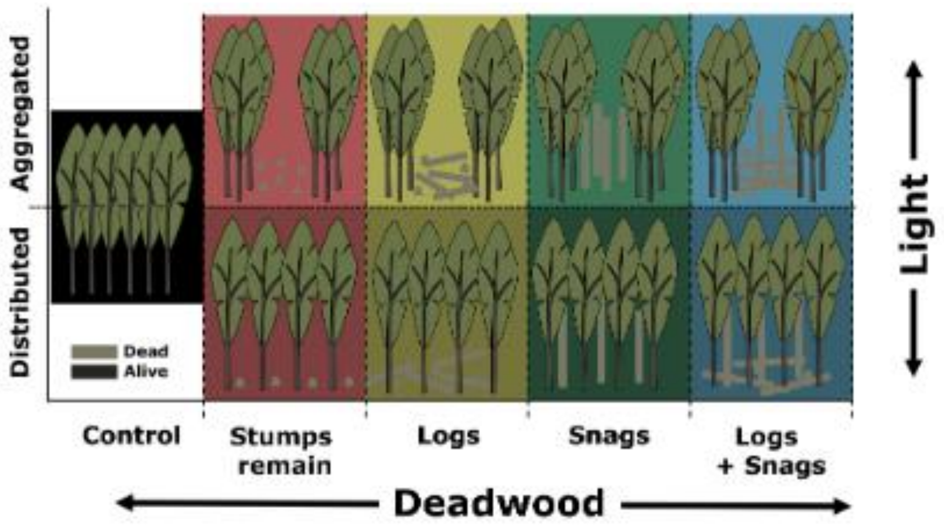


Figure 1: Schematic illustration of the aggregated or distributed tree removal, which results in different amounts of light availability and the different forms of remaining deadwood (adopted from Müller et al., 2023, 1443).

The research design consists of 75 experimental plots (Figure 4), with 51 of the plots having undertaken a distributed treatment of canopy gaps. Therefore, these sites remain shady, whereas 21 plots are sunny forest areas due to the aggregated treatment. Another three plots were not treated at all, serving as control plots, thus they can be seen as shady plots.

In spring 2019, fences were installed of six times six meters sized areas to prevent ungulate browsing. Each patch spans a size of 50 times 50 metres and has two subplots of four square-metres. One subplot is ten metres outside the fence, called control area, the second subplot is inside the fence, called fenced or exclosure plot. The centre of each plot is marked with a large tree trunk, located either inside the fenced or inside the control area (Figure 2) (Müller et al., 2023; University Würzburg).

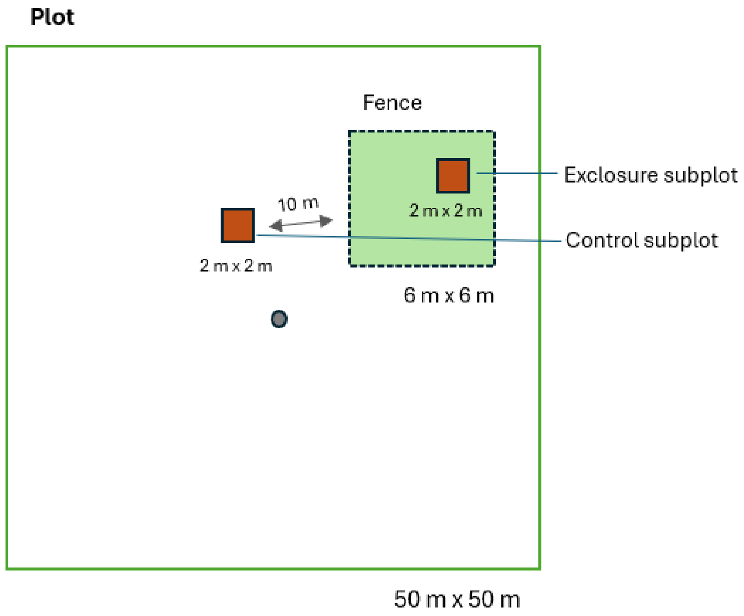


Figure 2: Experimental design of a plot consisting of one exclosure subplot and one control subplot (own creation with Microsoft Office).

The two interventions in the University Forest resulted in the following four treatment combinations, making a quantity of 150 experimental units in total (Table 1). Figure 3 shows the treatment combinations.

Table 1: Treatment combinations and their quantity of occurrence within the University Forest Würzburg.

Treatment	***Quantity***
Control (no fence) and shady (closed canopy) forest	54
Exclosure (fence) and shady (closed canopy) forest	54
Control (no fence) and sunny (open canopy) forest	21
Exclosure (fence) and sunny (open canopy) forest	21

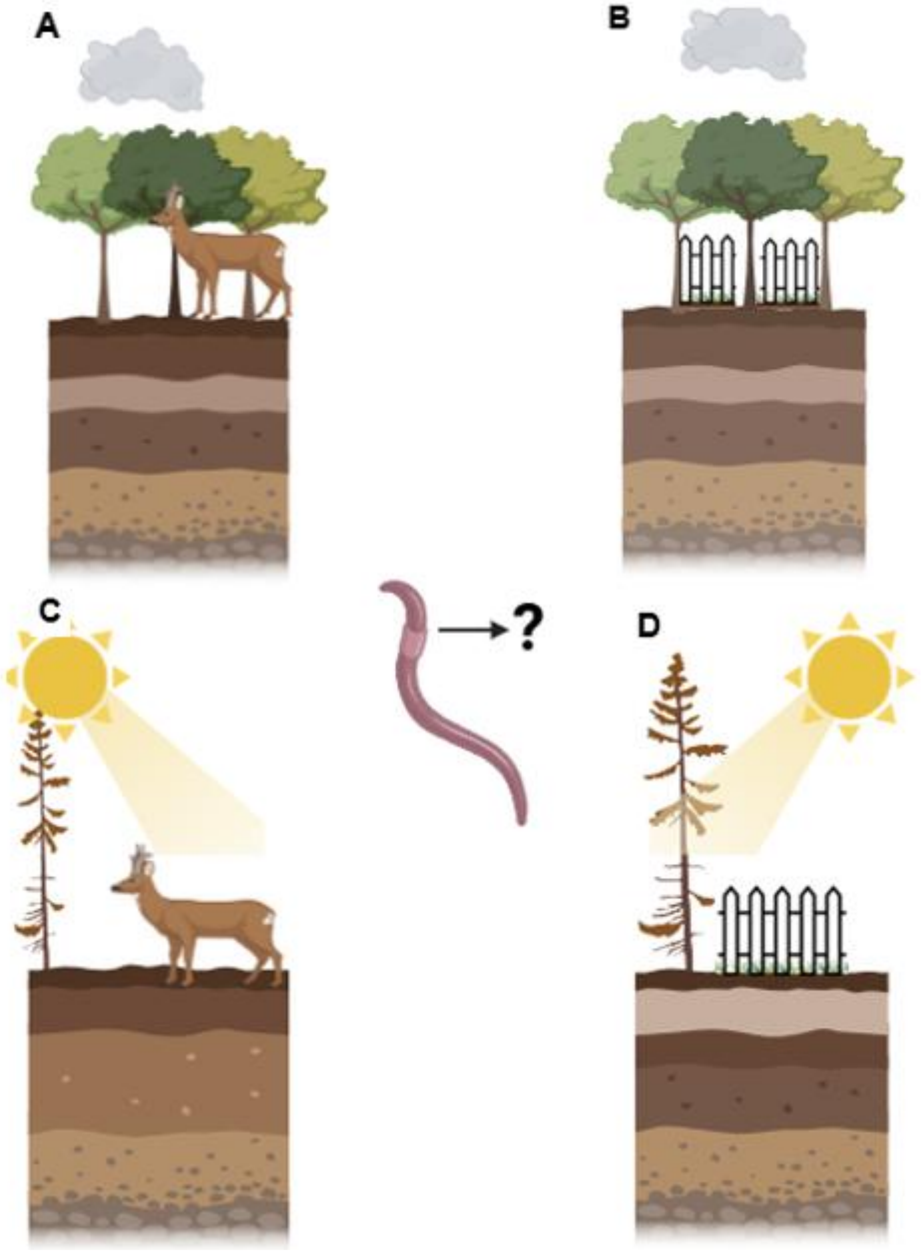
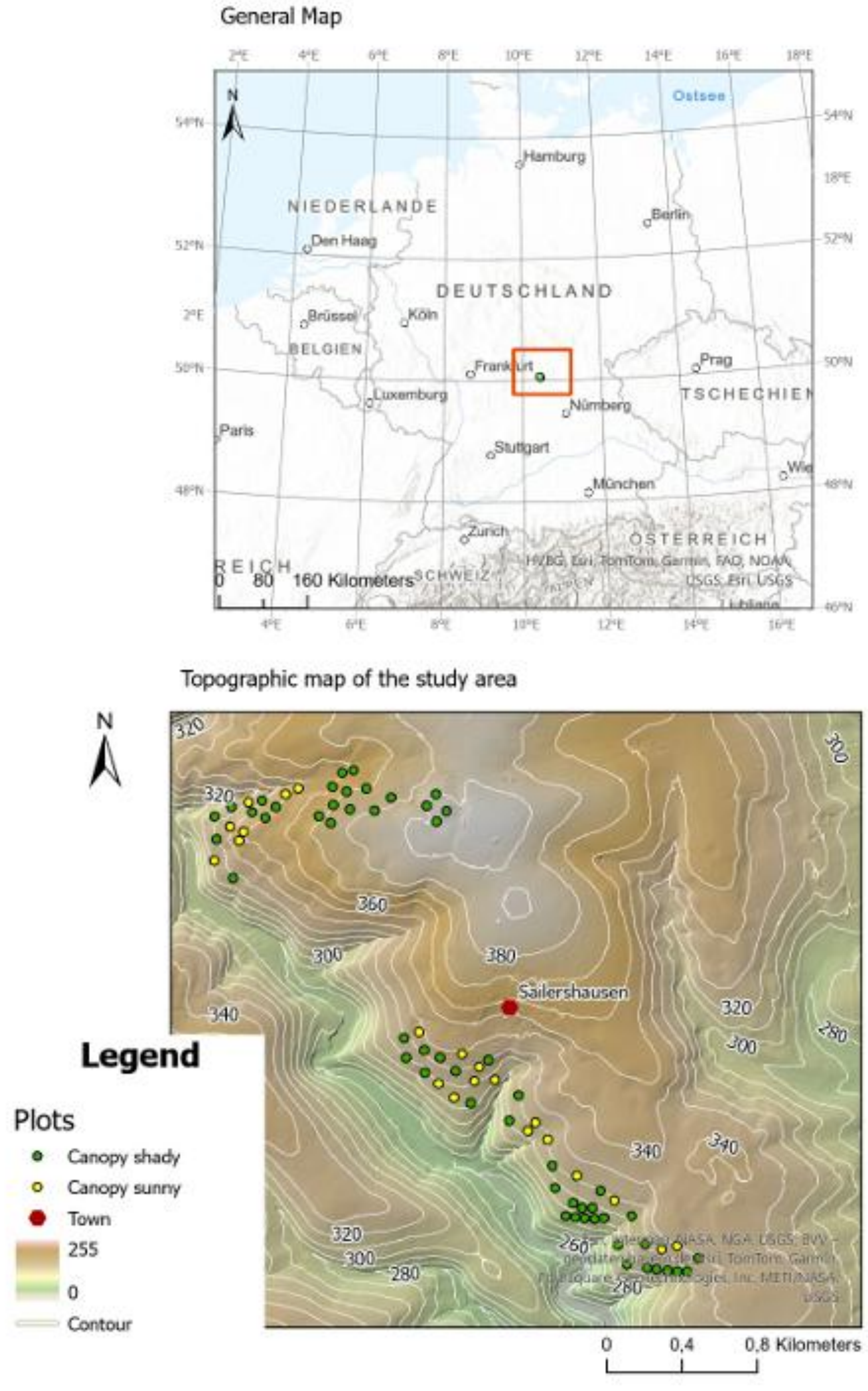


Figure 3: The four possible treatment combinations. A: Shady control. B: Shady exclosure. C: Sunny control. D: Sunny exclosure (own creation with BioRender.com).



References: opengeodata bayern, ESRI basemap, BETA-FOR

Figure 4: Topographic map of the study area with contours showing 75 plots (bottom) and a general map (top) (own creation with ArcGIS).

The plots are located on a ridge between 275 and 385 metres above sea level based on a digital terrain model with one metre resolution (DGM1) (Bayerische Vermessungsverwaltung). As seen in the profile of a cutout of the University Forest (Figure 5), the terrain of the plots differs slightly in elevation, slope and aspect which hence likely causes variations in soil temperature and moisture level.

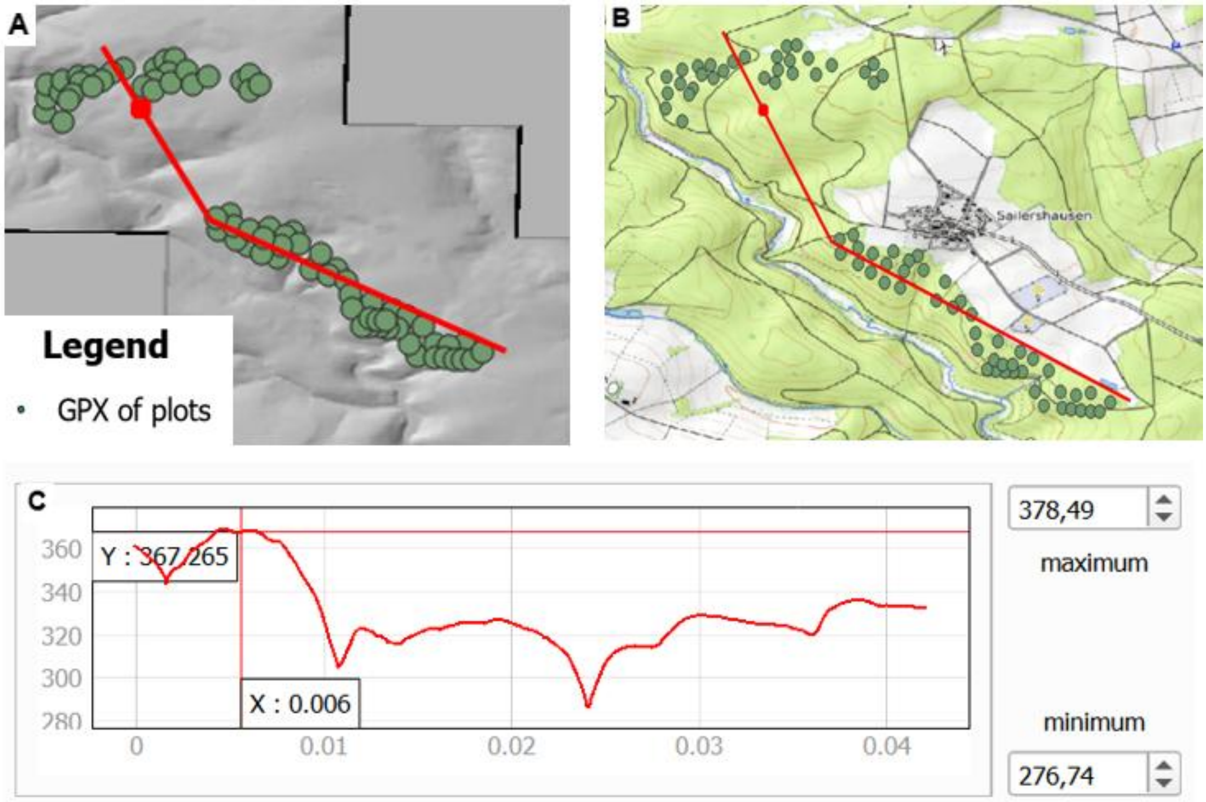


Figure 5: C: Profile of a cutout of the terrain of the University Forest Sailershausen. The red line shows the location of the profile in A: DGM as hillshade with the plots, and B: Topographic map with the plots (Own generation with QGIS, google terrain base map, DGM1 from Bayerische Vermessungsverwaltung, n.d.).

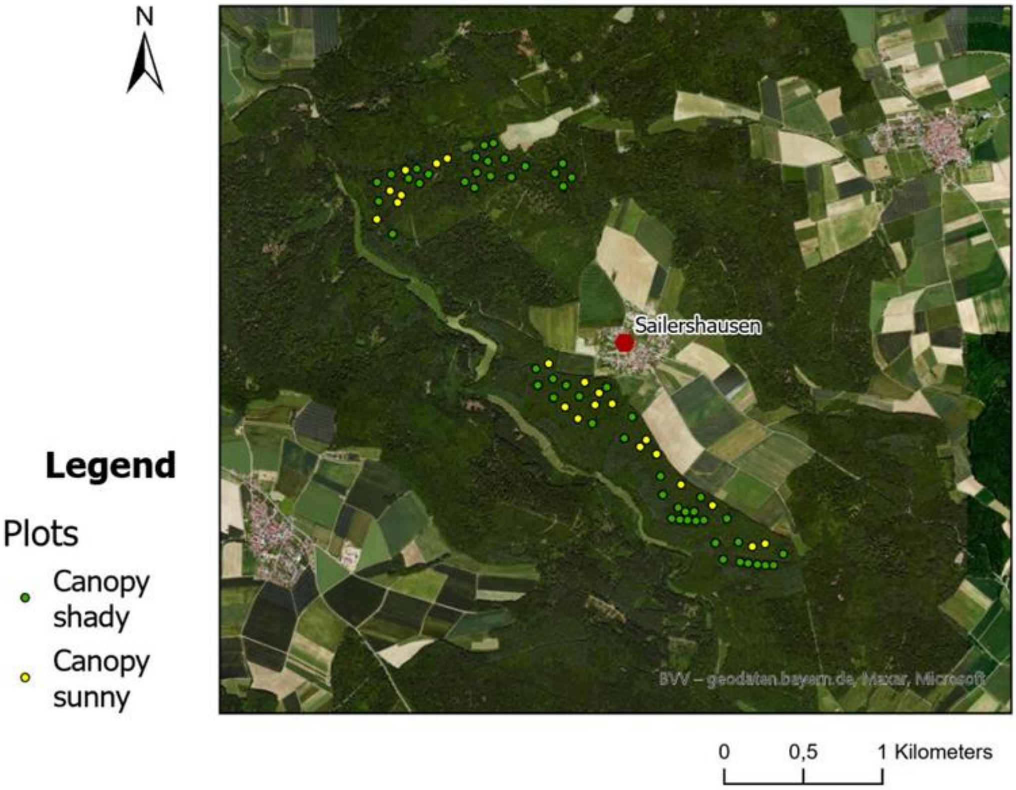
3.1.2 Climate, Flora & Fauna

Sailershausen has a moderate continental seasonal climate with maximum temperature in the Northern hemispheric summer. Mean annual temperature of this region is 10.7 °C with the highest average temperature of 19.9 °C in August and lowest average temperature of 2.1 °C in January while absolute temperatures range from 37.9 °C in July to -13.7 °C in February. Mean annual precipitation is 55 mm with highest average precipitations of 70 mm in July and August and lowest average precipitation of 38 mm in November. The highest number of rainy days of 18 was in December, meaning it rained less but more often in Winter compared to Spring and Summer (based on weather station Schonungen-Mainberg, 305 m a.sl., with data between 12/2019 and 11/2024, Wetterdienst.de, 2024).

The woodland of the University Würzburg encompasses a total of 2176,2 hectars of forest area (Figure 6) and fulfils various forest functions with the biggest share being Special Protection Area (SPA) for birds, landscape conservation area, Flora-Fauna-Habitat (FFH)-area and recreational forest, to some amount also forest for water protection, climate protection and conservation area.

The tree structure shows 74% deciduous forest with 21% of European beech *(Fagus sylvatica L.)*, 19% of oak *(Quercus spp. L.)* and 11% of hornbeam (*Carpinus betulus L.)* as well as 19% of hardwood containing ash tree *(Fraxinus excelsior L.),* wild cherry *(Prunus avium L.)* and rowan *(Sorbus torminalis Garsault)*. Precious woods make 19 % with Sycamore maple *(Acer pseudoplatanus L.),* Norway maple *(Acer platanoides L.)* and Field maple *(Acer campestre L.).* The 26% of coniferous wood are dominated by 10% spruce *(Picea abies (L.) H. Karst.),* followed by pine *(Pinus spp.),* European larch *(Larix decidua (L.) Mill.)* and Douglas fir *(Pseudotsuga menziesii (Mirb.) Franco)* (Figure 7). The potential natural vegetation is either wood barley - beech forest or woodruff - beech forest and few plots show Scotch mist - oak - hornbeam forest (Arbeitsgemeinschaft Forsteinrichtung, 2016; Walentowski et al., 2020).

The hunt is carried out by around 20 independent hunters without their own hunting ground shooting approximately 260 deer per year (University Würzburg).



Reference: ESRI basemap worldwide image data; opengeodata Bayern; BETA-FOR.

Figure 6: Image data of the University Forest and surrounding area with plots (own generation with ArcGIS).

Figure 7: University Forest with A: rejuvenation in the control plot outside the fence and B: inside the exclosure (own images).

3.1.3 Geological and Pedological characteristics

Between April 2024 and June 2024 an extensive soil mapping was conducted in accordance with Forstliche Standortaufnahme (Arbeitsgemeinschaft Forsteinrichtung, 2016). Hence, a full data set of soil characteristics is available.

The geology shows Loess loam over Upper Muschelkalk apart from seven plots with Loess loam over lower yellow marl (Lower Keuper), determined with a drill stem and geological maps. The humus form is the soil organic layer structure and composition. It was determined by cutting out a block with a spade at approximately 25-30 cm deep with Ah and mineral soil. On most sites it is L- or F-Mull next to a few patches with F-Mull or mull-like moder, A-Mull and Rhizo-Mull. The litter thickness was estimated from the soil block with consistently zero cm. Similarly, the OF-thickness, the layer with decomposed organic matter, was estimated and differed from zero cm up to two-point-five cm. The OH- thickness, the layer with highly decomposed organic matter, was zero cm apart from one site with one cm.

The soil texture, a soil category based on physical characteristics, was determined by the tactile method of the finger test from soil samples taken with a one-metre-long soil corer of two centimetre diameter. By rolling a small amount of moist soil between the fingers it shows characteristics of its texture. The material's composition can be estimated by feeling the grain size, smoothness or coarseness. If the soil crumbles easily and cannot form a ribbon, it is sandy, whereas a short ribbon indicates a silty texture. If a long ribbon can be formed without breaking, it is clayey. Hence, the different soil texture classes can be categorized and visualized in the soil textural triangle, indicating the content of sand, silt and clay. Sand, a coarse particle, that lets water drain quickly, amounts to 30% apart from a few plots with 25%. Silt makes 55% next to a few plots with 52.5%. Clay, the smallest particle, which is highly plastic and cohesive, consequently amounts to 15% with few plots of 22.5%. Soil types of the sites differed quite evenly between Parabrown earth - Terra fusca and Brown earth - Terra fusca. For determining the individual soil horizons, a soil core with at least 50 cm, up to 100 cm length was extracted using a Pürckhauer soil corer. Most sites showed four different soil layers with a few sites of five or six layers, again specified by the finger test together with the standardized codes that describe the composition and texture.

The base saturation showed the class of one or two on all plots apart from four plots with class two to three. Base types consist of five main classes with class one describing soils with a very high base saturation over 80%, indicating high fertility with abundant nutrients, whereas a low base saturation under 20% represents very acidic and nutrient poor soils (Arbeitsgemeinschaft Forsteinrichtung, 2016; Walentowski et al., 2020).

Finally, the Calcium carbonate ($CaCO_3$) was estimated with a reaction of dilute hydrochloric acid (HCl) and carbonate minerals producing carbon dioxide gas with visible effervescence. $CaCO_3$ was present in almost all plots in the third or fourth soil layer. It can influence soil pH, nutrient availability, and overall soil health.

3.2 Field Work

The field work took place for nine full days from 24th of September until the 3rd of October 2024. For the earthworm extraction procedure, a 25 x 25 x 10 cm area was excavated in each subplot representative of the predominant vegetation. Plots were located with GPX data in the Locus Map application. The excavated soil was hand sorted for earthworms for a total of 30 minutes which were collected in a tube with 70 % ethanol. Part of the hand sorted soil was stored in falcon tubes for subsequent analyses (see soil sampling). In addition, 5 L mustard solution (10g mustard powder per 1 L water, activated by a shot of vinegar essence, prepared the day before usage) were poured evenly onto the excavated hole. For 15 minutes emerging earthworms were collected, rinsed with water and stored in the tube filled with 70 % ethanol. Subsequently, the addition of 5 L mustard solution and the collection of earthworms for another 15 minutes was repeated (Figure 8) (sampling modified and based on Ganault et al., 2024).

Figure 8: Field work. A: 25 x 25 x 10 cm excavation. B: Pouring in a total of 10 L of mustard solution. C: Hand sorting of the excavated soil for earthworms (Own creation with BioRender.com, own images).

3.3 Earthworm identification

After drying the earthworms with cell paper and weighing them, the identification was conducted one by one under a binocular microscope (Leica). I worked with taxonomic identification keys of Brohmer & Schaefer (2010), Sherlock (2018) and University of Minnesota (n.d.) and finally compared identified species with Dorow 's (2020) table of forest affinity of earthworm species in Germany to ensure their presence in German forests.

For the identification of earthworms, at first I checked whether the samples are juvenile or adult ones, as only adults can be identified to species level, while for juveniles the ecological group was determined. Looking at the colour of pigmentation, the headline and the distance of the setae as closely or widely paired classifies first categories of the family. If the headline of the prostomium, which is the head part before the first segment, reaches the second segment with two vertical lines, it is called tanylobic whereas for epilobic earthworms the headline does not reach the second segment. For the adult earthworms the species is classified depending on the location of the male pore and on the number of segments at which the clitellum including the Tubercula pubertatis starts and of how many segments it spans. Subadults only have the Tubercula pubertatis developed, which shape, for example as sucker or button like discs, is a distinguishing feature as well (Figure 9) (Sherlock, 2018).

Figure 9: Earthworms viewed from the binocular. A: Visible setae and clitellum. B and C: Different locations and shapes of the male pore, clitellum and Tubercula pubertatis, which are identification characteristics (own images).

3.4 Soil sampling

3.4.1 Soil preparation

Soils were collected during the earthworm hand sorting and transported in 50 mL falcon tubes to avoid soil compaction. Preparations for measuring soil variables included drying the soil samples in paper backs one per subplot in the dry oven at 30°C for a total of five days, as they should be air-dry for further measurements. To make sure all samples are comparable, they had to be analysed within 14 days after drying. Also, for the water stable soil aggregate measurement, soil must not be squeezed, which is why soil sampling had to be done carefully and a stable container, the falcon tube, was chosen for storing. Soil samples must not be frozen as this may break aggregates and no fungi should grow as this causes aggregation.

For both the pH-value measurements and the soil aggregates, soil has to be sieved. I used the sieving tower with a four millimetre and one millimetre sieve, with up to three samples fitting in at a time. Large, strongly attached aggregates from some sites were carefully crushed before sieving in order to get enough mass from the samples. For soil aggregates four grams of dry soil in the size of one to four millimetre is needed (Figure 10). For the pH-value I mixed the remaining sieved soil with soil smaller than four millimetre and weighed 10,0 g in labelled 40 mL vials.

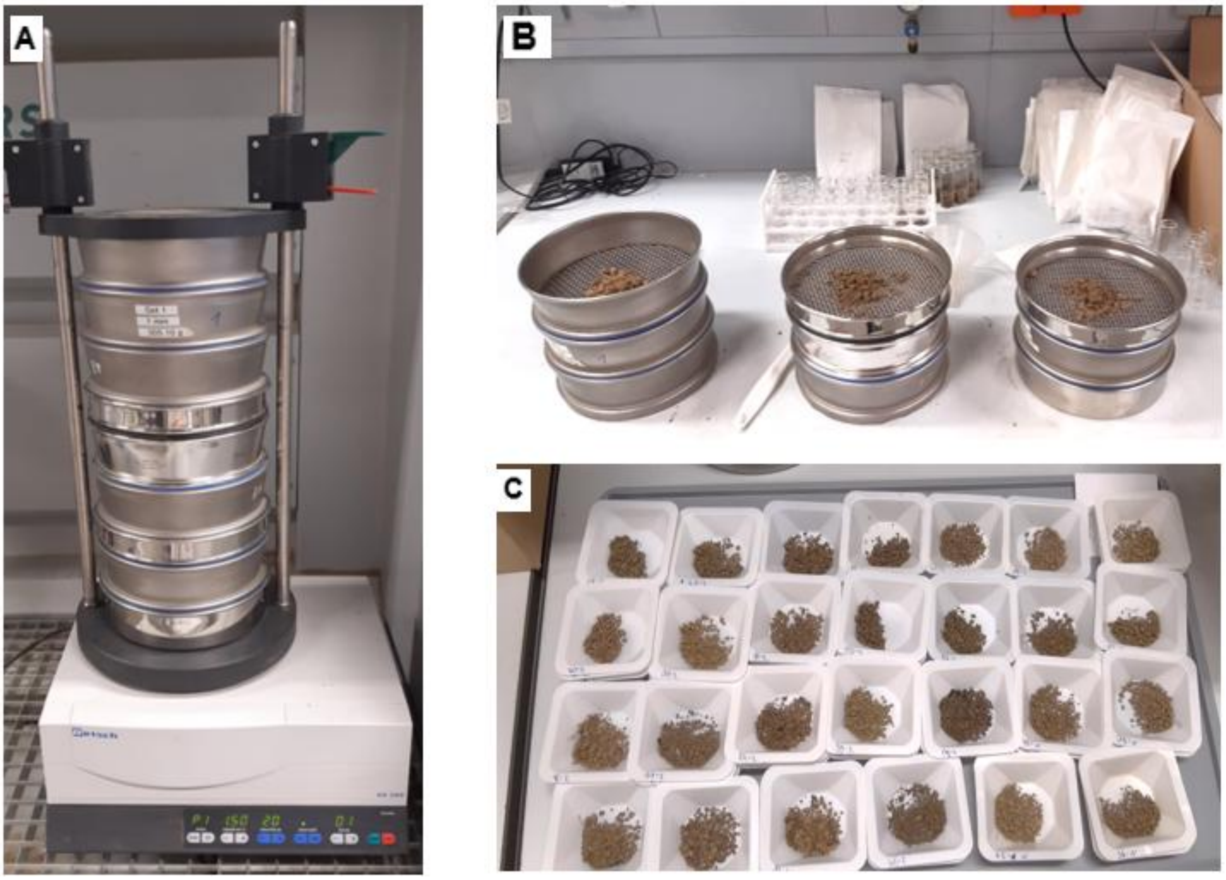
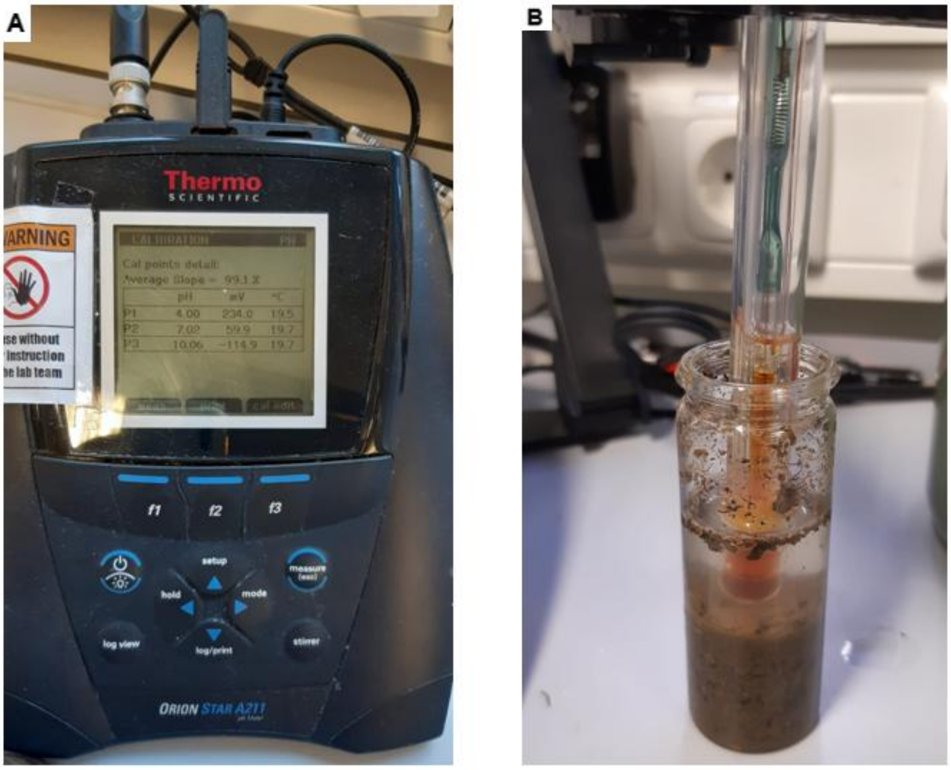


Figure 10: Soil preparation. A: Sieving tower. B: Sieves of four and one millimetre size. C: Prepared sieved samples for WSA measuring (Own images).

3.4.2 soil pH-measurement

For measuring the pH-value (with Orion Star™ A211 pH-Benchtop Meter, with measuring electrode Orion™ ROSS Ultra™ Triode™ pH/ATC-combination electrode - Thermo Scientific™), every morning the pH meter had to be calibrated with three different buffers of pH four, seven and ten, resulting in a slope of the calibration of 99.1% and 98.8 % depending on the day of calibration (Figure 11A).

For the processing, 25 mL calcium chloride solution ($CaCl_2$) with the concentration of 0.01 mol/L were added to every vial, which were then shaken vigorously and let stand for around one hour. After swirling up the samples again, the pH-value could be measured with the electrode of an accuracy of two decimal places, together with the temperature, once the values were stable. The electrode had to be rinsed with deionized water and pat dried before measuring the next sample (Figure 11B).



Cal points detail:
Average Slope = 99.1 %

	pH	mV	°C
P1	4.00	234.0	19.5
P2	7.02	59.9	19.7
P3	10.06	-114.9	19.7

Figure 11: A: Monitor with measured pH-values of the buffers. B: Measuring electrode in the soil sample solution (own images).

3.4.3 Water stable soil aggregate (WSA) measurement

For the measuring process of the water stable soil aggregates with the sieving machine, based on Kemper and Rosenau (1986), Nimmo and Perkins (2018) and Rieke et al. (2022), around four grams of sieved soil were weighed in the small apparatus' sieves, testing eight samples per time. For each sample two beakers of 150 mL were weighed empty, one of them for unstable, the other one for stable aggregates. The metal bins of the sieving machine were filled with 75 mL distilled water (H_2O), in which the soil inside the small sieves was soaked for three minutes and another five minutes with the machine running which moves the sieves up and down. The water of the metal bins containing the possible dissolved soil was poured into the beakers for unstable aggregates, thoroughly rinsing them with distilled water. In the second round, the sieves with the same soil samples were soaking in 75 mL of a dispersing agent of 2,0 g/L $(NaPO_3)_n$ and 0,45 g/L Na_2CO_3 solution for five minutes in the running machine. The aggregates remaining on the sieve not yet dissolved were stirred and crushed carefully and rinsed through with distilled water until only sand and organic minerals were left. The metal bin's content was poured into the beakers for stable aggregates, again thoroughly rinsing them with distilled water. After drying all beakers in the oven at 105° C for at least 24 hours until all the liquid was evaporated, the dry beakers now only containing the soil aggregates were weighed again (Figure 12).

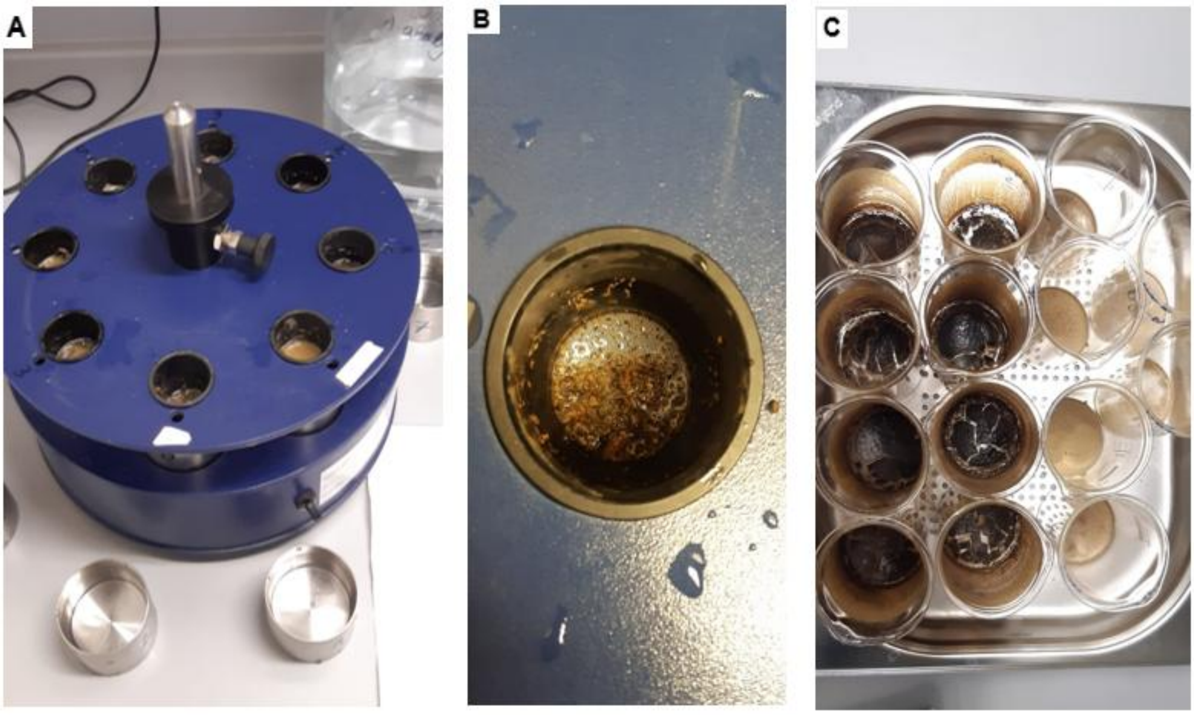


Figure 12: A: Sieving machine with eight metal bins and sieves. B: Sieve with remaining sand and organic minerals. C: Dried beakers with stable (left) and unstable aggregates (right) (own images).

A calculation for the percentage of water-stable aggregates as well as overall aggregates was carried out, considering the weight of the sample, weight of fraction one, which are the unstable aggregates, weight of fraction two, which are the stable aggregates and the mass of the dispersant solution of 0,18375 g. The formula are as follows:

$$WSA\,\% = \frac{(mass\ of\ stable\ aggregates - mass\ of\ dispersant)}{(sum\ of\ both\ fractions - mass\ of\ dispersant)} * 100$$

$$Overall\ aggregates\ \% \ = \frac{(sum\ of\ both\ fractions - mass\ of\ dispersant}{(weight\ of\ the\ sample)}) * 100$$

The percentage of overall aggregates describes how much stable and unstable aggregates are contained in the sample, which is the whole soil apart from sand and organic rest. The percentage of water stable aggregates is their share related to the overall aggregates amount. The numbers are generally quite high in all my samples which is led back to the relatively high amounts of loam on the study area. However, it also has to be considered that while the soil samples were tested within fourteen days after drying compliant to the protocol, the drying itself took place around six weeks after the soil sampling. Kemper and Koch (1966) proved that aggregate stability rises slowly the longer soil samples are stored, which is why measurements should be made as soon as possible after drying. Therefore, my results might be a bit higher than the actual value (Kemper and Koch, 1966; Kemper and Rosenau, 1986).

3.5 Statistical analysis with R software

The data evaluation and statistical analyses were performed with Microsoft Office 365 Excel and the statistical software RStudio 2024.09.1+394. The packages “openxlsx” (Schauberger and Walker, 2014), “readxl” (Wickham and Bryan, 2015), “tidyverse” (Wickham et al., 2019), “dplyr” (Wickham et al., 2014), “ggeffects” (Lüdecke, 2018), “ggplot2” (Wickham, 2016), “glmm” (Knudson, 2015), “glmmTMB” (Brooks et al., 2017), “DHARMa” (Hartig, 2016), “ordbetareg“ (Kubinec, 2022), “performance“ (Lüdecke, Ben-Shachar, et al., 2021), “see“ (Lüdecke, Patil, et al., 2021), “patchwork“ (Pedersen, 2019), “rr2” (Ives and Li, 2018) and “car” (Fox and Weisberg, 2019) were used under R Version 4.4.2.

For the data frame I created an extensive excel file with all relevant metadata for each subplot such as the treatment of fence and canopy, soil properties, as well as the analysed variables of soil pH-value, water stable soil aggregates and aggregates overall. Also, it contained earthworm abundance and biomass, each again subcategorised for the living form of anecic, endogeic and epigeic earthworms and for the live cycle of juvenile and adult. Further columns included every earthworm species as well as the genera. Tree species as vegetation data were incorporated, too.

For descriptive analysis, the sum, mean, median and standard deviation of abundance and of biomass of total earthworm community and of each genus were calculated. For visualisation as well as for checking normal distribution, histograms showing the frequency of occurrence were created, further also boxplots. Species richness, shannon and evenness indices were calculated for each subplot as well as their means categorised by the four treatments. Also, means for soil pH-values were calculated classified by each treatment.

To test the significance of both soil pH-value and soil type on the abundance (i.e., the number of individuals) of earthworms, initially a model was performed with total abundance as response variable. Either soil type or soil pH-value or both variables were used as fixed effects in order to reduce the possible influence of different site properties to earthworms' respons to the treatments. The model was coupled with analysis of variance (ANOVA) Type II Wald chisquare (Chisq) test. Also, a model testing for an interaction between soil pH-value and soil type was conducted.

For investigating the effects of light availability and deer exclosure on the abundance, I performed generalized linear mixed-effects models (GLMM) in the glmmTMB package in R (Brooks et al., 2017) with a tweedie error distribution, which allows for zero-inflated, continuous data, coupled with analysis of variance (ANOVA) Type II Wald chisquare tests with approximation for degrees of freedom for all models. The GLMM had negative binomial family distribution since count values consist of integer numbers, thus follow a Poisson distribution. I checked for overdispersion and fitted the abundance as the response variable. Canopy gap, deer exclosure and their interaction as well as soil pH-value were fitted as the fixed effects. The treatments were categorical variables, the soil pH-value was a continuous variable. To account for the nested design, plots were included as a random effect with general differences amongst them. With the Shapiro-Wilk test normal distribution of my response variables was tested, which is a necessary assumption of the ANOVA.

To investigate the same explanatory variables on biomass as well as on bodymass, I performed linear mixed effects models (LMM) with Gaussian family, which is used for a normal distribution, with the same model structure as mentioned above. Biomass and bodymass were transformed with square root (sqrt) and fitted as dependent variables.

To investigate if earthworm abundance generally had an effect on WSA, I performed a model with zero-inflation with the function of glmmTMB and ordbetareg (Kubinec, 2022) following a beta regression distribution to account for the percentage values of WSA, conducted only for the plots 1 – 47. The model was again coupled with ANOVA Type II Wald chisquare tests. WSA were fitted as response variable and total abundance as the independent variable. A similar model was conducted for WSA with the dependant variable of total biomass, whereby no zero-inflation was necessary.

All models were checked with the DHARMa package in R (Hartig, 2016), with simulateResiduals whether the model assumptions were correct, which created a fitted model showing QQ plot residuals and DHARMa residuals. For visualisation, boxplots were created for each dependent variable.

Since earthworms were collected from a 25 x 25 cm excavation, for further analyses biomass and abundance were multiplied by 16 for scaling up to one square metre which is a common standard.

4. Results

4.1 Descriptive results

In total, 1,643 individuals were sampled in the university Forest. However, 131 individuals were cut or damaged, resulting in 1,512 intact individuals. 824 individuals could be identified to species level, 725 individuals could be identified as either *Aporrectodea sp*. or *Allolobophora chlorotica* due to their juvenile stadium, 51 individuals could not be identified at all since they were cut or damaged too severely. One plot showed on both subplots an absence of earthworms. Ten distinct species could be identified with *Lumbricus terrestris* having the highest abundance and biomass, followed by *Aporrectodea rosea* and *Aporrectodea calliginosa* (Table 2). Thus, six genera, consisting of *Allolobophora*, *Aporrectodea*, *Dendrobaena*, *Dendrodrilus*, *Lumbricus* and *Octolasion*, can be assigned to the four treatment combinations with varying numbers of occurrence depending on the sites (Table 3). Further tables show statistical sum, mean, median and standard deviation of abundance and biomass of all sampled earthworms and classified by each genus (Table 4) as well as of bodymass (Table 5).

As originally aimed to differentiate between the three ecological groups and measure their different variation between the treatments, this was not possible since epigeic species with an occurrence of nine individuals were too rare to have statistical power. Genus-specific analyses were hence conducted for the most common species namely *Aporrectodea sp*., representing the endogeic life form, and *Lumbricus sp*., representing the anecic life form.

Table 2: Total abundance, total biomass and bodymass of each earthworm species from sampling of all plots (individuals only identified to genus level are excluded here).

Species	**Abundance** (number of individuals)	**Total biomass [g]**	**Bodymass** (individual biomass) **[g]**
Lumbricus terrestris	568	419.99	0.739
Aporrectodea rosea	148	23.139	0.156
Aporrectodea calliginosa	70	23.31	0.333
Octolasion tyrtaeum	19	9.54	0.502
Allolobophora chlorotica	9	2.16	0.24
Lumbricus rubellus	5	3.07	0.614
Octolasion cyaneum	2	1.05	0.525
Aporrectodea longa	1	0.32	0.32
Dendrobaena octaedra	1	0.05	0.05
Dendrodrilus rubidus	1	0.12	0.12

Table 3: Total sampled numbers of the six genera appearing in the four treatment combinations (juveniles, that could not be assigned to a genus are excluded here).

	Shady and control	**Shady and exclosure**	**Sunny and control**	**Sunny and exclosure**
Allolobophora	2	3	2	2
Aporrectodea	59	89	39	34
Dendrobaena	0	0	0	1
Dendrodrilus	0	0	0	1
Lumbricus	157	242	115	84
Octolasion	17	6	2	12
Total	235	340	158	134

Table 4: Sum, mean, median and standard deviation of abundance and biomass for total earthworm samples and for each genus.

Treatment	**Total abundance**	**Mean abundance**	**Median abundance**	**Standard deviation abundance**	**Total biomass**	**Mean biomass**	**Median biomass**	**Standard deviation biomass**
Total earthworm samples								
Shady control	452	8.370	8.500	4.696	144.790	2.681	2.040	2.337
Shady exclosure	573	10.611	10.500	6.764	220.749	4.088	2.640	4.082
Sunny control	353	16.810	15.000	11.797	102.690	4.890	4.980	3.150
Sunny exclosure	265	12.619	13.000	5.608	91.451	4.355	3.520	2.858
Allolobophora sp.								
Shady control	2	0.037	0.000	0.191	0.760	0.014	0.000	0.074
Shady exclosure	3	0.056	0.000	0.302	0.690	0.013	0.000	0.066
Sunny control	2	0.095	0.000	0.301	0.330	0.016	0.000	0.055
Sunny exclosure	2	0.095	0.000	0.301	0.380	0.018	0.000	0.057

Table 4 continued: Sum, mean, median and standard deviation of abundance and biomass for total earthworm samples and for each genus.

Treatment	Total abundance	Mean abundance	Median abundance	Standard deviation abundance	Total biomass	Mean biomass	Median biomass	Standard deviation biomass
Aporrectodea sp.								
Shady control	59	1.093	1.000	1.233	11.880	0.220	0.150	0.281
Shady exclosure	89	1.648	1.000	2.030	20.819	0.386	0.270	0.492
Sunny control	39	1.857	1.000	2.128	8.010	0.381	0.140	0.475
Sunny exclosure	34	1.619	1.000	1.499	6.610	0.315	0.130	0.362
Dendrobaena sp.								
Shady control	0	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Shady exclosure	0	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sunny control	0	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sunny exclosure	1	0.048	0.000	0.218	0.050	0.002	0.000	0.011
Dendrodrilus sp.								
Shady control	0	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Shady exclosure	0	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sunny control	0	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sunny exclosure	1	0.048	0.000	0.218	0.120	0.006	0.000	0.026

Table 4 continued: Sum, mean, median and standard deviation of abundance and biomass for total earthworm samples and for each genus.

Treatment	Total abundance	Mean abundance	Median abundance	Standard deviation abundance	Total biomass	Mean biomass	Median biomass	Standard deviation biomass
Lumbricus sp.								
Shady control	157	2.907	2.000	2.735	108.450	2.008	1.295	2.161
Shady exclosure	242	4.481	4.000	3.835	177.130	3.280	1.370	3.847
Sunny control	115	5.476	4.000	6.088	77.620	3.696	3.490	2.668
Sunny exclosure	84	4.000	3.000	4.393	63.260	3.012	2.320	2.801
Octolasion sp.								
Shady control	17	0.315	0.000	0.696	5.950	0.110	0.000	0.275
Shady exclosure	6	0.111	0.000	0.372	2.340	0.043	0.000	0.205
Sunny control	2	0.095	0.000	0.301	0.960	0.046	0.000	0.168
Sunny exclosure	12	0.571	0.000	1.630	4.770	0.227	0.000	0.528

Table 5: Sum, mean, median and standard deviation for bodymass of total earthworm community.

Treatment	Total bodymass	Mean bodymass	Median bodymass	Standard deviation bodymass
Shady control	20.231	0.382	0.255	0.466
Shady exclosure	19.463	0.374	0.326	0.237
Sunny control	7.535	0.359	0.375	0.207
Sunny exclosure	9.191	0.438	0.275	0.359

Soil pH-values ranged from 3.4 to 6.76, while subplots of control and exclosure differed between ±0.5. The mean differences of the measured soil pH-values depending on the treatments were only slightly visible (Table 6) with the highest value in in sunny control plots (pH 5.839), while the least is shown in shady control plots (pH 5.622).

Table 6: Mean soil pH-value depending on the plots, regarding treatments separately (left column) and the interaction of both treatments (right column).

Treatment	Mean soil pH-value	Treatment combinations	Mean soil pH-value
Control	5.622	Shady control	5.622
Exclosure	5.626	Sunny exclosure	5.836
Sunny	5.842	Sunny control	5.839
Shady	5.626	Shady exclosure	5.626
Total	5.626		

The richness of earthworms showed slight differences depending on the treatments (Table 7). Sunny control plots had the highest mean richness (3.013), while the lowest mean richness was in shady exclosures (2.839). Mean Shannon index was highest in sunny exclosures (2.481) as well as mean evenness index (2.224).

Table 7: Mean richness regarding treatments separately (left column) and mean richness, shannon and evenness indices regarding as an interaction of both treatments (right column).

Treatment	Mean richness	Treatment combinations	Mean richness	Mean shannon	Mean evenness
Control	2.846	Shady control	2.846	2.406	2.201
Exclosure	2.839	Shady exclosure	2.839	2.398	2.193
Sunny	3.013	Sunny control	3.013	2.478	2.223
Shady	2.847	Sunny exclosure	3.000	2.481	2.224
		Total	2.847	2.407	2.202

4.2 Inferential results

My results show a positive significant effect of soil pH-values on total earthworm abundance using a model with the family of negative binomial distribution (p = 0.009). Soil type shows a marginal positive significance on total earthworm abundance in the model transformed with square root and with the family of gaussian distribution (p = 0.076). If both soil characteristics are added to the model as independent variables with the family of gaussian distribution, they lose their significant differences as they take away each other's explanatory power, but soil pH-value remains significant (Table 8). An additionally created model with soil pH-value as response variable and soil type as explanatory variable showed a high significance (p = 3.275e-11), meaning that pH-values differ strongly within soil types and due to their correlation, soil pH-value covers soil type as well. Therefore, I was only using the soil pH-value for further models (Figure 13).

Table 8: ANOVA, Analysis of Deviance Table (Type II Wald chisquare tests), of the model testing for significance of soi pH-value and soil type on total earthworm abundance per 1 m².

Response: abundance total*16				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Soil pH-value	4.2047	1	0.04031	*
Soil type	1.2694	5	0.93805	

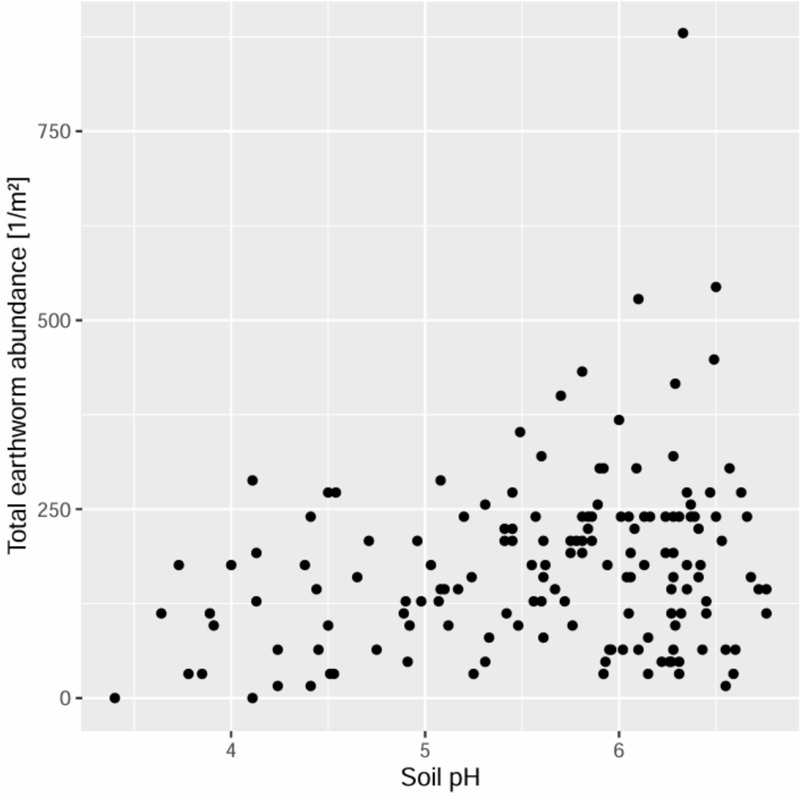


Figure 13: Plot of total earthworm abundance depending on the soil pH-value (own creation).

A zero-inflated model testing for total abundance as a function of canopy, fence, an interaction of both variables and soil pH-values with the family of negative binomial distribution was conducted. The ANOVA found significant differences for all variables besides fence (Table 9). This means that abundance does not significantly change with either fenced or control plots, but it does significantly increase with higher pH-values, with canopy openness and with the interaction of canopy and fence (Figure 14). Abundance was highest in sunny control plots with a mean of 268,96 [1/m²] (Figure 15).

Table 9: ANOVA of the model testing for significance of canopy, fence, soil pH-value and canopy fence interaction on total earthworm abundance per 1 m².

Response: abundance total*16				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Canopy	*9.9531*	1	*0.001606*	**
Fence	*0.7471*	1	*0.387411*	
Soil pH	*4.8698*	1	*0.027331*	*
Canopy:fence	*5.6810*	1	*0.017150*	*

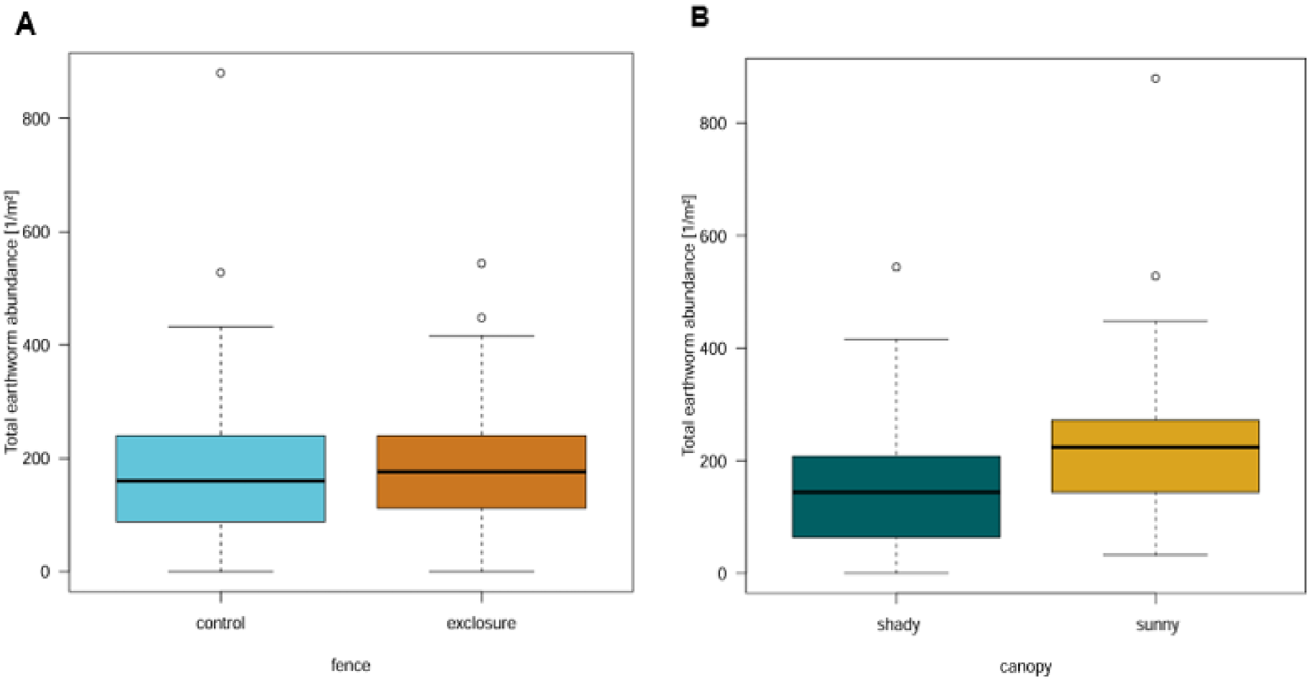


Figure 14: Boxplots showing total earthworm abundance depending on A: treatment of fence and B: treatment of canopy (own creation).

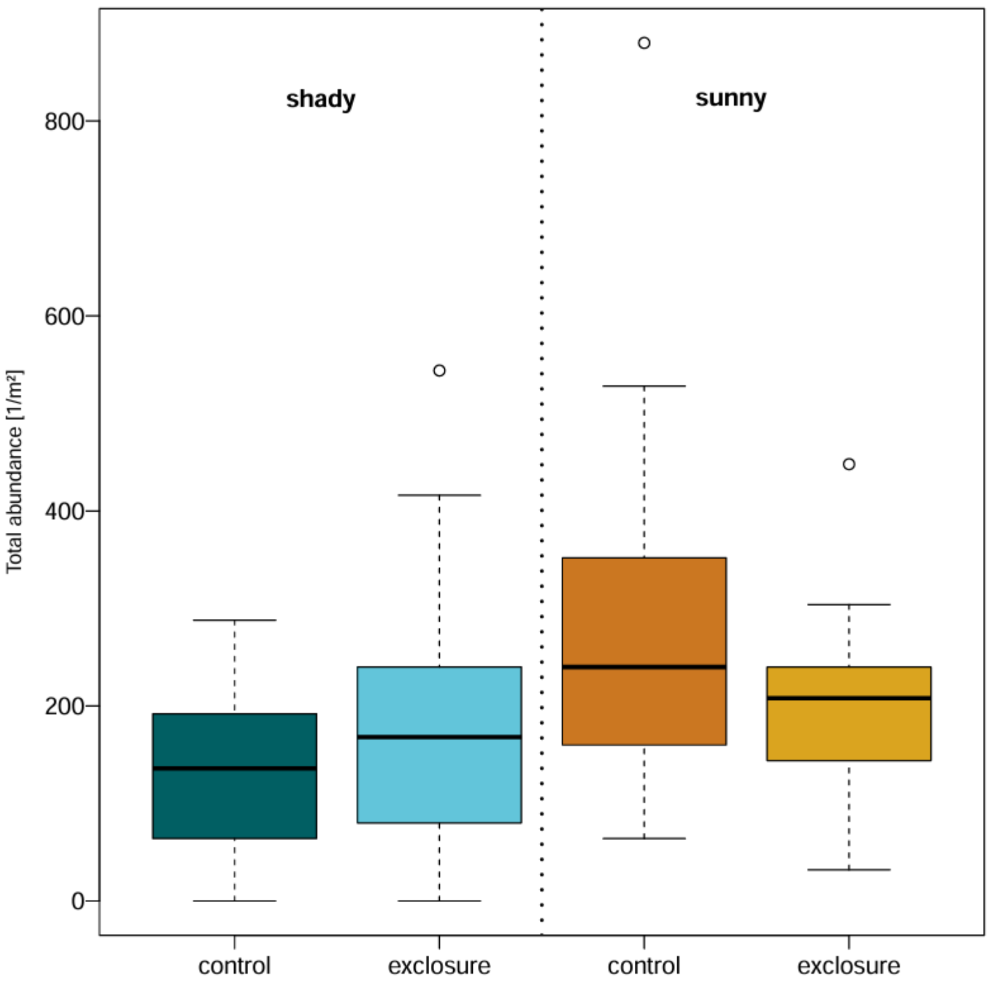


Figure 15: Boxplot showing total earthworm abundance depending on the interaction of the treatment of fence and canopy (own creation).

The response patterns of the two earthworm genera were different to the total earthworm community. Testing abundance of *Lumbricus sp*. with the same function as above-mentioned showed marginal significance for the interaction of canopy and fence (Table 10) with highest numbers of abundance in sunny control plots with a mean of 87.616 [1/m²] (Figure A 3).

Table 10: ANOVA of the model testing for significance of canopy, fence, soil pH-value and canopy fence interaction on Lumbricus sp. abundance per 1 m².

Response: *Lumbricus* abundance *16				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Canopy	0.2660	1	0.60601	
Fence	2.4053	1	0.12093	
Soil pH	1.5642	1	0.21104	
Canopy:fence	3.1746	1	0.07479	.

Testing abundance of *Aporrectodea sp*. with the same function had marginally significant interaction of canopy and fence (Table 11) and showed almost similar high abundance on all treatments apart from a bit lower number in control shady. The highest mean of 29.712 [1/m²] was found in sunny control plots (Figure A 4).

Table 11: ANOVA of the model testing for significance of canopy, fence, soil pH-value and canopy fence interaction on Aporrectodea sp. abundance per 1 m².

Response: *Aporrectodea* abundance*16				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Canopy	0.0069	1	0.93384	
Fence	1.0524	1	0.30496	
Soil pH	1.1943	1	0.27446	
Canopy:fence	2.9094	1	0.08806	.

Regarding biomass, a mixed effects model without zero-inflation was created with the biomass as a function of canopy, fence, an interaction of both variables and soil pH-value, with the family of Gaussian. The ANOVA for total biomass found significant differences for canopy and soil pH-variables and marginally significant differences for fence and the interaction of canopy and fence (Table 12). Biomass is higher in sites with higher soil pH-value, in sunny sites and in deer exclosure sites if regarded separately (Figure 16) and tends to be highest in their interaction in sunny control plots with a mean of 78.240 [g/m²] (Figure 17).

Table 12: ANOVA of the model testing for significance of canopy, fence, soil pH-value and canopy fence interaction on total earthworm biomass per 1 m².

Response: sqrt(biomass total*16)				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Canopy	4.5228	1	0.03345	*
Fence	3.0443	1	0.08102	.
Soil pH	6.4201	1	0.01128	*
Canopy:fence	3.6561	1	0.05586	.

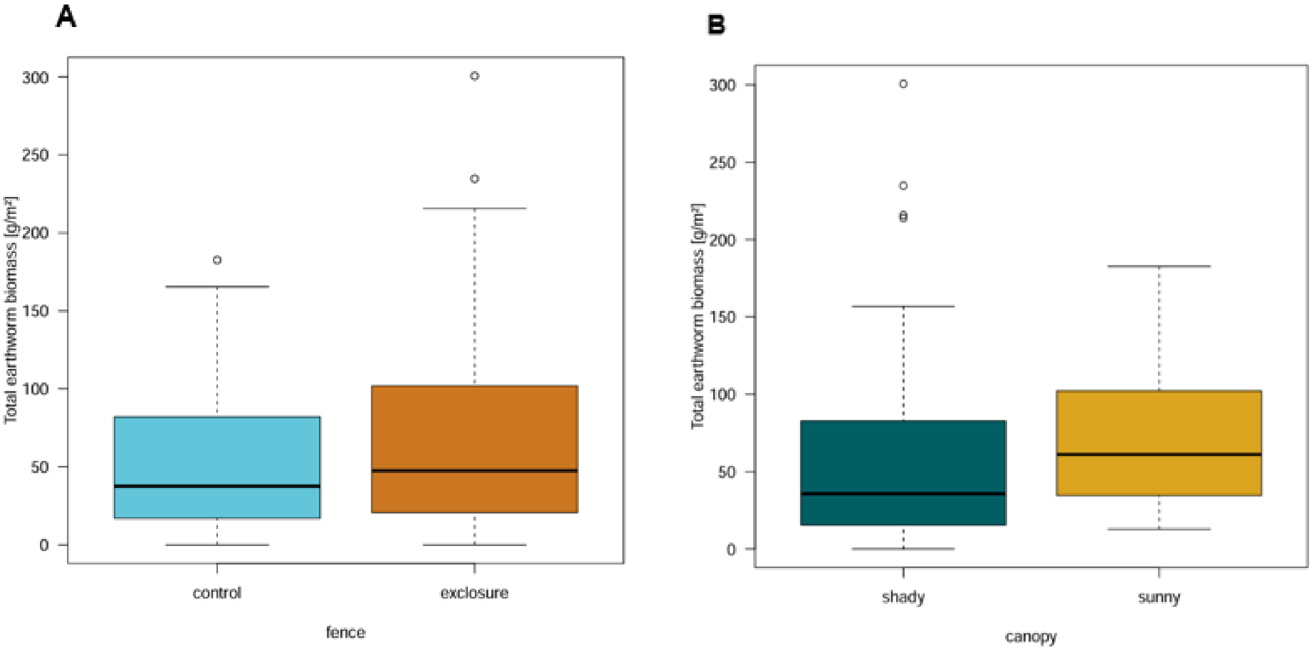


Figure 16: Boxplots showing total earthworm biomass depending on A: treatment of fence and B: treatment of canopy (own creation).

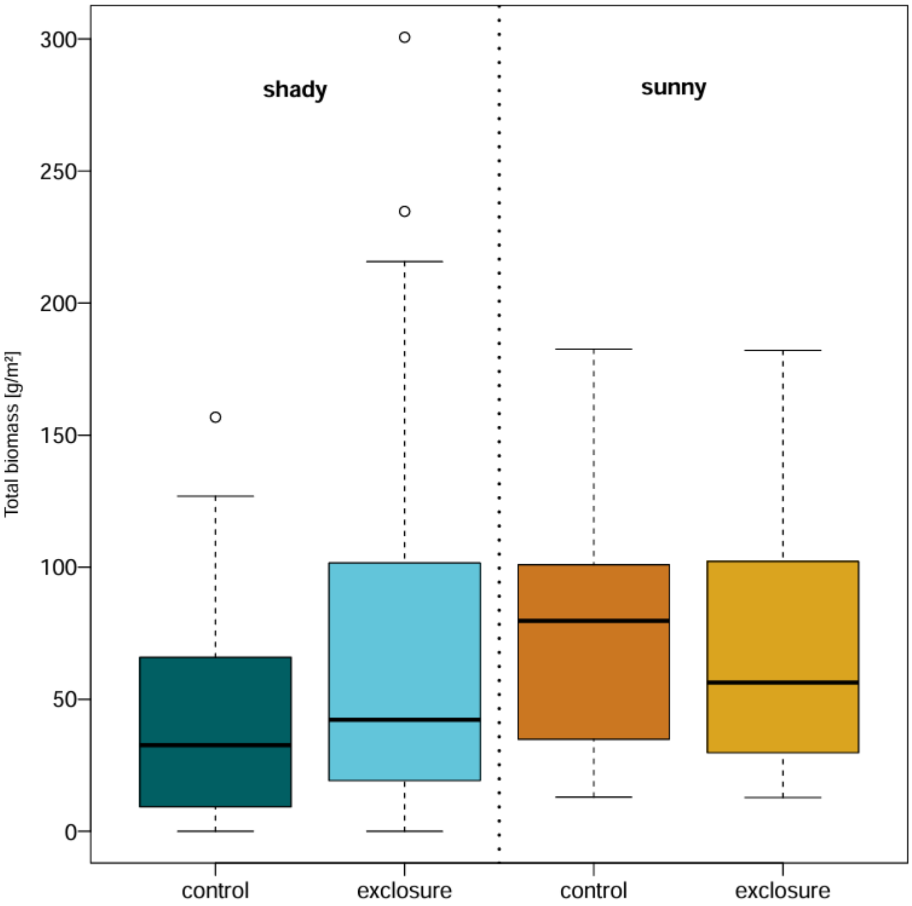


Figure 17: Boxplot showing total earthworm biomass depending on the interaction of the treatment of fence and canopy (own creation).

A similar LMM for the biomass of *Lumbricus sp*. indicated significant differences for soil pH variables and the interaction of canopy and fence (Table 13) with highest mean biomass of 59.136 [g/m²] in sunny control plots (Figure A 5). With a similar LMM with zero-inflation for the biomass of *Aporrectodea sp.* a marginally significant interaction effect could be shown (Table 14) with highest mean biomass of 6.176 [g/m²] in shady exclosures (Figure A 6). Hence, *Lumbricus sp.* showed stronger effects of the disturbance treatments than *Aporrectodea sp*. regarding their biomass.

Table 13: ANOVA of the model testing for significance of canopy, fence, soil pH-value and canopy fence interaction on Lumbricus sp. biomass per 1 m².

Response: sqrt(*Lumbricus* biomass*16)				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Canopy	1.8181	1	0.17754	
Fence	1.7723	1	0.18310	
Soil pH	5.4527	1	0.01954	*
Canopy:fence	5.5891	1	0.01807	*

Table 14: ANOVA of the model testing for significance of canopy, fence, soil pH-value and canopy fence interaction on Aporrectodea sp. biomass per 1 m².

Response: sqrt(*Aporrectodea* biomass*16)				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Canopy	0.4155	1	0.51918	
Fence	2.2771	1	0.13129	
Soil pH	0.5870	1	0.44358	
Canopy:fence	3.6318	1	0.05668	.

A similar LMM for bodymass of the whole earthworm community could not find any statistically significant effects (Table 15), the highest mean bodymass of 0.438 [g/m²] was found in sunny exclosures (Figure 18).

Table 15: ANOVA of the model testing for significance of canopy, fence, soil pH-value and canopy fence interaction on earthworm bodymass per 1 m².

Response: sqrt(bodymass)				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Canopy	0.1545	1	0.6943	
Fence	1.4083	1	0.2353	
Soil pH	0.1685	1	0.6814	
Canopy:fence	0.0136	1	0.9071	

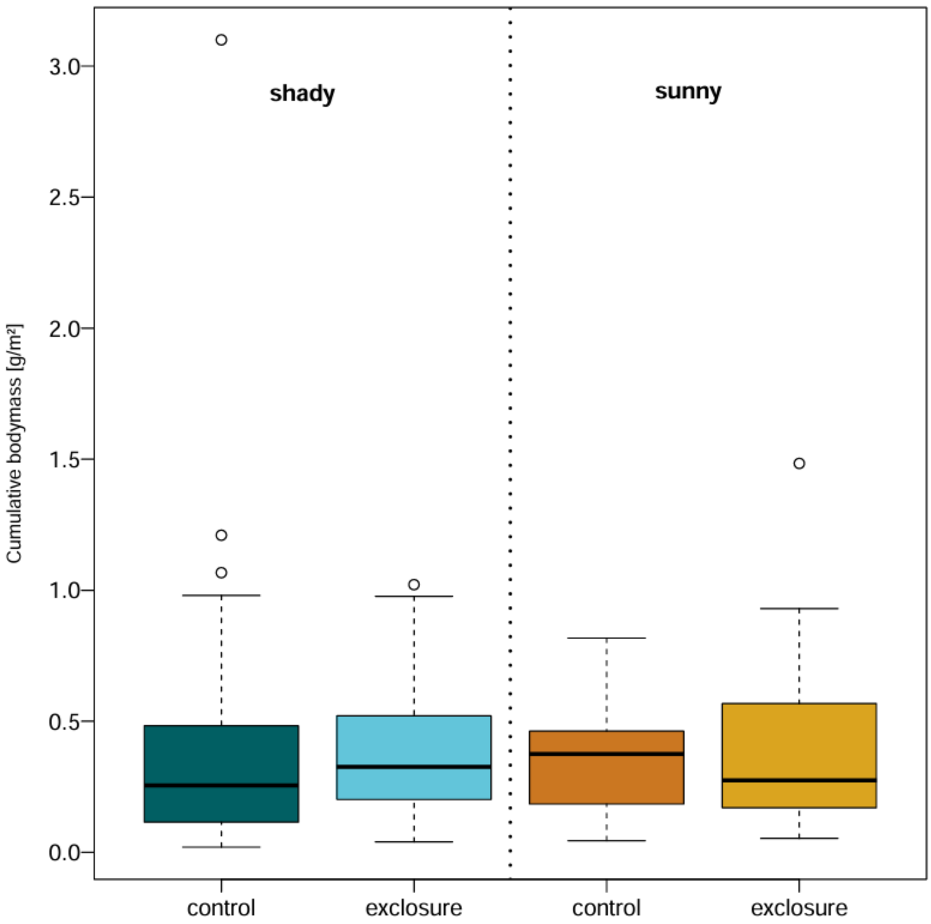


Figure 18: Boxplot showing earthworm bodymass depending on the interaction of the treatment of fence and canopy (own creation).

Finally, the significance of water stable soil aggregates was tested as a function of either total earthworm abundance or total biomass. The models did not find any statistical significance (Table 16 & 17).

Table 16: ANOVA of the model testing for significance of total earthworm abundance on WSA.

Response: water stable soil aggregates				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Abundance total	0.1	1	0.7518	

Table 17: ANOVA of the model testing for significance of total earthworm biomass on WSA.

Response: water stable soil aggregates				
	Chisq	**Df**	**Pr(>Chisq)**	**Significance**
Biomass total	1e-04	1	0.9916	

5. Discussion

5.1 Results related to hypotheses

The outcomes of our research supported the assumption of linked disturbance events in temperate forests and bring new insights into earthworm community shifts through ecosystem dynamics. According to the experimental research with canopy gap creation and roe deer exclosures located in a temperate forest in Bavaria, I could not approve my hypotheses stating that both canopy gaps and deer exclosures result in lower total earthworm abundance and biomass. The first hypothesis had to be neglected as I found that canopy gaps creating sunny forest sites increased both total earthworm abundance and biomass significantly.

My second hypothesis can only partially be accepted since deer exclosures increased total biomass marginally, while for total abundance no significant difference was observed.

Yet if considered the interaction of both treatments it was vice versa, hence exclosures decreased earthworm abundance which means that control plots with deer present in sunny forests showed the highest abundance and biomass. Thus, I found a significant interaction effect between canopy gaps and deer exclosure opposed to the study of Reed et al. (2023). As I was relying on results of this study on which I build my hypothesis on, I might have expected different effects at our research. However, since Reed et al.'s study took place in North America, where only invasive earthworm species are home to, it is very plausible that we have different results as we were investigating on native German earthworm communities. Further, dominant tree species in the University Forest differed from the testing areas in North Wisconsin forests, which might account for the different outcomes as well (Reed et al., 2023).

The assumption of a higher soil pH-value resulting in an increased abundance and biomass of earthworms could be proven. This conclusion was expected, as it is known that soils at the University Forest of Würzburg are quite acidic and that earthworms do not favour too low soil pH-values.

The last hypothesis of a higher earthworm abundance or biomass leading to an increase in WSA in the plots both had to be negated as no significant differences were tested.

5.2 Results connected to literature

Earthworms are mainly constrained by vegetation such as low quality and nutrient-poor food resources, by unsuitable climate patterns with droughts and colds and by soil characteristics and structure too compact to move. Generally, their abundance and richness depend on these external abiotic factors (Lavelle, 1988).

The ten different species we have found are within the average spectrum of eight to twelve species in optimal environmental conditions. In temperate forests, species richness also gets higher with higher quality of litter which might be an explanation why we have found slightly higher mean richness of earthworms in sunny sites given their different understory vegetation (Lavelle, 1988). Our most dominant earthworm species, namely *Lumbricus sp., Aporrectodea sp.* and *Allolobophoridella sp.,* are conform with Dorow's table (2020) of forest attachment in Germany, indicating *Dendrobaena sp., Lumbricus sp., Allolobophoridella sp.* and *Aporrectodea sp.* as species mainly found in forests, which accounts for 20.4 % of all species (Figure A 7) (Dorow, 2020).

My outcomes of roe deer leading to increased total earthworm abundance in sunny sites, less distinct for total biomass, are supported by studies of the eastern United States such as Cope & Burns (2019), Dávalos et al. (2015) and Mahon & Crist (2019) as well as by a Japanese study of Seki & Koganezawa (2013). Even though most investigations are done on the effects of ungulates on vegetation, invertebrates and soil organisms are focused on as well (Reed et al., 2023).

However, my result of an increase due to roe deer was only found in sunny sites, whereas in shady sites, earthworm abundance and biomass were increased in exclosures, which contrasts above-mentioned studies and again differs from results of Reed et al. (2023), thus existing studies show different outcomes. Indeed, Wardle et al. (2001) observed a decline in soil macrofauna because of deer presence as well. This can be explained since overall, herbivores cause many different effects on ecosystems and decomposer biota which can be positively, neutral or negatively affected by browsing as studies implementing fences as research design such as Bardgett et al. (2001), Bressette et al. (2012), Stark et al. (2000) and Suominen (1999) have shown and thus accord with my ambiguous findings. Deer presence strongly affects vegetation and nutrients of ecosystems. Depending on plants' tolerance and robustness they grow slower or dye (Augustine and McNaughton, 1998). Alterations of the early successional forest vegetation through browsing can remain long-term and impact the structure of the future forests, showing reduced diversity in the understory and overstory. Open tree canopies increase due to smaller leaf areas, thus deer pose a press disturbance continuously harming vegetation (Reed et al., 2022, 2023). This leads to decreased herb diversity and to a rise in unpalatable, more browsing resistant vegetation (Dávalos et al., 2015). This might be an unfavourable habitat and food resource for earthworms and hence explain their decrease in shady control plots. Further, the overabundance of deer might cause soil compaction through their trampling and the pressure of their hooves could be an unfavourable disturbance for earthworm communities (Dávalos et al., 2015; Shelton et al., 2014; Wardle et al., 2001).

On the other side, the most likely reason why earthworms generally increase in sunny sites where deer are present could be indirect by changes in soil composition as plants store nutrients and carbon next to their roots to offset their damages in leaves due to browsing. This again can have positive effects on microbial biomass in the rhizosphere and soil biota density

(A’Bear et al., 2014; Bardgett and Wardle, 2003), what might be the reason of higher earthworm abundance since they use microorganisms as a support for their digestion (Lavelle, 1988). Reduced plant density attributed to deer browsing means less soil nutrient usage by vegetation. Thus, nutrients might remain available for earthworms and lead to more prospering communities (Bardgett and Wardle, 2003). A likely direct positive impact by deer is the addition of organic matter and soil nutrients, especially nitrogen, through deer urine and faeces, which is more easily decomposed. However, it would be rather heterogeneously distributed but favours soil biota activity which again are part of the diet of earthworms and fasten decomposing processes (Dávalos et al., 2015; Wardle et al., 2001). On the other hand, the study of Mueller et al. (2016) found a negative correlation of earthworm richness and the nitrogen availability. Furthermore, deer hooves might transport earthworm cocoons favouring their populations (Murray et al., 2013).

Regarding earthworms at their life form groups, abundance of *Aporrectodea sp.* and *Lumbricus sp.* were marginally affected by the interaction of canopy and fence. The biomass of *Aporrectodea sp*. showed a marginally significant interaction effect. The biomass of *Lumbricus sp.* was significantly influenced by the interaction effect and by soil pH-value. This again shows different results as the study of Reed et al. (2023).

Aporrectodea sp. as endogeic life form inhabit the upper soil up to 15 cm deep which offers buffered and more constant living conditions. Also, they mostly feed on soil organic matter with humic molecules inside the soil mineral matrix (Lavelle, 1988; Reed et al., 2023). This might be a reason why *Aporrectodea sp*. show no significant differences within the treatments as they live rather independently from these outside factors.

Lumbricus sp. representing anecic life forms, mostly feed on plant litter and inhabit different soil layers (Lavelle, 1988; Reed et al., 2023). Herbivore influences on the accumulation, quality and decomposition of plant litter, also resulting in a different soil pH-value, might be one reason for the stronger dependence of *Lumbricus sp.* biomass on treatment variables (Bardgett and Wardle, 2003; Suominen, 1999). Moreover, Wardle et al. (2001) found that shifts of litter layers lead to less diverse habitats again affecting the diversity of soil biota. However, as mentioned above, the increased microbial biomass due to herbivores might favour *Lumbricus sp.* as they feed on bacteria and other soil biota as well (Satchell, 1983).

To follow up, deer and earthworms are both ecosystem engineers and linked to each other’s presence. Given the large variety of effects by deer, it seems plausible that studies such as Wardle et al. (2001) or Shelton et al. (2014) have observed idiosyncratic or no effects and that still more insight in the mechanisms is needed. Nevertheless, recent studies have indicated that earthworms and deer have interactive connections through legacy effects on each other and on ecosystems, such as deer favouring earthworm abundance which accelerates litter decomposition and nutrient cycling and enhances plant consumption by deer (Dávalos et al., 2015; Mahon et al., 2020).

My findings that canopy gaps significantly increase both earthworm abundance and biomass did not coincide with my hypothesis nor with the results of Reed et al.'s study (2023), where earthworm abundance grew the most, the furthest away from the canopy gap centre. Studies suggest that earthworms' abundance is low because of migration from gap centres towards closed canopies and because hatchlings survive less under open canopies due to environmental and climatic conditions (Reed et al., 2023). Despite this, Mueller et al. (2016) found positive correlations between soil invertebrate diversity as well as earthworm richness and the understory average light availability between April and November, which supports my finding. The reasons for this are several interconnected ecological characteristics, such as increased soil temperature by more light availability which accelerates metabolism and decomposition rates and in turn availability of resources. As many studies have shown, light availability is strongly enhancing natural regeneration in tree gaps which can be seen on a higher plant diversity with successional understory herbs, shrubs and saplings and thus brings a reorganization of ecosystems (Muscolo et al., 2014; Seidl et al., 2017; Thom and Seidl, 2016). Seedlings respond differently to higher light exposure amounts depending on their species but most show taller heights, some also a bigger biomass and diameter (Annighöfer et al., 2019; Orman et al., 2021; Xu et al., 2023). Fast or high growing species will spread more thanks to better light competition while smaller plants remaining in the shade grow slower or decease (Weiner, 1990). The increased plant cover and plant species richness of the understory change the chemical compounds that are part of the soil food web (Hooper et al., 2000; Mueller et al., 2016). Further, open canopies because of tree mortality can positively affect biodiversity, due to early stages of forest dynamics. Especially if deadwood remains on the site, which is however rather rare in European forests due to intensive wood extraction, gaps foster heterogeneity and structural complexity within the forest which is likely to favour earthworms (Muscolo et al., 2014; Senf et al., 2018). Generally, the quality, quantity and diversity of resources influences soil biodiversity (Mueller et al., 2016). Hence it is plausible, that the more diverse vegetation which is prospering in sites with less light competition provides a more nutritiously balanced diet for earthworms.

On top of that, more open forest canopies are likely to attract deer to a greater extent given a higher saplings' quality. Hence, this is showing the interconnection of different disturbances (Ohse et al., 2017).

Since earthworms are poikilothermic, which means having a varying body temperature according to the outside temperature, their metabolism, growth, reproduction and activity rely on temperature (Edwards and Bohlen, 1996). Depending on the species, earthworms have their optimal temperature range between 10 °C and 35 °C, but generally, modest warmer soil temperatures can lead to growing biomass and activity of earthworms if ranging within their optima. Earthworms digest with the help of microflora inside their gut, which gets activated better at higher temperatures (Lavelle, 1988). However, temperatures above 40 °C can stop earthworms' reproduction and connected with droughts, soil moisture hast to be enough to enable their activity (Boström and Lofs, 1996; Singh et al., 2019).

Forests are among the most preferred living environments for earthworms thanks to optimal soil temperatures and high moisture and given the warming of a few degrees in canopy gaps, it might accelerate the activity of earthworms while still being within the ideal habitat conditions (Singh et al., 2019).

All these alterations depend on the size of the gap, on its slope and the height of the trees next to it (Muscolo et al., 2014). However, if disturbance changes are too big and tipping points are reached, forest ecosystems could lose their resilience and collapse (Seidl et al., 2017). Moreover, the provision of ecosystem services is generally impacted negatively by disturbance events and not all species flourish in the changed conditions (Thom and Seidl, 2016).

Further, the correlation of higher soil pH-values and higher earthworm abundance visible in our study was proven in several studies such as Dávalos et al. (2015) or De Wandeler et al. (2016) who found preferred soil pH-values of five to six. The highest abundance and biomass in sunny control plots followed by sunny exclosures might therefore be partly explained by the soil pH-value, which is highest in sunny control plots (pH 5.839) and lowest in shady control plots (pH 5.622). The soil pH-value again might be affected by different vegetation compositions as well as by soil properties. While deciduous forests mainly show soils of mull, coniferous forests as higher shade donators mostly show moder soils, which have lower pH-values and support acidification of soils due to different litter properties. Consequently, there will be a lower abundance and biomass of earthworms (Augusto et al., 2002; Frelich et al., 2012).

That might also be one potential explanation for the interaction between canopy and exclosure. The outcome of the study of Dávalos et al. (2015) stating that deer presence is favourable for earthworms at plots with low soil pH, while it is vice versa with higher soil pH, could not be supported by our study. This stresses the need for further research but it also does show interactive effects and approves the connection of food webs above- and below-ground (Van Der Putten et al., 2013). As deer overabundance impacts the biodiversity in forests rather negatively, the sunny sites with increased structural diversity might have led to more varied ecosystems which show greater resilience to disturbance regimes. Following, the more resistant earthworms inhabiting sunny plots might be better able to make use of the effects of deer browsing such as nutrients of their droppings (Reed et al., 2022; Thom and Seidl, 2016).

Earthworms enhance structural stability of soils through building casts. These generally consist of higher amounts of organic matter as well as of clay and silt minerals compared to undigested soil. Casts are built through mixing, compacting and glueing soil matrix together with mucopolysaccharides resulting in augmented development of aggregates. Thus, we would have expected to find a larger amount of water stable soil aggregates on sites with higher earthworm abundance, which however was not the case. An explanation might be the seasonal variation as well as dependence on the soil type. Further, the cast's structure depends on the earthworm species and the granular casts are easily dissolved by rain which might have been the case in the soils of our sites (Heydari et al., 2014; Lavelle, 1988).

5.3 Methodological validation

Regarding the research design and the field work, it was conducted based on the sampling recommendations by (Ganault et al., 2024) according to a common scientific approach. The sampling number of 150 plots was quite high enabling representative statistical analysis and deductions. Nevertheless, it would always be more powerful if a greater number of plots, preferably over different landscapes and regions could be included.

Earthworms' distribution varies a lot tempo-spatially depending on environmental factors as well as on seasonal changes of moisture and temperature within the soil and on vegetation (Cesarz et al., 2007; Edwards and Bohlen, 1996). Thus, I would suggest repeating the sampling a few times at the same plots, possibly during the same season in two different years to account for an evolving climate and vegetation change as well as at different seasons to account for the earthworms' cycle of live with different stages in their development and differing activity levels. Also, several rounds of earthworm sampling could prevent possible mistakes connected to identification, especially if samples have not been adults yet or if they were bruised from sampling.

The same applies to soil samples, for which it would be advisable to take a few samples over the year, as well as a greater amount of soil to be able to conduct at least three rounds of the measurement of water stable soil aggregates which is often recommended due to the rather inexact method. Also, the aggregates should be measured as soon as possible after drying (Kemper and Koch, 1966; Kemper and Rosenau, 1986).

In addition, if more time is available for the study, other effects could be taken into account as well since earthworm compositions are influenced by a variety of parameters. Amongst vegetation, for example tree and shrub species or the litter quality could be tested for significant differences. Also, soil temperature and humidity, soil carbon and the carbon to nitrogen ratio and microbial activity or further soil parameters such as the amount of sand, silt and clay or the base saturation could be used as independent variables, since studies found positive correlations (De Wandeler et al., 2016; Heydari et al., 2014; Mueller et al., 2016).

Another possibility would be to sample at a second year after experimental set ups including climate change consequences. Similar to the Jena Experiment, plots could be manipulated by heat and dryness to get further insights of possible future scenarios under a hotter climate. Additionally, species distribution models could be conducted. They intend to show the spatial and temporal changes of distribution of species depending on their habitat with the help of environmental predictor variables used to determine which living environments are selected by species and how communities are composed. However, all these factors are scale-dependent, thus several studies should be performed on different regional scales to get a broader knowledge on earthworm distribution (Edwards and Bohlen, 1996; Schröder, 2008).

5.4 Future prospects

As my results show links between the forest disturbances and prove their existing effects on earthworm compositions, they should be of important usage and guidance for long-term sustainable forest management practices. Supplying ecosystem services to humans in a sustainable manner and ensuring the protection and prospering of soil biodiversity is challenging (Thom and Seidl, 2016). An understanding of the earthworm's quantitative development due to practices of land owners is necessary, since they are also strongly impacted by landscape scaled management decisions and land use changes (Mueller et al., 2016; Singh et al., 2019). Under future hotter and drier climates, not only plant species composition, productivity and quality but also soil characteristics are likely to change. This has strong effects on ecosystem functions as well as on other organisms, like herbivores and earthworms that rely on these resources (A'Bear et al., 2014; Singh et al., 2019). Earthworms play a more important role within the ecosystem the warmer the climate gets, which is why they are one of the dominating soil biota in temperate regions (Lavelle, 1988) and given climate change, they might get more vital and present in many regions of the world.

Forests are a powerful tool in climate mitigation and protection of climate risks, e.g. flood risks, and silviculture enables these forest functions (Hanson and Weltzin, 2000). Particularly large tree mortality events severely decrease the carbon sink function and release CO_2 since forests are a "high-carbon ecosystem" (Calvin et al., 2023b, 29). By keeping our forests healthy and by avoiding the rapid deforestation, carbon dioxide emissions can be reduced drastically. Therefore, forest restoration and conservation together with improved management are vital and can lead back to fortified ecosystem services. The goal should be to keep forests resilient against climate change and more resistant to pests, which is best given under a high tree species diversity with fertile soils. Management practices should be sustainable and up to date with newest scientific research (Calvin et al., 2023a; Wirth et al., 2024).

As a protection of heavy rainfall events, earthworms will get even more vital with increasingly irregular precipitation patterns because by building casts and burrows, mainly done by anecic earthworms, they increase structural stability and the pore space immensely which helps aeration and water infiltration (Lavelle, 1988). Since the different ecological groups of earthworms show different activities, they also have specific impacts to the environment. The particular desirable functions should be identified in order to impose habitat protection strategies especially adopted to certain species (Lavelle, 1988).

Regarding the well-being of earthworms, further results of our broader study should be adopted by management principles advocating heterogeneous forests with structural diversity. This is encouraged by canopy gaps and especially by deadwood, which favours biodiversity and hence should remain inside the forests to some extent. However, with hotter climates litter and deadwood dry out quickly, thus larger amounts of deadwood increase fire hazards which has to be considered thoroughly in management decisions (Amiro et al., 2010; Hauck et al., 2019; Reed et al., 2023). On the other hand, if forests are heterogeneous and support different microclimates with sunny patches in between, they might be more robust and resilient and hence have no need to keep roe deer outside with fenced areas. Nevertheless, deer populations should be observed and monitored precisely to avoid overabundance which is causing negative effects on biodiversity (Reed et al., 2022).

As the results have shown that sunny sites increased earthworm abundance, more light availability could also be reached through practices of forest management regarding the density and age of stands and the occurring tree species. Gap-cutting of different shapes and sizes as an imitation of natural disturbances is a tool that brings a profit to the whole forest structure and biodiversity. However, due to the disturbance paradox such interventions should only be done at a medium frequency and at low severity, since disturbances mostly impact forest ecosystem services and carbon storage negatively (Mueller et al., 2016; Muscolo et al., 2014; Thom and Seidl, 2016). Regarding the species, deciduous trees enable higher light availability while evergreen trees cast more shade which is why the growing numbers of conifer plantations should be questioned if one is focusing on keeping soil fertility high with the help of earthworms as well as other invertebrates (Augusto et al., 2002; Mueller et al., 2016; Paquette and Messier, 2010). This also applies to the soil pH-value which gets more acidic with coniferous trees and might even be toxic for anecic earthworms. Thus, their planting should be well considered and adopted to the predominant environment as prevailing tree species have a big impact on soil biodiversity. Also, forest monocultures are to be eliminated since besides their detrimental impacts on diversity, such forests are less resistant to any external disturbances (Augusto et al., 2002; De Wandeler et al., 2016; Mueller et al., 2016). Further, the soil acidity as well as nutrients availability strongly differ with global change and land use practices. Therefore, sustainable land management becomes vital, including the reduction of environmental pollution by nitrogen or sulphur (Augusto et al., 2002; Mueller et al., 2016; Paquette and

Messier, 2010). Especially land degradation can influence the chemical soil properties resulting in decreasing earthworm populations. This stresses the severe impacts of human activities which should therefore be guided towards conservation practices (Heydari et al., 2014).

The increasing sustainable silvicultural management decisions are visible in a change from monoculture to now 79 % mixed forests in Germany, in deciduous trees rising to 48%, as well as in increased structural diversity and deadwood over the last years and is a development that should be continued (BMEL, 2024).

Conclusion

To sum up, in order to keep soil fertility high and to have healthy and resilient forests, earthworms play a vital role with their manifold functions. This thesis provides insights in the interconnection of disturbance factors to native earthworm communities in German forests and proves links in between. My results have shown that earthworms are affected by the two treatments of canopy opening and deer browsing. Earthworms occur with highest abundance and biomass in sunny control plots. However, they are influenced by a complex, interwoven network of not only the two treatments but verisimilar by a variety of factors with soil properties, habitats and food resources being an important part thereof. The interactions between earthworms, deer, plants, other fauna, soil characteristics and their feedbacks are still largely unknown to us, as it is for example not yet clear if earthworms in turn influence deer populations. One might follow, that below-ground responses to above-ground activities such as deer browsing take longer or are less pronounced than above-ground vegetational responses (Shelton et al., 2014). Also, specific studies on the behaviour of individual earthworm species might help to better interpret their different affections by deer and canopy openness (Dávalos et al., 2015). For a more detailed understanding of all underlying mechanisms, further research should be carried out by comprehensively addressing the different influencing factors. The use of novel techniques as well as transdisciplinary approaches is important for a better protection and restoration of ecosystems given that disturbances are likely to be more frequent with future climate. Regarding the possible disturbance threats, forest canopy gaps as well as deer browsing pressure are mainly manmade and can to some part be controlled via sustainable forestry management.

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Appendix

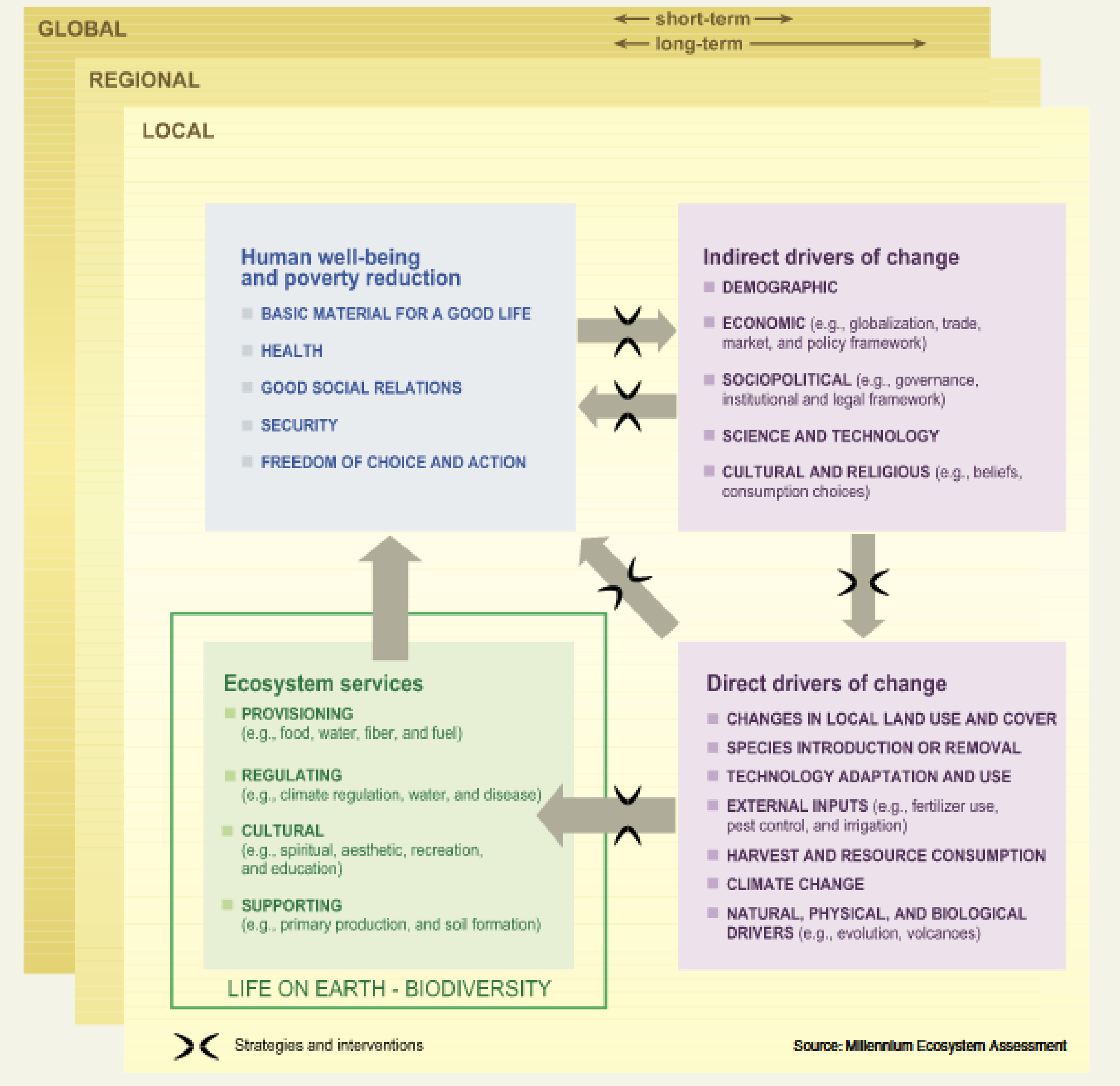
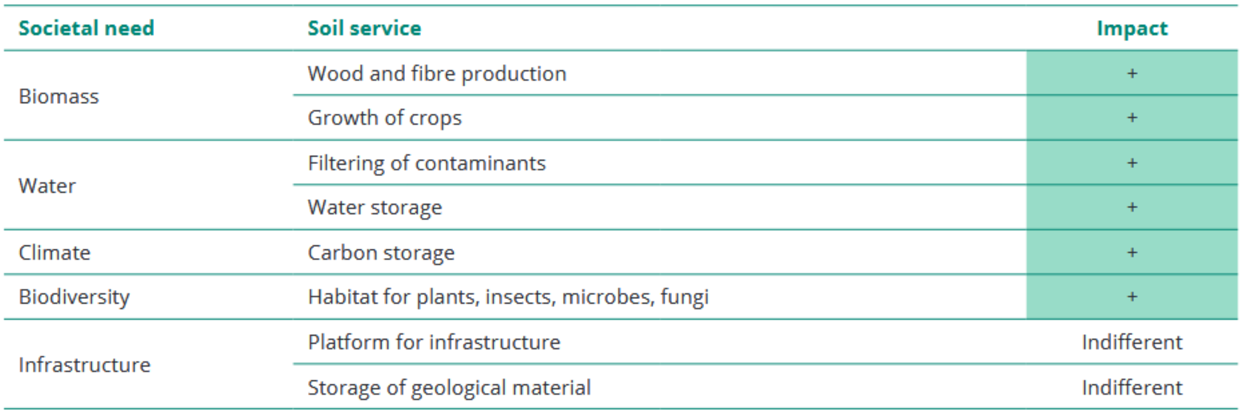


Figure A 1: Millennium Ecosystem Assessment Conceptual Framework of Interactions between Biodiversity and Ecosystem Services, Human Well-being and Drivers of Change. The bottom boxes are of highest relevance for my thesis (Millennium Ecosystem Assessment, 2005, Sec1:xvi).

Table A 1: Impacts of an increase in soil biodiversity to key societal needs and soil functions (European Environment Agency, 2023, 91).



Societal need	**Soil service**	**Impact**
Biomass	Wood and fibre production	+
	Growth of crops	+
Water	Filtering of contaminants	+
	Water storage	+
Climate	Carbon storage	+
Biodiversity	Habitat for plants, insects, microbes, fungi	+
Infrastructure	Platform for infrastructure	Indifferent
	Storage of geological material	Indifferent

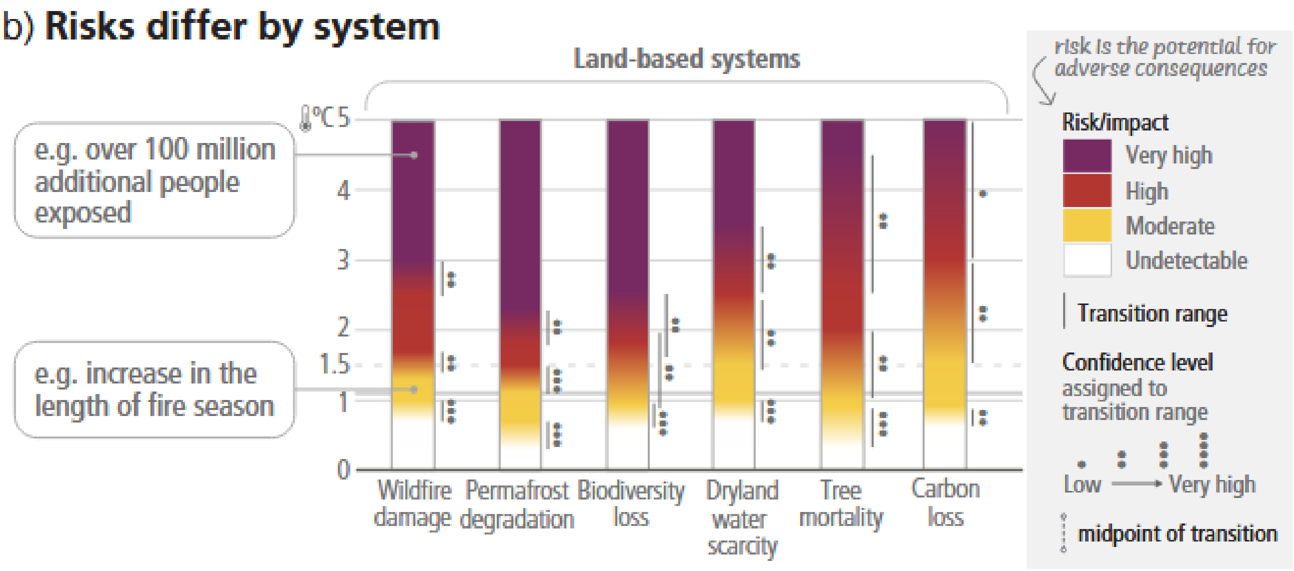


Figure A 2: Risks for land-based systems with increased global warming (Calvin et al., 2023a, 75).

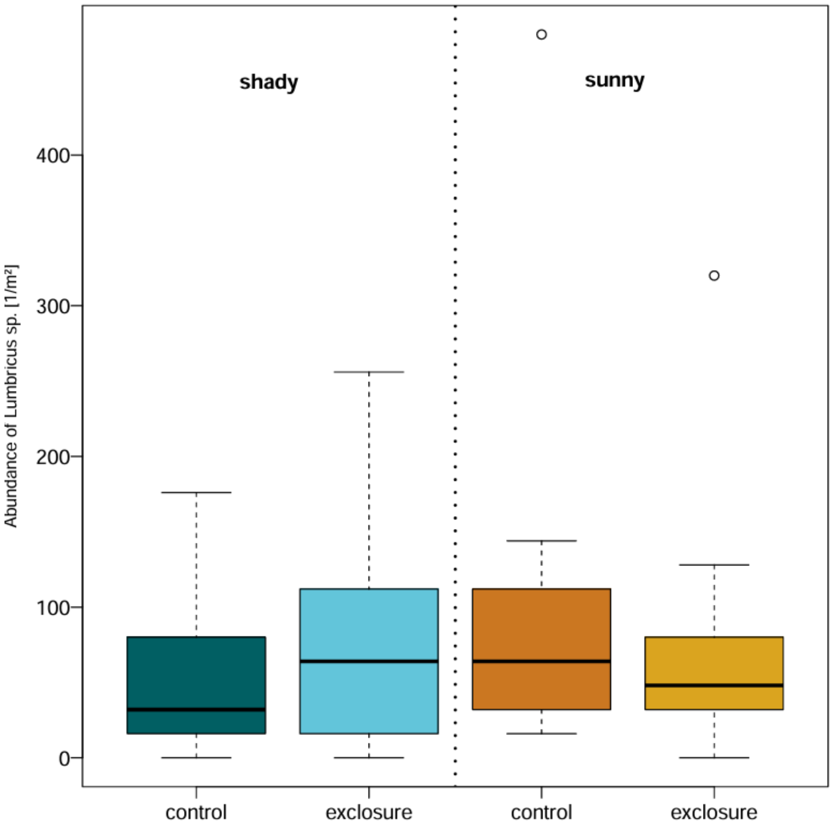


Figure A 3: Boxplot showing abundance of Lumbricus sp. depending on the interaction of the treatment of fence and canopy (own creation).

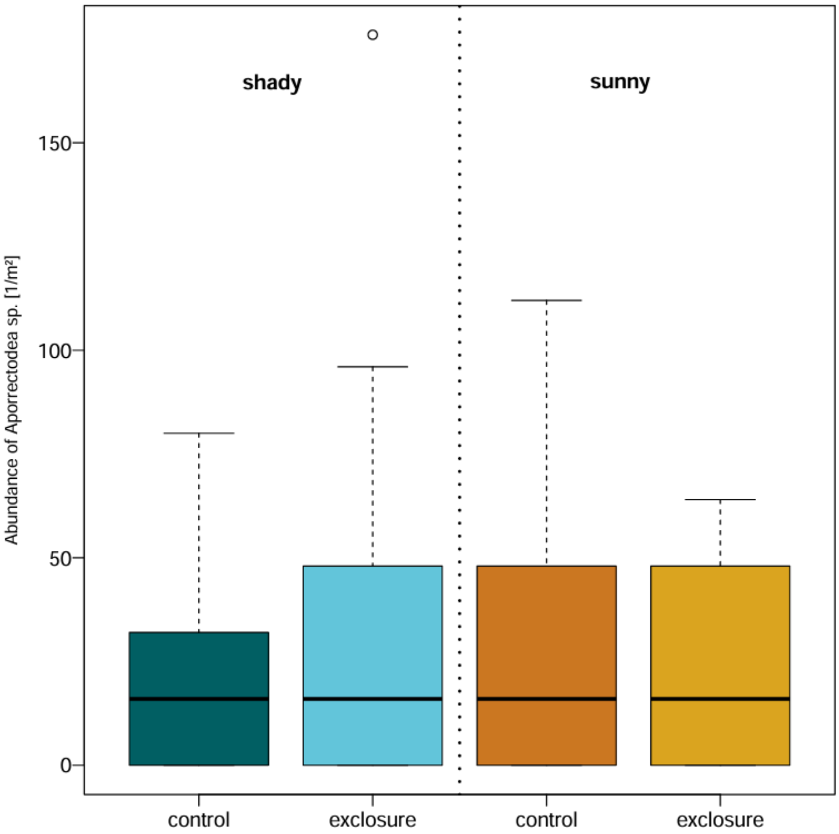


Figure A 4: Boxplot showing abundance of Aporrectodea sp. depending on the interaction of the treatment of fence and canopy (own creation).

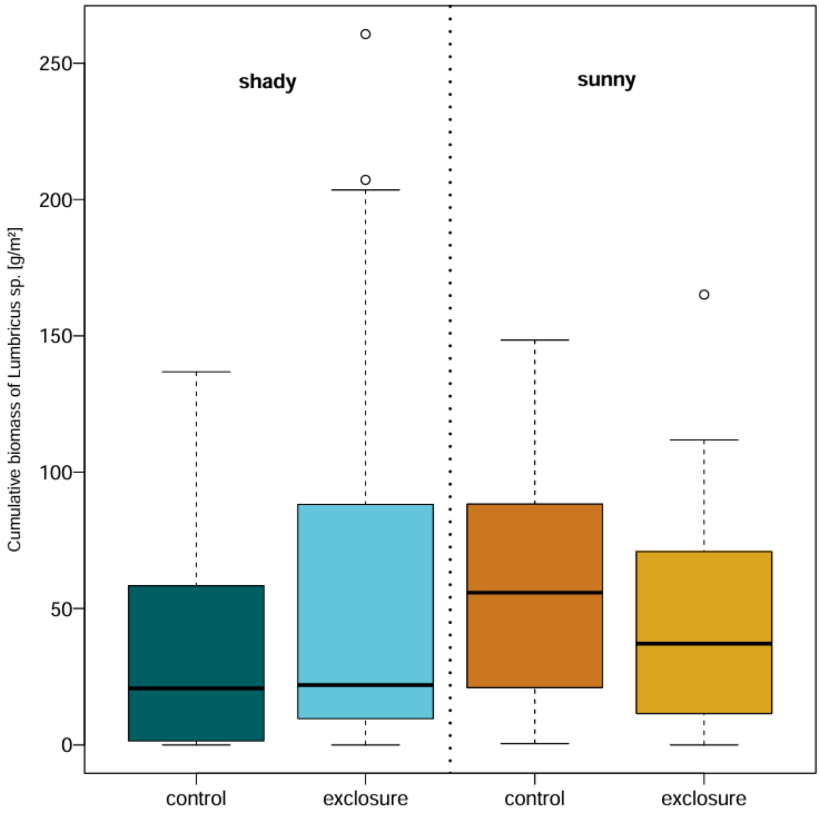


Figure A 5: Boxplot showing cumulative biomass of Lumbricus sp. depending on the interaction of the treatment of fence and canopy (own creation).

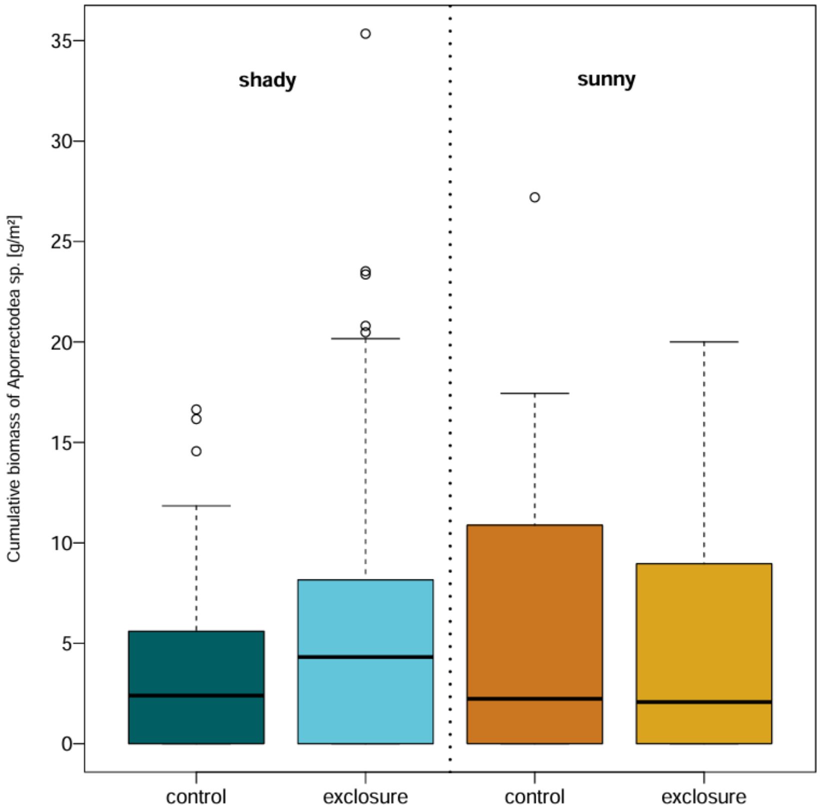
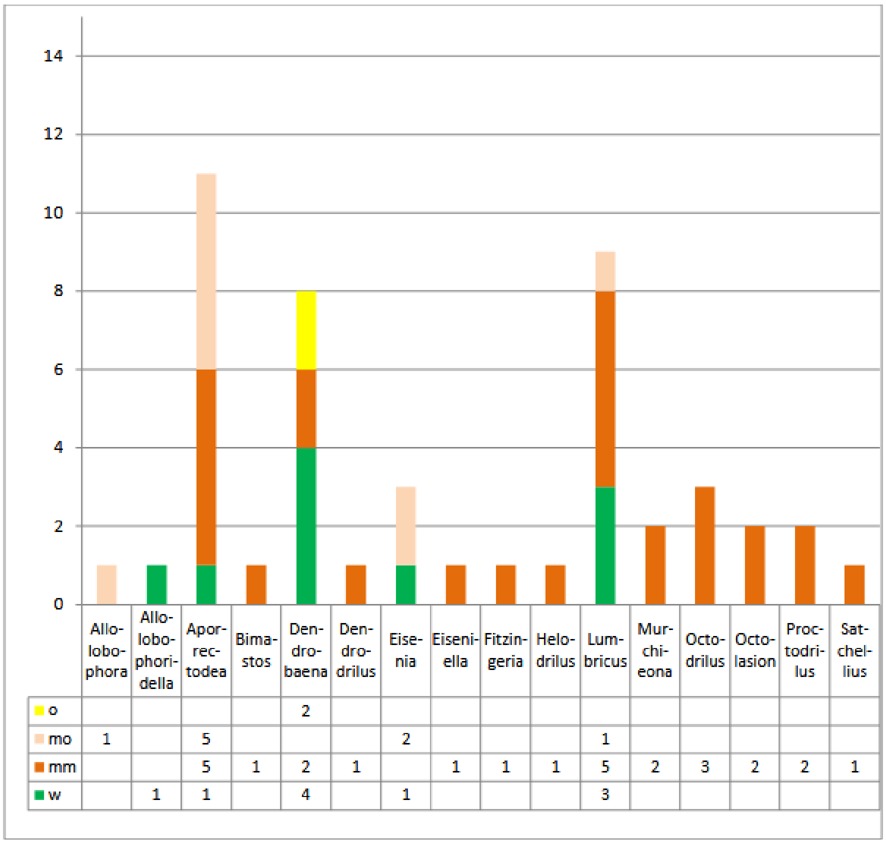


Figure A 6: Boxplot showing cumulative biomass of Aporrectodea sp. depending on the interaction of the treatment of fence and canopy (own creation).



	Allolobophora	Allolobophoridella	Aporrectodea	Bimastos	Dendrobaena	Dendrodrilus	Eisenia	Eiseniella	Fitzingeria	Helodrilus	Lumbricus	Murchieona	Octodrilus	Octolasion	Proctodrilus	Satchellius
🟨 o					2											
◻ mo	1		5				2				1					
🟧 mm			5	1	2	1		1	1	1	5	2	3	2	2	1
🟩 w		1	1		4		1				3					

Figure A 7: Distribution of earthworm species found in Germany by genus (Dorow, 2020, 22)..

“Categories of forest attachment:
w: mainly found in forests, mm: found equally in forests and open land, mo: mainly found in open land, but also regularly occurring in forests, on forest edges or in clearings, o: only found in open land or other non-forested habitats such as caves or buildings” (Dorow, 2020, 22).